Reproductive Biology and Ecology of the Endemic New Zealand Tree *Ixerba brexioides* (tāwari)

A thesis submitted in partial fulfilment

of the requirements for the degree

of

Masters of Science

in Biological Sciences

at

The University of Waikato

by

Rachel Elizabeth Thomson

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2013

Frontispiece: Tāwari morphology: A) tree in flower; B) foliage; C) leaf with glands visible between marginal teeth; D) mature buds; E) flowers; F) capsules with persistent style; G) dehiscent capsule showing viable seeds. Photo C) courtesy of Catherine Bryan.

Abstract

This research investigated the ecology of *Ixerba brexioides* (tāwari) with regard to pollination, breeding strategy, seed biology, and forest composition. Research was focused around three main questions:

1. How is tāwari pollinated with regard to vector and pollen source? How is it adapted for this?
2. How is seed dispersal of tāwari achieved and under what conditions is germination most successful?
3. What are the dominant community associations of tāwari what how are they constrained by environmental variables?

The first research question was addressed using video surveillance, nectar analysis, and artificial pollination experiments in a small tract of tāwari forest at Tūī Ridge Park in the Mamaku Range, North Island, New Zealand. Analysis of 125 hours of video footage showed that tāwari is predominantly insect pollinated with occasional bird visitation. The most frequent flower visitors were flies and nocturnal moths. Tāwari nectar volume peaked at midday, and declined toward the late afternoon, before increasing again at dusk. This pattern of nectar secretion followed closely the activity patterns of flies during the day and moths at night. Nectar sugar concentration was 11% on average (range 3% to 20%) which is considered low, but is suited to moths, bats, birds, and bees. Exclusion experiments demonstrated that tāwari is capable of producing viable seed under cross-fertilisation, self-fertilisation, and agamospermy. Breeding system indices demonstrated that tāwari is medium pollen limited (PLI = 0.31), self-compatible (SCI = 0.93), and autonomously selfing (ASI = 0.65).

Question two was addressed by video surveillance of tāwari seed capsules, morphological observation, and by a series of germination experiments. Video failure meant that with limited footage (mostly at night) no dispersal activity was captured on film. However, using available literature and observations of seed morphology birds were considered the most probable effective disperser. Germination trials included standard conditions, shade, seeds left in fruit, seeds deposited on soil surface, and seeds buried at 5 cm soil depth. Germination was

most effective in the buried treatment (average 85% germination) and the soil surface treatment (average 75% germination).

Cluster analysis and NMS (Non-Metric Multi-Dimensional Scaling) ordination of 641 plots of tāwari forest from the NVS (National Vegetation Survey) database was used to assess the community associations of tāwari. Based on plot species assemblage, the analysis showed four main forest types that are largely separate in geographical space: Northland, Coromandel, Kaimai, and Urewera. Each type had significant indicator species that were constrained in range by latitudinal limits. Recent literature suggests that environmental variables that most influence tāwari forest distribution are annual temperature and rainfall in conjunction with solar radiation. Tāwari forest occupies only areas which are cool and moist, and seedlings are biased toward high light conditions. In the central North Island tāwari had the highest probability of occurrence in sites with a mean annual temperature of 11° to 13° Celsius, mean annual rainfall between 2000 and 2250 mm annually, and mean solar radiation of 143 to 145 MJ m^2 per day. Parent material also plays an important part, especially the depth of Taupō Pumice deposits as tāwari forest is more prone to occur in areas of mature soil where depth of volcanic deposits is not excessive.

Information on tāwari from the present thesis combined with other published and unpublished sources is presented in the form of a New Zealand Biological Flora Series journal contribution.

Recommendations for further research on tāwari and New Zealand reproductive biology in general are given.

Acknowledgements

This Master of Science has been the most challenging, but most rewarding experience of my life. I never thought I was capable of something this big – and I was right. Alone it would not have been possible, but with all the incredible support I received I have finally made it!

First of all, my respect, admiration, and gratitude go to my supervisor Professor Bruce Clarkson. When I started at university my dream was to be a zoo keeper until a class taught by Professor Clarkson inspired in me a love of plants that I have fostered ever since. A Master of Science wasn't part of the plan but with encouragement from Professor Clarkson I made the choice to go ahead with it and have never looked back. Thank you for introducing me to tāwari - the tree that has inspired this research and become my favourite of all trees. Thank-you for your guidance, for the many hours of proof-reading, and for all the things you have taught me about research, writing, and about having a love of nature and of learning that compels you to search for answers.

Over the last two years of research I have had the pleasure of working in the field with many willing hands including Catherine Bryan, Fiona Clarkson, Toni Cornes Brad Day, Dave Thomson, Sue Thomson, Celeste Mulipola, Nathan Day, Scarlet Sharland, and Blake Terry. I have enjoyed your company, your enthusiasm, and your willingness to help. Thanks to my sweet office companions Olivia Henwood and Ella Grierson – it has been a pleasure! Special thanks to Toni Cornes for all the maps, field gear, and advice, and for the frights that kept me awake and laughing. Thanks also to my dear friend and my mentor Catherine Bryan. I could write a thesis on how you've helped me, but I'll just keep it simple. Thank you.

Tūī Ridge Park and the amazing staff there played a huge part in the research for this thesis. It was an incredible place to live, conduct research, and to continue to foster my love of the great New Zealand outdoors. I am grateful for all the kind staff there that maintained such a beautiful park and that were always so helpful.

I would like to thank those from the Chemistry Department at the University of Waikato for helping me with nectar analysis, particularly Marilyn Manly-Harris and Jess King who demonstrated methods in a way that was clear and easy to understand.

I am grateful for the organisations that provided the funding which has made it possible for me to study something which has truly caught my fascination. Thanks to the University of Waikato for the summer research scholarship which prepared me for my Masters research, and for the scholarship contributions to my university fees and research. Thanks also to the Perry Foundation and the Waikato Branch of the New Zealand Federation of Graduate Women whose generous contributions made this research possible.

Technology and I have never quite clicked so I am grateful for the assistance of Bruce Patty, Neil Fitzgerald, and David Pattemore in designing the set-up of my video surveillance system. The many hours of watching the fascinating footage was very rewarding and could not have been undertaken without your help.

My sanity was preserved during this research by the love, laughs, and good company of my wonderful friends – you know who you are! You make my life such a joy to live in – my cheeks are cramping from the extent of my smile as I write this. Thanks for understanding my need to hermit myself away in my office, but always being ready to distract me when necessary.

I have the most incredible family! This thesis is something that I could never have completed without their love and support. They are my friends, my flat-mates, teachers, advisors, and anchors. Somehow they managed to still love me through all my cranky and stressed moments when experiments failed and deadlines loomed. Mum and Dad supplied packed lunches (every day!) for the long days at university, proof-read, made me laugh, and always gave me the encouragement to succeed. They even helped with the field work on occasion! But the biggest service my parents have rendered to me is in the faith that they have fostered through my entire life. Through all the stormy nights camping out, all the days I spent staring at a computer screen struggling to find the right words to write, all the times when I thought I couldn't do this, it was my God that pulled me through. No matter how hectic it got, I knew I could always find peace in God. I am grateful for the opportunity He has blessed me with to pursue this Master of Science. I have learned so much, I have grown, and with everything I learn about the natural world I grow closer to the God that created it.

This experience has been a switch-point for the rest of my life and I am grateful for everyone, named and unnamed here, that has contributed. .

Table of Contents

List of Figures

List of Tables

Chapter One: Introduction

This thesis presents a reproductive biology case study focused on the distinctive endemic New Zealand tree *Ixerba* brexioides[*], New Zealand's sole representative of the plant family Strasburgeriaceae. This introductory chapter provides an overview of reproductive biology, with a New Zealand focus. It also gives background information on *Ixerba brexioides* as the focal species in this case study. Finally, this chapter introduces the questions and objectives which have guided this research project and provides a thesis outline.

1.1 Reproductive Biology in New Zealand

Reproductive biology of island floras is a topic that has piqued the interest of naturalists for centuries and which includes in its scope pollination, seed dispersal, and germination – processes essential for the successful reproduction of plants. The New Zealand vascular flora has a number of unusual reproductive biology characteristics including small, simple and inconspicuous flower structure, high incidence of dioecy, and unusually frequent instances of fleshy fruits and masting (Webb and Kelly, 1993). Seed biology of New Zealand plants also differs from northern hemisphere counterparts in the relative absence of dormancy mechanisms and winter chilling, and the relatively short-lived nature of seed banks (Burrows, 1994). These characteristics reflect New Zealand's long history of isolation, oceanic climate, and relatively depauperate pollinator and disperser fauna (Webb and Kelly, 1993).

As efforts are made to close knowledge gaps in the field of reproductive biology, evidence from New Zealand's unique plant reproductive systems is mounting against several long-held hypotheses. Two examples are pollination syndromes, and Bakers Rule of long-distance colonisation. The concept of pollination syndromes was initiated by Frederico Delpino in the late eighteenth century as a way to classify the diversity of flowering plants he saw, based on the idea that flowering plants and their pollinators co-evolve because of their relationship with one another. Pollination syndromes are groups of floral traits (such as flower colour and structure) that are assessed to give information about what type of pollinators might be expected to pollinate certain plants, in the absence of

[*] Species nomenclature follows New Zealand Plant Conservation Network (NZPCN 2013)

empirical evidence. Pollination syndromes have been challenged as the available data on pollination systems increases. A study by Ollerton et al. (2009) examined flowers in six communities from three continents for floral traits and pollinators and interestingly found that almost none of these fit within the classification of pollination syndromes. Other reviews have similarly suggested that the applicability of pollination syndromes is less than previously thought, particularly with regard to flora of the southern hemisphere (Newstrom and Robertson, 2005, Kingston and McQuillan, 2000).

Island floras have been generalised as having low rates of self-incompatibility in breeding systems and a lack of specialised pollination, as well as little pollinator dependence. These conditions are based largely on Bakers Rule of long-distance colonisation which surmises that those plants that are self-compatible are more likely to establish populations after long distance dispersal because only one individual is sufficient to start a self-perpetuating colony (Baker, 1955, Baker, 1967). However in New Zealand at least 18% of the flora have separate sexes (Lloyd, 1985), and the level of self-incompatibility is, rather than being unusually low, more accurately described as moderate because about 36% of hermaphroditic populations are self-incompatible (Newstrom and Robertson, 2005).

Research on plant reproductive systems in New Zealand also presents a unique opportunity for understanding the functioning of plant reproduction in modified ecosystems. New Zealand has a short but concentrated history of disturbance which has seen the fragmentation and decline of what was once almost continuous forest covering 85-90% of the land surface (McGlone, 1989). This affects not only plant communities but also faunal communities that interact with them and provide essential ecosystem services such as pollination, and dispersal. For example, pollen limitation has been documented for a number of endemic plant species that rely on pollination relationships with native bird species which have been limited in population and range by forest fragmentation and the effects of introduced mammalian predators (Kelly et al., 2010, Pattemore and Anderson, 2013, Robertson et al., 2008). Changes are better documented for the avifauna than for the insect fauna of New Zealand. However, insects have long been recognised as the major force in pollination in New Zealand (Thomson, 1927, Heine, 1938) and native insect biodiversity and abundance has seen negative effects from the introduction of invasive plants and animals (Toft et al., 2001,

Atkinson and Cameron, 1993, Brockerhoff et al., 2010, Leschen et al., 2012). Tūī Ridge Park is an example of a small relict of native bush fragmented from a more extensive area of native bush that has been affected by logging and land clearance. Research from the present thesis is based in Tūī Ridge Park and demonstrates a case study of New Zealand plant reproductive biology in an area of modified mainland forest.

Pollination and reproductive biology has only been investigated in depth in a small proportion of the New Zealand flora. Therefore, the current *Ixerba brexioides* study makes a valuable contribution to the growing pool of information in this field.

1.2 *Ixerba brexioides*

Ixerba brexioides, commonly known as tāwari, was first described by Allan Cunningham in 1839 and was noted to be "one of the most remarkable plants of New Zealand" (Cunningham 1839). It is a small flowering tree which grows to between 10 and 20 m in height and has a scattered distribution across the top half of the North Island of New Zealand, mainly occupying areas of mature soil, at altitudes above 400 m above sea level. Several features of its physiognomy make it a particularly striking plant. Leaves are long and toothed with glands between each serration. They are arranged spirally, for the most part, around the stems, ascending upward to frame the conspicuous inflorescences. Flowers are arranged as umbellate inflorescences composed of between 3 and 20 florets. Each floret is about 5 cm in diameter with 5 creamy-white petals arranged in a star shape about the nectary. The stigma is five-locular with 5 styles entwined together to form a point (Allan, 1982). These flowers appear *en masse* between November and January each year.

Tāwari is unique in the New Zealand flora and for a time represented the monotypic plant family Ixerbaceae, which was endemic to New Zealand. However, more recent molecular studies have revealed a close affinity of tāwari to the New Caledonian family Strasburgeriaceae (Oginuma et al., 2006, The Angiosperm Phylogeny Group, 2009). Tāwari is still the only New Zealand representative in Strasburgeriaceae.

Despite the unique nature of tāwari, little is understood about its biology, and much of what is known – particularly with regard to reproductive biology – is

based largely on conjecture. Various sources have identified tāwari as being a predominantly bird pollinated (ornithophilous) species (Schneider, 2007, Dawson and Lucas, 2011). However, there is currently no data available to support this assertion. To address this uncertainty and the lack of information on breeding strategy, seed dispersal, and germination the current thesis investigates the reproductive biology of tāwari through the following research objectives and questions.

1.3 Research Objectives and Questions

The objective of this research is to increase knowledge of the endemic native tree *Ixerba brexioides* by focusing on three main questions:

1. How is *Ixerba brexioides* pollinated with regard to vector and pollen source? How is it adapted for this?
2. How is seed dispersal of *I. brexioides* achieved and under what conditions is germination most successful?
3. What are the dominant community associations of *I. brexioides* and how are they constrained by environmental variables?

1.4 Thesis Outline

Research that addresses each of the focus questions above is presented in six chapters:

Chapter 1: Introduction

Chapter one gives background information relevant to the current thesis. It also outlines research questions and objectives and gives a brief overview of the content of this thesis.

Chapter 2: Pollination of *Ixerba brexioides*

This chapter presents a review of the current situation of New Zealand ecosystems with regard to pollination services. Data from a pollination survey of *Ixerba brexioides* is presented from research in a modified mainland forest ecosystem.

Chapter 3: Seed ecology of *Ixerba brexioides*

Chapter three presents a review of seed dispersal services in New Zealand. *Ixerba brexioides* is used as a case study to examine this process. Results from germination trials are also presented.

Chapter 4: Composition of *Ixerba brexioides* forest

This chapter presents the results of an analysis of National Vegetation Database plot data to classify types of *Ixerba brexioides* forest, their distribution, and the environmental variables that constrain them.

Chapter 5: Biological Flora of New Zealand. *Ixerba brexioides,* tāwari, whakou (flowers)

Chapter five presents a comprehensive literature review on *Ixerba brexioides* alongside the key findings from the current research. This chapter is presented in the style and format of a New Zealand Journal of Botany Biological Flora article and will be submitted to this journal for possible publication.

Chapter 6: Synthesis and Recommendations

This final chapter presents a summary of the findings of this research project and their implications for the management and ecological restoration of tāwari forest in modified mainland forest ecosystems of New Zealand. It also gives recommendations for further research.

Chapter Two: Pollination of *Ixerba brexioides*

2.1 Introduction

Thomson (1927) remarked with surprise on the lack of information about pollination systems of New Zealand plants and said:

> "Botanists, as a rule, do not trouble themselves with the insects that visit the flowers which they collect; and entomologists are seeking the insects themselves, and seldom notice the flowers they are found on. Yet the subject is one of great interest to the naturalist, as it displays in a marked degree the principle of adaptation in nature."

Thomson and other early New Zealand biologists understood the importance of pollination research in understanding the functioning of ecosystems and their history and urged botanists and entomologists alike to study pollination systems in the New Zealand flora before the system changed irreparably (Thomson, 1927, Thomson, 1880, Heine, 1938). Today momentum is gathering on the research into pollination systems in New Zealand fuelled by agricultural issues affecting bees (such as the varroa mite and colony collapse disorder) which threaten pollination systems in agricultural production. Other ecological issues such as the decline of native bird species are also significant.

Recent reviews on the reproductive biology of New Zealand plants suggest the New Zealand flora has been relatively well studied in terms of reproductive systems (Godley, 1979, Lloyd, 1985, Newstrom and Robertson, 2005, Webb and Kelly, 1993). However, tāwari remains an unstudied element of the flora with regard to reproductive biology. This is surprising given the distinctiveness of the species in the flora, and the conspicuousness of the floral display which caught the attention of several early botanists (Cheeseman and Hemsley, 1914, Cunningham, 1839, Cockayne, 1923). Only a few publications mention the pollination system of tāwari (Dawson and Lucas, 2011, Schneider, 2007, Kelly et al., 2010) and none describe the breeding system of tāwari.

2.2 Aims and Objectives

This chapter aims to improve understanding of the pollination and reproductive biology of tāwari. The data deficiency on this topic was addressed by the

execution of an in-depth survey including observational aspects as well as measures of nectar properties, and experimental pollination trials to delineate the breeding system of tāwari. The findings of the study are then discussed with reference to the unique character of the pollination and breeding systems of the New Zealand flora.

In particular, this chapter aims to:

a) Identify the main functional group or groups performing the pollination service for tāwari;
b) Illustrate the floral adaptations that support the plant-pollinator mutualism;
c) Present findings on the breeding system of tāwari and implications of that system for the longevity of tāwari populations in the future.

2.3 Materials and Methods

2.3.1 Study site

The pollination studies for this project were undertaken at Tūī Ridge Park on the Mamaku Range. This park covers an area of 120 hectares, a large portion of which is dominated by native forest. The park backs onto a large area of pine plantation which is contiguous with the native forest of the Kaimai-Mamaku forest park, less than 10 km away. The native vegetation at Tūī Ridge Park is dominated by *Beilschmiedia tawa* and tāwari with scattered podocarps *Dacrydium cupressinum* and *Prumnopitys ferruginea.* The understory is dominated by *Coprosma grandifolia, Carpodetus serratus, Fuchsia excorticata, Pseudopanax crassifolius, Weinmannia racemosa, Pseudopanax arboreus, Schefflera digitata,* and tree ferns *Dicksonia squarrosa*, *Cyathea medullaris,* and *Cyathea smithii.* The ground tier is dominated by leaf litter but with frequent native ferns such as *Blechnum novae-zealandiae, Blechnum discolor, Blechnum fluviatile, Leptopteris superba,* and *Asplenium bulbiferum.* The climbers *Ripogonum scandens* and *Clematis paniculata* are also common. Edges of the vegetation in many places have been planted with ornamental exotics such as *Rhododendron* but these do not persist in the areas of native vegetation. Tracks criss-cross the park to accommodate walkers and mountain bikers. Possums and mustelids have been reported in the park, with possums particularly common. Tūī Ridge Park was an ideal location for this research because of the preponderance of and accessibility

of tāwari trees, the close proximity to and connectivity with a larger tract of native vegetation (Kaimai-Mamaku Forest Park), and the convenience of on-site accommodation.

Measurements of flower structure and osmophores were carried out as well as video surveillance, observations of plant-pollinator interactions, and exclusion experiments. Artificial pollination trials and nectar analysis measurements were also undertaken. The methods used are described in more detail in the following paragraphs.

2.3.2 Flower morphology and osmophores

Flowers were photographed at various stages in development. Also, main floral parts (including anthers, filaments, stigma, petals, and sepals) were measured to compare with published descriptions of flower dimensions. The internal structure of tāwari flowers has already been described in detail (Dravitzki, 1967, Matthews and Endress, 2005).

Osmophores are the glands in plant reproductive structures that are responsible for scent production. Detection of the areas of osmophores was determined using a simple protocol involving the collection of ten tāwari flowers and submergence of these flowers in a stain bath of 1:1000 neutral red: tap water for 2-12 hours. The tissues responsible for the production of scent stain red while other tissues remain unstained (Lehnebach & Robertson 2004; Ascensão et al. 2005). Following the treatment, the flowers were photographed and the areas of staining were described.

2.3.3 Video surveillance

To date tāwari pollination has not been described or measured in detail. For this reason, video surveillance was selected as an appropriate method of observation to capture flower visitation 24-hours each day. Two surveillance cameras were secured to the trunk of a tawa tree at Tūī Ridge Park. Cameras were facing in opposite directions to gain footage of two tāwari trees. The cameras were protected by camouflaged housing. This housing was connected to an automated external LED light source producing infra-red light. At the base of the tree the cameras were connected to a video recording device in a water-tight pelican case

and a 12 volt battery. This system allowed easy access to the recording device and battery while the camera remained secure in the canopy.

Collection of video footage began on the 2nd of December 2012 when the first of the filmed buds burst, and concluded on the 19th of January when all petals and anthers had dehisced. Technical difficulties meant that footage was not continuous for the entire flowering period, but sporadic and mostly in two to three hour bursts. In total 125 hours of footage was recorded. All video footage was viewed at 8 times speed. Information for each video segment was recorded including date recorded, start and finish time (and hence duration), weather conditions, which camera the segment was recorded from, whether day or night vision was used, and the flower visits observed within that video segment. Each flower visitor was recorded to the highest identifiable level, which in most cases was only to functional group because of the quality of the image. Functional groups included flies, bees, wasps, native bees, beetles, birds, and moths. The start and finish time of each visit was recorded, and if visible, the flower structures that were contacted (including stigma, nectar, anther, petal, bud, or the underside of the flower). Video surveillance data was pooled with field observation data (see section 2.3.4).

Data from the video footage was analysed in terms of visitor rate in visits per flower per hour of observation. The significance of the differences in visitor rate at different times of the day, calendar date, and location, and visitor type were analysed using ANOVA. The data required transformation to fit the assumptions of this test. For test of significance for time, date, and location a square root transformation was used. For significance of visitor type, a log transformation was used.

2.3.4 Field observation

Field observations were carried out over two flowering seasons (December to January 2011-12 and November to December 2012) at Tūī Ridge Park. In the first season, observations were made either from the ground (using binoculars) or from a position in the canopy which afforded good views of flowers without the aid of binoculars. Two to three focal inflorescences were selected and visitors to these inflorescences were recorded in terms of functional group, flower structures contacted, and any additional notes. Duration of visits was not recorded.

2.3.5 Exclusion experiments

A combination of flower bagging, caging, and emasculation in concert with different pollination regimes was used to assess the ability of tāwari to set seed under different pollination conditions. These methods were based largely on the work of Boulter et al. (2006). Eight trees in total were selected to be part of the exclusion experiments. The selection of the experimental trees was based on reproductive stage and accessibility. Trees that were in bud, and had inflorescences within reach of a ladder were selected. In November of 2011 inflorescences on these eight trees which were within 3.5 m from the ground (accessible with a ladder) were tagged and randomly assigned to one of eleven treatments (from Table 2.1). Each inflorescence was allocated a number indicating the tree it belonged to and its order on the tree. For example, inflorescence 5.1 was the first inflorescence number on tree five. The number of buds on each inflorescence was also recorded.

Table 2.1: Exclusion experiments

No.	Treatment	Bagged	Emasculated	Pollen source	Inflorescences
1	unmanipulated	no	no	open	7
2	cage control	no	no	open/bird	6
3	bag control	yes	no	none	5
4	emasculation control	yes	yes	different tree	4
5	cross-natural/ emasculation control	no	yes	open	4
6	diurnal	6pm to 6am	no	open	5
7	nocturnal	6am to 6pm	no	open	5
8	induced selfing	yes	yes	self-pollinated	11
9	geitonogamy	yes	yes	same tree	8
10	cross-artificial	yes	no	different tree	7
11	agamospermy	yes	yes	none	5

Bagged treatments were enclosed in mesh bags. Each bag had adjustable openings at either end to allow the bag to enclose the inflorescence and be fastened around the branch and one end, and allowing easy access at the other end. Caged inflorescences were enclosed in a mesh cage that was fastened with wire partway down the branch of the inflorescence.

Emasculation refers to the removal of the male anthers. The colour of the anthers changes throughout the period of flowering from purple early on, to yellow once the pollen has formed. In each emasculation treatment anthers were removed when purple using tweezers. In treatment 8 anthers were removed when yellow and used to pollinate the flowers from which they were removed.

Artificial pollination is an essential part of these exclusion experiments. Pollen was collected from the designated experimental trees. Anthers were removed using tweezers and transferred to Eppendorf tubes. Paintbrushes were then used to pollinate treatment inflorescences with this pollen.

When capsules were mature they were collected and the seeds removed. Viability of the seeds was assessed using two methods: dissection and staining. Dissection was the main method of assessing seed viability. Two main kinds of seeds were found in tāwari capsules: large, black seeds with an orange aril attached; and small, brown or yellow seeds with little or no fruit attached. On occasion medium sized seeds were also found which had the same dark black colour as the large seeds and often had an orange fleshy aril, but were obviously smaller in size. After the dissection of a large number of these smaller seeds it became clear that none were viable. Of the large seeds, however, it was very rare to find a seed which was not viable. Therefore, after the initial trials only large seeds were dissected. Seeds were measured and a number from 0 to 5 was given to denote the stage of embryo development with 0 meaning no embryo, and 5 meaning a fully formed embryo was present.

Visual examination of these dissected seeds was followed by staining with a tetrazolium chloride stain (TZC). This stain is commonly used in estimations of seed viability. It works by the reduction of a colourless tetrazolium salt to formozan by the action of dehydrogenases in cellular organelles like the mitochondria. Formozan is a non-diffusible, red-coloured substance which allows the identification of living tissues in seeds (Freeland, 1976). In this experiment seeds were soaked in distilled water for 24 hours beforehand and then dissected and submerged in 1% TZC solution. The seeds were then left to soak for four hours, and finally examined under a stereo microscope. Viability was visually assessed based on the appearance of the staining in the seed tissues.

Statistical analysis of seed production under exclusion treatments used non-parametric Kruskal-Wallis ANOVA because the data did not fit a normal distribution. No data transformation was applied.

2.3.6 Nectar analysis

Nectar analysis is an indirect way of discerning pollination vectors because of the role it plays in attracting pollinators and essentially 'rewarding' them for their pollination service. In particular, nectar data included measurements of volume, pH, concentration, and ratios of three main sugars. Nectar measurements were constrained by the availability of tāwari florets that were within reach.

The volume of nectar produced by tāwari was measured as nectar standing crop. This is defined as the "quantity and distribution of nectar determined by randomly sampling flowers that have not been protected from pollinators by bagging, at a given moment" (Kearns and Inouye, 1993). These measures were also compared with values from flowers that were bagged. Nectar volume was measured by removing the nectar droplets using a glass pipette and transferring the liquid to a plastic Eppendorf tube with graduated volume markings. The volume was then estimated using these markings. Samples were collected from 13 florets from 4 different trees and were taken every 3 hours over a 24 hour period in late December 2011. Nectar volume data did not fit a normal distribution initially, so ANOVA was carried out using square root transformed data, at a significance level of 0.05.

Nectar pH was measured using litmus paper. Nectar droplets were collected using a glass pipette and transferred to plastic Eppendorf tubes. A small piece of litmus paper was added to the solution and the pH determined using the colour guide supplied with the litmus paper. Nectar from 10 florets was collected between 1230 and 1500 hours on the 3rd of January 2012 and each sample was measured separately. Because of the limited number of pH samples obtained, the data did not fit a normal distribution and the statistical analysis was undertaken using non-parametric methods.

Sugar concentration of nectar samples was determined using a handheld refractometer. Nectar was collected from individual tāwari florets using a glass pipette and transferred to the refractometer and a reading was obtained. Readings from 28 different flowers were taken 67 times between 21st December 2011 and

4th January 2012 over a range of times to give an indication of any diurnal fluctuations in sugar concentration. Flowers measured for nectar concentration were categorised by flower condition into four generalised categories:

- Immature -buds just opened, or anthers purple and not yet bearing pollen
- Pollen-bearing anthers
- Past maturity – petals and anthers starting to dehisce
- Emasculated

The significance of changes in nectar concentration were then assessed with regard to date collected, time of collection, location of collection, and the condition of the flowers. Nectar concentration data did not fit a normal distribution; hence, non-parametric methods were used.

A pilot study on the sugar composition of tāwari nectar was carried out using GCMS (gas chromatography/mass spectrometry).

2.4 Results

2.4.1 Osmophores

Soaking flowers in a 1:1000 neutral red: tap water solution produced staining 50-60% of the time on the anthers, sepals, and the tip of the stigma. Petals also often had a light pink appearance.

Figure 2.1: Osmophore treatment – Left) flowers were soaked in a solution of 1:1000 neutral red: tap water for 5-12 hours; Middle) red staining on top; Right) red staining on back.

2.4.2 Flower visitors

Over 140 hours of observation, 395 visits from flower visitors from 10 functional groups were recorded. Functional groups included: bird, bumble bee, wasp, honey bee, large fly, moth, beetle, native bee, small fly, and spider. The most common

visitors were large flies and moths which accounted for 27% and 20% of the total number of visits respectively.

The average visitation rate was 0.18 visits per flower per hour. The maximum visitation rate was 1.02 visits per flower per hour and the minimum was 0.024 visits per flower per hour. Large flies and moths had the highest maximum visitation rate (1.056 and 1.05 visits per flower per hour respectively) and the highest average visitation rates (0.288 and 0.276 visits per flower per hour respectively) of all visitor groups. Beetles had the lowest minimum, average, and maximum visitation rates of all groups (0.03, 0.048, and 0.06 visits per flower per hour respectively).

Flower visits peaked between 0900-1200 hours and 1800-2100 hours (as shown in Figure 2.2). Visitation rate was also lower in wet conditions and slightly higher when there was a wind or breeze. None of these trends was statistically significant.

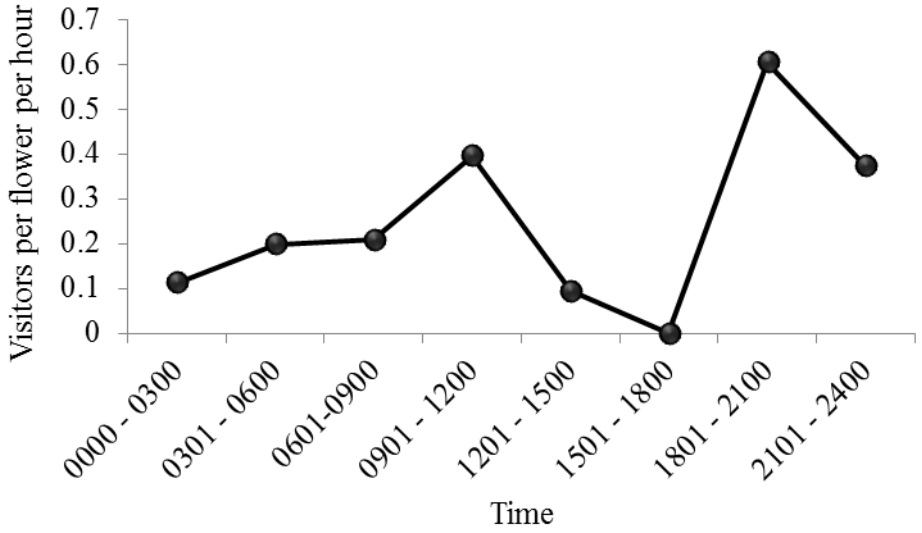

Figure 2.2: Flower visitors per flower per hour at different times of the day

Visitor rate was not significantly different between locations, observation dates, or observation times. However, when categorised by visitor type, visitor rate was significantly different with a *p*-value of 0.025. Post-hoc analysis using Duncan's test showed that the main source of this significance was from the visit rate of large flies and moths in comparison to beetles because beetle visitation was only recorded on two occasions, compared with the frequent visitation by large flies and moths. The latter two groups had the highest visitation rates, but these were

not significantly different to other groups of visitors including small flies, honey bees, bumble bees, and wasps. Birds did not feature in the analysis because the birds either did not come in contact with tāwari flowers, or bird visitation was observed in passing, outside a formal observation period.

2.4.3 Exclusion experiments

The exclusion experiments yielded an average of 43% seed viability for each capsule, with a maximum of 90% viability and a minimum of 0% viable seeds per capsule. Standard deviation was 21%.

2.4.3.1 Pollination treatments

Non-parametric methods were used to discern differences in production of viable seed between the different pollination treatments performed on tāwari (Figure 2.3). The *p* value was 0.0006 showing a strongly significant result. Post-hoc analysis showed that the main source of this significant difference was from treatment 1 (control) which had lower seed viability than most other treatments, and a significantly lower viability than treatments 9 and 10.

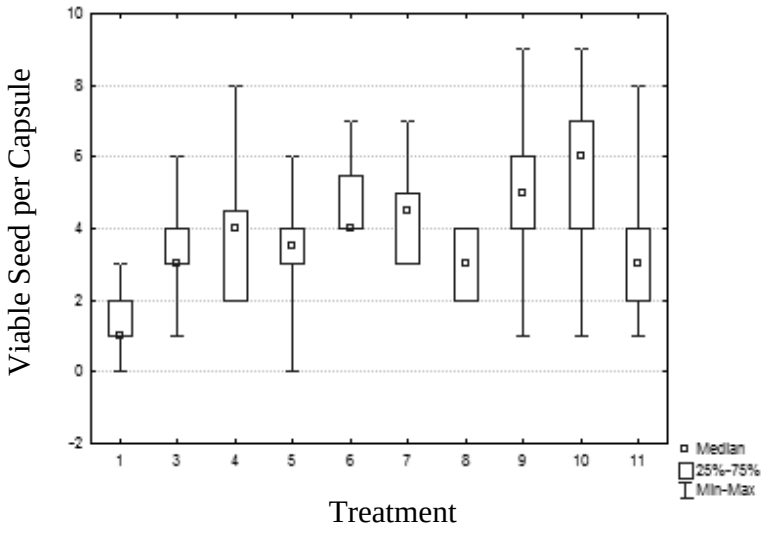

Figure 2.3: Comparative box and whisker plot showing the pollination treatments (see Table 2.1) performed on tāwari and the differences in viable seed produced from these treatments

Non-parametric analysis also showed a significant difference in the seed set of different pollination treatments based on the nature of pollination or pollen source, with a *p* value of 0.0021. Post-hoc analysis demonstrated that the significance of this difference comes from the disparity between the hand pollinated treatments and the other pollination types, with hand pollination yielding higher seed

viability than natural pollination and no pollination. There was no significant difference between the viable seed set of naturally pollinated flowers and flowers that had pollen excluded from them (Figure 2.4).

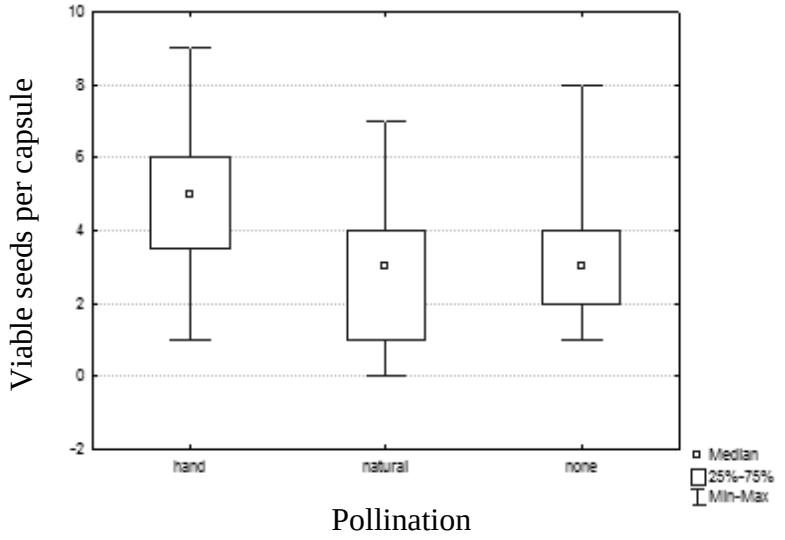

Figure 2.4: Average viable seeds per capsule for hand pollinated, naturally pollinated, and un-pollinated tāwari flowers

Non-parametric analysis was used to assess the significance of differences in viable seed production from different pollen sources: none, natural, cross, and self (Figure 2.5). There was a significant difference between the seed set of naturally pollinated flowers, and the seed set of self-pollinated flowers (with selfed flowers significantly higher).

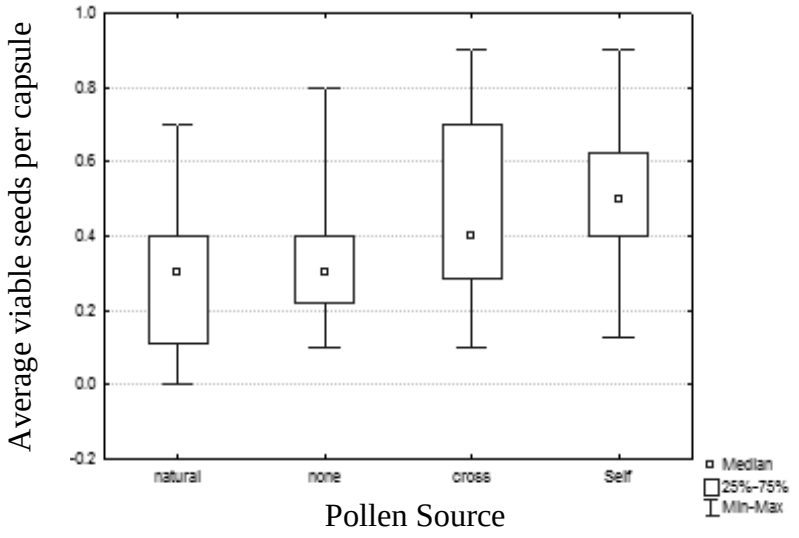

Figure 2.5: Box and whisker plot showing the differences in viable seed production from flowers pollinated with different source pollens: natural, none, cross and self.

Collection date made no difference to viable seed set, though capsule source tree was significant with a *p*-value of 0.0004. Post-hoc analysis showed that of the eight study trees tree 7 was significantly lower in viable seed set than tree two and tree four. Tree 7, however, had a lower sample size than both tree 2 and tree 4 which may have affected this difference (Table 2.2).

Table 2.2: Table showing the number of capsules collected from each study tree (n) and the average seed viability of the collected capsules.

Tree	n	Viability
1	1	20%
2	48	47%
3	13	35%
4	18	51%
5	8	29%
6	1	80%
7	7	16%
8	2	55%

2.4.3.2 Breeding system indices

Exclusion experiments and artificial pollination made it possible to calculate a range of indices that characterise the breeding system of tāwari.

The pollen limitation index compares the seed set of hand pollinated flowers and naturally pollinated flowers, levelled at zero. A value of zero means there is no limitation as the same seed set would be determined for natural and hand pollinated flowers. Tāwari has a PLI value of 0.31 and viable seed set was 15% higher in hand pollinated treatments than in naturally pollinated treatments.

ASI is the autonomous selfing index and compares pollinator excluded treatments with cross pollinated treatments to give an indication of the level of autonomous selfing occurring. The ASI value was calculated at 0.65 for tāwari and viable seed set was 18% higher in hand crossed treatments than in pollinator excluded treatments.

Finally, SCI is a self-compatibility index. This index is calculated by comparing the viable seed set from hand crossed and hand selfed flowers. Tāwari has an SCI of 0.93. Further indices were calculated to separate out the compatibility for self-pollination using pollen from the same flower, and using pollen from the same

tree. These two indices had very different results. SCI for the same flower was 0.57 compared with SCI for the same tree of 0.98.

2.4.4 Nectar analysis

2.4.4.1 Volume

Of the 45 nectar samples collected from tāwari flowers, volume of nectar collected ranged between 0 μL and 70 μL, with an average of 18 μL and a standard deviation of 16.4 μL.

Measurement of nectar volume at different times of the day showed a strong trend in the production of nectar over time on a daily scale. Nectar volume began at an average of 13 μL before dawn, which steadily increased to an average of 29 μL toward day-break, and peaking at 32.5 μL at mid-late morning. Toward the afternoon, average nectar volume began to decrease, bottoming out at 4.7 μL in the late afternoon before beginning a slow rise in volume collected toward dusk. The strength of this trend is decreased somewhat by the large variation recorded in these samples (Figure 2.6). ANOVA revealed that the many of these changes are significantly different (Table 2.3). Post-hoc analysis showed that the peak nectar volume between 0700 and 1300 is significantly different from most other times (exceptions between 0430 and 0700 and 1300; also 1300 and 2200) (Table 2.3).

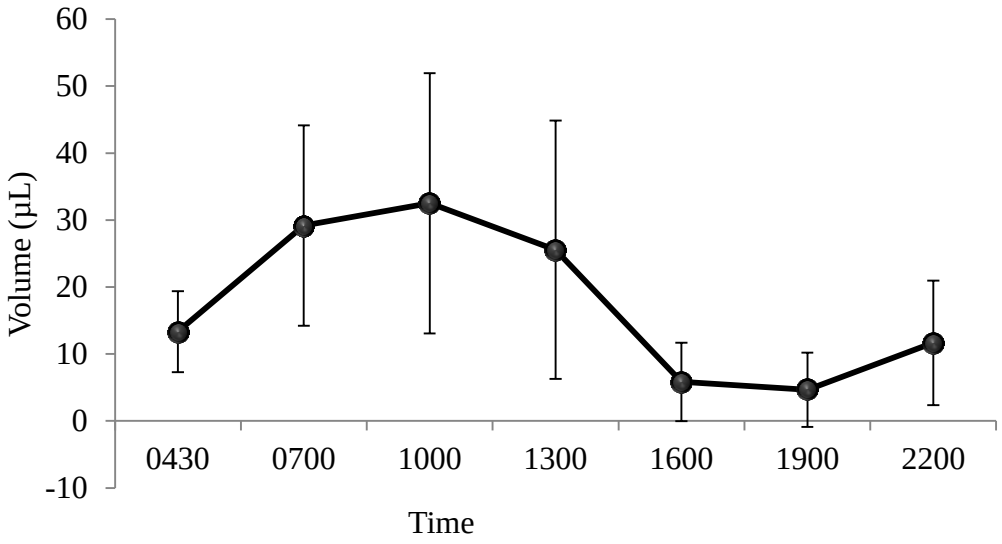

Figure 2.6: Average volume of nectar collected from tāwari flowers at different times of the day

Table 2.3: Post-hoc Duncan's test for differences in diel patterns of nectar volume collection. Significant values (p<0.05) are in bold type.

	0430	0700	1000	1300	1600	1900	2200
0430		0.055	**0.025**	0.116	0.36	0.307	0.828
0700	**0.055**		0.664	0.638	**0.008**	**0.006**	**0.04**
1000	0.025	0.664		0.396	**0.003**	**0.002**	**0.017**
1300	0.116	0.638	0.396		**0.021**	**0.017**	0.092
1600	0.36	**0.008**	**0.003**	0.021		0.879	0.448
1900	0.307	**0.006**	**0.002**	0.017	0.879		0.392
2200	0.828	**0.04**	**0.017**	0.092	0.448	0.392	

Statistical analysis showed overall no significant differences in nectar volume collected from different flowers, with a p value of 0.57. However a post-hoc Duncan's test showed that flower 11 (from inflorescence 7.2) is significantly higher than 7 out of 12 other flower measurements. However, the sample size from each flower was low, and in the case of inflorescence 11 only two samples were taken from this tree. A comparison of average nectar volume collected from flowers of different trees showed overall no statistical difference (p=0.15). Further analysis with both Duncan's test and Newman-Keul's test showed that the volume of nectar collected from flowers on tree 7 was significantly higher than the volume collected from all other trees in the survey. However, again the sample size for this tree was much lower than for the other trees in the study, and all flowers tested from tree 7 were covered, whereas the measurements from other trees had a mixture of covered and uncovered inflorescences.

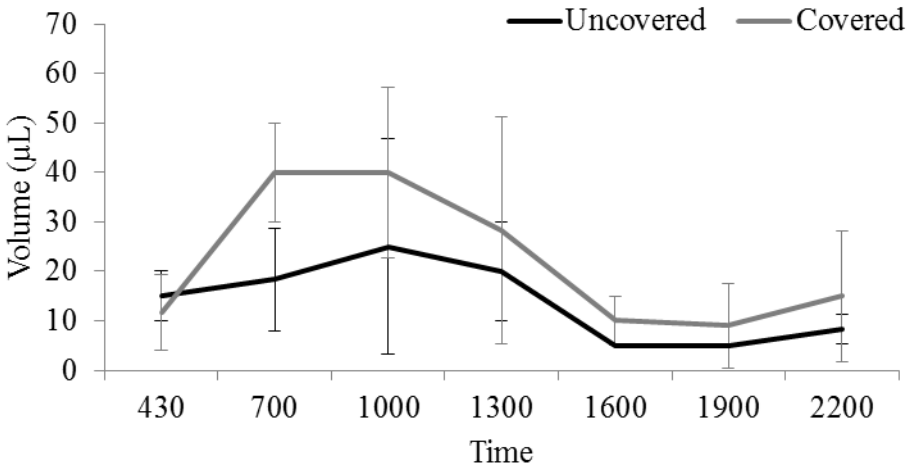

Figure 2.7: Average volume of nectar collected from tāwari flowers at different times of the day and separated by covered inflorescences versus uncovered inflorescences. Covered inflorescences were enclosed in a fine mesh bag to prevent nectar collection by flower visitors.

The diurnal trend in nectar volume is consistent in covered and uncovered flowers though more exaggerated in the covered specimens (Figure 2.7). ANOVA tests revealed that the difference in values between covered and uncovered flowers was not statistically significant, with a *p* value of 0.1.

2.4.4.2 Concentration

Tāwari had an average nectar concentration of 11.02% with a standard deviation of 4.64%. The highest recorded concentration was 20% and the lowest was 3%. Nectar concentrations over 20% could not be detected because they were outside the range of the refractometer. This occurred only on one occasion.

Non-parametric analysis was used to determine any statistically significant differences in nectar concentration between: sampling dates, sampling times, source flower, source tree, and flower condition. The difference between sampling dates was highly significant with a *p* value of 0.000000. The trend overall, was decreasing trend in sugar concentration over the sampling time-period. A post-hoc Duncan's test revealed that measurements from the first two sampling days (21 Dec and 23 Dec 2012) were significantly different from all other days.

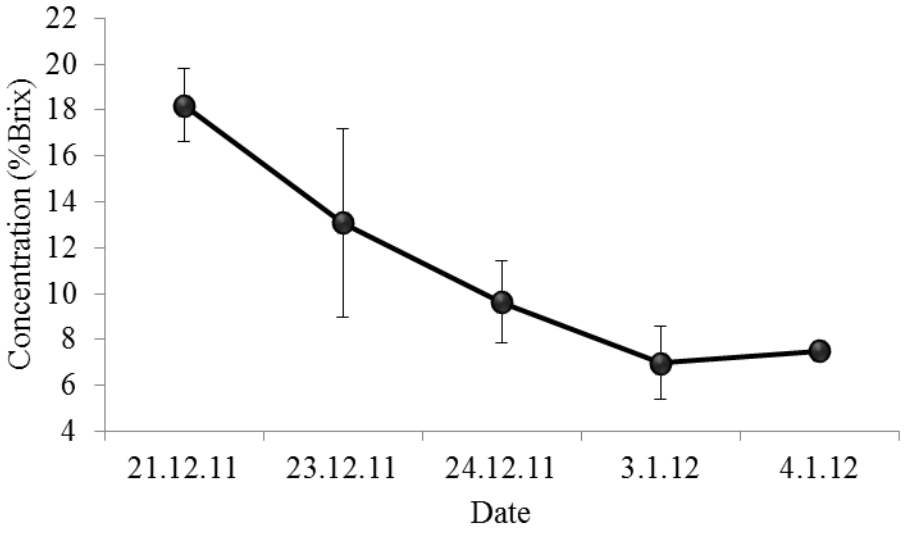

Figure 2.8: Concentration (%Brix) of tāwari nectar between 21 Dec 2012 and 4 Jan 2012.

