Structure and function of wood in mangroves

Nadia Silvana Santini González
BSc. Hons

A thesis submitted for the degree of Doctor of Philosophy at
The University of Queensland in 2012
The School of Biological Sciences
Abstract

Mangrove forests are communities of halophytic woody plants distributed along tropical and subtropical riverine and coastal shores. They are exposed to a wide variation in environmental conditions that influence tree structure and productivity. Mangroves provide a range of ecosystem services, including coastal protection from waves, wind and extreme events such as cyclones and tsunamis. The degree of protection they offer to the coast partly depends on their wood density.

The woody tissues of trees perform a range of functions including resistance to breakage and water transport. In addition, wood constitutes a high proportion of forest aboveground biomass. The properties of the woody tissue can be directly related to tree growth and forest productivity, rates of transpiration, vulnerability to water stress, pathogen resistance and rates of decomposition. This thesis explored the wood functions of water uptake (Chapter 2), mechanical strength (Chapter 3) and growth rates (Chapter 2, Chapter 4, Chapter 5 and Chapter 6) across a range of locations.

Firstly, I investigated the extent of freshwater utilization by A. marina across a range of sites in eastern and western Australia by using stable oxygen isotopes. My results suggest that A. marina used a combination of fresh and saline water sources for growth. In addition, stem growth was enhanced by the amount of rainfall, indicating that high levels of mangrove productivity rely on access to freshwater.

Secondly, I studied how the wood structure of mangroves influenced wood density and mechanical strength in South East Queensland mangroves. I found that mechanical strength was correlated with wood density in mangrove branches. Higher mechanical strength and wood density in mangrove branches were explained by reductions in xylem vessel lumen areas, which may have costs through reducing water uptake, carbon gain and growth and with lower pith content (where synthesis can occur, e.g. hormones, enzymes, pigments). In addition, higher mechanical strength and wood density were associated with increases in fibre wall thickness. These associations between wood strength and anatomical characteristics in mangrove branches may indicate trade-offs between mechanical strength and water supply, both of which are linked to tree growth and survival.

Thirdly, in order to understand the anatomical bases of variation in wood density and how wood...
density varied with tree growth rates, the wood structure of the widespread mangrove species *Avicennia marina* was investigated. *Avicennia marina* has an uncommon wood structure in which increments in xylem vessel diameter (and fibre wall thickness) significantly increased wood density and growth rates. My fourth study evaluated climatic influences on the historical growth rates and wood density of *A. marina* in the arid Exmouth Gulf in Western Australia. By assessing wood density profiles and utilizing radiocarbon dating across stems profiles (from pith to bark), I established that *A. marina* wood density decreases towards the bark and over time, and that wood density was positively correlated with growth rates, reductions in growth rates were linked to less rainfall availability (positive Pacific Decadal Oscillation index values). Finally, the hypothesis that differences in growth rates and nutrient use among species with increases in nutrient availability result in the dominance of *A. marina* over *Rhizophora stylosa* in western Moreton Bay was investigated with an individual based model. This modelling approach indicated that, when nutrients are low, *R. stylosa* grows faster and dominates, but when nutrients become highly available *A. marina* grows faster and becomes the dominant species.

Overall, this work contributes to the understanding of wood structure and its associated functions in mangrove trees. This work demonstrated that wood density can be used as a proxy for mechanical strength in mangroves. In addition, the particular wood structure of the mangrove *A. marina* leads to a positive relationship between wood density, xylem vessel diameter and growth rates. Growth rates, productivity and species dominance of *A. marina* are enhanced by freshwater sources and nutrient availability.
Declaration by Author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

I acknowledge that an electronic copy of my thesis must be lodged with the University Library and, subject to the General Award Rules of The University of Queensland, immediately made available for research and study in accordance with the Copyright Act 1968.

I acknowledge that copyright of all material contained in my thesis resides with the copyright holder(s) of that material. Where appropriate I have obtained copyright permission from the copyright holder to reproduce material in this thesis.

Nadia Silvana Santini González
Publications during candidature


Santini NS, Schmitz N, Bennion V, Lovelock CE. The anatomical basis of the link between wood density and mechanical strength in mangrove branches. Submitted to *Functional Plant Biology*.


Santini NS, Hua Q, Schmitz N, Lovelock CE. Historical growth rates of mangrove trees in the arid zone of Western Australia: Sensitivity to climatic cycles. To be submitted to *Annals of Botany*.


Conference proceedings

Talks

Santini NS, Lovelock CE, Lockington D. Groundwater is important for mangrove growth. National Centre for Groundwater Research and Training, Canberra, ACT, Australia. 4-5 November 2010.


Santini NS, Schmitz N, Lovelock, CE. Wood density responses to climate and an intertidal gradient. 41st Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. Oldenburg, Germany. 5-9 September 2011.


**Poster presentations**

**Santini NS**, Lovelock CE. Effects of seasonal climate variability on vessel diameter and density of *Avicennia marina*. Australian Marine Sciences Association Conference AMSA. Adelaide, SA, Australia. 5-9 July 2009.

**Santini NS**, Lovelock, CE. Variation in vessel diameter and density of *Avicennia marina* in a Seasonal Climate. 10th International Congress of Ecology (INTECOL). Brisbane, QLD, Australia. 16-21 August 2009.

**Santini NS**, Lovelock CE, Lockington D. Understanding the groundwater dependance of mangroves using $\delta^{18}O$ as a tracer for water sources. National Centre for Groundwater Research and Training. Summer School Adelaide, SA, Australia. 28 November - 2 December 2011.


**Publications included in this Thesis**

Prof. Lovelock and Prof. Lockington contributed to the planning of the project. I was responsible for the collection and analyses of the data as well as for writing the manuscript. Dr. Reef critically revised the manuscript.

Santini NS, Schmitz N, Bennion V, Lovelock CE. The anatomical basis of the link between wood density and mechanical strength in mangroves. Submitted to *Functional Plant Biology*. Incorporated as *Chapter 3*.

Prof. Lovelock and Dr. Schmitz contributed to the planning of the project. I was responsible for collecting the samples, performing the data analyses and writing the manuscript. Prof. Lovelock and Dr. Schmitz revised the manuscript. Vicki Bennion helped to perform fieldwork.

Santini NS, Schmitz N, Lovelock CE. Variation in wood density and anatomy in a widespread mangrove species. Published in *Trees, Structure and Function*. DOI: 10.1007/s00468-012-0729-0 Incorporated as *Chapter 4*.

Prof. Lovelock contributed to the planning of the project and provided the wood samples. Dr. Schmitz provided advice on how to process the samples. I was responsible for processing the samples, performing the data analyses and writing the manuscript. Prof. Lovelock and Dr. Schmitz revised the manuscript.

Santini NS, Hua Q, Schmitz N, Lovelock CE. Historical growth rates of mangrove trees in the arid zone of Western Australia: Sensitivity to climatic cycles. To be submitted to *Annals of Botany*. Incorporated as *Chapter 5*.

Prof. Lovelock and Dr. Hua contributed to the planning of the project. Dr. Hua and I prepared the samples. I was responsible of analysing the data and writing the manuscript. Dr. Schmitz critically revised the manuscript.


Prof. Lovelock and Prof. Uta Berger contributed to the planning of the project, Juliane Vogt and Dr. Ruth Reef provided advice during the development of the model. I was responsible for analysing the data, and the writing of the manuscript.
Contributions by others to the thesis

Dr. Nele Schmitz provided advice on how to process the samples for Chapter 3 and Chapter 4. Dr. Julieta Rosell helped during the planning of the project of Chapter 3. Vicki Bennion and Mitchell Zischke participated in the fieldwork while collecting material for Chapter 2. Dr. Tim R Mercer, Dr. Ruth Reef, Lucy Hurrey and Mitchell Zischke provided editorial assistance.

Statement of parts of the thesis submitted to qualify for the award of another degree

None.
Acknowledgements

I dedicate this work to my parents, Miguel A. Santini and Norma T. González, for inspiring me to travel, to explore, for always being a support.

I would like to thank The National Council for Science and Technology (CONACYT, Mexico), The Secretary of Public Education (SEP, Mexico), The School of Biological Sciences at the University of Queensland (UQ, Australia), The Graduate School (UQ, Australia) The National Centre for Groundwater Research and Training (NCGRT, Australia) and The Australian Nuclear Science and Technology Organisation (ANSTO, Australia) for financial support. Additionally, I thank the Brisbane City Council for permitting using the Point Halloran Reserve, the Nundah Wetlands Reserve and the Tinchi Tamba Reserve.

It is a pleasure to thank my generous and stimulating supervisors, Prof. Catherine Lovelock and Dr. Nele Schmitz for their constant help and support, for engaging with my work, for being involved in my trips and discussions by air, by boat, by car and by foot. Thanks Cath and Nele for opening me the door of mangrove curiosity and excitement and for giving me your friendship.

This work would not have been possible without the support of the members of the Coastal Plant Lab: Vicki Bennion, Dr. Ruth Reef, Dr. Fernanda Adame, Frida Sidik and Matt Hayes, and without the valuable thoughts of Prof. Susanne Schmidt and Prof. David Lockington. I am very thankful to Mitchell Zischke for being the boat captain whenever I needed to collect mangrove samples and Dr. María Gómez-Cabrera for providing me with technical advice and assistance.

I would like to acknowledge all the people that in one or another way helped with the completion of this thesis, Jennifer and Denver Blake from Giralia Station; Dr. Tim R. Mercer, Lucy Hurrey, Dario Hugg, Robert Gould, Richard Webb, Robyn Webb, Wendy Armstrong and Kay Hodge from the University of Queensland. Andrew Swales and Nicole Hancock from the National Institute of Water and Atmospheric Research (New Zealand). Prof. Uta Berger, Dr. Juliane Vogt and Yue Lin from the Technische Universität Dresden. Prof. Marilyn Ball and Jack Egerton from the Australian National University. I am also thankful to Dr. Greg Skrzypek and Douglas Ford from the University of Western Australia and Prof. Peter Wells (retired) and Dr. Jeroen Hostens from SkyScan.
I thank Tim for sharing these PhD years with me, for transforming hard times into mellow ones, for your willing to construct and create things together.

I thank my mum Norma and my sisters Bianca and Carla because with them everything is always more fun and meaningful. I thank my dad Miguel for his infinity.

I thank all my friends who let me share stories with them, because they are now part of my family in Australia.
Keywords
Growth rates, mangroves, wood density, wood anatomy, mechanical strength, oxygen isotopes, radiocarbon, KiWi, *Avicennia marina*

Australian and New Zealand Standard Research Classifications (ANZSRC)

060205 *Marine and Estuarine Ecology* 40%; 060703 *Plant Developmental and Reproductive Biology* 40%; 069902 *Global Change Biology* 20%

Fields of Research (FoR) Classification

0602 *Ecology* 50%; 0607 *Plant Biology* 50%
# Table of contents

Abstract ........................................................................................................................................... II
Declaration by author ..................................................................................................................... IV
Publications during candidature .................................................................................................. V
  *Conference proceedings* ........................................................................................................... V
Publications included in this thesis ............................................................................................ VI
Contributions by others to the thesis ......................................................................................... VIII
Statement of parts of the thesis submitted to qualify for the award of another degree .......... VIII
Acknowledgements ....................................................................................................................... IX
Keywords .......................................................................................................................................... XI
Australian and New Zealand Standard Research Classifications (ANZSRC) ......................... XI
Fields of Research (FoR) Classification ..................................................................................... XI
Chapter 1. Background ................................................................................................................ 1
Chapter 2. Dependence of the mangrove *Avicennia marina* on fresh and saline water sources .... 11
  *Abstract* ..................................................................................................................................... 12
  *Introduction* ............................................................................................................................... 13
  *Methods* .................................................................................................................................... 15
  *Results* ....................................................................................................................................... 19
  *Discussion and Conclusions* ..................................................................................................... 21
Chapter 3. The anatomical basis of the link between wood density and mechanical strength ..... 32
  *Abstract* ..................................................................................................................................... 33
  *Introduction* ............................................................................................................................... 34
  *Methods* .................................................................................................................................... 36
  *Results* ....................................................................................................................................... 40
  *Discussion and Conclusions* ..................................................................................................... 41
Chapter 4. Variation in wood density and anatomy in a widespread mangrove species ............ 54
  *Abstract* ..................................................................................................................................... 55
  *Introduction* ............................................................................................................................... 56
  *Methods* .................................................................................................................................... 58
Results........................................................................................................................................................................62
Discussion and Conclusions................................................................................................................................................63
Chapter 5. Historical growth rates of mangrove trees in the arid zone of Western Australia: Sensitivity to climatic cycles ............................................................................................................................................76
Abstract..............................................................................................................................................................................77
Introduction......................................................................................................................................................................78
Methods.............................................................................................................................................................................80
Results...............................................................................................................................................................................82
Discussion and Conclusions.............................................................................................................................................83
Chapter 6. *Avicennia marina* dominance over *Rhizophora stylosa*: A response to high nutrient availability in western Moreton Bay, Australia........................................................................................................................................92
Introduction......................................................................................................................................................................93
Methods.............................................................................................................................................................................95
Results and Discussion....................................................................................................................................................98
Chapter 7. Discussion and Final Remarks...........................................................................................................................................103
References.......................................................................................................................................................................109
List of figures

Fig. 1.1 A) Typical and B) atypical secondary growth ................................................................. 4
Fig. 1.2 Study sites: The Exmouth Gulf in Western Australia, the Noosa River and Moreton Bay in Queensland, Australia and the Firth of Thames in New Zealand ................................................................. 9
Fig. 2.1 Conceptual diagram of the water sources available to mangroves. Mangroves have access to a range of water sources, including a) tidal water, b) pore-water, c) rainwater and d) groundwater .......................................................................................... 26
Fig. 2.2 Study sites in estuaries of Moreton Bay, the Noosa River and the Exmouth Gulf, Australia ................................................................. 27
Fig. 2.3 Mean daily minimum and maximum temperature and rainfall during the collection period at Giralia Bay in the Exmouth Gulf, Western Australia .................................................................. 28
Fig. 2.4 δ¹⁸O values of Avicennia marina mangroves from Giralia Bay, Western Australia before and after a rainfall event .......................................................................................... 29
Fig. 2.5 Relationship between δ¹⁸O and salinity for estuaries of Moreton Bay, the Noosa River and the Exmouth Gulf ................................................................. 30
Fig. 2.6 Relationship between daily stem circumference increment and Log (Rainfall [mm] +1) .................................................................. 31
Fig. 3.1 Spearman correlations between A) Log (Modulus of Elasticity) and wood density and, B) Log (Modulus of Rupture) and wood density .................................................................. 48
Fig. 3.2 A) Modulus of elasticity of branches from the dominant mangrove species in South East Queensland from the low intertidal and the B) high intertidal zones. C) Wood density of branches from the dominant mangrove species in South East Queensland from the low intertidal and the D) high intertidal zones .................................................................. 49
Fig. 3.3 A) Modulus of Elasticity of Avicennia marina from the high and the low intertidal zones. B) Wood density of Avicennia marina from the high and the low intertidal zones .................................................................. 50
Fig. 3.4 Relationship between Log (Modulus of Elasticity) and A) pith content, B) fibre wall thickness, C) xylem vessel lumen area and D) bark content .................................................................. 51
Fig. 3.5 Relationship among wood characteristics (modulus of rupture, modulus of elasticity, wood density, pith content, bark content, vessel lumen area and fibre wall thickness) of the studied mangrove species along two axes determined by principal component analyses .................................................................. 52
Fig. 3.6 Relationship between Log (Modulus of Elasticity) and the proportion of phloem in the wood layer……………………………………………………………………………53

Fig. 4.1 A) Sanded wood disc of *Avicennia marina* with inset showing the last layers in which wood was sampled, B) complete band of xylem and phloem and C) transverse wood section of *Avicennia marina*……………………………………………………………………………69

Fig. 4.2 Mean wood density of trees at sampling sites in New Zealand and Western Australia……70

Fig. 4.3 Relationship between A) wood density and xylem vessel diameter, B) wood density and total vessel lumen area, C) wood density and fibre wall thickness and D) wood density and the proportion of phloem per wood layer……………………………………..…...71

Fig. 4.4 Relationship among wood characteristics (wood density, total vessel lumen area, fibre wall thickness and phloem percentage per wood layer) in *A. marina* along two axes determined by principal component analyses (PCA)…………………………………………………………………..72

Fig. 4.5 Proportion of phloem per growth layer over the sampling sites in New Zealand and Western Australia………………………………………………………………………73

Fig. 4.6 Relationship between A) tree growth rate and xylem vessel diameter, and B) tree growth rate and wood density……………………………………………………………………..74

Fig. 4.7 Relationship between A) wood density and stem radius and B) xylem vessel diameter and stem radius for the mangrove *Avicennia marina*…………………………………………………………………….75

Fig. 5.1 Mean monthly air temperature and mean monthly precipitation in the Exmouth Gulf, Western Australia…………………………………………………………………….87

Fig. 5.2 Relationship between A) wood density and distance from pith and B) wood density and tree age for *Avicennia marina* collected in Giralia Bay, Western Australia………………………………………………………………………88

Fig. 5.3. Relationship between growth rate and wood density of *Avicennia marina* collected in Giralia Bay, Western Australia……………………………………………………….89

Fig. 5.4. Wood density and growth rate of the *Avicennia marina* mangrove from the Exmouth Gulf, Western Australia…………………………………………………………………90

Fig. 5.5. Relationship between A) growth rate and the Pacific Decadal Oscillation Index, B) growth rate and the Southern Oscillation Index, C) wood density and the Pacific Decadal Oscillation Index and D) wood density and the Southern Oscillation Index for *A. marina* trees collected in Giralia Bay, Western Australia…………………………………………91

Fig. 6.1. KiWi simulation experiments show variation in A) number of trees per hectare, B) weighted-mean dbh, and C) Importance Value in a mixed forest comprised by *Avicennia marina* and *Rhizophora stylosa* ……………………………………101
Fig. 6.2 Field data of A) diameter at breast height (dbh) in western and B) eastern Moreton Bay and C) growth rates in western and D) eastern Moreton Bay expressed as basal area gain per year (cm$^2$ year$^{-1}$) for *Avicennia marina* and *Rhizophora stylosa*..........................102
List of tables

Table 1.1 Climatic characteristics of the study sites (including the common mangrove species that occur in each site) that were used in this thesis and the corresponding Chapters in which they were used.................................................................10

Table 2.1 δ18O isotope values from different water sources in Moreton Bay, the Noosa River and the Exmouth Gulf.................................................................24

Table 2.2 Proportion of different water sources used by Avicennia marina mangroves in estuaries of Moreton Bay, the Noosa River and the Exmouth Gulf.................................25

Table 3.1 Wood anatomical basis of the differences in mechanical strength for five dominant mangrove species from South East Queensland........................................46

Table 3.2 Stepwise multiple regression models for Log (Modulus of Elasticity) and wood characteristics, Log (Modulus of Rupture) and wood characteristics, and wood density and wood characteristics in mangroves from South East Queensland...............47

Table 4.1 Tree age, tree height, number of growth layers, phloem percentage per wood layer, stem diameter and radius increment of Avicennia marina trees from the seaward and landward sites of the mangrove forests in New Zealand and Western Australia.................................................................66

Table 4.2 Parameters of the regression analysis of wood density and vessel diameter, wood density and total vessel lumen area, wood density and fibre wall thickness, wood density and proportion of phloem per wood layer, wood density and growth rates, vessel diameter and growth rates, stem radius and wood density and stem radius and vessel diameter.................................................................67

Table 4.3 Results of the stepwise multiple regression analyses for wood density...............68

Table 6.1. Species-specific parameters for Avicennia marina and Rhizophora stylosa used in the KiWi model based on field data from Moreton Bay, Queensland, Australia..............100
Abbreviations

WA: Western Australia

NZ: New Zealand

MOE: Modulus of Elasticity

MOR: Modulus of Rupture

PDO: Pacific Decadal Oscillation Index

SOI: Southern Oscillation Index
Chapter 1. Background
Mangroves are halophytic, woody plants distributed along the tropical and subtropical tidal margins, between ~25°N to 38°S (Duke 2006). They are exposed to winds and tides and to extreme events such as cyclones, hurricanes and tsunamis (Alongi 2002). Mangroves provide a range of ecosystem services (Ewel et al. 1998), including coastal protection from waves, wind and weather events (Koch et al 2009). The degree of coastal protection provided by mangroves and their survival partly depends on their wood density and mechanical strength. Wood maintains the structure of the trees by providing resistance to breakage and flexibility when strong winds and other environmental forces act upon trees (Curran et al. 2008; Chave et al. 2009).

