STRUCTURE, COMPOSITION AND DYNAMICS OF *METROSIDEROS EXCELSA* (PŌHUTUKAWA) FOREST, BAY OF PLENTY

Rebecca Bylsma
Waikato University

As a recipient of funding from the John Nicholls Memorial Research Grant, I would like to thank the Rotorua Botanical Society for their generosity.

The objective of my MSc research was to investigate the structure, composition and dynamics of pōhutukawa (*Metrosideros excelsa*) forest, and provide new insight into pōhutukawa forest ecology and development. Currently, pōhutukawa forest is thought to represent a mere 10% of its original, pre-human distribution and is primarily restricted to the warm coastal zone. However, pōhutukawa stands bordering some Rotorua lakes, Lake Taupo and along the Tarawera River margins, could suggest the forest type was once far more widespread inland, as a coloniser of new volcanic surfaces (Clarkson & Clarkson 1994). The rarity and limited extent of pōhutukawa forest on the mainland has resulted in the forest type being mostly left out of nationwide forest classification schemes. The Bay of Plenty Region however, hosts some of the most intact regenerating pōhutukawa forest and forest remnants, providing the perfect setting for this research.

During my field research we surveyed a broad range of coastal and semi-coastal pōhutukawa forests and stands; these spanned from Waihi Beach in the west, to the Opape headlands in the east of the region (Figure 1). Many of the reserves we visited had previously been the focus of Rotorua Botanical Society fieldtrips and the forest descriptions/species lists produced were a great help. The real highlight of my research however, was visiting some of the less accessible offshore islands, such as Tuhua (Mayor Island), Motuotau (Rabbit Island), and Moutohora (Whale Island); these provided an opportunity to examine pōhutukawa forest development largely in the absence of mammalian pests. The opportunity also arose to survey pōhutukawa forest on Great Barrier Island, and although pōhutukawa forest there was mostly confined to narrow bands on the coastal margins, it served as a good comparison site for the Bay of Plenty data.

Within each study site, pōhutukawa forest was comprehensively sampled within randomly located quadrats; quadrats were predominantly 20 x 20 m, however on a couple of occasions this was reduced to avoid topographic barriers or when the site became too steep. We were also able to re-measure permanent quadrats within pōhutukawa forest on Tuhua (Three quadrats) and Motuotau (One quadrat). These quadrats were installed by Bruce Clarkson 18 and 21 years ago respectively, and the resulting data was invaluable in predicting and confirming long term developmental

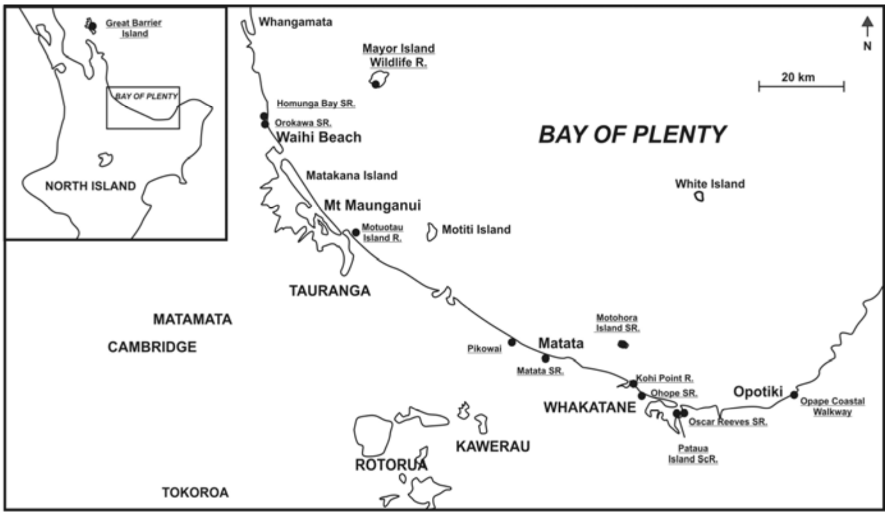

Figure 1: Map showing the location of study sites within the Bay of Plenty. Black dots indicate study sites. R= Reserve, SR= Scenic Reserve, Sci R= Scientific Reserve

trends. By the end of my field research we had surveyed a total of 39 quadrats and these had a combined area of 14,200 m^2.

In addition to the forest survey, the shade tolerances of pōhutukawa and key forest associates (e.g. *Litsea calicaris*, *Dysoxylum spectabile* and *Beilschmiedia tawa*) juveniles were also investigated. This was done using hemispherical photography. Digital photographs were taken directly above randomly selected juveniles apices, looking upward through an extreme wide-angle lens. The proportion of canopy openness was then calculated from the photographs using computer software. This data then allowed the relationship between a species regeneration strategy and shade tolerance to be identified. An example of a hemispherical photograph is illustrated in figure 2.