Nectar concentration across different sampling times was also shown to be statistically significant with a *p* value of 0.005. Duncan's test revealed that most

the of the difference arises from measurements taken at 2200 hours, where nectar concentration was significantly higher than at 0130, 0700, 1000, 1300, and 1600.

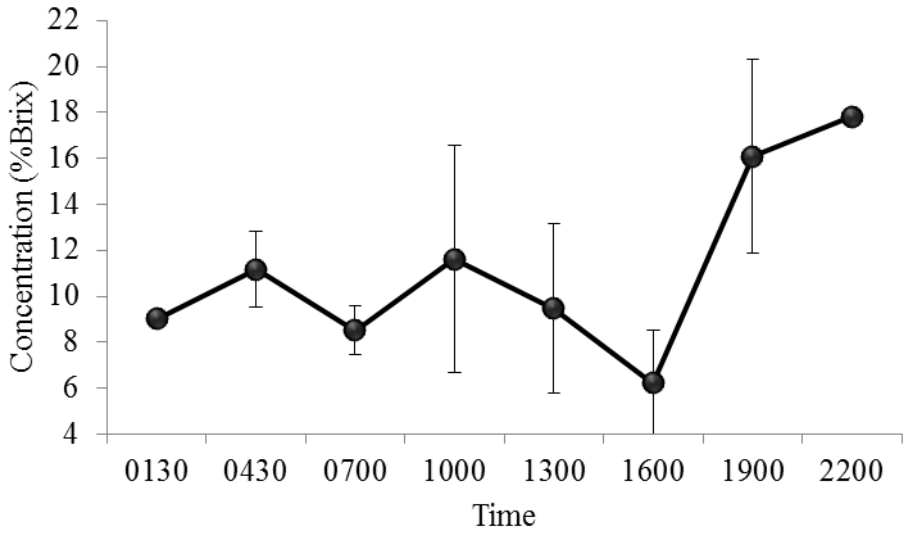

Figure 2.9: Diel pattern of tāwari nectar concentration (% Brix)

Differences in nectar concentration between trees were statistically significant with a *p* value of 0.000000. Post-hoc analysis using Duncan's test showed that the main source of this difference was from tree 9 which was significantly higher than all other trees, and tree 5 which was significantly higher than trees 3, 6, and 7.

Nectar concentration was also significantly different between different flowers with a *p* value of 0.000007. Again, the main differences reflected in this difference are from flowers on tree 9, flower 3.1, and flower 4.5 which were significantly higher in nectar concentration than most other flowers.

Flower condition elicited some significant differences in flower nectar concentration, showing a *p* value of 0.007. Concentration of nectar seemed to increase with increasing maturation stage, and to be lower in emasculated flowers. Post-hoc analysis using a Duncan's test showed that the most significant difference was between flowers bearing pollen and immature flowers, and emasculated flowers.

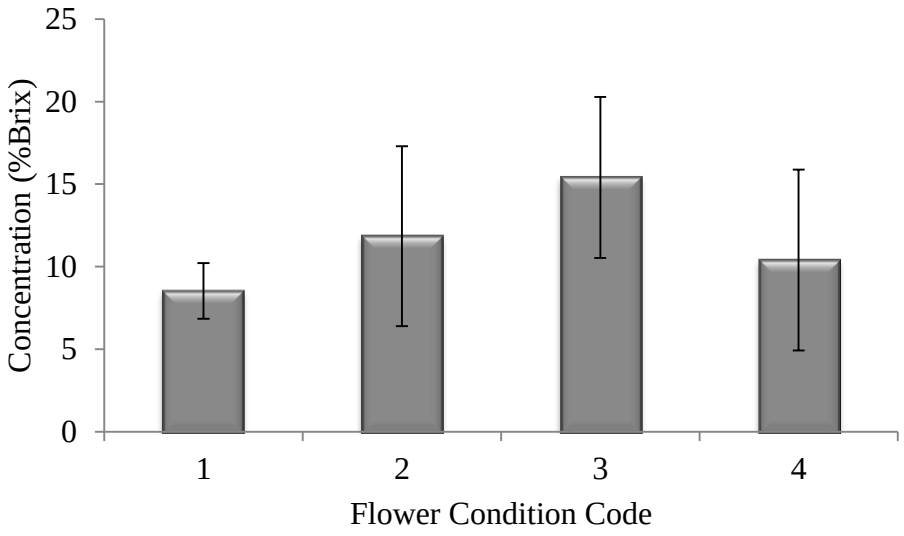

Figure 2.10: Tāwari nectar concentration at different flower conditions. 1) Immature; 2) Pollen bearing anthers; 3) Past maturity; 4) Emasculated.

A pilot study on the nature of the sugar content of tāwari nectar demonstrated a dominance of hexose sugars (fructose and glucose) (Figure 2.11).

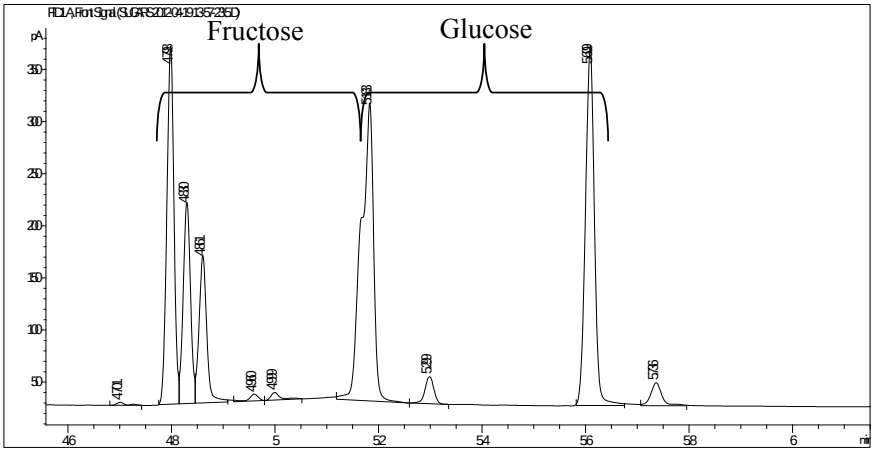

Figure 2.11: Gas chromatography readout showing peaks representing fructose and glucose as the major constituents of tāwari nectar.

2.4.4.3 pH

The pH measurements for tāwari nectar fell between 7 and 9 on the pH scale with an average of 8.5 and a standard deviation of 0.71. Non-parametric analysis showed no significant difference in nectar pH between different flowers or trees sampled, and between different times of the day.

2.5 Discussion and Conclusions

2.5.1 Flower visitors

Harder and Johnson (2008) estimated that <1% of collected pollen reaches a conspecific stigma. Functional pollinators are those that transfer this pollen effectively and accurately. When flower visitors consume floral rewards (such as nectar and pollen) without performing the pollination service this is characterised as either nectar robbing, or pollen theft. Most pollen theft occurs by vectors that pollinate other plants and the most frequent pollen thieves are bees (Hargreaves et al., 2009). Pollen theft occurs because of mismatched pollination vectors and flowers in terms of flower structure (particularly with regard to sexual dichotomy) and timing of differential sex maturation. Several strategies have been documented which allow plants to either tolerate pollen theft or resist pollen theft. One tolerance strategy is increasing pollen production (through an increase in flower numbers or pollen quantity per flower). This is suggested as a form of masting and an adaptive advantage of a mass-flowering strategy (Hargreaves et al., 2009). Other more active approaches resisting pollen theft include timing pollen availability outside the foraging season or time of pollen thieves; eliminating pollen attractants to make pollen less conspicuous to pollen thieves; hiding pollen in flower structures or packaging pollen in a way that makes it accessible to only effective pollinators; or chemical defences which guard against pollen thieves. Tāwari is known for the abundance of inflorescences in its floral display. This mass flowering strategy of tāwari may be part of a tolerance strategy against the potential for pollen theft and as insurance against inefficient pollinators.

2.5.1.1 Fly pollination

Flies were the most frequent visitors of tāwari flowers in this study. The importance of flies as floral visitors was early noted by Robertson (1924) who identified them as the next most frequent visitors of flowers and flowering plant species than any other insect group after bees. New Zealand has a great diversity of Diptera and a number of the prominent Dipteran groups make an important contribution to pollination in New Zealand (Heine, 1938, Thomson, 1927, Thomson, 1880, Godley, 1979, Newstrom and Robertson, 2005).

Hoverflies (Syrphidae) are said to make a high percentage of non-pollinating visits (Robertson, 1924). Small hoverflies with sparse hairs and simple bristles, and a short proboscis collect high levels of anemophilous (wind dispersed) pollen (99%); whereas large hoverflies with more hairs and spirally grooved bristles, and a longer proboscis collected pollen from nectar bearing flowers (Holloway, 1976, Hickman et al., 1995). These larger flies share morphological (such as branched hairs and spirally grooved bristles) and behavioural (such as the leg-scraping practice) similarities with honey-bees which have been attributed to convergent evolution as a result of similar food-gathering requirements. They also share the characteristics of flower constancy that have been observed in other pollinators such as bees and beetles (Goulson and Wright, 1998).

The Tabanidae (horse flies) are also important flower visitors (Johnson and Morita, 2006, Morita, 2008) and have been recorded visiting flowers such as *Leptospermum* in New Zealand (Mackerras, 1956) despite their reputation as biters or bloodsuckers elsewhere in the world (Lessard and Yeates, 2012).

Other groups of flies that have been recorded visiting New Zealand flowers include the Tachinidae, Goniinae, Phasiinae, Tachininae, Voriinae, Sarcophagidae, Asilidae, Bibionidae, Empididae, Stratiomyiidae, Dolichopodidae, Cyrtidae, Calliphoridae, Tabanidae, Muscidae (Primack, 1983) but effectiveness of these groups in the movement of pollen has not been investigated (Newstrom and Robertson, 2005). Muscoidea are valuable as flower visitors (Primack, 1978, Primack, 1983) which has been suggested to be due to structures like the thick proboscis to which pollen adheres (Percival, 1979).

Short-tongued flies are more frequent visitors of flowers with open structures and readily accessible nectar, which are grouped in inflorescences (Percival, 1979). This is consistent with the observations of Heine (1937), Godley (1979) and Lloyd (1985) in the New Zealand flora which coupled Dipteran visitation with white or pale flowers of the dish/bowl class (see section 2.5.1.8.5). Flies of the genus *Calliphora* also use textural visual cues and are attracted to surfaces with a liquid appearance (Percival, 1979).

The high levels of fly visitation to tāwari during the 2011-2012 sampling season may be attributable to a number of variables including altitude and climate of the study area. Pollinator fauna changes with altitude; in particular at increasing

altitudes fewer bees were observed visiting flowers, and flies and butterflies became more frequent (Primack, 1983, Delph, 1988, Delph, 1990). In subalpine and montane habitats of the South Island flies represent up to 50% - 80% of flower visitors (Primack, 1983). Climatic conditions also affect the pollinator assemblage available for pollination services. In cold, rainy weather flies are frequent floral visitors compared with the relative inactivity of bees in these conditions. Winter is not the only time when these conditions occur, and as a result of New Zealand's changeable weather pollinator assemblages can often fluctuate on much smaller time scales (Primack, 1978, Primack, 1983, Lloyd, 1985). The summer of 2011-2012 was a particularly cold and wet season. The summer mean temperature was between 0.5°C and 1.2°C below average and was a very wet summer across the North Island (Griffiths and Tait, 2012).

2.5.1.2 Lepidopteran pollination

New Zealand has a striking diversity of moths, particularly in comparison to their Lepidopteran counterparts the butterflies. In all, New Zealand has over 1800 species of Lepidoptera, only 17 of which are butterflies (Parkinson and Patrick, 2000). Butterfly pollination has been documented by a number of authors (Thomson, 1927, Heine, 1938, Godley, 1979, Primack, 1978, Primack, 1983) but no specialist relationships have been described (Lloyd, 1985). No butterfly visitations were observed on tāwari flowers; however moths did make an important contribution to the visitor fauna of tāwari.

Moths are an important group in the pollination of the New Zealand flora. In other areas of the world hawk moths are a major contributor to pollination, however, in New Zealand this group is largely absent with the exception of one exotic species found in some parts of the North Island (Newstrom and Robertson, 2005, Primack, 1978). Moth pollination has been demonstrated in the New Zealand flora (Godley, 1979, Heine, 1938, Lloyd, 1985, Newstrom and Robertson, 2005, Thomson, 1927) including some cases where flowers are adapted to moth pollination (Primack, 1978, Godley, 1979). In the present research moths played a key role as the nocturnal visitors of tāwari flowers, accounting for 20% of the total visitations observed. Tāwari flowers showed some evidence of adaptation for moth pollination in the way that the flowers remain open at night, and in the increase in nectar volume and concentration observed at dusk and into the night,

when moth pollinators were most active. During the flowering season at dusk clouds of moths would descend upon tāwari trees, and moth visitation continued throughout the night. During visitation moths would land in the nectary of tāwari flowers and the beating of their wings would create contact between the flower visitor and the anthers and stigma.

2.5.1.3 Bird pollination in New Zealand

Kelly et al. (2010) compiled a list of New Zealand birds known to act as pollinators. These included native species: tūī, bellbird, silvereye, kākā (*Nestor meridionalis),* stitchbird (*Notiomystis cincta),* saddleback (*Philesturnus carunculatus),* red-crowned parakeet (*Cyanoramphus novaezelandiae),* yellow-crowned parakeet (*C. auriceps)* , kea (*Nestor notabilis),* whitehead (*Mohoua albicilla),* yellowhead (*M. ochrocephala),* fantail (*Rhipidura fuliginosa),* and kokako; as well as introduced birds: house sparrow (*Passer domesticus,* starling (*Sturnus vulgaris),* chaffinch (*Fringilla coelebs),* eastern rosella (*Platycercus eximius),* and myna (*Acridotheres tristis).* But of this extensive list of pollinating avifauna only three species are responsible for most flower visitations: bellbirds (32%), silvereyes (31%), and tūī (25 %).

However, the bird fauna of New Zealand has been modified to the point where it has been described as being the "wreckage of an avifauna" (Diamond, 1984). From 428 taxa a total of 20 species of native birds have become extinct since 1800, while 77 species are endangered, and 93 species are at risk (Miskelly et al., 2008). Similar trends in other areas around the world have caused increasing concern regarding the fate of plant-bird mutualisms such as pollination and seed dispersal. A study of global bird extinction showed that on record 141 monotypic species and 138 subspecies of polytypic species have gone extinct since 1500 (Szabo et al., 2012). The main drivers of this extinction are colonisation of non-native predator species, hunting, and agricultural expansion causing habitat decline. Though declining rates of extinction on oceanic islands have been reported, New Zealand's bird-fauna has already seen significant losses. Other studies predict that with the current conditions of New Zealand ecosystems birdlife will continue to decline without large-scale management of pests, and of other factors limiting bird populations such as habitat size, food availability, disease, and the genetic effects of small population size (Innes et al., 2010).

In New Zealand the effects of avian extinctions on bird-mediated seed dispersal have been overestimated, but effects on bird-mediated pollination are significantly underestimated (Kelly et al., 2010). Birds were once thought to play a minimal role in pollination (Godley, 1979, Lloyd, 1985, Clout and Hay, 1989). However, more recent publications present case-studies that assert the importance of bird pollination for a number of native species including species outside of the typical bird specialist flowers (Anderson, 2003, Kelly et al., 2010, Kelly et al., 2004, Ladley and Kelly, 1996, Robertson et al., 2001).

In the present research tāwari was shown to be entomophilous with infrequent bird visits and medium pollen limitation. Because bird exclusion trials failed in this experiment it is impossible to gauge the effect of birds on the effective pollination and seed set for tāwari. But it is possible that the missing bird-tāwari mutualism has negative impacts on the effective pollination and seed set of tāwari. The birds that have been observed visiting tāwari trees include tūī and bellbirds – common nectar drinking birds in the New Zealand fauna. The present research recorded one instance of North Island robin visitation. These birds are known as insectivores, so their flower visitation may be in pursuit of the insect visitors attracted by the nectar of tāwari flowers.

2.5.1.4 Bat pollination

Bat pollination is a mechanism that has been suggested to have a minor role in the pollination of New Zealand plants (Godley, 1979, Lloyd, 1985, Newstrom and Robertson, 2005), but which has received more attention in recent times and has now been shown to be more important than previously thought (Pattemore, 2011). Bat pollination in New Zealand is unusual because of the unique characteristics of the bat fauna in New Zealand. New Zealand has two extant endemic species of bat (*Chalinolobus tuberculatus* and *Mystacina tuberculata*), and a third endemic species that is now believed extinct (*Mystacina robusta*). *Chalinolobus tuberculatus* is a strict insectivore, and *Mystacina tuberculata* is an omnivore feeding on insects as well as floral nectar and pollen (King, 1990). Several New Zealand flowering plants have been recorded as visited by bats including *Knightia excelsa, Metrosideros* spp., *Freycinetia banksii*, and *Collospermum hastatum* (Newstrom and Robertson, 2005). Godley (1979) characterised flowers that were suited for bat pollination as having exposed pollen, accessible nectar, and flowers

aggregated in large or prominent inflorescences. This description matches the characteristics of tāwari florets. In the video footage of tāwari inflorescences one bat (*Mystacina tuberculata*) was seen and this was on a night with very poor video quality, and when camera displacement meant that flowers were outside of the camera shot, hence no claim of bat visitation can be made.

2.5.1.5 Beetle pollination

Beetles are not thought to play an important role in the pollination of New Zealand plants. One study attributed this to low density on the flower, morphology incompatible with the transfer of pollen (e.g. lacking in body hairs), and low rates of movement between flowers (Primack, 1983). However, flower visitation by beetles has been reported by a number of authors (Heine, 1938, Newstrom and Robertson, 2005, Primack, 1983, Thomson, 1927, Wilton, 1997, Webb, 1994, Delph, 1990, Gaffney et al., 2011, Thomson, 1881) though the relative effectiveness of beetles as pollinators is unstudied.

In the present study beetle pollination was rarely observed, but included visitation on different occasions from longhorns, cockroaches, and weevils. These visitors accounted for 2% of the total flower visitations that were observed. The pattern of visitation reflects the above descriptions of low density, infrequent visits, with low rates of movement between flowers. In one period of observation a longhorn remained on one inflorescence in excess of 30 minutes and visited 3 separate flowers. The effectiveness of these beetles as flower pollinators was not assessed because of the rarity of observation of these interactions.

2.5.1.6 Small insect pollination

The role of very small insects (such as thrips) has often been overlooked in pollination studies, though they have been suggested to play an important role in pollination for *Pseudowintera colorata* (Norton, 1980, Norton, 1984). Despite the small pollen loads they are able to carry, high population numbers and capacity for rapid population expansion seem to compensate. Another study on *Pseudowintera*, however, did not see a significant effect of thrips in pollination (Lloyd and Wells, 1992). In the present research, small insects accounted for 2.5% of all visits. There was insufficient camera resolution to identify insect groups more specifically. The effectiveness of these small flower visitors was not investigated, but for the most part, these visitors were stationed in the nectaries of

tāwari flowers and did not come in contact with the reproductive floral parts. This observation, coupled with the low rate of visitation and the large size of tāwari flowers, makes pollination by small insects improbable.

2.5.1.7 Spider visitation

Spider visitation on tāwari flowers was observed on ten occasions. On one occasion, a flower spider was camouflaged against the green nectary of a tāwari flower and caught a moth when it came to land. In other cases of flower visitation on tāwari the circumstances were similar in that rather than feeding on nectar, or pollen the spiders were predating flower visitors. Thomson (1927) mentioned a similar interaction occurring on *Nematoceras macranthum*; and Primack (1978) observed the same on several species of *Celmisia* and *Helichrysum selago*. Spider visitors have also been mentioned for the native orchids *Microtis unifolia* and *Pterostylis banksii* though no mention of pollination was made (Heine, 1938).

2.5.1.8 Flower characteristics

2.5.1.8.1 Pollen morphology

Tāwari pollen occurs singly (rather than in aggregates or tetrads) and is isopolar (Moar, 1993). It has four to five apertures, arranged in an angulaperturate fashion. The exine is 2 µm thick, thinning to 1 µm at ectoapertures. The surface structure is tectate, baculate with the tectum perforate. Tāwari pollen ranges in size from 37-40 µm on the polar axis, and 43-45 µm on the equatorial axis. According to Erdtman's (1952) classification tāwari pollen is medium in size and suboblate in shape. Tāwari pollen morphology is unique in the New Zealand flora, and is typical of insect pollination (Moar, 1993). Tāwari pollen is classified as only occasionally observed in the pollen record, distributed by insects or other invertebrates, produced in low quantities, and having a limited distribution (Moar et al., 2011).

Based on whether the percentage of collected pollen exceeds, is approximately equal to, or is less than the percentage of the source plant in the vegetation, pollen types can be classed as over-represented, well-represented, or under-represented respectively (Macphail and McQueen, 1983). Macphail and McQueen had insufficient information to offer a classification for tāwari pollen; however other studies have demonstrated under-representation of tāwari pollen in palynological

surveys (Macphail, 1980, Deng, 2004, Ogden et al., 2003). This trend of underrepresentation is characteristic of insect pollinated trees (Macphail and McQueen, 1983).

2.5.1.8.2 Flower colour

Many studies have shown the impact of flower colour in the attraction of pollinators and the impact of pollinators in the selection of the colour morphs displayed by some flowering plant species (Jones and Reithel, 2001, Irwin and Strauss, 2005, Hoballah et al., 2007, Bradshaw and Schemske, 2003, Ashman and Majetic, 2006). Developing genetic techniques make it ever more possible to discern these effects. Hoballah et al. (2007) manipulated a single gene locus coding for flower colour in flowering plants of the genus *Petunia* and observed a shift in pollinators. This relationship demonstrates the importance of flower colour in plant-pollinator mutualisms.

One of the often quoted anomalies of the New Zealand flora is the paucity of brightly coloured flowers compared with flora from other parts of the world. This difference is particularly notable in genera which are dominated by brightly coloured flowers outside of New Zealand, such as *Myosotis, Gentiana,* and *Veronica.* Early estimates by Thomson (1880) characterised the flora as 33% white flowers, 11 % yellow, 5 % red, 2.5% blue or purple, and the remainder green or inconspicuous. Estimates of New Zealand's 'showy' flowers by Cockayne (1921) suggested that 61% were white. Recent arrivals from Australia have been highlighted as the conspicuous coloured component, with large sized flowers (Lloyd, 1985). Two examples include *Solanum laciniatum* which has blue petals and *Solanum aviculare* which has pink petals (Newstrom and Robertson, 2005). This "[striking deficiency] in gaily-coloured blossoms" is a feature of New Zealand flowering plants that was observed by A. R. Wallace and was attributed by him to the similar deficiency in insect variety – a view not shared by Thomson (1881).

Tāwari flowers fall into this majority category of white flowers, though they are large and conspicuous in their presentation. Traditional pollination syndromes suggest that white flower colour is linked to pollination by bats, bees, beetles, and moths (Faegri and Van der Pijl, 1979, Proctor et al., 1996).

2.5.1.8.3 Floral scent

Floral scent is an understudied phenotypic trait that is important in many pollination mechanisms. Not only has scent been identified as a pollinator attractant (Adler and Irwin, 2012, Gaskett, 2011, Parachnowitsch et al., 2012), but research has also demonstrated a synergistic effect of floral scent in conjunction with floral colour and form (Leonard et al., 2011, Spaethe et al., 2007). Even flower-emitted volatiles which escape the sensitivity of the human nose can have important roles in pollinator attraction (Ashman et al., 2005) and in plant microevolution (Parachnowitsch et al., 2012).

Thomson (1880) reasoned, based on Wallace's arguments on floral colour and insect diversity, that if the paucity of brightly coloured flowers in the New Zealand flora was linked to insect diversity, then floral scent should reflect the same trend. In other words, if flower colour is an adaptation for attracting pollinators, then the New Zealand flora should also be lacking a strong component of highly scented flowers. To back up this reasoning Thomson quoted Dr Joseph Hooker, an authority on the New Zealand flora: "New Zealand plants are remarkably scentless, both in regard to the rarity of scented flowers, of leaves with immersed glands containing essential oils, and of glandular hairs." There are a number of exceptions to this rule. This is of particular interest in groups that are known to attract pollinators through scent in other parts of the world. For example, several members of the genus *Pterostylis* have demonstrated an ability to imitate the scent of fungus, acting as an attractant for fungus gnats which then pollinate the orchids via pseudocopulation. However, this has not been demonstrated in any of the New Zealand species of the same genus (Lehnebach et al., 2005). Thomson (1881) observed 232 species of plants in Dunedin, New Zealand and identified 64 as being scented, but also noted that often scent was a feature observable only under certain climatic conditions. Flowers that were small and inconspicuous were more often scented, and most likely to be visited by Diptera (Thomson, 1881). Further study may yet identify examples of the New Zealand flora where scent is an important character for pollinator mutualisms.

Floral scent is just beginning to be researched in detail, though no current studies offer information on the volatile chemistry or scent profile of tāwari. Osmophore analysis identified that tāwari has scent producing tissues, but the usefulness of these tissues in producing pollinator-attracting odours is unknown.

2.5.1.8.4 Flower structure

Tāwari has perfect (with both male and female parts) and complete (with distinguishable petals and sepals) flowers, and represents the simple characteristics of New Zealand's flowering plants in flower morphology with radial symmetry, free and exposed anthers and stigma, white colour, and its open dish structure. New Zealand flowering plants are characterised by having a low level of bilateral symmetry. Bilateral symmetry is a structural mechanism whereby flowers can manipulate the behaviour of the pollinator and potentially improve pollinator effectiveness and efficiency. In radially symmetric flowers the pollinator can enter from any direction, but in bilaterally symmetric flowers pollinators are generally forced in a particular direction which will favour the pollinator contact with flower reproductive parts (Kampny, 1995). Nectar guides work in a similar way (Waser, 1983). In most cases radial symmetry appears to be the basal condition (c.f. Scrophulariaceae) (Kampny, 1995) in plant families, while bilateral symmetry is associated with specialisation and diversification (Cubas, 2004).

Blossom classes were outlined in Faegri and Van der Pijl (1979) and used by both Lloyd (1985) and Newstrom and Robertson (2005) with relation to the New Zealand flora. New Zealand flowers fall most commonly into the class of dish flowers or tube flowers, and lack the more complex and specialised bell, gullet, and flag blossom structure (Lloyd, 1985, Newstrom and Robertson, 2005).

The radial symmetry and open dish structure of tāwari flowers is consistent with a generalised insect pollinating visitor fauna. The free and exposed anthers and stigma of tāwari flowers also demonstrate a non-exclusive pollination strategy and leave the nectar reward openly available for a generalised pollinator fauna.

2.5.1.8.5 Floral rewards

Floral rewards are important characteristics in determining floral visitor fauna. Floral rewards come in a number of forms including pollen, nectar, and other exudates. Nectar is a common floral reward that is discussed in depth in section 2.5.2. Other exudates include for example stigmatic exudates that attract pollinators and reward them for pollination. *Pseudowintera colorata* is a New Zealand example of a flowering plant which produces stigmatic exudates in this manner (Lloyd and Wells, 1992). Pollen is not a reward as such because it is

intended for delivery and pollination rather than to be consumed by the vector. When pollen becomes the main benefit for a flower visitation by a visitor it crosses the line from pollination to pollen theft (see section 2.5.1).

Floral rewards are not necessarily involved in pollination mutualisms. Anemophilous (wind pollinated) and hydrophilous (water pollinated) flowers operate without the use of animal pollination vectors and do not require floral rewards. Other flowering plants that are dependent on animal pollination vectors use deceptive tactics to ensure pollination, rather than offering a reward. Classic examples are the sexually deceptive orchids including *Arthrochilus*, *Caladenia*e, *Caleana*, *Calochilus*, *Chiloglottis*, *Drakaea*, *Leporella*, *Paracaleana*, *Pterostylis*, and *Spiculaea* that mimic the females of their pollinator species to elicit pollination by pseudocopulation (Gaskett, 2011). Other forms of deception can involve the mimicry of a flowering species that does offer pollinator rewards, such as in *Disa nervosa* (Johnson and Morita, 2006).

The New Zealand flora has been characterised as having flowering plants with a low level of specialisation which is well represented with tāwari. With its open structure and copious nectar as a reward, tāwari attracts a generalist pollinator assemblage rather than rewarding one group or another.

2.5.1.8.6 Pollination syndromes

Pollination syndromes are groups of floral traits (such as flower colour and structure) that are assessed to give information about what type of pollinators might be expected to pollinate certain plants, in the absence of observational data. Numerous studies have shown the selective pressure of pollinator groups on different flower traits including among other things corolla tube length (Alexandersson and Johnson, 2002), and flower colour (Jones and Reithel, 2001, Irwin and Strauss, 2005, Bradshaw and Schemske, 2003, Melendez-Ackerman and Campbell, 1998, Campbell et al., 1997).

The applicability of pollination syndromes is less than previously thought, particularly with regard to flora of the southern hemisphere (Kingston and McQuillan, 2000). Newstrom and Robertson (2005) suggest that classification based on blossom class first and then with the finer points of syndromes would be a more helpful way to organise the diversity of plant-pollinator relationships in

New Zealand and provide a way to make meaningful predictions about these relationships (Table 2.4).

Table 2.4: Blossom class-Functional group matrix from Newstrom and Robertson (2005) which shows plant-pollinator assocations based on flower structure including acces to rewards, landing faciilities, and protection of the ovary. Symbols are based on the effective pollination potential: ○ ineffective pollination potential; ● good pollination potential; ☼ association atypical on a global scale, though observed in New Zealand; blank: little to no visitation or pollination expected.

	Open access to center and rewards (depends on limitations by size)						Direct access to centre or other rewards				Closed or partially closed, access restricted				
Functional groups of visitors and pollinators	Brush inflorescence	Aggregation of dish/ bowls	Aggregation of tubes in capitula	Brush/ fluffy cup flowers	Dish/bowl/"knob" flowers	Inconspicuous flowers < 3 mm	Bell/funnel flowers	Gullet/ tube flowers	Trumpet/ salverform flowers	Spurred flowers	Trap flowers (orchid)	Complex flowers (e.g., flag)	Poricidal anthers, pollen only	Expolsive closed buds (mistletoe)	Syconium (figs)
Insects															
Fig wasps															●
Chewing mouthparts (thrips, weevils, beetles)	○	●	●	●	●	●	○	○	○		○				
Short sucking mouthparts (flies, bees)	○	●	●	●	●	●	○	○			●	●		☼	
Long tongues (flies, bees, moths,	●	○	●	○	○	○	●	●	●	●		●	●	○	
Hovering with long tongue (hawkmoths)	●						●	●	●	●					
Birds															
Hovering hummingbirds	●			●			●	●							
Perching birds	●	☼		●			●	●						☼	
Bats															
Bats	●	●		●			●								
Non-flying vertebrates															
Lizards	●	●													
Mammals (e.g., possums, rodents)	●	●		●	●										

Tāwari fits the description of flowers with open access to the flower centre and rewards, in particular the aggregation of dish/bowl shaped flowers. The classification from Table 2.4 thus indicates that the expected associations would be from insects with chewing mouthparts (including thrips, weevils, and beetles), short sucking mouth parts (including flies and bees) and long tongues (including flies, bees and moths) though the latter group are identified as less effective. Bats and non-flying vertebrates such as rodents and lizards were also identified as potentially suitable pollinators. Perching birds occur in New Zealand in

association with the open aggregate dish flower type, but this is uncommon elsewhere in the world.

2.5.2 Nectar analysis

Floral nectar is a pollinator reward exuded from nectaries and containing as its main constituents sugar and water. Nectar also contains a host of other components including amino acids, lipids, antioxidants, and other potentially toxic substances including non-protein amino acids, alkaloids, phenolics, and glycosides. With the identification of these components in nectar, additional roles of nectar besides providing caloric requirements are being identified. The amino acid component is found in all nectars and has been linked to the protein requirements of flower visitors. This is reflected by the changes in amino acid content relative to the diet of the flower visitors – for example flowers pollinated by bees and bats have a lower amino acid content as their pollinators supplement their protein intake with pollen. The non-sugar components of nectar are also associated with defining the taste of the nectar which can be an important factor for building flower visitor constancy. Non-sugar components have also been associated with defence and deterrence of nectar robbers (Baker, 1977).

The honey industry in New Zealand is based on a combination of contributions from introduced pasture crops such as white clover (*Trifolium repens*) and indigenous trees including *Metrosideros, Weinmannia, Leptospermum,* and *Ixerba.* Most nectar studies relevant to the New Zealand flora have been conducted only for the purpose of honey research, or in cases of bee poisoning, with little attention to the role of nectar chemical components in plant-pollinator mutualisms (Godley, 1979). This section will discuss the nectar properties of tāwari flowers with relation to flower structure and nectar presentation, and nectar volume, sugar concentration, and pH.

2.5.2.1 Flower structure and nectar presentation

Flower structure and nectar presentation are two structural factors that affect the attraction of flower visitors. Three general categories of nectary location were identified by Fahn (1979): at surface level; forming an outgrowth; and sunken. Within these categories are other specific forms of nectar presentation, including presentation outside the nectary (secondary presentation), in a spur, or at the end of a nectary duct (Pacini and Nepi, 2007). Tāwari flowers have sunken nectaries

that are visible as slight depressions in each of the five lobes of the disc at the base of the style. Nectar is presented on the nectary surface and forms large droplets. The structure of tāwari flowers is open, and nectar is not hidden. This structural adaptation makes tāwari available for promiscuous pollination from a range of insect visitors (Percival, 1979).

2.5.2.2 Volume

Nectar standing crop can be affected by environmental factors, changes in nectar production and reabsorption throughout the day, and animal foraging activity. Bergquist (1987) classified flowers producing <10 µl as low volume producers and >10 µl as high volume producers. With an average volume of 18 µL nectar standing crop tāwari is a high volume nectar producer. The fate of the nectar produced can follow a number of pathways including: a) consumption by a pollinator; b) consumption by a nectar thief; c) dripping from the flower; or d) no removal where nectar remains in the nectary and may be reabsorbed (Pacini and Nepi, 2007). High volume producers reduce the risk of all nectar being taken by nectar thieves (in a similar fashion to the masting habit of some trees); but high volume nectar production can also attract nectar robbers and increase loss from gravity-induced dripping. Nectar volume and nectar concentration work together to influence flower visitor fauna assemblage. Nectar concentration is discussed in section 2.5.2.3 of this chapter.

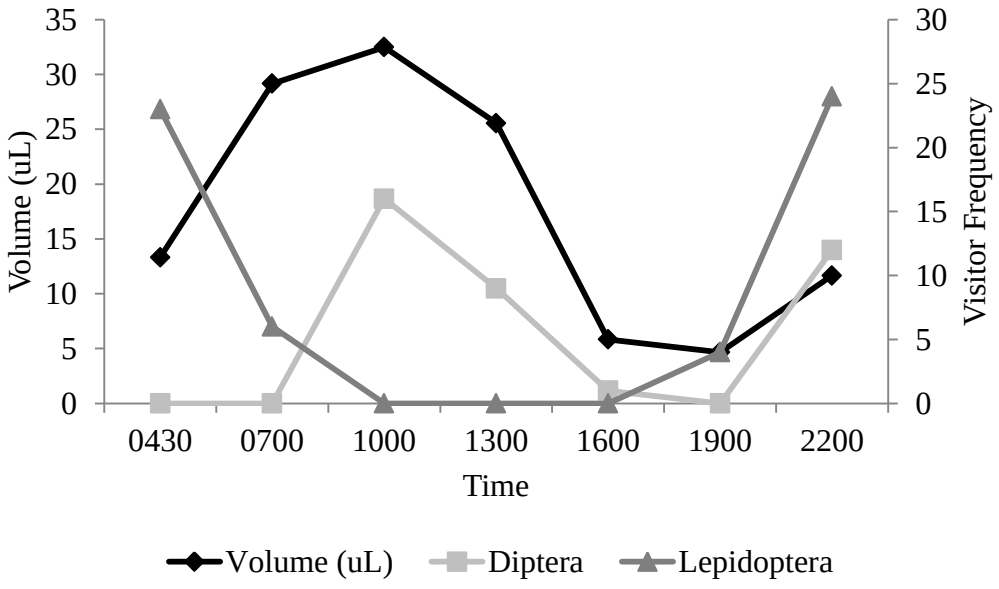

Figure 2.12: Activity periods of main floral visitors against the average volume of tāwari nectar produced throughout the day

The extent of regulation on floral nectar production varies between species. Tāwari exhibits a degree of control in the production of floral nectar which is seen in the diurnal pattern of secretion. Nectar standing crop peaked during mid-late morning, troughed late afternoon, and began to increase again toward dusk. These peaks in nectar production reflect the activity patterns of some of the key visitors of tāwari flowers – Diptera and Lepidoptera (Figure 2.12).

The measurements on covered and uncovered flowers indicated that the removal of nectar has no effect on the nectar secretion pattern of tāwari flowers. Flowers with nectar removal had lower standing crops than flowers which were covered, but overall followed the same diel trend. Nectar quantity in flowers is a function of secretion and removal by insect forage or reabsorption. Hence, when protected from forage by bagging, nectar standing crop is a function of secretion and reabsorption. Burquez and Corbet (1991) suggest that if nectar quantity decreases throughout the day in the absence of insect forage then reabsorption must be occurring. This is a trend which is also seen in tāwari flowers. In bagged flowers there is a marked decline in the volume of nectar collected at some times of the day even in the absence of insect visitors.

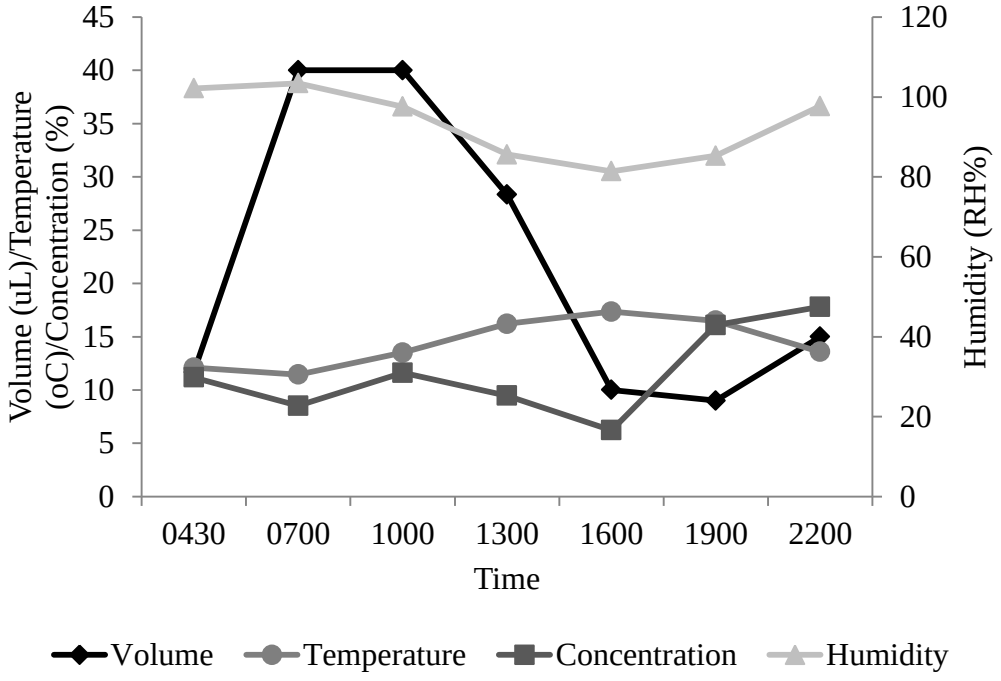

Figure 2.13: Diel pattern of nectar volume collected from bagged tāwari flowers plotted with nectar concentration, daily average temperature (°C) and daily average humidity (% relative humidity) recorded during the flowering period of tāwari.

Nectar reabsorption has been suggested as a mechanism for the recovery of plant resources and the maintenance of a constant concentration and volume of nectar presented (Burquez and Corbet, 1991, Corbet, 2003, Pacini and Nepi, 2007). However, it is difficult to separate the environmental effects of changes in nectar volume from the potential reabsorption mechanism. The present research showed that changes in tāwari nectar standing crop are concurrent with changes in temperature and humidity. During afternoon hours these environmental factors contribute to a decline in presented nectar volume by increasing the evaporative rate of nectar water which is mirrored by an increase in nectar concentration.

Bergquist (1987) presented a study of the foraging patterns of the tūī and demonstrated a lack of selectivity in flower visitation. There was no obvious preference for flowers of a particular colour, and the nectar concentration varied from 7-47% w/w. Tūī generally visited flowers that produced nectar in volumes above 10 µl. Bergquist identified that tāwari nectar was a resource extensively used by tūī.

2.5.2.3 Concentration

Nectar concentration is connected to nectar volume and in turn, to environmental fluctuations in relative humidity and temperature. This relationship is touched on in section 2.5.2.2 where peaks and troughs in tāwari nectar volume are mirrored by alternate troughs and peaks in tāwari nectar sugar concentration (Figure 2.13). Rain is another environmental variable that has a marked effect on nectar properties (Nicolson and Thornburg, 2007). As nectar measurements in the current research were undertaken over a notably cold and wet summer (Griffiths and Tait, 2012) this may have affected the dilution of tāwari nectar.

Tāwari nectar is a relatively dilute solution and a number of adaptive advantages have been suggested for this condition. Bolten and Feinsinger (1978) suggest that producing dilute nectar may deter nectar-robbers that cannot satisfy energy requirements on low caloric nectar, leaving it instead for other pollinators. Dilute nectar has also been suggested as a means of increasing cross pollination by fostering fewer between-flower movements, and more between-plant movements by pollination vectors. This has been demonstrated to be successful even in extreme cases where no floral nectar is produced (Jersakova and Johnson, 2006). Details of pollinator movements and pollen dispersal distances have not been

investigated for tāwari. However, artificial pollination treatments undertaken in the present research demonstrated that the average viable seed set from self-pollinated flowers was comparable to the seed set from cross-pollinated flowers. Therefore, the selective advantage of increasing out-crossing would only be valid if the fitness of individuals resulting from self-pollination was lower (i.e. inbreeding depression). This is an interesting area for future research.

Table 2.5: Types of pollinators predicted based on nectar concentration. From Percival (1979)

Visitor Type	Preferred Nectar Sugar (%)
Moth	8-18
Bat	14-16
Bird	13-40
Butterfly	21-48
Honeybee + bumble bees	10-74
Short tongued flies	(Higher)
Long tongued flies	(Higher still)

Percival (1979) summarised the types of pollinators which show preference for nectar of different sugar concentrations (Table 2.5). Under this classification, the average concentration of tāwari nectar of 11% (range 3% to 20%) is very low, but includes in its scope moths, bats, birds, and bees. In addition to sugar concentration, the constituents of nectar can indicate potential flower visitors. The pilot study (Section 2.4.4.2, pg. 22) on the sugar constituents of tāwari showed that nectar is dominated by hexose sugars. Nectars of this nature are generally sought by passerine birds, microchiropteran bats (such as the New Zealand *Mystacina tuberculata*), and short-tongued bees or flies (Baker and Baker, 1983). This is consistent with the range of pollinators associated with the sugar concentration of tāwari nectar.

2.5.2.4 pH

The pH of nectar is an understudied component of nectar chemistry which is not well understood. The known pH range of floral nectars is between 3 (as in *Silene alba*) and 10 (as in *Viburnum costaricanum*). However, *Lathraea clandestina* nectar has since been identified outside of this range (pH 11.5) for part of the flowers lifecycle (Nicolson and Thornburg, 2007). This anomalous flower bursts

at ground level and initially produces weakly acidic nectar (pH 6.5). As the flowers age, the nectar becomes alkaline (pH 11.5). This increase in pH is attributed to high levels of dissolved ammonia produced by the break-down of amino acids. This unusual nectar characteristic is thought to be related to the deterrence of certain flower visitors, particularly ants (Prŷs-Jones and Willmer, 1992). Tāwari nectar with its often neutral pH is unlikely to play a similar role in flower visitor deterrence.

2.5.3 Breeding system

2.5.3.1 Pollen limitation index

Part of the reproductive cycle of seed plants requires that an adequate quantity and quality of pollen is deposited on the receptive female structures in order for fertilisation, seed development, and ultimately plant reproduction to take place. Pollen limitation results when an inadequate quantity or quality of pollen is deposited in this process. These explanations derive from the theory of sexual selection and the concept that resource availability should limit female reproductive success rather than access to mates (Bateman, 1948). Therefore, if access to mates is increased (in this case, if increased quantities of pollen were delivered to receptive female floral structures) no increase in seed set would be observed because no additional resources are available to foster additional ovules. Assessments of pollen limitation use this principle by assuming that hand-pollination delivers excess pollen than required. So by comparing seed set of flowers pollinated by hand and flowers that are naturally pollinated it is possible to discern whether resources are limiting the development of additional fertilised ovules (i.e. no additional seed set from hand pollinated flowers) or whether access to pollen is the limiting factor (i.e. additional set from hand pollinated flowers).

Assessments of pollen limitation have been used as a measure to gauge the effectiveness of pollination and the flow on effects of that on seed set and population dynamics. Two factors that can affect the limitation of pollen are inadequate quantity of pollen deposited (usually by the means of fewer or less effective pollinator visits) and inadequate quality pollen deposited (either by incompatibility of pollen source or by pollen manipulation by the pollination vector). These factors are driven by environmental variables such as the presence of other flowering plant species either as competitors for pollination or as additive

inciters for pollination; plant population size and density; pollinator loss; resource availability; habitat size and isolation; plant pathogens and herbivores; plant mutualists (e.g. mycorrhizal fungi); pollinator predators; non-native plant species which may lack effective pollinators or have a higher frequency of autogamy; and non-native pollinators which may compete with native pollinators and yet be less effective (Knight et al., 2005).

Interpretation of the breeding system indices derived for tāwari (Section 2.4.3.2) was based on the parameters set out in Newstrom and Robertson (2005). PLI values were classified as low pollen limitation if PLI <0.2, medium pollen limitation if 0.2<PLI<0.75, and high pollen limitation if PLI>0.75. The PLI value for Tāwari was calculated as 0.36 and is classified as having medium pollen limitation. Between 62 -73% of flowering plants are significantly pollen limited (Burd, 1994, Ashman et al., 2004, Knight et al., 2005). However Aizen and Harder (2007) suggest that this figure overestimates the current situation because of a failure of current methods of pollen limitation analysis to delineate pollen quantity and pollen quality issues. Factors affecting pollen quantity received by receptive female floral parts were treated in Knight et al. (2005). Aizen and Harder (2007) review the factors affecting pollen quality and the circumstances where pollen quality affects pollen limitation. Often, due to either autonomous mechanisms or vector mediation flowers receive selfed pollen or pollen from closely related plants rather than crossed pollen. This can be an issue for many plants and can reduce seed production by competitive exclusion of crossed pollen or death of embryos after fertilisation (Aizen and Harder, 2007). The development of embryos into seed may also be subject to parental selection based on mates (Obeso, 2004). Also, plants with generalised pollination systems and pollinators with low constancy can have the issue of heterospecific pollen interference. In a longer-term scope, inbreeding depression can also be manifested as a result of self-pollination or pollination from closely related plants. In addition to these problems outbreeding depression may arise when the pollen source is located from too distant a population producing offspring that are unsuited to the present environs. These effects are identified as a potential confounder of the current concept of pollen limitation because under hand supplementation, higher quantities of pollen are supplied which is often of a higher quality than plants would receive through natural processes. As a result the current measures of

pollen limitation may overestimate the maximal seed production, providing an unhelpful comparison with natural seed set and overestimating the current state of pollen limitation in the global flora.