The wood of angiosperms is comprised of different cell types that arise from the secondary growth of the vascular cambium. These cell types include: the xylem vessels that provide transport of water and of soluble minerals such as Na⁺, Cl⁻, Mg²⁺, Ca²⁺ and SO₄²⁻; the phloem, which transports nutrients (e.g. organic nitrogen as amino acids, proteins and carbohydrates) and other organic materials such as ribonucleic acid; the fibres, thick-walled cells that offer support to the plant and that can be involved in water transport; and the parenchyma, linking the xylem and the phloem and acting as nutrient storage tissue (Carlquist 2001; Chave et al. 2009).

Wood density is of significant economic and ecological importance. Wood density is one of the most important parameters in quantifying aboveground forest biomass (with tree diameter and height) as it reflects the amount of carbon stored in the wood (Chave et al. 2005) and is an indicator of tree growth rate (Enquist et al. 1999; King et al. 2006). Denser wood can increase the survival of trees because it increases their mechanical strength and resistance to collapse, but denser wood is energetically more expensive to construct than lighter wood (King et al. 2006).
Typically, denser woods have smaller xylem vessels, which constrain canopy transpiration rates, photosynthesis and tree growth (Enquist et al. 1999). Dense wood is also characterized by a high abundance of fibres (Jacobsen et al. 2007). Both xylem vessels and fibres are produced during secondary growth, which refers to the radial expansion of woody stems. Secondary growth is the result of meristematic activity that produces xylem and phloem, and varies among angiosperms resulting in a variety of life forms, i.e. lianas, shrubs and trees (Spicer and Groover 2010). The typical pattern of secondary growth is characterized by a single cylindrical cambium (meristematic cells which can perpetuate) producing phloem externally and xylem internally (Carlquist 2001).

In mangroves, secondary growth is typical with the exception of *Avicennia* and *Aegialitis*, which display successive cambia (Tomlinson 1986). The wood structure of *Avicennia marina*, characterized by successive cambia, displays consecutive bands of xylem and conjunctive tissue that includes phloem strands (Fig. 1.1A, B). Phloem within the wood of *Avicennia* is a potential site for starch depolymerisation, which is the basis of the mechanism for refilling embolized xylem vessels that can occur in water-limited and under highly saline conditions. Successive cambia, have been proposed as a mechanism of drought tolerance in plants and salinity tolerance in *A. marina* (Nardini et al. 2011; Robert et al. 2011a).

Secondary growth varies as a result of cambial dormancy, which is a response to environmental conditions. In temperate forests, where seasons are defined, cambial dormancy is periodic, producing annual growth rings. These rings facilitate age determination in trees from temperate zones (Spiecer and Groover 2010). However, age assessment of tropical mangroves is difficult because of the lack of annual rings and / or low confidence in the regular timing of rings (e.g. Lovelock et al. 2010; Robert et al. 2011b). Rings in mangroves are defined as alternate layers of narrow-highly frequent vessels and wide-low density of vessels, the presence/absence and
regularity of these rings (layers) varies with salinity conditions (Menezes et al. 2003; Verheyden et al. 2005). Under low salinity conditions, mangroves exhibit wider xylem vessels and low vessel density (Melcher et al. 2001; Schmitz et al. 2008). Under higher salinity conditions, an increase in vessel density and a decrease in vessel diameters have been observed for a number of mangroves, including *Avicennia marina*, *Rhizophora mucronata* and *Laguncularia racemosa* (Verheyden et al. 2005; Schmitz et al. 2006; Sobrado 2007; Robert et al. 2009).

![Figure 1.1](image)

**Fig. 1.1** A) Typical secondary growth, the cambium (C) produces xylem (X) internally and phloem (P) externally. B) Atypical secondary growth with successive cambia in which alternating xylem and phloem layers are formed. In *A. marina* successive cambia are reticulate, forming a tridimensional network (Figure modified from Robert et al. 2011a).

Although mangroves are remarkably salt tolerant, high salinity can have negative effects on mangrove growth rates (e.g. López-Portillo and Ezcurra 1989; Lin and Sternberg 1992). Menezes et al. (2003) found annual increments in stem circumference to be lower in mangrove trees growing in infrequently inundated sites compared to those occurring in more frequently inundated forests. Salt reduces the water potential of the soil. This exerts similar effects as drought stress (Ball 1988a). Consequently, plant growth is reduced because low soil water potentials reduce the capacity for...
water uptake and transport, thereby reducing cell turgor, cell expansion and growth (Naidoo 2006; Sobrado and Ewe 2006). High osmotic concentrations in the soil subject mangroves to large xylem tensions, which can lead to xylem embolisms that reduce water flow and photosynthesis (Ewers et al. 2004; López-Portillo et al. 2005; Lovelock et al. 2006). Due to the energetic costs associated with maintaining water uptake under saline conditions, mangroves have been observed to preferentially utilize water sources of lower salinity to support their growth (e.g. Ewe et al. 2007).

**Stable oxygen isotopes to determine water sources**

Determining the use of different water sources (e.g. rainwater) by mangroves has been possible by investigating the $^{18}O/^{16}O$ ratio ($\delta^{18}O$) composition of xylem water, which remains unaltered during plant water uptake (Ehleringer and Dawson 1992). Water is comprised of three different stable oxygen isotopes, $^{16}O$, $^{17}O$, and $^{18}O$. In the environment, the proportion of $^{16}O$ is the highest 99.74%, while $^{17}O$ and $^{18}O$ occur in minimum proportions of 0.05% and 0.21% respectively (Barbour 2007). The isotopic composition of water is different depending on its provenance and stages (i.e. liquid, vapour, solid). Seawater is enriched in the heavier isotope $^{18}O$ given the lighter isotope $^{16}O$ evaporates, forming the clouds that are therefore depleted in $^{18}O$. Precipitation is enriched with the heavier oxygen isotopes when compared to values of the originating cloud. Groundwater is typically fed by annual rainwater inputs and therefore the isotopic signature of groundwater may be similar to that of the rainwater of origin (Craig 1961).

**Nutrient availability and mangrove growth**

Another environmental parameter controlling mangrove growth is nutrient availability (Feller et al. 1999; Lovelock et al. 2006; Naidoo 2009). Nutrient availability affects photosynthetic performance and resource utilization of species and can alter species composition in forests (Chen and Twilley 1998; Lovelock and Feller 2003). In mangrove forests, nutrient availability depends on the geomorphological setting (e.g. Adame et al. 2010). In addition, agriculture and urban development
close to the catchments can increase nutrient concentrations in the water bodies (Cloern 2001; Brodie and Mitchell 2005).

**Radiocarbon dating of wood**

For mangroves and other tropical trees, radiocarbon dating has been used as a tool to accurately determine tree age and tree growth rates (Biondi 1999; Menezes et al. 2003). Radiocarbon dating is possible due to the relative abundance of three carbon isotopes in nature. The most abundant is $^{12}$C (98.9% of total C), followed by $^{13}$C (1.1% of total C) and radiocarbon ($^{14}$C, which occurs in low abundances, i.e. $1.2 \times 10^{-10}$% in the troposphere). Radiocarbon is formed in the atmosphere by the interaction of carbon and $^{14}$N with the flux of neutrons from the cosmic rays. Plants incorporate radiocarbon as carbon dioxide ($^{14}$CO$_2$) by metabolic processes; therefore radiocarbon concentration in wood reflects the atmospheric radiocarbon concentration at the time the wood was formed. During the 1950’s and 1960’s, nuclear detonations caused a remarkable increase of radiocarbon concentrations in the atmosphere. The highest concentration peak of this carbon isotope was in 1955. The observed reduction of radiocarbon concentrations in the atmosphere after 1955 offers the possibility of dating recent terrestrial samples with a resolution of one to a few years (Hua 2009).

This thesis consists of seven chapters including Chapter 1, the general background of the thesis; Chapter 2 to Chapter 6 have been or will be published as papers.

In Chapter 2, I aimed to evaluate the extent of freshwater utilization by *A. marina* using stable oxygen isotopes as tracers for water sources and measuring stem growth with automatic logging dendrometer bands. My results showed that *A. marina* uses a mix of rainwater/groundwater and tidal water sources for metabolic processes. In addition, my study found that freshwater sources enhanced stem growth, predicting that mangroves will be sensitive to changes in rainfall patterns due to climate change.
In Chapter 3, I investigated how wood mechanical strength and wood density relate to wood anatomy in mangroves from South East Queensland and whether mechanical strength of wood varies among five mangrove species. By using plant anatomy techniques and an electromechanical strength-testing instrument, this work demonstrated that wood density is a good predictor of mechanical strength and that mangrove species exhibit a range of mechanical strength. Higher mechanical strength was correlated with fibre wall thickness and with reductions in percentage of pith and lumen area of xylem vessels, although these associations varied among species. These associations between wood strength and anatomical characteristics in mangroves may reflect trade-offs between mechanical strength and water supply, both of which are linked to tree growth and survival.

In Chapter 4, I used polished wood stem discs and wood micro-sections to understand how variation in anatomical characteristics of *A. marina* wood influence wood density and tree growth rates in the mangroves of the Firth of Thames, New Zealand and at the Exmouth Gulf, Western Australia. In the majority of angiosperms species, low wood density is linked to large xylem vessel diameters. Allometric scaling theory predicts that larger lumen areas would allow higher rates of transpiration and photosynthetic carbon gain, supporting large canopies and high growth rates (e.g. Enquist et al. 1999; King et al. 2006). However, my work shows that the atypical wood structure of *A. marina* results in contrasting relationships among these characteristics. The high wood density of *A. marina* is linked to increases in xylem vessel diameters, which allow faster growth rates. *Avicennia marina* can maintain high wood density with wide xylem vessels by forming thick fibre walls. In addition, *A. marina* growing in the high intertidal, where frequency of inundation is lower and salinities are higher, exhibited lower wood densities and therefore may have a greater likelihood of physical damage than trees growing in the low intertidal.
In Chapter 5, I used X-Ray densitometry and bomb-pulse radio carbon dating techniques to assess how growth of *A. marina* in the Exmouth Gulf varies with wood density and its link to historical climatic variability. My results suggest that growth rates of *A. marina* trees over long periods of time are positively correlated with wood density. Additionally, *A. marina* trees in the Exmouth Gulf, Western Australia, despite multiple intense cyclones in the region, are relatively old, 68 ± 8.6 years old. Their growth is slow but is enhanced with increases in rainfall during low phases of the Pacific Decadal Oscillation Index as access to freshwater sources increase and water salinities are reduced.

Finally, in Chapter 6, a computer model simulation of mangrove species competition in Moreton Bay Australia was used to test whether species dominance could be due to variation in nutrient availability. I parameterized the individual based model KiWi with data from Moreton Bay mangroves. By simulating changes in nutrient availability with the KiWi model in east and western Moreton Bay I found that high nutrient availability in western Moreton Bay resulted in the dominance of *A. marina* over *R. stylosa*. This leads to the hypothesis that *A. marina* dominance over *R. stylosa* is a response to the high nutrient discharge in west Moreton Bay caused by urban development.

The final Chapter 7 provides a summary of my findings and provides a list of questions that arose from this work to be addressed in future research.

**Study sites**

This thesis explored the wood functions of water uptake (Chapter 2), mechanical strength (Chapter 3) and growth rates (Chapter 2, Chapter 4, Chapter 5 and Chapter 6) across a range of locations (Fig. 1.2). The study sites were chosen as for the aims of each Chapter, climatic characteristics and common mangrove species of each site are shown in Table 1.1.
Fig. 1.2 Study sites: the Exmouth Gulf in Western Australia, the Noosa River and Moreton Bay in Queensland, Australia and the Firth of Thames in New Zealand.
Table 1.1 Characteristics of the study sites (including the common mangrove species that occur at each site) that were used in this thesis and the corresponding Chapters in which they were used. Temperature and rainfall data were obtained from the Australian Bureau of Meteorology (2012). The southernmost distribution of the mangrove species *A. marina* is in the Firth of Thames, New Zealand.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Mean minimum temperature (ºC)</th>
<th>Mean maximum temperature (ºC)</th>
<th>Mean rainfall (mm year⁻¹)</th>
<th>Common species</th>
<th>Chapter</th>
</tr>
</thead>
<tbody>
<tr>
<td>The Exmouth Gulf, Western Australia</td>
<td>18</td>
<td>32 with peaks of 45ºC in summer</td>
<td>230</td>
<td><em>Avicennia marina</em></td>
<td>2, 4, 5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Rhizophora stylosa</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Ceriops australis</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Ceriops australis</em></td>
<td></td>
</tr>
<tr>
<td>Moreton Bay, Queensland Australia</td>
<td>16</td>
<td>25</td>
<td>1016</td>
<td><em>Avicennia marina</em></td>
<td>2, 3, 6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Rhizophora stylosa</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Ceriops australis</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Bragulera gymnorrhiza</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Aegiceras corniculatum</em></td>
<td></td>
</tr>
<tr>
<td>The Noosa River, Queensland, Australia</td>
<td>17</td>
<td>25</td>
<td>1628</td>
<td><em>Avicennia marina</em></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Rhizophora stylosa</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Ceriops australis</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Bragulera gymnorrhiza</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Aegiceras corniculatum</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Excoecaria agallocha</em></td>
<td></td>
</tr>
<tr>
<td>The Firth of Thames, New Zealand</td>
<td>13</td>
<td>22</td>
<td>1400</td>
<td><em>Avicennia marina</em></td>
<td>4</td>
</tr>
</tbody>
</table>
Chapter 2. Dependence of the mangrove *Avicennia marina* on fresh and saline water sources
Abstract

Mangrove forests are distributed along the tropical and subtropical riverine and coastal shores. Although mangroves are highly adapted to saline environments, maintaining water uptake under highly saline conditions is nevertheless energetically expensive (Ball 1988a). Therefore, salinity is an important limiting factor for mangrove growth and productivity, and access to freshwater sources, such as rainwater and groundwater, which reduce water salinity, increase mangrove ecosystem productivity. Given the predicted changes to rainfall patterns associated with climate change, I investigated the extent of freshwater utilization by mangroves in order to better predict current and future mangrove distributions and productivity. I used the abundance of \(^{18}\text{O}\) isotope in xylem sap to quantify the freshwater utilization by *Avicennia marina*. Secondly, I also assessed whether growth, measured as increments in stem circumference, was sensitive to variation in rainfall. The \(\delta^{18}\text{O}\) isotopic composition of xylem water indicated mangroves use both rainwater/groundwater and tidal water/seawater for metabolic processes. In addition, stem growth was correlated with rainfall \((r^2 = 0.34 \text{ and } r^2 = 0.35, p < 0.0001)\). My results indicate that high levels of mangrove productivity rely on access to freshwater (whether rainwater or groundwater) and predict mangrove productivity and distribution will be highly sensitive to changes in patterns of rainfall with climate change.

**Keywords:** groundwater, rainfall, stem growth, Moreton Bay, Noosa River, Exmouth Gulf
Introduction

Mangrove forests inhabit the coastal and riverine shores of the tropics and sub-tropics (Alongi 2009). Due to their position in the intertidal zone, mangroves can access water from a range of different sources, such as soil pore-water (sediment interstitial water), rainwater (surface water), groundwater and tidal water from the adjoining rivers, creeks or sea (Fig. 2.1). Groundwater from the tidal mangrove systems is fed by surface and subsurface seepage, which originates from rainfall. Groundwater would otherwise be hypersaline (Semeniuk 1983; Saenger and Moverley 1985; Méndez Linares et al. 2007; Humphreys et al. 2009).

Salinity of the pore-water surrounding the roots of mangroves varies according to rainfall, evaporation (and transpiration), and frequency of tidal inundation. Low in the intertidal zone, mangrove soils are regularly inundated and subject to relatively constant salinity values similar to the salinity of the water in the adjoining creek or sea. Higher in the intertidal, where soils are less frequently inundated, pore-water salinities fluctuate depending on rainfall and evaporation. In more arid environments, pore-water salinity can become hypersaline due to high levels of evaporation, however even with high evaporation, where fresh groundwater enters the mangroves (due to seepage), or during periods of rainfall, pore-water salinity can be reduced (Semeniuk 1983; Alongi and Brinkman 2011).

Mangroves are adapted to highly saline environments. Mangroves can exclude up to 97% of the salt in the soil pore-water from entering the xylem stream (Ball 1988a) and use salt ions for osmoregulation and for maintaining sufficiently low tissue water potentials for water uptake (Scholander 1968). Due to the energetic costs associated with maintaining water uptake and under
saline conditions, soil salinity has long been recognized as an important factor that limits mangrove growth and productivity (Ball 1988a; Lin and Sternberg 1992; Lovelock et al. 2006).

The widespread mangrove *Avicennia marina* can tolerate salinities up to 90 practical salinity units (PSU) (Hutchings and Saenger 1987), the optimum salinity levels for *A. marina*’s growth range from 3.5 to 17.5 PSU (Clough 1984; Ball 1988a) and decline with increasing salinity (Morrisey et al. 2010). Therefore, mangroves growing at salinities higher than those optimal for growth benefit greatly from enhanced freshwater availability. Which is why productivity (Menezes et al. 2003; Méndez-Alonso et al. 2008), diversity and distribution of mangroves (e.g. Smith and Duke 1987; Eslami-Andargoli et al. 2009) have been found to increase with increasing rainfall. Given variation in rainfall is expected with climate change, understanding how much freshwater mangroves use for sustaining their metabolic processes is important for the maintenance and management of these ecosystems (Lovelock and Ellison 2007).

It is possible to determine the use of different water sources by mangroves by investigating the natural oxygen (O) stable isotopes within their tissues. The abundances of $^{18}$O and $^{16}$O stable isotopes can vary greatly between water sources. Because no evidence for oxygen fractionation has been observed during water uptake in plants (Lin and Sternberg 1993, Ellsworth and Williams 2007), the $^{18}$O/$^{16}$O ratio ($\delta^{18}$O) of the xylem water reflects the $\delta^{18}$O of the water sources taken up by the plant. There have been three previous studies of uses of different water sources by mangroves, all conducted in the Everglades in Florida, where the wetland system is underlain by highly permeable limestones (Obeysekera et al. 1999). Sternberg and Swart (1987) found that the $\delta^{18}$O of stem xylem water of *Rhizophora mangle, Avicennia germinans* and *Laguncularia racemosa* were determined by the relative availability of seawater and freshwater at each sampling location. Using analysis of natural stable isotopes of oxygen, Lin and Sternberg (1992) demonstrated seasonal variation in water source utilization in the mangrove *R. mangle* growing high in the intertidal.
Rhizophora mangle in the high intertidal relied more heavily on seawater during the dry season while during the wet season, freshwater utilization increased. The $\delta^{18}O$ values of stem water from R. mangle trees in the fringing forest (which is frequently inundated by tides) were similar to values typical of seawater during both seasons. A more recent study of seasonal variation in water source utilization in mangroves in the Everglades presents a model where during the dry season R. mangle uses a mix of shallow hypersaline water and saline groundwater, while during the wet season when shallow water is comprised of rainwater, R. mangle used only the shallow freshwater for growth (Ewe et al. 2007).

In this study, my goals were 1) to measure the extent of freshwater utilization by A. marina and 2) to assess whether growth, measured as daily increments in stem circumference, were sensitive to rainfall. I studied $\delta^{18}O$ in A. marina xylem water in five sites from three locations with varying hydrological settings: Moreton Bay and the Noosa River in Queensland, Australia and the Exmouth Gulf in Western Australia.