Figure 2: Hemispherical photograph taken in pohutukawa forest, Ohope Scenic Reserve 2011.

A total of 122 indigenous species were recorded in the field survey (excluding herbaceous species), however only a minority of these were considered common and widespread in the forest understories. Such species included *Coprosma macrocarpa*, *Coprosma robusta*, *Cyathea dealbata*, *Melicytus ramiflorus*, *Myrsine australis*, *Pseudopanax lessonii*, *Pseudopanax arboreus*, *Beilschmiedia tawa*, *Dysoxylum spectabile* and *Litsea calicaris*.

Quadrat data could be divided into nine distinct forest types (using ordination and classification techniques) with groupings being partially explained by geographic position, distance from the sea, topographic landform and forest age. Below the forest types are described using the Atkinson (1985) vegetation classification system:

1. <u>Pōhutukawa</u>/ *Pseudopanax lessonii* forest
2. <u>Pōhutukawa</u>/ *Melicytus ramiflorus – Pseudopanax lessonii* forest
3. <u>Pōhutukawa</u> / *Myrsine australis – Melicytus ramiflorus* forest
4. <u>Pōhutukawa</u> / *Myrsine australis – Coprosma macrocarpa – Coprosma lucida* forest
5. <u>Pōhutukawa</u> / *Melicytus ramiflorus – Cordyline australis* forest
6. (*Kunzea*) <u>Pōhutukawa</u> / *Pseudopanax arboreus – Pseudopanax lessonii* forest
7. (*Knightia*) Pōhutukawa/ *Myrsine australis – Melicytus ramiflorus* forest

8. <u>Pōhutukawa</u> / *Coprosma macrocarpa – Cyathea dealbata – Myrsine australis* forest
9. <u>Pōhutukawa</u> / *Dysoxylum spectabile – Beilschmiedia tawa – Cyathea dealbata* forest

Understories within young pōhutukawa forest generally had a sparse shrub layer, overtopped by a sub-canopy dominated by either tree-ferns in steep inland localities, *Pseudopanax lessonii*, *Coprosma lucida*, *Coprosma macrocarpa* and *Melicytus ramiflorus* on coastal headlands, or *Coprosma* spp. (*C. lucida*, *C. Macrocarpa*, *C. robusta*) and *Myrsine australis*, in semi-coastal locations. *Myrsine australis* was far more prevalent in semi-coastal locations whereas the *Pseudopanax* spp. and *Melicytus ramiflorus* were more common in coastal locations. This trend may be attributed to the damaging effects of salt laden winds, from which, *Melicytus ramiflorus* recovers more hastily and may competitively exclude *Myrsine australis* from the seaward facing areas (Atkinson 2004). Interestingly, *Melicytus novae-zelandiae* as opposed to *Melicytus ramiflorus* was present in the Motuotau quadrat. Mature pōhutukawa forests had far denser understories and significant contributions of mid and late successional species, such as *Beilschmiedia tawa*, *Litsea calicaris* and *Dysoxylum spectabile.*

The ground layer within pōhutukawa forest was often sparse, particularly in young and coastal forest where characteristically pōhutukawa leaf litter dominated. However, *Adiantium cunninghamii*, *Asplenium polyodon*, *Doodia australis*, *Astelia banksii* and *Machaerina sinclairii* were generally the most wide-spread and common ground cover species. On Motuotau, *Asplenium haurakiense* was present, but the species was not found elsewhere. The paucity of the understories beneath young pōhutukawa forest, is in part the result of slowly decomposing leaf litter, which creates a forest floor environment sub-optimal for seedling germination, retarding the rate at which a diverse understory can develop (Atkinson 2004).

Stand development

It would have been useful to determine the exact age of the stands surveyed, however pōhutukawa wood is far too hard for normal increment coring. Alternatively, sixteen pōhutukawa stem disks were sourced from fallen trees on the mainland. Stem discs were sanded back until growth rings became distinct enough to count. It was assumed that a single ring represented one year's growth, however it is possible pōhutukawa may be capable of producing multiple growth rings per year (Bergin & Hosking 2006), but this has yet to be investigated. Growth ring data was combined with Clarkson & Clarkson's (1994) data set (collected on Tuhua and Whakaari) and the resulting diameter increment relationship is illustrated on Figure 3. Initially pōhutukawa stems had high annual growth rates, which could exceed 0.5 cm on the mainland. However, diameter growth decreased with increasing stem age. The diameter growth rates on Whakaari were, as expected, much lower than those on the mainland due to the harsh and frequently disturbed environment on the island.

