

THE SUSTAINABLE MANAGEMENT AND CONSERVATION OF
SANTALUM YASI (SANDALWOOD) IN FIJI AND TONGA:
A COMBINED ECOLOGICAL AND GENETIC APPROACH

by

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

THE SUSTAINABLE MANAGEMENT AND CONSERVATION OF *SANTALUM YASI* (SANDALWOOD) IN FIJI AND TONGA: A COMBINED ECOLOGICAL AND GENETIC APPROACH

by

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Advisor: Dr. Michael Balick

Valued internationally for the aromatic oil found within its heartwood, Sandalwood (*Santalum*, Santalaceae) is one of the most heavily exploited groups of plants across its range. While historically, most oil has been harvested from *Santalum album* in Southeast Asia and India, the decrease of *S. album* sources has caused a widening gap between supply and demand, which creates profitable market opportunities and increasing harvest pressure for alternative sandalwood oil sources. *Santalum yasi*, a quality alternative, has been harvested extensively in Fiji and Tonga, yet is vastly understudied. The absence of basic data on population dynamics and genetic variation for remnant populations remains a major constraint to the sustainable management of this culturally and economically valued resource. This dissertation focuses on the ecological and genetic data and analyses that can aid in developing sustainable management strategies.

Population size-class structure data was collected using transects in the three densest natural populations of *Santalum yasi*. Population dynamics, current species distribution, and ecological threats were investigated to find that the few remaining wild stands display discontinuous size class structures, are under regenerative stress and that

the natural distribution has diminished significantly, even to local extinction in some areas.

Using a nuclear microsatellite analysis, genetic variability within and between populations was investigated. Results suggest that there is no significant genetic variation between populations, but that most of the genetic variation lies within populations. This genetic distribution suggests that there is a significant level of gene flow between and among populations, most likely through human induced dispersal, showing a more panmictic trend than previously supposed. This may provide molecular evidence confirming the Western documentation and traditional oral history of extensive interaction between Fiji and Tonga and their trade of plants and culture.

Based on these dwindling levels of yasi population size and unstructured genetic variation in Fiji and Tonga, further enumerations and resource surveys are not practical to conduct at this time. Rather, forestry and governmental efforts should be focused on promotion of local involvement in assisted natural regeneration of wild stands and preservation of genetic variation through *in situ*, community-mediated conservation.

Preface

The Fijian and English vernacular “yasi” is used throughout this thesis to refer to *Santalum yasi*. The term “sandalwood” will refer broadly to any species within the genus *Santalum*. When referring to several different *Santalum* species in the same sentence, each will be referred to by their Latin binomial.

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Many thanks go to Heimuli Likiafu and Taniela Hoponoa of Tongan Forestry for instilling within me the passion to study sandalwood. This research could not have come to fruition without the kind cooperation of the many forestry officers, sandalwood collectors, and village participants who were so valuable in the formulation and carrying out of this project, namely Sanjana Lal, Eliko Senivasa, Binesh, Josevata Mateboto, Balram, Peni Cawani, and Temo Gade Raravula of the Fiji Ministry of Forests; Tevita Faka'osi, Heimuli Likiafu, Taniela Hoponoa, Sunia Napa'a, Leody Vainikolo, Ketoni Akau'ola, Sione Fauolo Fotofili, and others from the Tonga Ministry of Forests; and also for the crew members who aided in the collection of the field data including Tupou Fifita, Mesui Faka'iloatu'u, Kepueli Tupou, Losi Finau, Soni Tuamei'api, Talafungani Finau,

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Dedication

*To my dear wife, Katie, and children,
Ammon, Magnolia, and Abraham
for accompanying me in the field,
unlocking doors of understanding with the
people of Tonga and Fiji, and
for their patient love and support over the years*

*We know nothing of the Viti [Fiji] Islands botanically, except that
they contain rich forests of sandalwood; and it is not a little remarkable that
it was this single fact which led to the existing intercourse
between the savage Vitian and the rest of mankind....”*

Endlicher, *Flora of the South Sea Islands*, 1836.

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CHAPTER 1

INTRODUCTION AND BACKGROUND

“The trade in this fragrant wood has been going on since the dawn of history and will probably not cease until the connection between the sandal trees and the idolaters existing from time immemorial, shall have been broken up, by one or another becoming extinct as a race as the Archaeopteryx or the [Dodo].” ~Sawyer, 1892

1.1 Introduction

This study addresses the current distribution, basic ecological analysis and genetic structure of remaining, wild populations of *Santalum yasi* Seem. in Fiji and Tonga.

[*Santalum yasi* will hereafter be referred to as the Fijian and English vernacular “yasi”.

The term “sandalwood” will refer broadly to any species within the genus *Santalum*.

When referring to several different *Santalum* species in the same sentence, each will be referred to by their Latin binomial.]

This chapter begins with the background and significance of research on yasi including a general history of the exploitation of the genus and species. Then, a discussion of the goals and broader impacts addressed by this dissertation will be followed by a list of research questions. A botanical description is then presented for yasi which includes current available information on size, habit, foliage, flowering and fruiting, seed dispersal and viability, germination and seedling survival rates, growth rates, environmental tolerances and considerations, heartwood and oil production, silvicultural potential, and folk varieties. Then, a comment on the unique natural range of the genus *Santalum* across the Asia Pacific region is followed by a brief summary of the natural range of yasi and a discussion of land use and tenure in Fiji and Tonga. The

chapter concludes with a discussion on the ethnobotany of yasi and a summarized introduction to the dissertation.

1.2 Background and Significance

The genus *Santalum* (the sandalwoods; Santalaceae) is represented by 16 semi-parasitic species occurring throughout various parts of India, Southeast Asia, Australia, and the Pacific (Figure 1.1). The aromatic oil contained in the mature heartwood is greatly valued both locally and internationally for its medicinal, religious, ceremonial, cosmetic and perfumery uses (McKinnell, 1990; Butaud et al., 2005). Sandalwood has been sought after for centuries, sometimes to the point of extinction as in *S. fernandezianum* (Juan Fernandez Is., Chile) in the 20th century (Darwin, 1839; Stuessy et al., 1992; Woodward, 1969; for a more detailed history of *S. fernandezianum* see Federico Johow, 1893 & 1896), or near extinction as in the case of *S. insulare* (French Polynesia), *S. boninense* (Bonin Islands) and *S. macgregorii* (Papua New Guinea) (Maina et al., 1988; Waldren et al., 1995; Butaud et al., 2005). Indeed, *Santalum* is one of the most heavily exploited groups of plants across its range (Brennan & Merlin, 1992).

Due to an inability to synthesize a high quality substitute, sandalwood oil must be extracted from harvested wood (Barrett & Fox, 1994). Most oil has been and is harvested from *Santalum album* in Southeast Asia and India, which has consequently been the focus of most sandalwood study and intense regulation (Burfield, 2005). However, these supplies are decreasing while market demand remains steady at 5000 - 6000 tons creating a widening gap between market supply and demand (Radomiljac et al., 1998; Thomson et

al., 2005). As supply is dropping, prices have also increased significantly across the market (Jiko, 1991; Radomijac, 1995). Furthermore, this supply dilemma has negatively affected the quality of oil available on the market. In recent harvests, *Santalum album* heartwood and oil, the long held standard for sandalwood oil, has been decreasing in quality due in part to limited regeneration and subsequent harvest of younger, smaller trees with underdeveloped heartwood (Howes et al., 2004).

This widening gap between supply and demand creates increasing pressure for harvesting of alternative *Santalum* species (Burfield, 2005). *Santalum album* and *S. yasi* (the latter in Fiji and Tonga) both have the highest concentrations of merchantable oil, each with an average of 5 – 7% oil content (McKinnell, 1990) and promising oil composition (Doran et al., 2005). Furthermore, *S. album* and *S. yasi* are sister taxa forming a well-supported clade within the genus (Harbaugh & Baldwin, 2007), making *S. yasi* a clear, high quality alternative when compared with other *Santalum* species

Yasi is a current export for Fiji and Tonga yet it is vastly under-studied and the harvesting is unregulated (McKinnell, 1990; Jiko, 1993; Thomson, 2002; Sanjana Lal, Senior Scientific Officer, Fiji Department of Forestry, personal communication, 2006). Only four peer-reviewed, scientific journal articles have been published that deal to any degree with yasi. These include a morphological and embryological study on various species within Santalaceae (Paliwal, 1956), an oil quality evaluation which compared historic and trade samples of various sandalwood oils including one historic sample of yasi oil (Howes et al., 2004), a recent study on the phylogenetic relationships of all

sandalwood species (Harbaugh & Baldwin, 2007), and a study on the polyploid and hybrid origins of Pacific island sandalwoods (Harbaugh, 2008).

The worldwide demand for sandalwood production creates extensive opportunities for smaller nations across the Asia Pacific region to diversify and boost economies. The relative low maintenance to high harvest value makes sandalwood cultivation a superior option compared to high input/low output crops with uncertain market value. In fact, sandalwood has the highest value for bulk products compared to all other wood producing species (Barrett & Fox, 1994). Yet without sustainable utilization of these valuable resources, illegal and improper harvesting threatens the future of the market, and endangers species and genetic resources.

The sandalwood trade was one of the initial lures attracting Europeans into the South Pacific. Fiji was the first of the Pacific islands to feel the effect of this scramble for sandalwood. During the early nineteenth century, the heartwood of yasi was a major export (Shineberg, 1967). Harvesting of yasi has been almost exclusively from wild populations, due to the difficulty of successfully raising trees with a semi-parasitic trophic mode, and has followed a characteristic, cyclical pattern of short, but intense, exploitation and over-harvesting when supply is high and then subsequent periods of regeneration (Thomson et al., 2000). Excessive harvesting without management or replanting was one of the main causes for the extinction of *Santalum fernandezianum* from the Juan Fernandez Islands in the early 20th century (Skottsberg, 1956; Munoz, 1973). Excessive harvesting may also be the reason why yasi never became established in Samoa, or became extinct there pre-Western contact, despite the proximity of the

species in Tonga and Fiji and the frequent trade of yasi to Samoa from those neighboring islands (Brennan & Merlin, 1992). (For further discussion on sandalwood in Samoa, see sections 1.8, 1.10, and 2.6.1.) Considering current economic pressures and yasi's value in local and international markets, extant wild populations in Fiji and Tonga are threatened with further, rapid depletion without a scientifically based management strategy (Thomson et al., 2000).

1.3 History of Exploitation

The advent of trade in sandalwood began in the 1st century when Buddhism and the need for sandalwood incense to burn in the Buddhist temples was brought to China from India (Shineberg, 1965 & 1967) and Southeast Asia (Harbaugh, 2007). Specifically for yasi, sandalwood products such as scented coconut oil, powder or heartwood, and even seedlings were exchanged and bartered among islanders of Tonga, Fiji, and Samoa by boat before European influences (Seeman, 1869; Brennan & Merlin, 1992; Kaufusi, 1995). Much later, European, American and Australian traders, seeking lucrative items to barter for Chinese goods, discovered and exploited sandalwood resources on various islands throughout the Pacific from 1790 to 1865, exhausting supplies in only 75 years (Bradley, 1968; Brennan & Merlin, 1992). During the early nineteenth century, yasi was discovered in Fiji and Tonga by European sailors and the tree was harvested extensively, but for only a decade, as populations of mature trees quickly became rare (Bulai, 1995; Tuisese et al., 2000; Jiko, 2000). The island of Vanua Levu in Fiji was even designated

as “Sandalwood Island” by European sailors, because of the former abundance of sandalwood on the island.