Methods

Study sites

Two of the study sites were located on the western side of Moreton Bay, Queensland, two sites encompassed a salinity gradient along the Noosa River, Queensland and one site was within Giralia Bay in the Exmouth Gulf, Western Australia (Fig. 2.2).

Moreton Bay is a large semi open bay that extends 90 km from north to south. The bay is well flushed through three passages to the open ocean and also influenced by five rivers that drain into the bay (Dennison and Abal 1999). Mangrove forests are well developed on the western side of the
bay. My first site was the Nudgee Creek forest within the Boondall Wetlands Reserve, the Nudgee Creek is 3 km inland from the coast (27.35ºS, 153.08ºE). My second site in Moreton Bay is a forest fringing the Brisbane River, at The University of Queensland, 25 km from the mouth of the Brisbane River (27.50ºS, 153.02ºE). The climate is subtropical with a dry winter and a warm, wet summer. The mean minimum temperature in this region is 16º C and the mean maximum temperature is 25 ºC with a mean annual rainfall of 1016 mm year⁻¹ (Australian Bureau of Meteorology 2012).

Two other sites in Queensland than span a salinity gradient are located along the Noosa River, approximately 120 km north of the Moreton Bay study area. The Noosa River is an estuarine system characterized by a sand bar in the mouth of the river, which restricts seawater exchange (Hewson et al. 2001). The Noosa River is comprised of shallow embayments and lakes (mean depth ~ 1 m) connected by a deeper river channel. One of my sites is in Lake Cooroibah (26.36ºS, 153.04ºE) 8 km away from the river mouth and the other less saline site is situated at Lake Cootharaba (26.31ºS, 152.98ºE) 19 km away from the river mouth. The climate is wet, compared to the other sites, with a mean annual rainfall of 1628 mm year⁻¹. The mean minimum temperature in Noosa is 17 ºC and the mean maximum temperature is 25 ºC (Australian Bureau of Meteorology 2012).

My fifth site is located in Giralia Bay in the Exmouth Gulf, Western Australia (22.53ºS 114.3ºS). The Exmouth Gulf is a large, open inverse estuary with infrequent river flows that occur during cyclones (Brunskill et al. 2001). The study site was on the edge of a tidal creek within Giralia Bay. The climate in this region is arid and warm, with a mean annual rainfall of 230 mm year⁻¹. The mean minimum temperature in the region is 18 ºC and the mean maximum temperature is 32 ºC with peaks of 45ºC in summer (Australian Bureau of Meteorology 2012).
Sample collection

In the Moreton Bay sites (Brisbane River and Nudgee Creek) and in the Noosa River sites (Lake Cootharaba and Lake Cooroibah) I sampled during March- April 2010. While in Giralia Bay, I sampled during a dry period and then re-sampled (only mangrove twigs) after a 3-day period of rain (21\textsuperscript{st} of August 2010 and 25\textsuperscript{th} of August 2010, Fig. 2.3).

To establish the $\delta^{18}$O isotopic composition of water used by \textit{A. marina} I sampled twigs from 3-10 fringing mangrove trees at each site. The twigs were collected 40 cm away from transpiring leaf surfaces and were 150 mm long with stem diameters of $\sim$ 8 mm. Immediately following collection the twigs were sealed with Parafilm M (SPI Supplies, PA USA) and put in collection tubes and kept at - 20$^\circ$ C until further analysis. Xylem water was extracted from each twig sample by cryogenic distillation using a vacuum system at the Stable Isotope Laboratory at the University of Western Australia following the procedures of West et al. (2006). The water extracted from the twigs was analyzed for $\delta^{18}$O abundance and results of $\delta^{18}$O were normalized with the international standards (Eqn 2.1) provided by the International Atomic Energy Agency (IAEA): Vienna Standard Mean Ocean Water (VSMOW), Standard Light Antarctic Precipitation 2 (SLAP2) and Greenland Ice Sheet Precipitation (GISP).

\begin{equation}
\delta^{18}O = \left( \frac{^{18}O_{sample}}{^{16}O_{standard}} \right) - 1 \times 1000 \text{‰} \tag{Eqn 2.1}
\end{equation}

Simultaneously with twig collection I collected water from the different water sources at each site in 10 mL vials ($n = 3 \text{–} 6$). I collected tidal water (river water or creek water), seawater, rainwater (directly in vials during the rainy periods) and soil pore-water. Vials were completely filled in with water and sealed with Parafilm after collection to avoid evaporation. Soil pore-water was collected at 30 cm depth from the surface using a suction device (McKee 1988). In the Exmouth Gulf, I also sampled groundwater from the Giralia Pastoral Station homestead bores (- 22.75 $^\circ$ S, 114.39 $^\circ$ E).
which were 25 km away from the study site. I was unable to sample groundwater at the Queensland sites. Instead, I used values obtained from other estuarine sites in the region \((n = 3)\). For the Brisbane River and Nudgee Creek sites, Wei et al. \((In rev.)\) provided values from the Tinchi Tamba Wetlands Reserve located within 15 km of the Moreton Bay sites. For the Noosa River sites, I used data from the literature from the Buttha and Poona coastal aquifers that are located within 24 km south and 50 km north from our Noosa River sites (Larsen and Cox 2011). All the values of groundwater for my study correspond to shallow groundwater, from aquifers of unconsolidated coastal deposits (1 - 4 m depth). Salinity of the different water sources was measured using a Refractometer W/ATC 300011, SPER Scientific (Scottsdale, USA).

**Stem growth**

I monitored daily increments in stem circumference for 2 months (November-December 2010) at the sites along the Noosa River and in Moreton Bay, using electronic dendrometer bands (ICT International, Australia) (Lagergren and Lindroth 2004). I recorded the increment in stem circumference of a total of 10 *A. marina* trees of \(~30\) cm circumference. To assess the sensitivity of stem circumference increments to rainfall I obtained daily rainfall records from the meteorological stations that were closest to my sites: Brisbane Aero (station 40842), 3 km away from the Brisbane River site and 6 km away from the Nudgee Creek site and Noosaville (station 40995), 5 km away from the Corooibah Lake and 12 km away from the Cootharaba Lake (Australian Bureau of Meteorology 2012).

**Data analyses**

To assess the variation in \(\delta^{18}O\) and salinity among water sources at each site I performed a Kruskal–Wallis one-way analysis of variance (ANOVA) followed by a Dunn’s post-test. I used the package SIAR from the software R (The R Foundation for Statistical Computing) that uses a Bayesian approach based on Gaussian likelihood to determine which sources of water mangroves use (Parnell
et al. 2010). Seawater, rainwater, tidal water (from the adjoining creek or river) and groundwater were considered as water sources for the model. Soil pore-water was not included in the model to avoid duplication of water sources (because the $\delta^{18}$O signature of the pore-water was the same to that of the tidal water, $r^2 = 0.99$, $p < 0.05$). I evaluated the response of mangrove stem circumference increment to the amount of daily rainfall using linear regression analyses with the software R. Rainfall was log transformed prior to analysis to normalize the variance of the data.

**Results**

Within sites, the $\delta^{18}$O values of the xylem water were significantly similar to more than one source of water, indicating that *A. marina* uses a mixture of water sources for metabolic processes. In addition, the isotopic signature of xylem water across sites was at all times depleted in $^{18}$O and varied from $-2.73 \pm 0.25 \%e$ (mean $\pm$ standard error) in the Brisbane River to $-1.28 \pm 0.17 \%e$ in Giralia Bay (Table 2.1). In Giralia Bay, Western Australia, I was able to test whether water use was altered by a rainfall event. Values of $\delta^{18}$O in mangrove tissues were significantly more depleted in $^{18}$O after rain (Fig. 2.4).

Salinity of the tidal water was higher in Giralia Bay than in the Moreton Bay and Noosa River sites. Among the Moreton Bay sites, the Nudgee Creek exhibited slightly higher tidal water salinities than the Brisbane River. Lake Cooroibah was more saline than the Lake Cootharaba, which had the lowest salinities of all sites (Fig. 2.5). More saline waters were more enriched in the heavier isotope $^{18}$O. The relationship between $\delta^{18}$O and salinity of the water sources was different between sites (Fig. 2.5).
To further evaluate the proportional use of different water sources for metabolic processes by *A. marina* I used the SIAR package. SIAR calculates confidence intervals of water sources used by *A. marina* considering the $\delta^{18}O$ values of the different water sources and of *A. marina*. These confidence intervals are based on posterior distributions using a Bayesian approach (Moore et al. 2008; Parnell et al. 2010). The $\delta^{18}O$ values of rainwater and groundwater at all sites were indistinguishable. Also, the isotopic signatures of tidal water and seawater at the Nudgee Creek, the Cooroibah Lake and Giralia Bay were indistinguishable. Because it was not possible to differentiate between the $\delta^{18}O$ values of rainwater/groundwater across sites and between the $\delta^{18}O$ values of tidal water/seawater at some sites, I grouped the results as rainwater/groundwater (for all sites) and tidal water/seawater (for the Nudgee Creek, the Coroibah Lake and the Giralia Bay sites) in the following paragraphs. I found that across sites *A. marina* used a mix of rainwater/groundwater and tidal water/seawater for metabolic processes. In the Moreton Bay and in the Noosa River sites, *A. marina* used 4 – 58% rainwater/groundwater. In Giralia Bay, after the rain event *A. marina* used from 13 – 36% rainwater/groundwater, and during the dry period (when rainfall was not available and therefore was not included in the model) *A. marina* was highly reliant on groundwater sources, using 31 - 49%.

In upstream regions of the Brisbane River and Lake Cootharaba, SIAR modelling differentiated between tidal water and seawater. At these two sites, the contribution of seawater to the tidal water mix is likely to be small. At these sites, tidal water was depleted in $^{18}O$, in the Brisbane River $\delta^{18}O = -1.61 \pm 0.31 \%e$ and in Lake Cootharaba $\delta^{18}O = -0.73 \pm 0.02 \%e$; compared to the values enriched in $^{18}O$ of the adjoining seawater $\delta^{18}O = 0.70 \pm 0.07 \%e$ for the Brisbane River and $\delta^{18}O = 0.96 \pm 0.13 \%e$ for Lake Cootharaba. At these two sites, tidal water was used by the trees in lower amounts (0 – 41%) than rainwater/groundwater (4 – 58%).
Consistent with the high level of rainwater/groundwater used by trees, indicated by our SIAR analysis of $\delta^{18}O$, I found that the relationship between rainfall and stem growth was significant in the Moreton Bay and in the Noosa River sites (Fig. 2.6). The slope of the regression between stem growth and rainfall amounts was significantly different between sites but trees at all sites responded to increasing rainfall in a consistently positive way. Stem growth varied, but was mostly zero or slightly negative with zero rainfall.

**Discussion**

The $\delta^{18}O$ values for *A. marina* and the confidence intervals calculated by SIAR, indicated that at all times mangroves use rainwater/groundwater for growth. In Giralia Bay, rainfall events are scarce. However, the xylem water of *A. marina* mangroves from Giralia Bay was depleted in $^{18}O$, which suggests that even during dry periods *A. marina* uses a proportion of freshwater (groundwater) for metabolic processes. The SIAR model indicated that during the dry period, *A. marina* uses from 31 – 49 % groundwater.

In mangroves, hyper saline water increases energetic costs associated with water uptake and therefore decreases growth and productivity (Ball 1988a; Lovelock et al. 2006). However, because mangroves grow in saline environments, they also need salt ions for osmoregulation (Scholander 1968). My results support the hypothesis that *A. marina* mangroves have a flexible water-use strategy that uses both freshwater and saline water to maintain both growth and tissue salt balance in saline environments (Ball 1988a).

At Giralia Bay, the $\delta^{18}O$ of *A. marina* xylem water varied significantly before and after a rainfall event. This difference in $\delta^{18}O$ values indicated that *A. marina* is able to utilize water delivered in
rainfall events. However, the isotopic signature of the xylem water was significantly higher than the rainfall isotopic signature ($p = 0.007$), indicating that *A. marina* used tidal water simultaneously with water delivered in recent rainfall. Mangroves root distributions and the association of roots with soil macropores, where rainfall, tidal water and groundwater infiltrate the soils (e.g. crab burrows and old root channels) may be features of mangrove root systems that enhance access to intermittently available water sources (i.e. surface water, soil pore-water, groundwater) as well as performing other functions such as nutrient uptake (Ridd et al. 1996; Middleton and McKee 2000).

Previously groundwater and rainfall have been recognized as important factors contributing to the salt balance in the mangrove environment (Semeniuk 1983; Susilo et al. 2005). In the sandy permeable soils of the Moreton Bay and Noosa River sites, yearly precipitation is relatively high and shallow groundwaters have been widely recognized to be from local origin (Larsen and Cox 2001). In Giralia Bay, groundwater stores occur in porous and cavernous substrates (e.g. limestone) where groundwater reaches the sea. These groundwater systems are recharged with episodic rainfall, e.g. cyclonic periods (Humphreys et al. 2009).

There was significant variation in isotopic signatures of water sources between sites. The $\delta^{18}O$ of rainwater was lowest in Giralia Bay, reflecting the high evaporative demand in the region (McGuire and McDonnell 2007). Seawater and tidal water in Giralia Bay were more enriched in $^{18}O$ and exhibited higher salinity values than seawater and tidal water from the Moreton Bay and the Noosa River study areas. These broad regional differences in $^{18}O$ of water are due to variation in evaporative demand associated with higher temperatures in the Exmouth region (McGuire and McDonnell 2007). Additionally, the highly saline and more $^{18}O$ enriched tidal water and seawater in Giralia Bay, may also reflect the limited freshwater inputs that limit $^{16}O$ sources (Wolanski 1986).
Stem growth in mangroves was larger in the Noosa River, where conditions are less saline than in Moreton Bay. In both sites increasing rainfall led to increases in the size of the daily stem increments. Freshwater is essential for maintenance of turgidity of cells and tissues, assuring the presence of a driving force for cell enlargement, stomata opening and therefore photosynthetic carbon gain (Pallardy 2008). Zero and negative growth were also observed when rainfall was zero. Negative growth (shrinkage of stems) may indicate use of stored water in stems to support transpiration and carbon gain during periods without rain (Bucci et al. 2004).

**Conclusions**

My results strongly suggest that *A. marina* mangrove productivity is dependent on access to freshwater, whether rainwater, groundwater or surface water. In Giralia Bay, where mangroves inhabit a tropical arid biogeographic region, groundwater aquifers may be of greater importance than in the Moreton Bay and the Noosa River, where rainfall is more abundant (Semeniuk 1983). My results contribute to the understanding of the sensitivity of mangroves to climatic gradients (Smith and Duke 1987) and indicate that mangroves will be highly sensitive to changes in patterns of rainfall with climate change.
Table 2.1 δ¹⁸O isotope values from different water sources in our study sites. Values are means and standard errors and are expressed in ‰. Different letters along each row indicate that δ¹⁸O values were significantly different among sources of water within sites. Values for groundwater at the Brisbane River and Nudgee Creek were obtained from the Tinchi Tamba Wetlands Reserve (Wei et al. *In rev.*). Values for groundwater data for Lake Cootharaba and Lake Cooroibah were obtained from the Buttha and Poona coastal aquifers (Larsen and Cox 2011). *These values were not included in the ANOVA statistical tests.*

<table>
<thead>
<tr>
<th>Site</th>
<th>Rainfall</th>
<th>Tidal Water</th>
<th>Seawater</th>
<th>Groundwater</th>
<th>A. marina</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brisbane River</td>
<td>-4.12 ± 1.50</td>
<td>a</td>
<td>-1.61 ± 0.31</td>
<td>ab</td>
<td>0.70 ± 0.07</td>
<td>-1.2 ± 0.20</td>
</tr>
<tr>
<td>Nudgee Creek</td>
<td>-4.12 ± 1.50</td>
<td>ac</td>
<td>0.18 ± 0.19</td>
<td>bc</td>
<td>0.70 ± 0.07</td>
<td>-1.2 ± 0.20</td>
</tr>
<tr>
<td>Lake Cootharaba</td>
<td>-1.86 ± 0.59</td>
<td>ab</td>
<td>-0.73 ± 0.02</td>
<td>ab</td>
<td>0.96 ± 0.13</td>
<td>-4.4 ± 0.44</td>
</tr>
<tr>
<td>Lake Cooroibah</td>
<td>-1.86 ± 0.59</td>
<td>a</td>
<td>-0.37 ± 8 *10⁻³</td>
<td>abc</td>
<td>0.96 ± 0.13</td>
<td>-4.4 ± 0.44</td>
</tr>
<tr>
<td>Giralia Bay</td>
<td>-9.42 ± 0.07</td>
<td>a</td>
<td>2.38 ± 0.08</td>
<td>bd</td>
<td>1.29 ± 0.19</td>
<td>-6.43 ± 0.06</td>
</tr>
</tbody>
</table>
Table 2.2 Proportion of different water sources used by *A. marina* mangroves in our study sites. Values are 10% - 90% percentiles as calculated by SIAR (Parnell et al. 2010).

<table>
<thead>
<tr>
<th>Site</th>
<th>Rainfall Water</th>
<th>Tidal Water</th>
<th>Sea Water</th>
<th>Groundwater</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brisbane River</td>
<td>(7 –55)</td>
<td>(0 – 36)</td>
<td>(0 – 26)</td>
<td>(11 – 58)</td>
</tr>
<tr>
<td>Nudgee Creek</td>
<td>(4 – 38)</td>
<td>(4 – 48)</td>
<td>(9 – 44)</td>
<td>(5 – 38)</td>
</tr>
<tr>
<td>Lake Cootharaba</td>
<td>(4 – 48)</td>
<td>(1 – 41)</td>
<td>(1 – 34)</td>
<td>(6 – 50)</td>
</tr>
<tr>
<td>Lake Cooroibah</td>
<td>(5 – 45)</td>
<td>(2 – 44)</td>
<td>(1 – 36)</td>
<td>(7 – 46)</td>
</tr>
<tr>
<td>Giralia Bay-Before Rain</td>
<td>-</td>
<td>(12 – 50)</td>
<td>(5 - 47)</td>
<td>(31 - 49)</td>
</tr>
<tr>
<td>Giralia Bay- After Rain</td>
<td>(13 – 36)</td>
<td>(17 – 48)</td>
<td>(7 - 41)</td>
<td>(2 - 34)</td>
</tr>
</tbody>
</table>
Fig. 2.1 Mangroves have access to a range of water sources, including a) tidal water, b) pore-water, c) rainwater and d) groundwater, which occurs in mangroves due to seepage of water moving from the hinterlands into the tidal mangrove lands.
Fig. 2.2 Location of the five study sites in the estuaries of Moreton Bay, the Noosa River and the Exmouth Gulf.
Fig. 2.3 Mean daily minimum (filled diamonds) and maximum temperature (open diamonds) and rainfall (bars) during the collection period at Giralia Bay in the Exmouth Gulf, Western Australia. Dates of twig collection are marked with arrows. During the previous months (May, June and July) rainfall events were rare, with rainfall only during May and June. Rainfall occurred on May 19th (0.4 mm), May 23rd (3.2 mm), June 4th – 7th (50 mm), June 15th (0.2 mm), June 16th (95 mm) and June 17th (0.2 mm). Data were obtained from the Australian Bureau of Meteorology (2012).
Fig. 2.4 $\delta^{18}$O values of *Avicennia marina* mangroves from Giralia Bay, Western Australia before and after a rainfall event. Values are mean and standard errors. The $\delta^{18}$O mean values were significantly lower before the rainfall event ($t = 3.57, n_{total} = 20$).
Fig. 2.5 Relationship between δ¹⁸O and salinity for three study regions. Each line indicated the best fit for every site. Between the Moreton Bay, the Noosa River and the Exmouth Gulf sites, the slopes of the regression lines were significantly different ($p < 0.05$). For Moreton Bay, the regression was: $\delta^{18}O = 0.12$ Salinity $- 3.16$ ($r^2 = 0.61$, $p = 0.0009$, $n = 14$). For the Noosa River the regression was: $\delta^{18}O = 0.06$ Salinity $- 1.33$ ($r^2 = 0.72$, $p = 0.0005$, $n = 12$). For the Exmouth Gulf the regression was: $\delta^{18}O = 0.25$ Salinity $- 8.49$ ($r^2 = 0.97$, $p < 0.0001$, $n = 15$). Different symbols represent different water sources, rainwater (circles); tidal water (triangles); seawater (squares) and groundwater (upside down triangles).
Fig. 2.6 Relationship between daily stem circumference increment and Log (Rainfall [mm] +1). The slopes of the relationships for the Moreton Bay and Noosa River study areas were significantly different ($p < 0.05$). For Moreton Bay, the regression was: \[\text{Increment} = 34 \log (\text{Rainfall [mm]} +1) - 10.5 \quad (r^2 = 0.34, p = 0.001)\] and for the Noosa River, the regression was: \[\text{Increment} = 62 \log (\text{Rainfall [mm]} +1) - 20 \quad (r^2 = 0.37, p = 0.001)\].
Chapter 3. The anatomical basis of the link between wood density and mechanical strength
Abstract

Wood performs a range of important ecosystem functions including mechanical support and water transport (Chave et al. 2009). Mangroves are subject to strong tidal flows and waves as well as high wind speeds that can cause structural damage to trees. Therefore, survival and establishment of mangrove trees under different environments partly depend on their wood density and mechanical strength. In addition to the wind and wave forces, mangroves grow in soils that vary in salinity. Highly saline conditions increase the tension on the water column therefore imposing mechanical stresses on the xylem vessels. Here, I investigated how wood mechanical strength and wood density relate to wood anatomy in five common mangrove species from South East Queensland (*Rhizophora stylosa*, *Bruguiera gymnorrhiza*, *Avicennia marina*, *Ceriops australis* and *Aegiceras corniculatum*) and whether mechanical strength of wood varies among mangrove species. I found mechanical strength to be correlated with wood density in mangrove branches. Mechanical strength and wood density increased with reductions of pith content (where synthesis can occur, e.g. hormones, enzymes, pigments) and increases in fibre wall thickness. In addition, higher mechanical strength and wood density were associated with reductions in xylem vessel lumen areas. These associations between wood strength and anatomical characteristics support the hypothesis that there is a trade-off between mechanical strength and water supply among species, both of which are linked to tree growth and survival.