While PLI gives a basic understanding of whether the pollination process is functioning adequately for tāwari, it does not offer a complete picture of the successfulness of pollination or long-term effects in terms of plant demography and population persistence, and ecosystem functioning. Ecological consequences of pollen limitation can occur when pollen limitation affects seed production, creating a shift in species dominance in affected ecosystems. Evolutionary changes associated with pollen limitation occur at particularly the severe limitation end of the scale where populations can evolve mechanisms to minimise or avoid pollen limitation (such as autonomous reproductive strategies), or severe pollen limitation can lead to local extinction (Ashman et al., 2004). PLI also does not separate out the contributions of pollen quantity and pollen quality to the overall pollen limitation (Aizen and Harder, 2007). These are pertinent considerations for tāwari because of the characteristics of its breeding system that have been demonstrated in the current research. In particular, though tāwari is self-compatible there is a difference between the viable seed set of cross-pollinated flowers and self-pollinated flowers (especially when pollen from the same flower is used).

Fernandez et al. (2012) analysed the pollen limitation of an endangered species and demonstrated a degree of variability in the PLI across different populations due to factors such as changes in the composition or ratios of the pollinator assemblage, climatic variation, and soil cover. Accordingly, the classification of tāwari as medium pollen limited may vary at different sites, and particularly at sites with variable conservation value. The study site where the PLI was determined for tāwari is a highly modified forest environment of small size and minimal pest management. Because of the higher altitudinal range of tāwari most of the sites where it is found are protected forest areas and are more intact and less disturbed systems than the one found at the study site. As a consequence, the PLI demonstrated at the study site may represent a base level of pollen limitation, and a lower level of limitation might be expected at more protected sites throughout its range (another interesting point for future research). Garcia-Camacho and Totland (2009) also looked at the variation of pollen limitation with altitude and

with breeding strategy to investigate claims of pollen limitation in alpine areas based on the dependence of alpine plants on pollinating insects and the climate of alpine environments as a pollinator deterrent. Contrary to previous suggestions, they found no difference between alpine and lowland plants, and no difference between self-fertilising and self-incompatible species.

In some pollination systems the presence of a key pollinating species is more important than a wide variety or abundance in the pollinator assemblage for avoiding pollen limitation. A study on *Erysimum popovii* showed variable pollen limitation between study sites. The key character of less pollen limited sites was the higher proportion of bee flies (Bombyliidae; only one species is represented in New Zealand) in the flower visitor assemblage. These bee flies are effective pollinators which have a high rate of inter-plant movement (Fernandez et al., 2012).

2.5.3.2 Self-compatibility index and autonomous selfing index

The interpretation of the self-compatibility and autonomous selfing indices was based on the parameters set out by Newstrom & Robertson (2005). Self-compatible species demonstrate an SCI >0.8; partially compatible species have a 0.2<SCI<0.8; and self-incompatible species demonstrate an SCI<0.2. With an SCI value of 0.93 tāwari is classed as a self-compatible species. Plants with an ASI value of greater than 0.5 were classified as '*autonomously selfing'*. An ASI value of 0.65 shows that tāwari is autonomously selfing, which is not common for New Zealand trees and shrubs.

SCI and ASI appear synonymous, but there is an important distinction. SCI denotes self-compatibility, whereas ASI denotes the ability of a plant species to facilitate pollination without the aid of a pollinator. Hence, plants with a high SCI are self-compatible, but not necessarily capable of autonomous selfing due to characters such as herkogamy (where male and female parts are separated in time e.g. by staggered maturation of anthers and stigma) or dichogamy (where male and female parts are separated in space). Though self-compatibility is known from the limited number of New Zealand trees that have been surveyed, few demonstrate autonomous selfing (Newstrom and Robertson, 2005).

2.5.3.3 Pollinator dependance

The breeding system indices determined above contribute to an understanding of the dependence relationship of tāwari to pollination vectors. This dependence-relationship is demonstrated in Figure 2.14 in model form. Each assessed character (right) represents a potential barrier to low pollinator dependence. Sexual dimorphism and monoecy represent reproductive strategies that separate male and female organs in space, either by separation of the sexes on separate plants (dioecy), or on separate flowers on the same plant (monoecy). In each of these cases pollination vectors are required to bridge the spatial gap between the male and female parts to allow fertilisation to take place. The next three characters represent a different kind of barrier. Self-incompatibility is a character which means that out-crossing is required. This creates pollinator dependence unless pollination by anemophily (wind) or hydrophily (water) is possible. Autonomous selfing is a feature of plants that are able to achieve pollination without the assistance of a pollination vector.

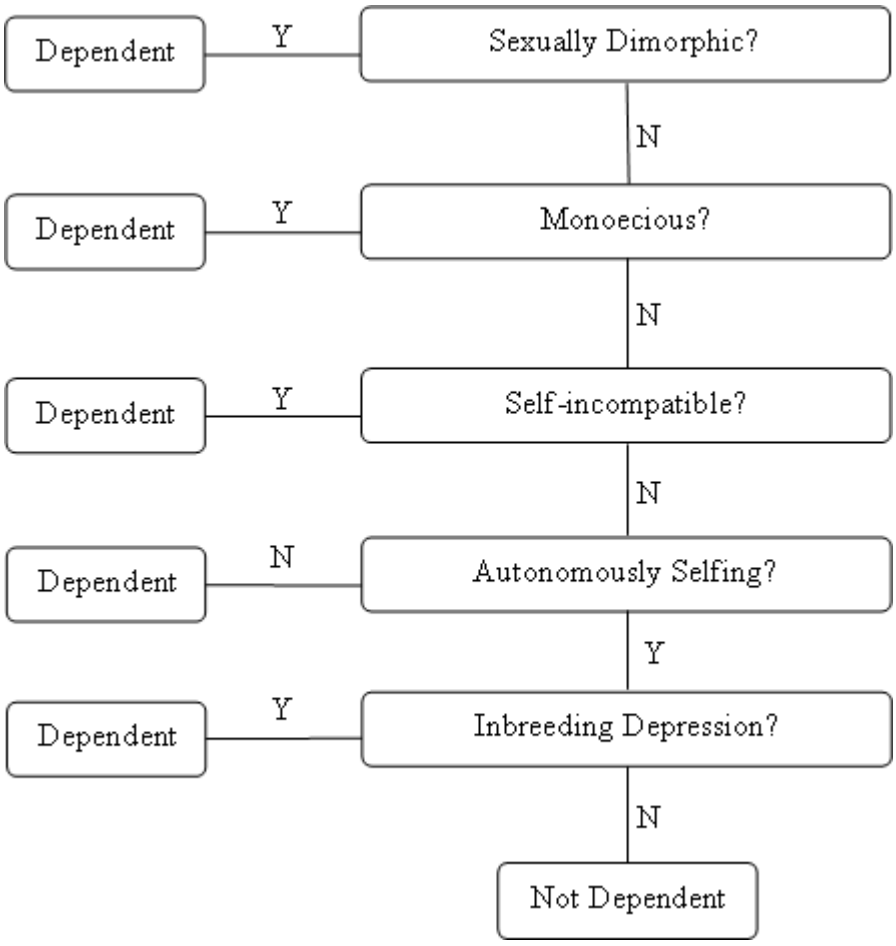

Figure 2.14: Model of plant-pollinator dependence. N=No, Y=Yes. Adapted from Newstrom & Robertson (2005)

Using this model for tāwari (Figure 2.14) we follow the route of no sexual dimorphism, hermaphrodite flower condition, self-compatibility, and autonomous selfing. However, the last phase in the model, inbreeding depression, has not been investigated. So while pollinator dependence appears to be low, the effect of pollination stress on the successful reproduction of tāwari is an incomplete picture. Schmidt-Adam et al. (2000) investigated the out-crossing rates of pōhutukawa (*Metrosideros excelsum*) and found a high rate of geitonogamous selfing. Investigation into the potential effects of inbreeding depression, however, found that because of selection pressure against the individuals resulting from inbreeding, the high levels of selfing did not contribute to an inbreeding depression, and did not affect the fitness or longevity of the populations in the long-term. There is no data on the rates of selfing or the long-term effects (such as inbreeding depression) in tāwari populations; however the healthy regeneration of tāwari gives no indication of detrimental long-term effects.

In addition, Newstrom and Robertson (2005) correctly identified that the divisions between the categories given in the model (Figure 2.14) in most circumstances are not clear cut, but occur in varying degrees and confer varying degrees of pollinator dependence. *Fuchsia excorticata* is an example of a native tree with a breeding system which is not typically monoecious. *F. excorticata* demonstrates a gynodioecious system where flowers and individual trees are either female or hermaphrodite. In this case the female trees will be completely pollinator dependent, whereas hermaphrodite trees may not be completely dependent. The same trend of incomplete dependence follows through the other categories of the model where species may demonstrate only weak abilities for self-compatibility and autonomous selfing, and low levels of inbreeding depression. Tāwari showed no difference in viable seed set from flowers that received no pollen, and flowers that were naturally pollinated. However, seed set from hand pollinated flowers was significantly higher than both natural pollination, and no pollination. This demonstrates that while tāwari may not be pollinator-dependent, seed set is not being maximised with either no pollinator assistance, or with pollinator assistance – an instance of partial pollinator-dependence.

2.5.3.4 Breeding system and climate change

Global climate change is a phenomenon with the potential for marked effects on ecosystem mutualisms such as pollination. Hegland et al. (2009) reviewed the effects of climate change on pollination, identifying in particular the potential problem of timing and distributional discrepancies in the activity periods of plants and their pollinators. Because the reproductive system of tāwari, which allows for self-pollination, has low dependence on pollinators, and is adapted to attract a range of visitors from different functional groups, the pollination system of tāwari is one that has the robustness to withstand the potential perturbations of global climate change.

2.6 Summary

In summary, the results from this study are in agreement with the classification given by Kelly et al. (2010) that tāwari is entomophilous and occasionally visited by birds. More in-depth study of the breeding system of tāwari demonstrated an uncommon system among the woody trees of the New Zealand flora – a condition of self-compatibility and autonomous selfing. The characteristics the breeding strategy of tāwari suggest robustness against global climate change and likely long term survival.

Chapter Three: Seed ecology of *Ixerba brexioides*

3.1 Introduction

Seed plants make up a large proportion of the New Zealand flora. In all, the New Zealand seed plant flora has 1896 species (1566 endemic and 330 non-endemic), (Wilton and Breitwieser, 2000). Of the woody species of the New Zealand flora 48% are fleshy fruited, and 70% of New Zealand trees are fleshy fruited (Burrows, 1994). Tāwari fruits are coriaceous and capsular with a long persistent style. As the seeds within the capsule grow, the capsule swells, the twisted styles begin to unravel, and the capsule splits down five seams located in the centre of each locule, exposing the mature seeds inside (Figure 3.1). Following on from Chapter Two on pollination, this chapter explores the next step in the reproductive cycle of tāwari – seed dispersal and germination.

Figure 3.1: Tāwari fruits and seeds: A) swelling capsules; B) an open tāwari capsule showing two locules – the top containing two viable seeds, and the bottom containing two empty seeds; C) twisted styles on a tāwari capsule (bottom) and a dehiscent tāwari capsule showing the separation of the twisted styles, exposing the seeds (top). Photos A) & B) courtesy of Catherine Bryan.

3.2 Aims and Objectives

This chapter addresses the current deficiency in data on the later stages of the reproductive cycle of tāwari including phenology and the dispersal, and germination of tāwari seeds. This was undertaken by a period of observation of the reproductive structures of tāwari in a tract of forest at Tūī Ridge Park, video surveillance of seed capsules, and experiments observing seed germination in different conditions.

In particular this chapter aims to:

a) Present a timeline for the reproductive cycle of tāwari including the magnitude of survival of these structures through various stages of development
b) Identify potential seed dispersers for tāwari and fruit and seed adaptations associated with this mutualism
c) Comment on successful conditions for tāwari seed germination

3.3 Materials and Methods

3.3.1 Phenology

Phenology is the study of events in plant life such as flowering, and seed production and requires quantitative recording of reproductive characters such as buds, flowers, nectar, fruits, and seeds (Stiles, 1975, Sakai et al., 2005). Tāwari trees were closely monitored between November 2011 and July 2012. The developmental stage of the flowers and capsules was regularly recorded in order to produce a timeline of the major events in the reproductive cycle of tāwari. The following stages of development were recorded:

- Bud: floret closed
- Flower: petals fully extended and all reproductive parts visible. Other details of flower condition included the state of the anthers (immature, pollen producing, or past maturity), anther and petal dehiscence, browning of the stigma, sepal yellowing, and cessation of nectar production.
- Small capsule: all anthers and petals dehisced, no swelling
- Swelling capsule: one or more locules swelling beyond the original dimensions of a small capsule
- Split capsule: capsule split revealing seeds

Measurements were done every two to three days during the flowering period of tāwari and then every seven days after flowering because of the slower progression in capsule condition compared to flower condition. All measurements were compiled to show weekly totals of reproductive structures in each of the categories given above. These totals were plotted against environmental averages for temperature and humidity measured using data-loggers for the duration of the study to assess the relationship between flower development and environmental cues.

3.3.2 Video surveillance

Two surveillance cameras were secured to the trunk of a tawa tree at Tūī Ridge Park. A description of this site is given in Section 2.3.1. Cameras were facing in opposite directions to get footage of two tāwari trees. The cameras were protected by camouflaged housing. This housing was connected to an automated external LED light source producing infra-red light. At the base of the tree the cameras were connected to a video recording device in a water-tight pelican case and a 12 volt battery. This system allowed easy access to the recording device and battery while the camera remained secure in the canopy.

These cameras collected footage of tāwari capsules between 31st December 2011 and 30 May 2012. A total of 50 hours of footage was collected across various stages of the capsule development and at a range of times throughout the day. All collected footage was then watched at high speed and any fruit-visitor interactions were recorded including duration of the visit and fruit parts visited.

3.3.3 Germination trials

Germination trials were set up in May 2012 (Table 3.1, Figure 3.2).

Table 3.1: Seed germination experiment treatments and conditions

Treatment	Conditions
Standard	Pericarps removed, seeds washed, set in petri dishes on filter paper in wet, well-lit conditions
Shade	As in standard, except light excluded from petri dishes
Soil	As in standard, except seeds were sown on the surface moist soil in petri dishes
In-fruit	As in standard, except pericarps left around seeds
Buried	Pericarps removed, seeds washed, and set 5 cm deep in a pot filled with soil collected from Tūī Ridge Park. Soil kept moist and left in well-lit conditions.

The five treatments were set up with four replicates of twenty seeds each. Seeds were collected from Tūī Ridge Park between the 8th and 11th of May 2012. Each treatment was maintained with regular watering. Treatments were regularly examined and the number of seeds which had germinated was recorded. Germinated seeds were removed, replanted in separate containers, and maintained with regular watering.

Germination data did not fit a normal distribution; hence non-parametric methods were used for data analysis. A Kruskal-Wallis ANOVA and a Median Test were the methods used to assess the significance of differences in germination success between the different germination treatments.

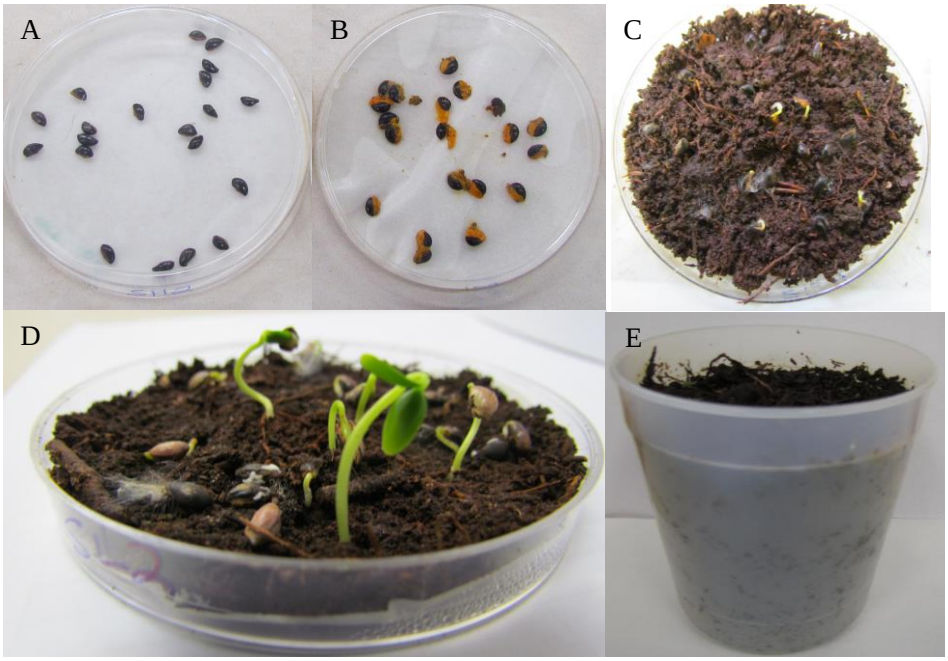

Figure 3.2: Germination treatments: A) standard/shade; B) in fruit; C) soil surface; D) germinating seeds; E) buried

3.4 Results

3.4.1 Phenology

Development of tāwari flowers as observed between December 2011 and July 2012 shows a sequence of distinct stages (Figure 3.3). Observations started with 460 buds. After a period of 5 weeks the number of flowers open peaked at 395 flowers. Flowers had an average lifespan of two weeks, and after that the petals and anthers fell off leaving developing seed capsules with a long persistent stigma. The number of these small capsules peaked at 268. Small capsules took

approximately 5 weeks to become swelling capsules and then a further average of 18 weeks to dehisce. In each mature capsule 10 seeds were produced (two per locule) and between 1 and 9 of these were fully formed and viable. Two other kinds of seeds were produced: medium sized seeds with the same appearance of the viable seeds (i.e. purple-black on the outside with an orange fleshy aril partially covering the seed) but which were empty inside, and very small seeds that were light yellow in colour with little or no fleshy aril that (if present) was light yellow or orange in colour. The two non-viable seed types made up between 10 and 90 per cent of the seeds present in each capsule.

The relative humidity recorded at the study site remained consistently high throughout the duration of the study (Table 3.2). Temperature declined from December 2011 to July 2012 with an average of 14.15°C in the summer months (December-February), 9.52°C in autumn months (March-May), and 6.19°C in winter months (June-July) and 13.08°C in spring months (temperature and humidity measurements only available for November 2011).

Table 3.2: Seasonal averages in temperature and relative humidity at Tūī Ridge Park, Mamaku plateau, averaged from hourly recordings at four sites

Season	RH%	Temperature (°C)
Summer	94.62	14.15
Autumn	98.10	9.52
Winter	102.17	6.19
Spring	85.50	13.08

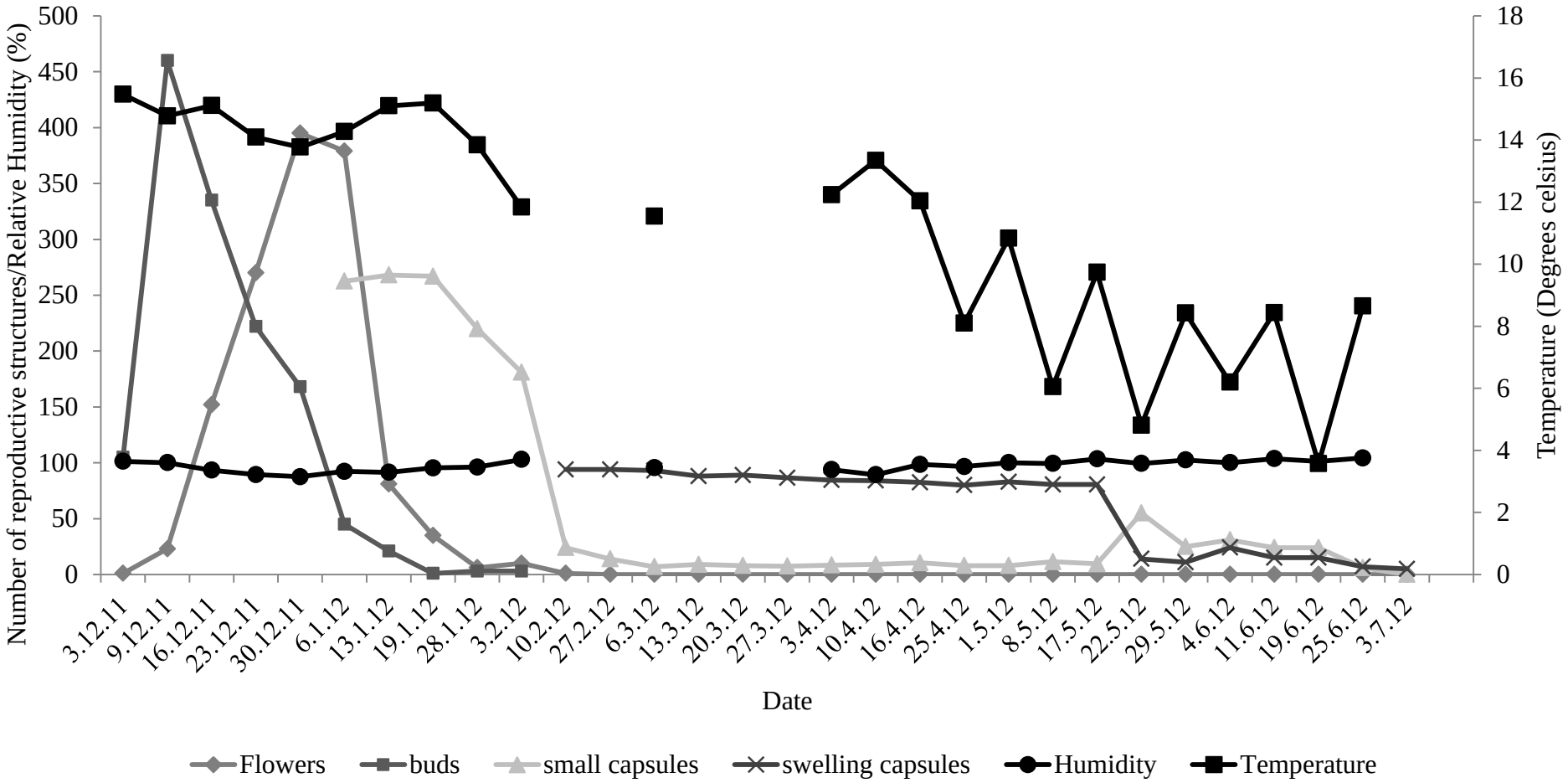

Figure 3.3: Timeline of events in the reproductive cycle of tawari at Tui Ridge Park in the Mamaku Range between December 2011 and July 2012

3.4.2 Video surveillance

Video surveillance techniques attempted to identify the dispersal vector for tāwari seeds at Tūī Ridge Park in the Mamaku region of the North Island. A total of 50 hours of footage of capsules at various stages of development was viewed and no interactions were observed. Because of technical difficulties and the way that the recorders were set up to begin recording at midnight each day the most sampled time frame was between midnight and 0300 hours (45% of total footage duration), with 0900 to 1200 hours the second most sampled (23% of total footage duration).

3.4.3 Germination

Tāwari seeds began to germinate one month after seed collection. Average per cent germination of tāwari seeds varied under different treatment conditions (Figure 3.4). The buried seeds had the highest germination rate at an average of 75% success followed by seeds on the soil surface (50%), under standard conditions (34%), shade (15%) and finally seeds left in fruit (8%). Germination treatments showed a statistically significant difference in successful germination with a *p* value of 0.0089. Multiple group-wise comparisons demonstrated that buried seeds had significantly higher germination than the seeds left in fruit.

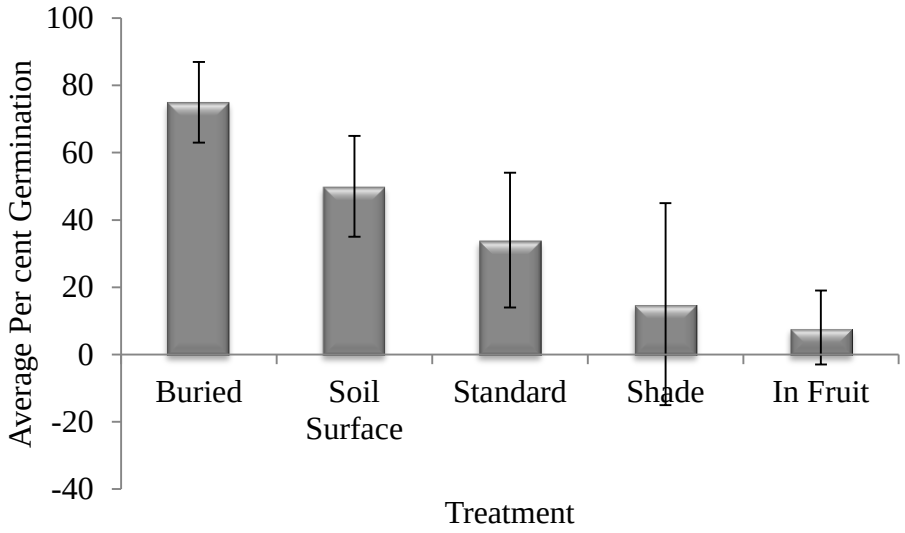

Figure 3.4: Average per cent germination of tāwari seeds under different treatments

The seeds that were left embedded in fruit had the lowest germination rate of all treatments. The fruit that was left on the seeds encouraged mould growth which may have had an inhibitory effect on seed germination. Seeds in the shade also had low rates of germination on average but this was linked to desiccation of the

seeds that was apparent in three out of the four replicates. One shade treatment replicate that was unaffected by desiccation had a good overall rate of germination (60%). Desiccation and mould also occurred in the standard treatment.

Seeds that underwent desiccation turned from dark purple-black to a pale purple-grey colour. Rehydration of the desiccated seeds returned the normal dark colour but the embryo inside, instead of the usual fleshy green, became clear and jelly-like (Figure 3.5B). Desiccated and rehydrated tāwari seeds were assessed for viability using the TZ test and no staining was observed (Figure 3.5C).

Figure 3.5: Tāwari seeds: A) tāwari seeds from one capsule with 8 viable seeds and 2 non-viable (far right); B) comparison of desiccate/rehydrated seed and a normal viable seed; C) desiccated/rehydrated seeds after TZ staining test; D) a dehiscent tāwari capsule; E) tāwari seed embryos following TZ staining test.

3.5 Discussion and Conclusions

Tāwari – "a New Zealander of New Zealanders" (Cockayne, 1923) - exemplifies the unusual features of the New Zealand seed flora in its fleshy fruits and absence of dormancy mechanisms. Burrows (1994) describes the comparative abundance of fleshy fruits trees in the New Zealand seed flora (with 70% of tree species fleshy fruited) with the seed flora of the Northern Hemisphere where fleshy fruits often accompany the marginal, or small understory species rather than forest dominants. Tāwari contributes to this statistic as a dominant canopy or sub canopy species of the New Zealand flora with fleshy seed accessory tissues. Dormancy mechanisms are also an area of difference. Northern woody species generally demonstrate delayed germination after a period of winter chilling, whereas many New Zealand woody species demonstrate germination during autumn or winter months without any period of delay. Burrows (1994) also compared the development of long-term (years) seed banks by northern tree species with the short lived (weeks or months) seed banks of New Zealand forests. This characteristic has not been investigated for tāwari.

The following paragraphs discuss other aspects of the seed biology of tāwari that were investigated in the present research including: production of empty seeds, mass flowering strategy and masting, potential seed dispersal agents, and germination behaviour of tāwari seeds.

3.5.1 Empty seeds

The production of empty seeds seems wasteful on the part of the plant, and is generally a result of either limited pollen access, or limited resources for seed development (Bateman, 1948). However, the production of empty seeds has been advantageous for *Juniperus osteosperma* (Utah juniper). Plants of this species with high proportions of empty seeds were not as heavily attacked by birds as were the plants with high proportions of filled seeds – demonstrating predator-selection based on whole plant seed production (Fuentes and Schupp, 1998). Another documented benefit from the production of empty seeds is reducing viable seed damage by insect larvae browse (Coetzee and Giliomee, 1987) and wasp oviposition (Traveset, 1993) because of indiscriminate seed selection by browsers and wasps, and because of avoidance of infertile seeds which often leads to abandoning plants with high proportions of empty seeds (Ziv and Bronstein,

1996). Tāwari was found to be a medium pollen limited species (PLI = 0.31) (Thomson, 2013: Chapter 2), so pollen limitation may be a factor in the production of empty seeds by tāwari trees. The advantageous effects of empty seed production have not been investigated for tāwari.

3.5.2 Mass flowering and masting

Phenological results showed the numbers of reproductive units (buds, flowers, and capsules) that reach the various life stages in the reproductive cycle of tāwari. To reiterate - 85% of buds made it to flowers, 70% remained as capsules, 30% of these swelled to mature capsules. Each capsule can produce 10 seeds of which an average of 38% are viable. Though 40% seed viability is normal for the New Zealand flora, when the whole reproductive cycle is considered, a very small proportion of reproductive units have the potential to produce new tāwari progeny.

Masting is intermittent variation in seed production that can be synchronised between individuals and genera, even across large distances (Schauber et al., 2002). It is a strategy that has been suggested as a protection from seed predation by swamping predator populations with seed one year (and thus satiating predator populations to allow the survival of some seed), and not producing enough seed to maintain a viable predator population another year. Masting has been reported as an apparently common feature of the New Zealand forest (Webb and Kelly, 1993, Burns, 2012), potentially because of the long life-spans of the flora that are required to make masting effective, or because of an underestimated effect of masting elsewhere in the world (Schauber et al., 2002). Altitude is strongly correlated with masting, and many of the associates of tāwari have demonstrated a masting pattern in seed production including *Nothofagus solandri, N. menziesii, N. fusca, Dacrydium cupressinum, Prumnopitys ferruginea, Podocarpus totara,* and *Elaeocarpus dentatus* (Webb and Kelly, 1993). Variability in tāwari flowering density has been observed previously (Mead, 1963), as well as in the present study. However, in all cases the observation is anecdotal, and the extent of the variability cannot be quantified. A comparison of one particular tree was carried out at Tūī Ridge Park in the present study that is shown in Figure 3.6. Photographs were taken of the same tree, at the same time in 2011 and 2012 (20th – 21st December). The difference in the floral load was obvious to the naked eye,

and a count of the visible flower bunches showed 96 in 2011 but only 8 in 2012. The same pattern was observed for tāwari trees in the surrounding area, extending beyond Tūī Ridge Park and into the wider Mamaku Plateau. Further research that quantifies the variability in seed production between reproductive seasons and the effective cues is recommended.

Mckone et al. (2004) present a case study on the effects of climate change on mass-flowering and masting species of New Zealand grass in the genus *Chionochloa*. They suggested that increased annual temperatures could reduce the inter-annual variation in seed production, allowing populations of insect seed-predators to increase, and the overall level of predation to increase. There are currently no studies which investigate the palatability of tāwari seeds for common seed predators such as mice and rats or the effect that such predation would have on the reproductive success of tāwari. This is another area that would be beneficial to investigate.

Figure 3.6: A comparison of a tāwari tree inflorescence load between 2011 and 2012 at Tūī Ridge Park, Mamaku, New Zealand.

3.5.3 Seed dispersal

The lack of interactions observed in the video footage of tāwari fruits may be attributable to a few crucial difficulties in the execution of the project. Firstly, the on-going failure of the video recording equipment meant that after months of video surveillance only 50 hours of footage was available for analysis. Secondly,

almost half of the duration of this footage occurred at midnight when many common New Zealand fruit dispersers are inactive e.g. tūī, kererū.

There is currently no available information on the chemistry or composition of tāwari fruit or seeds. Therefore, in the absence of observational data, fruit and seed morphology may offer some clues about the potential seed dispersal vectors for tāwari. A summary of fruit characteristics preferred by types of fruit dispersers (von Bethlenfalvy, 2006) can be used to predict dispersal vectors (Table 3.3). Tāwari trees produce capsular fruits which dehisce at maturity to reveal up to ten black seeds which are partially covered in an orange-red flesh. From the morphological characteristics of tāwari fruits, the most probable candidate for a seed dispersal vector is birds. This is a trait that is characteristic of the New Zealand flora because of the paucity of native frugivorous mammals that are present in New Zealand ecosystems.

Table 3.3: Fruit trait preferences of frugivorous animals. From von Bethlenfalvy (2006)

Disperser	Fruit/Seed Characteristics
Mammals	Duller colours; yellow; green; strongly aromatic; poor lipid content
Arboreal frugivorous mammals	Brown; green; white; orange; yellow; aromatic; often arillate seeds or drupes; aril or pulp rich in protein, sugar, or starch
Terrestrial frugivorous mammals	Often green or brown; tough; in-dehiscent; often >50 mm long; pulp rich in lipid
Bats (flying foxes)	Green; white; pale-yellow; strong smelling; aromatic or musty; sourish; rancid; often pendant; exposed; soft; juicy; sugary; weakly protected; arillate seeds; multi-seeded; small; pulp rich in lipid or starch
Rodents	Yellow; green; relatively larger and heavier drupes; few seeds
Birds	**Black**; purple; blue**; red**; scentless**; <2cm in diameter**; no or thin husk; permanent attachment; **attractive edible part signalling ripeness**

Dijkgraaf (2002) identified tāwari fruits in a list of foods utilised by the kererū. A study by McEwen (1978) also demonstrated this mutualism with a study on the diet of the kererū. Two birds were found with digestive tracts containing tāwari seeds. One bird had a total of 174 seeds in its digestive tract. Oliver (1955) described the diet of the whitehead, though mostly insectivorous, as also containing the fruit of some trees including tāwari. Similar observations were made for kākā by McLean (1911b) and Oliver (1955). However, Oliver (1955)

also notes that kākā may destroy the seeds during ingestion by cracking them with their beaks. Best (1942) described historical records of kākā eating tāwari fruits in large quantities: "He kākā tāwari ki Hikurangi, he moki ki te moana (a kākā feeding on the tāwari berries of Hikurangi is as fat as the moki fish of the ocean". Hihi have been seen taking the fruit of tāwari (Perrott and Armstrong, 2000). Greene (1989) included tāwari flowers and fruit in a list of high quality foods for kākāpō but did not give any observations of this taking place. Bergquist (1987) identified tūī as nectar feeders on tāwari, but saw no indication of fruit ingestion by tūī. Thomson and Challies (1988) observed tāwari foliage as a significant food source for feral pigs (particularly during the winter), but no significant use of tāwari seeds was noted.

Table 3.4: Bird species observed ingesting tāwari fruit

Species	Reference
Kererū *Hemiphaga novaeseelandiae*	Dijkgraaf (2002) McEwen (1978)
Whitehead *Mohoua albicilla*	Oliver (1955) McLean (1907)
Kākā *Nestor meridionalis*	Oliver (1955) Best (1942) McLean (1911b) McLean (1907)
Hihi *Notiomystis cincta*	Perrott and Armstrong, (2000)
Kākāriki *Cyanoramphus auriceps*	McLean (1911a) McLean (1907)
Kākāpō *Strigops habroptilus*	Greene (1989)

While a number of New Zealand birds have been shown to utilise tāwari seeds as a food source (Table 3.4), there is currently no data to show the survival and viability of seed post-digestion.

Reptiles were not included in the summary table 3.3. However, a thesis by Marshall (2009) investigated the sensory cues used by frugivorous New Zealand lizards of the genus *Oligosoma* in fruit selection and demonstrated a preference for white and pale coloured fruits over red. While the applicability of this finding

is very limited because of the diversity of New Zealand's reptile fauna and the range of niches they occupy, this general trend in fruit colour preference is visible in other studies. Figure 3.7 shows a comparison of fruit colours in the New Zealand flora with those fruit colours known to be consumed by lizards. This shows again the dominance of white blue and transparent over red and orange fruits. Tree habit is another factor influencing the preference of frugivorous lizards. In particular, low-lying shrubs with a divaricating habit have been described as having successful mutualisms with frugivorous lizards in fruit dispersal (Lord et al., 2002). In light of this research, lizard dispersal of tāwari seeds is unlikely.

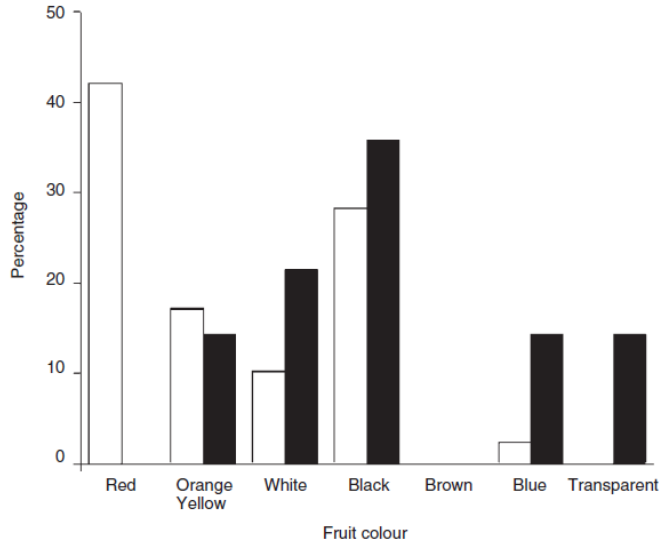

Figure 3.7: The proportion of fruit colours in the New Zealand flora (open bars) compared with the proportion of those colours eaten by lizards (solid bars). From Valido and Olesen et al.

New Zealand is also home to over seventy species of wēta which have been shown to be seed dispersers of a number of New Zealand species including *Fuchsia excorticata, F. procumbens, Gaultheria antipoda, Pratia angulata,* and *P. physaloides* (Duthie et al., 2006). Experiments on the fruit selection showed that wēta preferentially select fruits of blue hues over red hues (Fadzly and Burns, 2010). This has been attributed to the inability of insects to see light in the red spectrum (Fadzly and Burns, 2010, Field, 2001, Willson and Whelan, 1990, Burns, 2006). Based on fruit colour, dispersal of tāwari fruit by wēta is also unlikely.

3.5.4 Germination

Tāwari seeds in the present study demonstrated rapid germination and did not exhibit a requirement for winter chilling, instead, germinating in autumn/winter. This finding is consistent with the research of Burrows (1994) who remarked on the contrast between Northern Hemisphere seeds requiring a period of dormancy and chilling before germination, and elements of the New Zealand flora that do not require this. In New Zealand there are 59 species with documented germination behaviours which range in days to first germination from 2 days (*Alectryon excelsus* and *Corynocarpus laevigatus*) to 303 days (*Rhopalostylis sapida*) (see Table 3.5). The propensity for some species in New Zealand to germinate soon after ripening is linked to the moist conditions during autumn and winter and the greater need to avoid drought conditions rather than freezing conditions for seedling establishment.

Rates of successful germination in many New Zealand woody species have been elucidated, particularly in the work of Burrows (1995b, 1996a, 1999, 1996b, 1996c, 1996d, 1995c, 1996e, 1996f, 1995a, 1995d). Most of the species included in these studies exhibited high rates of germination (91% average) under standard conditions, with slightly lower rates occurring in soil (70% average), and in fruit (31% average). Tāwari had comparably low rates of germination under standard conditions, but average rates in the soil treatments.

Table 3.5: Germination behaviour of New Zealand woody species compiled from Burrows (1995d, 1996a, 1999, 1996b, 1996f, 1996c, 1995a, 1996h, 1996i, 1995b, 1995f) and the present thesis. DFG = days to first germination; Other values represent the percentage germination success under different conditions: St=Standard germination conditions (see methods section 3.3.3); D=dark; IF=in fruit; S=soil.

Species	DFG	St	D	IF	S	Reference
Dodonaea viscosa	62	98	24	60	76	Burrows, 1995
Hedycarya arborea	33	100	92	2	98	Burrows, 1995
Pennantia corymbosa	122	100	96	36	82	Burrows, 1995
Pseudowintera colorata	139	98	98		82	Burrows, 1995
Rhopalostylis sapida	303	95		2	28	Burrows, 1995
Streblus heterophyllus	14	100	90		94	Burrows, 1995
Ixerba Brexioides	28	35	15	8	50	Thomson, 2013
Carpodetus serratus	68	90	6	8	70	Burrows, 1996
Coprosma lucida	99	100	94			Burrows, 1996
Pittosporum eugenioides	31	80	90	20	65	Burrows, 1996

Table 3.5: Continued

Species	DFG	St	D	IF	S	Reference
Pittosporum tenuifolium	83	94	100			Burrows, 1996
Plagianthus regius	54	96	88			Burrows, 1996
Pseudopanax arboreus	46	100	72		84	Burrows, 1996
Pseudopanax crassifolius	27	88	72			Burrows, 1996
Alseuosmia macrophylla	115	99			44	Burrows, 1996
Alseuosmia pusilla	113	98			84	Burrows, 1999
Cordyline banksii	26	100	100	12	96	Burrows, 1999
Geniostoma rupestre	57	99	90		2	Burrows, 1999
Lophomyrtus bullata	56	97	96		96	Burrows, 1999
Solanum aviculare	18	82	82		46	Burrows, 1999
Beilschmiedia tawa	40	100	100	0	100	Burrows, 1999
Dysoxylum spectabile	12	100		0	86	Burrows, 1999
Griselinia lucida	8	100	96	0	94	Burrows, 1999
Weinmannia racemosa	15	84.8	16		22	Burrows, 1999
Alectryon excelsus	2	48		8	56	Burrows, 1996
Corynocarpus laevigatus	2	94	75		98	Burrows, 1996
Kunzea ericoides	24	100	86		76	Burrows, 1996
Coprosma foetidissima	105	98	4	4	94	Burrows, 1996
Freycinetia banksii	101	92			12	Burrows, 1996
Hoheria angustifolia	80	93	88	93	84	Burrows, 1996
Myrsine australis	112	100	42	16	54	Burrows, 1996
Ascarina lucida	41	91	98	48	74	Burrows, 1996
Coprosma grandifolia	23	100	30	4	100	Burrows, 1996
Melicytus lanceolatus	68	100	8	20	80	Burrows, 1996
Solanum laciniatum	62	98	68	12	56	Burrows, 1996
Melicope simplex	242	77	56			Burrows, 1996
Myoporum laetum	155	90	18		94	Burrows, 1996
Myrsine divaricata	77	92	94	24	40	Burrows, 1996
Urtica ferox	35	59			32	Burrows, 1996
Coriaria arborea	6	100	98	93	93	Burrows, 1995
Coriaria sarmentosa	9	97	44	48	43	Burrows, 1995
Coriaria angustissima	25	94	57	60	78	Burrows, 1995
Coriaria sp. cf. *plumosa*	16	100	46	88	48	Burrows, 1995
Fuchsia excorticata	12	100	86	54	52	Burrows, 1995
Griselinia littoralis	9	92	96	2	72	Burrows, 1995
Macropiper excelsum	20	100	100	14.5	84	Burrows, 1995
Melicytus ramiflorus	11	99	96	24	84	Burrows, 1995
Aristotelia serrata	17	96	86	10	84	Burrows, 1995
Coprosma robusta	17	90	60	72	92	Burrows, 1995
Cordyline australis	26	96	96		88	Burrows, 1995
Lophomyrtus obcordata	34	100	94	12	92	Burrows, 1995

Table 3.5: Continued

Species	DFG	St	D	IF	S	Reference
Schefflera digitata	41	98	36	60	44	Burrows, 1995
Calystegia tuguriorum	8	18				Burrows, 1996
Clematis foetida	149	89			26	Burrows, 1996
Muehlenbeckia australis	35	97	72	88	68	Burrows, 1996
Parsonsia heterophylla	134	73	40	76	72	Burrows, 1996
Ripogonum scandens	18	98	82		88	Burrows, 1996
Rubus cissoides	57	82	40	38	58	Burrows, 1996
Passiflora tetrandra	30	98	92		80	Burrows, 1996

Seed properties and successional status are two plant characters which are inextricably linked. *Weinmannia* and *Griselinia* are examples of early colonisers that exhibit rapid germination and significantly lower rates of germination under buried conditions (Rowarth et al., 2007). In contrast, tāwari seeds germinated most successfully when buried – a trait connected with species occurring later in the successional sequence.

Seeds in some floras demonstrated a pattern between seed size and shape and a propensity for burial and longevity with small round/rounded seeds more commonly buried where they are less targeted by seed predators and hence more long-lived (Bekker et al., 1998, Thompson et al., 1993, Thompson and Grime, 1979). However, the same trend does not hold in the New Zealand flora where large and elongate seeds, such as tāwari seeds, are common (Moles et al., 2000). The occurrence of burial and longevity of tāwari seeds in a seed bank has not been investigated. Tāwari seeds are sensitive to desiccation, but because tāwari forest is distributed in moist areas of montane cloud forest, soil moisture ought to remain high enough to prevent desiccation occurring with burial, and in many cases burial may be a mechanism preventing desiccation.

Burrows (1995b, 1996a, 1999, 1996b, 1996c, 1996d, 1995c, 1996e, 1996f, 1995a, 1995d) made a considerable contribution to seed biology research in New Zealand with his investigations on the germination requirements of the seeds of New Zealand woody species. Many of the species he observed had lower rates of seed germination when the seeds were left in fruit than when under standard conditions e.g. *Hedycarya arborea* (98% lower), *Rhopalostylis sapida* (93% lower), *Carpodetus serratus* (82% lower), and *Pittosporum eugenioides* (60% lower). A similar trend was seen in the germination of tāwari seeds. Inhibition of

germination by fruit persistence is a character which has been described for some species (Yagihashi et al., 1998, Yagihashi et al., 2000, Paulsen and Högstedt, 2002). Some have suggested reasons for this inhibitory effect are the presence of an inhibitor or high osmotic pressure of flesh (Rowarth et al., 2007). The requirement of pericarp removal for seed germination has been linked to a dependence on seed dispersal by ingestion, gut passage, and defecation. Studies that go further than investigating only the effect of retention of fruit on the seed (i.e. as a result of the seed not being ingested), but also the changes that occur to the seed during the passage through the gut have demonstrated benefits to both germination and seedling establishment from this method of dispersal. *Sorbus aucuparia* seeds that were ingested and defecated by birds were 9% heavier than control seeds, emerged quicker, and grew faster than non-defecated seeds (Paulsen and Högstedt, 2002). Seed characteristics that make dispersal by ingestion and defecation necessary can also increase the chances of dispersal to longer distances from the parent tree which helps with colonisation of new sites, avoiding density-dependent seedling mortality, and directed dispersal to suitable sites (Wenny, 2001).

3.5.5 Summary

The results presented in this chapter provide some key insights into the reproductive strategy of tāwari and again highlight some unique features of the New Zealand flora. The overall seed-crop of the flowers studied in this project demonstrates an obvious reason for the mass flowering strategy of tāwari in ensuring an adequate seed crop to promote the continuity of tāwari populations. Birds are the most probable vectors for tāwari seed dispersal based on current observations and fruit morphology. The germination requirements of tāwari seeds demonstrates a species which, like many other species in the New Zealand flora, does not require a period of winter chilling, and its preference for burial conditions is indicative of a later successional element of the flora. Combined, these characteristics paint a picture that supports the arguments of Burrows (1994) that the New Zealand flora differs from Northern Temperate forest in several key areas of seed biology: fleshy fruits, dormancy mechanisms, and the formation of long-term seed banks.