The Western world’s hunger for sandalwood was driven, at least in part, by their thirst for tea, the main source coming from China at the time. As the demand for tea increased, the trade with China became more and more one-sided as it was very difficult to find any valuable commodity that was acceptable to the Chinese. This dilemma was epitomized in the famous remark of the Emperor Chien Lung to Lord Macartney in 1793: ‘Your Ambassador can see for himself that we possess all things’ (Shineberg, 1967). One of the commodities they did not possess, however, was sandalwood, and they paid a handsome price for it. For the Western merchants, it was as if they had come upon a goldmine (Shineberg, 1967).

This sandalwood trade has had significant influence on the historical and present interaction between the islanders and outsiders. Endlicher (1836), an early botanist to the Fiji islands, wrote, “Our botanical knowledge of the Viti [Fiji] group was limited to the fact that it abounded in rich forests of sandalwood; and it is not a little remarkable that it was this single fact which led to the existing intercourse between the savage Vitian and the rest of mankind....” And Dorothy Shineberg (1967), the author of *They Came for Sandalwood*, discussing the early sandalwood trade in the Pacific, summarized the early harvesting of sandalwood:

Sandalwooding has been stereotyped as a trade sullied by brutality and violence that left behind it a legacy of hostility to Europeans. The view of the Rev. John G. Paton that ‘it was a trade steeped in human blood and indescribable vice,’ is varied by later writers only in their choice of derogatory adjectives.

More detailed accounts of early harvesting can be found in Seeman (1867) and Horne (1881).

More recently, in the middle of the 20th century as wild populations of yasi had been replenished and prices for sandalwood products had increased, the trees were once again recognized as a lucrative source of revenue for rural communities. Modern exploitive sandalwood harvesting began in Fiji in May 1984 at Ram Jati Singh's freehold estate in Bua under special license and was quickly followed by harvest of all other naturally growing yasi habitat areas (Jiko, 1991). Yasi harvests returned F\$4.74 million (approximately US\$2.78 million) in foreign exchange between 1987 and 1990 (Jiko, 1993). Exportation of yasi from Fiji to markets in Singapore, Hong Kong, Taiwan, Korea and Japan between 1984 and 1993 totaled 1,115 tons of heartwood, selling at a value of F\$3,383/ton in 1984 (approximately US\$1,985), and then F\$13,452/ton in 1991 (approximately US\$7,896), and down to F\$2,700/ton in 1992 (approximately US\$1,584) (Bulai, 1995).

Similarly, export of wild yasi from Tonga during the 1960s and 70s caused the disappearance of nearly all mature trees on Tongatapu and 'Eua and was followed by subsequent harvesting of immature trees. Recent commercial harvesting of yasi in 'Eua in 1996 – 1997 grossed T\$2,000 – 3,000 per ton of heartwood (approximately US\$1,016-1,525) (Kaufusi et al., 1999). From 2003 – 2007, an average annual harvest level was 126 tons, which totals at 630 tons, some of which may have included the lesser quality sapwood in addition to the valuable heartwood (Likiafu, 2008; Tuita, 2005). In 2007 alone, after the ecological study for this thesis was conducted, 205 tons were

reported to have been exported from Tonga (MAFF, 2008). With resources dwindling again, a harvesting ban was placed on yasi in Tonga in 2008 (Tevita Faka'osi, Deputy Director of Forestry and Conservation Division, Head of Forestry, Tongan Ministry of Forests, personal communication, 2008).

1.4 International Market

The major commercial sandalwood products, valued across the world, include such items as perfume, incense, and carvings. These goods are produced mainly from the distilled essential oil or from the raw heartwood. The oil of sandalwood is most sought after in France and the United States (FAO, 1995; Thomson, 2006) and is one of the most highly priced items in essential oil trade (FAO, 1995). While currently no oil is being distilled from yasi in Tonga or Fiji at a commercial level, the heartwood of yasi is exported to markets in Taiwan, Japan, China and a lesser amount to the United States (Thomson, 2006). Some amount of yasi sapwood is also occasionally exported for use in the production of joss sticks, a lower grade form of incense, used in Asian religious ceremonies (Thomson, 2006).

Over the past two decades the market value of yasi heartwood has fluctuated significantly from US\$1/kg to US\$40/kg, but more often than not, yasi has been sold for much less than it is worth (Kaufusi et al., 1999; Bulai, 1994; Heimuli Likiafu, Tongan Forestry Officer personal communication, 2009). Yasi harvests returned F\$4.74 million (approximately US\$2.78 million) in foreign exchange between 1987 and 1990 (Jiko, 1993). Exportation of yasi from Fiji to markets in Singapore, Hong Kong, Taiwan, Korea

and Japan between 1984 and 1993 totaled at 1,115 tons heartwood, selling at a value of F\$3,383/ton in 1984 (approximately US\$1,985), and then F\$13,452/ton in 1991 (approximately US\$7,896), and down to F\$2,700/ton in 1992 (approximately US\$1,584) (Bulai, 1995). Export of wild yasi from ‘Eua, Tonga in 1996-97 grossed T\$2-3,000 per ton of heartwood (approximately US\$1,016-1,525) (Kaufusi et al., 1999). The fluctuation in price most plausibly reflects the inconsistency of resource supply and small-scale export. Detailed information on the export of yasi is not readily available, undocumented, and/or generally undisclosed by Fijian and Tongan governments. Illegal harvesting occurrences make accurate record keeping difficult.

With the current decreasing resource supply and increasing demand for sandalwood products, the potential outlook for market value of yasi seems positive. Most oil has been and is harvested from *Santalum album* in Southeast Asia and India. Yet, *S. album* supplies are decreasing while market demand remains steady at 5000-6000 tons, creating a widening gap between market supply and demand (Radomiljac et al., 1998; Thomson et al., 2005), and creating frequent associated increases in market price (Jiko, 1991; Radomijac, 1995). Future research, tracking the processing and consumers of yasi products, needs to be performed to determine the more detailed market of yasi.

1.5 Research Goals and Broader Impacts

Yasi is one of the priority species for the South Pacific Regional Initiative on Forest Genetic Resources (SPRIG), which asserts that “a major constraint to the successful implementation of a genetic conservation and management program for

Santalum yasi remains a dearth of detailed information on the current distribution and basic data of each population including age/class structure and the genetic structure of the species, i.e. the distribution of genetic variation within and between remnant populations in Fiji and Tonga” (Thomson et al., 2000). The research on the extant, wild yasi populations presented in this dissertation aims to provide these crucial ecological and genetic data and analyses. As part of this research, population size/class structure data were collected along transects through the three densest natural populations and population dynamics, species distribution, and evident ecological threats are investigated. Also, nuclear microsatellites were used to determine genetic variability within and between populations. Elucidating the current ecological and genetic conditions of yasi populations will facilitate the conservation and sustainable management of this valuable resource by increasing the currently limited published methodologies and data on yasi for the benefit of scientists worldwide, local government agencies in Fiji and Tonga, and also for SPRIG which is working with Fijian and Tongan forestry departments to develop the ongoing “Action Plan (2007-2020) for the Conservation, Management and Sustainable Utilization of Forest Genetic Resources in the Pacific Islands,” of which yasi is a focus species. This project also aims to build the capacity of local Tongan and Fijian officials, forestry workers, and village leaders through their active participation in the research process.

1.6 Research Questions

The following questions are addressed in this study:

1. What is the current distribution of wild/naturalized *Santalum* species in Fiji, Tonga, and Niue? How has the natural distribution of these sandalwood species changed over time?
2. What are the current densities and size-class structures of remaining, wild yasi populations? Are regeneration rates under current harvest regimes sufficient to maintain the populations *in situ*?
3. What are the observed ecological threats to remnant yasi populations?
4. What are the estimated heartwood yield losses from premature harvesting?
5. What is the distribution of genetic variation within and between remnant populations of yasi in Fiji and Tonga and what implications does this have for its conservation?
6. Does intraspecific genetic data shed light on the historical migrations of yasi?
7. What factors have constrained past and present management strategies and how can they be addressed?

1.7 Botanical Description

1.7.1 Size, Foliage, and Habit

Santalum yasi Seem. is a small, semi-parasitic tree with a light, spreading crown reaching 8 – 12 m across (Thomson, 2006a) (Figure 1.2a). However, in open, exposed habitats it may be reduced to a bushy, multi-stemmed shrub. Mature specimens reach about 10 m tall, sometimes to 13-15 m, and can attain stem diameters of > 40 cm after

40-50 years growth, developing rich heartwood (Usumaki, 1981) (Figure 1.2b). The root system is fairly shallow and wide spreading, which allows for water and nutrient uptake and extensive grafting onto various host species (Thomson, 2006a) (Figure 1.2c). Bark is smooth to slightly fissured and grayish-brown in color. Bole taper, based on a limited sample, is reported at -4.8cm/m or less (Usumaki, 1981).

Mature leaves are simple, opposite, and narrow to broadly lanceolate (Figure 1.3 & Figure 1.4a). Considerable variation exists in foliage size with a range from 5 x 1 cm to 8 x 2.5 cm (Thomson, 2006a). The foliage color and shape is also variable, possibly genetic and/or dependant on shade conditions, appearing more yellowish in light abundant situations and glossy green in more shaded environments. Juvenile leaves are very slender and light green (Ehrhart, 1998).

Growth habit of yasi is variable depending on the growing conditions. The young branches are slender and often pendulous, and some plants display a characteristic semi-weeping habit. When in open environments, yasi frequently forms multiple leaders with the lateral branches frequently overtaking the main branches (Ehrhart, 1998). Multiple leader formation may be induced by wounding from insects or animals, falling branches, or dieback (Jiko, 1991). In laterally-shaded environments, the main leader remains dominant with larger lateral branches, while the crown is thin and weak in over-shaded environments (Ehrhart, 1998). A shade to light ratio of 40-60% is physiologically ideal for cultivating a taller tree with a single straight leader and well-developed crown (Ehrhart, 1998). Tree growth from root suckers off coppiced trees can form (Jiko, 1991; Thomson, 2006a), though suckers usually lack main leaders (Ehrhart, 1998).

1.7.2 Flowering and Fruiting

The bell shaped, monoecious flowers are small and clustered in panicles in the axils of leaves. The flowers are 4- or 5-parted, and greenish white turning pink then red at maturity with yellow and red-tinged anthers and cream styles, stamens adnate (Thomson, 2006a) (Figure 1.3, 1.4a, 1.4b). The two major flowering peaks in Fiji are February and October-November (Bulai, 1995) and one main peak in June to September in Tonga (Thomson, 2006a). Flowering may begin as early as 3 to 4 years but significant fruiting requires 7 to 10 years and may occur throughout the year (Smith, 1985; Bulai, 1995; Thomson, 2006a). It has been suggested that insects are the main pollinators of *Santalum* species (Sedgley, 1982; Veerendra, 1996), though the specific pollinators of yasi have not been determined. Pollinators for *Santalum album* include bees, butterflies and beetles (CAB International, 2000).