**Keywords:** Modulus of elasticity, Modulus of rupture, wood anatomy, Queensland
Introduction

Mangroves grow on the coasts of tropical and sub-tropical shores. They are subject to strong tidal flows and waves as well as high wind speeds, although variation in exposure to these forces depends on their position in the intertidal region. In Queensland, wind gusts can reach 90 km h\(^{-1}\) during thunderstorms and > 200 km h\(^{-1}\) during cyclonic activity (Australian Bureau of Meteorology 2012), and can cause structural damage to trees (Bardsley 1985; Baldwin et al. 2001). Therefore, trees’ survival and establishment under different environments partly depends on their wood density and mechanical strength (Van Gelder et al. 2006; Curran et al. 2008). In addition to the wind and wave forces, mangroves are exposed to soils that vary in salinity. Mangrove trees that grow low in the intertidal area are more frequently inundated than trees growing in positions that are higher in the intertidal zone. When rainfall run-off is limited, soil pore-water high in the intertidal zone becomes highly saline due to evaporation of the seawater (Robert et al. 2009). Highly saline conditions are conditions similar to drought and result in an increase in the tension on the water column within the xylem, which can impose mechanical stresses on the xylem vessels (Hacke et al. 2001; Jacobsen et al. 2005).

Wood performs vital functions during the life of a tree and it also determines important ecosystem properties (Chave et al. 2009). Wood density is an important characteristic defining the mechanical properties of the wood and its performance, e.g. resistance to breakage during high winds (Curran et al. 2008; Niklas and Spatz 2010) and to boring insects and pathogens (Augspurger and Kelly 1984; Bell et al. 2006). The density of wood also influences its physiological functions because of its role in water transport (Pratt et al. 2007). For instance, high wood density has been found to decrease vessel implosion by reducing mechanical stresses associated with the negative pressure in the water column during drought (Hacke et al. 2001; Jacobsen et al. 2005).
Wood density is dependent on the anatomical characteristics of wood such as xylem vessels and fibres (Jacobsen et al. 2005; Preston et al. 2006). In angiosperms, wood density has been observed to decline with increasing vessel area, water transport occurs in the xylem vessels (Preston et al. 2006), also wood density increases with increments in fibre wall thickness, that provide mechanical strength (Jacobsen et al. 2007; Martínez-Cabrera et al. 2009). Studies of wood structure and function have focused in the relationship between wood anatomy and hydraulic conductivity (Hacke and Sperry 2001). The anatomical bases of mechanical strength have been poorly studied, but may offer insights into the variation in wood density over environmental gradients and the trade-offs between traits for mechanical strength (e.g. fibres) and water transport (xylem vessels).

The mechanical properties of stems can be described by measuring their modulus of rupture (MOR) and their modulus of elasticity (MOE). The MOR measures the maximum load that stems can resist depending on their circular cross sectional area (Eqn 3.1, Eqn 3.2) (Gere and Goodno 2009).

\[
MOR = \frac{F_{\text{max}}LR}{4I}
\]  

(Eqn 3.1)

Where \(F_{\text{max}}\) is the maximum load [N], \(L\) is the span length [m], \(R\) is the radius of the stem [m] and \(I\) refers to the second moment of area \([m^4]\) of a stem with a circular cross section, with

\[
I = \frac{\pi R^4}{4}
\]  

(Eqn 3.2)

In contrast to MOR, MOE is a material property (Gere and Goodno 2009). The MOE indicates how much a stem can bend and it is defined as the slope of the linear elastic region of load \((F)\) in \([N]\) and deflection \((\delta)\) in \([mm]\) (Eqn 3.3).

\[
MOE = \frac{FL^3}{48I\delta}
\]  

(Eqn 3.3)
Here, I studied mechanical strength, wood density and wood anatomy in canopy branches of mangroves in South East Queensland. The studied species include: the most widely distributed mangrove across the Indo-West Pacific shores, *Avicennia marina* (Acanthaceae); three members of the family Rhizophoraceae, *Rhizophora stylosa*, *Bruguiera gymnorrhiza* and *Ceriops australis*; and, *Aegiceras corniculatum* from the Myrsinaceae (Shi et al. 2005; Duke 2006).

I assessed: 1) the relationship between wood mechanical strength, wood density and wood anatomy in mangroves; 2) whether mechanical strength of wood varies among mangrove species, and 3) whether wood mechanical strength and wood density varies between *A. marina* growing low in the intertidal zone and *A. marina* from the high intertidal zone.

**Methods**

*Site description and sample collection*

The study sites were located in South East Queensland, where the mean air temperature is 21°C (mean minimum temperature of 15°C and mean maximum temperature of 25°C) and the mean rainfall is 1150 mm year$^{-1}$. The study sites were in Tinchi Tamba Wetlands Reserve (27.23°S, 153.02°E) and Point Halloran Reserve, 35 km to the south of the Tinchi Tamba site (27.56°S, 153.28°E). These sites were chosen as they contain five of the most abundant mangrove species in South East Queensland. Mangroves in this study were selected to include both species with typical (*R. stylosa*, *B. gymnorrhiza*, *C. australis* and *A. corniculatum*) and atypical (*A. marina*) secondary growth. Typical secondary growth refers to a single cylindrical cambium that produces phloem externally and xylem internally, whereas atypical secondary growth displays successive cambia, i.e. forming consecutive bands of xylem and phloem connected by a band of parenchyma tissue (Fig. 1.1; Carlquist 2001).
At each site and on the basis of elevation relative to mean sea level, I defined two intertidal zone habitats: low and high intertidal. I assessed salinity of soil pore-water at each intertidal zone from each site. In addition, I collected pore-water samples at 30 cm depth using a suction device (McKee et al. 1988) and measured salinity with a handheld refractometer (W/ATC 300011, SPER Scientific Scottsdale, USA).

I collected canopy branches from each species in each intertidal zone (low and high intertidal) during July 2010 (n = 166). I tested for mechanical strength (MOE and MOR) and wood density differences between species as described in the data analyses section. I made a second collection of branches to assess the relationship between mechanical strength, wood density, and anatomical characteristics (n = 38).

I chose straight branches with diameters 8 to 10 mm and length 20 times larger than branch diameter to minimize shear during the measurements (Rosell and Olson 2007; Onoda et al. 2010). After cutting the branches, I covered them with a moist paper towel and stored them in sealed plastic bags inside an insulated container. Branches were then stored in a refrigerator at 8°C until laboratory analyses of mechanical strength were performed, within 2 days of sample collection. After analyses of the mechanical properties of the branches, I stored two subsamples of approximately 7 cm length for analysis of wood density and anatomical analyses. I analysed wood density, fibre wall thickness, xylem vessel diameter, the proportion of the branches diameter comprised by pith and bark. In addition, for A. marina I assessed the proportion of phloem per layer of wood as described in Santini et al. (2012).
**Measurement of mechanical properties**

I measured the modulus of elasticity (MOE) and the modulus of rupture (MOR) of the stems using an Electromechanical Testing Machine (INSTRON 5584, Chicago, USA). For each branch, I performed a three point bending test. For this test a vertical force of 25 mm min\(^{-1}\) was applied (Onoda et al. 2010).

**Measurement of wood characteristics**

I measured wood density from the 7 cm length subsamples of the collected stems. I determined the mass of water displaced by the wood as green volume, and then dried the subsamples in an oven at 60ºC for 5 days (until constant weight was attained). Finally, I calculated wood density as the ratio of dry mass over green volume following Chave et al. (2006).

To assess wood anatomy I made transverse sections of 25 µm thickness with a Reichert-Jung sliding microtome. I photographed the sections using an Olympus BX61 microscope (Tokyo, Japan). From the photographs I measured 100 – 200 xylem vessels and 100 – 200 fibres for each stem.

I calculated the xylem vessel diameter \((D_h)\) following Lewis (1992) (Eqn 3.4), and the total vessel lumen area \((XA)\) considering the vessel area \((VA)\) and the vessel density \((VD)\) (Eqn 3.5, Eqn 3.6).

Letters \(a\) and \(b\) in Eqn 3.4 are the short and long axes of each vessel

\[
D_h = \sqrt{\frac{2a'b^2}{a^2 + b^2}} \tag{Eqn 3.4}
\]

\[
XA = VAVD \tag{Eqn 3.5}
\]

With vessel density and vessel area calculated as the area of an ellipse,

\[
VA = \pi ab0.25 \tag{Eqn 3.6}
\]

Fibre wall thickness was calculated as double fibre wall thickness dividing the total distance by two (Lei et al. 1997; Luo et al. 2005).
For pith and bark measurements, I first smoothed the branch transversal surface with a blade, removing any protrusions. The proportion of pith and bark were determined as the width of the pith and the mean width of the bark (measured at three different points separated by the same distance around the stem circumference) divided by the total branch diameter.

I measured proportion of wood comprised of phloem for *A. marina*. The proportion of phloem per growth layer was calculated as the width of the phloem band divided by the total width (xylem + phloem) of the growth layer. All anatomical characteristics were measured using Image Pro Plus version 5.0.1 (MediaCybernetics, Maryland, USA).

**Data analyses**

To assess the variation in Modulus of Elasticity (MOE), Modulus of Rupture (MOR) and wood density between a) species within the same intertidal zone; and b) among *A. marina* occurring in two different intertidal zones, we performed a Kruskal–Wallis one-way analysis of variance (ANOVA) followed by a Dunn’s post-test. I assessed the relationship between MOE, MOR, wood density, and the anatomical characteristics using Pearson correlation tests based on mean values of species to avoid pseudoreplication (Crawley 2007). I performed these analyses with the software Prism 5.0 (La Jolla, CA, USA). Additionally, I used general linear models, where species were nested factors by using the *nlme* package and the function *lme* with the software R (The R Foundation for Statistical Computing). When necessary I performed bootstrap analyses with the function *boot* from the software R to demonstrate that the sample size was adequate for analyses (bias <0.01). Further, I performed stepwise multiple regression analyses to investigate the contribution of anatomical characteristics to the variation in MOE, MOR and wood density with the software R. Independent variables used for the multiple regression analyses were not correlated. In addition, a principal component analysis was done to visualize the relationship among MOE, MOR, wood density and the wood structural characteristics of mangrove branches. I performed
D'Agostino–Pearson normality tests to confirm that my data were normally distributed (D’Agostino and Ralph 1970).

Results

Both MOE and MOR increased with wood density (Fig. 3.1A, B). Additionally, MOE and MOR were strongly correlated ($r^2=0.99$, $p<0.0001$). Therefore, in the following results I only present results for MOE.

The modulus of elasticity (MOE) varied from 536.8 ± 39.23 MPa in *R. stylosa* and 554 ± 58.20 MPa in *B. gymnorrhiza* to 2079±177 MPa in *A. marina*. In the low intertidal zone, *R. stylosa* and *B. gymnorrhiza* exhibited a similar MOE, which was significantly lower from *A. corniculatum* and *A. marina* (Fig. 3.2A). In the high intertidal zone *A. marina* and *C. australis* exhibited a similar MOE (Fig. 3.2B). Similar to MOE, wood density varied between species from the same intertidal zone (Fig. 3.2C, D).

The tall *A. marina* growing in the low intertidal zone had higher MOE values than *A. marina* growing high in the intertidal zone (Fig. 3.3A). However, wood density values of *A. marina* from the high intertidal zone were similar than for *A. marina* low in the intertidal (Fig. 3.3B).

Assessment of the relationship between MOE, wood density and xylem vessel lumen area found that increases in MOE were associated with decreased xylem vessel lumen area (Fig. 3.4A). In addition, MOE decreased as the proportion of pith increased (Fig. 3.4B). I found that the proportion of stem that was pith varied significantly among species. The pith comprised 13.3 ± 0.3 (%) of the branch diameter in *A. corniculatum* to 47.2 ± 3 (%) in *B. gymnorrhiza* (Table 3.1).
MOE and wood density increased as fibre wall thickness increased (Fig. 3.4C, Table 3.2). Fibre wall thickness varied from 2.40 ± 0.13 (µm) to 5.47 ± 0.16 µm, with fibre walls from *C. australis* being the thickest of the species examined (Table 3.1). Finally, I evaluated how variation in MOE was explained by proportion of bark of the stem diameter. I found that MOE declined as the proportion of bark increased (Fig. 3.4D). *Bruguiera gymnorrhiza* exhibited the highest proportion of bark per stem diameter (9.26 ± 0.69 %) of our studied species (Table 3.1).

Multiple regression analyses of MOE over all species found that xylem vessel lumen area and fibre wall thickness explained 87% of the variation in MOE. Similar to MOE, the multiple regression model for MOR found that 89% of the variation could be explained by xylem vessel lumen area and fibre wall thickness. Finally, 88 % of the variation in wood density was explained by pith content and fibre wall thickness (Table 3.2). A principal component analysis was done to visualize the relationship among MOE, MOR, wood density and the wood structural characteristics of mangrove branches (Fig. 3.5).

In *A. marina*, in which phloem is an important component of the wood, I found MOE to decrease with the proportion of phloem (expressed as a percentage) per wood layer (Fig. 3.6).

**Discussion**

We found wood density to be a good indicator of mechanical strength (MOE and MOR) of mangrove species from South East Queensland.

Mechanical strength decreased with increases in xylem vessel lumen area. This accounted for a large part of the variation in mechanical strength (64%); as also reported in other studies (Jacobsen et al. 2007; Chave et al. 2009). Allometric scaling theory predicts that larger lumen areas would
allow higher rates of transpiration and photosynthetic carbon gain, supporting large canopies and high growth rates and this seems to occur in a number of species (e.g. Enquist et al. 1999; King et al. 2006). Therefore, decreases in xylem vessel lumen area results in increased mechanical strength but potentially at the cost of a reduced growth in mangroves. This trade-off between mechanical strength and vessel area appears to be absent in roots; Pratt et al. (2007) found that increments in vessel area do not explain decreases in root mechanical strength and suggested that hydraulic demands are more important than mechanical demands in roots given they can experience extremely low water potentials.

Overall the species in our study we found mechanical strength to decrease with increasing proportion of pith in the wood. Pith in woody plants is composed of parenchyma tissue with thin cellulose walls. The parenchyma of the pith can be responsible for various metabolic processes including storage of water, synthesis (i.e. hormones, enzymes, pigments), photosynthesis, respiration and communication with the vascular system of the trees via the pit structures of the cells (Forest et al. 1970; Dalessandro and Roberts 1971; Metzler et al. 1995; Olson 2005). Associations between pith content and mechanical strength in mangrove branches may indicate that supporting metabolic activity within the vascular system, has associated costs of reducing mechanical strength.

Mechanical strength increased with the wall thickness of the fibres. Fibres provide structural support in secondary wood of angiosperms (Jacobsen et al. 2007; Beck 2010). Additionally, thick fibre walls have been proposed to provide mechanical strength to the xylem vessels under negative pressure (Jacobsen et al. 2005). The thickest fibres of all species were found in the wood of *C. australis*, which grows high in the intertidal where soil pore-water salinity is hypersaline. In our study sites *C. australis* occurred at 41 - 50 ppt but has been observed to persist in salinities of over 90 ppt (Ball 1998b). In this species, which tends to occur in landward, hypersaline environments,
thick fibre walls may protect xylem from implosion under extreme negative pressure, although this remains to be tested experimentally.

A previous study found that fibre wall thickness increased with increasing salinity (up to 23 ppt) in the mangrove *A. corniculatum* (Sun and Lin 1997). In this study I did not observe significant increases in fibre wall thickness in *A. marina* in more saline high intertidal environments compared to trees growing low in the intertidal, although mean fibre wall thickness was higher in the high intertidal. The salinity of the high intertidal habitat was 11 - 19 ppt higher than the low intertidal. However, increases in fibre wall thickness may not vary linearly with salinity (or with water potential in the xylem) and variation in fibre wall thickness with salinity may vary among species with differing levels of salinity tolerance.

The wood anatomical characteristics of the studied mangrove species have a range of mechanical strength. *Avicennia marina*, *C. australis* and *A. corniculatum* exhibited higher wood mechanical strength and wood density than *R. stylosa* and *B. gymnorrhiza* which may provide enhanced resistance to wind and water forces (tidal flows and waves) as well as to high tensions on the water column that occur in highly saline environments. In contrast, *R. stylosa* and *B. gymnorrhiza*, with their wood of low mechanical strength and wood density, are potentially more likely to be damaged during cyclones or storms when high wind speeds and waves occur. Bardsley (1985) compared the degree of damage in 13 mangrove species after a tropical cyclone. She found that *R. stylosa* was particularly sensitive to damage by wind gusts. In contrast, she found *A. marina* to be the less damaged by extreme wind speeds. Stilt and buttress roots in *R. stylosa* and *B. gymnorrhiza* may play a role in mechanical resistance that compensate for their weaker, less strong branches.

Mechanical strength of *A. marina*, which has successive cambia, was negatively correlated with the proportion of phloem per wood layer. The proportion of phloem was higher in branches from the
high intertidal zone and therefore trees in the high intertidal zone had lower mechanical strength compared to those in the low intertidal zone. The decline in mechanical strength could be due to the phloem bands, which may create areas of weakness between the xylem / fibre matrix thereby lowering the mechanical strength in *A. marina* branches in high intertidal, saline habitats.

Finally, the proportion of the stem that was comprised of bark was loosely negatively correlated to wood density and mechanical strength. Niklas (1992) found that bark contributes positively to mechanical strength, but only in old stems, when bark comprised at least 32% of the stem, which far exceeds the range of 3.96 ± 0.24 % (*A. marina* shrubs) to 9.26 ± 0.69 % (*B. gymnorrhiza*) in the mangrove branches of this study.