Chapter Four: Composition of *Ixerba brexioides* forest

4.1 Introduction

New Zealand's history of forest monitoring and analysis of forest composition began with the inauguration of the National Forest Inventory in 1923 by the New Zealand Forest Service, and then the National Forest Survey in 1945-1955 (Masters et al., 1957). But initially, New Zealand's forests captured attention purely for the timber industry products that were plentiful there. McGlone (1989) estimated that before human settlement in New Zealand forest covered 85-90% of the land surface. Since that time large-scale decline of this vegetation cover has occurred as a result of processes such as fire, logging, and clearing and drainage of land for conversion to pasture. In the mid-1900s the ecological aspect of forest monitoring was introduced which included the study of trees not considered as first class forestry products. With data from these surveys came classifications of the New Zealand forest ecosystems (McKelvey and Nicholls, 1957, McKelvey and Nicholls, 1959, Nicholls, 1976).

Information about vegetation patterns is important for understanding the history of change, current ecosystem functioning, and projected impacts of introduced weeds and browsers, climatic change, and continued disturbance. Analysis of forest composition is an area of research that Allen et al. (2003) identified as a crucial part of biodiversity monitoring to inform policy-makers on both a national and a worldwide stage. Walker et al. (2006) demonstrated that despite significant historical rates of deforestation in New Zealand, forest cover continued to decline in 49% of environments in the late 1990s and early 2000s and this loss was most concentrated where vegetation was already highly impacted. This condition, coupled with poor levels of land protection, creates a general need for current studies on the composition, structure, and functioning of New Zealand forest ecosystems.

Because the earliest classifications of New Zealand forests focused on the timber industry potential they did not pay much attention to tāwari forest (McKelvey and Nicholls, 1957, McKelvey and Nicholls, 1959, Nicholls, 1976, Wiser and Hurst, 2008, Wiser et al., 2011, Campbell-Walker, 1877, Cockayne, 1908). More recent classifications overlooked tāwari forest because of its restricted range (Wiser and

Hurst, 2008, Wiser et al., 2011). In this chapter tāwari forest is the focus in a series of analyses to define the composition of tāwari forest throughout its range in the North Island of New Zealand.

4.2 Aims and Objectives

This chapter aims to improve understanding of the composition, structure, distribution, and dynamics of tāwari forest in the North Island of New Zealand. This is done by the analysis of an extensive data set sourced from the National Vegetation Survey database administered by Landcare Research.

In particular, this chapter aims to:

a) Provide analysis on the composition of tāwari forest in the North Island of New Zealand
b) Classify tāwari forest types occurring throughout its range and the environmental variables that are correlated with these vegetation types
c) Discuss the distribution of tāwari with regard to current environmental constraints, historical patterns, and future considerations.

4.3 Methodology and Analysis

4.3.1 NVS database

Data from the Nation Vegetation Survey database was used to assess the composition of tāwari forest throughout its range in the North Island, New Zealand. This database is a collection of approximately 94,000 vegetation survey plots assessed across New Zealand in a range of ecosystems and beginning over 50 years ago. Originally, this data was conducted by the New Zealand Forest Service, Department of Lands & Survey, and the DSIR Botany Division, but in more recent times the vegetation survey data is made available by sources such as the Department of Conservation, Landcare Research, universities, regional councils, and by private parties. A database search identified all of the plots within the NVS database that contain tāwari. Permission was obtained to use the data from all of these plots, and this data then became the base of the forest composition assessment of tāwari. Vegetation plots came from the following projects:

- Coromandel/Moehau Forest 1999

- Kaimai Exclosures Forest 2002
- Kaimai Exclosures Forest-1981 1980
- Kaimai Forest 1974
- Kaimai Forest-1985 1984
- Kaimai/Wharawhara Forest 1974
- Kaimai/Wharawhara Forest-1985 1984
- Kaimanawa/Windfall Forest-1984 1983
- Maungatautari 2004
- Moehau 2010
- Motu Forest-1984 1983
- Pirongia 2008
- Pirongia Exclosures Forest 1999
- Pukeamaru Forest-1985 1964
- Puketi (Kokako) Forest-1984 1983
- Raukumara Forest 1984
- Raukumara Forest-1983 1982
- Rotoehu Forest-1980 1979
- Rotorua Lakes Forest-1984 1983
- Tairua Forest-1989 1988
- Te 88
- Te Hoe Forest 2002
- Urewera Exclosures Forest 1997
- Urewera Exclosures Forest-1981 1980
- Urewera, South Forest-1981 1980
- Urewera, South Forest-1982 1981
- Urewera/Waikare Forest-1981 1980
- Waitakere Forest 1989
- Waipoua Exclosures Forest 1986
- Waipoua Forest-1985 1984

Details of specific plots used from this data set can be found in Appendix 1.

Only recce (reconnaissance) inventory data from the NVS database was used in this analysis (Hurst and Allen, 2007). Recces can be bounded or unbounded and

include a range of measures including recce identification information, site descriptions and stand parameters, and vegetation descriptions. The identification information gives a reference that would make the site re-locatable in the future. The site description and stand parameters describe the physical characteristics of the location including aspect, slope, altitude, ground cover and parent material, and other information such as disturbance and treatments occurring at the site. Vegetation descriptions include information about the structure and composition of the vegetation within the bounds (actual or variable) of the recce. The components of the vegetation are described using fixed height tiers and modified Braun Blanquet cover classes (shown in Table 4.1) (Mueller-Dombois and Ellenberg, 1974, Hurst and Allen, 2007).

Table 4.1: Standard tiers (m) and cover classes (per cent canopy cover) used in recce inventories. Adapted from Hurst and Allen (2007)

Tier	Standard tiers	Cover-class	Per cent (%) Canopy Cover
1	>25	1	<1
2	12-25	2	1-5
3	5-12	3	6-25
4	2-5	4	26-50
5	0.3-2	5	51-75
6	<0.3	6	76-100
7	epiphytes (any height)		

4.3.2 NMS ordination

The aim of the analysis of the data obtained from NVS was to delineate types of tāwari forest by undertaking analysis of community associations using multivariate techniques. Only plots that contained tāwari were used. Of these plots, many had been re-measured on multiple occasions. In these cases, only the most recent plot data was used. Recce survey data was used to create a matrix of species occurring in tāwari forest plots throughout the range of tāwari with calculated abundance values based on the number of tiers the species were represented in and the average abundance of the species in the plot. Recce inventory data was used so that species indicative of tāwari forest types that would not be measured in stem diameter surveys could be included in the analyses. Species that occurred in fewer than 5% of plots were not included in the analysis. In total, the recce inventory data set included 641 plots and 159 species.

NMS (Non-metric Multidimensional Scaling) was used to analyse compositional patterns of the plots using PC-Ord ver. 6 software. It is a method which is recommended as effective for ordination of ecological community data (McCune et al., 2002). NMS is a technique used to present complex relationships by mapping plots based on differences in composition. The advantage of NMS over other ordination techniques (such as Principal Component Analysis) lies in the ability of NMS to maximise rank-order correlations rather than linear correlations, detect patterns in community structure that are unrelated to environmental variables, and cope with zero rich data sets (McCune et al., 2002).

In this analysis the NMS ordination was run on the slow and thorough autopilot setting which has as a default a maximum of 6 axis, and 500 iterations. Sorensen (Bray-Curtis) was selected as the distance measure. The slow and thorough method completes 250 runs with the real data and then conducts a randomisation test. The randomisation test completes 250 runs with randomised data to calculate the probability of a similar stress level being produced with random data. The solution that was presented indicated that 3-dimensions would best display the patterns observed in the ecological data. The 3-dimensional solution had an average stress value of 13.817 for the real data and the randomisation test produced an average stress value of 30.212 ($p = 0.004$). The final 3-dimensional solution had a stress value of 13.77222 with a final instability of 0.0000 over 110 iterations. The Monte Carlo test demonstrates that this stress level could not have been reached using randomised data.

The interpretation of the ordination was done using a joint-plot function to overlay environmental variable vectors to assess the contribution of these variables to the compositional patterns of the vegetation. This contribution is indicated by the direction and length of the vector. The variables used in this analysis included plot latitude, longitude, altitude, species richness, aspect, slope, drainage, disturbance, vegetation cover, bare soil cover, bare rock cover, litter cover, moss cover, canopy cover, and top height but variables were only displayed on the ordination when the correlation was significant. Coefficients of determination for the ordination axis and r-values for the correlation of species and variables with the axis were calculated.

The significance of the relationship between the environmental variables and ordination scores produced in the NMS analysis was tested using a Mantel test. The first matrix contained the ordination scores for the three NMS axis, and the second matrix contained an environmental variable. Each variable was tested individually. Variables included latitude, longitude, altitude, slope, top height, aspect, percentage bare soil cover, percentage vegetation cover, percentage rock cover, drainage score, and disturbance score. Drainage scores were given as 1 for poor drainage, 2 for medium drainage, and 3 for good drainage. Disturbance scores were given as 0 for no disturbance, 1 for low level disturbance (e.g. grazing and tracks), and 2 for higher level disturbance (e.g. fire, logging, mining). Mantel's asymptotic approximation method was used to evaluate the test statistic. The distance measure used was Euclidean.

4.3.3 Classification of forest types

Cluster analysis was used in conjunction with NMS ordination to identify discrete groupings for tāwari forest types based on the similarity of the composition of the plots used in the analysis. To make these analyses comparable they were done using the same software (PC-Ord ver. 6) and using the same distance measure (Sorensen (Bray Curtis)). The significance of the difference between these groups was tested using a PerMANOVA test (Anderson, 2001) and pairwise comparison. Because this test requires equal group sizes 56 plots (the smallest group size) were randomly selected from each group for this analysis. Sorensen (Bray-Curtis) was the distance measure used.

Indicator Species Analysis (ISA) (Dufrêne and Legendre, 1997) is a method used to assess the degree to which certain species may indicate environmental conditions. This was analysed using the same recce data set as the cluster analysis and ordination. Tāwari was excluded from the analysis because it occurred in every plot. An indicator value (IV) is calculated as measure of the faithfulness and exclusivity of a species to a particular group between zero (no indication value) and 100 (perfect indication value). In this analysis IVs were calculated using the Tichý and Chytrý (2006) method in PC-Ord ver. 6 software (McCune and Mefford, 1999). A Monte Carlo test was done with 4999 randomisations to test probability of the same values occurring by chance and hence demonstrate the significance of the values.

4.4 Results

4.4.1 Flora

The plot data used in this study showed a total of 395 species of which 20 were adventive. These adventive species, however, in total were present in less than 5% of plots and in all cases occupied less than 1% of the cover in the tier in which they were found. The most common life form were native trees and shrubs (153 species), though there was a great diversity of ferns and fern allies (103 species). Recce data also included 49 species of monocots, 21 species of lianes and climbers, and 48 herb species. Although the total number of species observed was high, only 159 species occurred in greater than 5% of plots.

The epiphytic tier had 191 species represented and of these 68 could be classified as true epiphytes. Forty per cent of species in the epiphytic tier were trees and shrubs, but of these only 8 species are classed as true epiphytes while the others may be accidental or ephemeral epiphytes. Ferns and fern allies were the next most common with 67 species in total and 40 species which could be classed as truly epiphytic. Orchids, lianes and climbers, and nest epiphytes were also common. The average number of species in the epiphytic tier for each plot followed a decreasing north to south trend with plots in the Northland group averaging 26 epiphyte species per plot to the Urewera group averaging 3 species per plot (Table 4.2). Forest groups are explained in section 4.4.2.

Table 4.2: Average and standard deviation of epiphyte species per plot for each vegetation group identified in the cluster analysis and ordination for tāwari forest in the North Island of New Zealand.

Group	Species	St.Dev.
1	26.07	10.20
2	23.98	7.20
3	4.22	6.41
4	2.73	3.02

Of the native species observed in the recce plots 2 were data deficient, 7 were naturally uncommon, 1 was nationally vulnerable, 1 was in decline, and 1 was nationally critical (Table 4.3). Trees and shrubs had the most threatened species followed by herbs. The majority of threatened species were found in the Northland group (75%). The Coromandel group had no threatened species.

Table 4.3: Status of threatened species occurring in areas of tāwari forest across its range in the North Island of New Zealand with the number of plots they were recorded in and the vegetation group they were most commonly found in.

Status	Species	Plots	Group
Data Deficient	*Lachnagrostis tenuis*	7	1
	Nematoceras rivulare	54	1
Naturally Uncommon	*Halocarpus kirkii*	18	1
	Libocedrus plumosa	13	1
	Lindsaea viridis	2	3
	Petalochilus alatus	1	1
	Pittosporum ellipticum	2	3
	Pittosporum virgatum	9	1
	Schizaea dichotoma	8	1
Nationally Vulnerable	*Libertia peregrinans*	14	4
Declining	*Pittosporum kirkii*	11	1
Nationally Critical	*Senecio scaberulus*	1	1

4.4.2 Forest Classification and Ordination

4.4.2.1 Cluster analysis

The cluster dendrogram that was produced in PC-Ord was pruned to the 4 group level. The number of groups was selected based on a comparison between the cluster analysis output and the ordination output to discern how many distinct groups were present. A PerMANOVA test demonstrated a *p* value of 0.0002 showing a strong difference between the 4 forest groups. Pairwise comparison showed that the significance of this result stemmed from equally significant differences between each of the groups in the analysis (shown in Table 4.4).

Table 4.4: Pairwise comparison of forest classification groupings.

Groups	t	*p*
1 vs. 2	4.23	0.0002
1 vs. 3	6.90	0.0002
1 vs. 4	6.07	0.0002
2 vs. 3	6.93	0.0002
2 vs. 4	7.24	0.0002
3 vs. 4	6.51	0.0002

4.4.2.2 Indicator species analysis (ISA)

Of 158 species included in the ISA 149 had significant IVs and 120 of these had an IV over 25%. These are the species classified as characteristic of the vegetation groups, following Dufrêne and Legendre (1997), and are included in the results Table 4.5. The Northland group had the most characteristic indicator species with

67 species (56% of all characteristic species). Groups 2, 3, and 4 had 36, 5, and 12 characteristic species respectively.

Table 4.5: Indicator values (IV) are between 0 (no indication) and 100 (perfect indication). Maxgroup is the vegetation group for which each species has the highest indicator value. IVs that are significant ($p>0.05$) and above 25% are considered characteristic of their vegetation group and are included in the table.

Species	MaxGroup	IV (%)	*p*
Beilschmiedia tarairi	1	92.7	0.0002
Ackama rosifolia	1	81.2	0.0002
Melicytus macrophyllus	1	76.6	0.0002
Hymenophyllum dilatatum	1	74.7	0.0002
Weinmannia silvicola	1	71.5	0.0002
Hymenophyllum revolutum	1	69.7	0.0002
Notogrammitis pseudociliata	1	69.2	0.0002
Blechnum fraseri	1	69	0.0002
Gahnia xanthocarpa	1	66.4	0.0002
Hymenophyllum flabellatum	1	66.1	0.0002
Metrosideros albiflora	1	64.9	0.0002
Hymenophyllum demissum	1	64	0.0002
Loxogramme lanceolata	1	60	0.0002
Hymenophyllum sanguinolentum	1	58.9	0.0002
Rubus australis	1	58.4	0.0002
Griselinia lucida	1	57.4	0.0002
Asplenium oblongifolium	1	57.3	0.0002
Mida salicifolia	1	56.3	0.0002
Elaeocarpus dentatus	1	56	0.0002
Rhopalostylis sapida	1	55.9	0.0002
Winika cunninghamii	1	55.8	0.0002
Podocarpus cunninghamii	1	55.4	0.0002
Notogrammitis heterophylla	1	54.7	0.0002
Hymenophyllum scabrum	1	54.2	0.0002
Dysoxylum spectabile	1	53.3	0.0002
Pittosporum cornifolium	1	52.9	0.0002
Clematis paniculata	1	51.2	0.0002
Abrodictyum elongatum	1	50.8	0.0002
Hymenophyllum rarum	1	50.1	0.0002
Tmesipteris lanceolata	1	50.1	0.0002
Astelia solandri	1	49.6	0.0002
Dacrycarpus dacrydioides	1	49.1	0.0002
Ichthyostomum pygmaeum	1	48.8	0.0002
Polyphlebium venosum	1	48.8	0.0002
Dicksonia lanata	1	48.3	0.0002
Agathis australis	1	47.5	0.0002

Table 4.5: Continued

Species	MaxGroup	IV (%)	*p*
Nestegis lanceolata	1	46.5	0.0002
Tmesipteris sigmatifolia	1	46	0.0002
Collospermum hastatum	1	45.7	0.0002
Acianthus sinclairii	1	44.4	0.0002
Cardiomanes reniforme	1	42.1	0.0002
Freycinetia banksii	1	40.3	0.0002
Alseuosmia quercifolia	1	40	0.0002
Astelia trinervia	1	39	0.0002
Lophomyrtus bullata	1	38.8	0.0002
Asplenium polyodon	1	38.6	0.0002
Nestegis montana	1	38.1	0.0002
Earina mucronata	1	37.7	0.0002
Nematoceras rivulare	1	34.5	0.0002
Lygodium articulatum	1	34.1	0.0002
Pseudopanax crassifolius	1	33.9	0.0002
Cyathea medullaris	1	33.8	0.0002
Myrsine australis	1	32.9	0.0002
Dracophyllum latifolium	1	32	0.0002
Ripogonum scandens	1	32	0.0002
Microsorum pustulatum	1	30.3	0.0002
Uncinia uncinata	1	29.8	0.0002
Metrosideros robusta	1	29.2	0.0002
Dacrydium cupressinum	1	28.6	0.0002
Metrosideros perforata	1	28.5	0.0002
Asplenium flaccidum	1	26.9	0.0002
Prumnopitys ferruginea	1	26.1	0.0002
Schefflera digitata	1	25.7	0.0002
Cyathea dealbata	1	25.6	0.0002
Geniostoma ligustrifolium	1	25.6	0.0002
Pneumatopteris pennigera	1	25.3	0.0002
Lindsaea trichomanoides	1	25.1	0.0002
Ascarina lucida	2	81.6	0.0002
Uncinia banksii	2	77.9	0.0002
Hymenophyllum multifidum	2	77.6	0.0002
Uncinia clavata	2	73.3	0.0002
Collospermum microspermum	2	65.1	0.0002
Dracophyllum traversii	2	64.8	0.0002
Notogrammitis billardierei	2	59.5	0.0002
Nertera dichondrifolia	2	58.5	0.0002
Huperzia varia	2	57.6	0.0002
Gahnia pauciflora	2	56.3	0.0002
Coprosma dodonaeifolia	2	56.2	0.0002

Table 4.5: Continued

Species	MaxGroup	IV (%)	*p*
Myrsine salicina	2	51.7	0.0002
Brachyglottis kirkii	2	51.4	0.0002
Hymenophyllum frankliniae	2	51.3	0.0002
Coprosma colensoi	2	50.2	0.0002
Earina autumnalis	2	50.2	0.0002
Rumohra adiantiformis	2	49.9	0.0002
Tmesipteris elongata	2	48	0.0002
Microlaena avenacea	2	47.6	0.0002
Raukaua edgerleyi	2	47.4	0.0002
Pseudopanax laetus	2	47.1	0.0002
Libocedrus bidwillii	2	46.6	0.0002
Pseudopanax arboreus	2	45.9	0.0002
Blechnum fluviatile	2	44.1	0.0002
Quintinia serrata	2	43.1	0.0002
Metrosideros fulgens	2	42.3	0.0002
Corokia buddleioides	2	41.5	0.0002
Coprosma arborea	2	40	0.0002
Cyathea smithii	2	38.8	0.0002
Libertia micrantha	2	37.3	0.0002
Alseuosmia macrophylla	2	36.2	0.0002
Tmesipteris tannensis	2	34.1	0.0002
Olearia rani	2	33.7	0.0002
Raukaua simplex	2	33.1	0.0002
Brachyglottis repanda	2	29.4	0.0002
Lastreopsis hispida	2	25.3	0.0002
Beilschmiedia tawa	3	33.8	0.0002
Hedycarya arborea	3	33	0.0002
Melicytus ramiflorus	3	32.8	0.0002
Cyathea colensoi	3	26	0.0002
Parsonsia heterophylla	3	25	0.0002
Nothofagus fusca	4	60	0.0002
Griselinia littoralis	4	56.6	0.0002
Nothofagus menziesii	4	54.5	0.0002
Pseudowintera colorata	4	46.2	0.0002
Phyllocladus toatoa	4	42.5	0.0002
Coprosma foetidissima	4	38.4	0.0002
Coprosma parviflora	4	37.9	0.0002
Polystichum neozelandicum	4	35.9	0.0002
Carpodetus serratus	4	32.2	0.0002
Weinmannia racemosa	4	31.4	0.0002
Pseudopanax colensoi	4	29.9	0.0002
Leucopogon fasciculatus	4	26.7	0.0002

4.4.2.3 Forest types

Cluster analysis identified four main vegetation types that are separate in geographical space. These were named: Northland, Coromandel, Kaimai, and Urewera respectively. Table 4.6 defines some of the main characteristics of these types including latitude, longitude, altitude, slope, and species richness. Because of the large size of the data set used to generate the classifications the defined groups represent a broad-scale division of the types of tāwari forest occurring throughout the North Island of New Zealand and include substantial variation in geographic range, environmental conditions, and species compliments. However, the four vegetation types identified represent four obvious splits in the range of tāwari (Figure 4.1). The characteristics of these vegetation types are described in the paragraphs that follow.

Table 4.6: Summary characteristics for the four main forest types identified by cluster analysis and NMS ordination, including the number of plots in each group, ranges for latitude (WG 84), longitude (WG 84), altitude (m), slope (degrees), and average canopy height (m), and a measure of average species richness for the group ± standard deviation.

	n	Latitude	Longitude	Altitude	Slope	Species	Top height
1	129	34.96-35.68	173.48-173.75	374.64±91.22	0-45	67±19	10-37
2	56	36.54-36.50	175.34-175.40	691.82±112.59	2-44	56±9	2.5-22
3	281	38.50-36.53	174.49-178.17	451.19±150.44	0-58	32±9	2-40
4	175	38.99-36.96	174.52-178.25	724.19±219.52	0-50	25±9	0.7-45

4.4.2.3.1 Group 1 – Northland

The Northland group is a very closely associated group and has 129 plots from various locations in Waipoua Forest, and Puketi Forest. Group 1 forest is the most northern forest type. It occurs at an average of -35.47 degrees latitude and 173.64 degrees longitude but extends in range from 34.96 degrees south to 35.68 degrees south and from 173.48 degrees east to 175.75 degrees east. The altitudinal range is between 43 and 640 m with an average of 374.64 m and a standard deviation of 91.22 m.

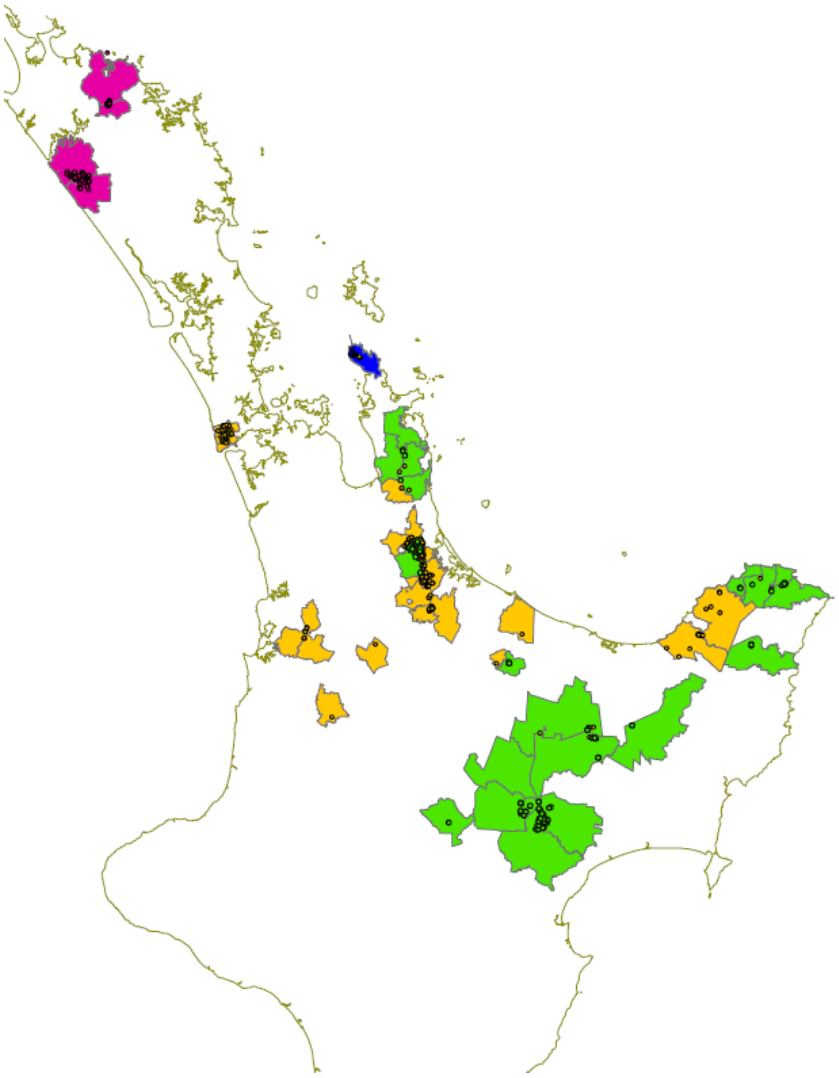

Figure 4.1: Map showing the vegetation types identified by cluster analysis and ordination of 641 plots and 159 species in tāwari forest throughout the North Island, New Zealand. Pink: Northland; Blue: Coromandel; Yellow: Kaimai; Green: Urewera. From Thomson (2013

Group 1 had 236 species in total. It had the highest average species richness at 68 species average per plot. The Northland type had 48 novel species (20% of the total species list for the Northland Group) that were found in no other groups which was the highest proportion of novel species for all groups. Indicator Species Analysis demonstrated that 67 species of the Northland group could be called characteristic of that vegetation type because they had indicator values higher than 25% and were significant to the 0.05 level. The strongest indicator species were *Beilschmiedia tarairi, Ackama rosifolia, Melicytus macrophyllus,* and *Weinmannia silvicola.* A number of *Hymenophyllum* species were also strong indicators.

The emergent layer had 25 different species represented. Species that dominated this layer (>25 m) include *Dacrycarpus cupressinum,* (rimu), *Agathis australis* (kauri), *Metrosideros robusta* (northern rātā), *Prumnopitys ferruginea* (miro), and *Podocarpus cunninghamii* (mountain totara). These emergent species were also prominent features of the canopy layer (12 to 25 m). Dominant species in the canopy layer included *Weinmannia silvicola* (tōwai), *Beilschmiedia tarairi* (taraire), *Beilschmiedia tawa* (tawa), *Knightia excelsa* (rewarewa), *Ackama rosifolia* (makamaka), *Elaeocarpus dentatus* (hīnau), *Dysoxylum spectabile* (kohekohe), *Laurelia novae-zealandiae* (pukatea), *Olearia rani* (heketara), tāwari, and others (listed in order of occurrence across the plots). The sub-canopy layer (5 to 12 m) had 87 species represented. This included the species already described in higher tiers as well as a number of tree fern species such as *Cyathea smithii, C. dealbata, C. medullaris, C. cunninghamii, Dicksonia squarrosa,* and other woody species such as *Coprosma grandifolia* (kanono), *Melicytus macrophyllus* (large-leaved māhoe), *Rhopalostylis sapida* (nīkau), *Myrsine salicina* (toro), and *Raukaua edgerleyi* (raukawa).

The understory layer (2 to 5 m) in the Northland forest group had 99 species across the range of plots. *Freycinetia banksii* (kiekie) was the most universally present species. Dominant species in the understory layer of Group 1 forest included juvenile forms of the species represented in higher tiers as well as other species such as *Myrsine australis* (maupo), *Geniostoma ligustrifolium* (hangehange), *Dracophyllum latifolium* (neinei), *Leucopogon fasciculatus* (mingimingi), and *Brachyglottis kirkii* (kohurangi). The shrub layer (30 cm to 2 m) was represented by 165 species. Again, this layer was dominated by representatives from the higher layers. In addition, ferns and monocots became a prominent fixture including *Blechnum fraseri, Lygodium articulatum, Gahnia xanthocarpa, Astelia trinervia, Blechnum discolor, Blechnum novae-zealandiae, Microlaena avenacea, Asplenium bulbiferum, Uncinia clavata, B. filiforme, B. fluviatile* and others (listed in order of occurrence in the total plots for Group 1). The ground tier was the most speciose (221 species) and was dominated by native ferns such as *Blechnum fraseri, Lygodium articulatum, Asplenium bulbiferum, B. discolor, B. novae-zealandiae* (kiokio), and *A. oblongifolium,* with other native species such as *Nertera dichondrifolia, Astelia trinervia, Metrosideros diffusa,*

Uncinia uncinata, and *Microlaena avenacea.* Seedlings of the species in higher tiers were also well represented in the ground tier.

The epiphytic tier of the Northland tāwari forest group had 113 species recorded including a diversity of ferns and fern allies, lianes and climbers, nest forming species, and woody species. Of these 59 species were considered true epiphytes. The true epiphytes were mainly ferns and fern allies (61%), but there were also lianes and climbers (14%), shrub epiphytes (12%), orchids (8%), and nest epiphytes (5%). The most common epiphyte species were *Hymenophyllum* species, *Asplenium flaccidum, Collospermum hastatum, Cardiomanes reniforme,* and *Microsorum pustulatum.* The average epiphyte diversity per plot was 26 species with a standard deviation of 10.

4.4.2.3.2 Group 2 – Coromandel

The Coromandel group is the smallest of the vegetation groups in plot numbers and geographic area. It includes 56 plots all from the Coromandel Peninsula. This type occurs at an average of -36.52 degrees latitude and 175.37 degrees longitude but extends in range from 36.49 to 36.54 degrees south and from 175.34 to 175.40 degrees east. The altitudinal range is from 485 to 890 m with an average of 691.82 m and a standard deviation of 112.59 m. The slope of plots in this group ranges from 2 to 44 degrees.

The Coromandel group had high species diversity given the small number of plots included in the group. In total there were 176 species encountered and the average species richness was 56.07 per plot with a standard deviation of 9 (the second highest species richness of all four groups). The Coromandel group had 14 novel species that were found in no other plots. Indicator Species Analysis demonstrated 36 species that were characteristic of the Coromandel forest group. This included a range of trees and shrubs, ferns and fern allies, lianes and climbers, monocots, and herbs. Some of the strongest indicators species include *Ascarina lucida, Dracophyllum traversii, Coprosma dodonaeifolia, Myrsine salicina,* and *Brachyglottis kirkii.*

An emergent layer was recorded in only two plots where *Dacrydium cupressinum* was the dominant species. In the canopy the most frequent dominant species included tōwai, tawa, rewarewa, and rimu. The sub-canopy was dominated by tōwai, *Cyathea smithii*, and tāwari, with heketara, māhoe, kanono, and raukawa

also common. The understory resembled the sub-canopy with a dominance of tōwai, *Cyathea smithii*, and tāwari. Other species that were common included *Dicksonia squarrosa*, *Quintinia serrata* (tāwheowheo), heketara, kanono, toro, and *Libocedrus bidwillii* (pāhautea). The shrub layer was commonly dominated by *Microlaena avenacea* with saplings of species from the higher tiers. *Alseuosmia macrophylla* (toropapa) was also common. The ground tier was again dominated most commonly by *Microlaena avenacea* with seedlings of the dominant species from higher tiers.

The Coromandel forest group had 97 species recorded in the epiphytic tier. True epiphytes (43 species) were mainly ferns and fern allies (72%) with shrubs (12%), orchids (9%), and nest epiphytes (7%) also occurring. The most common epiphyte species included *Hymenophyllum* species, *Collospermum microspermum, Earina autumnalis, Cardiomanes reniforme,* and *Notogrammitis billardierei.* The average number of epiphytes per plot was 24 with a standard deviation of 7.

4.4.2.3.3 Group 3 - Kaimai

The Kaimai group is the largest group and includes 281 plots. These plots are mainly from the Kaimai Range but include some plots from Waitakere, Maungatautari, Pirongia, Motu, Moehau, Puketi, Raukumara, Rotorua, Tairua, Te Aroha, and Urewera. Group 2 forest occurs at an average of -37.56 degrees latitude and 175.74 degrees longitude but extends in range from 38.50 degrees south to 36.53 degrees south and from 174.49 degrees east to 178.17 degrees east. The altitudinal range is between 5 and 900 m with an average of 451.19 m and a standard deviation of 150.44 m. The slope of plots in Group 2 ranges from 0 degrees to 58 degrees.

The Kaimai group had 260 species occurring across the range of the vegetation type. The average species richness was 32 species per plot with a standard deviation of 9. Of the total species complement for this group 17% were novel. Being the middle-ground for tāwari forest, there were few species that were truly indicative of this forest group as it included components of the northern and southern tāwari forest types such as kauri and beeches respectively. The main indicator species include *Beilschmiedia tawa, Hedycarya arborea, Melicytus ramiflorus, Cyathea colensoi,* and *Parsonsia heterophylla.*

The emergent tier of the Kaimai group vegetation was very diverse and included tawa, rimu, miro, kauri, rewarewa, kāmahi, *Nothofagus fusca* (red beech), tāwari, and *Nothofagus truncata* (hard beech). Other less commonly recorded emergent species included pukatea, *Podocarpus totara* (totara), *Phyllocladus trichomanoides* (tānekaha), and *Cyathea cunninghamii.* The canopy layer is dominated by tawa, tāwari, kāmahi, and rewarewa. Other common species included rimu, hard beech, miro, kauri, hīnau, *Cyathea medullaris* (mamaku) and kohekohe. The most common sub-canopy species were tāwari, tawa, pigeonwood, kāmahi, and māhoe. The understory was most commonly dominated by tawa, tāwari, kanono, pigeonwood, *Dicksonia squarrosa, Cyathea dealbata*, and māhoe. The shrub layer was most commonly dominated by saplings of the prominent sub-canopy species including tāwari, tawa, kāmahi, and pigeonwood but was also frequently dominated by *Blechnum discolor,* kiekie, *Lygodium articulatum,* toropapa, kiokio, hangehange, mingimingi, *Microlaena avenacea,* and *Asplenium bulbiferum.* The ground tier was the most speciose tier of the Kaimai forest group (225 species) where the most common species were seedlings from higher tiers with *Blechnum discolor,* kiekie, *Uncinia uncinata, Microlaena avenacea* and kiokio also very dominant.

The epiphytic component of the Kaimai forest group had 125 species in total with 52 of these species considered true epiphytes. Of the true epiphytes 50% were ferns and fern allies, 11% were lianes and climbers, 7% were shrub epiphytes, 5% were epiphytic orchids, and 3% were nest epiphytes. The most common epiphyte species were *Asplenium flaccidum* (hanging spleenwort), *Microsorum pustulatum* (hounds tongue), *Collospermum hastatum, Metrosideros fulgens* (rātā), *Cardiomanes reniforme* (kidney fern), and *Asplenium polyodon* (sickle spleenwort). The average species richness of epiphytes per plot was 4 species with a standard deviation of 6.

4.4.2.3.4 Group 4 – Urewera

The Urewera forest group covers 175 plots predominantly from the Urewera Range but with others from the Kaimai Range, Rotorua, Raukumara, Waitakere, Puketi, Te Hoe, Tairua, and Te Aroha. Group 4 forest occurs at an average of -38.19 degrees latitude and 176.47 degrees longitude but extends in range from 38.99 degrees south to 36.96 degrees south and from 174.52 degrees east to

178.25 degrees east. The altitudinal range is between 220 and 1190 m with an average of 724.19 m and a standard deviation of 219.52 m. The slope of plots within this vegetation type ranges from 0 to 50 degrees.

Group 4 was the most speciose group with 272 species represented in total but the average species richness per plot was the lowest at 24.7 with a standard deviation of 9 species. The Urewera forest group had 17% novel species. Indicator species analysis identified 12 species that were characteristic of the Urewera forest group including 11 species of trees and shrubs and 1 fern species. The most prominent indicators included red beech, *Griselinia littoralis* (kāpuka), *Nothofagus menziesii, Pseudowintera colorata,* and *Phyllocladus toatoa.*

The emergent layer was dominated by *Nothofagus* species including red beech, silver beech, and hard beech with kauri, tāwari, toatoa, miro, and rimu also occurring. The canopy was again dominated by *Nothofagus* species including red beech, silver beech, hard beech and *Nothofagus solandri* along with tāwari, kāmahi, tāwheowheo, toatoa, and tawa. In the sub-canopy the dominant species was tāwari in most plots. Other dominant species included kāmahi, silver beech, tāwheowheo, and toatoa. The understory resembled the canopy and sub-canopy with tāwari, tāwheowheo, kāmahi, silver beech, and mingimingi common. Other species included *Pseudowintera colorata* (mountain horopito), toatoa, *Coprosma foetidissima* (stinkwood), kāpuka, neinei, marbleleaf, kanono, *Cyathea smithii,* and *Aristotelia serrata* (wineberry). The shrub layer in Group 4 forest was dominated in many plots by mountain horopito, *Blechnum discolor,* mingimingi, tāwheowheo, and kiokio. Other species included kāmahi, tāwari, stinkwood, red beech, and *Carpodetus serratus* (marbleleaf). The ground tier was dominated by *Blechnum discolor*, and seedlings of trees from higher forest tiers, in particular *Nothofagus*, tāwari, and tāwheowheo. Other species from the higher tiers were also well represented in the ground tier.

The epiphytic tier of the Urewera forest group had 88 species recorded, but over half of these were classed as ephemeral or accidental epiphytes. The true epiphytes (42 species) included a range of ferns and fern allies (60%), lianes and climbers (17%), shrubs (10%), orchids (7%), and nest epiphytes (7%). The most common epiphytic species included *Asplenium flaccidum, Microsorum pustulatum, Earina autumnalis, Collospermum microspermum,* and *Astelia*

trinervia. The average richness of epiphytes per plot was 3 species with a standard deviation of 3.

4.4.2.4 Ordination

The final 3-dimensional solution (Figure 4.2) had a stress value of 13.7722 with a final instability of 0.0000 over 110 iterations. The Monte Carlo test demonstrates that this stress level could not have been reached using randomised data. Table 4.8 shows the coefficients of determination for the three axes of the NMS ordination. The values demonstrate that the three axes explain 82% of the total variance in the analysed data. Axis one explains the largest proportion of this variation (46%) and has a very strong correlation with plot latitude, longitude, altitude, and species richness as demonstrated by Pearson and Kendall correlations of the environmental variables with the ordination axes (shown in Table 4.7).

Table 4.7: Pearson and Kendall correlations with ordination axes. Significant values (r>0.5) are given in bold type.

Axis:	1		2		3	
	r	tau	r	tau	r	tau
Latitude	**-0.805**	-0.591	0.302	0.181	-0.239	-0.227
Longitude	**0.742**	0.543	-0.279	-0.188	0.213	0.211
Species	**-0.707**	-0.565	0.39	0.277	0.023	-0.003
Altitude	**0.602**	0.386	0.322	0.172	0.339	0.241
Vegetation	0.323	0.155	0.071	0.047	0.217	0.136
Soil	-0.282	-0.192	0.072	-0.04	-0.011	0.052
Slope	0.16	0.099	-0.11	-0.062	0.052	0.032
Top Height	-0.154	-0.153	0.267	0.212	0.153	0.089
Litter	-0.14	-0.066	-0.098	-0.081	0.237	0.164
Disturbance	0.063	0.078	-0.104	-0.095	-0.113	-0.081
Moss	-0.059	-0.081	0.255	0.185	0.031	0.055
Rock	0.04	-0.057	-0.125	-0.032	0.079	0.11
Drainage	0.035	0.037	-0.007	-0.029	0.255	0.16
Aspect	0.019	0.007	0.144	0.098	-0.014	0.009
Canopy Cover	-0.019	-0.001	0.046	0.029	0.11	0.105

Table 4.8: Coefficients of determination for three NMS ordination axes

	r^2	
Axis	Increment	Cumulative
1	0.458	0.458
2	0.226	0.684
3	0.133	0.817

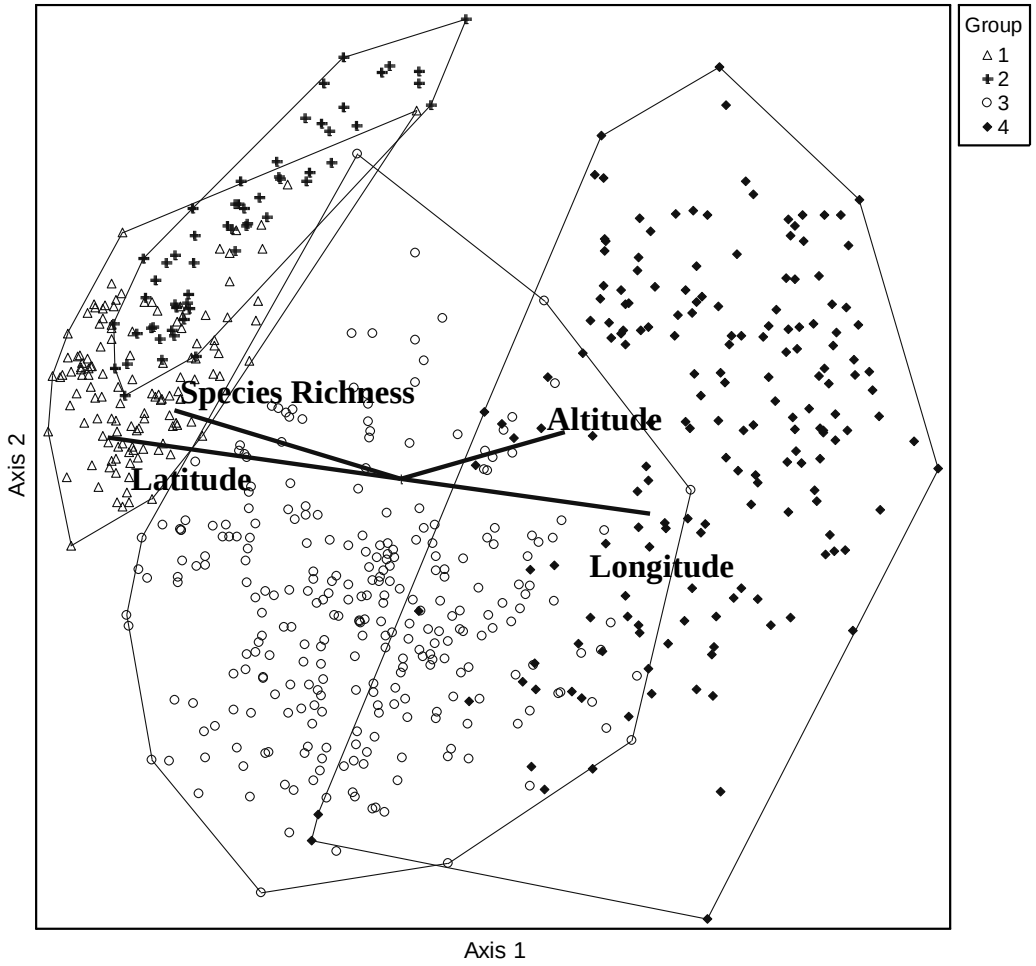

Figure 4.2: NMS ordination of 159 species in 641 plots located throughout the range of *Ixerba brexioides* in the North Island of New Zealand. Quadrat groupings obtained from cluster analysis of the same dta set are shown by solid-line polygons.

The Mantel test showed significant correlation between the ordination points generated in the NMS analysis and a number of the environmental variables assessed (Table 4.9). In particular, latitude, longitude, altitude, aspect, percentage

vegetation cover, and top height were the most significant, followed by rock cover and slope. Soil cover, drainage, and disturbance were not significant.

Table 4.9: Results from Mantel test of correlation between NMS ordination scores and environmental variables. Significant values are in bold type.

Variable	*p*
Latitude	**0.000000**
Longitude	**0.000000**
Altitude	**0.000000**
Aspect	**0.000000**
Percentage vegetation cover	**0.000000**
Average Top Height	**0.000000**
Percentage rock cover	**0.000062**
Slope	**0.002995**
Percentage bare soil cover	0.057067
Drainage Score	0.245831
Disturbance Score	0.805403

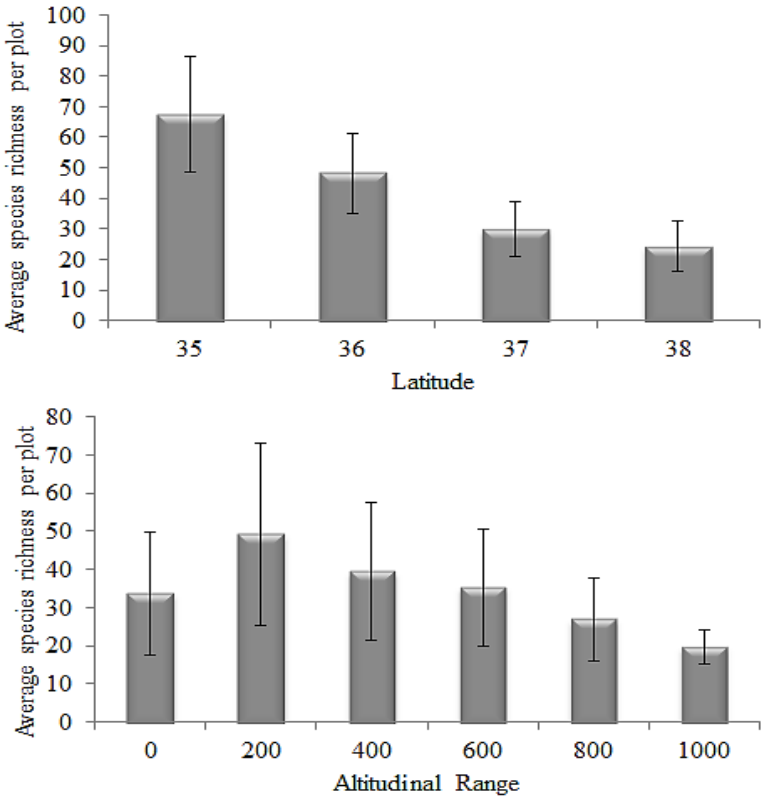

Figure 4.3: Column graphs showing the changes in species richness across the latitudinal (top) and altitudinal range (bottom) of tāwari in the North Island, New Zealand from 641 recce survey plots.

Latitude and altitude had a strong relationship with the change in species richness across these gradients (Figure 4.3). After an initial increase in species richness by an average of 28% per 100 m increase in altitude for the first 300 m, species richness decreased by an average of 12% per 100 metre increase in altitude. Latitudinal trends showed an average decrease of 28% in species richness per degree of latitude.

Table 4.10 shows the correlation coefficients for species that were significantly correlated with at least one axis of the NMS ordination for recce data collected in tāwari forest throughout the range of tāwari in the North Island, New Zealand. The strongest correlations for most species were with axis one. Axis one is correlated strongly with latitude, longitude, species richness, and altitude so this axis follows a broad pattern of the north to south and west to east plot transitions and a transition from lower altitude to higher altitude locations. The species most sensitive to these variations included *Freycinetia banksii, Ripogonum scandens, Hedycarya arborea, Coprosma grandifolia, Weinmannia silvicola, Dicksonia squarrosa, Hymenophyllum demissum, Lygodium articulatum, Cyathea dealbata, Geniostoma ligustrifolium, Blechnum fraseri, Prumnopitys ferruginea, Beilschmiedia tawa, Beilschmiedia tarairi, Knightia excelsa, Hymenophyllum dilatatum, Asplenium oblongifolium, Melicytus macrophyllus, Olearia rani, Rhopalostylis sapida, Pseudopanax crassifolius, Elaeocarpus dentatus, Metrosideros fulgens,* and *Nothofagus fusca*.