The fruit is a fleshy one-seeded drupe, ellipsoid in shape (9-11 x 6-8 mm) with a small, round, calyx scar (c. 2 mm diameter) at the apex, enclosing a rather stout, cone-shaped point. Seed volume is about 50% of the mature fruit (Usumaki, 1981). Immature fruits are light-green in color, turning reddish-purple, and finally dark purple or black at full maturity four months after flowering (Smith, 1985; Bulai, 1995; Jiko, 1993; Thomson, 2000 & 2006a) (Figure 1.4b). The main fruiting season corresponds to the wet season, January-March, with light fruiting in the cooler, dry season of June-August. In Tonga the fruiting season varies regionally, but is mainly from October-December. (Thomson, 2006a). Seed production can also be induced by tree wounding. This practice

can be combined with pruning efforts to encourage natural regeneration and has been practiced in Tonga (Heimuli Likiafu, personal communication, 2006).

Usumaki observed in his ecological survey of yasi that trees in open or exposed areas bear more flowers and fruit than those growing in forest cover (1981). Some fruit loss is also experienced due to destructive hurricanes and other storms, which occur in untimely correspondence with the main fruiting season (Jiko, 2000).

1.7.3 Seed Dispersal and Conservation Viability

The seeds are largely dispersed by various bird species and, to a lesser extent, flying foxes. Extinct pigeons may have played an important role in sandalwood seed dispersal in the Pacific (Tassin et al., 2008). Some Fijian birds reportedly responsible for dispersal include Miti, Kaisevau, Beka, Ruve, Seasea, and Kula (Tabunakawai & Chang, 1984). Tassin et al. (2008), based on their own study, suggested that the ingestion of sandalwood seeds by certain birds is likely to improve germination.

Plants begin fruiting from about 3-4 years but only have high levels of fertility after 7-10 years (Smith, 1985; Jiko, 1993; Bulai, 1995; Thomson, 2006a). Seed storage viability is undocumented for yasi but is presumably highly variable as in other *Santalum* species, and sowing is recommended as soon as possible after harvesting (Thomson, 2006a). *Santalum austrocaledonicum*, which has similar size and habitat preferences to yasi, shows marked differences in long term seed viability across the species based on physiological differences perhaps induced by growing conditions or genetic differences between different populations of the mother trees (Chauvin & Ehrhart 1997; Thomson,

2006a). *Santalum austrocaledonicum* seed viability ranges from 18 months to 3-4 years (Ehrhart, 1998; Chauvin & Ehrhart, 1997). Ehrhart (1998) speculated that seed viability is associated with the probable genetic superiority of “better-shaped trees” and suggested that seed collection be conducted from the “best-shaped trees”. However, Ehrhart’s (1998) suggestion does not account for the effects of growing conditions on yasi form and is contradictory to the general association of greater heartwood formation on slower growing, less healthy-looking trees, which may therefore be genetically preferable if one is interested in heartwood production.

1.7.4 Germination and Seedling Survival Rates

Germination rates specific to yasi are not well known but, according to some estimates from studies of various sandalwood species, may be potentially high with pretreatment including scarification (Tassin et al, 2008). According to Thomson (2006a), extracted embryos from newly collected seeds showed 80-90% germination after 2-3 months, but rates decreased to 60-70% for nicked seeds and were much lower and slower for untreated seeds. In one propagation test conducted through the Fiji Forestry Department with 250 seeds, germination began at 14 days and rates were 100% after 31 days using pretreated seeds according to the methods of Barrett (1987). However, germination rates were extremely low in all treatment methods according to a report from the Nawailevu Yasi Project (Seruwaqa, 1993), perhaps due to loss of viability during seed storage. Seed sowing is recommended as soon as possible after collection (Thomson, 2006a).

A study on nursery seedlings in Fiji showed survival rates varying from 40 to 100% depending on the host species and plant spacing in one trial group after two years. Survival rates dropped from less than 30% after two years to less than 10% after five years in another trial group planted with mixed host species (Jiko, 1991). No information on sample size in this study is given.

In natural forest settings, Usumaki (1981) reported very little regeneration from coppicing or seeds, even under trees that have plentiful fruit. He noted that this might be due perhaps to poor seed viability, undergrowth thickness, or soil conditions. When seedlings are found they are often growing under bushes and shrubs, due perhaps to the perching locality of the birds dispersing the seeds, or the afforded protection against heat and browsing animals (Jiko, 1991; Tabunakawai & Chang, 1984). Seedling mortality is mainly caused by prolonged heat or drought, excessive moisture, herbivory by rats or other animals, or falling branches (Jiko 1991). Seedling mortality can occur in open grassy areas that have a higher incidence of fires and susceptibility to environmental extremes, and also by indiscriminate or purposeful destruction or removal of saplings and seedlings when land is cleared for gardening (Thomson et al., 2000). Seedlings do not compete well with monocotyledons such as grasses and palms (Thomson, 2006a).

1.7.5 Growth Rates

Growth rate can vary significantly based on host quality and environmental factors and is not well understood. In a nursery in Fiji, seedling growth rates varied with host and spacing (Jiko, 1991). Early growth is reported as slow at 0.5 to 0.7m in height

per year (Thomson, 2006a). Usumaki (1981) reported a faster early height growth rate of up to 1m per year, which slows until full maturity at age 50-60 years and a maximum height of 13-15m. Limited data from plots in Fiji show low levels of girth increase of 1cm diameter and height increase of 0.5m annually in natural stands but growth is noted as variable according to host suitability (Jiko, 1991). Thomson (2006a) suggests tree diameter can reach 20-25cm near ground level after 25 years. A discussion of growth rate estimation is included in chapter 2.

1.7.6 Habitat

Found in drier, open lowland forest types, yasi prefers a warm to hot climate with a distinct dry season of 3 to 5 months and annual rainfall between 125–175cm (Thomson, 2006a). Yasi trees are also occasionally found in dense forests, but these have most likely established themselves when the surrounding trees were smaller and the canopy was more open (Ehrhart, 1998). Yasi grows with various associated, and possibly host, species. Associated species include *Acacia sp.*, *Casuarina sp.*, *Calophyllum sp.*, *Cocos nucifera*, *Fagraea gracilipes*, *Storckiella vitensis*, *Hibiscus tiliaceus*, *Thespesia populnea*, and *Dodonea viscosa* *Broussonetia papyfera*, *Citrus sp.*, *Diospyros spp.*, *Hernandia nymphaeifolia*, *Inocarpus fagiferus*, *Morinda citrifolia*, *Pandanus tectorius*, *Pometia pinnata*, and *Rhus taitensis* (Thomson, 2006a; Jiko, 1993) (Figure 1.2c). Yasi also grows well intercropped with *Pinus caribaea* plantations in both Fiji and Tonga (Thomson, 2006a) (Figure 2.15).

Yasi is often found in secondary forests and disturbed areas and frequently in home gardens and bush allotments among fruit trees or cultural species such as *Cordyline*, *Croton*, *Euodia*, and *Polyscias* (Ehrhart, 1998; Thomson, 2006a). While adequate drainage is necessary, yasi can tolerate acidic or alkaline soils (pH 4.0 – 7.4) (Thomson, 2006a) and has a broad edaphic range (Likiafu & Robson, 2005). Yasi is found frequently in shallow and infertile soils such as those over rocky outcroppings and ridge slopes, sandy coastal soils and sometimes near the edges of swamps (Jiko, 1991; Tabunakawai & Chang, 1984; Brennan & Merlin, 1992), perhaps due mainly to the lower levels of competition with other species in these areas. Yasi also grows well in the deep volcanic ash soils of ‘Eua (Ehrhart, 1998). Usumaki (1981) reported a possible preference for elevations below 1000 ft.

1.7.7 Environmental Tolerances and Considerations

Depending on the quality and tolerance levels of the hemi-parasitic host species, yasi can potentially endure many environmental conditions including a dry season of 5-6 months and full sun or up to 70% shade (Thomson, 2006a). Yasi is sensitive to frost, but the shorter growth habit makes it more resistant to the cyclone force winds that frequent the area. Yasi growing in coastal areas can also often recover successfully from defoliation and salt scorching by cyclonic, salt-laden winds, making them a good choice for cultivation in plantations (Thomson, 2006a). However, strong winds can damage trees with forked trunks, or growing in open areas, and fire also causes casualties, particularly to seedlings and saplings (Jiko, 1991; Thomson, 2006a).

Seedlings can contract root rot fungi in cool moist conditions, and mature yasi trees are susceptible to the tropical basidiomycete *Phellinus noxius* which can spread to other trees through root grafting. No studies have shown whether or not yasi is susceptible to the phytoplasma-caused sandal spike disease, currently absent in the South Pacific, which has damaged populations of *Santalum album* in India (Thomson, 2006a).

With a high tolerance for variation in habitat and prolific seed production, yasi has the potential to be an invasive species in disturbed or open areas (Thomson, 2006a).

1.7.8 Heartwood and Oil Production

Sandalwood oil is produced by the inner, yellowish brown, hard heartwood, which is strongly scented, while oil is absent from the outer, white sapwood and is unscented (Jiko, 1991; Doran, 2005) (Figure 1.2b). Heartwood formation is variable from tree to tree according to growing conditions, or other factors, but generally begins after 10 years in stem wood greater than 7cm in diameter (Doran et. al., 2005; Usumaki, 1981). However, trunk size and age are not always reliable indicators of heartwood formation. Doran et al's study (2005) of oil composition in young trees in Fiji, Tonga, and Niue shows yasi trees 10 to 20 years old with diameters of 9.5 to 17.8cm with no detectable heartwood formation at the tree base. The most concentrated levels of sandalwood oil is reputedly found in the heartwood of the roots and main bole, and levels decrease towards the outer branches, not extending far along the length of stems of younger trees (Usumaki, 1981) (Figure 1.5).

Heartwood production rates and yield levels are also variable and understudied. Thomson (2006a) suggests a heartwood production rate of 1-2kg per year after age 10 years (15-30kg of heartwood in a 20-25 year old tree). Usumaki calculated an average 35% heartwood to volume ratio in a limited sampling but notes that while growth in diameter may slow noticeable at full maturity of 50-60 years the heartwood development may actually increase at this time (1981). Heartwood formation, however, has also been noted as much as 40% of total volume in basal stem sections after 15 to 20 years growth in pine plantations (Thomson 2006a). While growth and heartwood yield is highly variable between individual trees, a reasonable look at the probable yield of an average individual yasi tree according to age may be obtained using the more detailed growth data available for *Santalum austrocalidonicum*, a closely related species from New Caledonia of almost identical size, life span and habitat preference as discussed in Chapter 2 (Thomson, 2006a; personal conversation with Lex Thomson, 2008).

While generally reported to have an oil quantity of 5-7%, comparable to the market standard *Santalum album* (McKinnell, 1990), oil composition and quality of yasi is currently undecided and is difficult to analyze due to variations caused by methods of extraction and age and heartwood maturity of sample material (Howes et. al., 2004), and possibly from physiological changes induced by environmental factors (Ehrhart, 1998). Alpha (1997) reports low variation in oil composition across provenances in Tonga, but Doran (2005) notes significant variation in composition of α -santalol and β -santalol levels in trees selected from Tonga, Fiji and Niue. Lower quality was generally associated with younger trees, with 6 of 17 samples containing α -santalol and β -santalol

levels below International Standard of 41-55% and 16-24% respectively. The variation present in Doran's samples may provide an opportunity for improvement in santalol levels through breeding selection if santalol production is heritable (Doran, 2002 & 2005).