While in general wood density was a good indicator of mechanical strength, *A. marina* trees growing in the low intertidal zone, where tidal forces are usually stronger than higher in the intertidal, exhibited higher mechanical strength values than *A. marina* trees growing high in the intertidal, but wood density in both intertidal zones was similar. Mechanical strength differences between *A. marina* from the low and the high intertidal can be due to a reduction in the inclination angle of microfibrils in the low intertidal zone (Déjardin et al. 2010). In addition, wood density is the result of variation in a range of anatomical traits (i.e. xylem vessel lumen area, fibre wall thickness, phloem content), which can vary independently with environmental variables. For example, in *A. marina* there may be no change in wood density with increasing fibre wall thickness if this occurs concurrently with increases in the proportion of phloem content in the wood.

**Conclusions**

Mechanical strength varied with wood density in mangrove species from South East Queensland. In the low intertidal zone *A. marina* and *A. corniculatum* exhibited the highest mechanical strength in
contrast to *B. gymnorrhiza* and *R. stylosa* (which exhibited the lowest mechanical strength). In the high intertidal, *A. marina* and *C. australis* exhibited similar mechanical strength. Higher mechanical strength and wood density in mangrove branches were mainly explained by reductions in xylem vessel lumen areas, which may have costs through reducing water uptake, carbon gain and growth and with lower pith content (where synthesis occurs, e.g. hormones, enzymes, pigments). In addition, higher mechanical strength and wood density were associated with increases in fibre wall thickness. These associations between wood strength and anatomical characteristics in mangrove branches suggest trade-offs between mechanical strength and water supply, both of which are linked to tree growth and survival.
Table 3.1 Wood anatomical basis of the differences in mechanical strength for the five dominant mangrove species from South East Queensland. Species are ordered from low to high mechanical strength. Values are means and standard errors. Different letters indicate that means were significantly different following the Tukey’s test (p<0.05).

<table>
<thead>
<tr>
<th>Species</th>
<th>Fibre wall thickness (µm) ± SE</th>
<th>Total vessel lumen area (µm²) ± SE</th>
<th>Pith content (%) ± SE</th>
<th>Bark content (%) ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizophora stylosa</td>
<td>2.40 ± 0.13 a</td>
<td>83211 ± 5387 a</td>
<td>38.45 ± 1.2 a</td>
<td>5.1 ± 0.3 a</td>
</tr>
<tr>
<td>Bruguiera gymnorrhiza</td>
<td>4.09 ± 0.23 d</td>
<td>82323 ± 11415 a</td>
<td>47.23 ± 2.8 b</td>
<td>9.3 ± 0.7 c</td>
</tr>
<tr>
<td>Avicennia marina (High intertidal)</td>
<td>4.05 ± 0.27 cd</td>
<td>46855 ± 2983 b</td>
<td>22.84 ± 1.9 cd</td>
<td>4.0 ± 0.2 a</td>
</tr>
<tr>
<td>Ceriops australis</td>
<td>5.47 ± 0.16 b</td>
<td>68752 ± 7499 ab</td>
<td>18.88 ± 1.0 de</td>
<td>4.2 ± 0.2 a</td>
</tr>
<tr>
<td>Aegiceras corniculatum</td>
<td>3.99 ± 0.14 c</td>
<td>58361 ± 7596 ab</td>
<td>13.34 ± 0.3 e</td>
<td>6.9 ± 0.8 b</td>
</tr>
<tr>
<td>Avicennia marina (Low intertidal)</td>
<td>4.18 ± 0.26 d</td>
<td>61871 ± 2130 ab</td>
<td>18.82 ± 0.7 cde</td>
<td>4.6 ± 0.2 a</td>
</tr>
</tbody>
</table>
Table 3.2 Stepwise multiple regression models for Log (Modulus of Elasticity) and wood characteristics, Log (Modulus of Rupture) and wood characteristics, and wood density and wood characteristics in mangroves branches from South East Queensland. Only wood characteristics that contributed significantly to the models are shown, $p < 0.05$, standard error $< 0.01$.

<table>
<thead>
<tr>
<th>$y$ – Dependent variable</th>
<th>Estimate (Original)</th>
<th>t-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Log Modulus of Elasticity (MPa)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.74</td>
<td>73.4</td>
</tr>
<tr>
<td>Fibre wall thickness (µm)</td>
<td>0.92</td>
<td>362</td>
</tr>
<tr>
<td>Vessel lumen area (µm²)</td>
<td>$2.40 \times 10^{-5}$</td>
<td>186</td>
</tr>
<tr>
<td>Fibre wall thickness (µm)* Vessel lumen area (µm²)</td>
<td>$-1.11 \times 10^{-5}$</td>
<td>-335</td>
</tr>
<tr>
<td><strong>Log Modulus of Rupture (MPa)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-2.61</td>
<td>-11.9</td>
</tr>
<tr>
<td>Fibre wall thickness (µm)</td>
<td>1.31</td>
<td>23.7</td>
</tr>
<tr>
<td>Vessel lumen area (µm²)</td>
<td>$4.73 \times 10^{-5}$</td>
<td>16.8</td>
</tr>
<tr>
<td>Fibre wall thickness (µm)* Vessel lumen area (µm²)</td>
<td>$-1.63 \times 10^{-5}$</td>
<td>-22.5</td>
</tr>
<tr>
<td><strong>Wood density (g/cm³)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.36</td>
<td>16.1</td>
</tr>
<tr>
<td>Fibre wall thickness (µm)</td>
<td>0.07</td>
<td>2.12</td>
</tr>
<tr>
<td>Fibre wall thickness (µm)* Pith content (%)</td>
<td>$-1.78 \times 10^{-3}$</td>
<td>-10.7</td>
</tr>
</tbody>
</table>

1 Final model, $r^2 = 0.87$

2 Final model, $r^2 = 0.89$

3 Final model, $r^2 = 0.88$
Fig. 3.1 The relationship between A) Log Modulus of Elasticity (MOE) and Wood density and B) Log Modulus of Rupture (MOR) and Wood density. Symbols represent species, *A. marina* (filled circles), *A. corniculatum* (open diamonds), *B. gymnorrhiza* (open upside down triangles), *C. australis* (squares) and *R. stylosa* (filled triangles). Each point represents mean ± standard error of $n = 30 - 72$. Values of $r^2$ and $p$ are based on Pearson correlation tests.
Fig. 3.2 A) Modulus of elasticity of branches from the dominant mangrove species in South East Queensland from the low intertidal and the B) high intertidal. C) Wood density of branches from the dominant mangrove species in South East Queensland from the low intertidal and the D) high intertidal. Values are means and standard errors ($n = 30 - 36$). Different letters indicate that the means were significantly different ($p<0.05$).
Fig. 3.3 A) Modulus of elasticity of *A. marina* from the high and the low intertidal. B) Wood density of *A. marina* from the high and the low intertidal. Values are means and standard errors. Different letters indicate that the means were significantly different (*n* = 31 – 41, *p*<0.05).
Fig. 3.4 Relationship between Log Modulus of Elasticity (MOE) and A) Xylem vessel lumen area B) Pith content (expressed as total %), C) Fibre wall thickness and D) Bark content (expressed as total %) of mangroves. The lines represent the linear regressions where A) Log MOE = -2.14 x 10^{-5} Xylem vessel lumen area + 4.53, B) Log MOE = -2.16 x 10^{-2} Pith content + 3.64, C) Log MOE = 0.16 Fibre wall thickness + 2.38, and D) Log MOE = -8.86 x 10^{-2} Bark content + 3.53. Symbols represent species, A. marina (filled circles), A. corniculatum (open diamonds), B. gymnorrhiza (open upside down triangles), C. australis (squares) and R. stylosa (filled triangles). Each point represents mean ± standard error of n = 4 - 10.
Fig. 3.5 Relationship among wood characteristics (modulus of rupture, modulus of elasticity, wood density, pith content, bark content, vessel lumen area and fibre wall thickness) of the studied mangrove species along two axes determined by principal component analyses (PCA).
Fig. 3.6 Relationship between Log modulus of elasticity (MOE) and the proportion of phloem per growth layer expressed as a percentage. The line represents the linear regression where Log MOE = -4.0 x 10^{-2} Phloem%/layer + 4.47, n = 10. Confidence Intervals for the slope and the intercept after bootstrapping the sample 1000 times are as follows (CI 95 % for slope: -0.06, -0.01) and (CI 95 % for intercept: 3.2, 5.7). Symbols represent A. marina branches from the low-intertidal zone (filled circles) and A. marina from the high-intertidal zone (open circles).
Chapter 4. Variation in wood density and anatomy in a widespread mangrove species
Abstract

Wood density is an important plant trait that influences a range of ecological processes, including resistance to damage and growth rates. Wood density is highly dependent on anatomical characteristics associated with the conductive tissue of trees (xylem and phloem) and the fibre matrix in which they occur. Here, I investigated variation in the wood density of the widespread mangrove species *Avicennia marina* in the Exmouth Gulf in Western Australia and in the Firth of Thames in New Zealand. I assessed how variation in xylem vessel diameter, fibre wall thickness and proportion of phloem within the wood contributed to variation in wood density and how these characteristics were linked to growth rates.

I found the wood density of *A. marina* to be higher in Western Australia than in New Zealand and to be higher in taller seaward fringing trees than in scrub trees growing high in the intertidal. At the cellular level, high wood density was associated with wide xylem vessels and thick fibre walls. Additionally, wood density increased with decreasing proportions of phloem per growth layer of wood. Tree growth rates were positively correlated with xylem vessel diameter and wood density. I conclude that *A. marina* can have large xylem vessel diameters and high growth rates while still maintaining high wood density because of the abundance and thickness of fibres in which vessels are found.

**Keywords:** Firth of Thames, Exmouth Gulf, successive cambia, xylem vessels, fibre wall thickness, growth, mangroves.
Introduction

Wood density is an ecologically and economically important trait in plants. High wood density increases resistance to physical damage (Niklas 1992), and pathogen resistance (Hillis 1987; Augspurger and Kelly 1984) and thereby contributes to plant survival. Additionally, wood density is an important parameter for estimating the biomass of trees and is used to calculate the carbon stocks in forests (Fearnside 1997). Within a species wood density can vary across environmental gradients, as its variation depends on the anatomy of the wood, which is in turn linked to functions such as water transport, mechanical strength and growth (Chave et al. 2009).

The density of wood in many species is largely determined by fibres, which are thick-walled cells composed of cellulose and lignin, that provide mechanical support (Barnett and Bonham 2004; Beck 2010). Other tissue types can also influence wood density. The abundance of xylem vessels, which have lumen areas for water transport, decreases wood density. Previous studies over a range of species have shown increasing wood density correlates with decreasing xylem vessel lumen area (Hacke et al. 2001; Preston et al. 2006).

Wood density has also been linked to tree growth rates. In a survey of 21 rain forest species from Malaysia King et al. (2006) found tree growth rates decreased with increasing wood density. The relationship between wood density and tree growth rates reflects the presence of wide xylem vessels, which allow for high rates of transpiration and photosynthetic carbon gain, that supports large canopies and high growth rates (Enquist et al. 1999; King et al. 2006).
Mangrove forests dominate the coasts of tropical and subtropical coastlines, where they are exposed to a range of physical disturbances, including ocean waves, strong winds and tidal currents. Mangroves provide valuable coastal protection services (Mazda et al. 2006) and are increasingly recognized for their role in carbon sequestration (Mcleod et al. 2011). The density of mangrove wood is key to the provision of these ecological services, yet the anatomical basis of variation in wood density in mangroves is poorly known. In this study I assessed variation in wood density of the mangrove species, Avicennia marina.

The Indo-pacific mangrove species A. marina has the widest geographical distribution of all mangroves with a latitudinal distribution from ~25°N to 38°S. Avicennia marina reaches its southernmost distribution at Corner Inlet, Victoria, Australia and in the North Island of New Zealand (Duke 2006). The species tolerates a wide range of soil water salinity and is the dominant species where aridity and/or cool temperatures limit the productivity of mangroves (Morrisey et al. 2010). The wide distribution of A. marina has been linked to its special wood structure, characterized by successive cambia (Tomlinson 1995; Robert et al. 2011a). This peculiar wood structure comprises consecutive bands of xylem, interspersed with phloem strands that are connected by a band of parenchyma tissue (Schmitz et al. 2007; 2008). Based on the occurrence of this wood structure in tree species that occur in arid or saline habitats (i.e. only 34 families are known to have this wood structure), it has been proposed that successive cambia are associated with tolerance to water deficits (Robert et al. 2011a). The presence of phloem in the successive cambia may have implications for wood density.

Here I assessed variation in wood density of A. marina in two locations with different climatic conditions and across an intertidal gradient. My goals were to 1) assess the variation in wood density between and within locations, 2) investigate the contribution of anatomical features to
variation in wood density, and 3) test for linkages among variation in wood density, anatomy and
tree growth rates in *A. marina*.

**Methods**

*Site descriptions and sample collection*

My study compares the density and structure of the wood of *A. marina* and its correlation with tree
growth rates at two sampling locations where *A. marina* is dominant, the Firth of Thames, New
Zealand and Giralia Bay, Exmouth Gulf in Western Australia.

The Firth of Thames (37.18°S, 175.4°E) is an embayment of about 19 km wide in the northern part
of the Hauraki Depression, NZ (Hochstein & Nixon 1979). In this site, an extensive mangrove
forest with varying forest structure (ranging between ~ 0.3 to 3 m in height) has developed since the
1950’s (Lovelock et al. 2010). The climate is wet, with a mean annual rainfall of 1400 mm year⁻¹
and cool, with a mean annual air temperature of 15°C (National Institute of Water and Atmospheric
Research 2011). My second sampling location at Giralia Bay in the Exmouth Gulf, Western
Australia (WA) (22.4°S, 114.3°E) is arid, with a mean annual rainfall of 300 mm year⁻¹ and warm,
with a mean annual air temperature of 25°C. Cyclones occur every two to three years in the
Exmouth region causing short periods of intense rainfall and flooding (Lovelock et al. 2011) and
wind gusts in excess of 90 km/h (Australian Bureau of Meteorology 2012).

In January 2007, five mature stems from each of three sites across the intertidal zone in NZ were
collected. The sites encompassed trees of differing sizes but within each site stems were relatively
homogeneous in diameter (Lovelock et al. 2011). The forest at the Firth of Thames, NZ is older
towards the landward side (trees recruited in ~1978) and younger on the seaward edge (trees
recruited ~1996). In the NZ forests tree size varies in a typical manner for mangroves (Feller et al. 2010), with tall trees (~1.9 m height and ~6.6 cm stem diameter) on the seaward, more frequently inundated site (NZ-Seaward) to scrub forests ~0.3 m in height and ~ 1.9 cm stem diameter in the landward, less frequently inundated site (NZ-Landward-1, 350 m from the seaward edge). The older 1978 forest is a relict fringing forest (NZ-Landward-2, 620 m from the seaward edge) that has tall trees (~ 3.2 m in height and ~ 6.2 cm stem diameter) but is inundated less frequently due to sediment accretion and forest development in a seaward direction over time. At Giralia Bay in WA, wood from 6 mature stems with similar diameters (~8.6 cm) and similar heights (~3.3 m) from the seaward edge of the forest (WA-Seaward) was collected in October 2008. Similar to the fringing site in NZ, the seaward fringing forest at Giralia Bay is inundated by the tide twice daily. Given differences in tree height from the different forests, the height in mangrove trees in which wood was collected varied; however, wood from all trees was attached to the main stems (second order branches).

At each site (three at NZ and one in WA), I assessed the porewater salinity. Water samples were collected from 30 cm depth using a suction device (McKee et al. 1988) and were analyzed with a handheld refractometer (W/ATC 300011, SPER Scientific Scottsdale, USA).

Measurement of wood characteristics

All measurements were made in the 3 - 4 outermost layers of wood (Fig. 4.1A). Wood density was measured for each tree from 1 cm x 1 cm x 2 cm rectangular prisms cut from the outer layers of the wood. Wood density was calculated as the ratio of the oven-dry mass of the wood sample divided by the mass of water displaced by its fresh (green) volume (Chave et al. 2006). Using oven-dried (60°C) and sanded wood discs (Fig. 4.1A, B), the number of growth layers, defined as ontogenetic units of phloem and xylem, was counted using an Olympus SZH10 microscope (Tokyo, Japan). A growth layer was counted if it crossed a line drawn from pith to bark along the maximum radius of
the stem disc (Schmitz et al. 2007). The proportion of phloem per growth layer was calculated as the width of the phloem band divided by the total width of the growth layer, including both xylem and phloem, measured along the radius of the stem disc.

Given it can be difficult to resolve small vessels from sanded wood discs, ~1 cm³ cubes were cut from the discs to make transverse microsections (Fig. 4.1C) that were double stained with Safranin – Alcian blue. I photographed the sections with an Olympus BX61 microscope (Tokyo, Japan). From the photographs I measured 100-200 xylem vessels and 100-200 fibres for each stem. Xylem and phloem area was measured per layer. The number of vessels was counted and the perpendicular axes of the vessel lumina were measured (Fig. 4.1C). All the measurements were done using Image Pro Plus version 5.0.1 (MediaCybernetics, Maryland, USA).

I calculated the xylem vessel diameter \((D_h)\) following the ellipse equation of Lewis (1992) (Eqn 4.1), and the total vessel lumen area \((X_A)\) accounting for vessel density \((V_D)\) and vessel area \((V_A)\) (Eqn 4.2, Eqn 4.3), \(a\) and \(b\) are the short and long axes of each vessel.

\[
D_h = \sqrt[4]{\frac{2a^2b^2}{a^2 + b^2}} 
\]  
\text{(Eqn 4.1)}

\[
X_A = V_A V_D 
\]  
\text{(Eqn 4.2)}

with vessel density and vessel area of an ellipse,

\[
V_A = \pi ab0.25 
\]  
\text{(Eqn 4.3)}

Fibre wall thickness was calculated as double fibre wall thickness dividing the total distance by two (Fig. 4.1C; Lei et al. 1997; Luo et al. 2005).
Tree growth rates

For the *A. marina* trees from NZ the pith of each sampled tree was dated using bomb-pulse radio carbon dating with Accelerator Mass Spectrometry (AMS) $^{14}$C analysis (Table 4.1) (Lovelock et al. 2010). Wood samples were dated with a resolution from 1 - 2 years, which is possible given the significant changes in atmospheric $^{14}$C after 1955 (when the last bomb-pulse was released) (Hua and Barbetti 2004; Hua 2009). Growth rates were estimated as stem radius divided by tree age. For the trees from the WA-Seaward site, growth rates were estimated from the mean circumference increment in the period April 2008 – August 2010, as recorded with 27 mechanical dendrometer bands and converted to radius increment per year.

Data analyses

Differences in wood density, xylem vessel diameter and the proportion of phloem per growth layer between sites were tested using a Kruskal-Wallis test and a Dunn's post hoc test. These analyses were performed with the software package Prism 5.0 (La Jolla, CA, USA).

To analyse the influence of anatomical characteristics on variation in wood density I used linear regression, stepwise multiple regression and principal component analyses with the software R (The R Foundation for Statistical Computing). Linear regression analyses were performed using the package *lmodel2* (Major Axis Regression). Bootstrap analyses were performed to assess the suitability of the sample size. Confidence intervals of the slope and the intercept were calculated for the linear regressions using *lmodel2* and the bias was calculated for the multiple regressions with the R software (bias after bootstrap in all cases was < 0.001). These tests indicated that the sample size was adequate and the results were independent of sample size. Prior to analysis I tested for normality using the D'Agostino-Pearson normality test ($p > 0.05$, which indicated that the deviation from the Gaussian ideal was not more than what I would expect to see by chance alone). Independent variables (total vessel lumen area, fibre wall thickness and proportion of phloem per layer) used in the stepwise multiple regression for wood density were not correlated.
Results

Wood density was higher in WA than in NZ \((n=19, \ p<0.005)\). Between the NZ sites wood density was similar in the tall trees from NZ-Seaward and NZ-Landward-2, but wood density was significantly lower in the NZ-Landward-1 scrub trees (Fig. 4.2).