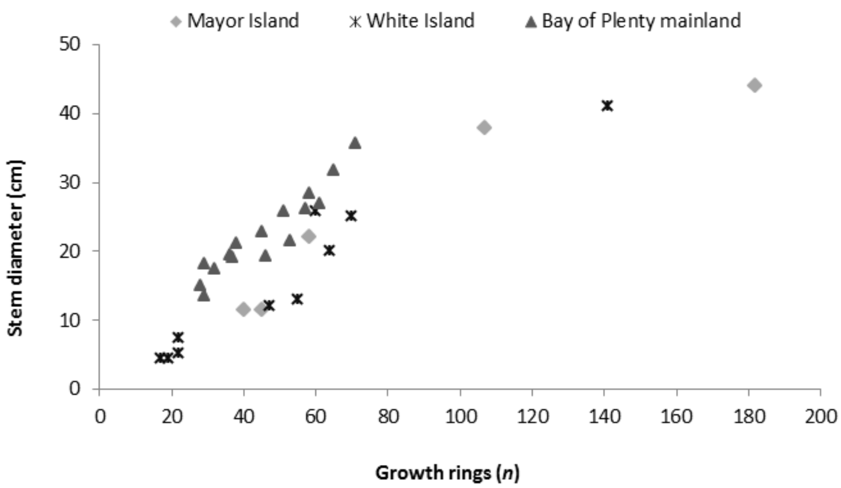

Figure 3: Stem diameter (cm) and age relationship, for *Metrosideros excelsa* stems disks, Tuhua (Mayor Island) n=5, Whakaari (White Island) n=10, Bay of Plenty mainland (n=16).

Because pōhutukawa seedlings characteristically establish on open sites following disturbance (the majority of pōhutukawa seedlings sampled were occupying sites with 16–32% canopy openness) the estimated age of the most frequently occurring stem size class was considered analogous with stand age. Stands surveyed were estimated to be between 20 years to >300 years old, however the majority were <60 cm diameter and likely to be <200 years old, suggesting current pōhutukawa forest had mostly arisen following burning episodes in the 1900s. A a small number of relict trees were also encountered in the Matata, Kohi Point and Ohope Reserves, these trees had diameters greater than 1.5 metres and were likely to exceed 1000 years and probably nearing the end of their life span.

The sequence of pōhutukawa forest development showed mature pōhutukawa forest could develop within 250–300 years. Forest development was characterised by a decline in pōhutukawa stems from >2000 to <400 stems ha^{-1}, the result of natural self-thinning. This decrease in pōhutukawa stems was coupled with an increase in the total basal area of pōhutukawa stems, from <20 m^2 ha^{-1} to an average of 50 m^2 ha^{-1}. Basal area appeared to plateau after approximately 70 years; the result of the diameter increase of live stems balancing those lost to self-thinning (Figure 4).

Self-thinning of pōhutukawa stems was the most prolific in the high density young stands (<180 years), with approximately 11% of stems sampled being dead and an equivalent number showing signs of deterioration. Developing pōhutukawa forest on Moutohora, estimated to be 35 years old, had even higher proportions, with one quadrat having >40% dead or deteriorating stems (Figure 5). The self-thinning process in young forest involved the loss of entire trees, whereas self-thinning in mature forest generally involved the sequential loss of tree limbs, which would slowly eventuate to the demise of the tree. It was not uncommon for mature trees to have more than 50% of their limbs missing, and the loss of a single limb could create a canopy gap >10 m^2. Such gaps created light environments which favoured the establishment of mid-late succession tree species and stands which exceeded 300 years had significant canopy contributions from such species; showing a compositional shift away from pōhutukawa dominated forest.
Early colonist species were successively being replaced by mid- late successional species and this replacement directly reflected species' differing shade tolerances and juvenile establishment at different phases of forest development.

Forest succession

Results from the hemispherical photographs showed that the distribution of light environments occupied by pōhutukawa and key canopy species juveniles all differed significantly (P <0.001) from the distribution of light environments found to be available in the forest understory. Species had the following order of shade tolerance: *Kunzea ericoides* < pōhutukawa < *Corynocarpus laevigatus* =*Dysoxylum spectabile* < *Litsea calicaris* > *Beilschmiedia tawa*. This order strongly reflects arrival and establishment patterns in forest succession.