The best oil production is reputedly found in specimens on stony, drier soils, which are slower growing, and is sometimes a characteristic noted in distinguishing between folk varieties (Jiko, 1991; Brennan & Merlin, 1992; Usumaki, 1981; Seruwaqa, 1993; personal conversation with forestry officer Heimuli Likiafu, 2006). A field-friendly technique for quick, non-invasive, easy identification of high oil yielding *Santalum album* individuals has been developed by Angadi (2002) using peroxidase reagents and twig samples, which may also be appropriate for testing yasi.

A high quality, synthetic substitute for naturally derived sandalwood oil has not yet been successfully produced and prospects appear unlikely (Barrett & Fox, 1994). Sandalwood oil components contributing to the overall odor include α -santalol (50-60%), (-)-(Z)- β -santalol (20-25%) and minor levels of (-)-(E)- β -santalol and β -santalene (Krotz and Helmchen, 1990). Research on synthesis of α -santalol and β -santalene has been partially successful, while β -santalol synthesis including enantiomers and double bond isomers has been successfully made by Krotz and Helmchen (1990). However, β -santalol is prone to racemization via carbocation rearrangement, and while synthesized (-)-(Z)- β -santalol and (-)-(E)- β -santalol compounds showed similar or lesser scent qualities, the enantiomers produced were scentless, only developing a weak scent after several months of storage.

1.7.9 Silvicultural Potential

The habitat versatility and relative low maintenance to high harvest value of sandalwood cultivation on a large or small scale make it a superior option compared to high input/low output crops with uncertain market value (Barrett & Fox, 1994).

Silvicultural methods for yasi are complex due to the hemi-parasitic nature of the species, and are currently being developed by Fiji and Tonga Forestry. Thus far yasi has been seen to act much like other *Santalum* species and can be propagated by seed (Jiko, 1991), and also by vegetative cuttings from young plants or root cuttings from mature plants (Thomson, 2006a). Wildlings can also be encouraged to grow under heavy-bearing mature trees by occasional weeding and watering for later transplanting (Thomson, 2006a). Grafting has also been noted as a plausible way of retaining genetics from mature harvest ready trees in a breeding program (Thomson, 2006a). Silviculture methods for *Santalum spicatum*, *S. austrocaledonicum*, *S. ellipticum*, *S. freycinetianum*, and *S. album* may be resources for general cultivation practices until further species specific data are available (Jiko, 1991; Thomson, 2006a). The major constraint to successful propagation of yasi is seed availability, due to lack of mature, fruiting trees, and the remote location of remaining mature trees (Jiko, 1991; personal communication with Tevita Faka'osi and Sanjana Lal, 2006).

1.7.10 Folk Varieties

Several folk varieties of *Santalum yasi* have been documented in Fiji and Tonga though none has been documented in Niue. While particular characteristics of folk

varieties may be reported slightly differently by individuals in different villages and islands, recorded folk varieties referring to *Santalum yasi* are listed here.

The folk varieties for yasi in Fiji include *yasi dina* (or true sandalwood referring to the genus *Santalum*, as opposed to other genera with sweetly fragrant wood), *yasi buco*, *yasi vula* (white), *yasi boi* (fragrant), *yasi damu* (red), and *yasi kula* (red) (Thomson, 2006a; Orr, 1977; Smith, 1985). The reddish leaves of the latter varieties may come from a micronutrient deficiency, which may be a factor affecting the particularly potent scent of the *yasi kula* variety (Thomson, 2006a). Varieties may differ significantly in the quality of heartwood (Orr, 1977) though phytochemical analysis is needed to quantify any oil quality differences specific to varieties.

Bua harvesters (Vanua Levu, Fiji) note the two main local varieties to be *yasi buco*, also called *yasi vula*, and *yasi kula*. *Yasi buco* is more abundant and vigorous than other varieties with a dense crown, dense green leaves, smooth bark, and more abundant flowers and seeds. Seed size is also larger. However, heartwood scent is weaker in *yasi buco*. *Yasi kula* is the opposite of *yasi buco* in that it has a sparse crown and sparse light green leaves which often have a reddish discoloration. Growing slower than *yasi buco*, *yasi kula* also has fewer flowers, seeds, and less sapwood making it a more desirable harvest tree with a stronger scent. (Seruwaqa, 1993).

In Tonga, significant morphological variation exists between yasi individuals. The several folk varieties refer mainly to individual tree characteristics more so than whole populations and consist of *ahi fefine* (literally female, with small leaves), *ahi tangata* (with large, long leaves), *ahi kolo* (sweet smelling), *ahi lau lahi*, *ahi uhiuhi*, and *ahi vao*

(Thomson, 2006a). The characteristics appear very similar to the two distinctive folk varieties *yasi buco* and *yasi kula* found in Fiji. The darker, broader leaved individuals or varieties appear healthier and develop larger stems faster, but contain significantly less heartwood while the thinner, yellow leaved trees with more reddish bark can be smaller but contain as much as twice the amount of heartwood (personal conversation with Tongan forestry officer Heimuli Likiafu, 2006).

1.8 Natural Range

The genus *Santalum* has a curious, scattered distribution pattern across the South Pacific region. The genus is found across long distances to the isolated islands of Hawaii and Juan Fernandez Islands and north to the Ogasawara Islands, while major island groups between, such as Micronesia and the Solomon Islands, remain devoid of *Santalum* species despite suitable habitats (Brennan & Merlin, 1992) (Figure 1.1). This scattered distribution may reflect the occurrence of prehistoric, chance or human-mediated dispersal or may be an indication of prehistoric or more recent extinction events as is the case in *S. fernandezianum* (Brennan & Merlin, 1992). The similar disproportion in concentrations of *Santalum* populations between various islands may also be better explained by associated levels of human impact, such as exploitation or conservation (Brennan & Merlin, 1992), rather than environmental conditions for this versatile and potentially invasive plant group (Thomson, 2006a).

The natural range of yasi is Fiji and Tonga in the South West Pacific. Yasi has also recently been introduced in Niue Islands around Hakupu village (Thomson et al.,

2005; Doran, 2005) (Figure 1.6). Despite prehistoric and historic trade in yasi from Tonga to neighboring Samoa, there is surprisingly only one record of its presence there as an introduction on Savai'i (Brennan & Merlin, 1992; Thomson, 2006a), but currently there are no natural stands of yasi found in Samoa. Further details regarding the current distribution across Fiji, Tonga, and Niue as investigated in this research will be discussed in chapter two.

1.9 Land, Land Use and Tenure in Fiji and Tonga

1.9.1 Fiji

The 332 South Pacific islands of Fiji combine for a total land area of 18,270 square kilometers. Only one third of the islands are inhabited and approximately 90% of the over 931,000 people live on the two largest islands, Viti Levu and Vanua Levu, which also contain 87% of the land area (Jiko, 1991). The country has four divisions: Northern Division (Vanua Levu and surrounding islands), Central Division (southeastern half of Viti Levu and nearby islands), Western Division (western half of Viti Levu and outer islands) and Eastern Division (Kadavu, Lau Group islands and Ono-i-Lau islands). Lying between 178 - 179°W longitude and 16 - 22°S latitude, most islands have a volcanic origin from the Eocene to Pleistocene eras with steeply dissected topography, while some are raised limestone, and most have fairly fertile soils (Jiko, 1991).

Climatic variation in Fiji includes a wet, warm season from November to March, with mean temperatures around 29°C and a cooler, drier season from July to August when mean temperatures drop to 24°C (Jiko, 1991). Average annual rainfall can vary

based on topography but ranges from 165 to 330cm with hardwood forests usually having more than 25cm rainfall a month with a short dry period (Jiko, 1991; Duikoro, 2002).

While 7.4% of land in Fiji is under government ownership and 10% is freehold, almost 83% is native-owned and managed by land owning units, mataqali, with rights to occupy and use the land under customary tenure. One third of this native land is for use by native Fijians only and may not be leased to outsiders. (Thomson et. al., 2000)

Land use includes a large amount of subsistence farming by native Fijians of traditional, staple food crops such as cassava, taro, yam and occasionally rice farming. Some areas have been under cultivation of coconut for the copra industry, and grazing. The most notable change in land use recently comes from the increasing numbers of pine plantations, which provide reliable income to landowners. Indian Fijian freehold properties often have coconut groves and sandalwood plantations, which were often originally planted by European landlords (Usumaki, 1981).

Four different authorities administer land use including the Native Lands and Fisheries Commission (native land ownership), Native Land Trust Board for Native Land (on behalf of the native owners), Department of Lands and Surveys for Crown Land, and Registrar of Titles for Freehold Land. This four-fold administration creates some difficulty in maintaining current records accurately and thoroughly. In 1992, the development of a national land information system began in coordination with New Zealand's Department of Survey and Land Information, which is helping to streamline land administration issues (Masikerei et al., 1996).

The Native Land Commission was established in 1880 to determine boundaries between land areas and to record names of individuals forming each mataqali. The Native Land Trust Act endorsed in 1940 designated land reserves to provide for the future needs of each unit and created an administrative body called the Native Land Trust Board (NLTB). The NLTB extends land leases, which by 1987 covered almost 32,000 ha of land and were used mostly for agricultural purposes. The NLTB also distributes logging royalties and collects regeneration levies proscribed by the Native Forest Regeneration Fund Ordinance of 1965. (Thomson et al., 2000)

1.9.2 Tonga

The Kingdom of Tonga consists of an expanse of 171 islands with a total land area of 747 km² scattered across 347,282 km² of ocean. The islands lie east of Fiji and southwest of Samoa between 15-23°S latitude and 173-176°W longitude. The islands are of mixed origin of both young andesitic volcanoes up to 1030m above sea level and older raised limestone (Drake et al., 1996). First populated by humans ca. 3000 years ago, the 119,000 inhabitants today dwell on 36 islands, which contain about 90% of the total land area of the Kingdom (Franklin et al., 1999). While the northern most island group, including Niuatoputapu and Niuafu'ou, lies closer to Fiji than the rest of Tonga, the 17 main islands form 3 groups including the Vava'u group, Ha'apai group, and Tongatapu and 'Eua.

The urban areas of the Kingdom of Tonga are Neiafu in Vava'u and the growing capitol city Nuku'alofa, the most densely populated area, which lies on the northeastern

corner of the largest island Tongatapu. Outside of these cities, the inhabited islands are characterized by small, scattered villages and agricultural allotments. The remaining stands of indigenous tropical hardwood forests are now found only in patches on the islands of Vava'u, 'Eua and on a few uninhabited islands such as Tofua and Late (Drake et al., 1996).

All of the land of the Kingdom of Tonga is legally owned by the King. This Crown Land includes the hereditary estates of the King, royal family, nobility and also government land. Under the Land Act each Tongan male upon reaching the age of 16 is granted a town allotment of approximately 1,600 m² for residence and bush allotment of 3.3 ha. for farming purposes (Thomson et al, 2000). The allotments may be leased but not sold and are the basis for subsistence agriculture frequently used in cultivating staple crops of yams, sweet potatoes, cassava, papaya, mango, coconut, and bananas among other fruits, vegetables, and medicinal herbs. Yasi is occasionally planted in these plots and along the edge of bush allotments among fruit trees. Population growth and changes in land use are causing pressure on land resources (Robson, 2004; TNR, 2002). Changes in land use include the creation of large scale coconut plantations at the turn of the 20th century and more recently pine plantations and the cash cropping developments of squash, kava, watermelon, and vanilla cultivation. These endeavors oblige land clearing and have replaced much of the traditional subsistence farmland and nearly all of the indigenous forest land (TNR, 2002).