My analysis of the anatomical factors that contribute to wood density showed that over all our sites wood density was positively related to mean xylem vessel diameter and total vessel lumen area (Table 4.2; Fig. 4.3A, B; Fig. 4.4). Variation in total vessel lumen area can be due to variation in vessel density and/or variation in vessel diameter. Vessel density varied from \(57 \pm 13 \) vessels mm\(^{-2}\) (mean \pm standard deviation) in NZ-Seaward to \(64 \pm 13 \) vessels mm\(^{-2}\) in WA-Seaward but these values were not significantly different between sites. Therefore variation in total vessel lumen area between locations was due xylem vessel diameter.

I also observed that \textit{A. marina} trees with high wood density had thicker fibre walls (Table 4.2; Fig. 4.3C; Fig. 4.4) and a lower proportion of phloem per growth layer (Table 4.2; Fig. 4.3D; Fig. 4.4). The proportion of phloem per growth layer was highest in landward forests from NZ (Fig. 4.5). The three components together: total vessel lumen area, fibre wall thickness and the proportion of phloem per growth layer explained 76% of the variation in the wood density of \textit{A. marina} (Table 4.3).

Tree growth rates increased with wider xylem vessels and were associated with higher wood density over all sites (Table 4.2; Fig. 4.6A, B). However, the regression of growth rates and wood density was significant only for the NZ sites. In contrast, over all sites wood density and xylem
vessel diameters were significantly positively correlated with tree size (Fig. 4.7A, B).

**Discussion**

Over the contrasting sites I found that wood density of *A. marina* varied. In the same habitat (seaward fringe) *A. marina* tended to have higher mean wood density in WA than in NZ. In different sites within the same location in NZ, landward scrub mangroves (NZ-Landward-1) had lower wood density than tall trees in seaward fringing forest (NZ-Seaward) and those in a taller landward forest (NZ-Landward-2). Using the variation in wood density over all sites I found that wood density increased with total vessel lumen area and fibre wall thickness but was negatively correlated with the proportion of phloem per growth layer of wood.

The positive relationship between wood density and total vessel lumen area and xylem vessel diameter observed in *A. marina* is in contrast to previous studies that have found high wood density is associated with low total vessel lumen areas and small vessel sizes (Preston et al. 2006; Jacobsen et al. 2007). However, by increasing fibre wall thickness, *A. marina* maintains high wood density even with large xylem diameters. By investing in thick fibre walls and reducing the proportion of phloem per growth layer in wood, *A. marina* could maintain both high water conductivity and mechanical strength. Other studies have also observed that high wood density is not always associated with low xylem lumen area, indicating that trees may achieve high wood density using a range of anatomical strategies (Jacobsen et al. 2005; Martínez-Cabrera et al. 2009).

Wood density of *A. marina* increased with increasing fibre wall thickness as has been observed in other tree species (Jacobsen et al. 2005; Martínez-Cabrera et al. 2009). The walls of fibres of *A. marina* are very thick compared to other trees species and their fibre lumina is almost completely
lost (IAWA 2012). For example, in this study mean fibre wall thickness in WA-Seaward trees was 5.27 ± 0.55 mm (mean ± standard deviation) in *A. marina* compared to 2 mm in *Rollinia rensoniana* (Barajas-Morales 1985). The thick-walled fibres of *A. marina* may increase resistance to breakage by wind and tidal waters during storms, even in rapidly growing trees with large total vessel lumen areas. In WA the large vessels observed in *A. marina* trees occurred within a dense fibre matrix. In addition to protection from breakage and attack from wood boring invertebrates, fibres add strength to xylem walls that may increase their resistance to collapse under the high tensions that may occur on the xylem water column with water deficits (Jacobsen et al. 2005).

Tree growth rates increased with xylem vessel diameter and wood density at the NZ site. Stronger correlations (over all sites) were observed between xylem vessel size and stem radius and wood density and stem radius, possibly because stem radius is an integrated measure of tree growth over the entire life time of trees compared to growth rates calculated from changes in stem radius over 2.3 years of observations, as they were for the WA trees. The relationship between large lumen areas and fast growth rates and tree size is predicted by theoretical analyses of tree growth (Enquist et al. 1999) and has been observed in other species (Poorter et al. 2010; Russo et al. 2010).

Low wood density of *A. marina* in my study was strongly associated with high proportions of phloem tissue per growth layer in the wood. Phloem is a major constituent of *A. marina*’s wood tissue and results from secondary growth via successive cambia. Successive cambia have been described in shrubs and tree species of which ~84% have been found to grow under conditions where drought is common (Robert et al. 2011a). Phloem within the wood may be a site for starch depolymerisation, which is the basis of the mechanism for refilling of embolized xylem vessels (Nardini et al. 2010, Nardini et al. 2011) and therefore phloem in wood has been proposed to be important in tolerating salinity stress in *A. marina* (Robert et al. 2011a), and drought stress in other species (Salleo et al. 2004). The proportion of phloem per growth layer in the wood varied across
the intertidal gradient in NZ, being significantly higher in landward trees compared to seaward trees. Additionally, previous studies found higher proportions of phloem per growth layer in landward *A. marina* trees from Kenya (Schmitz et al. 2007; Schmitz et al. 2008). My results indicate a high level of phloem in wood is associated with reduced wood density. This may have negative consequences for withstanding damage from wind and waves and also pathogens and pests. Trees growing in suboptimal habitats (high intertidal) with low wood density may have a greater likelihood of physical damage than trees growing in more seaward sites.

**Conclusions**

Wood density of *A. marina* varied between locations and across an intertidal gradient in NZ. High wood density of *A. marina* was associated with large xylem vessel diameters (and total lumen area), thick-walled fibres, low proportion of phloem in the wood, faster growth rates and larger tree sizes. In contrast, low wood density was associated with large areas of phloem within the wood, smaller xylem vessels, thin-walled fibres, slower growth rates and small tree sizes.
Table 4.1 Description of the characteristics of *A. marina* trees from the seaward and landward sites of the mangrove forests in New Zealand (NZ) and Western Australia (WA). NZ-Landward-1 trees grow 350 m from the seaward edge of the forest, while NZ-Landward-2 trees grow 620 m from the seaward edge. The age of NZ trees was estimated using bomb pulse $^{14}$C dating (Lovelock et al. 2010). The age of WA trees was estimated from measurement of circumference increments for 2.3 years using 27 mechanical dendrometer bands.

<table>
<thead>
<tr>
<th>Site</th>
<th>Estimated tree age (years)</th>
<th>Mean tree height (m)±SD</th>
<th>n</th>
<th>Mean no. growth layers / mm ± SD</th>
<th>n</th>
<th>Phloem % / mm ± SD</th>
<th>n</th>
<th>Mean stem diameter (mm) ± SD</th>
<th>n</th>
<th>Radius increment (range) (mm year$^{-1}$)</th>
<th>n</th>
<th>Salinity (ppt) ± SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>NZ-Seaward</td>
<td>9-13</td>
<td>1.87± 0.29</td>
<td>4</td>
<td>0.58 ± 0.08</td>
<td>5</td>
<td>18 ± 1</td>
<td>5</td>
<td>66.2±10.9</td>
<td>5</td>
<td>3.11 (2.12-4.28)</td>
<td>3</td>
<td>44 ± 2</td>
<td>4</td>
</tr>
<tr>
<td>NZ-Landward-1</td>
<td>8-12</td>
<td>0.35±0.04</td>
<td>4</td>
<td>0.89 ± 0.17</td>
<td>5</td>
<td>38 ± 2</td>
<td>5</td>
<td>19.4±2.50</td>
<td>5</td>
<td>1.01 (0.70-1.37)</td>
<td>3</td>
<td>50 ± 4</td>
<td>4</td>
</tr>
<tr>
<td>NZ-Landward-2</td>
<td>27-30</td>
<td>3.22±0.05</td>
<td>4</td>
<td>0.69 ± 0.06</td>
<td>5</td>
<td>29 ± 1</td>
<td>5</td>
<td>61.8±5.01</td>
<td>5</td>
<td>1.08 (0.94-1.23)</td>
<td>3</td>
<td>53 ± 4</td>
<td>4</td>
</tr>
<tr>
<td>WA-Seaward</td>
<td>47-67</td>
<td>3.30±0.70</td>
<td>27</td>
<td>0.97 ± 0.29</td>
<td>6</td>
<td>35 ± 2</td>
<td>6</td>
<td>86.4±2.05</td>
<td>6</td>
<td>1.04 (0.05-3.18)</td>
<td>27</td>
<td>53 ± 3</td>
<td>5</td>
</tr>
</tbody>
</table>
Table 4.2 Parameters of the regression analysis of wood density, xylem vessel diameter and growth rates. I show the 95% confidence intervals (CI) of the parameters after running a bootstrap 1000 times. In each case, units are as follows: Vessel diameter (µm), Total vessel lumen area (µm²), Fibre wall thickness(µm), Proportion of Phloem per wood Layer (%), Stem radius (cm), Growth rates (mm year⁻¹).

<table>
<thead>
<tr>
<th>X – variable</th>
<th>y - dependent variable</th>
<th>Regression Equation</th>
<th>²</th>
<th>p</th>
<th>n</th>
<th>CI 95% For slope</th>
<th>CI 95% For Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vessel diameter</td>
<td>Wood density</td>
<td>y = 1.2 x 10⁻² X + 0.04</td>
<td>0.67</td>
<td>0.0001</td>
<td>19</td>
<td>(-1.50 x 10⁻¹, 0.25)</td>
<td>(8.2 x 10⁻¹, 1.70 x 10⁻¹)</td>
</tr>
<tr>
<td>Total vessel lumen area</td>
<td>Wood density</td>
<td>y = 2.6 x 10⁻⁴ X + 0.43</td>
<td>0.59</td>
<td>0.0001</td>
<td>19</td>
<td>(1.52 x 10⁻⁴, 3.76 x 10⁻⁶)</td>
<td>(0.34, 0.51)</td>
</tr>
<tr>
<td>Fibre wall thickness</td>
<td>Wood density</td>
<td>y = 0.21 X – 0.44</td>
<td>0.38</td>
<td>0.01</td>
<td>16</td>
<td>(0.14, 0.33)</td>
<td>(-1.04, -0.06)</td>
</tr>
<tr>
<td>Proportion of Phloem per Layer</td>
<td>Wood density</td>
<td>y = -2.0 x 10⁻³ X + 0.97</td>
<td>0.35</td>
<td>0.009</td>
<td>21</td>
<td>(-1.6 x 10⁻³, -2.6 x 10⁻³)</td>
<td>(0.71, 1.23)</td>
</tr>
<tr>
<td>Vessel diameter</td>
<td>NZ Growth rates</td>
<td>y = 0.10 X – 2.84</td>
<td>0.23</td>
<td>0.01</td>
<td>12</td>
<td>(0.05, 0.25)</td>
<td>(-3.80, -2.50)</td>
</tr>
<tr>
<td>Vessel diameter</td>
<td>WA Growth rates</td>
<td>y = 0.04 X – 1.5</td>
<td>0.40</td>
<td>0.02</td>
<td>6</td>
<td>(0.01, 0.06)</td>
<td>(-2.10, -1.05)</td>
</tr>
<tr>
<td>Wood density</td>
<td>NZ Growth rates</td>
<td>y = 17.5 X – 8.29</td>
<td>0.57</td>
<td>0.0045</td>
<td>12</td>
<td>(12.7, 20.1)</td>
<td>(-9.20, -7.50)</td>
</tr>
<tr>
<td>Stem radius</td>
<td>Wood density</td>
<td>y = 0.05 X + 0.46</td>
<td>0.62</td>
<td>0.0001</td>
<td>19</td>
<td>(0.03, 0.07)</td>
<td>(0.40, 0.53)</td>
</tr>
<tr>
<td>Stem radius</td>
<td>Vessel diameter</td>
<td>y = 4.51 X + 30.4</td>
<td>0.76</td>
<td>0.0001</td>
<td>21</td>
<td>(3.55, 6.10)</td>
<td>(25.2, 33.6)</td>
</tr>
</tbody>
</table>

¹ Growth rates had a positive relationship with wood density over all sites but the regression was significant only for the NZ sites.
Table 4.3 Results of the stepwise multiple regression analyses for wood density. The final model for wood density (g/cm$^3$) explains 76% of the wood density variation. In each case, units are as follows: Total vessel lumen area (µm$^3$), Fibre wall thickness (µm), Proportion of Phloem per wood Layer (%).

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Estimate (Original)</th>
<th>SE</th>
<th>t-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.37</td>
<td>0.9</td>
<td>-2.62</td>
</tr>
<tr>
<td>Phloem% / Layer</td>
<td>7.30 x 10$^{-2}$</td>
<td>0.02</td>
<td>2.94</td>
</tr>
<tr>
<td>Fibre wall thickness</td>
<td>0.58</td>
<td>0.01</td>
<td>3.22</td>
</tr>
<tr>
<td>Total vessel lumen area</td>
<td>2.25 x 10$^{-6}$</td>
<td>4.5 x 10$^{-7}$</td>
<td>4.92</td>
</tr>
<tr>
<td>Phloem% / Layer * Fibre wall thickness</td>
<td>1.50 x 10$^{-3}$</td>
<td>5.1 x 10$^{-3}$</td>
<td>-3.00</td>
</tr>
</tbody>
</table>
Fig. 4.1  A) Sanded wood disc of *Avicennia marina*. Inset shows the last layers in which I sampled the wood. B) I defined a “layer” as a complete band of xylem (X) and phloem (P) that is composed of conjunctive tissue including phloem strands. C) Transverse wood section of *Avicennia marina*. Insets show how I measured double fibre wall thickness and xylem vessel axes to calculate fibre wall thickness and xylem vessel diameter (Lewis 1992).
Fig. 4.2 Mean wood density of trees at sampling sites in New Zealand and Western Australia. Values are the means and standard deviations from 3-6 individual trees. Different letters indicate that the means were significantly different ($p<0.05$, $n=19$).
Fig. 4.3 The relationship between A) wood density and xylem vessel diameter, B) wood density and total vessel lumen area, C) wood density and fibre wall thickness and D) wood density and the proportion of phloem per wood layer expressed as a percentage (Phloem%/Layer) (Details of regression lines are presented in Table 4.2). Different symbols represent different sites and different positions in the intertidal: WA-Seaward (closed circles), NZ-Seaward (open squares), NZ-Landward-1 (open diamonds) and NZ-Landward-2 (open triangles).
Fig. 4.4 Relationship among wood characteristics (wood density, total vessel lumen area, fibre wall thickness and phloem percentage per wood layer) in *A. marina* along two axes determined by principal component analyses (PCA).
Fig. 4.5 The proportion of phloem per growth layer expressed as a percentage (Phloem% / Growth Layer) over the sampling sites in New Zealand (NZ) and Western Australia (WA). Values are the means and standard deviations from 5-6 individual trees. Different letters indicate that the means were significantly different ($p<0.05$, $n=21$).
Fig. 4.6 The relationship between A) tree growth rate and xylem vessel diameter, and B) tree growth rate and wood density (Details of regression lines are presented in Table 4.2). Different symbols represent different sites and different positions in the intertidal: WA-Seaward (closed circles), NZ-Seaward (open squares), NZ-Landward-1 (open diamonds) and NZ-Landward-2 (open triangles).
Fig. 4.7 The relationship between A) wood density and stem radius and B) xylem vessel diameter and stem radius for the mangrove *Avicennia marina* (Details of regression lines are presented in Table 4.2). Different symbols represent different sites and different positions in the intertidal: WA-Seaward (closed circles), NZ-Seaward (open squares), NZ-Landward-1 (open diamonds) and NZ-Landward-2 (open triangles).
Chapter 5. Historical growth rates of mangrove trees in the arid zone of Western Australia: Sensitivity to climatic cycles
Abstract

Mangrove trees tend to be larger and communities more diverse in tropical latitudes, particularly where there is high rainfall. Variation in the structure, growth and productivity of mangrove forests over climatic gradients suggests they are sensitive to variation in climate, however evidence of changes in forests in response to variation in climate is scarce. Bomb-pulse radiocarbon dating techniques offer advances in the examination of the response of tropical and subtropical trees to variation in climate by providing accurate dates of wood formation and tree age. Here, I used bomb-pulse radiocarbon techniques, combined with X-ray densitometry, to test the following hypotheses, that growth rates of \textit{A. marina} trees co-vary with the density of wood and that growth rates of \textit{A. marina} are sensitive to two indices of rainfall in the Exmouth Gulf, Western Australia.

We found the relatively small seaward fringing \textit{A. marina} trees (~ 10 cm diameter) were $68 \pm 8.6$ (mean $\pm$ standard error) years old. The growth rates of \textit{A. marina} increased with increasing wood density. Growth rates decreased with the Pacific Decadal Oscillation Index, which is an indicator of low rainfall in central Australia. We conclude that growth rates of \textit{A. marina} trees have significantly decreased between 1984 and 2008 consistent with a drying trend in Western and Central Australia, supporting the idea that mangroves are highly dependent on freshwater sources for growth and that periods of low rainfall reduce tree growth.

Keywords

\textit{Avicennia marina}, rainfall, wood density, Pacific Decadal Oscillation Index, Southern Oscillation Index, radiocarbon dating
Introduction

Mangrove forests are an important component of tropical and subtropical coastal ecosystems. They have high rates of primary production, provide habitat for fauna and increase fisheries production (Ewel et al. 1998; Alongi 2002). Mangrove forest stature and productivity is correlated with temperature over latitude (Twilley et al. 1992; Saenger and Snedaker 1993; Méndez-Alonzo and López-Portillo 2008) with trees tending to be larger and communities more diverse in tropical latitudes, particularly where there is high rainfall (Duke et al. 1981).

In arid areas growth of trees has also been observed to be enhanced after large rain-bearing cyclonic events, possibly due to delivery of nutrients and to increased availability of freshwater that can enhance metabolic rates (Lovelock et al. 2011b). Additionally, I have found that mangroves use freshwater sources for growth, such as groundwater in arid regions (Chapter 2). Variation in the structure and productivity of mangrove forests over climatic gradients suggests they will be highly sensitive to climate change (Lovelock et al. 2007; Gilman et al. 2008), but direct evidence of their sensitivity to variation in climate is not often available.

On the east coast of Australia the El Niño – Southern Oscillation (ENSO) cycle, which occurs every 3 to 7 years, has a strong influence over rainfall amounts and therefore on the productivity of many ecosystems, including mangroves (e.g. Eslami-Andargoli et al. 2009). When the Southern Oscillation Index (SOI) is high (La Niña periods) there is an increase in freshwater availability and higher than normal sea level (Feng et al. 2004). During La Niña periods mangrove forests expand in area due to high rainfall (Eslami-Andargoli et al. 2009). The Pacific Decadal Oscillation Index (PDO), analogous to the SOI, indicates temperature fluctuations in the Pacific Ocean but for longer
periods of time (20 to 30 years). Positive values of PDO link to cooler ocean temperatures, lower than normal sea level and decreased rainfall in Australia while negative values are related to warmer ocean temperatures, increased rainfall and higher than average sea level (McGowan et al. 2009). In my study site in the arid North West of Australia, in the Pilbara region, climatic patterns are complex. High rainfall (> 600 mm yr⁻¹) occurs in the austral summer associated to tropical cyclones, but in some years rainfall may also be associated with low-pressure southern climatic systems during the winter months (Gentilli 1971). Because of this complexity, the instrumental rainfall record (which begins in 1945) is not correlated with variation in ENSO (Tobin 2010). However, sea level is influenced by ENSO, and may decrease down to 20 cm in Western Australia depending on the intensity of El Niño events (Feng et al. 2004), therefore reducing tidal inundation of mangroves.