Axis two did not have any correlations with environmental variables as strong as those shown by the first axis. Again, the strongest correlates were latitude, longitude, altitude, and species richness. Two other factors that had higher correlations with the second axis than with the first were moss cover and canopy top height – both of which had a positive relationship with the axis. Species that had significant correlations with the second axis included *Astelia trinervia, Brachyglottis kirkii, Hymenophyllum revolutum, Quintinia serrata,* and *Weinmannia silvicola.*

Axis three had no significant correlations either with environmental variables or with the species that were included in the analysis.

Table 4.10: Species correlation coefficients (r value) for NMS ordination axes. Significant values (r>0.5) are in bold type. Only species with a significant value for at least one axis are included.

Species	Axis 1	Axis 2	Axis 3
Asplenium oblongifolium	**-0.529**	0.208	0.053
Astelia trinervia	-0.265	**0.525**	-0.297
Beilschmiedia tarairi	**-0.541**	0.242	-0.018
Beilschmiedia tawa	**-0.546**	-0.248	0.262
Blechnum fraseri	**-0.55**	0.236	-0.103
Brachyglottis kirkii	-0.405	**0.504**	-0.089
Coprosma grandifolia	**-0.603**	0.301	0.172
Cyathea dealbata	**-0.553**	0.069	-0.088
Dicksonia squarrosa	**-0.577**	0.258	0.21
Elaeocarpus dentatus	**-0.505**	0.217	-0.084
Freycinetia banksii	**-0.765**	0.205	0.037
Geniostoma ligustrifolium	**-0.55**	0.148	-0.057
Hedycarya arborea	**-0.643**	-0.017	0.184
Hymenophyllum demissum	**-0.565**	0.263	0.123
Hymenophyllum dilatatum	**-0.53**	0.322	0.088
Hymenophyllum revolutum	-0.458	**0.51**	0.07
Knightia excelsa	**-0.538**	0.135	-0.088
Lygodium articulatum	**-0.561**	0.087	0.051
Melicytus macrophyllus	**-0.523**	0.238	-0.082
Metrosideros fulgens	**-0.505**	0.291	0.036
Nothofagus fusca	**0.524**	0.174	0.268
Olearia rani	**-0.521**	0.264	-0.026
Prumnopitys ferruginea	**-0.548**	0.259	-0.076
Pseudopanax crassifolius	**-0.52**	0.296	-0.133
Quintinia serrata	0.039	**0.57**	0
Rhopalostylis sapida	**-0.521**	0.092	0.005
Ripogonum scandens	**-0.673**	0.129	0.216
Weinmannia silvicola	**-0.579**	**0.522**	0.048

The northern-southern split was most evident for a number of species including *Beilschmiedia tarairi*, *Weinmannia silvicola*, *Ackama rosifolia* (which were restricted to northern plots), and the *Nothofagus* species (which occurred only in the southern-most plots. Some species showed similar trends with a west-east gradient such as *Coprosma foetidissima*, and *Griselinia littoralis* (Figure 4.4)

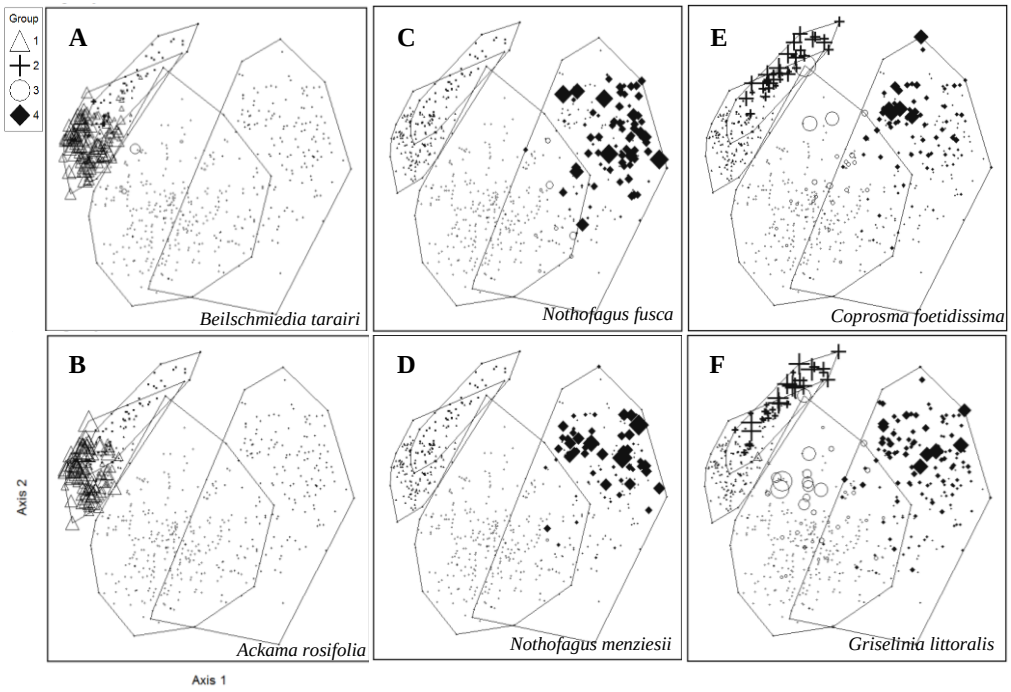

Figure 4.4: NMS ordinations showing the association of some species with strong latitudinal or longitudinal trends: A-B *Beilschmiedia tarairi*, and *Ackama rosifolia* occurring in only northern plots; C-D *Nothofagus fusca* and *Nothofagus menziesii* occurring only in the southern-most plots; E-F *Coprosma foetidissima* and *Griselinia littoralis* occurring in the eastern-most plots.

4.5 Discussion and Conclusions

Cluster analysis and NMS ordination identified 4 broad categories of tāwari forest with distinct species compliments. The composition of these groups was influenced mainly by the combined effects of gradients in latitude, longitude, and altitude and the environmental changes associated with these gradients. The following paragraphs discuss the compositional changes in tāwari forest based on environmental constraints; outline previous vegetation classifications that include tāwari in their scope; illustrate the historical differences in the distribution of tāwari based on palynological data and the fossil record; and comment on the potential for future change.

4.5.1 Factors affecting the distribution of tāwari

The strongest correlate with the ordination of vegetation plots in the NMS analysis was latitude, or the north to south variation in plot situation which followed the same direction as the trend in species richness (decreasing north to south). This latitudinal trend is a longstanding one that is not unique to New Zealand. In general, species diversity decreases with latitude and with increasing

altitude. Some recorded exceptions include vascular epiphytes in South America (Ibisch et al., 1996), woody species in South Africa, (Brien et al., 1998), and rock outcrops in West Africa (Porembski et al., 1995). In this study the latitudinal correlate with species richness was more consistent than the altitudinal correlate, likely because this analysis was restricted to tāwari forest which is already confined in altitudinal range.

New Zealand vegetation patterns have been summarised by Wardle (1991, 1964) in relation to altitudinal and latitudinal zones. Latitudinal zones are shown in Figure 4.5. They reflect the decrease in temperature and solar radiation that accompany the north to south trajectory. From this diagram tāwari forest occurs exclusively in the Northern latitudinal belt. This belt extends from Three Kings Islands to 39° S and includes the southern limits of a number of species that co-occur with tāwari such as makamaka, taraire, kauri, tānekaha, and toatoa. Figure 4.5 also shows how tāwari is absent from the west of the North Island. The gardens of the Pukeiti Rhododendron Trust have a planted specimen of tāwari that was in full flower in January 2012. This garden is located at approximately 39.2° S latitude, and 174 ° E longitude – outside the natural range of tāwari which suggests tāwari has the potential for establishment on Taranaki but is perhaps absent as a result of re-colonisation failure after a history of volcanic activity at Mt Taranaki.

Altitudinal zones reflect a similar decrease in temperature with increasing altitude. The main divisions identified by Wardle (1991) include warm-temperate, cool-temperate or montane, subalpine, penalpine, and alpine. Tāwari forest extends from areas of warm-temperate altitude to cool temperate or montane altitudes but is most common in the montane belt. Freezing limits of some New Zealand species in relation to their distribution in New Zealand, including some species that are found growing with tāwari, have been determined by Sakai and Wardle (1978) (Table 4.11). As tāwari forest progresses into higher altitude zones the associates change from lowland broadleaved species, such as taraire, to the hardier species such as the beeches, and *Phyllocladus* species.

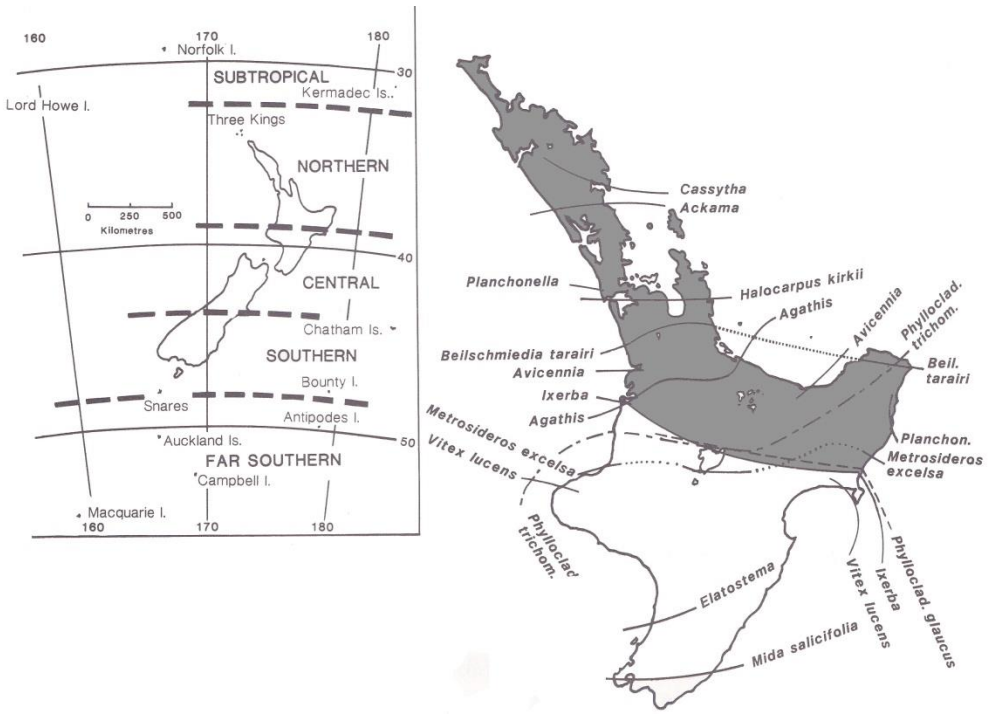

Figure 4.5: Latitudinal zones and natural southern limits of some common New Zealand woody plants, including tāwari (grey shading). Adapted from Wardle (1991).

Altitudinal effects have also been described as a factor influencing the distribution of tāwari on the Waikato volcanic remnants. The apparent absence of tāwari on Mount Karioi, in particular, has been questioned by a number of botanists. Gudex reported instances of tāwari high up on Karioi, (Gudex, 1960) and at Bridal Veil Falls (Gudex, 1962). However B. D. Clarkson searched and corresponded with A. Caldwell, an associate of Gudex, who agreed that the record was dubious and unsupported by any collected specimens (Clarkson pers. comm.). An herbarium specimen of a tāwari sapling collected from western Mt Karioi is lodged in AK but a search of the area did not locate the species. Clarkson (1981) suggested that the lack of tāwari here is a result of the lower altitude giving tāwari insufficient opportunity to be permanently established because of the under-developed and under-represented montane belt.

Table 4.11: Freezing points (and altitudinal limits of some plant associates with tāwari. Adapted from Sakai and Wardle (1978)

Species	Leaf	Bud	Cortex	Twig	Xylem	Altitude Limit
Ascarina lucida	-3	-3	-5		-3	450
Hedycarya arborea	-3	-3	-10		-3	400
Beilschmiedia tarairi	-4	-4	-5		-5	Lowland
Elaeocarpus dentatus	-5	-5	-5		-5	300
Knightia excelsa	-5	-8	-8		-8	Montane

Table 4.11: Continued

Species	Leaf	Bud	Cortex	Twig	Xylem	Altitude Limit
Agathis australis	-7	-7		-7		750
Libocedrus plumosa	-7	-7		-7		Lowland
Podocarpus totara	-7	-7		-7		600
Quintinia serrata	-8	-8	-8		-8	700
Weinmannia racemosa	-8	-8	-8		-10	800
Dacrydium cupressinum	-8		-10		-10	600
Griselinia littoralis	-8	-10	-10		-12	950
Nothofagus fusca	-8	-10	-10		-17	750
Prumnopitys ferruginea	-10	-7		-10		600
Phyllocladus trichomanoides	-10	-10	-10		-10	Montane
Dracophyllum longifolium	-10	-10	-10		-10	1100
Podocarpus cunninghamii	-13	-13		-13		800
Libocedrus bidwillii	-13	-13		-13		950
Halocarpus biformis	-13	-13	-13		-15	1050
Phyllocladus alpinus	-18 ~ -20		-20		-23	1300
Fuchsia excorticata		-5		-5		750

Leathwick and Mitchell (1992) investigated the relationships between forest pattern and environment in the central North Island, New Zealand which includes in its range one of the strongholds of tāwari in New Zealand. They found that sites dominated by the *Beilschmiedia tawa-Weinmannia racemosa-Ixerba brexioides* vegetation type occurred in poorly drained sites with high rainfall and low levels of Taupō Pumice deposits. The effect of the Taupō Pumice deposit is particularly significant and can be visually observed in the arc of tāwari absence surrounding the areas most affected by this volcanic deposit (Figure 4.1). Leathwick and Mitchell (1992) quantified this effect by testing the significance of regression models using the depth of the Taupō Pumice as a predictor of tāwari distribution (Table 4.12). This showed that Taupō Pumice is a significant predictor for tāwari distribution (p=0.05). In another study by Leathwick (1995) tāwari was demonstrated to be biased toward sedimentary substrates.

Experiments on the light environments occupied by tāwari seedlings showed a marginal bias toward high light environments, and an underrepresentation of tāwari seedlings in the most shaded regions of the vegetation (Lusk et al., 2009). Leathwick and Mitchell's (1992) investigations also demonstrated that light environment was an important factor affecting tāwari distribution beyond the seedling stage. Table 4.12 shows a t-value of 3.08 for solar radiation indicating

significance to the level of 0.01. Solar radiation was identified by Leathwick (1995) as a variable of potentially greater importance than previously noted and potentially behind the anomalous trend of increasing altitude at more southern latitudes in the range of tāwari.

Table 4.12: t-values indicating the significance of regression coefficients from models based on environmental values and their prediction value for the distribution of *Ixerba brexioides* in the central North Island, New Zealand. T=temperature; S=solar radiation; R=rainfall; T*R=interaction between temperature and rainfall. The second value for S is the quadratic term. Topography values indicate significance for topography that is rolling, moderately steep, steep, and very steep respectively. The numbers in brackets represent the order of inclusion in the stepwise fitting process. From Leathwick and Mitchell (1992). The siginificance of the results is as follows: >1.96: $P \leq 0.05$; >2.576: $P \leq 0.01$; >3.291: $P \leq 0.0001$.

Species	T	S	R	T*R	Taupō pumice	Topography	Residual mean deviance
Ixerba brexioides	0.96 (4)	3.08/ -4.12(2)	0.44 (4)	3.98 (4)	-2.56(1)	-1.29, -0.74, 1.52, 1.62(3)	0.340

Stress experiments on tāwari and how they affect its distribution in the Kaimai Range showed a dependence on cooler, wetter climates and a low tolerance of drought stress (Jane and Green, 1983b). However, variability in these results between seasons indicated flexibility or adaptability to drought conditions. This was supported by Leathwick and Mitchell (1992) as the most significant variable for the distribution of tāwari in the central North Island, New Zealand was the interaction between temperature and rainfall. The centroid of probability of tāwari occurrence is approximately 12 °C mean annual temperature and 2000 mm mean annual rainfall (Figure 4.6). Tāwari was shown to be more frequent in areas where large-scale temperature fluctuations were uncommon (Leathwick, 1995). In the central North Island tāwari had the highest probability of occurrence in sites with a mean annual temperature of 11° to 13° Celsius, mean annual rainfall between 2000 and 2250 mm annually, and mean solar radiation of 143 to 145 MJ m^2 per day.

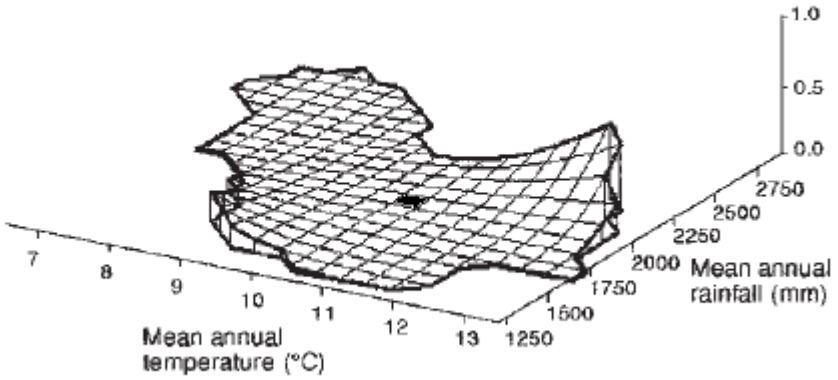

Figure 4.6: Probability of tāwari occurrence based on mean annual temperature and mean annual rainfall. Values were calculated assuming flat topography, good drainage, and 50 cm depth of Taupō Pumice (the mean depth of deposits in the study area). From Leathwick and Mitchell (1992). The black shaded square shows the centroid value of 12 °C mean annual temperature and 2000 mm mean annual rainfall.

Topography was one of the less significant variables contributing to the ordination of tāwari plots in the present study. However, again because the analysis was limited to tāwari forest, the assumption is that this broad forest type will occupy the same general environmental niche throughout its range. In the analysis by Leathwick and Mitchell (1992) topography was also found to be insignificant (see Table 4.12). However, finer scale classification of forest types within the Waipoua Forest sanctuary was shown to be highly affected by topography (Burns, 1995). This interaction was linked to the topographical impact on soil fertility as upper slope areas with higher leaching experience lower pH, lower base saturation, and lower phosphorous than areas further down the slope.

4.5.2 Previous classifications of the New Zealand flora

Several classifications of New Zealand forest ecosystems have been developed in the last sixty years (McKelvey and Nicholls, 1957, McKelvey and Nicholls, 1959, Nicholls, 1976, Wiser and Hurst, 2008, Wiser et al., 2011). The first major classification of New Zealand forest ecosystems (McKelvey and Nicholls 1957) breaks down the major forest classes into a number of groups based on the dominant species. The groups are then further broken down into different types. Tāwari features in 7 groups encompassing 11 different types of vegetation. The dominant species co-occurring with tāwari in this classification include kauri, tōwai, rimu, miro, tawa, red beech, silver beech, kāmahi, and northern rātā.

A refined classification by Nicholls (1976) recorded the prominence or presence of tāwari in 42 different forest groups categorised into the following types:

- Kauri forest (3)
- Kauri-Softwoods-Hardwoods (6)
- Kauri-Softwoods-Hardwoods-Beeches (3)
- Softwoods (1)
- Rimu-Tawa (3)
- Rimu-General Hardwoods (1)
- Lowland Steepland and Highland softwoods and Hardwoods (6)
- Rimu-Tawa-Beeches (3)
- Rimu- General Hardwoods-Beeches (7)
- Highland softwoods-Hardwoods-Beeches (5)
- Beech forest (4).

A 1992 classification of vegetation in the central North Island, New Zealand identified tāwari dominating one vegetation type with *Beilschmiedia tawa* (tawa) and *Weinmannia racemosa* (kāmahi) (Leathwick and Mitchell, 1992).

A broader classification (2001) identified five main divisions in forest composition across New Zealand which encompassed 20 different vegetation types (Leathwick, 2001). Tāwari was classified in two of these types: Upland Conifer Forests, and Northern Nothofagus-Conifer-Broadleaved forests. The former category occurs in the group named 'Conifer-broadleaved forests of warm climates' and occupies higher altitude areas of the central North Island with forest associates such as miro, rimu, mataī, kahikatea, totara, tawa, kāmahi, and hīnau. The latter type occurs in the group named 'Mixed forests of cool, wet climates' and occurs in lowland to montane sites throughout eastern Bay of Plenty, Taranaki, Wellington, Marlborough, Nelson, and Buller. Tāwari is a feature of only the northern most region of this forest type where it is found with *Nothofagus* species, rimu, miro, kāmahi, and tawa. These classifications reflect the Northland and Urewera forest types respectively but are broader in extent.

The most recent classification by Wiser et al. (2011) mentions tāwari only once as a diagnostic species for forest dominated by kāmahi, *Cyathea smithii*, and miro over *Blechnum discolor*. The sampling method used in this classification,

however, is based on a systematic approach which neglects forest types that are restricted in range, such as tāwari forest.

4.5.3 Historical records

A significant question associated with the forest classifications outlined is: how does the current classification reflect the historical distribution and extent of tāwari forest? Palynological data is a helpful tool in answering such questions. In the case of tāwari, pollen is limited and uncommon in palynological surveys (Macphail, 1980, Deng, 2004, Ogden et al., 2003). However in places where it has been found inference can be made about the kinds of forest that tāwari historically grew in, and the locations that it was found.

Palynological records of tāwari pollen have been found both within the current range of tāwari: Frankton, Waikato (Couper and Harris, 1960); Limestone Downs, Port Waikato (Lees et al., 1998); Lake Ohia and Tauanui, Northland (Elliot, 1997); Whangapoua Estuary, Great Barrier Island (Deng et al., 2006); Waipoua, Northland (Ogden et al., 2003); Motutangi and Awanui, Northland (Horrocks et al., 2007); and outside the current range of tāwari: Rangitawa Stream, South Wanganui Basin (Bussell, 1986); Tadmore Saddle, and Ruby Bay, Tasman (Mildenhall and Suggate, 1981); Petone, Lower Hutt (Mildenhall, 1995); Pohangina, Manawatū (Mildenhall, 1975); and Five-Fingers Peninsula, Fiordland (Turnbull et al., 1985). The samples that lie below the current southern limit of tāwari are commonly estuarine in nature and hence would receive pollen via water transport from surrounding upland areas of vegetation. This makes it difficult to pinpoint a precise location of the source vegetation.

The historical community associates described from the pollen record of tāwari resemble the current species complement; however the distributional range is different. This is linked to climatic changes through the glacial and interglacial periods of New Zealand's history. For example, cores from Petone Drillhole, Wellington represent the period of the last interglacial (Oturi or Kaihinu) and contain, with tāwari, pollen from species including *Libocedrus* and *Metrosideros* along with *Ascarina lucida, Dodonaea viscosa, Fuchsia,* and *Quintinia* – species characteristic of the Northern and Coromandel tāwari vegetation groups but which in this case occur with tāwari as far south as Wellington.

Climate change patterns, such as the ones described above, continue today. Studies have reported warming by 0.6 degrees worldwide and increasing by 1.4 to 5.8 °C by 2100 (IPCC, 2001) while in New Zealand warming is reported at 0.5 °C degrees in summer and winter months (Wardle and Coleman, 1992). Forest classifications, such as the one done in this chapter, can be helpful tools as inventories and measuring sticks with which to compare future forest patterns. The ecological data from palynological records demonstrates the history of change that has dominated New Zealand patterns in vegetation. As these natural processes continue to take place in years to come the range of tāwari forest has the potential to expand and contract, as it has previously done, and the classifications provided in this chapter may be useful tools for identifying these changes.

4.5.4 Summary

Forest classification, though a useful tool, has inherent danger of dividing into discrete groups systems that in reality represent a gradient or continuum. This is often the case with vegetation analysis. In the analysis of tāwari forest there is a clear north to south gradient with changes in species richness and composition of tāwari forest. While the groups make it easy to visualise the kinds of variation in forest composition that accompany this gradual change, they are still arbitrary delineations of a continuous trend in forest pattern. The classifications presented in this chapter shed light on the distribution of tāwari and the factors affecting this, as well as offer a point of comparison for future inventories of tāwari forest in the North Island of New Zealand.

Chapter Five: Biological Flora of New Zealand. *Ixerba brexioides*, tāwari, whakou (flowers)

Rachel E. Thomson
Department of Biological Sciences
University of Waikato
Private Bag 3105
Hamilton 3240, New Zealand

5.1 Abstract

A review of the morphology, reproductive biology, classification, history, distribution, traditional and current uses of *Ixerba brexioides* (A. Cunn.) (Strasburgeriaceae) assembled from published and unpublished sources is presented. *Ixerba brexioides* (tāwari) is a small tree endemic to the North Island, New Zealand and restricted to lowland and montane forest north of 39° S latitude. The most conspicuous feature of tāwari is the white flowers that are displayed *en masse* between November and January each year. These with their dark green, long, and toothed leaves arranged in whorls have earned tāwari recognition as one of New Zealand's most remarkable trees. Tāwari occupies areas of mature soil in in warm, moist climates with the highest probability of occurrence in sites with a mean annual temperature of 11° to 13° Celsius, mean annual rainfall between 2000 and 2250 mm annually, and mean solar radiation of 143 to 145 MJ m^2 per day. Four main forest types can be delineated that reflect compositional changes in the geographic distribution of tāwari forest: Northland, Coromandel, Kaimai, and Urewera. Inflorescences are predominantly insect pollinated, though occasionally visited by birds. The reproductive strategy of tāwari is one which allows for pollen limitation by enabling self-fertilisation and autonomous selfing. The capsular fruit of tāwari dehisce to reveal dark black-purple seeds with an orange fleshy aril that are reportedly bird dispersed. Tāwari flowers (whakou) were historically used in garlands and necklaces and used to time the harvest of crops. They are also used to produce honey crops in areas where the trees are abundant. Because of the range of tāwari in higher altitude areas (not suitable for agriculture) tāwari so far has not been affected by post-settlement land disturbance and reproductive back-up systems have allowed it to avoid pollen limitation and continue to reproduce successfully.

Keywords: biological flora, *Ixerba*, tāwari, morphology; taxonomy; distribution; associations; conservation;

5.2 Morphological Description

Ixerba brexioides (tāwari) has a small tree habit, and reaches 10 to 20 m in height at maturity. Trunk diameter at breast height may reach up to 60 cm. Tāwari has a decurrent form, often with young offshoots growing from the base of the trunk. Branchlets may be pilose-pubescent when young (Allan, 1982). Leaves are petiolate and exhibit alternate, opposite, or whorled arrangements. They are long (6 cm to 16 cm), and narrow (1 cm to 4 cm) lanceolate, and with coarse, gland-tipped serrations on the margin. The leaf surface is glabrous and dark green with a coriaceous lamina (Allan, 1982). Petioles may be pilose-pubescent when young.

5.2.1 Inflorescence and fruit

Inflorescences are compound, arranged in terminal subumbellate panicles with 5 - 10 florets per panicle. Each floret is 2.5 cm to 3.5 cm in diameter, with 5 overlapping petals. Petals are white, 1.5 cm to 2 cm in length, obovate-spathulate in shape, and with a distinctive claw on the tip. Each petal is attached to a five-lobed calyx tube. The ovary is generally superior (Allan, 1982, Cunningham, 1839) though it is also reported to be partially inferior by one quarter to one half (Bensel and Palser, 1975). The ovary is five-lobed, and with five locules, each containing two ovules. The ovary merges into a twisted, five-grooved style. The androecium contains five stamens inserted alternately with the disk lobes. Florets are pedicilate, with articulate pedicels. Peduncles and pedicels are covered in pilose pubescence when young (Allan, 1982). Tāwari produce coriaceous, capsular fruit 1 cm to 1.5 cm in diameter that retain the protrusive style on the capsule apex. Capsules contain ten glossy dark purple-black seeds that are partially covered with orange flesh (Allan, 1982).

5.2.2 Leaves

Leaves are classified as mesophylls (between 20 and 180 cm^2) (Raunkiaer, 1934), the size class most common in mixed forest of upland environments (Wardle, 1991). In these environments, leaves play an important role in water balance. Some canopy trees, such as *Nothofagus*, retain water moisture in dense canopies in the cloud forests of the Kaimais, thus reducing flooding of roots. Tāwari is less inclined to hold moisture in the canopy but can withstand root flooding and has thick leaves to buffer water loss (Jane and Green, 1983a). Finer scale observations

have identified a single-layered epidermis, with anomocytic stomata on leaf undersides. The mesophyll layers have 1-3 layers of palisade parenchyma with both simple and crystal druses. The vascular arrangement of leaf nodes is trilacunar with 3 leaf traces (Schneider, 2007).

5.2.3 Wood

The wood of tāwari has been described as a white wood with a pale-brown or reddish heart (Kirk, 1889). It is a dense and heavy wood with the live wood average density of 623 kg m^{-3}, similar to the mean live wood density of other New Zealand trees such as *Elaeocarpus dentatus* (622 kg m^3), *Weinmannia silvicola* (627 kg m^3), *Weinmannia racemosa* (636 kg m^3), and *Knightia excelsa* (642 kg m^3) (Richardson et al., 2009) and is comparable to the mean live wood density of 645 kg m^3 for 2456 tree species form Central and South America (Chave et al., 2006). Though the durability of the wood has not been tested, tāwari was historically used for mine props in the Thames Goldfield (Kirk, 1889) and was recommended for general use by Kirk (1886).

Main features of the wood anatomy include indistinct to distinct growth rings; numerous vessels in the early wood; scalariform perforation plats with on average 37 bars (range 22-57); and heterogeneous rays 1-3 cells wide (Patel, 1973) (Figure 5.1).

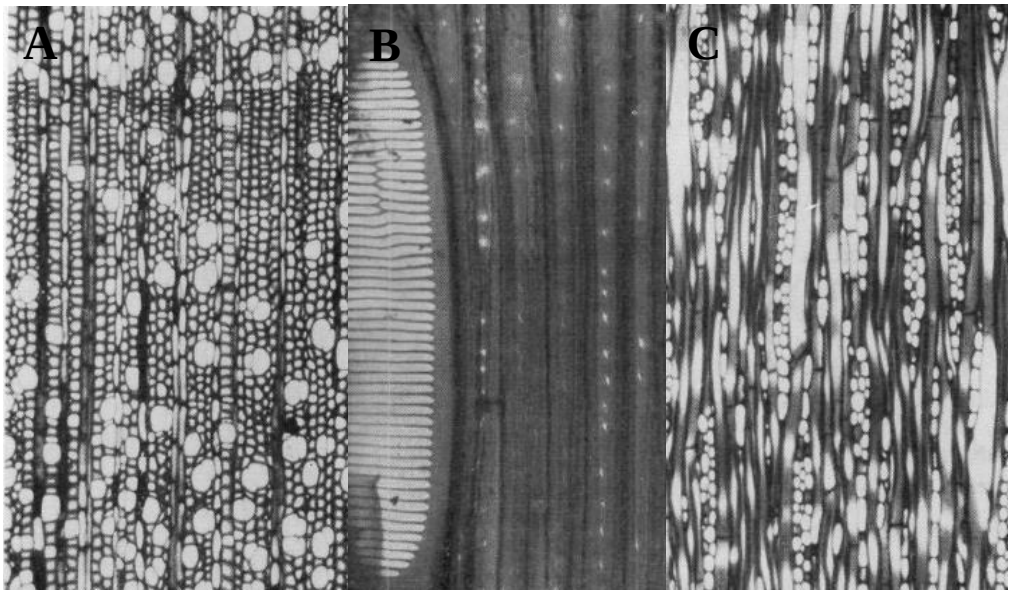

Figure 5.1: Characteristics of the wood structure of tāwari: A) Growth ring showing numerous vessels in early wood; B) Scalariform perforation plate; C) Rays 1-3 cells wide. From Patel (1973).

5.2.4 Roots

Tāwari roots have not been described in detail. Wardle (1991) noted roots of Kaimai Range trees were concentrated in the upper 10 – 20 cm of the soil. Seedlings in the Kaimai Range were shown to have root to shoot ratios of 0.04 on poor sites, and 0.24 in good sites (Jane and Green, 1986).

5.3 Chemistry

Chemicals associated with tāwari include ursolic acid in tāwari leaves and proanthocyanidins in the leaf cortex (Schneider, 2007, Cambie, 1976). Ursolic acid is a pentacyclic triterpenoid carboxylic acid that has been linked to a number of medicinal properties including anti-inflammation, anticancer activity, anti-diabetic symptoms, and as an antioxidant (Ullevig et al., 2011, Ikeda et al., 2008). Proanthocyanidins (condensed tannins) are precursors to plant pigments that are found in leaves, fruits, cereals, and legumes. Research on proanthocyanidins has shown roles in bioavailability of minerals, cancer prevention, and prevention of cardiovascular disease (Santos-Buelga and Scalbert, 2000). Oxidation of the compounds by laccases also produces polymers that inhibit proteolytic enzymes in herbivores and slow fungal and bacterial growth (Gleason and Chollet, 2012).

5.4 Cytology

The chromosome number for tāwari is 2n=50 (Oginuma et al., 2006, Beuzenberg, 1966).

5.5 Reproductive Biology

The present thesis (Thomson, 2013) contains the only known study of tāwari reproductive biology. The section below summarises the findings of this thesis with regard to reproductive biology, while incorporating information from other relevant sources.

5.5.1 Pollen morphology

The pollen type for tāwari, that is unique in the New Zealand flora, suggests insect pollination (Moar, 1993). Tāwari pollen occurs singly (rather than in aggregates or tetrads) and is isopolar (Moar, 1993). It has four to five apertures, arranged in an angulaperturate fashion. The exine is 2 µm thick, thinning to 1 µm at ectoapertures. The surface structure is tectate, baculate with the tectum perforate.

Tāwari pollen ranges in size from 37-40 µm on the polar axis, and 43-45 µm on the equatorial axis. According to Erdtman's (1952) classification tāwari pollen is medium in size and suboblate in shape.

5.5.2 Pollination and seed biology

Various publications have stated that tāwari is bird pollinated (ornithophilous) (Dawson and Lucas, 2011, Schneider, 2007). However, the contribution of birds to tāwari pollination has been overestimated, particularly in modified, mainland ecosystems. Instead, tāwari has a general breeding strategy that attracts a range of pollinators. On the Mamaku Range the most frequent visitors to tāwari flowers are large flies and moths, followed by honey bees, bumblebees, native bees, wasps, other flies, beetles (including longhorns, weevils, and cockroaches) and spiders. Tāwari is not pollen limited (with a PLI value of 0.14), which means that seed set is not limited by the availability of pollen to tāwari flowers. This may be in part due to the breeding system of tāwari which has in-built back-ups (Thomson 2013: chapter 2).

Tāwari is self-compatible and autonomously selfing based on breeding indices (SCI = 0.78; ASI = 0.68). This means that tāwari can produce viable seed even when the pollen source is from the same tree or same flower, and this can happen in the absence of pollen vectors (Thomson 2013: chapter 2). Seed production was also observed from agamospermy. The longevity and successful growth of seeds produced in this way has not been investigated.

The present thesis attempted to identify the vector for this service. Footage of capsules at various stages of development totalling 50 hours was viewed but no interactions were observed. However, from the fruit structure and colour it appears to be best suited to bird dispersal. Though no studies are available on the logistics of tāwari seed dispersal (including dispersal distance, consequences of ingestion, and seed longevity), several papers have identified instances of ingestion of tāwari seeds by native birds. Dijkgraaf (2002) identified tāwari fruits in a list of foods utilised by the kererū. McEwen (1978) earlier demonstrated this mutualism with a study on the diet of the kererū. Two birds were found with digestive tracts containing tāwari seeds. One bird had a total of 174 seeds in its digestive tract. Oliver (1955) described the diet of the whitehead, though mostly insectivorous, as also containing the fruit of some trees including tāwari. Similar

observations were made for kākā by McLean (1911b) and Oliver (1955). However, Oliver (1955) also noted that kākā may destroy the seeds during ingestion by cracking them with their beaks. Best (1942) described historical records of kākā eating tāwari fruits in large quantities: "He kākā tāwari ki Hikurangi, he moki ki te moana (a kākā feeding on the tāwari berries of Hikurangi is as fat as the moki fish of the ocean". Hihi also have been seen taking the fruit of tāwari (Perrott and Armstrong, 2000). Thomson and Challies (1988) observed tāwari foliage as a significant food source for feral pigs (particularly during the winter), but no seed ingestion was noted.

Germination trials showed tāwari seeds germinate in autumn/winter without a dormancy period. Different germination treatments (following (Burrows, 1995a)) showed that buried seeds had the highest germination rate at an average of 75% success followed by seeds on the soil surface (50%), under standard conditions (34%), shade (15%) and finally seeds left in fruit (8%). These findings support a later successional status for tāwari and a preference for dispersal by ingestion and defecation (Thomson, 2013: Chapter 3).

Inter-annual variability in tāwari flowering density and seed set has been observed previously (Mead, 1963), and in the present study. However, in all cases the observation is anecdotal, and the extent of the variability cannot be quantified. A comparison of a single tree was carried out at Tūī Ridge Park in the present study which showed 96 inflorescences in 2011 and 8 inflorescences in 2012. The same pattern was observed for tāwari trees in the surrounding area, extending beyond Tūī Ridge Park and into the wider Mamaku Plateau. Further research that quantifies the variability in seed production between reproductive seasons and the effective cues is recommended (Thomson, 2013: Chapter 3).

5.5.3 Phenology

Development of tāwari flowers was observed between December 2011 and July 2012 (Chapter 3, Figure 3.3). Observations started with 460 buds on eight different trees. After a period of 5 weeks the number of open flowers peaked at 395. Flowers had an average lifespan of two weeks, after which time the petals and anthers fell off, leaving the beginnings of capsules with a long persistent stigma. The number of these immature capsules peaked at 268. Capsules took approximately 5 weeks to start swelling and then a further 18 weeks, on average,

to dehisce. This occurred as the locules began to split down a centre groove and as the twisted style began to unravel. Dehiscence of the capsule revealed ten seeds dark black-purple in colour and partially covered by a red-orange aril.

5.6 Nomenclature and Taxonomic Relationships

Since its original description tāwari has been a taxonomic challenge. Cunningham (1839) observed that although it appeared to be more similar to *Brexia* than to any other published genus, it still differed from *Brexia* in a few respects: it does not have an indefinite number of ovules attached to the placental axis in two rows; and it lacks toothed or fringed lobes between the bases of the stamens. Similarities between *Brexia* and tāwari included aestivation and formation of the calyx and petals, hypogynous stamens, and the structure and position of the anthers, and the ovarium structure with a basal disk. The name *Ixerba* reflects this similarity, being an anagram of *Brexia,* and the specific epithet (*brexioides*) meaning 'similar to *Brexia*'.

Cunningham also recognised affinities with *Celastrineae,* supported by several shared characteristics: aestivation of the floral envelopes, number and alternating pattern of the stamens, perigyny, and ovules ascending from the ovarium axis (Cunningham, 1839).

A study of the wood anatomy of New Zealand members of the family Escalloniaceae (Patel, 1973) included tāwari and confirmed the separation of *Ixerba* and *Brexia* based on elements of the wood structure of *Brexia*: vessels with simple perforations, homogenous rays, crystals in ray and axial parenchyma, and banded axial parenchyma one to six cells wide. Retention of *Ixerba* in Escalloniaceae because of similarities in wood anatomy was recommended, though *Ixerba* appeared less primitive than other New Zealand members of the Escalloniaceae (Patel, 1973).

Research on the floral anatomy of Saxifragaceae *s.l.* by Bensel and Palser (1975) also highlighted the difficulty in placing tāwari. At this time (1975), *Brexia* and *Ixerba* were both in the subfamily Brexioideae within the family Saxifragaceae. It was recommended that *Brexia* and *Ixerba* be dissociated and that a more appropriate phylogenetic placement for *Ixerba* would be within Escallonioideae rather than with either *Brexia* or the Saxifragaceae. This was based on marked differences in structure between *Ixerba* and *Brexia*: spirally arranged sepals in

Ixerba c.f. whorled sepals in *Brexia;* carpels in petal plains in *Ixerba* c.f. in sepal plains in *Brexia*; lignified unicellular hairs on the abaxial surface of outer sepals in *Ixerba*, c.f. lacking in *Brexia;* and other morphological differences related to male and female reproductive structures.

Cronquistian classification (Cronquist, 1981) placed tāwari in the family Grossulariaceae, considered a group with close affinities to Saxifragaceae *s.s.* This interpretation continued with the classification by Al-Shammary and Gornall (1994) who used trichome morphology to resolve placement issues for tāwari, and found affinities with Grossulariaceae, and Hydrangeaceae. However, neither one nor the other was definitive.

The monotypic family Ixerbaceae was erected by Takhtajan (1997) and held till 2009. At a similar time Koontz and Soltis (1999) also used molecular analyses to attempt to elucidate the taxonomic relationships of *Ixerba*. Data suggested that there is no close relationship between *Ixerba* and Escallonioideae (as suggested by Bensel and Palser (1975)). Instead it was suggested to be a sister affinity to families of Eurosid I (including taxa such as Celastraceae, Cucurbitaceae, Fabaceae, Fagaceae, Malpighiaceae, Oxalidaceae, and Roasaceae). However, again no definite phylogenetic placement was given and the result was a request for further taxon sampling of rosids.

Soltis et al. (2000) placed *Ixerba* with *Aphloia* as sister to Crossosomatales but left both unplaced as to order. This relationship was supported by Wikström *et al.* (2001) whose research quantified the divergence of *Ixerba* in geological time, placing its origin at about 85 mya, during the late cretaceous. This supports a relationship as sister to *Aphloia* and within Crossosomatales.

The Angiosperm Phylogeny Group (2003) classification identifies *Ixerba* as unplaced within the rosids – represented by no order and within the monotypic family Ixerbaceae.

Genetic analyses by Oginuma *et al.* (2006) identified a chromosome number of 2n=50 for Ixerbaceae and 2n=500 for Strasburgeriaceae and suggested this was the result of polyploidy because the other taxa within Crossosomatales have x=12 or 13. The common base number between Ixerbaceae and Strasburgeriaceae (x=25) gives evidence to the close relationship between these two monotypic families. This finding is also supported by morphological assessments. Matthews

and Endress (2005), for example, described the flowers of *Strasburgeria* as "a giant version of *Ixerba* flowers with some features more exaggerated." Because high ploidy has often been linked with increased organ size, this genetic analysis may provide some insight into the close affinity of *Strasburgeria* and *Ixerba*, and the origin of the morphological divergence between these genera, but more elucidation is required.

The most current classification (The Angiosperm Phylogeny Group, 2009) places *Ixerba* with the previously monotypic New Caledonian family Strasburgeriaceae. This was based on the similarity in several characters including base chromosome number, wood structure, and stamen and gynoecial morphology. Fossilised leaf material found in Southland, New Zealand also showed affinities to *Strasburgeria* in the structure and arrangement of stomata and stomatal complexes on the leaf surface (Pole, 2008). This material is dated around the Miocene. It was not compared with *Ixerba* (Heads, 2010).

Palynological studies have also contributed to the discussion on the relationship of *Ixerba* and *Strasburgeria* with the identification of *Bluffopollis scabratus* pollen in Palaeocene-Miocene deposits in New Zealand and the southern coast of Australia. *B. scabratus* and *S. robusta* share a number of commonalities in pollen morphology including the number and position of apertures, exine structure, and surface sculpture. The arrangement of the exine layers is similar in structure and thickness in all pollen types, has similar arrangement of apertures (though tāwari has 4-5 apertures rather than 3) and the pollen grains are free in all types (c.f. existing in aggregates). There is some variability in size between the pollen types with an increasing trend in size from *Bluffpolis* to *Ixerba* to *Strasburgeria*. This evidence, in concert with other genetic and morphological evidence of the relationship of tāwari and *Strasburgeria,* has identified *Bluffpolis scabratus* as a potential common ancestor of *Strasburgeria* and tāwari. It has been suggested that the ancestor of *Strasburgeria* evolved prior to the Gondwanan breakup and by the Miocene was restricted to New Zealand, and then since that time become further restricted to the main island of New Caledonia (Jarzen and Pocknall, 1993, Cameron, 2002).

5.7 Distribution

Tāwari is endemic to North Island, New Zealand, where it is restricted in range and found only in the lowland and montane forest north of 39 °S latitude (Chapter 4, Figure 4.5). This distribution is shared with a number of other New Zealand tree species such as *Agathis australis, Metrosideros excelsum, Phyllocladus toatoa,* and *Beilschmiedia tarairi*. The altitudinal range is between 5 to 1200 m, with an average of 531 m (±214 m) above sea level. Because of the upland nature of the environments inhabited by tāwari, in comparison with lowland zones its distribution has been largely unaffected by urban encroachment, or land clearance for agricultural use. However, changes in geographic distribution of tāwari forest have occurred in the past related to climatic changes through the glacial and interglacial periods. For example, cores from Petone Drillhole, Wellington represent the period of the last interglacial (Oturi or Kaihinu) and contain, with tāwari, pollen from species including *Libocedrus* and *Metrosideros* along with *Ascarina lucida, Dodonaea viscosa, Fuchsia,* and *Quintinia* – species characteristic of more northern tāwari forest types, but which in this case occur with tāwari outside the current range, as far south as Wellington.

Little Barrier Island (Hauturu) is an offshore home for tāwari. Above altitudes of about 600 m the forest is dominated by *Quintinia serrata*, tāwari, and southern rātā. The conditions in this area are characterised by high wind, ridge topography, high humidity, and prevalence of deep semi-humified organic soils. The key factor in this vegetation type is the hygrophytic shade element which relies on the moisture of the cloud cap at this altitude (Hamilton & Atkinson, 1961). Tāwari is also found nearby on Great Barrier Island where it grows in regenerating kauri forest.

An outlier pocket of tāwari forest has been observed in the Waimonoa basin of Pureora State Forest Park (Clarkson, 1985) though further descriptions of the site and vegetation associations have not been made.

Tāwari has been introduced in other areas outside of the natural range in New Zealand and overseas: Pukeiti, Taranaki (Bruce Clarkson pers comm.); Kāpiti Island (Wildlife Service, 1970); John Slow Garden, Richmond (New Zealand Biodiversity Recording Network); Edinburgh Botanical Gardens, Scotland (Wall, 1930).

5.8 Environmental Requirements and Limitations

In altitudinal range tāwari forest extends from areas of warm-temperate altitude to cool temperate or montane altitudes but is most common in the montane belt. As tāwari forest progresses into higher altitude zones the associates change from lowland broadleaved species, such as taraire, to the hardier species such as the beeches, and *Phyllocladus* species. Altitudinal effects have also been described as a factor influencing the distribution of tāwari on the Waikato volcanic remnants. The apparent absence of tāwari on Mount Karioi, in particular, has been questioned by a number of botanists. Gudex reported instances of tāwari high up on Karioi, (Gudex, 1960) and at Bridal Veil Falls (Gudex, 1962). However B. D. Clarkson searched both locations and corresponded with A. Caldwell, an associate of Gudex, who agreed that the record was dubious and unsupported by any collected specimens (Clarkson pers. comm.). An herbarium specimen of a tāwari sapling collected from western Mt Karioi is lodged in AK but a recent search of the area did not locate the species. There seems little doubt that tāwari stands or forest dominated by tāwari is absent from Mt Karioi. Clarkson (1981) suggested that the lack of tāwari here is a result of the lower altitude giving tāwari insufficient opportunity to be permanently established because of the under-developed and under-represented montane belt.