The Ministry of Lands and Surveys and Natural Resources (MLSNR) oversee all land use and allocation. The Ministry of Agriculture and Forestry (MAF) controls

agricultural and forest land including plantation land, and the two natural parks in Vava'u and 'Eua. The MAF is a key force in the Kingdom for conducting research and promoting education. The newly formed Department of Environment (DoE) coordinates collaborative environmental projects with international and regional agencies.

1.10 Ethnobotany of Yasi

Known as *yasi* in Fiji and *ahi* in Tonga, *Santalum yasi* holds a significant place in cultural traditions of both Fiji and Tonga and has played a role in the continued interaction within and between these two island groups. Trading between Fiji and Tonga has persisted since prehistoric times and is the reputed source of the yasi in Tonga, which, according to some sources was brought as seedlings from its origins in Fiji (Seemann, 1869; Brennan & Merlin, 1992). Tongan sailors would bring barkcloth, whales teeth, ornamental shells, sail masts, fish stingers used for spearheads, and other goods to Fiji in exchange for various items including canoes, red feathers, mats, baskets, pottery, and sandalwood (Tippett, 1968; Thompson, 1940; Brennan & Merlin, 1992). Tongan boatmen also traded yasi to islanders north in Samoa, and exchange between islands of each archipelago was common with the southern Lau islands of Fiji trading for the yasi from Vanua Levu, Fiji (Thompson, 1940; Brennan & Merlin, 1992).

A highly prized commodity, the yasi heartwood was an important, prestigious, cultural item in Tonga for weddings and funerals, and was a valuable gift to chiefs (Bennett, 1932). Vason (1810) noted that yasi-scented oil was used to anoint chiefs (Whistler, 1991b). The successful acquisition of yasi supplies, therefore, may have

played an important role in facilitating the control of the island kingdom of Tonga by dominant chiefs (Brennan & Merlin, 1992). The significance of yasi's political role was paramount during the early 19th century when trade in the resource was an easy opportunity for aspiring elites (Sahlins, 1988).

While yasi wood was used for carving and even for fuel or building materials at times in Fiji (Jiko, 1991), a major traditional utilization of sandalwood in Tonga, Samoa, and the Lau islands of Fiji was for scenting coconut oil (Bennett, 1932; Seeman, 1869; Yunker, 1959; Thompson, 1940; Brennan & Merlin, 1992). By grating the heartwood on a mushroom coral a fine powder was produced and mixed with the coconut oil to create an aromatic product for various uses including body lotion, perfume, and hair oil (Seeman, 1869; Brennan & Merlin, 1992). In Tonga, often a yasi log is stored in the *fata*, the loft of a home, where the other valuables, such as fine mats, kava, and ngatu (traditional bark cloth or "tapa cloth"), are kept between use for funerals, marriages, or other important ceremonies. One yasi branch would last perhaps 10-20 years or longer, as only small amounts of grated dust is needed to make the scented coconut oil, and sometimes one log was passed from one generation to the next (personal correspondence with Sunia Napa'a, 2006). In Tonga, oil from yasi heartwood is used to scent tapa cloth (traditional bark cloth) on special occasions and to anoint bodies in royal funerals. Yasi is also featured in Tongan songs and legends (Thomson, 2006). Sandalwood has also been used in Fiji as an insect fumigant and medicinally to clear dandruff and head lice (Jiko, 2000). Fijian women, when marrying, reputedly brought yasi with them to the

village of their new husband. It is unclear whether yasi seedlings, heartwood, or both were brought into the marriage (Sisa Rayaquayaga, personal communication, 2006).

Although prehistoric and historic trade with yasi occurred from Tonga to neighboring Samoa (Brennan & Merlin, 1992), it either never established in Samoa, or was established, then since became locally extinct. Interesting insights into the possible history of yasi in Samoa can be found in several historical records. References to the fragrant *asi* (Samoan vernacular for yasi) are found in Samoan traditional songs. [For example in Kramer 1901, “Afoafouvale’s Song” (p283) referenced to *asi* along with other fragrant plants. The footnotes to the use of the word *asi* clarify it is referring to sandalwood (p415)]. In the article “In search of Tagaloa: Pulemelei, Samoan Mythology and Science”, written by the Honorable Tui Atua Tupua Tamasese Taisi Tupuola Tufuga Efi, several ceremonial uses for *asi* are described. Tamasese explains:

In Samoa, one of the essential ingredients for performing liutofaga would be sandalwood and sandalwood leaves. This is evidenced in the Samoan word for funerals falelauasi, meaning the house that is lined with sandalwood leaves. Sandalwood like incense is one of the essences of Samoan culture, particularly Samoan spiritual culture. Fire is another core ingredient. The ritual making of fire is a direct inheritance from the Tagaloa mythology where Tiitiatalaga brought fire from the underworld for the use of man. The purification ritual thus involved the ritualistic lighting of flares, bonfires and asi wood fires—all symbolic of the Tagaloa mythology. ...The purification ritual had associated rituals. Putting together the purification ritual itself was as much a search as was the sequel. There were three sequel rituals: the fono ma aitu (conference with the sprits), lolo sa (making of holy oil) and sami lolo (making of containers for the oil). The asi or sandalwood leaves and wood which were presented at the purification ritual, were carefully stored for the sequel rituals. (Tamasese, 2007; see also Stair, 1896, 1898; Turner 1884; Kramer, 1999).

Although *asi* in Samoan vernacular refers to several other ethnobotanically valuable plants, it seems clear that this article is referring to sandalwood (most likely *Santalum yasi*) as the wood from other Myrtaceaeous *asi* would not normally be used in ritual burning as sandalwood is in many cultures. Talie Foliga, a Samoan forestry officer, has confirmed the use of *yasi* for the uses described above and added that it has also been used traditionally to make scented coconut oil (personal communication, 2009). It is interesting to note that no similar uses for *yasi* have been documented in Fiji or Tonga. For further discussion on the distribution of sandalwood in Samoa, refer to section 2.6.1.

1.11 Introduction to Dissertation

Chapter 2 of this dissertation, titled “Population Dynamics of Wild *Santalum yasi* Stands,” discusses the current distribution of *yasi*, and the growth rates and heartwood yield estimates, and reports on population dynamics, including size-class structure, of remnant, wild populations as well as observed threats. Chapter 3, titled “Population Genetics of *Santalum yasi*,” details the genetic structure and distribution of genetic variation within and between remnant populations in Fiji and Tonga. Chapter 4, “Discussion and Conclusions on the Sustainable Management of *Santalum yasi*,” focuses on the past and present efforts towards the conservation and sustainable management of *yasi*, builds on the recommendations of chapters two and three within the context of conservation strategies, and presents the complete, combined list of all the recommendations of this dissertation as well as the summarized findings and conclusions.

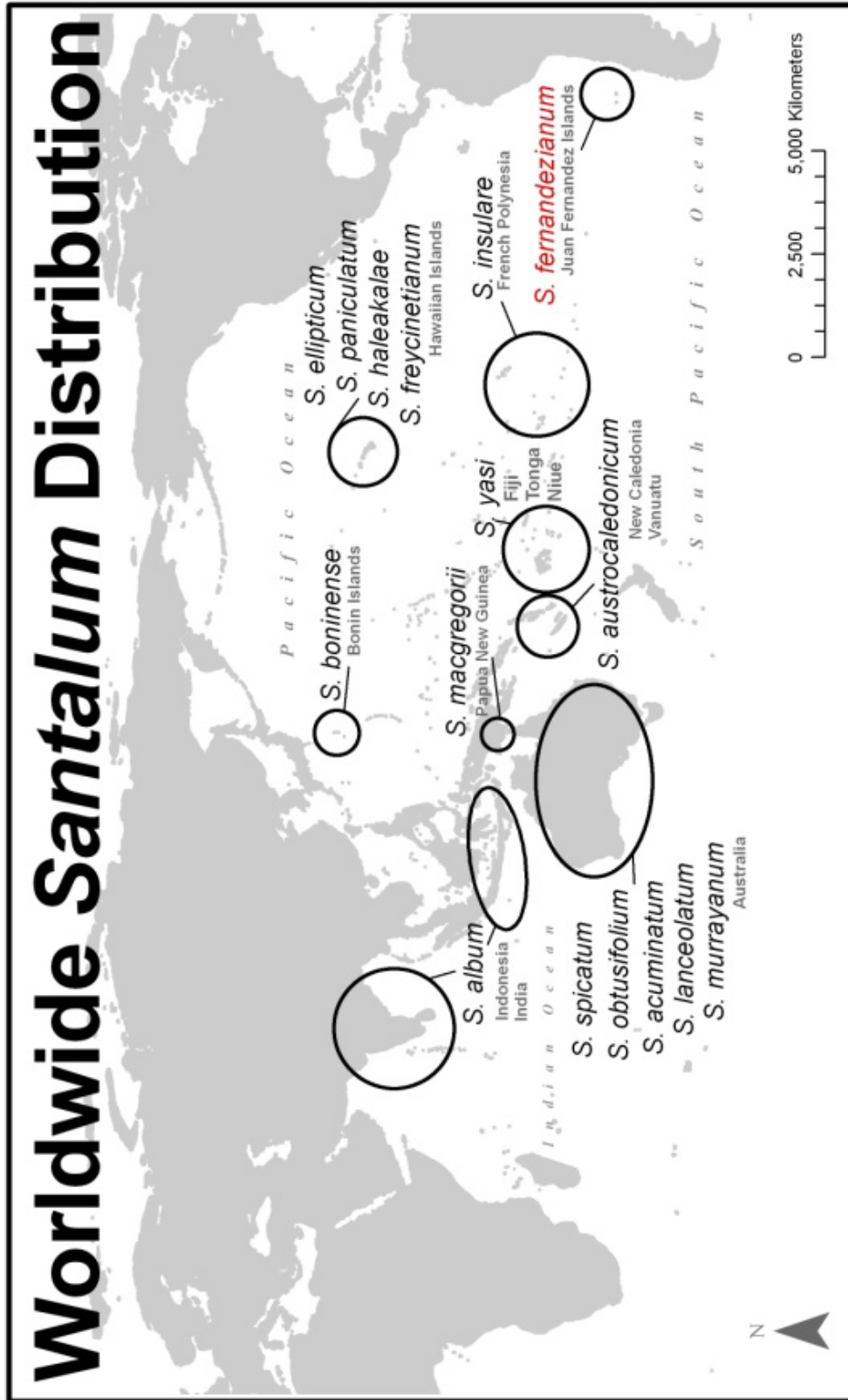


Figure 1.1 Distribution of the Genus *Santalum* (Santalaceae)



Figure 1.2 Growth Form and Habit of *Santalum yasi*.

a. Growth Habit of *Santalum yasi* (photo credit: Ryan Huish). *b.* Darker heartwood surrounded by lighter sapwood in *S. yasi* (photo credit: Lex Thomson). *c.* *Santalum yasi* parasitizing host of *Citrus* species (photo credit: Lex Thomson).



Figure 1.3 Illustration of *Santalum yasi* by Walter Fitch (Seeman, 1873).