The use of rings in wood to determine sensitivity of trees to environmental change in mangroves and other tropical tree species (Worbes et al. 2002) can be difficult because of 1) the lack of annual growth rings or low confidence in the regular timing of tree rings, and 2) for the widely distributed mangrove *Avicennia marina*, its unique wood structure, characterized by successive cambia, i.e. concentrically alternating xylem and phloem bands (Carlquist 2001; Robert et al. 2011a). Examination of wood from another widespread mangrove family, the Rhizophoraceae, indicates that changes in xylem vessel density throughout the life of trees can reflect changing environmental conditions, most likely freshwater inputs (Menezes et al. 2003; Verheyden et al. 2004, 2005; Yu et al. 2004, 2007; Chowdhury et al. 2008). My work from Chapter 4 with *A. marina* suggests that variation in tree growth rates are correlated with predictable changes in wood density, and therefore wood density may be used as a proxy for tree growth over time.

The development of highly accurate radiocarbon dating techniques that use the last atomic bomb pulse (1955) of radiation that occurred in the atmosphere to date wood and other organic materials
(Hua and Barbetti 2004; Hua et al. 2009) has offered advances in the examination of the response of tropical and subtropical trees to variation in climate (Clarke et al. 2012). Here I used radiocarbon techniques combined with X-ray densitometry (which allows analyses of continuous and high-resolution wood density profiles from tree stems over time, Steppe et al. 2004; Nock et al. 2009) to test the following hypotheses: 1) Growth rates of *A. marina* trees co-vary with the density of wood; 2) growth rate of *A. marina* is sensitive to the PDO, growth rate increases when the PDO is low (when rainfall in Central Australia is high); and, 3) growth rate of *A. marina* is sensitive to ENSO (Southern Oscillation Index), decreasing with strong *El Niño* (low SOI) events associated with lower sea level and reduced tidal inundation.

**Methods**

*Site description and sample collection*

The study site was located in Giralia Bay, in the east of the Exmouth Gulf, Western Australia (WA) (22.4°S, 114.3°E). The climate of the site is warm and dry, with a mean air temperature of 25°C, a mean minimum temperature of 17°C, and a mean maximum temperature of 32°C, with peaks of up to 47°C in summer. The mean annual rainfall in the site is 250 mm yr\(^{-1}\) (Fig. 5.1). In the region, cyclones bringing wind gusts in excess of 300 km h\(^{-1}\) and heavy rainfall (> 600 mm yr\(^{-1}\)) occur every two to three years (Australian Bureau of Meteorology 2012).

In October 2008, four mature stems of the widespread mangrove species *A. marina* were collected. The sampling was 7 months after tropical cyclone *Pancho*, which flooded the region in March 2008. I chose mangrove trees of ~ 10 cm diameter and ~ 4 m tall from the seaward edge of the forest. From the tree stems, I cut rectangular bars of 4 mm x 4 mm x (maximum radius, 41 – 57 mm) of the stem with a bandsaw (CarbaTec, Wakerley, QLD Australia), excluding pith and bark. I put the wood samples within glass containers with distilled water under vacuum for one day
(sufficient time to fully saturate the samples) before scanning the samples with a compact micro CT scanner 1174 (SkyScan, Belgium). The wood rectangular bars were covered with Parafilm to avoid desiccation and exposed to X-rays (45KV, 800µA) for 30 minutes. I obtained four wood density profiles from each wood sample (expressed as 256 grey values) from the CT scanner (resulting in a resolution of ca. 22 grey values for each mm of rectangular woody bar). The four wood density profiles were averaged and calibrated with the actual fresh (green) wood density values (Chave et al. 2006) from the samples using Eqn 5.1, where $A$ is the calculated wood density, $B$ is the grey value along the stem (0 - 256) and $k$ is a constant calculated as mean grey value times mean fresh wood density (Shalbot 1988).

$$A = k \cdot \frac{1}{B}$$  \hspace{1cm} \text{(Eqn 5.1)}

The high resolution of assessed wood density (ca. 22 values for each mm of rectangular woody bar) allowed me to perform wood density averages a) per mm and after obtaining the radiocarbon dates, b) at dates established using bomb-pulse dating.

**Tree age and growth rate estimation**

From the scanned rectangular prisms, I cut cross-sections along the radius of 1 mm length (resulting in 4 mm x 4 mm x 1 mm bars) at homogeneous intervals of ~7 mm to obtain ~6 dates per stem, which were representative of their growth history. From each sample, the age of the wood was estimated using bomb-pulse $^{14}$C techniques (Hua et al. 2001). The wood samples were chemically pre-treated with the standard acid-alkali-acid method to obtain holo-cellulose and alpha-cellulose. Following this pre-treatment, the samples were combusted to CO$_2$ and reduced to graphite for $^{14}$C analysis, see Hua et al. (2001) for details on chemical sample treatment and preparation.

Accelerator Mass Spectrometry measurements were performed using the Small Tandem Accelerator for Research (STAR) facility of the Australian Nuclear Science and Technology Organisation (ANSTO; Fink et al. 2004). Values of $^{14}$C were converted to calendar ages using the
updated Southern Hemisphere bomb radiocarbon data set (Hua and Barbetti 2004) and the CALIBomb program (Reimer et al. 2004). Growth rates were calculated as radius increment per year.

**Data analyses**

I used linear regressions to assess the relationship between wood density and distance from the pith to the bark and wood density and growth rate over time using dates established with bomb-pulse dating. Regression analyses were also used to evaluate the response of growth rate to climatic variables over time: the Pacific Decadal Oscillation Index, PDO (Mantua et al. 1997) and the Southern Oscillation Index, SOI, measured as the standardised anomaly of the Mean Sea Level Pressure difference between Tahiti and Darwin (Australian Bureau of Meteorology 2012). Analyses were performed with the software package *lmodel2* from R (The R Foundation for Statistical Computing). In addition, I grouped wood density and growth rate values within the following periods of time: 1936 – 1959, 1960 – 1983 and 1984 – 2008, this grouping was performed aiming to have representative values from the inner, mid and outer sections of stems and to obtain representative means of wood density and growth rates of the four *A. marina* trees together. Differences between growth rate and wood density between the three periods of time were tested using a Kruskal–Wallis test and a Dunn’s post hoc test. These analyses were performed with the software Prism 5.0 (La Jolla, CA, USA).

**Results**

I found wood density to decrease from pith to bark and with age (Fig. 5.2A, B) in fringing *A. marina* trees from the Exmouth Gulf, Western Australia. In addition, higher growth rates were correlated with higher wood density values (Fig. 5.3).
The dating results showed that the relatively small trees of *A. marina* in the Exmouth Gulf were 68 ± 8.6 (mean ± standard error) years old. Growth rates measured as increases in radius were significantly lower during the most recent period (between 1984 – 2008) than growth rates in older periods of time (between 1936 – 1959 and 1960 – 1983) and varied from 0.44 ± 0.1 mm yr\(^{-1}\) in the most recent period (1984 – 2008) to 1.07 ± 0.23 mm yr\(^{-1}\) in the period between 1960 – 1983 (Fig. 5.4). Additionally, wood density values ranged from 0.71 ± 0.02 g/cm\(^3\) to 0.87 ± 0.01 g/cm\(^3\).

Regression analyses indicated that growth rate decreased as the PDO Index increased (Fig. 5.5A). In contrast to what we expected, we found that growth rate and the SOI were not significantly correlated, however higher growth rates appear to be associated with positive SOI values (Fig. 5.5B). In addition, the regression analysis between wood density and PDO index was not significant, while wood density significantly increased with SOI values (Fig. 5.5 C, D).

**Discussion**

Wood density decreased from the pith towards the bark and over time in *A. marina* trees from the Exmouth Gulf, Western Australia. My previous work from Chapter 4 indicated that denser wood in *A. marina* can be maintained even with large xylem vessel diameters, which are embedded within a thick fibre matrix which maintains higher wood densities. I also found that larger trees exhibited larger wood density values. In addition and consistent with previous results, analyses of the relationship between wood density and growth rates indicated higher growth rates were associated with denser wood. However, in contrast to previous results, here I found decreases in wood density from the pith towards the bark. Because trees are subject to environmental variation while growth occurs and wood structure may change in response to climatic changes. These reductions in wood density while *A. marina* trees grow in size suggested wood density in *A. marina* to be sensitive to climatic factors, which are important for growth and productivity. In *A. marina* occurring in the arid...
Exmouth Gulf, rainfall availability is likely key to determining growth rates (Chapter 2).

To corroborate if there was a link between growth rates, wood density and climatic variability, I analyzed the relationship between growth rate and two climatic indices: the PDO Index and the SOI. In addition I analyzed the relationship between wood density and these climatic indices. I found that growth rate decreased with positive values of the PDO index, which is negatively correlated to rainfall in other arid regions of Australia (McGowan et al. 2009). The relationship between growth rates of *A. marina* and the SOI was not significant, however I observed that positive growth was linked to positive SOI values. Previous studies have shown that rainfall and SOI do not correlate in the Exmouth Gulf, Western Australia (Chiew et al. 1998; Hughes et al. 2003; Tobin 2010), because the atmospheric pressure patterns in Western Australia are complex (Arblaster et al. 2002). However, positive values of SOI have been found to be associated with high sea levels in Fremantle, Western Australia (Feng et al. 2004), changes in sea level may not have the same magnitude of positive impact on mangrove growth as variation in freshwater inputs (Chapter 2; Menezes et al. 2003).

I also tested for correlations between wood density and PDO and wood density and SOI, the general pattern was similar to that of growth rates, but the linear regression between wood density and climatic indices was significant only for SOI. Decreases in wood density from the pith towards the bark and the significant correlations between climatic indices, growth rate and wood density in *A. marina*, strongly support the idea that in the tropics, freshwater inputs enhance mangrove growth (Menezes et al. 2003; Lovelock et al. 2006, Lovelock et al. 2011b; Chapter 2). High rainfall (freshwater) and the higher relative humidity associated with rainfall would assist trees to maintain a favorable salinity balance and stomatal conductance, in addition to releasing nutrients in floods that enhance mangrove growth (Ball and Farquhar 1984; Lovelock et al. 2011b). My results indicate that in the arid zone mangroves may be extremely sensitive to changes in annual rainfall
and to changes in the frequency of rain bearing cyclones predicted with climate change (Chapter 2; Knutson et al. 2010).

My data indicated that the relatively small trees (~10 cm diameter) from the Exmouth Gulf (fringe canopy is ~4 m tall) are 68 ± 8.6 (mean ± standard error) years old. Despite the occurrence of cyclones every two to three years in the Exmouth Gulf, and the devastating cyclone in 1998 (Cyclone Vance) that directly struck the site, these trees have persisted through these cyclonic events. The age of *A. marina* mangrove forests in the Exmouth Gulf, may be due to their resistant and flexible wood compared to other mangrove species (Chapter 3; Bardsley 1985). Mangrove forests are typically comprised of fringing taller trees and scrubby landward trees (Feller et al. 2010). Scrub trees in the Exmouth Gulf, WA, although relatively small (<1.5 m) may be as old or older than fringing trees as previously found in other mangrove forests in New Zealand (Lovelock et al. 2010). Some trees at the site are greater than 20 cm in diameter, even in the scrub forest from the Exmouth Gulf (C.E. Lovelock *unpublished data*), indicating these trees may be ~100 years old (based on radius increment of 1 mm yr\(^{-1}\)) or more than 200 years old considering radius increment of 0.44 mm yr\(^{-1}\). Discrepancy between size and age in mangrove forests (smaller trees can be older than larger trees) has been linked to the environment (Lovelock et al. 2010). Lugo (1997) suggested taller fringing trees could be younger than scrub trees because they could access freshwater or less saline water than scrubby landward trees. Additionally, Jiménez and Lugo (1985) suggested large-scale mortalities to be common in mangrove forests. This turnover would be associated to severe weather events such as episodic cyclones, extreme drought and sea level changes. Fringing trees in the Exmouth Gulf, Western Australia have experienced a large number of cyclones since 1918 (~8, Australian Bureau of Meteorology 2012), however, there is a relatively large gap between 1909 – 1943 in which there are no recorded cyclonic events. During this period (~1918 – 1943) my studied fringing mangrove forest could have been established and stems could have become relatively resistant to cyclones that occurred after ~1918. Major mangrove forests establishments during
episodes of reduced wind and wave forces have been previously reported in a New Zealand forests (Lovelock et al. 2010).

The comparison among *A. marina* stems showed that, overall, the range of growth rates in *A. marina* from the Exmouth Gulf varied from $0.44 \pm 0.1$ mm yr$^{-1}$ to $1.07 \pm 0.23$ mm yr$^{-1}$ these growth rates are comparable to growth rates observed previously in Moreton Bay, Australia (Lovelock et al. 2011a; Chapter 6). Growth rates from the last period of time (1984 – 2008) were the lowest growth rates recoded in fringing *A. marina*, reflecting the drying trend and therefore less rainwater availability in the Exmouth Gulf, Western Australia.

**Conclusions**

Fringing trees of *A. marina* in the Exmouth Gulf, Western Australia, despite multiple intense cyclones in the region, are relatively old (68 ± 8.6 years old). Their growth is slow but is enhanced with increases in rainfall during low phases of the PDO as access to freshwater sources increase (Semeniuk 1983; Chapter 2). My study indicates there has been a prolonged drying trend in the Exmouth region and that wood density and tree growth of *A. marina* has declined over time.
Fig. 5.1 Mean monthly maximum air temperature (open diamonds), mean monthly minimum air temperature (filled diamonds) and mean monthly precipitation (bars) in the Exmouth Gulf, Western Australia. Data were obtained from the Australian Bureau of Meteorology (2012).
Fig. 5.2 Relationship between A) wood density and distance from pith and B) wood density and time for *Avicennia marina* collected in Giralia Bay, Western Australia. The lines represent the linear regressions where A) Wood density = \(-4.2 \times 10^{-3} X + 0.92\), \(r^2=0.41\), \(p<0.0001\), \(n = 196\), dashed line: standard error and B) Wood density = \(-2.6 \times 10^{-3} X + 6.07\), \(r^2=0.43\), \(p = 0.0001\), \(n = 25\).
Fig. 5.3. Relationship between growth rate and wood density of *Avicennia marina* collected in Giralia Bay, Western Australia. Points are at dates established using bomb-pulse dating. The line represents the linear regression where: Growth rate = 2.44 X - 1.15, $r^2=0.3$, $p=0.01$, $n=25$. 
Fig. 5.4. Wood density (white bars) and growth rate (filled bars) of the *Avicennia marina* mangrove from the Exmouth Gulf, Western Australia. Values are the means and standard errors of *n* = 6 – 7, wood density and growth rate values were significantly lower from the period between 1984 – 2008, *p* <0.05, ***p* <0.0001.
Fig. 5.5. Relationship between A) Growth rate and the Pacific Decadal Oscillation Index, B) Growth rate and the Southern Oscillation Index, C) Wood density and the Pacific Decadal Oscillation Index and D) Wood density and the Southern Oscillation Index for *Avicennia marina* trees collected in Giralia Bay, Western Australia. The lines represent the linear regressions where A) Growth rate = 0.67 X - 1.47, $r^2=0.92$, $p = 0.03$ and D) Wood density = 0.84 X - 0.07, $r^2=0.95$, $p = 0.04$. Each point represents mean ± standard error of $n = 6 – 7$. 
Chapter 6. *Avicennia marina* dominance over *Rhizophora stylosa*: A response to high nutrient availability in western Moreton Bay, Australia
Introduction

One of the hypotheses of how species can coexist in the same habitat is that some species can persist with lower resource concentrations than others (Tilman and Pacala 1993). Species that can persist with lower resources have efficient resource use and minimize resource loss (which occurs during senescence or with herbivory). In mangrove forests, the dominance of different species has been widely proposed to be associated with competitive displacement, which involves tolerance for growth in low nutrient environments and ability to compete in high nutrient environments (Chen and Twilley 1998; Lovelock and Feller 2003).

Sediment and nutrient availability in mangrove forests depends on geomorphological settings. Geomorphology influences sedimentation patterns, delivery of nutrients and the import and export of organic matter (Eyre 1993; Adame et al. 2010). In addition, agriculture and urban development within catchments increase nutrient concentrations in coastal waters (Brodie and Mitchell 2005).

In western and eastern Moreton Bay, Queensland, nutrient availability and sediment inputs vary as a function of the different geomorphological settings as well as different anthropogenic influences. Moreton Bay is semi-closed and extends 90 km from north to south. In the western side of the bay, high nutrient availability is associated with river inputs from highly modified catchments, which support agriculture as well as urban development associated with the city of Brisbane, (Costanzo et al. 2001). In the west side of the bay, mangroves grow in muddy sediments of terrestrial origin.
which contain high concentrations of total nitrogen (N) and phosphorous (P) (You 2005). Additionally, water residence times are high, within the Brisbane River ~70 days (Denison and Abal 1999). In contrast, the mangroves of eastern Moreton Bay occur on sandy islands that have near oceanic water quality due to flushing of the bay from the Pacific Ocean (Denison and Abal 1999).

Mangrove growth with varying nutrient availability has been previously assessed in the Caribbean with experiments in growth chambers and under field conditions. McKee (1995) studied mangrove growth in absence of inter and intra-specific competition (in potted plants). She found that *Rhizophora mangle* exhibited higher relative growth rate, leaf production and branch growth than *Avicennia germinans* and *Laguncularia racemosa* under high nutrient availability, optimal salinity values for growth (10% seawater) and with no competitors. Lovelock and Feller (2003) studied growth of *A. germinans* and *L. racemosa* in nutrient enrichment field experiments. They found that *L. racemosa* had higher photosynthetic rates than *A. germinans* in control trees, but that *A. germinans* responded to nitrogen additions by increasing leaf nitrogen concentrations and rates of photosynthesis while *L. racemosa* was not responsive to nitrogen additions, supporting the idea that *A. germinans* is a better competitor when nutrients are highly available and salinity is high.

Computational models have been used as a tool in understanding the distribution of mangrove species along intertidal gradients, including nutrient availability (Berger et al. 2008). Using the FORMAN model, Chen and Twilley (1998) simulated the effects of soil salinity and nutrient availability on mangrove succession and found that *R. mangle* mainly occupied regions with poor soil fertility and that *A. germinans* achieved maximum basal area in plots where soil salinity and fertility were high.
Chen and Twilley (1998) did not consider species replacement by competition, which is important since the competitor may have a negative effect on the neighbouring trees by reducing resource availability (Keddy 2001). Species competition in simulations of mangrove forest succession was addressed later with the individual based model KiWi (Berger and Hildenbrandt 2000), which introduced the field of neighbourhood approach for individual competition.

With the KiWi model, Berger et al. (2006) studied secondary succession of mangroves in abandoned rice fields, and found that current mangrove forests differed in composition from the former mangrove forests and that the original dominant species (*R. mangle*) occurred sporadically. In the mature forest, species dominance changed from a mixed mangrove forest of *L. racemosa* and *A. germinans* to an almost monospecific stand of *A. germinans*. This study suggested that species replacement was a consequence of a decrease in nutrient availability, but that further data was needed to test this hypothesis (Berger et al. 2006).

Previous simulations with the KiWi model have focused in the Atlantic East Pacific biogeographic province, including *R. mangle*, *A. germinans* and *L. racemosa*. The work I present here concerns mangrove forest dynamics in Moreton Bay, Queensland, Australia. I used KiWi to simulate and understand the causes of alternative mangrove species dominance in western and eastern Moreton Bay. In west Moreton Bay mangrove forests are dominated by *A. marina*, while the dominant species in the eastern side of the Bay is *R. stylosa* (Denison and Abal 1999; Manson et al. 2003). My goal was to test if higher nutrient availability could be responsible for *A. marina*’s dominance in the western side of the bay.

**Methods**

I parameterized the KiWi model with field data from Moreton Bay (Table 6.1) (Lovelock et al. 2011a). In the simulated scenario, the relative nutrient availability was initially low and increased
significantly after a defined period, corresponding to half the simulated time. This scenario reproduced changing conditions in western Moreton Bay, in which nutrient discharge has increased since European colonization as a consequence of urban development (Neil 1998).