Leathwick and Mitchell (1992) investigated the relationships between forest pattern and environment in the central North Island, one of the strongholds of tāwari. They found that sites dominated by the *Beilschmiedia tawa-Weinmannia racemosa-Ixerba brexioides* vegetation type occurred in poorly drained sites with high rainfall and low levels of Taupō Pumice deposits. The effect of the Taupō Pumice deposit is particularly significant and is evident as an arc of tāwari absence surrounding the areas most affected by this volcanic deposit (Chapter 4, Figure 4.1). Leathwick (1995) suggested a bias toward sedimentary substrates in tāwari distribution.

Measurements of the light environments occupied by tāwari seedlings showed a marginal bias toward high light environments, and an underrepresentation of tāwari seedlings in the most shaded regions of the vegetation (Lusk et al., 2009). Leathwick and Mitchell's (1992) investigations also demonstrated that light environment was an important factor affecting tāwari distribution beyond the

seedling stage. Solar radiation was identified by Leathwick (1995) as a variable of potentially greater importance than previously noted, and suggested that solar radiation may be behind the anomalous trend of increasing altitude at more southern latitudes in the range of tāwari.

Stress experiments on tāwari and how they affect its distribution in the Kaimai Range showed a dependence on cooler, wetter climates and a low tolerance of drought stress (Jane and Green, 1983b). However, variability in these results between seasons indicated flexibility or adaptability to drought conditions. This result is supported by the study of Leathwick and Mitchell (1992) which showed that the most significant variable for the distribution of tāwari in the central North Island was the interaction between temperature and rainfall. Tāwari was shown to be more frequent in areas where large-scale temperature fluctuations were uncommon (Leathwick, 1995). In the central North Island tāwari had the highest probability of occurrence in sites with a mean annual temperature of 11° to 13° Celsius, mean annual rainfall between 2000 and 2250 mm annually, and mean solar radiation of 143 to 145 MJ m^2 per day (Leathwick and Mitchell, 1992). This was the highest average solar radiation for the plot groups recorded by Leathwick and Mitchell (1992).

Topography was one of the less significant variables contributing to the distribution of tāwari in an analysis by Leathwick and Mitchell (1992). However, finer scale classification of forest types within the Waipoua Forest sanctuary was shown to be highly affected by topography (Burns, 1995). This pattern was linked to the topographical impact on soil fertility as upper slope areas with higher leaching experience lower pH, lower base saturation, and lower phosphorus levels than lower slopes.

5.9 Plant Communities

In the McKelvey and Nicholls (1957) forest type classification tāwari features in 7 groups encompassing 11 different types of vegetation. The dominant species co-occurring with tāwari in this classification include kauri, tōwai, rimu, miro, tawa, red beech, silver beech, kāmahi, and northern rātā. A 1992 classification of the central North Island forests identified tāwari dominating a single type with *Beilschmiedia tawa* (tawa) and *Weinmannia racemosa* (kāmahi) (Leathwick and Mitchell, 1992).A broader classification (2001) identified five main divisions in

forest composition across New Zealand which encompassed 20 different vegetation types (Leathwick, 2001). Tāwari was prominent in two of these types: Upland Conifer Forests, and Northern Nothofagus-Conifer-Broadleaved forests. The former category occurs in the group named 'Conifer-broadleaved forests of warm climates' and occupies higher altitude areas of the central north island with forest associates such as miro, rimu, mataī, kahikatea, totara, tawa, kāmahi, and hīnau. The latter type occurs in the group named 'Mixed forests of cool, wet climates' and occurs in lowland to montane sites throughout eastern Bay of Plenty. Tāwari is a feature of only the northern most region of this vegetation type where it is found with *Nothofagus* species, rimu, miro, kāmahi, and tawa.

Vegetation analysis from cluster analysis and ordinations of 641 NVS plots from the present thesis identified four main forest types that are essentially separate in geographical space. These were named: Northland, Coromandel, Kaimai, and Urewera respectively. Table 4.6 (Chapter 4) defines four main characteristics of these types: latitude, longitude, altitude, slope, and species richness while Figure 4.1 (Chapter 4) maps these types. These represent a broad-scale division of the types of tāwari forest occurring throughout the North Island of New Zealand and include substantial variation in geographic range, environmental conditions, and species complements. Composition and structure is summarised below incorporating some information from areas not covered by NVS, such as Little Barrier Island.

In the Northland forest type tāwari is a feature of kauri forest occurring in areas with medium to low fertility on ridges and plateaux (Burns, 1995, Burns and Leathwick, 1996). The emergent layer (>25 m) is dominated by *Dacrycarpus cupressinum,* (rimu), *Agathis australis* (kauri), *Metrosideros robusta* (northern rātā), *Prumnopitys ferruginea* (miro), and *Podocarpus cunninghamii* (mountain totara). These emergent species are also prominent in the canopy layer (12 to 25 m). Dominant species in the canopy layer include *Weinmannia silvicola* (tōwai), *Beilschmiedia tarairi* (taraire), *Beilschmiedia tawa* (tawa), *Knightia excelsa* (rewarewa), *Ackama rosifolia* (makamaka), *Elaeocarpus dentatus* (hīnau), *Dysoxylum spectabile* (kohekohe), *Laurelia novae-zealandiae* (pukatea), *Olearia rani* (heketara), tāwari, and others. The sub-canopy layer (5 to 12 m) includes species already described in higher tiers as well as a number of tree fern species such as *Cyathea smithii, C. dealbata, C. medullaris, C. cunninghamii, Dicksonia*

squarrosa, and other woody species such as *Coprosma grandifolia* (kanono), *Melicytus macrophyllus* (large-leaved māhoe), *Rhopalostylis sapida* (nīkau), *Myrsine salicina* (toro), and *Raukaua edgerleyi* (raukawa).

The understory layer includes juvenile forms of the species represented in higher tiers as well as other species such as *Myrsine australis* (maupo), *Geniostoma ligustrifolium* (hangehange), *Dracophyllum latifolium* (neinei), *Leucopogon fasciculatus* (mingimingi), and *Brachyglottis kirkii* (kohurangi). In the shrub layer (30 cm to 2 m) ferns and monocots become a prominent fixture including *Blechnum fraseri, Lygodium articulatum, Gahnia xanthocarpa, Astelia trinervia, Blechnum discolor, Blechnum novae-zealandiae, Microlaena avenacea, Asplenium bulbiferum, Uncinia clavata, B. filiforme, B. fluviatile* and others. The ground tier is dominated by native ferns such as *Blechnum fraseri, Lygodium articulatum, Asplenium bulbiferum, B. discolor, B. novae-zealandiae* (kiokio), and *A. oblongifolium,* with other native species such as *Nertera dichondrifolia, Astelia trinervia, Metrosideros diffusa, Uncinia uncinata,* and *Microlaena avenacea.*

Tāwari is found in a significant proportion of native forest on Little Barrier Island in communities dominated by *Quintinia serrata*, tāwari, and southern rātā. This vegetation covers about 70 hectares. The range of tāwari lies between 800 m about 175 m above sea level, extending into *Quintinia/Ixerba/Metrosideros* forest, tōwai/tawa forest, and rātā/tawa forest (Hamilton & Atkinson, 1961).

The Coromandel forest type has the most restricted range, occurring only on the tip of the Coromandel Peninsula in areas above 485 m altitude. In the canopy the most frequent dominant species include tōwai, tawa, rewarewa, and rimu. The sub-canopy is dominated by tōwai, *Cyathea smithii*, and tāwari, with heketara, māhoe, kanono, and raukawa also common. The understory resembles the sub-canopy with a dominance of tōwai, *Cyathea smithii,* and tāwari. Other species that are common included *Dicksonia squarrosa, Quintinia serrata* (tāwheowheo), heketara, kanono, toro, and pāhautea. The shrub layer is commonly dominated by *Microlaena avenacea* with saplings of species from the higher tiers. *Alseuosmia macrophylla* (toropapa) is also common. The ground tier is again dominated most commonly by *Microlaena avenacea* with seedlings of the dominant species from higher tiers.

The Kaimai vegetation type is most widespread in the Kaimai range but also includes the Waikato, Waitakere, and some areas of the Eastern Bay of Plenty. The emergent tier of the Kaimai forest group is very diverse and includes tawa, rimu, miro, kauri, rewarewa, kāmahi *Nothofagus fusca* (red beech), tāwari, and *Nothofagus truncata* (hard beech). Other less commonly recorded emergent species include pukatea, *Podocarpus totara* (totara), *Phyllocladus trichomanoides* (tānekaha), and *Cyathea cunninghamii.* The canopy layer is dominated by tawa, tāwari, kāmahi, and rewarewa. Other common species include rimu, hard beech, miro, kauri, hīnau, *Cyathea medullaris* (mamaku), and kohekohe. The most common sub-canopy species are tāwari, tawa, pigeonwood, kāmahi, and māhoe. Tawa, tāwari, kanono, pigeonwood, *Dicksonia squarrosa, Cyathea dealbata*, and māhoe are common in the understory. The shrub layer is most commonly dominated by saplings of the prominent sub-canopy species including tāwari, tawa, kāmahi, and pigeonwood but *Blechnum discolor,* kiekie, *Lygodium articulatum,* toropapa, kiokio, hangehange, mingimingi, *Microlaena avenacea,* and *Asplenium bulbiferum* are also common. The most common species in the ground tier were seedlings of species from higher tiers but with *Blechnum discolor,* kiekie, *Uncinia uncinata, Microlaena avenacea* and kiokio also very abundant.

5.10 Other Biotic Relationships

Baylis (2002) described the potential mycorrhizal association of tāwari with *Griselinia littoralis* – a New Zealand tree species known to have mycorrhizal endophytes (Greenall, 1963, Baylis, 1959). He speculated that tāwari only grows when linked with a network of *Griselinia* arbuscular mycorrhizal fungi in the soil. No experiments have been undertaken to verify this interesting observation. However, analysis of data from NVS database plots showed that *Griselinia* occurred in 57% of plots where tāwari was found. So while they commonly grow together, it does not appear to be an obligatory mutualism.

Tāwari hosts a number of epiphytic species. In the Mamaku Range the most commonly observed species included *Astelia solandri, Metrosideros diffusa, Asplenium flaccidum,* and *Collospermum hastatum.* Like many other tree species, given the right conditions tāwari may also be found growing epiphytically, particularly on tree fern trunks.

5.11 Historical Records

Ixerba represents one of the few endemic genera with a long fossil record. Most sources agree that the origin of *Ixerba* is between the Eocene to mid-Miocene eras (Lee et al., 2001, Schneider, 2007, Wardle, 1991). The earliest species of the genus was found by W. R. B. Oliver in the Kaikorai Valley deposits in Otago in 1929 and was named *Ixerba semidentata* (Oliver, 1936). The deposit included a leaf impression of the basal portion of a leaf which resembles *Ixerba brexioides*. The noted points of difference were in the narrowing of the leaf base, widely spaced secondary veins, and the increased space between teeth on the leaf margin.

Tāwari pollen is uncommon in palynological surveys (Macphail, 1980, Deng, 2004, Ogden et al., 2003). However, palynological records of tāwari pollen have been found both within the current range of tāwari: Frankton, Waikato (Couper and Harris, 1960); Limestone Downs, Port Waikato (Lees et al., 1998); Lake Ohia and Tauanui, Northland (Elliot, 1997); Whangapoua Estuary, Great Barrier Island (Deng et al., 2006); Waipoua, Northland (Ogden et al., 2003); Motutangi and Awanui, Northland (Horrocks et al., 2007); and outside the current range of tāwari: Rangitawa Stream, South Wanganui Basin (Bussell, 1986); Tadmore Saddle, and Ruby Bay, Tasman (Mildenhall and Suggate, 1981); Petone, Lower Hutt (Mildenhall, 1995); Pohangina, Manawatū (Mildenhall, 1975); and Five-Fingers Peninsula, Fiordland (Turnbull et al., 1985). The samples that lie below the current southern limit of tāwari are commonly estuarine in nature and hence would receive pollen via water transport from surrounding upland areas of vegetation. This makes it difficult to pinpoint a precise source.

5.12 Traditional and Historic Uses and Cultivation

Historical records show the Māori have a special name for the flowers of tāwari, which is an uncommon practice and hints at the conspicuous nature of these flowers and their importance to Māori. Whakou (as the flowers were called) were used for decorative purposes as garlands and ornamental necklaces (Cockayne, 1910, Salmon, 1993). The flowering of tāwari was also used as an environmental indicator for many Māori. Best (1902) described how the Māori cultivated fern root as a food source. Every third year the fern would be burnt off to prevent other vegetation dominating the fern, and to promote the whitening of the roots. The

timing for this burning was set by the flowering of the tāwari. If left too late the root would become brown and unpalatable.

Several historical records note the importance of tūī in the spiritual world of the Māori. Tūī have an unusual ability to mimic sounds, including the human voice, in a startlingly accurate manner. This ability was often enhanced by the trimming of hairs on the end of the forked tongue of the tūī to improve annunciation of certain sounds. Māori forest lore describes how baby tūī were captured, raised by Māori and trained to speak karakia and to offer blessings at the time of crop sowing and harvest (Best, 1907, Best, 1934, Best 1942). One account of this practice identified tāwari nectar as a food source on which to raise baby tūī. Tāwari nectar was collected using grass straws or equivalent (by capillary action) and used to feed baby tūī (R. Forbes pers. comm.). This makes sense because the normal hatching time for tūī and the flowering time for tāwari overlap considerably.

Historically, tāwari was also a source of food for Māori. Best (1907) recounts that tāwari was considered by the Māori as producing the finest honey, along with rātā, and *Clematis indivisa.* Accounts have also been given where the fruit of the tāwari tree lured kākā to be speared by Māori hunters. Trees in which this technique was used were called kaihua or rākau wero (Best, 1942).

Several historical sources indicate that a "handsome" blue dye may be produced from the bark and wood of tāwari (Brooker et al., 1989, McKillop, 1849).

Leonard Cockayne identified tāwari as a "plant of special beauty of flower, fruit, or form; the elite of the flora" and recommended it as a species which should be a "familiar city tree" used in municipal plantings (Cockayne, 1923). However, tāwari is difficult to cultivate and is hence not common as a garden plant. However, increased understanding of reliance on mycorrhizal association could improve the ease of cultivation, as indicated by Baylis (2002). Tāwari has been cultivated and included in at least two botanical gardens: Pukeiti Rhododendron Trust in Taranaki, and John Slow Garden in Richmond.

Timber surveys of New Zealand in the eighteen and nineteen hundreds identified tāwari among the range of available timber species. An assessment by Kirk (1886) categorised tāwari as a Class II timber product. This category was defined by limited durability though acceptable for general building or special purposes.

However, in the individual tree description the author comments on the hard, dense, and heavy characteristics of tāwari wood – characteristics which are generally associated with durability – though it had not been utilised enough to demonstrate these characteristics. Thomas Kirk's 'The Forest Flora of New Zealand' noted tāwari wood as used for mine-props in the Thames Goldfield mines.

5.13 Economic Importance

Just as honey was an important food source for Māori in the early settlement of New Zealand, it remains an economically important commodity today. New Zealand and Enterprise (2010) quantified this as being worth $94 million in export revenue in the year 2009. A small proportion of this market includes the production and export of tāwari honey. Chemical analysis of tāwari honey has shown a mean mineral content of about 1050 mg per kg, a pH of approximately 4.57, conductivity of 0.46 mS/cm, and a Pfund colour of 3.72 mm (Vanhanen et al., 2011). Though it has not been identified as having health benefits outside of the regular properties of honey, tāwari honey is still a popular choice because of its reputed butterscotch taste, light colour, and the attractiveness of the tāwari flower.

Sale of tāwari at plant nurseries is limited by the difficulty in growing this species. Hence it is often not economically viable despite the popularity and visual charm of tāwari. Tāwari was identified in a circular by the 'Trees for Bees' initiative as a good option for increasing on-farm biodiversity and to benefit the health of honeybees. They recommend the planting of tāwari and a number of other native trees in waterway margins, windbreaks, field edges, and along roadsides to provide food for bees during the spring when bees are gearing up for agricultural crop pollination (Trees for Bees, 2009), but because of the difficulty of growing tāwari this recommendation may not be a realistic one.

5.14 Conservation and Further Research

Tāwari is listed as non-threatened in de Lange et al. (2009). Given its preference for higher altitude forest, much of the area inhabited by tāwari is currently protected in reserve or is unsuitable for agricultural production so is not threatened by land clearance for conversion to pasture. No known research

investigates the susceptibility of tāwari to browse or pest species, though browsing by feral pigs has been recorded (Thomson and Challies, 1988). Further research on the potential for inbreeding depression from self-fertilisation is a topic for further research to ensure that in cases of low pollinator activity the back-up reproductive systems of tāwari can produce functional populations.

Chapter Six: Synthesis and Recommendations

6.1 Discussion

Research from the present thesis has made a new contribution to understanding of the reproductive biology of the New Zealand flora, and specifically tāwari. As well, classification of tāwari forest plot data has defined the predominant types of tāwari forest, where they occur, and the environmental variables that the forest is most sensitive to.

The pollination strategy of tāwari exemplifies the common characteristics of the New Zealand flora with its open, white flowers attracting a generalised pollinator assemblage that is dominated by flies and moths. This assessment differs from records of tāwari pollination vectors in the literature where tāwari is reported as predominantly bird pollinated. Birds however, are the most likely vectors for seed dispersal, based on seed morphology and records of tāwari seed ingestion from the literature. Post-dispersal germination percentage is average to low, occurs without a period of dormancy, and is most successful in buried conditions.

The present study demonstrates the low degree of pollinator dependence exhibited by tāwari which is mediated by a reproductive strategy where self-fertilised capsules are as successful in seed set as cross-pollinated capsules and that seed can be produced in the absence of pollinators and the absence of pollen. These back-up systems are a probable contributing factor to the low level of pollen limitation seen in the tāwari forest surveyed at Tūī Ridge Park. Further investigation into the breeding system of tāwari and comparison with its closest relative *Strasburgeria robusta* could shed some much-needed light on the origin and relationships of tāwari and its unique New Caledonian relative.

The main compositional differences in the North Island range of tāwari forest occur in four distinct geographical areas: Northland, Coromandel, Kaimai, and Urewera. Each of these forest types exhibited different species assemblages with unique indicator species. This was most significant for the Northland and Coromandel groups where species like *Weinmannia silvicola, Ackama rosifolia,* and *Beilschmiedia taraire* were found growing with tāwari up to their southern limits. Conversely, below this southern limit different associates with tāwari became predominant such as *Nothofagus* species.

Recent literature suggests that environmental variables that most influence tāwari forest distribution are annual temperature and rainfall in conjunction with solar radiation. Tāwari forest occupies only areas which are cool and moist, and seedlings are biased toward high light conditions. In the central North Island tāwari had the highest probability of occurrence in sites with a mean annual temperature of 11° to 13° Celsius, mean annual rainfall between 2000 and 2250 mm annually, and mean solar radiation of 143 to 145 MJ m^2 per day. Parent material also plays an important role in forest distribution, and in particular the depth of Taupō Pumice deposits. Tāwari forest occurs in areas of mature soil where volcanic deposits are not too deep. In addition, tāwari is missing from some areas of New Zealand because of a probable recolonisation failure after recent volcanism for example in the Taranaki region.

The decline of both insect and avian populations in New Zealand coupled with the fragmentation and disturbance of native forest ecosystems has threatened a number of pollination and seed dispersal mutualisms. It is necessary to take an inventory of pollination and dispersal processes to monitor how they are functioning in the face of such threats. Understanding how the pollination process works makes it possible to gauge whether or not the process is functioning as it should. The present thesis has demonstrated a pollination system in tāwari that is resilient to disturbance - catering to a generalised pollinator assemblage and demonstrating a low level of pollinator dependence.

The pollination process may not be particularly useful as an indicator of ecosystem health because it has the potential to be affected at so many different points. Pollination failure can occur with insufficient pollen quantity or quality, poor timing of pollen delivery, few or inconsistent pollination vectors, plant or vector population fragmentation, or climatic events that deter pollinators (Wilcock and Neiland, 2002). This makes it difficult to trace reproductive failure back to the source. This is a different story in agricultural systems where pollination services can be measured in terms of the cost benefits gained, the pollinator numbers observed, and the cost of supplemental pollination (Dale and Polasky, 2007). Development of methods for monitoring and quantifying the value of pollination as part of an overall measure of ecosystem health in natural ecosystems is recommended. Most of the work done in quantifying the value of pollination services has been done on crops, such as coffee, and the value of forest

ecosystems in pollination supplementation for these crops (Ricketts, 2004, Ricketts et al., 2004). Pollinators and pollination in New Zealand natural forest ecosystems have economic value in the bush honey industry, in supplementing populations of pollinators in nearby agricultural systems, in maintaining the vegetation that is part of the image and tourism value of New Zealand, and in ecosystem services that are yet to be quantified.

6.2 Recommendations for Further Research

In-depth studies of this nature have a way of opening up areas for further research – such is the case with the present thesis. One important avenue for further research is a comparison of the pollination mechanism of tāwari in the mainland modified environments and an intact forest ecosystem such as that of Little Barrier Island (Hauturu). Students and DOC personnel from Hauturu have reported a preponderance of bird visitation to tāwari flowers – in particular by tūī and bellbirds. Passerine birds and microchiropteran bats were included in the range of potential pollinators identified from tāwari nectar properties and the relative contributions of these groups to tāwari pollination is an area of interest. Bat pollination, in particular, has been largely ignored or underestimated in past appraisals of the reproductive biology of the New Zealand flora (Godley, 1979, Lloyd, 1985, Newstrom and Robertson, 2005). However, recent data suggests conservation of bat populations should be higher on the priority list because of their important role in pollination that has been observed in offshore islands like Hauturu (Pattemore, 2011, Pattemore and Wilcove, 2012).

Lack of pollinator dependence is a characteristic that has been linked to island floras (Baker, 1955, Baker, 1967, Cheptou, 2012) but which is not universally applicable. In the New Zealand flora in particular evidence has shown a high degree of pollinator dependence in the reproductive strategies of many species (Newstrom and Robertson, 2005, Thomson, 1881). Evidence given in the present thesis outlines a pollination and breeding strategy for tāwari that is consistent with this finding and which shows a low level of pollinator dependence due to an ability to produce seed from autonomous selfing and even agamospermy. However, the picture of pollinator dependence for tāwari is incomplete because the flow-on effects of selfing and agamospermy on seedling and tree health have not been investigated. This is an information gap that ought to be filled.

Godley (1979) remarked on the need for further study on the role of nocturnal pollinators and scent in relation to pollination. This is a plea that has not yet been answered in any great detail for the New Zealand flora. Nocturnal moths played a leading role in the pollination of tāwari. Because of this, further investigation on the mechanisms of pollination by nocturnal moths would be an interesting avenue for further research.

Recommendations for the use of tāwari in urban and rural plantings are currently unrealistic because of the difficulty of growing tāwari. Baylis' (1959) suggestion of the necessity of mycorrhizal association between tāwari and kāpuka is a topic that Baylis never had an opportunity to test experimentally. Investigation into this apparent relationship between tāwari and kāpuka mycorrhizal networks may be an opportunity to improve the cultivation of tāwari, making it more accessible for planting programs.

Studies on the nectar properties of New Zealand native trees are not common, and reported to only occur in the case of honey research or honeybee poisoning (Godley, 1979). Further work on nectar properties of tāwari and other native trees would make an interesting contribution to data on the reproductive biology of New Zealand's native flora. Particular areas for tāwari nectar that require work include the elucidation of results from the pilot GCMS study, and the identification and quantification of the non-sugar constituents of tāwari nectar.

Masting is a life history trait that has been well studied in New Zealand for species of *Nothofagus* (Burrows and Allen, 1991, McQueen and Lawrence, 2008, Monks and Kelly, 2006, Murphy and Dowding, 1995, Sweetapple, 2003) and which has been demonstrated for a number of other native species including associates of tāwari such as *Dacrycarpus cupressinum*, and *Elaeocarpus dentatus* (Schauber et al., 2002, Webb and Kelly, 1993). Community level studies on the extent of masting in New Zealand forest ecosystems could demonstrate wider ecological effects on community structure, and faunal populations (both native and introduced). This has implications for management of pest seed predator populations such as rats and mice, and for the native species that compete with them. A comparison of community masting events and the ecological effects of these events on faunal populations in predator-proof islands and in unprotected forest remnants would inform on the usefulness of predator-proof fencing for

protecting against seed predation and protecting plant regeneration. Temperature is a strong correlate with the occurrence of masting in New Zealand trees (Schauber et al., 2002) but analysis of the potential effects of global climate change on masting in New Zealand need revisiting.

It may be too late to follow the admonition of Thomson (1927, 1880) to study the pollination of the New Zealand flora before it is irreparably changed, but we can continue to work towards building a database of pollinators, dispersers, and plant reproductive characteristics as a marker for future studies. Also, more careful monitoring of Dipteran and Lepidopteran diversity in New Zealand is advisable to conserve these genera that have proved to be important pollinators in the present study.

References

Adler, L. S. & Irwin, R. E. 2012. What you smell is more important than what you see? Natural selection on floral scent. *New Phytologist,* 195**,** 510-511.

Aizen, M. A. & Harder, L. D. 2007. Expanding the limits of the pollen-limitation concept: Effects of pollen quantity and quality. *Ecology,* 88**,** 271-281.

Al-Shammary, K. I. A. & Gornall, R. J. 1994. Trichome anatomy of the Saxifragaceae *S.l.*from the Southern Hemisphere. *Botanical Journal of the Linnean Society,* 114**,** 99-131.

Alexandersson, R. & Johnson, S. D. 2002. Pollinator-mediated selection on flower-tube length in a hawkmoth-pollinated *Gladiolus* (Iridaceae). *Proceedings of the Royal Society B-Biological Sciences,* 269**,** 631-636.

Allan, H. H. 1982. *Flora of New Zealand Volume I,* Wellington, New Zealand, P. D. Hasselberg, Government Printer.

Allen, R. B., Bellingham, P. J. & Wiser, S. K. 2003. Developing a forest biodiversity monitoring approach for New Zealand. *New Zealand Journal of Ecology,* 27**,** 207-220.

Anderson, M. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology,* 26**,** 32-46.

Anderson, S. H. 2003. The relative importance of birds and insects as pollinators of the New Zealand flora. *New Zealand Journal of Ecology*, 27**,** 83-94.

Ascensão, L., Francisco, A., Cotrim, H. & Salome Pais, M. 2005. Comparative structure of the labellum in *Ophrys fusca* and *O. lutea* (Orchidaceae). *American Journal of Botany,* 92**,** 1059-1067.

Ashman, T. L., Bradburn, M., Cole, D. H., Blaney, B. H. & Raguso, R. A. 2005. The scent of a male: the role of floral volatiles in pollination of a gender dimorphic plant. *Ecology,* 86**,** 2099-2105.

Ashman, T. L., Knight, T. M., Steets, J. A., Amarasekare, P., Burd, M., Campbell, D. R., Dudash, M. R., Johnston, M. O., Mazer, S. J. & Mitchell, R. J. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology,* 85**,** 2408-2421.

Ashman, T. L. & Majetic, C. J. 2006. Genetic constraints on floral evolution: a review and evaluation of patterns. *Heredity,* 96**,** 343-352.

Atkinson, I. A. E. & Cameron, E. K. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends in Ecology & Evolution,* 8**,** 447-451.

Baker, H. G. 1955. Self-compatibility and establishment after 'long-distance' dispersal. *Evolution,* 9**,** 347-349.

Baker, H. G. 1967. Support for Baker's Law - As a Rule. *Evolution,* 21**,** 853-856.

Baker, H. G. 1977. Non-sugar chemical constituents of nectar. *Apidologie,* 8**,** 349-356.

Baker, H. G. & Baker, I. 1983. Floral nectar sugar constituents in relation to pollinator type. *In:* JONES, C. E. & LITTLE, R. J. (eds.) *Handbook of experimental pollination biology.* New York: Van Nostrand Reinhold.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity,* 2**,** 349.

Baylis, G. 1959. Effect of vesicular-arbuscular mycorrhizas on growth of *Griselinia littoralis* (Cornaceae). *New Phytologist,* 58**,** 274-278.

Baylis, G. 2002. Ixerba brexioides. *Botanical Society of Otago Newsletter,* 33**,** 4-4.

Bekker, R. M., Bakker, J. P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. & Willems, J. H. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology,* 12**,** 834-842.

Bensel, C. R. & Palser, B. F. 1975. Floral Anatomy in the Saxifragaceae *Sensu Lato*. I. Introduction, Parnassioideae and Brexioideae. *American Journal of Botany,* 62**,** 176-176.

Bergquist, C. A. L. 1987. Foraging tactics of tūī (Meliphagidae). *New Zealand Journal of Zoology,* 14**,** 299-303.

Best, E. 1902. Food products of Tuhoeland. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 35**,** 49-53.

Best, E. 1907. Māori Forest Lore: being some Account of Native Forest Lore and Woodcraft, as also of many Myths, Rites, Customs, and Superstitions connected with the Flora and Fauna of the Tuhoe or Ure-wera District - Part 1. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 40**,** 201-239.

Best, E. 1934. *The Māori as he was: a brief account of life as it was in pre-European days*, Wellington, Dominion Museum.

Best, E. 1942. *Forest lore of the Māori : with methods of snaring, trapping, and preserving birds and rats, uses of berries, roots, fern-root, and forest products, with mythological notes on origins, karakia used etc.*, Wellington, New Zealand, E. C. Keating Government Printer.

Beuzenberg, E. J. 1966. Contributions to a chromosome atlas of the New Zealand flora—7. *New Zealand Journal of Botany,* 4**,** 255-266.

Bolten, A. B. & Feinsinger, P. 1978. Why Do Hummingbird Flowers Secrete Dilute Nectar? *Biotropica,* 10**,** 307-309.

Boulter, S. L., Kitching, R. L., Zalucki, J. M. & Goodall, K. L. 2006. Reproductive Biology and Pollination in Rainforest Trees: Techniques for a Community-level Approach. Cairns, Australia.

Bradshaw, H. D. & Schemske, D. W. 2003. Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature,* 426**,** 176-178.

Brien, E. M. O., Whittaker, R. J. & Field, R. 1998. Climate and Woody Plant Diversity in Southern Africa: Relationships at Species, Genus and Family Levels. *Ecography,* 21**,** 495-509.

Brockerhoff, E. G., Barratt, B. I. P., Beggs, J. R., Fagan, L. L., Kay, M. K., Phillips, C. B. & Vink, C. J. 2010. Impacts of exotic invertebrates on New Zealand's indigenous species and ecosystems. *New Zealand Journal of Ecology,* 34**,** 158-174.

Brooker, S. G., Cambie, R. C. & Cooper, R. C. 1989. Economic native plants of New Zealand. *Economic Botany,* 43**,** 79-106.

Burd, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *The Botanical Review,* 60**,** 83-139.

Burns, B. R. 1995. Environmental correlates of species richness at Waipoua Forest Sanctuary, New Zealand. *New Zealand Journal of Ecology,* 19**,** 153-162.

Burns, B. R. & Leathwick, J. R. 1996. Vegetation-environment relationships at Waipoua Forest, Northland, New Zealand. *New Zealand Journal of Botany,* 34**,** 79-92.

Burns, K. C. 2006. Weta and the evolution of fleshy fruits in New Zealand. *New Zealand Journal of Ecology,* 30**,** 405-406.

Burns, K. C. 2012. Masting in a temperate tree: Evidence for environmental prediction? *Austral Ecology,* 37**,** 175-182.

Burquez, A. & Corbet, S. A. 1991. Do Flowers Reabsorb Nectar? *Functional Ecology,* 5**,** 369-379.

Burrows, C. J. 1994. The seeds always know best. *New Zealand Journal of Botany,* 32**,** 349-363.

Burrows, C. J. 1995a. Germination behaviour of the seeds of six New Zealand woody plant species. *New Zealand Journal of Botany,* 33**,** 365-377.

Burrows, C. J. 1995b. Germination behaviour of seeds of the New Zealand species *Fuchsia excorticata, Griselinia littoralis, Macropiper excelsum, i Melicytus ramiflorus*. *New Zealand Journal of Botany,* 33**,** 131-140.

Burrows, C. J. 1995c. Germination behaviour of the seeds of four New Zealand species of *Coriaria* (Coriariaceae). *New Zealand Journal of Botany,* 33**,** 265-275.

Burrows, C. J. 1995d. Germination behaviour of the seeds of the New Zealand species *Aristotelia serrata, Coprosma robusta, Cordyline australis, Myrtus obcordata,* and *Schefflera digitata*. *New Zealand Journal of Botany,* 33**,** 257-264.

Burrows, C. J. 1996a. Germination behaviour of seeds of the New Zealand woody species *Alectryon excelsus, Corynocarpus laevigatus,* and *Kunzea ericoides*. *New Zealand Journal of Botany,* 34**,** 489-498.

Burrows, C. J. 1996b. Germination behaviour of seeds of the New Zealand woody species *Ascarina lucida, Coprosma grandifolia, Melicytus lanceolatus,* and *Solanum laciniatum*. *New Zealand Journal of Botany,* 34**,** 509-515.

Burrows, C. J. 1996c. Germination behaviour of seeds of the New Zealand woody species *Coprosma foetidissima, Freycinetia baueriana, Hoheria angustifolia,* and *Myrsine australis*. *New Zealand Journal of Botany,* 34**,** 499-508.

Burrows, C. J. 1996d. Germination behaviour of seeds of the New Zealand woody species *Melicope simplex, Myoporum laetum, Myrsine divaricata,* and *Urtica ferox*. *New Zealand Journal of Botany,* 34**,** 205-213.

Burrows, C. J. 1996e. Germination behaviour of the seeds of seven New Zealand vine species. *New Zealand Journal of Botany,* 34**,** 93-102.

Burrows, C. J. 1996f. Germination behaviour of the seeds of seven New Zealand woody plant species. *New Zealand Journal of Botany,* 34**,** 355-367.

Burrows, C. J. 1999. Germination behaviour of seeds of the New Zealand woody species *Alseuosmia macrophylla, A. pusilla, Cordyline banksii,*

Geniostoma rupestre, *Myrtus bullata*, and *Solanum aviculare*. *New Zealand Journal of Botany*, 37**,** 277-287.

Burrows, L. E. & Allen, R. B. 1991. Silver beech (*Nothofagus-menziesii* (Hook F) Oerst) seedfall patterns in the Takitimu Range, South Island, New Zealand *New Zealand Journal of Botany*, 29**,** 361-365.

Bussell, M. R. 1986. Palynological evidence for upper Putikian (middle Pleistocene) interglacial and glacial climates at Rangitawa Stream, South Wanganui Basin, New Zealand. *New Zealand Journal of Geology and Geophysics*, 29**,** 471-479.

Cambie, R. C. 1976. A New Zealand Phytochemical Register — Part III. *Journal of the Royal Society of New Zealand*, 6**,** 307-379.

Cameron, K. M. 2002. On the Phylogenetic Position of the New Caledonian Endemic Families Paracryphiaceae, Oncothecaceae, and Strasburgeriaceae: A Comparison of Molecules and Morphology. *The Botanical Review*, 68**,** 428-443.

Campbell-Walker, J. 1877. Report of the Conservator of State Forests with Proposals for the Organization and Working of the State Forest Department. Wellington, New Zealand.

Campbell, D. R., Waser, N. M. & MelendezAckerman, E. J. 1997. Analyzing pollinator-mediated selection in a plant hybrid zone: Hummingbird visitation patterns on three spatial scales. *American Naturalist*, 149**,** 295-315.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Steege, H. t. & Webb, C. O. 2006. Regional and Phylogenetic Variation of Wood Density across 2456 Neotropical Tree Species. *Ecological Applications*, 16**,** 2356-2367.

Cheeseman, T. F. & Hemsley, W. B. 1914. *Illustrations of the New Zealand Flora*, Wellington, New Zealand, Publisher for the Government of New Zealand.

Cheptou, P. O. 2012. Clarifying Baker's Law. *Annals of botany*, 109**,** 633-641.

Clarkson, B. D. 1981. A note on the distribution of some indigenous plant species in the Waikato District, New Zealand. *Journal of the Royal Society of New Zealand*, 11**,** 109-111.

Clarkson, B. D. 1985. Distribution of *Ixerba brexioides* (tāwari): information wanted. *New Zealand Botanical Society Newsletter*, 2**,** 34-35.

Clout, M. & Hay, J. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology,* 12**,** 27-33.

Cockayne, L. 1908. Department of Lands: Report on a Botanical Survey of the Waipoua Kauri Forest. Wellington, New Zealand.

Cockayne, L. 1910. *New Zealand Plants and Their Story,* Wellington, New Zealand, John Mackay, Government Printer.

Cockayne, L. 1921. *The vegetation of New Zealand,* Leipzig, Engelmann Press.

Cockayne, L. 1923. *The cultivation of New Zealand plants,* Auckland, New Zealand, Whitcombe & Tombs.

Coetzee, J. H. & Giliomee, J. H. 1987. Seed predation and survival in the infructescences of *Protea repens* (Proteaceae) *South African Journal of Botany,* 53**,** 61-64.

Corbet, S. A. 2003. Nectar sugar content: estimating standing crop and secretion rate in the field. *Apidologie,* 34**,** 1-10.

Couper, R. & Harris, W. 1960. Pliocene and Pleistocene plant microfossils from drillholes near Frankton, New Zealand. *New Zealand Journal Of Geology and Geophysics,* 3**,** 15-22.

Cronquist, A. J. 1981. *An integrated system of classification of flowering plants,* New York, Columbia Univeristy Press.

Cubas, P. 2004. Floral zygomorphy, the recurring evolution of a successful trait. *BioEssays,* 26**,** 1175-1184.

Cunningham, A. 1839. A Specimen of the Botany of the Islands of New Zealand. *Annals of natural history,* 3**,** 249-250.

Dale, V. H. & Polasky, S. 2007. Measures of the effects of agricultural practices on ecosystem services. *Ecological Economics,* 64**,** 286-296.

Dawson, J. & Lucas, R. 2011. *New Zealand's Native Trees,* Nelson, New Zealand, Craig Potton Publishing.

de Lange, P. J., Norton, D. A., Courtney, S. P., Heenan, P. B., Barkla, J. W., Cameron, E. K., Hitchmough, R. & Townsend, A. J. 2009. Threatened and uncommon plants of New Zealand (2008 revision). *New Zealand Journal of Botany,* 47**,** 61-96.

Delph, L. 1988. *The evolution and maintenance of gender dimorphism in New Zealand Hebe (Scrophulariaceae).* PhD, University of Caterbury.

Delph, L. F. 1990. The evolution of gender dimorphism in New Zealand hebe (Scrophulariaceae) species. *Evolutionary Trends in Plants,* 4**,** 85-97.

Deng, Y. 2004. *The temporal and spatial pattern of vegetation change in the transition from estuary to freshwater swamp: Whangapoua Estuary, Great Barrier Island, northern New Zealand.* PhD, University of Auckland.

Deng, Y., Horrocks, M., Ogden, J. & Anderson, S. 2006. Modern pollen–vegetation relationships along transects on the Whangapoua Estuary, Great Barrier Island, northern New Zealand. *Journal of Biogeography,* 33**,** 592-608.

Diamond, J. M. 1984. Distributions of New Zealand birds on real and virtual islands. *New Zealand Journal of Ecology,* 7**,** 37-55.

Dijkgraaf, A. C. 2002. *Phenology and frugivory of large-fruited species in northern New Zealand and the impacts of introduced mammals.* Doctor of Philosphy, University of Auckland.

Dravitzki, P. V. 1967. *A comparative study of the wood anatomy and floral vascular systems of the New Zealand genera of the Escalloniaceae, Carpodetus, Ixerba and Quintinia.* Master of Science, University of Canterbury.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* 67**,** 345-366.

Duthie, C., Gibbs, G. & Burns, K. C. 2006. Seed Dispersal by Weta. *Science,* 311**,** 1575.

Elliot, M. B. 1997. *The late Quaternary vegetational and climatic history of far northern New Zealand.* Doctor of Philosophy, Massey University.

Erdtman, G. 1952. *Pollen Morphology and Plant Taxanomy - Angiosperms: An Introduction to the Study of Pollen Grains and Spores,* Stockholm, Sweden, Almqvist & Wiksell.

Fadzly, N. & Burns, K. C. 2010. What weta want: colour preferences of a frugivorous insect. *Arthropod-Plant Interactions,* 4**,** 267-276.

Faegri, K. & Van der Pijl, L. 1979. *The principles of pollination ecology,* England, Pergamon Press.

Fahn, A. 1979. *Secretory tissues in plants*, London, Academic Press.

Fernandez, J. D., Bosch, J., Nieto-Ariza, B. & Gomez, J. M. 2012. Pollen limitation in a narrow endemic plant: geographical variation and driving factors. *Oecologia,* 170**,** 421-431.

Field, L. H. 2001. *The Biology of Wetas, King Crickets and Their Allies,* USA, CABI.

Freeland, P. 1976. Tests for the viability of seeds. *Journal of Biological Education,* 10**,** 57-64.

Fuentes, M. & Schupp, E. W. 1998. Empty seeds reduce seed predation by birds in *Juniperus osteosperma*. *Evolutionary Ecology,* 12**,** 823-827.

Gaffney, A., Allen, G. R. & Brown, P. H. 2011. Insect visitation to flowering hybrid carrot seed crops. *New Zealand Journal of Crop and Horticultural Science,* 39**,** 79-93.

Garcia-Camacho, R. & Totland, O. 2009. Pollen Limitation in the Alpine: a Meta-Analysis. *Arctic Antarctic and Alpine Research,* 41**,** 103-111.

Gaskett, A. C. 2011. Orchid pollination by sexual deception: pollinator perspectives. *Biological Reviews,* 86**,** 33-75.

Gleason, F. K. & Chollet, R. 2012. *Plant Biochemistry*, USA, Jones & Bartlett Learning.

Godley, E. 1979. Flower biology in New Zealand. *New Zealand Journal of Botany,* 17**,** 441-466.

Goulson, D. & Wright, N. P. 1998. Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). *Behavioral Ecology,* 9**,** 213-219.

Greenall, J. M. 1963. The mycorrhizal endophytes of *Griselinia littoralis* (Cornaceae). *New Zealand Journal of Botany,* 1**,** 389-400.

Greene, T. C. 1989. Science and Research Internal Report No.48: Kakapo booming activity, Little Barrier Island January - March 1989. Wellington, New Zealand: Department of Conservation.

Griffiths, G. & Tait, A. 2012. National Climate Summary - Summer 2011. Available: http://www.niwa.co.nz/climate/summaries/seasonal/summer-2011-12 [Accessed 26 November 2012].

Gudex, M. C. 1960. The Native Flora of Bryant House-Whale Bay Area. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 88**,** 357-362.

Gudex, M. C. 1962. The native flora of the Bridal Veil Falls Scenic Reserve. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 1**,** 323-326.

Hamilton, W. M. & Atkinson, I. A. 1961. Vegetation. *In:* HAMILTON, W. M. (ed.) *Little Barrier Island (Hauturu).* Wellington: New Zealand Department of Scientific and Industrial Research Bulletin 137: 87-121.

Harder, L. D. & Johnson, S. D. 2008. Function and evolution of aggregated pollen in angiosperms. *International Journal of Plant Sciences,* 169**,** 59-78.

Hargreaves, A. L., Harder, L. D. & Johnson, S. D. 2009. Consumptive emasculation: the ecological and evolutionary consequences of pollen theft. *Biological Reviews,* 84**,** 259-276.

Heads, M. 2010. The endemic plant families and the palms of New Caledonia: a biogeographical analysis. *Journal of Biogeography,* 37**,** 1239-1250.

Hegland, S. J., Nielsen, A., Lazaro, A., Bjerknes, A. L. & Totland, O. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters,* 12**,** 184-195.

Heine, E. M. 1938. Observations on the Pollination of New Zealand Flowering Plants. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 67**,** 133-148.

Hickman, J. M., Lövei, G. L. & Wratten, S. D. 1995. Pollen feeding by adults of the hoverfly Melanostoma fasciatum (Diptera: Syrphidae). *New Zealand Journal of Zoology,* 22**,** 387-392.

Hoballah, M. E., Gubitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M. & Kuhlemeier, C. 2007. Single gene-mediated shift in pollinator attraction in Petunia. *Plant Cell,* 19**,** 779-790.

Holloway, B. A. 1976. Pollen-feeding in hover-flies (Diptera: Syrphidae). *New Zealand Journal of Zoology,* 3**,** 339-350.

Horrocks, M., Nichol, S., Augustinus, P. & Barber, I. 2007. Late Quaternary environments, vegetation and agriculture in northern New Zealand. *Journal of Quaternary Science,* 22**,** 267-279.

Hurst, J. M. & Allen, R. B. 2007. The Recce Method for Describing New Zealand Vegetation - Expanded Manual. Lincoln, New Zealand: Landcare Research.

Ibisch, P. L., Boegner, A., Nieder, J. & Barthlott, W. 1996. How diverse are neotropical epiphytes? An analysis based on the 'Catalogue of the flowering plants and gymnosperms of Peru'. *Ecotropica,* 2**,** 13-28.

Ikeda, Y., Murakami, A. & Ohigashi, H. 2008. Ursolic acid: An anti- and pro-inflammatory triterpenoid. *Molecular Nutrition & Food Research,* 52**,** 26-42.

Innes, J., Kelly, D., Overton, J. M. C. & Gillies, C. 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology,* 34**,** 86-114.

IPCC 2001. Summary for Policymakers: A Report of Working Group I of the Intergovernmental Panel on Climate Change. http://www.ipcc.ch/pub/reports.htm: Intergovernmental Panel on Climate Change.

Irwin, R. E. & Strauss, S. Y. 2005. Flower color microevolution in wild radish: Evolutionary response to pollinator-mediated selection. *American Naturalist,* 165**,** 225-237.

Jane, G. T. & Green, T. G. A. 1983a. Vegetation mortality in the Kaimai Ranges, North Island, New Zealand. *Pac. Sci,* 37**,** 385-89.

Jane, G. T. & Green, T. G. A. 1983b. Utilisation of pressure-volume techniques and non-linear least squares analysis to investigate site induced stresses in evergreen trees. *Oecologia,* 57**,** 380-390.

Jane, G. T. & Green, T. G. A. 1986. Etiology of forest dieback areas within the Kaimai Range, North Island, New Zealand. *New Zealand Journal of Botany,* 24**,** 513-527.

Jarzen, D. & Pocknall, D. 1993. Tertiary *Bluffopollis scabratus* (Couper) Pocknall & Mildenhall, 1984 and modern *Strasburgeria* pollen: a botanical comparison. *New Zealand Journal of Botany,* 31**,** 185-192.

Jersakova, J. & Johnson, S. D. 2006. Lack of floral nectar reduces self-pollination in a fly-pollinated orchid. *Oecologia,* 147**,** 60-68.

Johnson, S. D. & Morita, S. 2006. Lying to Pinocchio: floral deception in an orchid pollinated by long-proboscid flies. *Botanical Journal of the Linnean Society,* 152**,** 271-278.

Jones, K. N. & Reithel, J. S. 2001. Pollinator-mediated selection on a flower color polymorphism in experimental populations of *Antirrhinum* (Scrophulariaceae). *American Journal of Botany,* 88**,** 447-454.

Kampny, C. M. 1995. Pollination and flower diversity in Scrophulariaceae. *The Botanical Review,* 61**,** 350-366.

Kearns, C. A. & Inouye, D. W. 1993. *Techniques for Pollination Biology*, University Press of Colorado.

Kelly, D., Ladley, J. J. & Robertson, A. W. 2004. Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae. *New Zealand Journal of Botany,* 42**,** 89-103.

Kelly, D., Ladley, J. J., Robertson, A. W., Anderson, S. H., Wotton, D. M. & Wiser, S. K. 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. *New Zealand Journal of Ecology,* 34**,** 66-85.