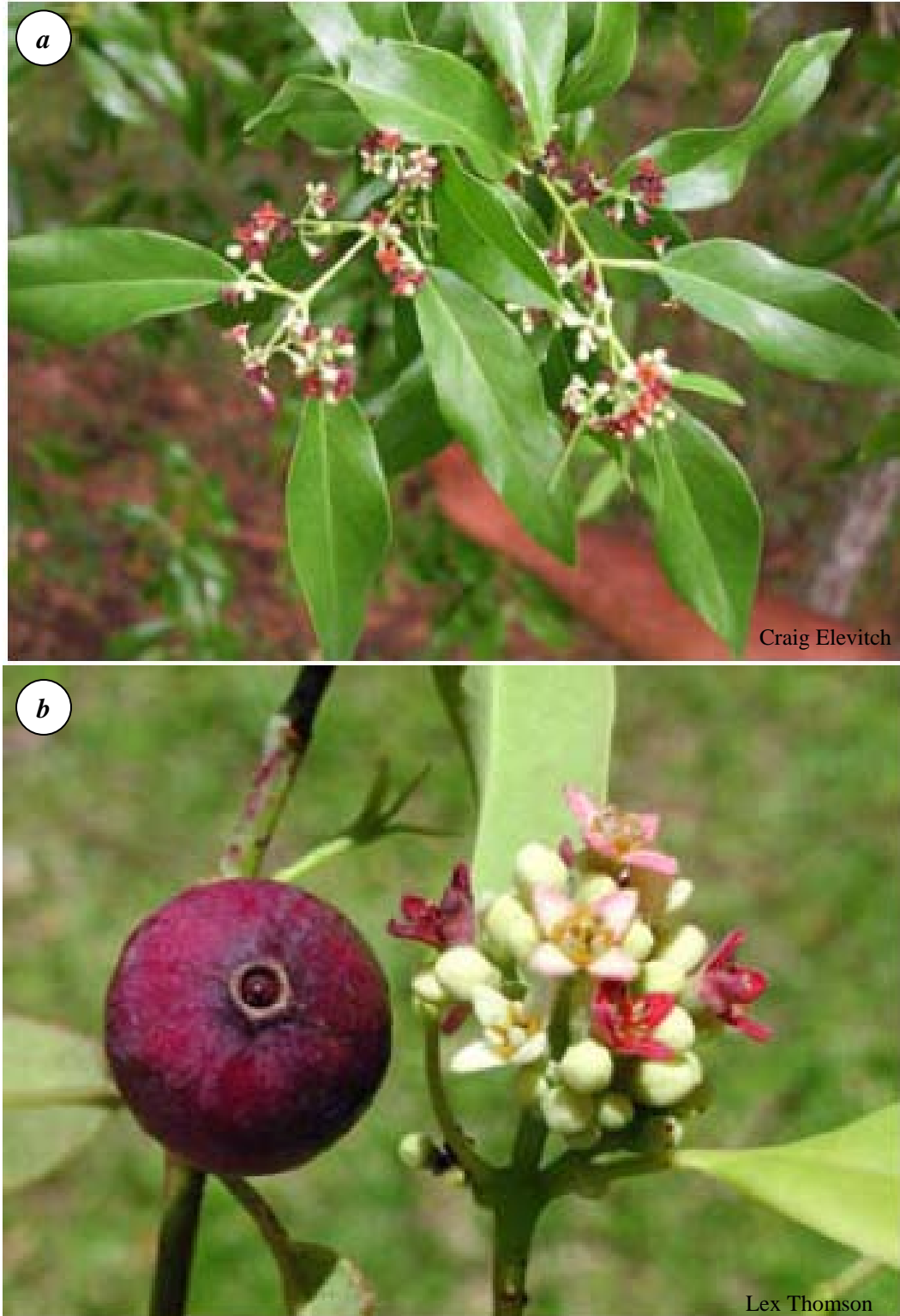


Figure 1.4 Flowers and Fruit of *Santalum yasi*

a. Flowering branch of *Santalum yasi* (photo credit: Craig Elevitch). *b.* Fruit and flowers of *S. yasi* (photo credit: Lex Thomson).



Figure 1.5 Preparing Heartwood of *Santalum yasi* for Export.

a. Heartwood from the roots (top left) and bole (right) (photo credit: Ryan Huish).
b. Sapwood is to be removed from heartwood before export (photo credit: Ryan Huish).

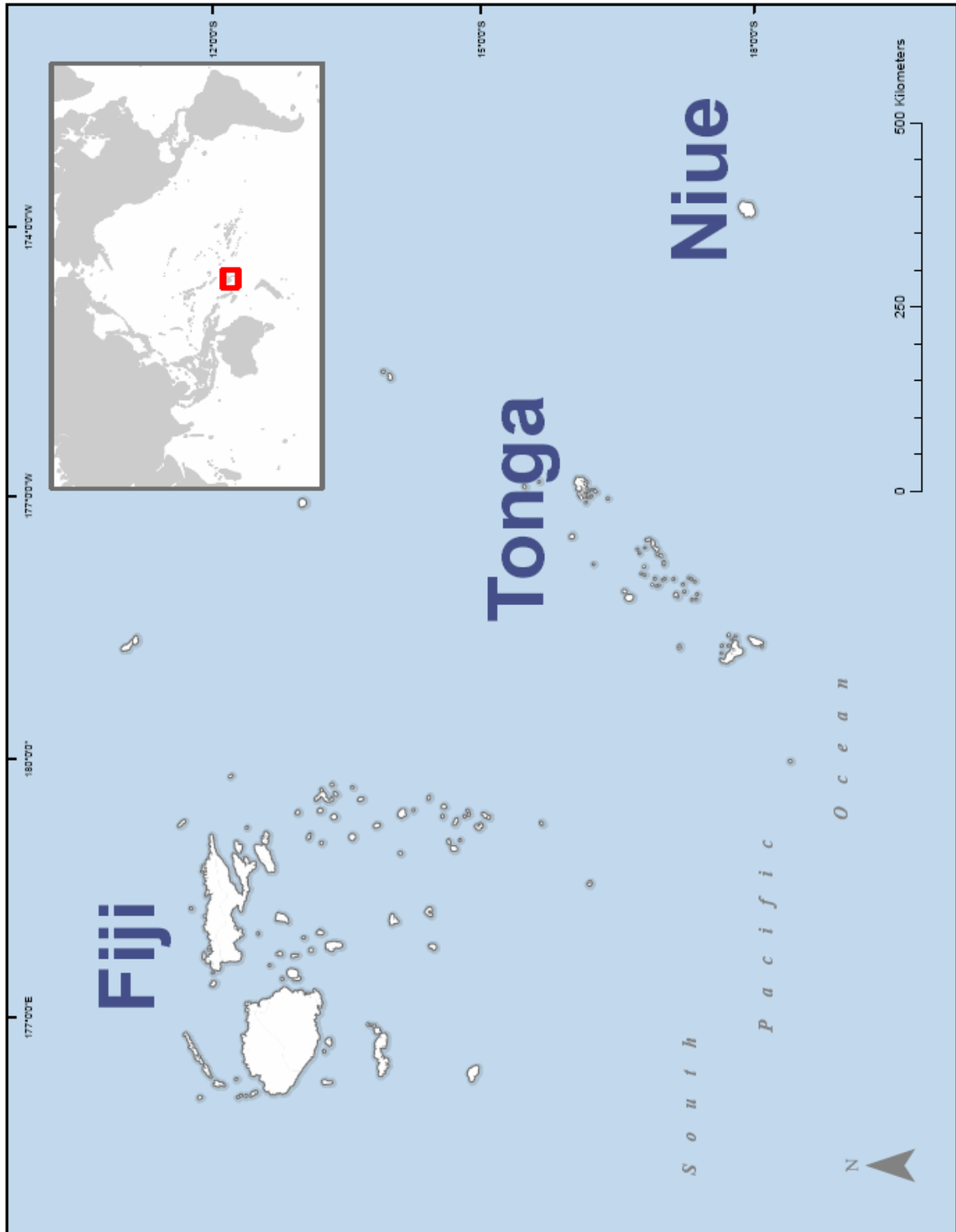


Figure 1.6 The Natural Geographic Range of *Santalum yasi* includes various islands within Fiji, Tonga, and Niue.

CHAPTER 2

POPULATION DYNAMICS OF WILD *SANTALUM YASI* STANDS

2.1 Introduction

This chapter will report on the collection and analysis of population dynamics data for the remaining wild yasi stands in Fiji and Tonga. The chapter begins with a discussion of the significance of population ecology in developing a sustainable management strategy for yasi and is followed by a review of previous ecological studies on yasi. The remainder of the chapter will cover the methods, results, and discussion of ecological analyses performed, including the current distribution of sandalwood in Fiji, Tonga, and Niue, size class structure and other transect data collection, and growth rate and yield estimates. The chapter will close with recommendations and conclusions on the implications the findings have on conservation management as well as future research areas.

2.2 Significance of Population Dynamics in Yasi Conservation Management

The long and turbulent history of yasi exploitation and waves of modern harvesting have caused populations to cycle through periods of abundance and decline. Determining the current population dynamics and inquiry into growth and yield rates for wild yasi stands will be imperative for the design of a sustainable management strategy, which could maintain and promote the growth of remaining stands.

These data can contribute to management in many ways. Determining the current distribution of yasi will help to identify how severe the decline of yasi has been, planning

for management strategies, and also for looking forward in identifying areas where yasi may potentially return. Information on the size, density, and size-class structure of a population can indicate regenerative capacity and recruitment levels. These data can also give insight into the general health of a population, and identify threats and priority areas for conservation to prevent future overexploitation and promote sustainable harvest levels for wild populations. Formulating growth rates and yield estimates according to tree age and diameter are of particular interest for harvest planning that maximizes yield.

As noted by Thomson et al. (2000), the current lack of ecological data on yasi is a major constraint to the successful development and implementation of a sustainable management strategy for this species. This chapter reports size-class structure data of the three densest remaining natural populations, the investigation into species distribution, evident ecological threats, and formulations of growth rates and yield estimates for yasi.

2.3 Research Questions

1. What is the current distribution of wild/naturalized *Santalum* species in Fiji, Tonga, and Niue? How has the natural distribution of these sandalwood species changed over time?
2. What are the current densities and size-class structures of remaining wild yasi populations? Are regeneration rates sufficient to maintain the populations in situ?
3. What are the ecological threats to remnant yasi populations?
4. What are the estimated heartwood yield losses from premature harvesting?

2.4 Previous Ecological Studies on Yasi

All ecological data previously collected on yasi consist of four reports and surveys from the Department of Forestry conducted in Fiji, which are unpublished and, with the exception of Jiko (1991), are difficult to access (Usumaki, 1981; Tabunakawai & Chang, 1984; Jiko, 1991; Duikoro & Tokairavua, 2002). All focus primarily on estimations of harvest volumes, distribution, and silviculture methods. Ecological data for yasi populations in Tonga and Niue are almost nonexistent beyond post harvest export data and brief comments on distribution (Ehrhart, 1997; Likiafu & Robson, 2005; Tuita, 2005; Thomson et al., 2005; Likiafu, 2008).