The KiWi model utilizes the growth function,

$$\Delta dbh = \frac{G \times dbh \times (1 - \frac{dbh \times H}{dbh_{\text{max}} \times H_{\text{max}}})}{274 + 3b_2 \times dbh - 4b_3 \times dbh^2} \cdot cF(nut)$$

(Eqn 6.1)

For Eqn 6.1, $\Delta dbh$ is the annual stem increment, $H$ is height of the tree in cm, $dbh$ is diameter at breast height of the tree in cm (for single stemmed $R. \text{stylosa}$ trees, $dbh$ is measured above the roots and below the branches), $dbh_{\text{max}}$ is the maximum diameter that trees can reach in cm; $H_{\text{max}}$ is the maximum height of trees in cm, and $G$, $b_2$ and $b_3$ are parameters for each species which can be calculated from Eqn 6.2 - 6.4.

$$b_2 = \frac{2(H_{\text{max}} - 137)}{dbh_{\text{max}}}$$

(Eqn 6.2)

$$b_3 = \frac{(H_{\text{max}} - 137)}{dbh_{\text{max}}^2}$$

(Eqn 6.3)

$$G = \frac{\Delta dbh_{\text{max}} \times H_{\text{max}}}{0.2 \times dbh_{\text{max}}}$$

(Eqn 6.4)

The growth function (Eqn 6.1) is multiplied by nutrient availability, represented here as the correction factor for nutrient availability or $cF(nut)$, this modifier is defined as,

$$cF(nut) = c_1 + c_2RNA + c_3RNA^2$$

(Eqn 6.5)

Where RNA is the Relative Nutrient Availability with values from 0 to 1 that KiWi assigns to each tree by the $(x, y)$ coordinates of its stem location within a simulated map and $c_1$, $c_2$ and $c_3$ are
constants for nutrient effect on growth. This equation is based on nutrient availability data from the species *A. germinans* and *R. mangle* (Chen and Twilley 1998).

The general settings of the simulation experiments were based on an initial area of 100 00m$^2$, with 1000 individuals from each species at time 0 and 1500 seedlings year$^{-1}$ (potential recruits) for each species (Chen and Twilley 1998). In addition, the KiWi model manages mortality as trees in which the annual increment in dbh is less than a specified amount for two successive years die (Chen and Twilley 1998). I simulated the forest development from time 0 to time 500 with low nutrient availability (RNA = 0.3) and from time 501 to 1000 with high relative nutrient availability (RNA = 1).

For each time, I calculated the number of trees, the weighted $dbh$ [cm] and the Importance Value (I.V.; Eqn 6.6) for, *A. marina* and *R. stylosa*. The I.V. indicates the relative structural importance of a species within a stand of mixed species and is calculated by adding the relative density ($De_{ri}$; Eqn 6.7), relative dominance ($Do_{ri}$; Eqn 6.8) and relative frequency ($Fr_{ri}$; Eqn 6.9) (Dahdouh-Guebas and Koedman 2006).

\[
IV_{ri} = De_{ri} + Do_{ri} + Fr_{ri}
\]  
(Eqn 6.6)

\[
De_{ri} = \frac{100n_i}{\sum_{i=1}^{m} n_i}
\]  
(Eqn 6.7)

\[
Do_{ri} = \frac{100Ba_i}{Ba}
\]  
(Eqn 6.8)

\[
Fr_{ri} = \frac{100F_i}{\sum_{i=1}^{m} F_i}
\]  
(Eqn 6.9)

To calculate the relative dominance it is necessary to calculate the basal area ($Ba$; Eqn 6.10).

\[
Ba = \frac{\pi \times (dbh/2)^2}{10000}
\]  
(Eqn 6.10)
In addition to the parameterization of the model, I determined growth rates from 15 A. marina and 15 R. stylosa trees in Western Moreton Bay and 44 A. marina and 44 R. stylosa trees in Eastern Moreton Bay. I tested whether dbh and the mean growth rates, expressed as biomass gain per year (cm² year⁻¹), differed in both sides of the bay by using t-tests with the software package Prism 5.0 (La Jolla, CA, USA).

**Results and Discussion**

Under low nutrient availability (RNA = 0.3), R. stylosa had the highest density and I.V. However, R. stylosa never reached larger dbh values than A. marina, even under low nutrient availability conditions (Fig. 6.1), this can be a consequence of the architecture of R. stylosa characterized by its stilt roots and relatively narrow trunk above the roots. The dominance of R. stylosa was maintained during periods when nutrient availability was low. When the nutrient availability increased after 501 years in the simulation, A. marina became the dominant species concerning tree density and I.V. This scenario is similar to the one observed in western Moreton Bay.

My field data support the results of the model. In western Moreton Bay, A. marina has larger dbh values than R. stylosa. In the eastern Bay, A. marina had larger dbh than R. stylosa but the difference was less pronounced (Fig. 6.2 A - B). In the western side of Moreton Bay, A. marina exhibited higher growth rates per year than R. stylosa, while at the eastern side R. stylosa grew faster (Fig. 6.2 C - D).

*Avicennia marina* has lower foliar nutrient resorption at sensecence than R. stylosa in the arid zones of Western Australia (Alongi et al. 2005). Faster turnover of leaves and other tissues (e.g. roots) may partially explain why A. marina grows more rapidly with higher nutrient availability compared
to lower nutrient availability. Slower turnover of nutrients (i.e. longer lived leaves and roots and higher resorption efficiencies) of *R. stylosa* may be important to its capacity for competitive growth rates under limiting nutrient environments. In addition, Lovelock and Feller (2003) found that *A. germinans* had higher water use efficiency than nutrient use efficiency. Previously, Field et al. (1983) suggested a trade-off between nutrient use efficiency (the ratio of photosynthetic capacity to leaf nitrogen content) and water use efficiency (the ratio of photosynthetic capacity to transpiration). In mangroves this trade-off has been found to occur in *A. germinans* (with a high water use efficiency) and *L. racemosa* (with a high nutrient use efficiency). A similar specialization of high water use efficiency compared to nutrient use efficiency may occur in *A. marina*, which has high water use efficiencies (Ball 1988a). Alternatively, its competitor *R. stylosa* has been found to exhibit higher nutrient use efficiency than *A. marina* (Alongi et al. 2005). Further experiments with individual base models remain to be done, for example, introducing the effect of salinity beside nutrient availability and exploring its effects in species dominance. However, my results with the KiWi model and data from the field support the idea that, when nutrients are low, *R. stylosa* grows faster and dominates, but when there is higher nutrient availability *A. marina* grows faster and dominates over *R. stylosa*.

According to the simulations carried out with the spatially explicit individual-based model KiWi, we were able to assess changes in forest structure under alternative environmental scenarios. These results suggest that pollution and nutrient enrichment in the coastal zone can clearly change structure and therefore function of mangrove forests. For example, if a shift of lower nutrient availability occurs, the change of forest composition from *R. stylosa* dominated to *A. marina* may protect the coasts from strong winds (since *A. marina* has high mechanical strength), but may reduce the diversity of fauna that spend part of their life cycle in the mangrove shores since is greater in the *R. stylosa* dominated forests (Ronnback et al. 1999).
Table 6.1. Species-specific parameters for *A. marina* and *R. stylosa* used in the KiWi model based on field data from Moreton Bay, Queensland, Australia.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th><em>Avicennia marina</em></th>
<th><em>Rhizophora stylosa</em></th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G$</td>
<td>Growth constant</td>
<td>85</td>
<td>286</td>
<td>Field data</td>
</tr>
<tr>
<td>$dbh_{max}$</td>
<td>Maximum dbh (cm)</td>
<td>100</td>
<td>15.63</td>
<td>Field data</td>
</tr>
<tr>
<td>$H_{max}$</td>
<td>Maximum height (cm)</td>
<td>1640</td>
<td>850</td>
<td>Field data</td>
</tr>
<tr>
<td>$b_2$</td>
<td>Constant in height to dbh relationship</td>
<td>30.06</td>
<td>91.23</td>
<td>Calculated from field data</td>
</tr>
<tr>
<td>$b_3$</td>
<td>Constant in height to dbh relationship</td>
<td>0.15</td>
<td>2.92</td>
<td>Field data</td>
</tr>
</tbody>
</table>
Fig. 6.1. KiWi simulation experiments show variation in A) number of trees per hectare, B) weighted-mean dbh, and C) Importance Value in a mixed forest comprised by *A. marina* and *R. stylosa* through a simulated period of 1000 years. From time 0 to time 500 the KiWi model experiments were run with low nutrient availability, while from time 501 to 1000, experiments were run with high nutrient availability.
Fig. 6.2 Field data of A) dbh in western and B) eastern Moreton Bay and C) Growth rates in western and D) eastern Moreton Bay expressed as biomass gain per year (cm² yr⁻¹) for *A. marina* and *R. stylosa*. Values are means ± standard error. *Rhizophora stylosa* dbh mean values were significantly lower than dbh values of *Avicennia marina*. Growth rates of *A. marina* were higher in Western than in Eastern Moreton Bay; *p* < 0.05, ***p* < 0.0001.
Chapter 7. Discussion and Final Remarks
This thesis has investigated the wood structure and its associated functions of mechanical strength (Chapter 2) and growth rates (Chapter 3, Chapter 4, Chapter 5 and Chapter 6) in mangrove species with typical secondary growth, i.e. *Rhizophora stylosa*, *Bruguiera gymnorrhiza*, *Ceriops australis* and *Aegiceras corniculatum* and atypical secondary growth, i.e. *Avicennia marina*.

Wood characteristics of mangroves, such as xylem vessel size and growth rates, are affected by a range of environmental factors, including water and nutrient availability (López-Portillo and Ezcurra 1989; Lovelock et al. 2006; Feller et al. 2007; Robert et al. 2011b). The results of growth in *A. marina* from Chapter 2 and Chapter 5 support the hypothesis that mangrove growth is enhanced by freshwater inputs. In Moreton Bay and in the Noosa River, rainwater enhances growth in *A. marina*. Additionally, in the arid Exmouth Gulf, in Western Australia, where rainfall events are scarce, groundwater sources may be essential for maintaining mangrove ecosystems function, both now and in the future.

Chapter 2 and Chapter 5 not only indicated that the growth of *A. marina* is enhanced by freshwater availability but that *A. marina* uses a mix of freshwater / saline water sources for metabolic processes. In contrast to *A. marina*, that uses a mix of freshwater / saline water during rainy periods, *R. mangle* appeared to use 100% fresh rainwater during the wet season in Florida (Ewe et al. 2007). Species of *Avicennia* may have a higher requirement for salt for osmoregulation than species within the genus *Rhizophora* and/or the availability of water sources may vary among sites. There remain a range of unknown factors that influence the use of different water sources in mangroves including the variation in the availability of different water sources in space and time and the root distributions of species. How the trees achieve flexibility in using different water sources may be dependent on variation in root morphology and distributions and rapid root growth. As yet there are
few observations of mangrove root morphology and growth and therefore this is an area for future research.

The results of Chapter 3 indicate that wood density varied among species, even when growing in the same intertidal zone. Wood plays a role in tree function determining rates of transport and storage of water and nutrients and providing defence properties (e.g. wood insect borers) and mechanical properties (Chave et al. 2009). Species with higher wood density exhibited higher mechanical strength. *Aegiceras corniculatum, A. marina* and *C. australis* had stronger wood that can resist stronger wind and water forces, while *R. stylosa* and *B. gymnorrhiza* branches are more vulnerable to damage. However, *R. stylosa* and *B. gymnorrhiza* exhibit stilt and buttress roots, which may provide mechanical stability. Given mangroves provide coastal protection from tidal and wind action as well as from cyclones and tsunamis, these results have implications for predicting mangrove ecosystems function and their responses to disturbance. Species with higher wood density and mechanical strength are less vulnerable to damage and may survive and maintain ecosystem services after cyclones or other natural forces damage species with lower wood density.

The combined results of Chapter 3 and Chapter 4 indicate which traits of the wood of mangroves were linked to mechanical strength and offer insights of trade-offs which may be occurring between traits associated with mechanical strength (fibres), water transport and tree growth (xylem vessels). Across species, wood density increases with increments in fibre wall thickness and decreases with xylem vessel lumen areas. *Ceriops australis*, constructs denser and stronger wood with thick fibre walls and tends to occur in landward, highly saline environments. The thick fibre walls of *C. australis* may protect xylem from implosion when exposed to intense negative pressures. In contrast, *R. stylosa*, has larger xylem vessel lumen areas which reduces its mechanical strength and therefore may affect survival of its branches after natural forces act upon this species.
Typically, increases in wood density are associated with decreasing growth rates (Enquist 1999, King et al. 2006). This association arises because increases in wood density are linked to decreasing xylem vessel size and xylem vessels are involved in water conductance, water transpiration and photosynthetic carbon gain. However, the results of my work indicate that secondary growth in *A. marina* results in contrasting associations of wood density and growth rates as increasing wood density in *A. marina* is associated with increasing growth rates. These contrasting associations emerge from the atypical wood anatomy of *A. marina* associated with successive cambia. *Avicennia marina* trees with higher wood density and higher growth rates had large xylem vessels, thick fibre walls and a reduction in the proportion of phloem content per wood layer. In addition, the results of Chapter 3 and Chapter 4 indicate that higher proportions of phloem per layer of wood in *A. marina* may be important in its role for salinity tolerance, but higher proportions of phloem per layer of wood reduce wood density and mechanical strength, suggesting a trade-off between higher salinity tolerance and reductions in mechanical strength for *A. marina* trees.

Another important environmental factor that affects wood characteristics is nutrient availability. Increases in phosphorus availability have been shown to increase xylem vessel size, rates of transpiration and growth in dwarf trees of *R. mangle* (Lovelock et al. 2006). In Chapter 6 my results using an individual based model and supporting field data, indicate that differences in growth rates and nutrient use among species with increases in nutrient availability result in the dominance of *A. marina* over *R. stylosa* in western Moreton Bay (and *R. stylosa* dominance over *A. marina* in eastern Moreton Bay). These results are a consequence of *A. marina*’s higher growth rates compared to *R. stylosa* under the higher nutrient availability observed in western Moreton Bay. My results indicate that changes in nutrient availability in Moreton Bay and elsewhere may have an impacts on mangrove species dominance and diversity and therefore on ecosystem function. Future
work in this area includes parameterization of the Relative Nutrient Availability equation (Eqn 6.5) for Indo-Pacific species.

Mangrove habitats are exposed to a range of climate change drivers that can influence their wood characteristics and growth rates. For instance, the increased intensity and frequency of cyclones has the potential to increase tree damage through defoliation, wood breakage and tree mortality. However, cyclones release freshwater and nutrients, resulting in enhanced mangrove growth and expansion (Paling et al. 2008; Lovelock et al. 2011b). In addition, a global increase in rainfall is predicted by 2050 but the regional distribution of rainfall will be uneven e.g. annual total rainfall has increased by 15% in New South Wales, South Australia, Victoria and the Northern Territory (Hennessy et al. 1999). Where drying is expected, for example along the central Queensland coast (Suppiah et al. 2007) decreased rainfall and increased evaporation will make mangrove habitats more saline decreasing net primary productivity and growth (Lovelock and Ellison 2007). Reduced rainfall will also reduce freshwater inputs from groundwater and rivers, which will have a negative impact in mangrove growth. In locations where rainfall increases, my data suggest that growth rates will increase, which may lead to increases in mangrove area and diversity. Higher fluvial sediment supply, increased nutrient availability as well as reduced salinity (e.g. Eslami-Andargoli et al. 2008, Lovelock et al. 2011b) are also likely to enhance growth. Changes in Pacific Ocean temperatures including, El Niño - Southern Oscillations (ENSO) events influence important weather events such as tropical cyclone activity, drought and flooding (Chen et al. 2001) as well as influencing sea level (Glynn 1984). My data from Chapter 5 investigating long term growth of mangroves from the Exmouth Gulf, Western Australia suggest that reductions in rainfall associated with positive values of PDO Index have reduced mangrove productivity over time in the region.

Future research in mangrove wood structure and function can focus on the following questions that have arisen from my thesis,
1) Test experimentally if there is a trade-off between mechanical strength and growth rates in mangroves and in woody plants generally.

2) Test experimentally if phloem is involved in salinity tolerance in the mangrove species *A. marina*.

3) Study the root distribution (depth and length) and wood anatomy of *A. marina* and *R. stylosa*, aiming to clarify if the water sources they use are determined by which sources of water their roots can access.

4) Further comparative studies of typical and atypical secondary growth, which might give rise to differing tree growth strategies and trade-offs among plant traits.

Overall, the combined results of this thesis, by using a range of techniques, provide an insight of the wood characteristics that determine tree function in mangrove species. By understanding responses of xylem vessel diameter, phloem in wood, wood density and wood growth to climatic factors this thesis provides a valuable comparative data set informing mangrove forest management in the future. Additionally, by determining the dependence of mangrove growth to freshwater availability, including how and when mangroves use different water sources, we can increase the knowledge needed to manage and preserve ecosystem function in Australia with changing rainfall patterns.
References


Larsen GR, Cox ME (2011) Hydrochemical and isotopic characterisation of groundwaters to define aquifer type and connectivity in a subtropical coastal setting, Fraser Coast, Queensland. Environmental Earth Sciences 64: 1885-1909


Lovelock CE, Bennion V, Grinham A, Cahoon DR (2011a) The role of surface and subsurface processes in keeping pace with sea level rise in intertidal wetlands of Moreton Bay, Queensland, Australia. Ecosystems 14: 745-757


Méndez-Linares AP, López-Portillo J, Hernández- Santana JR, Ortiz-Pérez MA, Oropeza-Orozco O


Robert E, Schmitz N, Boeren I, Driessens T, Herremands K, De Mey J, De Casteele EV, Beeckman H, Koedam N (2011a) Successive cambia: A developmental oddity or an adaptive structure? Public Library of Science ONE 6: e16558. DOI:10.1371/journal.pone.0016558

Robert E, Schmitz N, Kirauni HA, Koedam N (2009) Salinity fluctuations in the mangrove forest of


Santini NS, Schmitz N, Lovelock CE (2012) Variation in wood density and anatomy in a widespread mangrove species. Trees DOI: 10.1007/s00468-012-0729-0


Chisholm Institute of Technology. Monash University, Melbourne, p 268

mangroves: independent evolutionary origins of vivipary and salt secretion. Molecular
Phylogenetics and Evolution 34: 159-166

richness around the tropical coastline of Australia. Journal of Biogeography 14: 9-19

Sobrado M (2007) Relationship of water transport to anatomical features in the mangrove
*Laguncularia racemosa* grown under contrasting salinities. New Phytologist 173: 584-591

Sobrado MA, Ewe SML (2006) Ecophysiological characteristics of *Avicennia germinans* and
*Laguncularia racemosa* coexisting in a scrub mangrove forest at the Indian river lagoon,
Florida. Trees 20: 679-687

New Phytologist 186: 577-592

tomography for non-invasive determination of wood anatomical characteristics. Journal of
Structural Biology 148: 11-21

Sternberg LdSL, Swart PK (1987) Utilization of freshwater and ocean water by coastal plants of

Sun Q, Lin P (1997) Wood structure of *Aegiceras corniculatum* and its ecological adaptations to
salinity. Hydrobiologia 352: 61 - 66

(2007) Australian climate change projections derived from simulations performed for the

Susilo A, Ridd PV, Thomas S (2005) Comparison between tidally driven groundwater flow and
flushing of animal burrows in tropical mangrove swamps. Wetlands Ecology and
Management 13: 377 – 388

and geographical perspectives. In: Ricklefs RE, Schluter D (eds) Species diversity in
ecological communities: historical and geographical perspectives University of Chicago
Press, Chicago

summer; wetter than average for east north and central areas, dry in Western Australia and
Tasmania. Australian Meteorological and Oceanographic Journal 60: 289-299