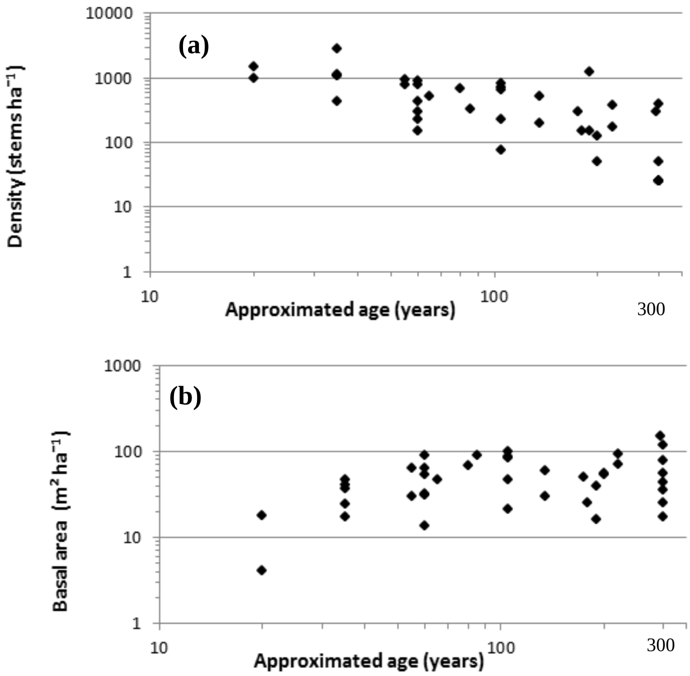

Figure 4: (a) Density versus approximated age of *Metrosideros excelsa* stands **(b)** Basal area versus approximated age of *Metrosideros excelsa* stands. All axis are log scales.

Following a disturbance (e.g. fire or landslide), young high density (Figure 5) pure or mixed pōhutukawa forest establishes (c. 30 years). Other primary immigrants may include *Kunzea ericoides* and *Leptospermum scoparium*, which also have small wind-dispersed seeds and high light requirements. These species are have shorter life spans and may only persist in semi-coastal and inland localities for approximately 200 years. The high light requirements of pōhutukawa juveniles' gives rise to cohort populations, as without any additional canopy disturbance stands develop without any additional pōhutukawa establishment.

Within the first 60 years of forest development, six predominantly bird-dispersed species commonly establish in the forest understory. These are *Myrsine australis, Pseudopanax lessonii, Pseudopanax arboreus, Melicytus ramiflorus, Geniostoma rupestre,* and *Macropiper excelsum*. Seedlings of all six species are considered shade-tolerant; species were found to occupy intermediate light environments relative to those occupied by early colonists (e.g. pōhutukawa) and later successional species (e.g. *Beilschmiedia tawa*). These species also share broadly similar lifespans of 80–180 years (Smale 1993; Atkinson 2004), and as expected, their presence was detected to be much lower in mature pōhutukawa stands. Mid-successional tree species that arrived following a

Figure 5: Photographs of pohutukawa forest, Moutohora 2011.

minimum 60 years of forest development included *Vitex lucens*, *Corynocarpus laevigatus*, *Litsea calicaris* and *Dysoxylum spectabile*, however only the latter two were common and wide-spread. These two species were common components of the mature forest canopy, however the light requirements of juveniles suggested their continued replacement may rely on canopy-gap formation. Conversely *Beilschmiedia tawa*, the most shade tolerant canopy species, commonly established in mature (>300 years) pōhutukawa forest and was capable of continued regeneration. Therefore, *Beilschmiedia tawa* is likely to be the dominant component of the forest community that replaces pōhutukawa if no further disturbance occurs. However, on the unstable coastal headlands and cliffs, pōhutukawa forest is likely to replace itself indefinitely (cyclic succession) as here the frequent disturbances (e.g. landslides) provide suitable regeneration sites. No other woody tree species are as capable of survival and establishment in such exposed and precarious locations.

We hope this research will enhance the understanding of pōhutukawa forest ecology, by providing new quantitative data determining the current composition and structure of *Metrosideros* forest in the Bay of Plenty, quantifying a sequence of forest development and providing a baseline for future research.

ACKNOWLEDGEMENTS

I would like to thank my supervisor Professor Bruce Clarkson for the guidance received throughout this research. I would like to acknowledge those who provided funding; The University of Waikato, the Rotorua Botanical Society and the Whakatane Historical Society, and those who provided access to the study forests; the Department of Conservation, Tuwharetoa Ki Kawerau Iwi, Ngati Awa Iwi and the Ngai Tamahaua hapu. And lastly, my partner Jackson Efford, for his support and assistance throughout this project.

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