2.4.1 Previous Ecological Studies on Yasi in Fiji

Resource surveys of Fijian yasi populations have been periodically conducted by the Fijian Ministry of Forests. In 1955, fifteen years after the establishment of the 1930 exportation ban and five years after the 1950 harvesting ban on yasi, the Forestry Department report on the status of yasi on Vanua Levu estimated that no more than 200 trees of yasi were present in Bua, with less than 10 exceeding 30 cm dbh (diameter at breast height) (this Forestry report was not accessible but was referred to by Usumaki (1981), Jiko (1991), and Thomson et al. (2000)). However, Thomson et al. (2000) in commenting on this report, noted that “it would seem that these were considerable underestimates, but they underscore the difficulty of estimating such a scattered and diffuse resource, which is heavily cut in more accessible areas.”

With the increasing inquiries into yasi for export by foreign traders, a resource survey was conducted in 1981 (September-October) by forestry officer J. T. Usumaki in the Bua Province of Vanua Levu, or “Sandalwood Island”, where the species has commonly been believed to have first originated and where the largest stands were supposed to have been. This survey sought to determine the quantity and distribution of yasi, ecology and regeneration potential, and to make recommendations for the species. The survey recorded size class distribution information by diameter and height according to sampling along transects.

Usumaki estimated 50,000-61,000 trees were growing in Bua of varied sizes but with very low regeneration (regeneration being defined as trees less than 7cm dbh (diameter at breast height)). The lack of seedlings/regeneration is suggested as an artifact of the dense forested conditions with thick underbrush or other environmental factors, which may inhibit seedling survival. This thick underbrush, however, may also obscure seedlings causing reporting errors. Usumaki further calculates a standing volume of 2600 m³ in Bua. This volume was scattered over 15,000 hectares and would yield at most 20 m³ or 1,080 tons of heartwood, according to his estimated 35% heartwood content and a 0.85 m³/ton heartwood conversion factor (1981). These tree and volume estimates are based on a sampling fraction of 0.11% to 2.14% of four separate forest areas, for a total area sampled of 26.7 hectares and total forest area of his extrapolation being 15,068 hectares, making the total sampling fraction less than 0.18%. These sampling fractions are significantly lower than Peters’ (1996a) suggested minimum of 5% sample of total habitat area necessary to accurately calculate values representative of whole populations.

The size class distribution reported by Usumaki (1981) is distinctly bell shaped with almost 45% of individuals falling in the size class of 10 to 15 cm dbh, and nearly 82% of all recorded, naturally occurring individuals having a dbh within 5 to 20 cm.

Size class distribution of forest population reported by Usumaki (1981) shows 8 regenerative individuals < 5cm dbh, 13 individuals 5 to < 10 cm dbh, 34 individuals 10 to < 15cm dbh, 15 individuals 15 to < 20cm dbh, 5 individuals 20 to < 25 cm dbh, and 1 individual > 25cm dbh.

Tabunakawai and Chang conducted a similar resource and distribution survey on the Ono-i-lau island group for the Fiji Ministry of Forests in 1984. On Onolevu, the main island of this group, they reported a standing volume of 11.5 m³ over 335 hectares, mainly on the south eastern parts of the island. Yasi was also found in sparse amounts on Udui, Mana, and Davura though most individuals were young trees less than 5cm dbh. Doi island was also sparsely populated with yasi of mostly less than 5cm dbh, but this island did reportedly have a few trees larger than 10cm dbh. Yasi was not found on the Yanuya island group, which is the farthest from Onolevu. The total standing volume for the whole Ono-i-lau island group totaled at 23m³ or 9.5 tons of heartwood.

In 1991, L. R. Jiko, a principal silviculturalist for the Fiji Ministry of Forests, compiled a report on the status and current interest in sandalwood in Fiji. (Different versions of this report are found in Jiko 1991, 1993, & 2000, but the original 1991 is the most comprehensive.) This timely report was compiled after the extensive sandalwood harvesting of 1987-90, which returned F\$4.74 million in foreign exchange. This harvesting consisted of sandalwood collected from areas in all four divisions of the

country. Jiko's (1991) report consists mainly of information gathered regarding yasi distribution.

The most recent report is the "*Santalum yasi* Enumeration Report on Kadavu Island" compiled by Joni Duikoro and Jone Tokairavua of the Fiji Ministry of Forests at the end of 2002, 14 years after the only commercial harvesting of yasi from Kadavu in 1987-1988. This report focused on determining current volume, distribution, regeneration potential and economic viability of the resource. The enumeration was conducted in four locations on the far eastern end of the central lobe of the island near the following neighboring villages: Muanisolo, Vunisei, Daku, and Naivakarauniniu. A 100% sampling method was attempted. All trees >7cm dbh were measured for dbh and height to calculate volume. All trees less than 7cm dbh, including any noticeable seedlings, were counted as regeneration.

In total, 455 trees ranging from 7 to 28 cm dbh were counted with an average dbh of 11.7cm. Almost 50% of these trees were in the lowest recorded size class of 7-10.9cm dbh and more than 82% of all trees were between 7 and 15cm dbh. Standing volume was calculated according to the formula $v=(\pi d^2 h)/40,000$ and totaled at 17.355m³ or 14.75 tons solid wood, or 5.16 tons heartwood. The land tenured by the Muanisolo village alone contained 54% of land surveyed and 78% of calculated yasi volume: 13.57m³, or 11.5 tons, which contains over 4 tons heartwood. This volume near Muanisolo was found across more than 762 hectares of forest.

Height, diameter, or other size-class distribution data was not collected for specimens < 7cm dbh, but 380 trees < 7cm dbh were counted as regeneration. Duikoro

and Tokairavua note, however, that seedlings could have easily remained unnoticed due to cover by overgrown shrubs, and further assert that regeneration capacity appeared low due to the dense forest conditions. Muanisolo and Daku had the greatest amounts of regeneration potential, with 217 individuals <7cm dbh reported for the Muanisolo location, amounting to .285 regenerative individuals per hectare. Regeneration was lower in Vunisei, and appeared to have been reduced by uncontrolled wildfires. Naivakarauniniu also had very low regeneration.

While these were the only village areas enumerated by the report, Duikoro and Tokairavua note that other villages on Kadavu Island had harvested some amount of yasi during the major harvest of 1987 – 1988 including the villages of Nalotu, Naqalotu, Yakita, Korovou, and Talaulia in the district of Yawe, and Vukavu in the district of Naceva, and Naioti and Levuka in the district of Yale. Duikoro and Tokairavua also found yasi growing in Nakaunakoro and Dravuvala villages and suggest that most areas across the island would be suitable yasi habitat if maintained appropriately (2002).

Another project lead by the Fiji Ministry of Forests sheds some light on the ecology of yasi. From 2006-2007, Rob McWilliam, the National Forest Inventory Coordinator for the Fiji Department of Forestry Management Services, led a team to assess and measure the indigenous forest cover across Fiji's main islands and to perform field samples of forests to estimate average and total volumes using a sample-plot methodology. According to McWilliam, the Fiji Conservator of Forests was considering a proposal to quantify the yasi resources to enhance planning and management, but after discussing the results from his forest inventories and the research presented in this thesis,

McWilliam was of the opinion that the yasi populations are so scattered it would be near impossible to find and sample the populations. He also suggested that finances would be better spent in awareness workshops, conservation of existing stands, the creation of seed orchards, and so forth (personal correspondence, 2008).

2.4.2 Previous Ecological Studies on Yasi in Tonga

Population dynamics of yasi in Tonga have been virtually undocumented, and resource information is generally available only post-harvesting as export values. Extensive harvesting occurred in the 1960s and 70s from ‘Eua and Tongatapu. In 2005, 52 tons of yasi heartwood was exported to China (Tuita, 2005). From 2003- 2007, an average annual harvest level was 126 tons, which totals at 630 tons, some of which may have included sapwood (Likiafu, 2008; Tuita, 2005). In 2007 alone, after the ecological data for this thesis was collected, 205 tons were exported (Likiafu, 2008).

Ehrhart (1997) visited stands of yasi in ‘Eua in 1996-1997 for his unpublished report on the consequences of silviculture practices on growth habit. He makes no quantitative measurements but states “stands are continuous and well stocked in number, but depleted in volume since trees are young and small and often badly shaped.” Regeneration was noted as plentiful, though more frequently in open areas, which would presumably produce less desirable, lower heartwood yielding trees. A stand in Vava’u was also reportedly located southwest of the main island with small trees, and Ehrhart speculates that trees may have been growing on the cliffs of other scattered, smaller islands around Vava’u, but not noted due to their hard-to-access location. Ehrhart reports

that yasi trees may be rarely found in the bush of islands in the Ha'apai group and speculates that the small population size of young trees has a narrow genetic base.

2.4.3 Previous Ecological Studies on Yasi in Niue

Beyond the report of less than 100 small yasi trees on Niue in early 2005, no other ecological or resource data is available for the small population of yasi in the forested area west of Hakupu, Niue. The extant trees were those left after Cyclone Heta struck Niue on January 1, 2004. Previously the population was noted to have been struggling, but the destruction of the greater forest canopy by Cyclone Heta may help the young yasi to grow and regenerate before the canopy closes (Thomson et al., 2005).

2.5 Methods

2.5.1 Determination of Current Distribution of *Santalum* and Study Site Selection

Yasi has historically grown naturally across multiple islands in Fiji and Tonga and has recently been found in Niue, however the current distribution has changed from the historic areas (Jiko, 1991; Thomson et al., 2000). The distribution of yasi as recorded in the historical records, floras, herbarium specimens, government reports, and management plans, was compared to the distribution of current remnant populations of wild sandalwood species, as determined through discussions with the Fiji and Tonga Ministry of Forests (Sanjana Lal, Eliko Senivasa, Binesh, and Temo Gade Raravula of the Fiji Ministry of Forests; Tevita Faka'osi, Heimuli Lifiaku, Leody Vainikolo, Sunia Napa'a, and Taniela Hoponoa of the Tonga Ministry of Forests), South Pacific botanical

researchers (Marika Tuiwawa, curator of the South Pacific Regional Herbarium at the University of the South Pacific; Lex Thomson of the Secretariat of the Pacific Community; Arthur Whistler of the University of Hawai'i), landowners, mataqali, sandalwood harvesters, and through personal observation.

Ecological study sites were selected to include remaining, naturally occurring populations, which were not so scattered as to allow for appropriate analysis by transects. Individuals cultivated in plantations, home gardens or bush allotments along forest edges were not included in this study. After a thorough investigation, the only remaining wild stands of yasi appropriate for this chosen form of ecological analysis were one on Kadavu Island in Fiji and two separate clusters on 'Eua island in Tonga. A description of the selected study site locations follows below.

Kadavu Island, Fiji

Muanisolo Population

The yasi population selected in Fiji is found near Muanisolo village on Kadavu Island, which lies 96km south of Suva, Viti Levu, the capitol of Fiji. This rugged island covers over 400km² of land, of which 83% was forested in 1992 but presumably less currently due to clearing for farming, and fire and hurricane damage (Duikoro & Tokairavua, 2002).

The island is divided into three distinct land masses by two isthmuses at Vunisea and Vunisei villages. The island has various peaks reaching 805m at its highest point on Delainabukelevu at the western end, and gentle slopes reaching 274m at the highest point

in the central area, and 634m at the highest point on the eastern end at Biloniyaqona peak. The annual rainfall ranges from 20.3 – 33cm on the windward side of the island, but 20.3 – 25.4cm on the leeward side with a three month dry season (Duikoro & Tokairavua, 2002). Kadavu is volcanic in origin and the soil is composed essentially of andesites. The yasi population is found approximately two kilometers north-northeast of Muanisolo village on the central lobe of Kadavu. The soil type around the village of Muanisolo is humic latosols derived from basic and intermediate parent materials (Duikoro & Tokairavua, 2002). Of the 18% non-forested land on Kadavu, the major form of land use is subsistence agriculture of traditional root crops, and occasionally fruit trees and vegetables. However, some land has recently been converted to pine plantations (*Pinus caribaea*) for lumber production.