King, C. M. 1990. *The handbook of New Zealand mammals,* New Zealand, Oxford University Press.

Kingston, A. B. & McQuillan, P. B. 2000. Are pollination syndromes useful predictors of floral visitors in Tasmania? *Austral Ecology,* 25**,** 600-609.

Kirk, T. 1886. New Zealand Timbers, Bark, and Secondary Forest Products. *Appendix to the Journals of the House of Representatives, 1886 Session I,* 1.

Kirk, T. 1889. *The forest flora of New Zealand,* Wellington, Government Printer.

Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Dudash, M. R., Johnston, M. O., Mitchell, R. J. & Ashman, T. L. 2005. Pollen limitation of plant reproduction: Pattern and process. *Annual Review of Ecology, Evolution, and Systematics,* 36, 467-497.

Koontz, J. a. & Soltis, D. E. 1999. DNA sequence data reveal polyphyly of Brexioideae (Brexiaceae; Saxifragaceae *sensu lato*). *Plant Systematics and Evolution,* 219**,** 199-208.

Ladley, J. J. & Kelly, D. 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. *New Zealand Journal of Ecology,* 20**,** 69-79.

Leathwick, J. 2001. New Zealand's potential forest pattern as predicted from current species-environment relationships. *New Zealand Journal of Botany,* 39**,** 447-464.

Leathwick, J. R. 1995. Climatic relationships of some New Zealand forest tree species. *Journal of Vegetation Science,* 6**,** 237-248.

Leathwick, J. R. & Mitchell, N. D. 1992. Forest pattern, climate and vulcanism in central North Island, New Zealand. *Journal of Vegetation Science,* 3**,** 603-616.

Lee, D. E., Lee, W. G. & Mortimer, N. 2001. Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany,* 49**,** 341-356.

Lees, C., Neall, V. & Palmer, A. 1998. Forest persistence at coastal Waikato, 24 000 years BP to present. *Journal of the Royal Society of New Zealand,* 28**,** 55-81.

Lehnebach, C. A. & Robertson, A. W. 2004. Pollination ecology of four epiphytic orchids of New Zealand. *Annals of botany,* 93**,** 773-81.

Lehnebach, C. A., Robertson, A. W. & Hedderley, D. 2005. Pollination studies of four New Zealand terrestrial orchids and the implication for their conservation. *New Zealand Journal of Botany,* 43**,** 467-477.

Leonard, A. S., Dornhaus, A. & Papaj, D. R. 2011. Forget-me-not: Complex floral displays, inter-signal interactions, and pollinator cognition. *Current Zoology,* 57**,** 215-224.

Leschen, R. A. B., Marris, J. W. M., Emberson, R. M., Nunn, J., Hitchmough, R. A. & Stringer, I. A. N. 2012. The conservation status of New Zealand Coleoptera. *New Zealand Entomologist,* 35**,** 91-98.

Lessard, B. D. & Yeates, D. K. 2012. Anzomyia (Diptera: Tabanidae: Pangoniinae: Scionini): a new genus of Australian and New Zealand horse fly, including the description of three new species. *Insect Systematics & Evolution,* 43**,** 101-116.

Lloyd, D. & Wells, M. 1992. Reproductive biology of a primitive angiosperm, *Pseudowintera colorata* (Winteraceae), and the evolution of pollination systems in theAnthophyta. *Plant Systematics and Evolution,* 181**,** 77-95.

Lloyd, D. G. 1985. Progress in understanding the natural history of New Zealand plants. *New Zealand Journal of Botany,* 23**,** 707-722.

Lord, J. M., Markey, A. S. & Marshall, J. E. 2002. Have frugivores influenced the evolution of fruit traits in New Zealand? *In:* LEVEY, D. J., SILVA, W. R. & GALETTI, M. (eds.) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation.* USA: CABI.

Lusk, C. H., Duncan, R. P. & Bellingham, P. J. 2009. Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp-broadleaved forest. *New Zealand Journal of Ecology,* 33**,** 83-89.

Mackerras, I. M. 1956. Tabanidae (Diptera) of New Zealand. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 84**,** 581-610.

Macphail, M. 1980. Fossil and modern *Beilschmiedia* (lauraceae) pollen in New Zealand. *New Zealand Journal of Botany,* 18**,** 453-457.

Macphail, M. K. & McQueen, D. R. 1983. The Value of New Zealand Pollen and Spores as Indicators of Cenozoic Vegetation and Climates. *Tuatara,* 26**,** 37-56.

Marshall, J. E. 2009. *The role of colour and odour in fruit selection by diurnal, endemic skinks (Oligosoma) in Aotearoa / New Zealand* Doctor of Philosophy, Otago University.

Masters, S. E., Holloway, J. T. & McKelvey, P. J. 1957. *The national forest survey of New Zealand, 1955,* Wellington, New Zealand Forest Service.

Matthews, M. L. & Endress, P. K. 2005. Comparative floral structure and systematics in Crossosomatales (Crossosomataceae, Stachyuraceae, Staphyleaceae, Aphloiaceae, Geissolomataceae, Ixerbaceae, Strasburgeriaceae). *Botanical Journal of the Linnean Society,* 147**,** 1-46.

McCune, B., Grace, J. B. & Urban, D. L. 2002. *Analysis of ecological communities,* MjM Software Design Gleneden Beach, Oregon.

McCune, B. & Mefford, M. 1999. *Multivariate Analysis of Ecological Data,* Oregon, USA, MjM Software Design.

McEwen, W. M. 1978. The food of the New Zealand pigeon. *New Zealand Journal of Ecology,* 1**,** 99-108.

McGlone, M. 1989. The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *New Zealand Journal of Ecology,* 12**,** 115-129.

McKelvey, P. & Nicholls, J. 1957. A provisional classification of North Island forests. *New Zealand Journal of Forestry,* 7**,** 84-101.

McKelvey, P. J. & Nicholls, J. 1959. The indigenous forest types of North Auckland. *New Zealand Journal of Forestry,* 8**,** 29-45.

McKillop, H. F. 1849. *Reminiscences of twelve month's service in New Zealand, as a midshipman, during the late disturbances in that colony,* London, Richard Bentley, New Burlington Street.

Mckone, M. J., Kelly, D. & Lee, W. G. 2004. Effect of climate change on mast seeding species: frequency of mass flowering and escape from specialist insect seed predators. *Global Change Biology,* 4**,** 591-596.

McLean, J. C. 1907. Field-Notes on some of the Bush-birds of New Zealand. *Ibis,* 49**,** 519-546.

McLean, J. C. 1911a. Bush birds of New Zealand. Part 1. *Emu,* 11**,** 1-17.

McLean, J. C. 1911b. Bush birds of New Zealand. Part 2. *Emu,* 11**,** 65-78.

McQueen, S. & Lawrence, B. 2008. Diet of ship rats following a mast event in beech (*Nothofagus* spp.) forest. *New Zealand Journal of Ecology,* 32**,** 214-218.

Mead, A. D. 1963. Flowering Time. *Auckland Botanical Society Newsletter,* 20**,** 4-5.

Melendez-Ackerman, E. & Campbell, D. R. 1998. Adaptive significance of flower color and inter-trait correlations in an *Ipomopsis* hybrid zone. *Evolution,* 52**,** 1293-1303.

Mildenhall, D. 1975. Palynology of the Acacia-bearing beds in the Komako district, Pohangina Valley, North Island, New Zealand. *New Zealand Journal of Geology and Geophysics,* 18**,** 209-228.

Mildenhall, D. 1995. Pleistocene palynology of the Petone and Seaview drillholes, Petone, Lower Hutt Valley, North Island, New Zealand. *Journal of the Royal Society of New Zealand,* 25**,** 207-262.

Mildenhall, D. & Suggate, R. 1981. Palynology and age of the Tadmor Group (Late Miocene-Pliocene) and Porika Formation (early Pleistocene), South Island, New Zealand. *New Zealand Journal of Geology and Geophysics,* 24**,** 515-528.

Miskelly, C. M., Dowding, J. E., Elliott, G. P., Hitchmough, R. A., Powlesland, R. G., Robertson, H. A., Sagar, P. M., Scofield, R. P. & Taylor, G. A. 2008. Conservation status of New Zealand birds, 2008. *Notornis,* 55**,** 117-135.

Mitchell, A. D., Frodin, D. G. & Heads, M. J. 1997. *New Zealand Journal of Botany,* 35**,** 309.

Moar, N. T. 1993. *Pollen grains of New Zealand dicotyledonous plants*, Lincoln, New Zealand, Manaaki Whenua Press.

Moar, N. T. & Wilmshurst, J. M. 2003. *New Zealand Journal of Botany,* 41**,** 325.

Moar, N. T., Wilmshurst, J. M. & McGlone, M. S. 2011. Standardizing names applied to pollen and spores in New Zealand Quaternary palynology. *New Zealand Journal of Botany,* 49**,** 201-229.

Moles, A. T., Hodson, D. W. & Webb, C. J. 2000. Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos,* 89**,** 541-545.

Monks, A. & Kelly, D. 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). *Austral Ecology,* 31**,** 366-375.

Morita, S. I. 2008. A phylogeny of long-tongued horse flies (Diptera: Tabanidae: *Philoliche*) with the first cladistic review of higher relationships within the family. *Invertebrate Systematics,* 22**,** 311-327.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology,* New York, John Wiley.

Murphy, E. C. & Dowding, J. E. 1995. Ecology of the stoat in *Nothofagus* forest: Home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology,* 19**,** 97-109.

New Zealand, T. & Enterprise 2010. The Complete Specialty Food and Beverage Industry Profile, June 2010. New Zealand.

Newstrom, L. & Robertson, A. 2005. Progress in understanding pollination systems in New Zealand. *New Zealand Journal of Botany,* 43**,** 1-59.

Nicholls, J. 1976. A revised classification of the North Island indigenous forests. *The New Zealand Journal of Forestry,* 21**,** 105.

Nicolson, S. W. & Thornburg, R. W. 2007. Nectar chemistry. *In:* NICOLSON, S. W., NEPI, M. & PACINI, E. (eds.) *Nectaries and Nectar.* The Netherlands: Springer.

Norton, S. A. 1980. *Reproductive biology of Pseudowintera (Winteraceae).* Msc, Victoria University of Wellington.

Norton, S. A. 1984. Thrips pollination in the lowland forest of New Zealand. *New Zealand Journal of Ecology,* 7**,** 157-164.

Obeso, J. R. 2004. A hierarchical perspective in allocation to reproduction from whole plant to fruit and seed level. *Perspectives in Plant Ecology Evolution and Systematics,* 6**,** 217-225.

Ogden, J., Deng, Y., Boswijk, G. & Sandiford, A. 2003. Vegetation changes since early Maori fires in Waipoua Forest, northern New Zealand. *Journal of Archaeological Science,* 30**,** 753-767.

Oginuma, K., Munzinger, J. & Tobe, H. 2006. Exceedingly high chromosome number in Strasburgeriaceae, a monotypic family endemic to New Caledonia. *Plant Systematics and Evolution,* 262**,** 97-101.

Oliver, W. R. B. The Tertiary flora of the Kaikorai Valley, Otago, New Zealand. Transactions of the Royal Society of New Zealand, 1936. 284-304.

Oliver, W. R. B. 1955. *New Zealand birds,* Wellington, New Zealand, Reed.

Ollerton, J., Alarcón, R., Waser, N. M., Price, M. V., Watts, S., Cranmer, L., Hingston, A., Peter, C. I. & Rotenberry, J. 2009. A global test of the pollination syndrome hypothesis. *Annals of botany,* 103**,** 1471-1480.

Pacini, E. & Nepi, M. 2007. Nectar production and presentation. *In:* NICOLSON, S. W., NEPI, M. & PACINI, E. (eds.) *Nectaries and Nectar.* The Netherlands: Springer.

Parachnowitsch, A. L., Raguso, R. A. & Kessler, A. 2012. Phenotypic selection to increase floral scent emission, but not flower size or colour in bee-pollinated *Penstemon digitalis*. *New Phytologist*.

Parkinson, B. J. & Patrick, B. 2000. *Butterflies and Moths of New Zealand,* Auckland, New Zealand, Reed Publishing.

Patel, R. N. 1973. Wood anatomy of the dicotyledons indigenous to New Zealand. 2. Escalloniaceae. *New Zealand Journal of Botany,* 11**,** 421-34.

Pattemore, D. E. 2011. *The endangered and the invasive: the importance of vertebrate pollinators in New Zealand*, Doctor of Philosophy, Princeton University.

Pattemore, D. E. & Anderson, S. H. 2013. Severe pollen limitation in populations of the New Zealand shrub Alseuosmia macrophylla (Alseuosmiaceae) can be attributed to the loss of pollinating bird species. *Austral Ecology*. 38, 95-102.

Pattemore, D. E. & Wilcove, D. S. 2012. Invasive rats and recent colonist birds partially compensate for the loss of endemic New Zealand pollinators. *Proceedings of the Royal Society B: Biological Sciences,* 279**,** 1597-1605.

Paulsen, T. & Högstedt, G. 2002. Passage through bird guts increases germination rate and seedling growth in *Sorbus aucuparia*. *Functional Ecology,* 16**,** 608-616.

Percival, M. S. 1979. *Floral biology*, New York, Pergamon Press.

Perrott, J. K. & Armstrong, D. P. 2000. Vegetation composition and phenology of Mokoia Island, and implications for the reintroduced hihi population. *New Zealand Journal of Ecology,* 24**,** 19-30.

Pole, M. 2008. Dispersed leaf cuticle from the Early Miocene of southern New Zealand. *Palaeontologia Electronica,* 11**,** 15A.

Porembski, S., Brown, G. & Barthlott, W. 1995. An inverted latitudinal gradient of plant diversity in shallow depressions on Ivorian inselbergs. *Plant Ecology,* 117**,** 151-163.

Primack, R. B. 1978. Variability in New Zelaand montane and alpime pollinator assemblages. *New Zealand Journal of Ecology,* 1**,** 66-73.

Primack, R. B. 1983. Insect pollination in the New Zealand mountain flora. *New Zealand Journal of Botany,* 21**,** 317-333.

Proctor, M., Yeo, P. & Lack, A. 1996. *The natural history of pollination,* Oregon, Timber Press.

Prŷs-Jones, O. E. & Willmer, P. G. 1992. The biology of alkaline nectar in the purple toothwort (*Lathraea clandestina*): ground level defences. *Biological Journal of the Linnean Society,* 45**,** 373-388.

Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer*. Oxford, Oxford University Press.

Richardson, S. J., Peltzer, D. a., Hurst, J. M., Allen, R. B., Bellingham, P. J., Carswell, F. E., Clinton, P. W., Griffiths, A. D., Wiser, S. K. & Wright, E. F. 2009. Deadwood in New Zealand's indigenous forests. *Forest Ecology and Management,* 258**,** 2456-2466.

Ricketts, T. H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology,* 18**,** 1262-1271.

Ricketts, T. H., Daily, G. C., Ehrlich, P. R. & Michener, C. D. 2004. Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences of the United States of America,* 101**,** 12579-12582.

Robertson, A. W., Kelly, D., Ladley, J. J. & Sparrow, A. D. 2001. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). *Conservation Biology,* 13**,** 499-508.

Robertson, A. W., Ladley, J. J., Kelly, D., McNutt, K. L., Peterson, P. G., Merrett, M. F. & Karl, B. J. 2008. Assessing pollination and fruit dispersal in Fuchsia excorticata (Onagraceae). *New Zealand Journal of Botany,* 46**,** 299-314.

Robertson, C. 1924. Flower Visits of insects II. *Psyche,* 31**,** 93-111.

Rowarth, J., Hampton, J. & Hill, M. 2007. New Zealand native seed germination requirements: a review. *New Zealand Journal of Botany,* 45**,** 485-501.

Sakai, A. & Wardle, P. 1978. Freezing resistance of New Zealand trees and shrubs. *New Zealand Journal of Ecology,* 1**,** 51-61.

Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid Karim, A. A., Nakashizuka, T. & Inoue, T. 2005. Plant reproductive phonology and general flowering in a mixed dipterocarp forest. *In:* ROUBIK, D., SAKAI, S. & HAMID KARIM, A. A. (eds.) *Pollination Ecology and the Rain Forest: Sarawak Studies.* New York, Springer.

Salmon, J. T. 1993. *The Native Trees of New Zealand,* Auckland, New Zealand, Reed Books.

Santos-Buelga, C. & Scalbert, A. 2000. Proanthocyanidins and tannin-like compounds – nature, occurrence, dietary intake and effects on nutrition and health. *Journal of the Science of Food and Agriculture,* 80**,** 1094-1117.

Schauber, E. M., Kelly, D., Turchin, P., Simon, C., Lee, W. G., Allen, R. B., Payton, I. J., Wilson, P. R., Cowan, P. E. & Brockie, R. E. 2002. Masting by eighteen New Zealand plant species: The role of temperature as a synchronizing cue. *Ecology,* 83**,** 1214-1225.

Schmidt-Adam, G., Young, A. G. & Murray, B. G. 2000. Low outcrossing rates and shift in pollinators in New Zealand pōhutukawa (*Metrosideros excelsa*; Myrtaceae). *American Journal of Botany,* 87**,** 1265-1271.

Schneider, J. 2007. Ixerbaceae. *The Families and Genera of Vascular Plants Volume 9.* Berlin: Springer-Verlag.

Soltis, D. E., Soltis, P. S., Chase, M. W., Mort, M. E., Albach, D. C., Zanis, M., Savolainen, V., Hahn, W. H., Hoot, S. B. & Fay, M. F. 2000. Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. *Botanical Journal of the Linnean Society,* 133**,** 381-461.

Spaethe, J., Moser, W. & Paulus, H. 2007. Increase of pollinator attraction by means of a visual signal in the sexually deceptive orchid, *Ophrys heldreichii* (Orchidaceae). *Plant Systematics and Evolution,* 264**,** 31-40.

Stiles, F. G. 1975. Ecology, Flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology,* 56**,** 285-301.

Sweetapple, P. J. 2003. Possum (*Trichosurus vulpecula*) diet in a mast and non-mast seed year in a New Zealand *Nothofagus* forest. *New Zealand Journal of Ecology,* 27**,** 157-167.

Szabo, J. K., Khwaja, N., Garnett, S. T. & Butchart, S. H. M. 2012. Global Patterns and Drivers of Avian Extinctions at the Species and Subspecies Level. *Plos One,* 7.

Takhtajan, A. 1997. *Diversity and classification of flowering plants,* New York, Columbia Univeristy Press.

The Angiosperm Phylogeny Group. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society,* 141**,** 399-436.

The Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society,* 161**,** 105-121.

Thompson, K., Band, S. R. & Hodgson, J. G. 1993. Seed size and shape predict persistence in soil. *Functional Ecology,* 7**,** 236-241.

Thompson, K. & Grime, J. P. 1979. Seasonal-variation in the seed banks of herbaceous species in 10 contrasting habitats. *Journal of Ecology,* 67**,** 893-921.

Thomson, C. & Challies, C. 1988. Diet of feral pigs in the podocarp-tawa forests of the Urewera Ranges. *New Zealand Journal of Ecology,* 11**,** 73-78.

Thomson, G. M. 1880. On the fertilization, etc., of New Zealand flowering plants. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 13**,** 241-288.

Thomson, G. M. 1881. The flowering plants of New Zealand and their relation to the insect fauna. *Transactions and Proceedings of the Botanical Society of Edinburgh,* 14**,** 91-105.

Thomson, G. M. 1927. The pollination of New Zealand flowers by birds and insects. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 57**,** 106-125.

Tichý, L. & Chytrý, M. 2006. Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science,* 17**,** 809-818.

Toft, R. J., Harris, R. J. & Williams, P. A. 2001. Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand. *Biological Conservation,* 102**,** 31-46.

Traveset, A. 1993. Deceptive fruits reduce seed predation by insects in *Pistacia terebinthus* L. (Anacardiaceae) *Evolutionary Ecology,* 7**,** 357-361.

Trees for Bees 2009. Smart Farming for Healthy Bees. *Bee Friendly Land Management.* Northland, New Zealand: Federated Farmers of New Zealand.

Turnbull, I., Lindqvist, J., Mildenhall, D., Hornibrook, N. B., Beu, A. & Mildenhall, D. 1985. Stratigraphy and paleontology of Pliocene—Pleistocene sediments on Five Fingers Peninsula, Dusky Sound, Fiordland. *New Zealand Journal of Geology and Geophysics,* 28**,** 217-231.

Ullevig, S. L., Zhao, Q., Zamora, D. & Asmis, R. 2011. Ursolic acid protects diabetic mice against monocyte dysfunction and accelerated atherosclerosis. *Atherosclerosis,* 219**,** 409-416.

Vanhanen, L. P., Emmertz, A. & Savage, G. P. 2011. Mineral analysis of mono-floral New Zealand honey. *Food Chemistry,* 128**,** 236-240.

von Bethlenfalvy, G. 2006. *Vertebrate seed dispersers in Mauritius: Fruit traits and fruit trait preferences.* University of Zurich.

Walker, S., Price, R., Rutledge, D., Stephens, R. T. T. & Lee, W. G. 2006. Recent loss of indigenous cover in New Zealand. *New Zealand Journal of Ecology,* 30**,** 169-177.

Wall, A. 1930. A Preliminary Catalogue of New Zealand Plants Cultivated in Britain. *Transactions and Proceedings of the Royal Society of New Zealand (1868-1961),* 60**,** 379-393.

Wardle, P. 1964. Facets of the distribution of forest vegetation in New Zealand. *New Zealand Journal of Botany,* 2**,** 352-366.

Wardle, P. 1991. *Vegetation of New Zealand,* Cambridge, Cambridge University Press.

Wardle, P. & Coleman, M. C. 1992. Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand Journal of Botany,* 30**,** 303-314.

Waser, N. M. 1983. The adaptive nature of floral traits: ideas and evidence. *In:* REAL, L. A. (ed.) *Pollination Biology.* Academic Press.

Webb, C. & Kelly, D. 1993. The reproductive biology of the New Zealand flora. *Trends in Ecology & Evolution,* 8**,** 442-447.

Webb, C. J. 1994. Pollination, self-incompatibility, and fruit production in *Corokia cotoneaster* (Escalloniaceae). *New Zealand Journal of Botany,* 32**,** 385-392.

Wenny, D. G. 2001. Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research,* 3**,** 51-74.

Wikström, N., Savolainen, V. & Chase, M. W. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings. Biological sciences / The Royal Society,* 268**,** 2211-20.

Wilcock, C. & Neiland, R. 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science,* 7**,** 270-277.

Wildlife Service 1970. An Incomplete List of Plants Introduced to Kapiti Island. New Zealand: Widlife Service.

Willson, M. F. & Whelan, C. J. 1990. The Evolution of Fruit Color in Fleshy-Fruited Plants. *The American Naturalist,* 136**,** 790-809.

Wilton, A. 1997. *An evolutionary investigation of the New Zealand Inuleae (Compositae): stem anatomy and flowering phenology.* PhD, University of Canterbury.

Wilton, A. & Breitwieser, I. 2000. Composition of the New Zealand seed plant flora. *New Zealand Journal of Botany,* 38**,** 537-549.

Wiser, S. & Hurst, J. 2008. Classification of New Zealand forest and shrubland communities based on national plot sampling on an 8-km grid. *Manaaki Whenua—Landcare Research, Lincoln, New Zealand*.

Wiser, S. K., Hurst, J. M., Wright, E. F. & Allen, R. B. 2011. New Zealand's forest and shrubland communities: a quantitative classification based on a nationally representative plot network. *Applied Vegetation Science,* 14**,** 506-523.

Yagihashi, T., Hayashida, M. & Miyamoto, T. 1998. Effects of bird ingestion on seed germination of *Sorbus commixta*. *Oecologia,* 114**,** 209-212.

Yagihashi, T., Hayashida, M. & Miyamoto, T. 2000. Inhibition by pulp juice and enhancement by ingestion on germination of bird-dispersed *Prunus* seeds. *Journal of Forest Research,* 5**,** 213-215.

Ziv, Y. & Bronstein, J. L. 1996. Infertile seeds of *Yucca schottii*: A beneficial role for the plant in the yucca-yucca moth mutualism? *Evolutionary Ecology,* 10**,** 63-76.

Appendices

Appendix 1: Details of 641 plots used in NMS ordination and cluster analysis. S=soil cover (%), L=litter cover (%), M=moss cover (%), R=rock cover (%), V=vegetation cover (%), D=disturbance, Lat=latitude (WG 84), Long=longitude (WG 84), Alt=altitude (m), Asp=aspect (degrees), Sl=Slope (degrees), Phys=physiography, Dr=drainage, G=vegetation group (from the classification given in Chapter Four of the current thesis).

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
1Mau	0	65	5	0	30		-38.045	175.557	400	186	25	Ridge	Good	3
2Kai	1	65	3	0	30	Logged	-37.836	175.924	585	68	4		Good	3
3Kai	1	60	2	0	37	Logged	-37.836	175.924	585	130	6	Face	Good	3
4Kai	1	62	2	0	35	None	-37.79	175.902	550	277		Terrace	Good	3
5Kai	1	44	5	0	50	None	-37.79	175.902	550	360	4	Terrace	Medium	3
6Te	5	50	25	0	20		-38.868	176.767	748	200	45	Face	Good	4
7Te	3	15	2	2	78		-38.873	176.756	740	330	45	Gully	Good	4
8Pir		74	1	0	25	Tracked	-38.434	175.281	300	110	6	Ridge	Good	3
9Cor		83	12	0	5	None	-36.523	175.352	490	354	17	Face	Good	2
10Cor		88	5	0	7	None	-36.523	175.352	490	285	23	Face	Good	2
11Cor		84	10	0	6	None	-36.496	175.351	560	327	28	Face	Good	2
12Cor		94	2	0	4	None	-36.523	175.353	550	340	22	Face	Good	2
13Cor		93	2	0	5	None	-36.523	175.353	540	14	36	Face	Good	2
14Cor		92	3	0	5	None	-36.523	175.355	570	2	28	Face	Good	2
15Cor	5	65	12	15	15	None	-36.524	175.355	610	282	15	Ridge	Good	2
16Cor		84	5	1	10	None	-36.524	175.357	610	340	28	Face	Good	2
17Cor	1	54	35	40	5	None	-36.523	175.358	620	216	5	Gully	Poor	2
18Cor	2	89	5	5	4	None	-36.523	175.358	630	301	44	Face	Good	2
19Cor		82	3	0	15	None	-36.523	175.358	630	235	22	Ridge	Good	2
20Cor	1	85	2	2	12	None	-36.522	175.358	615	284	31	Face	Good	2
21Cor		92	2	1	5	None	-36.529	175.363	715	287	33	Face	Good	2
22Cor	5	60	10	0	25	None	-36.527	175.364	715	229	14	Gully	Poor	2
23Cor	1	53	10	1	35	None	-36.527	175.366	735	354	8	Ridge	Good	2
24Cor		91	4	0	5	None	-36.527	175.367	745	227	7	Face	Good	2
25Cor		58	2	0	40	None	-36.526	175.367	750	282	18	Face	Good	2
26Cor	3	78	7	1	12	None	-36.526	175.368	785	300	29	Gully	Good	2
27Cor		77	15	0	8	None	-36.526	175.369	806	285	2	Ridge	Good	2
28Cor	3	79	15	0	3	None	-36.525	175.373	830	315	35	Face	Good	2
29Cor	3	68	25	0	4	None	-36.526	175.379	854	330	26	Face	Good	2
30Cor		65	30	0	5	None	-36.526	175.379	840	312	22	Face	Good	2
31Cor		76	20	0	4	None	-36.527	175.378	835	45	5	Ridge	Good	2
32Cor	1	79	15	0	5	None	-36.527	175.378	832	318	18	Face	Medium	2
33Cor	1	81	15	0	3	None	-36.527	175.378	805	6	32	Face	Good	2
34Cor	1	71	25	0	3	None	-36.526	175.376	805	3	25	Face	Good	2

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
35Cor		75	15	0	10	None	-36.525	175.371	735	283	30	Gully	Medium	2
36Cor		50	25	0	25	None	-36.525	175.371	750	275	10	Ridge	Good	2
37Cor		40	20	0	30	None	-36.526	175.37	775	11	28	Face	Good	2
38Cor		42	3	0	55	None	-36.524	175.362	740	322	3	Ridge	Good	2
39Cor	1	38	10	1	50	None	-36.524	175.362	730	29	10	Face	Good	2
40Cor	1	49	5	0	45	None	-36.523	175.361	735	281	5	Ridge	Good	2
41Cor	15	40	10	0	35	None	-36.521	175.362	715	300	6	Gully	Poor	2
42Cor	3	59	7	1	30	None	-36.521	175.361	705	302	21	Gully	Medium	2
43Cor		75	10	0	15	Fire	-36.54	175.402	885	66	20	Face	Good	2
44Cor	1	34	40	0	25	Fire	-36.539	175.403	890	58	15	Face	Good	2
45Cor		35	35	0	30	Fire	-36.54	175.401	865	215	17	Face	Medium	2
46Cor	1	57	10	2	30	Fire	-36.54	175.401	860	13	30	Face	Good	2
47Cor	1	44	30	10	15	Fire	-36.54	175.401	870	338	25	Face	Good	2
48Cor	1	69	15	10	15	None	-36.524	175.36	680	268	25	Gully	Good	2
49Cor		65	5	3	30	None	-36.523	175.359	670	267	30	Face	Good	2
50Cor	4	87	5	1	3	None	-36.521	175.36	680	201	37	Face	Good	2
51Cor	1	59	10	0	30	None	-36.521	175.36	675	327	29	Face	Good	2
52Cor	3	37	30	25	30	None	-36.521	175.36	675	322	18	Gully	Good	2
53Cor		70	5	0	25	None	-36.525	175.361	705	292	33	Face	Good	2
54Cor		56	4	0	40	None	-36.524	175.359	680	229	9	Ridge	Good	2
55Cor	3	88	4	3	4	None	-36.522	175.358	610	223	41	Face	Good	2
56Cor	2	67	6	4	25	None	-36.522	175.358	620	313	33	Face	Good	2
57Cor	7	55	25	30	3	None	-36.522	175.358	620	281	24	Gully	Poor	2
58Cor		71	4	2	25	None	-36.521	175.359	615	235	19	Ridge	Good	2
59Cor	3	87	6	3	4	None	-36.521	175.359	620	195	32	Face	Good	2
60Cor	1	62	30	0	7	None	-36.522	175.356	560	29	32	Face	Good	2
61Cor		89	3	1	7	None	-36.521	175.356	565	236	12	Ridge	Good	2
62Cor	1	88	3	1	7	None	-36.519	175.356	550	223	29	Ridge	Good	2
63Cor		67	2	1	30	None	-36.523	175.342	510	16	16	Ridge	Good	2
64Cor		70	15	0	15	None	-36.522	175.343	485	315	7	Ridge	Good	2
65Pir	1	48	1	0	50	Tracked	-38.434	175.281	300		0	Ridge	Medium	3
66Ure		75	10	0	15		-38.901	176.571	860	320	9	Ridge	Good	4
67Ure		75	5	0	20		-38.901	176.571	860	320	9	Ridge	Good	4
68Ure		60	20	0	20	None	-38.843	176.685	800	270	3		Good	4
69Ure		30	40	0	30		-38.843	176.685	800	270	3		Good	4
70Tai				0		Logged	-37.015	175.7	620	360	2			4
71Tai				0		None	-37.024	175.702	640	90	25			4
72Tai				0		Logged	-37.047	175.715	645	325				4
73Tai				0		Mined	-37.177	175.693	630	360	5			4
74Tai				0		Logged	-37.228	175.749	275		5			3
75Tai				0		Mined	-37.22	175.7	580	335	30			3
76Tai				0		Logged	-37.219	175.701	660	80	5			3
77TeA				0		Mined	-37.483	175.759	500	270	25			3
78TeA				0		Mined	-37.528	175.75	765	330	15			4
79TeA				0		Mined	-37.535	175.856	700	30	5			3

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
80TeA				0			-37.546	175.771	780	140	3			4
81TeA				0		Mined	-37.504	175.853	460	225	2			3
82TeA				0		Logged	-37.52	175.816	320	300	2			3
83TeA				0		Mined	-37.523	175.776	420		50			3
84TeA				0		Mined	-37.586	175.83	550	50	5			3
85TeA				0		Logged	-37.586	175.824	640	120	5			3
86TeA				0		Fire	-37.596	175.857	700	90				4
87TeA				0		Mined	-37.673	175.919	540	250	5			3
88TeA				0		Logged	-37.66	175.848	725	270	40			4
89TeA				0		Mined	-37.66	175.852	775	270	1			4
90TeA				0		Mined	-37.688	175.843	460	360	10			3
91Wat				0			-36.984	174.528	430	250	2	Seepage slope	6	3
92Wat				0			-36.982	174.527	410	0	0	Interfluve		3
93Wat				0			-36.984	174.535	400	0	10	Convex creep slope	6	3
94Wat				0			-36.985	174.537	410	240	2	Seepage slope	6	3
95Wat				0			-36.984	174.529	459	180	2	Seepage slope	6	3
96Wat				0			-36.987	174.528	420	310	5	Seepage slope	6	3
97Wat				0			-36.979	174.521	400	270	15	Convex creep slope	6	3
98Wat				0		Grazed	-36.983	174.516	280	340	9	Transport midslope	6	3
99Wat				0			-36.988	174.517	290	260	27	Transport midslope	6	3
100Wat				0			-36.986	174.516	310			Colluvial footslope	6	4
101Wat				0		Logged	-37.001	174.523	290	290	6	Transport midslope	6	3
102Wat				0		Fire	-36.995	174.518	310	240	19	Transport midslope	6	3
103Wat				0			-36.997	174.538	360	20	15	Transport midslope	6	3
104Wat				0		Logged	-36.997	174.537	300	20	10	Transport midslope	6	3
105Wat				0			-36.987	174.545	310	230	10	Convex creep slope	6	3
106Wat				0			-36.991	174.548	370	220	8	Seepage slope	6	3
107Wat				0			-37.002	174.53	380	90	35	Convex creep slope	6	3
108Wat				0		Logged	-37.005	174.542	360	130	6	Seepage slope	6	3
109Wat				0			-36.974	174.507	270	244	21	Transport midslope	6	3
110Wat				0			-36.943	174.493	290	270	12	Fall face		3
111Wat				0			-36.941	174.487	260	280	11	Transport midslope	6	3
112Wat				0			-36.919	174.514	220	320	35	Transport midslope	6	3
113Wat				0			-36.932	174.543	330	50	4	Seepage slope	6	3
114Wat				0			-36.942	174.55	340	130	20	Convex creep slope	6	3
115Wat				0			-36.931	174.562	370	65	5	Seepage slope	6	3
116Wat				0			-36.912	174.519	230	70	22	Transport midslope	6	3
117Wat				0			-36.926	174.532	220	260	3	Seepage slope	6	3
118Wat				0			-36.91	174.537	400	70	5	Interfluve		3
119Wat				0			-36.917	174.524	300	260	3	Seepage slope	6	3
120Wat				0			-36.915	174.555	300	80	20	Transport midslope	6	3
121Wat				0			-36.914	174.558	370	290	5	Seepage slope	6	3
122Wat				0			-36.909	174.542	320	240	7	Convex creep slope	6	3
123Wat				0			-36.975	174.54	280	20	3	Convex creep slope	6	3
124Wat				0			-36.977	174.543	360	100	16	Convex creep slope	6	3

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
125Wat				0			-36.957	174.551	320	120	5	Seepage slope	6	3
126Wat				0		Grazed	-36.952	174.546	220	135	25	Transport midslope	6	3
127Wat				0			-36.954	174.521	300	270	30	Convex creep slope	6	3
128Wat				0			-36.956	174.547	345	0	15	Convex creep slope	6	3
129Wat				0			-36.958	174.55	260	280	25	Convex creep slope	6	4
130Wat				0			-36.968	174.532	370	130	10	Transport midslope	6	3
131Wat				0			-36.97	174.535	240	350	15	Convex creep slope	6	3
132Wat				0			-36.966	174.518	270	155	35	Fall face		3
133Wat				0			-36.966	174.519	360	180	30	Convex creep slope	1	3
134Wat				0			-36.961	174.533	340	80	42	Fall face		3
135Wat				0			-36.935	174.574	360	300	5	Convex creep slope	6	3
136Wat				0			-36.943	174.557	340	110	17	Transport midslope	6	3
137Wat				0			-36.95	174.561	280	130	5	Transport midslope	6	3
138Wat				0			-36.959	174.575	300	0	5	Convex creep slope	6	4
139Wat				0			-36.956	174.576	340	110	17	Fall face		3
140Tai				0		Logged	-37.133	175.683	560	290	15			3
141Tai				0		Mined	-37.102	175.716	460	340	5			3
142Wai		20	30	0	50		-35.633	173.616	540	60	10	Face	Medium	1
143Wai		80		0	20		-35.632	173.576	280	54	1	Terrace	Good	1
144Wai		70	10	0	20		-35.632	173.576	280	41	3	Ridge	Good	1
145Wai		30	10	0	60		-35.633	173.616	540	240	0	Ridge	Medium	1
147Kai		13	7	0	80	Logged	-37.478	175.775	565	0	0	Terrace	Medium	3
148Kai	2	63	5	0	30	None	-37.691	175.869	530	100	14	Face	Good	3
149Kai	2	57	10	1	30		-37.555	175.809	680	120	30	Face	Medium	3
150Kai	5	44	10	1	40	None	-37.694	175.872	680	240	29	Face	Medium	3
151Kai	2	10	2	2	84	None	-37.69	175.872	720	280	30	Face	Medium	4
152Kai	5	55	25	0	15	None	-37.69	175.872	740	220	2	Ridge	Poor	4
153Kai		40	10	0	50		-37.69	175.873	520	260	9	Ridge	Poor	3
154Kai		80	5	0	15		-37.693	175.866	520	220	15	Face	Medium	3
155Kai		68	10	2	20	None	-37.692	175.867	520	220	15	Terrace	Medium	3
156Kai	5	50	20	0	25	None	-37.692	175.868	780	50	4	Ridge	Poor	4
157Kai	1	48	1	0	50	None	-37.689	175.875	560	200	28	Face	Good	3
158Kai		40	20	0	40	None	-37.691	175.87	760	45	10	Face	Medium	3
159Kai	5	40		3	52		-37.69	175.876	500	290	19	Ridge	Good	3
160Kai		65	5	0	30		-37.698	175.878	560	205	10	Face	Medium	3
161Kai		55	15	0	30	None	-37.697	175.877	550	190	18	Face	Medium	3
162Kai		65	5	0	30	None	-37.697	175.877	560	310	20	Face	Good	3
163Kai		80	2	1	17		-37.697	175.876	460	290	25	Face	Medium	3
164Kai	1	69	10	0	20	None	-37.697	175.875	500	110	8	Face	Good	3
165Kai	1	79	5	0	15	None	-37.705	175.883	480	200	5	Terrace	Medium	3
166Kai		80	3	0	17		-37.705	175.884	500	180	5	Face	Medium	3
167Kai		80	5	0	15		-37.704	175.885	500	160	2	Face	Poor	3
168Kai		65	5	0	30	None	-37.703	175.888	500	130	24	Face	Poor	3
169Kai		39	20	1	40	None	-37.69	175.878	540	230	45	Face	Good	3
170Kai		25	5	0	70	None	-37.703	175.889	720	55	33	Face	Good	3

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
171Kai		55	20	0	25	Logged	-37.69	175.878	580	290	3	Face	Medium	3
172Kai		38	2	0	60	Logged	-37.477	175.778	565	200	2	Ridge	Medium	3
173Kai		45	5	0	50	Logged	-37.478	175.774	580	300	13	Face	Poor	3
174Kai	7	33	20	0	40	Logged	-37.477	175.775	590	200	2	Terrace	Medium	3
175Wai		70	15	0	15	None	-35.593	173.581	445	40	45	Fall face	Good	1
176Wai		10	35	0	55	None	-35.593	173.58	450	100	4	Convex creep slope	Poor	1
177Wai		60	5	0	35	None	-35.587	173.486	400	290	4	Interfluve	Good	1
178Wai		50	15	0	35	None	-35.591	173.586	333	40	5	Seepage slope	Good	1
179Wai		30	30	0	40	None	-35.593	173.586	335	180	8	Seepage slope	Good	1
180Wai		75	5	0	20	None	-35.594	173.587	375	28	15	Convex creep slope	Good	1
181Wai		30	40	0	30	None	-35.595	173.588	400	20	10	Seepage slope	Medium	1
182Wai		65	20	0	15	None	-35.597	173.588	420	280	7	Convex creep slope	Medium	1
183Wai		65	20	0	15	None	-35.599	173.589	435	20	11	Seepage slope	Medium	1
184Wai		20	25	0	55	None	-35.602	173.591	470	290	14	Transport midslope	Medium	1
185Wai		65	5	0	30	None	-35.648	173.569	215	200	18	Seepage slope	Good	1
186Wai		30	50	0	20	None	-35.606	173.505	310	30	1	Seepage slope	Medium	1
187Wai		65		0	35	None	-35.604	173.505	340	0	3	Seepage slope	Good	1
188Wai		50	5	0	45	None	-35.601	173.505	310	90	5	Seepage slope	Good	1
189Wai		35	40	0	25	None	-35.6	173.484	310	142	8	Seepage slope	Good	1
190Wai		75	5	0	20	None	-35.614	173.505	310	340	4	Seepage slope	Good	1
191Wai		60		0	40	None	-35.608	173.505	380	40	8	Seepage slope	Good	1
192Puk				0		Grazed	-37.612	178.09	140	200	15	Convex creep slope	Good	3
193Puk				0			-37.647	178.039	280	10	10	Seepage slope	70	4
194Puk	40	40	10	0	10	None	-35.21	173.753	200	260	20	Ridge	Good	1
195Rot	0	85	0	0	15	Logged	-38.124	176.367	500	280	20		Good	3
196Rot	0	70	0	0	30	None	-38.114	176.447	594	280	30	Face	Good	3
197Rot	5	75	0	0	20	None	-38.116	176.448	701	280	35		Good	4
198Rot	0	90	0	0	10	Logged	-38.118	176.449	720	300	20		Good	4
199Rot	0	50	0	0	50	Logged	-38.12	176.449	819	180	30	Face	Good	4
200Rot	10	40	0	0	50	Logged	-38.121	176.45	790	300	25		Good	4
201Rot	0	50	0	0	50	Logged	-38.122	176.451	820	0	0		Medium	4
202Puk	30	30	10	5	15	None	-35.239	173.747	395	70	15	Face	Medium	1
203Puk	25	30	15	15	15	None	-35.239	173.747	390	55	25	Face	Good	1
204Puk	40	40	10	0	10	None	-35.239	173.747	400	310	10	Ridge	Good	1
205Puk	35	35	10	5	15	None	-35.239	173.747	405	60	10	Face	Good	1
206Puk	25	25	25	0	25	None	-35.23	173.74	395	170	35	Face	Good	1
207Puk	30	20	20	10	20	Tracked	-35.23	173.74	395	170	35	Face	Good	1
208Puk	30	20	20	10	20	Tracked	-35.23	173.74	395	120	35	Face	Good	1
209Puk	40	20	20	0	20	Tracked	-35.23	173.74	410	40	5	Ridge	Good	1
210Puk	30	25	20	0	25	Tracked	-35.23	173.74	400	90	15	Face	Medium	1
211Puk	45	20	15	0	20	Tracked	-35.23	173.74	405	200	5	Ridge	Good	1
212Puk	40	20	20	0	20	Tracked	-34.959	173.737	395	20	5	Ridge	Medium	1
213Puk	15	30	30	0	25	Tracked	-35.23	173.74	400	40	25	Face	Medium	1
214Puk	25	25	25	0	25	None	-35.23	173.74	395	110	10	Gully	Poor	1
215Puk	30	40	15	0	15	None	-35.23	173.74	400	170	20	Face	Good	1

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
216Puk	25	25	25	0	25	None	-35.23	173.74	395	130	10	Gully	Medium	1
217Puk	25	25	25	0	25	None	-35.23	173.74	405	75	15	Face	Good	1
218Puk	20	25	25	5	25	None	-35.23	173.74	400	40	10	Gully	Medium	1
219Puk	25	25	25	0	25	None	-35.23	173.74	395	180	20	Face	Medium	1
220Puk	20	20	20	20	20	None	-35.23	173.74	390	140	20	Gully	Good	1
221Puk	25	25	25	0	25	None	-35.23	173.74	405	110	5	Ridge	Good	1
222Puk	25	25	25	0	25	None	-35.23	173.74	400	20	15	Face	Good	1
223Puk	20	25	25	10	20	None	-35.23	173.74	390	350	30	Gully	Good	1
224Puk	25	25	25	0	25	None	-35.23	173.74	400	360	10	Face	Good	1
225Puk	35	40	5	10	10	None	-35.216	173.757	280	300	15	Face	Good	1
226Puk	25	25	25	0	25	None	-35.228	173.752	380	300	15	Face	Good	1
227Puk	30	25	20	0	25	None	-35.228	173.752	365	310	15	Face	Medium	1
228Puk	25	35	10	0	30	None	-35.228	173.752	335	340	10	Face	Good	1
229Puk	25	25	25	0	25	None	-35.228	173.752	390	290	15	Face	Medium	1
230Puk	25	25	25	0	25	None	-35.228	173.752	380	320	20	Face	Good	1
231Puk	35	30	10	0	25	None	-35.228	173.752	365	300	20	Ridge	Good	1
232Puk	38	37	10	0	15	None	-35.228	173.752	390	40	15	Face	Good	1
233Puk	35	35	13	2	15	None	-35.228	173.752	380	30	25	Face	Good	1
234Puk	38	37	8	2	15	None	-35.228	173.752	335	60	10	Face	Good	1
235Puk	35	35	10	0	20	None	-35.228	173.752	330	120	10	Face	Good	1
236Puk	35	35	10	0	20	None	-35.228	173.752	325	90	5	Face	Good	1
237Puk	30	30	15	0	25	None	-35.228	173.752	315	0	15	Face	Good	1
238Puk	35	35	10	0	20	None	-35.228	173.752	380	50	15	Face	Good	1
239Puk	40	40	8	2	10	None	-35.228	173.752	365	40	25	Face	Good	1
240Puk	30	30	15	5	20	None	-35.228	173.752	330	60	10	Face	Medium	1
241Puk	30	30	15	5	20	None	-35.228	173.752	320	110	10	Face	Good	1
242Puk	30	50	10	0	10	None	-35.228	173.752	315	70	10	Face	Medium	1
243Puk	40	40	5	5	10	None	-35.228	173.752	365	0	20	Face	Good	1
244Puk	30	30	15	10	15	None	-35.228	173.752	325	55	10	Gully	Medium	1
245Puk	35	35	10	10	10	None	-35.228	173.752	320	80	10	Gully	Medium	1
246Puk	40	40	10	5	15	None	-35.228	173.752	315	80	10	Gully	Good	1
247Puk	40	40	10	5	5	None	-35.228	173.752	315	130	15	Face	Good	1
248Puk	35	35	15	0	15	None	-35.228	173.752	310	20	10	Face	Good	1
249Mot				0			-38.004	177.493	76	110	30			3
250Mot				0			-38.046	177.576	46	24	45			3
251Mot				0			-37.803	177.833	244	10	15			3
252Mot				0			-37.788	177.741	244	110	15			3
253Mot				0			-37.775	177.774	122	300	20			3
254Mot				0			-37.694	177.823	46	0	0			3
255Mot				0			-37.699	177.826	5	195	45			3
256Rau	10	55	10	20	5	None	-37.926	177.701	420	90	55	Gully	Good	3
257Rau		75	5	0	20	None	-37.925	177.701	480	180	15	Ridge	Good	4
258Rau		60	5	0	35	None	-37.924	177.7	540		45	Ridge	Good	4
259Rau	5	45		45	5	None	-37.928	177.718	90	100	40	Face	Good	3
260Rau	10	40		40	10	None	-37.928	177.717	180	100	42	Face	Good	3

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
261Rau	20	35	5	5	35		-37.928	177.728	120	10	45	Face	Good	3
262Rau		40	5	35	20	None	-37.927	177.702	360	125	35	Ridge	Good	3
263Puk				0		Logged	-37.629	178.251	640	360	10	Interfluve		4
264Puk				0			-37.628	178.251	730	216	20	Seepage slope	70	4
265Puk				0		Tracked	-37.662	178.166	560	60	15	Interfluve		3
266Puk				0			-37.677	178.166	700	100	20	Seepage slope	70	4
267Puk				0			-37.667	177.958	320	340	15	Convex creep slope	Good	4
268Puk				0			-37.671	177.96	370	320	15	Interfluve	Good	4
269Kai		10	10	0	80		-37.556	175.809	700	280	15	Face	Poor	4
270Kai		20	55	0	25		-37.555	175.808	700	260	15	Face	Medium	4
271Kai		45	25	0	30		-37.555	175.809	660	260	18	Face	Medium	4
272Kai		25	5	0	70		-37.554	175.811	700	255	10	Face	Medium	4
273Kai		20	10	0	70		-37.553	175.808	660	300	15	Face	Medium	4
274Kai		40		0	60		-37.552	175.809	640	300	26	Face	Good	4
275Kai		60	20	0	20		-37.555	175.807	680	30		Face	Medium	4
276Kai		50	30	0	20	Logged	-37.556	175.806	750	300	13	Face	Poor	4
277Kai		40	10	0	50		-37.558	175.805	760	355	20	Face	Poor	4
278Kai	2	40	20	0	38	None	-37.559	175.804	780	30	26	Face	Poor	4
279Kai		20	30	0	50	None	-37.559	175.802	840	340	15	Face	Poor	4
280Kai		60	10	0	30	None	-37.554	175.807	660	130	14	Face	Medium	4
281Kai		55	15	0	30		-37.553	175.807	700	120	15	Face	Medium	4
282Kai		15	30	5	50	None	-37.562	175.808	820	270	24	Face	Poor	4
283Kai			10	0	90	None	-37.562	175.807	800	300	7	Face	Medium	4
284Kai		10		0	90		-37.562	175.804	780	120	20	Face	Good	4
285Kai		30	10	0	60	None	-37.562	175.804	800	90	9	Face	Medium	4
286Kai		30	10	0	60	None	-37.561	175.81	740	330	8	Face	Medium	4
287Kai		4	4	2	90	None	-37.561	175.812	800	170	5	Face	Medium	4
288Kai		10	5	0	85	None	-37.518	175.793	680	155	23	Face	Medium	4
289Kai		50	20	0	30	None	-37.523	175.79	760	50	31	Face	Good	4
290Kai	5	5		0	90		-37.523	175.787	800	25	20	Face	Medium	4
291Kai		15	5	0	80	None	-37.519	175.799	760	270	26	Face	Good	4
292Kai		63	5	2	30	None	-37.569	175.856	420	185	40	Face	Good	3
293Kai		78		2	20	Logged	-37.568	175.858	500	190	45	Face	Good	3
294Kai	2	77		1	20	Logged	-37.556	175.83	540	5	37	Ridge	Good	3
295Kai	1	80	4	0	15	None	-37.571	175.851	150	70	22	Face	Medium	3
296Kai	2	55	3	0	40	None	-37.57	175.849	250	90	22	Face	Good	3
297Kai		75		0	25		-37.569	175.848	300	120	20	Ridge	Good	3
298Kai		30	5	5	60	Logged	-37.551	175.834	400	230	44	Face	Good	3
299Kai	5	65		2	28	none	-37.545	175.842	300	290	25	Face		3
300Kai	10	50	10	1	29		-37.556	175.835	380	10	37	Face	Medium	3
301Kai		68	1	1	30	None	-37.556	175.832	450	360	36	Face	Medium	3
302Kai		50	20	0	30	none	-38.97	176.087	655	360	1	Terrace	Medium	4
303Wai	5	40	35	0	20	None	-35.629	173.569	350	320	2	Interfluve	Medium	1
304Wai	10	40	25	0	25	None	-35.629	173.568	350	0	3	Interfluve	Medium	1
305Wai	5	80	5	0	10	None	-35.628	173.567	335	340	12	Seepage slope	Good	1

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
306Wai	5	60	10	0	25	None	-35.626	173.562	300	230	11	Seepage slope	Good	1
307Wai		50		0	50	None	-35.631	173.537	255	240	5	Seepage slope	Good	1
308Wai		45	25	0	30	None	-35.628	173.537	270	235	11	Seepage slope	Medium	1
309Wai		30	20	0	50	Logged	-35.611	173.52	310	30	1	Alluvial toeslope	Poor	1
310Wai		40	30	0	30	Logged	-35.611	173.521	305	20	3	Seepage slope	Poor	1
311Wai		30	20	0	50	Logged	-35.61	173.521	300	20	1	Alluvial toeslope	Poor	1
312Wai	5	40	15	0	40	Logged	-35.61	173.522	300	0	0	Interfluve	Poor	1
313Wai		20	50	0	30	None	-35.609	173.524	320	210	4	Seepage slope	Medium	1
314Wai		40	10	0	50	None	-35.61	173.53	330	50	1	Interfluve	Medium	1
315Wai		50	10	5	35	None	-35.653	173.614	320	20	4	Colluvial footslope	Good	1
316Wai		65	10	0	25	None	-35.646	173.597	280	140	12	Convex creep slope	Good	1
317Wai		60	10	0	30	None	-35.681	173.625	440	200	2	Interfluve	Good	1
318Wai		40	15	0	45	None	-35.66	173.616	450	0	6	Seepage slope	Good	1
319Wai		70	5	0	25	None	-35.664	173.616	470	20	5	Colluvial footslope	Medium	1
320Wai		50	20	0	30	None	-35.665	173.616	495	30	22	Convex creep slope	Good	1
321Wai		75		0	25	None	-35.62	173.554	350	160	22	Convex creep slope	Good	1
322Wai		55	5	0	40	None	-35.619	173.556	370	85	4	Seepage slope	Good	1
323Wai		60	10	0	30	Logged	-35.617	173.558	400	260	2	Seepage slope	Medium	1
324Wai		35	20	0	45	None	-35.615	173.561	420	195	39	Convex creep slope	Good	1
325Wai	5	35	30	0	30	None	-35.613	173.563	440	74	26	Convex creep slope	Good	1
326Wai		45	15	0	40	None	-35.609	173.565	490	140	5	Seepage slope	Medium	1
327Wai		30	40	0	30	None	-35.614	173.603	510	60	3	Interfluve	Medium	1
328Wai		10	80	0	10	None	-35.615	173.612	550	280	1	Alluvial toeslope	Poor	1
329Wai	5	15	50	0	30	None	-35.615	173.613	560	325	3	Seepage slope	Poor	1
330Wai	5	50	5	0	40	None	-35.614	173.615	595	330	10	Seepage slope	Good	1
331Wai		40	40	0	20	None	-35.611	173.619	570	270	2	Colluvial footslope	Medium	1
332Wai	5	35	40	0	20	None	-35.608	173.625	580	230	18	Convex creep slope	Good	1
333Wai		5	40	0	55	None	-35.607	173.628	640	220	12	Convex creep slope	Good	1
334Wai		40	20	0	40	None	-35.636	173.616	510	75	7	Interfluve	Medium	1
335Wai		20	50	0	30	None	-35.636	173.618	485	110	14	Convex creep slope	Medium	1
336Wai		50	5	0	45	None	-35.636	173.619	460	170	2	Interfluve	Medium	1
337Wai		50	25	0	25	None	-35.637	173.623	435	340	5	Interfluve	Medium	1
338Wai		75	5	0	20	None	-35.637	173.624	400	146	6	Interfluve	Good	1
339Wai		60	20	0	20	None	-35.637	173.626	410	118	20	Transport midslope	Medium	1
340Wai		85	5	0	10	None	-35.637	173.626	390	60	20	Colluvial footslope	Good	1
341Wai		80	5	0	15	None	-35.642	173.606	460	252	13	Interfluve	Medium	1
342Wai		45	15	0	40	None	-35.643	173.604	380	195	14	Convex creep slope	Good	1
343Wai		50	10	0	40	None	-35.645	173.602	360	205	20	Convex creep slope	Medium	1
344Wai		50	5	0	45	None	-35.672	173.563	260	350	4	Seepage slope	Good	1
345Wai	5	40	30	0	25	None	-35.636	173.629	410	240	45	Fall face	Medium	1
346Wai		50	5	0	45	None	-35.635	173.63	430	170	17	Convex creep slope	Good	1
347Wai		75	5	0	20	None	-35.635	173.631	430	310	15	Convex creep slope	Good	1
348Wai	5	60	5	0	30	None	-35.635	173.581	275	350	16	Transport midslope	Good	1
349Wai		55	5	0	40	None	-35.634	173.583	270	160	4	Interfluve	Good	1
350Wai		30	20	0	50	None	-35.639	173.62	43	11	3	Interfluve	Medium	1

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
351Wai		30	30	0	40	None	-35.639	173.624	440	160	2	Interfluve	Medium	1
352Wai		35	30	0	35	None	-35.637	173.627	395	260	3	Colluvial footslope	Good	1
353Wai		60	10	0	30	None	-35.677	173.572	133	100	6	Alluvial toeslope	Good	1
354Wai		75	10	0	15	None	-35.676	173.571	170	52	9	Seepage slope	Good	1
355Wai		70		0	30	None	-35.675	173.571	195	45	30	Convex creep slope	Good	1
356Wai		70	5	0	25	None	-35.616	173.537	290	95	23	Convex creep slope	Good	1
357Wai		70	5	0	25	None	-35.613	173.535	325	280	6	Seepage slope	Good	1
358Wai		45	5	0	50	None	-35.612	173.535	330	180	15	Seepage slope	Good	1
359Wai		60		0	40	None	-35.6	173.533	235	30	6	Seepage slope	Good	1
360Wai		35	5	0	60	None	-35.592	173.534	485	205	18	Transport midslope	Good	1
361Wai	25	75		0			-35.589	173.534	535	180	8	Seepage slope	9	1
362Wai		65	5	0	30	None	-35.619	173.538	265	60	3	Colluvial footslope	Good	1
363Rau	10	70		0	20		-37.963	178.054	335	0	25	Ridge	Good	4
364Rau				0			-37.963	178.054	375	70	15	Ridge	Good	4
365Rau	10	35	10	5	40		-38.002	177.647	411	90	20	Face	Good	3
366Rau	10	80		0	10		-37.963	178.054	280	20	3	Ridge	Good	4
367Rau	10	65		5	20		-37.963	178.054	302	350	18	Face	Good	4
368Rau	15	45		5	35		-37.963	178.054	335	350	25	Face	Good	4
369Rau	2	15		3	80	None	-37.963	178.054	300	90	25	Face	Good	4
370Ure		15	5	0	80	Tracked	-38.951	176.746	671	95	18	Ridge	Good	4
371Ure		75	5	0	20	None	-38.953	176.745	732	20	22	Face	Good	4
372Ure		70	10	0	20	None	-38.952	176.74	838	205	32	Face	Good	4
373Ure		60	20	0	20	None	-38.953	176.735	1006	115	25	Ridge	Good	4
374Ure		60	25	0	15	None	-38.949	176.73	747	335	48	Ridge	Good	4
375Ure	5	40	10	0	45	None	-38.91	176.573	885	350	43	Face	Good	4
376Ure		40	25	0	35	None	-38.909	176.57	792	20	2	Face	Good	4
377Ure		65	5	10	20	None	-38.907	176.571	824	360	42	Face	Good	4
378Ure		25	15	0	60	None	-38.986	176.676	671	320	25	Face	Good	4
379Ure		35	5	0	60	None	-38.889	176.697	940					4
380Ure		60	10	0	30	None	-38.888	176.697	915	240	43	Face	Good	4
381Ure		20	10	0	70	None	-38.884	176.692	885	75	34	Face	Good	4
382Ure		65	20	0	15	None	-38.938	176.75	853	210	19	Ridge	Good	4
383Ure		60	15	0	25	None	-38.934	176.751	975	151	16	Ridge	Good	4
384Ure		40	5	0	55	Logged	-38.988	176.675	671	230	20	Face	Good	4
385Ure		65	20	0	15	None	-38.987	176.679	732	270	30	Face	Good	4
386Ure		65	15	0	20	None	-38.988	176.682	792	295	30	Face	Good	4
387Ure		70	20	0	10	None	-38.988	176.688	1068	315	40	Ridge	Good	4
388Ure				0		None	-38.988	176.694	1190	320	40	Gully		4
389Ure		50	15	0	35	None	-38.908	176.577	671	76	4	Terrace	Medium	4
390Ure		30		0	70	None	-38.979	176.726	914	110	10	Gully	Medium	4
391Ure		20	5	0	75		-38.979	176.721	975	100	45	Face	Good	4
392Ure		20	10	0	70	None	-38.979	176.72	823	95	40	Face	Good	4
393Ure		25	5	0	70		-38.964	176.686	853	50	0	Terrace	Poor	4
394Ure		20	5	0	75	None	-38.964	176.687	899	260	10	Face	Good	4
395Ure		60	5	0	35		-38.964	176.688	945	320	25	Face	Good	4

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
396Ure		30	5	0	65	None	-38.965	176.69	1021	330	5	Gully	Medium	4
397Ure		20	5	0	75		-38.966	176.694	762	325	10	Face	Good	4
398Ure		20	5	0	75	None	-38.895	176.6	793	165	10	Ridge	Good	4
399Ure		40	20	0	40	None	-38.897	176.603	1067	320	19	Face	Good	4
400Ure		20	5	5	70	None	-38.931	176.699	1097	20	30	Face	Good	4
401Ure		70	15	0	15	None	-38.931	176.698	1127	310	25	Face	Good	4
402Ure		45	5	0	50		-38.931	176.696	914	310	15	Ridge	Good	4
403Ure		30	30	0	40	None	-38.947	176.689	960	280	10	Terrace	Good	4
404Ure		40	15	0	45	None	-38.947	176.691	990	140	25	Face	Good	4
405Ure		50	5	0	45	None	-38.946	176.692	1097	250	20	Face	Good	4
406Ure		30	40	0	30	None	-38.904	176.711	792	100	30	Face	Good	4
407Ure	80	5	10	0	5		-38.928	176.734	853	25	20	Ridge	Good	4
408Ure	20		10	20	50		-38.928	176.731	914	50	20	Ridge	Good	4
409Ure		40	20	0	40		-38.929	176.73	975	340	0	Ridge	Good	4
410Ure				0			-38.93	176.728	1035	140	25	Face	Good	4
411Ure		40	5	0	55		-38.93	176.727	1097	110	50	Face	Good	4
412Ure		30	50	0	20		-38.931	176.724	1036	11	0	Ridge	Good	4
413Ure		30	30	0	40	None	-38.931	176.702	914	20	35	Face	Good	4
414Ure		20	10	0	70	None	-38.881	176.692	975	0	20	Face	Good	4
415Ure		10		0	90	None	-38.879	176.691	1006	40	25	Face	Good	4
416Ure		5		0	95	None	-38.878	176.69	792	50	20	Face	Good	4
417Ure		40	50	0	10	None	-38.908	176.719	884	16	45	Ridge	Good	4
418Ure	5	50	5	10	30	None	-38.907	176.718	975	80	35	Face	Good	4
419Ure	5	15		60	20	None	-38.906	176.715	1021		30	Face	Good	4
420Ure		30	15	0	55	None	-38.906	176.713	1067	20	40	Face		4
421Ure		45	5	20	30	None	-38.905	176.712	950	30	25	Face	Good	4
422Ure		25	5	0	70	None	-38.918	176.589	240	90	30	Ridge	Good	4
423Ure		70		0	30	None	-38.481	176.676	300	195	5	Ridge	Good	3
424Kai		40		0	60	Logged	-37.5	175.82	800	200	12	Ridge	Good	3
425Ure		50	5	0	45	None	-38.42	177.288	800		23	Face	Good	4
426Ure		25	15	0	60	None	-38.42	177.288	800	220	21	Face	Good	4
427Ure		30		0	70	None	-38.42	177.288	300	330	24	Face	Good	4
428Kai		50	20	0	30	None	-37.558	175.838	660	30	10	Face	Medium	3
429Ure		40	10	0	50		-38.442	177	800	60	25	Face	Good	4
430Ure		35	5	0	60	None	-38.452	176.993	825	70	15	Face	Medium	4
431Ure		75	5	0	20	None	-38.455	176.991	487	260	25	Ridge	Good	4
432Ure	5	70	5	0	20		-38.439	177.032	570	28	35	Face	Good	3
433Ure		80	10	0	10		-38.492	177.008	585	225	25	Face	Good	3
434Ure		90	5	0	5		-38.492	177.009	300	236	26	Ridge	Good	3
435Kai		45	10	0	45	Logged	-37.5	175.82	810	225	16	Face	Good	3
436Ure		40	10	0	50	None	-38.496	177.027	300	107	31	Face	Good	4
437Kai		35		0	65	None	-37.5	175.82	330	220	30	Face	Good	3
438Kai		65		0	35	None	-37.524	175.727	200	155	10	Face	Good	3
439Kai		30		0	70	None	-37.56	175.854	300	85	4	Terrace	Good	3
440Kai		30	10	0	60	None	-37.558	175.838	300	30	10	Face	Medium	3

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
441Kai		65	15	0	20	None	-37.558	175.838	900	30	10	Face	Medium	3
442Ure		20		0	80	None	-38.856	176.571	915	70	35	Face	Good	4
443Ure		15		0	85	None	-38.855	176.57	930	0	15	Face	Good	4
444Ure		40		0	60	None	-38.855	176.568	945	0	5	Face	Good	4
445Ure		30		0	70	None	-38.854	176.567	960	40	5	Face	Good	4
446Ure		80		0	20	None	-38.854	176.565	750	260	25	Face	Good	4
447Ure		20		0	80	None	-38.899	176.572	800	70	30	Face	Good	4
448Ure		85	5	0	10	None	-38.898	176.571	850	40	30	Face	Good	4
449Ure		10	5	0	85	None	-38.897	176.568	950	200	35	Face	Good	4
450Ure		10	5	0	85	None	-38.895	176.567	1000	70	30	Face	Good	4
451Ure		20	5	0	75	None	-38.895	176.567	975	140	10	Ridge	Good	4
452Ure		10	5	5	80	None	-38.853	176.565	950	80	45	Face	Good	4
453Ure		5		0	95	None	-38.866	176.63	955	290	5	Ridge	Good	4
454Ure		10	5	0	85		-38.597	177.071	950	350	5	Ridge	Good	4
455Ure		35	5	0	60		-38.597	177.071	580	265	9	Ridge		4
456Ure	5	30	5	0	60	None	-38.5	177.054	620	350	20	Ridge	Good	3
457Ure	5	50	15	0	30		-38.492	177.042	660	270	20	Ridge	Good	4
458Ure	10	30	20	0	40		-38.495	177.042	660	320	15	Ridge	Good	4
459Rot	5		45	0	50	Fire	-37.966	176.53	250	60	8	Ridge	Good	3
460Kai	5	73	2	0	20	None	-37.712	175.925	350	330	23	Face	Good	3
461Kai	20	65	5	0	10	Logged	-37.714	175.923	410	20	4	Face	Good	3
462Kai		30	10	0	60	None	-37.778	175.912	270	30	18	Face	Good	3
463Kai	5	75	5	0	15	None	-37.861	175.909	350	125	26	Face	Good	3
464Kai	5	85	5	0	5	None	-37.859	175.912	410	225	22	Face	Good	3
465Kai	5	80		0	15	None	-37.857	175.913	530	295	34	Face	Good	3
466Kai		40		0	60	Logged	-37.849	175.926	550		0	Terrace	Poor	3
467Kai		70	10	0	20	Logged	-37.85	175.925	560	60	15	Terrace	Good	3
468Kai		50	20	0	30	Logged	-37.85	175.924	430	160	5	Terrace	Poor	3
469Kai		40		0	60	Fire	-37.853	175.906	490	300	7	Ridge	Good	3
470Kai	5	80	5	0	10	None	-37.853	175.907	560	180	25	Face	Good	3
471Kai	5	80	5	0	10	None	-37.851	175.909	560	230	24	Ridge	Good	3
472Kai	10	20	10	10	50	Logged	-37.84	175.927	580	135	12	Terrace	Medium	3
473Kai		70	10	0	20	Logged	-37.839	175.926	590	155	5	Terrace	Medium	3
474Kai		70	10	0	20	None	-37.838	175.925	520		0	Terrace	Poor	3
475Kai		50	10	0	40	Logged	-37.845	175.932	520	90	5	Terrace	Medium	3
476Kai		85	5	0	10	Logged	-37.846	175.931	530	285	15	Gully	Poor	3
477Kai		60	20	0	20	None	-37.848	175.927	520	160	8	Terrace	Medium	3
478Kai		50	20	0	30	Logged	-37.848	175.928	635	215	10	Terrace	Medium	3
479Kai		20		0	80	None	-37.662	175.869	640	10	30	Ridge	Good	4
480Kai		45	5	0	50	None	-37.663	175.868	560	20	15	Ridge	Good	4
481Kai	2	92	1	0	5	None	-37.673	175.876	585	40	21	Face	Good	3
482Kai	5	84	5	1	5	None	-37.674	175.875	680	50	18	Face	Good	3
483Kai	5	91		2	2	None	-37.676	175.875	735	80	35	Face	Good	3
484Kai	24		5	70	1	None	-37.678	175.874	820	70	38	Face	Good	4
485Kai	10	50	30	0	10	None	-37.681	175.873	220	0	0	Ridge	Poor	4

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
486Kai		94	1	0	5	Logged	-37.673	175.907	270	60	37	Face	Good	3
487Kai	1	94		0	5	None	-37.674	175.904	300	140	10	Ridge	Good	3
488Kai	2	93		0	5	Logged	-37.675	175.901	430	130	6	Face	Good	3
489Kai	1	93	1	0	5	None	-37.688	175.889	480	40	27	Face	Good	3
490Kai		90	5	0	5	None	-37.688	175.888	620	60	8	Terrace	Good	3
491Kai	1	92	2	0	5	None	-37.682	175.884	650	80	3	Ridge	Good	3
492Kai	1	93	1	0	5	None	-37.682	175.883	700	80	19	Ridge	Good	3
493Kai	1	89	3	0	7	None	-37.683	175.881	270	60	12	Ridge	Good	3
494Kai	10	35	15	5	35	None	-37.687	175.849	330	195	42	Face	Good	3
495Kai		20	10	30	40	None	-37.685	175.85	390	160	42	Face	Good	3
496Kai	10	40	10	0	40	None	-37.685	175.851	450	190	30	Face	Good	3
497Kai		45	20	5	30	None	-37.683	175.852	510	215	11	Ridge	Good	3
498Kai		45	10	5	40	None	-37.682	175.854	570	35	5	Ridge	Good	3
499Kai	5	75		0	20	None	-37.713	175.855	630	210	15	Ridge	Good	3
500Kai		35	10	5	50	None	-37.713	175.856	690	0	0	Ridge	Good	3
501Kai		60	5	5	30	None	-37.712	175.857	730	250	20	Face	Good	3
502Kai	10	30	10	20	30	None	-37.71	175.858	460	220	40	Face	Good	3
503Kai	5	80	5	0	10	None	-37.704	175.869	490	60	16	Face	Good	3
504Kai		90	5	0	5	None	-37.705	175.87	490	300	11	Terrace	Good	3
505Kai	2	81	2	0	15	None	-37.706	175.871	440	70	15	Terrace	Good	3
506Kai	5	83	2	0	10	None	-37.724	175.883	440	0	0	Terrace	Good	3
507Kai		75	5	0	20	None	-37.723	175.884	430	360	2	Terrace	Good	3
508Kai	5	78	2	0	15	None	-37.723	175.886	400	10	42	Face	Good	3
509Kai	5	65	5	20	5	None	-37.722	175.889	410	120	20	Gully	Poor	3
510Kai		90		0	10	None	-37.722	175.888	410	50	5	Terrace	Good	3
511Kai	5	80	5	0	10	None	-37.731	175.886	430	240	2	Terrace	Medium	3
512Kai	5	80	5	0	10	None	-37.731	175.887	440	310	12	Face	Good	3
513Kai	2	78	5	0	15	None	-37.731	175.889	440	10	8	Face	Good	3
514Kai	5	75	5	0	15	None	-37.731	175.89	410	210	15	Face	Good	3
515Kai	5	80	5	0	10	None	-37.731	175.885	440	290	2	Face	Good	3
516Kai	5	80	5	0	10	None	-37.731	175.891	460	0	0	Face	Good	3
517Kai	2	78	5	0	15	None	-37.731	175.892	440	130	16	Face	Good	3
518Kai	5	79	5	1	10	None	-37.731	175.888	470	180	16	Face	Good	3
519Kai	5	75	5	0	15	None	-37.731	175.893	500	180	16	Terrace	Good	3
520Kai	5	80	5	0	10	None	-37.731	175.9	400	0	0	Face	Good	3
521Kai	10	65		0	25	None	-37.703	175.904	440	60	15	Face	Good	3
522Kai	5	70		0	25	None	-37.509	175.747	500	20	15	Face	Good	3
523Kai		67	5	3	25	None	-37.511	175.747	550	360	22	Ridge	Good	3
524Kai	5	72	3	0	20	None	-37.514	175.747	640	36	15	Ridge	Good	3
525Kai		80		0	20	None	-37.518	175.746	650	10	19	Face	Good	3
526Kai	2	78	5	0	15	None	-37.519	175.746	270	0	0	Terrace	Good	3
527Kai	5	73	5	2	15	None	-37.505	175.822	370	180	23	Face	Good	3
528Kai	5	72	3	0	20	None	-37.5	175.818	410	150	28	Ridge	Good	3
529Kai	2	58	25	0	15	None	-37.5	175.817	440	160	12	Ridge	Good	4
530Kai	2	83		0	15	None	-37.499	175.817	470	150	13	Ridge	Good	4

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
531Kai		75	5	0	20	None	-37.499	175.816	480	120	2	Terrace	Medium	3
532Kai		70	5	0	25	None	-37.498	175.816	330	120	5	Terrace	Medium	3
533Kai	5	65	5	0	25	None	-37.526	175.846	370	85	11	Ridge	Good	3
534Kai		75		0	25	None	-37.526	175.841	430	350	9	Ridge	Good	3
535Kai		78	2	0	20	None	-37.526	175.838	530	290	11	Ridge	Good	3
536Kai	10	80	5	0	5	None	-37.526	175.834	300	360	9	Ridge	Medium	4
537Kai	2	90	3	0	5	Fire	-37.545	175.842	520	180	22	Face	Good	3
538Kai		77	3	0	20	Logged	-37.555	175.842	550	190	10	Face	Good	3
539Kai		73	5	2	20	Logged	-37.552	175.842	560	80	12	Face	Good	3
540Kai		40	50	0	10	None	-37.545	175.842	390	180	5	Terrace	Poor	4
541Kai		80	5	0	15	Logged	-37.556	175.835	430	25	17	Ridge	Good	3
542Kai		95		0	5	Logged	-37.556	175.832	480	0	38	Ridge	Good	3
543Kai		70	10	0	20	Logged	-37.556	175.83	560	130	28	Ridge	Good	3
544Kai		75	5	0	20	Logged	-37.557	175.823	590	90	18	Ridge	Good	3
545Kai		45	5	0	50	None	-37.557	175.821	560	65	13	Terrace	Medium	3
546Kai	5	85	3	2	5	None	-37.578	175.829	590	120	58	Ridge	Good	3
547Kai		30	5	0	65	None	-37.579	175.806	320	260	29	Ridge	Good	4
548Kai	10	75	5	5	5	None	-37.591	175.846	480	40	45	Face	Good	3
549Kai		5		15	80	None	-37.621	175.852	230			Ridge	Good	4
550Kai		93	1	1	5	None	-37.626	175.86	240	40	25	Face	Good	3
551Kai		84	1	5	10	Logged	-37.626	175.859	200	30	12	Face	Good	3
552Kai		30	10	0	60	None	-37.624	175.87	380	30	2	Ridge	Good	3
553Kai	5	80		0	15	None	-37.64	175.858	500	290	27	Face	Good	3
554Kai	5	70		0	25	None	-37.644	175.861	570	260	25	Face	Good	3
555Kai		10		0	90	None	-37.653	175.851	660		0	Ridge	Good	3
556Kai	5	60	5	0	30	None	-37.655	175.851	700	315	27	Face	Good	3
557Kai	10			40	50	None	-37.656	175.851	790	320	30	Face	Good	4
558Kai	10	55	10	5	20	None	-37.658	175.852	850	320	36	Ridge	Poor	4
559Kai		5	5	0	90	None	-37.661	175.852	420			Ridge	Poor	4
560Kai	20	45	5	0	30	None	-37.664	175.84	478	215	39	Face	Good	3
561Kai	5	20	30	5	40	None	-37.663	175.84	550	140	35	Face	Good	3
562Kai	40	10	10	10	30	None	-37.662	175.84	610	320	21	Ridge	Good	3
563Kai	30	40	20	0	10	None	-37.661	175.84	670	240	5	Ridge	Good	3
564Kai	20	10	30	10	30	None	-37.66	175.84	485	240	15	Ridge	Good	4
565Kai		20	10	0	70	None	-37.659	175.877	315	280	0	Ridge	Good	3
566Kai		70		5	25	Logged	-37.498	175.777	350	40	40	Face	Good	3
567Kai		75	5	0	20	Logged	-37.499	175.776	515	140	5	Face	Good	3
568Kai		70	5	0	25	None	-37.503	175.771	560	55	34	Ridge	Good	3
569Kai	2	73	5	0	20	None	-37.509	175.765	600	10	20	Face	Medium	3
570Kai		65		0	35	None	-37.511	175.763	640	20	11	Ridge	Good	3
571Kai		75	5	0	20	None	-37.512	175.759	420	205	11	Ridge	Good	3
572Kai		55	15	10	20	Logged	-37.511	175.786	490	60	47	Face	Good	3
573Kai		40	10	0	50	Logged	-37.513	175.782	590	135	23	Ridge	Good	3
574Kai		45	15	0	40	Logged	-37.518	175.771	570	85	25	Face	Medium	3
575Kai		40	10	5	45	None	-37.516	175.775	570	180	40	Face	Medium	3

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
576Kai		50	20	0	30	None	-37.518	175.772	600	240	20	Face	Good	3
577Kai		30	5	0	65	None	-37.518	175.769	330	0	0	Ridge	Good	3
578Kai	5	75	10	0	10	Logged	-37.52	175.797	370	215	26	Face	Good	3
579Kai		10		0	90	Logged	-37.52	175.797	440	230	25	Ridge	Good	4
580Kai		20	20	0	60	Logged	-37.518	175.799	480	200	21	Ridge	Good	4
581Kai	10	10	40	20	20	Logged	-37.519	175.799	520			Ridge	Good	4
582Kai		40	10	0	50	None	-37.518	175.8	370	170	19	Face	Good	3
583Kai		30	30	10	30	None	-37.525	175.782	580	65	43	Face	Good	3
584Kai	10	10	30	20	30	None	-37.527	175.772	670	50	6	Ridge	Good	4
585Kai		70	10	0	20	None	-37.527	175.77	740	50	15	Ridge	Good	4
586Kai		50	10	0	40	None	-37.528	175.766	770	120	11	Face	Good	4
587Kai		80	10	0	10	None	-37.528	175.765	450	60	11	Ridge	Good	4
588Kai		50	10	0	40	None	-37.533	175.787	490	95	35	Face	Good	3
589Kai		60	20	0	20	None	-37.535	175.786	490	260	43	Face	Good	3
590Kai		60	10	0	30	None	-37.535	175.785	600	330	20	Face	Good	3
591Kai	10	80	5	0	5	None	-37.536	175.784	650	280	32	Face	Good	3
592Kai	10	40	20	0	30	Fire	-37.536	175.783	650	40	24	Ridge	Good	4
593Kai		35	40	0	25	None	-37.537	175.783	650	20	35	Ridge	Good	4
594Kai	10	30	20	10	30	None	-37.537	175.783	480	335	35	Face	Good	4
595Kai	3	75	2	0	20	None	-37.527	175.815	470	105	10	Face	Good	3
596Kai	2	76	2	0	20	None	-37.527	175.814	560	150	27	Face	Good	3
597Kai	2	78	2	0	18	None	-37.528	175.821	630	235	32	Face	Good	3
598Kai	10	53	2	20	15	None	-37.532	175.832	660	220	48	Face	Good	3
599Kai		88	2	0	10	None	-37.532	175.833	475	220	45	Ridge	Good	4
600Kai	5	30	5	0	60	Logged	-37.483	175.831	420	0	0	Ridge	Good	3
601Kai		80		0	20	None	-37.485	175.833	275	70	18	Face	Good	4
602Kai	10	30	5	0	55	Logged	-37.49	175.843	410	350	25	Face	Good	3
603Kai	20	45	5	0	30	Logged	-37.489	175.835	520	20	21	Face	Good	3
604Kai	10	50	5	0	35	Logged	-37.486	175.811	250	130	10	Face	Medium	3
605Kai	10	50	10	0	30	None	-37.503	175.848	300	40	0	Ridge	Good	3
606Kai	3	77	2	0	18	None	-37.505	175.747	320	360	18	Ridge	Good	3
607Kai	5	70	5	0	20	None	-37.506	175.747	360	50	32	Ridge	Good	3
608Kai	2	73	5	0	20	None	-37.507	175.747	850	35	6	Ridge	Good	3
609Puk				0			-37.642	178.233	800	0	35	Convex creep slope	70	4
610Puk				0		Tracked	-37.637	178.251	730	0	10	Convex creep slope	1	4
611Puk				0		Tracked	-37.635	178.252	700	0	30	Convex creep slope	1	4
612Puk				0			-37.634	178.249	445	265	5	Convex creep slope	1	4
613Pir	0	95	5	0	10	None	-38.055	175.47	445	265	5	Face	Good	3
614Pir				0		None	-38.061	175.47	510	45	10	Face	Good	3
615Pir	5	60	15	0	35	None	-38.203	175.475	530	120	5	Terrace	Medium	3
616Pir	15	70	20	10	30	None	-38.203	175.475	560	200	5	Terrace	Medium	3
617Pir	5	5	25	40	80	None	-38.022	175.083	690	120	38	Gully	Poor	3
618Pir	5	80	10	2	10	None	-38.203	175.475	640	130	35	Ridge	Medium	3
619Pir				0		None	-38.177	175.474	545	286	10	Ridge	Good	3
620Pir				0		None	-38.167	175.474	600	325	15	Ridge	Good	3

Appendix 1: Plot characteristics continued

ID	S	L	M	R	V	D	Lat	Long	Alt	Asp	Sl	Phys	Dr	G
621Pir				0		None	-38.157	175.474	690	360	25	Ridge		3
622Moe				0			-36.534	175.4	750	12	8	Face	Good	3
623Kai		60	5	0	35		-37.505	175.822	560	100	36	Ridge	Good	4
624Kai		30	10	0	60		-37.5	175.818	610	10	33	Face	Good	4
625Kai	5	30	5	0	60		-37.5	175.817	720	45	21	Face	Good	4
626Kai				0		None	-37.499	175.817	770	90	16	Ridge	Good	4
627Kai	25	45		0	30	Fire	-37.557	175.842	370	200	13	Ridge	Good	3
628Kai		40		0	60	None	-37.58	175.85	280	320	15	Ridge	Good	3
629Kai	5	50	10	5	30	None	-37.575	175.852	340	253	30	Face	Good	3
630Kai	10	45	20	5	20	None	-37.576	175.852	400	20	30	Face	Good	3
631Kai	10	55	10	5	20	None	-37.577	175.852	450	345	38	Face	Good	3
632Kai	10	60	10	0	20	None	-37.578	175.852	520	20	20	Ridge	Good	3
633Kai	5	75		0	20		-37.575	175.846	260	140	18	Ridge	Good	3
634Kai		65	5	0	30		-37.575	175.844	320	110	4	Ridge	Good	3
635Kai	5	60		0	35	None	-37.574	175.842	380	120	40	Face	Good	3
636Kai	5	30	5	0	60		-37.574	175.84	430	20	30	Face	Good	3
637Kai		40	10	0	50		-37.56	175.845	470	60	26	Face	Good	3
638Kai	5	50	10	0	35		-37.562	175.842	520	70	28	Face	Good	3
639Kai	5	50	5	0	40		-37.563	175.839	570	100	25	Face	Good	3
640Kai	10	50	5	5	30		-37.554	175.834	330	150	3	Face	Medium	3
641Kai	5	20	5	20	50		-37.549	175.834	440	220	32	Face	Good	4
642Kai		40		0	60	Logged	-37.572	175.848	390	200	24	Face	Good	3

Appendix 2: Complete species list compiled from recce data on tāwari forest in the North Island, New Zealand.

Trees and Shrubs
Ackama rosifolia
Agathis australis
Alectryon excelsus
Alseuosmia macrophylla
Alseuosmia pusilla
Alseuosmia quercifolia
Androstoma empetrifolia
Aristotelia serrata
Arthropodium candidum
Arthropodium cirratum
Ascarina lucida
Beilschmiedia tarairi
Beilschmiedia tawa
Brachyglottis kirkii
Brachyglottis repanda
Carpodetus serratus
Celmisia notcilenta
Coprosma arborea
Coprosma areolata
Coprosma chathamica
Coprosma cheesemanii
Coprosma ciliata
Coprosma colensoi
Coprosma crassifolia
Coprosma cuneata
Coprosma dodonaeifolia
Coprosma foetidissima
Coprosma grandifolia
Coprosma linariifolia
Coprosma lucida
Coprosma microcarpa
Coprosma parviflora
Coprosma propinqua
Coprosma rhamnoides
Coprosma robusta
Coprosma rotundifolia
Coprosma spathulata
Coprosma tayloriae
Coprosma tenuicaulis
Coprosma tenuifolia
Cordyline australis
Coriaria arborea
Corokia buddleioides
Cortaderia selloana
Corynocarpus laevigatus
Dacrycarpus dacrydioides
Dacrydium cupressinum
Dracophyllum latifolium
Dracophyllum lessonianum
Dracophyllum longifolium
Dracophyllum sinclairii
Dracophyllum traversii
Dysoxylum spectabile
Elaeocarpus dentatus
Elaeocarpus hookerianus
Fuchsia excorticata
Geniostoma ligustrifolium
Griselinia littoralis
Griselinia lucida
Halocarpus biformis
Halocarpus kirkii
Haloragis erecta
Hebe macrantha
Hebe macrocarpa var. *latisepela*
Hebe pubescens
Hebe salicifolia
Hebe stricta
Hedycarya arborea
Helichrysum lanceolatum
Hoheria populnea var. *populnea*
Hoheria sexstylosa
Ixerba brexioides
Juncus articulatus
Knightia excelsa
Kunzea ericoides
Laurelia novae-zelandiae
Leionema nudum
Lepidothamnus intermedius
Leptecophylla juniperina subsp. *juniperina*
Leptospermum scoparium
Leucopogon fasciculatus
Libocedrus bidwillii
Libocedrus plumosa
Litsea calicaris
Lophomyrtus bullata
Lophomyrtus obcordata
Macropiper excelsum
Manoao colensoi
Melicope simplex
Melicytus lanceolatus
Melicytus macrophyllus
Melicytus ramiflorus
Metrosideros parkinsonii
Metrosideros robusta
Metrosideros scandens
Metrosideros umbellata
Mida salicifolia
Monoao colensoi
Myrsine australis
Myrsine divaricata
Myrsine salicina
Neomyrtus pedunculata
Nestegis cunninghamii
Nestegis lanceolata
Nestegis montana
Nothofagus fusca
Nothofagus menziesii
Nothofagus solandri
Nothofagus truncata
Olearia furfuracea
Olearia ilicifolia
Olearia paniculata
Olearia rani
Olearia townsonii
Pennantia corymbosa
Phyllocladus alpinus
Phyllocladus toatoa
Phyllocladus trichomanoides
Pinus radiata
Pittosporum colensoi
Pittosporum cornifolium
Pittosporum divaricatum
Pittosporum ellipticum
Pittosporum eugenioides
Pittosporum kirkii
Pittosporum rigidum
Pittosporum tenuifolium
Pittosporum virgatum
Podocarpus cunninghamii
Podocarpus totara
Prumnopitys ferruginea
Pseudopanax arboreus
Pseudopanax colensoi
Pseudopanax crassifolius
Pseudopanax discolor
Pseudopanax laetus
Pseudowintera axillaris
Pseudowintera colorata
Quintinia serrata
Raukaua edgerleyi
Raukaua simplex
Rhabdothamnus solandri
Rhopalostylis sapida
Ruakaua anomalus
Schefflera digitata
Stellaria parviflora
Streblus heterophyllus
Syzygium maire
Toronia toru
Urtica ferox
Vitex lucens
Weinmannia racemosa
Weinmannia silvicola

Ferns and Fern Allies
Abrodictyum elongatum
Abrodictyum strictum
Adiantum cunninghamii
Adiantum fulvum
Asplenium appendiculatum
Asplenium bulbiferum
Asplenium flabellifolium
Asplenium flaccidum
Asplenium oblongifolium
Asplenium polyodon
Blechnum chambersii
Blechnum colensoi
Blechnum discolor
Blechnum filiforme
Blechnum fluviatile
Blechnum fraseri
Blechnum membranaceum
Blechnum minus
Blechnum nigrum
Blechnum novae-zealandiae
Blechnum procerum
Cardiomanes reniforme
Cyathea colensoi
Cyathea cunninghamii
Cyathea dealbata
Cyathea medullaris
Cyathea smithii
Cyrtostylis rotundifolia
Deparia petersenii subsp. congrua
Dicksonia fibrosa
Dicksonia lanata
Dicksonia squarrosa
Gleichenia dicarpa
Gleichenia microphylla
Gonocarpus incanus
Gonocarpus micranthus
Histiopteris incisa
Huperzia varia
Hymenophyllum armstrongii
Hymenophyllum bivalve
Hymenophyllum demissum
Hymenophyllum dilatatum
Hymenophyllum flabellatum
Hymenophyllum flexuosum
Hymenophyllum frankliniae
Hymenophyllum lyallii
Hymenophyllum multifidum
Hymenophyllum rarum
Hymenophyllum revolutum
Hymenophyllum rufescens
Hymenophyllum sanguinolentum
Hymenophyllum scabrum
Hymenophyllum villosum
Hypolepis ambigua
Hypolepis millefolium
Hypolepis rufobarbata
Lastreopsis glabella

Appendix 2: Complete species list compiled from recce data on tāwari forest in the North Island, New Zealand. Continued.

Lastreopsis hispida
Lastreopsis microsora
Leptopteris hymenophylloides
Leptopteris superba
Lindsaea linearis
Loxogramme dictyopteris
Loxogramme lanceolata
Loxsoma cunninghamii
Lycopodiella cernua
Lycopodiella lateralis
Lycopodium deuterodensum
Lycopodium fastigiatum
Lycopodium scariosum
Lycopodium volubile
Lygodium articulatum
Microsorum novae-zelandiae
Microsorum pustulatum
Microsorum scandens
Microtis unifolia
Notogrammitis angustifolia
Notogrammitis billardierei
Notogrammitis ciliata
Notogrammitis heterophylla
Notogrammitis pseudociliata
Paesia scaberula
Pneumatopteris pennigera
Polyphlebium endlicherianum
Polyphlebium venosum
Polystichum neozelandicum
Polystichum silvaticum
Polystichum vestitum
Polytrichum dendroides
Pteridium esculentum
Pteris macilenta
Pyrrosia eleagnifolia
Rumohra adiantiformis
Rumohra hispida
Schizaea dichotoma
Sticherus cunninghamii
Sticherus flabellatus
Tmesipteris elongata
Tmesipteris lanceolata
Tmesipteris sigmatifolia
Tmesipteris tannensis
Lianes and Climbers
Clematis cunninghamii
Clematis foetida
Clematis forsteri
Clematis paniculata
Freycinetia banksii
Metrosideros albiflora
Metrosideros carminea
Metrosideros diffusa
Metrosideros fulgens
Metrosideros perforata
Muehlenbeckia australis
Muehlenbeckia axillaris
Muehlenbeckia complexa
Parsonsia capsularis
Parsonsia heterophylla
Passiflora tetrandra
Ripogonum scandens
Rubus australis
Rubus cissoides
Rubus fruticosus
Rubus schmidelioides
Monocots
Astelia banksii
Astelia fragrans
Astelia grandis
Astelia nervosa
Astelia solandri
Astelia trinervia
Austroderia richardii
Axonopus fissifolius
Carex demissa
Carex dissita
Carex forsteri
Carex spinirostris
Chionochloa conspicua
Collospermum hastatum
Collospermum microspermum
Cordyline banksii
Cordyline indivisa
Cordyline pumilio
Dianella nigra
Gahnia lacera
Gahnia pauciflora
Gahnia procera
Gahnia setifolia
Gahnia xanthocarpa
Juncus edgariae
Juncus planifolius
Juncus prismatocarpus
Lachnagrostis tenuis
Libertia ixioides
Libertia peregrinans
Machaerina juncea
Machaerina rubiginosa
Machaerina sinclairii
Machaerina tenax
Machaerina teretifolia
Microlaena avenacea
Microlaena stipoides
Morelotia affinis
Phormium cookianum
Phormium tenax
Rytidosperma gracile
Schoenus maschalinus
Schoenus tendo
Uncinia banksii
Uncinia clavata
Uncinia filiformis
Uncinia rupestris
Uncinia uncinata
Uncinia zotovii
Herbs
Acaena anserinifolia
Acianthus sinclairii
Archeria racemosa
Cardamine debilis
Centella uniflora
Corybas acontiflorus
Diplodium trullifolium
Drymoanthus adversus
Earina autumnalis
Earina mucronata
Elatostema rugosum
Epacris pauciflora
Euchiton involucratus
Euchiton japonicus
Gaultheria antipoda
Hydrocotyle moschata
Hydroctoyle elongata
Hypericum pusillum
Ichthyostomum pygmaeum
Lagenifera strangulata
Leptostigma setulosa
Libertia micrantha
Lindsaea trichomanoides
Lindsaea viridis
Lobelia anceps
Luzuriaga parviflora
Microseris scapigera
Myriophyllum pedunculatum
Nematoceras macranthum
Nematoceras orbiculatum
Nematoceras rivulare
Nematoceras trilobum
Nertera depressa
Nertera dichondrifolia
Petalochilus alatus
Petalochilus carneus
Pterostylis banksii
Pterostylis graminea
Ranunculus reflexus
Senecio minimus
Senecio scaberulus
Simpliglottis cornuta
Singularybas oblongus
Thelymitra cyanea
Thelymitra longifolia
Urtica incisa
Viola filicaulis
Winika cunninghamii
Non-Vascular
Dawsonia superba
Adventives
Anthoxanthum odoratum
Calluna vulgaris
Cirsium vulgare
Critesion murinum
Erigeron floribunda
Gamochaeta coarctata
Hakea sericea
Holcus lanatus
Hypochaeris glabra
Hypochaeris radicata
Juncus effusus
Juncus tenuis
Lotus pedunculatus
Mentha australis
Mycelis muralis
Paspalum dilatatum
Plantago lanceolata
Prunella vulgaris
Senecio vulgaris
Ulex europaeus