Muanisolo village and surrounding villages and forest areas are only accessible via boats and by foot along dirt trails. The village of Muanisolo has approximately 35 households. The study site is found in an area consisting of 12 hectares (19°00'40"S 178°15'34"E, 50m elev.) within the lowland rain forest (mainly primary forest in the study site) 2.5km northeast of the village (Figure 2.1). This study area is included in the area previously reported by Jiko (1991) to have yasi, and the area enumerated by Duikoro and Tokairavua in 2002. This area is overseen by two Mataqali, both from Muanisolo village. The forested area near Muanisolo is frequently crossed by children traveling to school in Vunisei and villagers walking to and from neighboring villages and bush allotments, collecting forest products. Notably, the men and boys of Muanisolo manage the yasi populations by routinely visiting the forest and cutting down vines and non-host

trees that may be competing for light. They also remove young side branches, thus promoting one main leader to maximize heartwood content (for more details see section 4.5.2). Harvesting around the village is controlled by the mataqali. The first commercial harvesting of yasi in Kadavu occurred from 1987 to 1988 (Duikoro & Tokairavua, 2002).

'Eua Island, Tonga

The two yasi populations chosen for study in Tonga are on the island of 'Eua. Lying on the eastern margin of the continental Indian-Australian Plate approximately 20 km southeast of the main island Tongatapu, 'Eua is geologically unique in Tonga and is the highest and oldest limestone island of the Kingdom (Whistler, 1992). It is recognized as having originated from Gondwana, breaking off from Norfolk Ridge near New Caledonia about 40 million years ago. It then moved eastward, coming in close contact with Viti Levu (Fiji) 5 million years ago, and then settled at the southern end of the Tongan Trench. It is thus possible that 'Eua may have acted as a transfer agent of ancient floristic components to Fiji (Mueller-Dombois & Fosberg, 1998). 'Eua has the most diverse vegetation of any island in Tonga and still retains much of its original forest cover. It currently covers an area of approximately 81 km², the island has an oblong, triangular shape with a north-south orientation. One main paved road transverses the island from north to south along the western third of the island where the eight main villages are also located. The middle and eastern thirds of the island are accessible only by dirt roads and bush trails which give access to the 'Eua National Park, eastern ridge, and eastern beaches. While the microclimate of the highest ridge in 'Eua is slightly

cooler and moister, there is little seasonal variation in temperature, and south-east trade winds blow 65-75% of the time (Sykes, 1978). The only significant seasonal change is in mean rainfall, which is 90cm from May to October and 180cm from November to April (Drake et al., 1996).

Essentially a limestone formation, the island has a unique volcanic core and the rugged terraces across 'Eua are formed from periodic geologic uplifting of the eastern side of the island. The ridged outcroppings ascend gradually from the western coast in terraces as the elevation reaches 312m, forming an eastern ridge and then dropping quickly in steep cliffs towards the eastern coast (Bryan et al., 1972). The surface of the island from east to west consists of volcanic rock exposed along outcroppings of the eastern ridge, Eocene foramineral and algal limestones, Miocene tuffaceous and finally late Tertiary coral reef limestone along the western ridges, central valley and coast (Wilde & Hewiit, 1983). Quaternary andesitic tephra forms a complete layer 2m thick across the island, except where it has been eroded along cliffs, from which most soils are derived (Wilde & Hewiit, 1983). Alfisols and mollisols form the bulk of 'Eua's soils with entisols around the coastal regions and inceptisols on the steepest slopes (Wilde & Hewiit, 1983). The soils have well-developed profiles with an organically rich A horizon (Mueller-Dombois & Fosberg, 1998).

'Eua Coastal Population

The 'Eua coastal population is located on the western coast of 'Eua Island in Tonga in 16 hectares of littoral forest (mainly secondary forest) between the village of

Tuvuvai and the further-inland village of Ha'atu'a and is bordered on the west by the beach and on the east by bush allotments (21°21'S 174°58'W, 1-5m elev.) (Figure 2.2 & 2.3) The vegetation types included in this population are *Excoecaria-Tournefortia* littoral forest, *Hernandia-Terminalia* littoral forest, and some seedlings were observed out to the littoral scrub vegetation. This population is overlying Tertiary coral reef limestone and andesitic tephra formations and grows in soils consisting of a mixture of alfisols, mollisols and entisols and coralline sand (Mueller-Dombois & Fosberg, 1998; Wilde & Hewitt, 1983).

Minimal fencing separates native forest from bush allotments and the Deep Resort is located towards the northern end of the yasi population, which allows access to the habitat via a paved roadway. All of the forest is government estate land but is frequented by villagers collecting forest products or crossing to tidal areas.

'Eua Highland Population

The 'Eua highland population is located approximately two kilometers north-northeast of Houma village on the northern end of 'Eua island (21°18'S, 174°55'W, 380m elev.) in *Calophyllum*-mixed-species upland rain forest (mainly secondary forest) (Mueller-Dombois & Fosberg, 1998) (Figure 2.2 & 2.3). Pine plantations (*Pinus caribaea*) (not included in the transect readings) are encroaching in this area, replacing much of the native vegetation. The spatial distance (10km), difference in elevation, soil type, and surrounding vegetation merit treatment as a separate ecological population than the 'Eua coastal population. Located at a higher elevation than the 'Eua coastal population, this

area is subject to occasionally cooler and moister weather (Sykes, 1978). It is unknown whether seed dispersal occurs between the two populations. The population is found in 24 hectares of the forested area along the dissected slopes of the eastern ridge. Formed by uplifting of Eocene foraminiferal and algal limestones overlaid with Miocene submarine tuffs and tuffaceous limestones, the soils are mainly alfisols and mollisols with inceptisols in the steeper areas (Wilde & Hewitt, 1983).

2.5.2 Size-class Structure and Other Transect Data Collection

Ecological data on the size-class structure were collected September through October, 2006 on one site on Kadavu Island, Fiji, and November through December, 2006 on two sites on 'Eua Island, Tonga, as described in the previous sections. Methods followed those generally laid out by Peters (1996a & 1996b) and Hall & Bawa (1993). Data was collected with the assistance of forestry officers and local villagers (including village leaders and sandalwood harvesters).

For each habitat, a series of transects consisting of 10m x 20m contiguous plots were set. The number and placement of each transect was determined by the size and topography of each particular habitat. Measurement accuracy was maintained by correcting for slope using a clinometer and a prepared rope with corrected distance markers according to slope values (Peters, 1996b). The multiple transects ran parallel to each other, as determined by compass bearings, and were georeferenced using GPS coordinates. Transects were laid out to traverse the topographical and climatic gradients that existed (Hall & Bawa, 1993) and were spaced 50 or 200m apart to meet or exceed

the recommended 5% sample size of total habitat area necessary to accurately calculate statistics representative of the whole population (Peters, 1996a & 1996b).

The height of each individual sandalwood found within the plots was recorded using measuring tapes for shorter individuals and an extendable height pole for taller individuals. Diameter at breast height (dbh) of each tree 5cm dbh or above was recorded using a diameter tape. Other data also collected along the transects were presence of flowers and fruits on individuals, and other miscellaneous observations such as tree damage and vigor.

Size-class structures were characterized by the distribution of individuals into eight different size-classes (Table 2.1). Individuals in each population were classified according to height measurements for young trees and dbh measurement for mature trees to allow compilation into size-structure histograms (Peters, 1996a).

Table 2.1 Size-Class Assignments

Age class	Size class	Class Interval
Seedling	S ₁	< 0.5 m height
Sapling 1	S ₂	0.5 - < 1.0 m height
Sapling 2	S ₃	1.0 - < 2.0 m height
Juvenile	S ₄	2.0 - < 3.0 m height and dbh < 5cm
Adult 1	S ₅	5.0 - < 10 cm dbh
Adult 2	S ₆	10 - < 15cm dbh
Adult 3	S ₇	15 - < 20 cm dbh
Adult 4	S ₈	20 - < 25 cm dbh

Dendrometers were installed on six adult trees (at least one from every adult size class) in two populations in varying habitats from each Fiji and Tonga, for a total of 12 dendrometers in order to make monthly measurements of lateral bole growth through various seasons of the year to determine periodicity of growth. Unfortunately, since all

the dendrometers were on adult specimens, these trees were all harvested before adequate data could be obtained from them.

2.5.3 Growth Rates Estimation and Heartwood Yield Calculations

As discussed in the botanical description of Chapter 1, growth and heartwood yield of *Santalum yasi* is highly variable between individual trees and detailed information on mortality rates and growth rates within the different size classes is limited. A reasonable estimate of the growth rate of an average individual yasi tree according to age will be estimated using the more detailed growth data available for *Santalum austrocaledonicum*, another sandalwood species from neighboring New Caledonia and Vanuatu with almost identical size, life span, and habitat preference (Thomson, 2006a; personal communication with Lex Thomson, 2008). The *S. austrocaledonicum* growth rates at differing ages highlight the following timeframe for advancement between size classes for an average individual tree (Table 2.2). These values compare well with Thomson's report (2006a) that a 15-20 year old yasi tree appears to reach 15cm dbh.

Table 2.2 Estimated Years to Advance between Size Classes. (Size classes for adult trees follow the same pattern as found in Table 2.1: an additional 5cm dbh/size class.)

Initial Size Class	Ending Size Class	Time to advance (years)
S ₁	S ₄	3
S ₄	S ₅	3
S ₅	S ₆	6
S ₆	S ₇	6
S ₇	S ₈	6
S ₈	S ₉	6
S ₉	S ₉	7
S ₁₀	S ₁₁	7

Previous measurements for yasi heartwood volume have used a straight percentage (35%) of total tree bole volume according to Huber's formula for a cylinder using diameter at breast height and a height up to a bole diameter of 7cm. However, such calculations frequently return an overestimate of actual heartwood yields (Usumaki, 1981; Thomson, 2006a). The actual shape of the heartwood core most accurately resembles not a cylinder but rather a cone within a frustum-shaped volume tapering from 40% of the basal diameter (reflecting the 40% heartwood content of basal stem sections reported by Thomson (2006a)) to a point of 0% heartwood at the upper diameter of 7cm dob (diameter of bole) where heartwood presence generally reaches 0% (Usumaki, 1981). The measurement of heartwood volume for this report is therefore calculated by a formula for a cone with height being the total height minus the height at which the bole diameter is 7cm and basal diameter of the cone being 40% the basal diameter of tree. Heartwood yield contribution of roots, reported as being 25% to 33% of the total heartwood yield of a tree, is accommodated by adding a root factor to the formula (personal communication with Lex Thomson, 2008).

$$\text{Volume (m}^3\text{)} = \left(\frac{\pi * h * (.4*b)^2}{12,000,000} \right) * r$$

h= bole height to 7cm diameter (cm)

b= basal diameter (cm)

r= root factor =1.42

The diameter at breast height and tree height recorded from trees in the transects were used to help calculate estimations of growth rates and heartwood production. Basal

diameter was determined by adding 3.64cm to the diameter at breast height according to Usumaki's updated taper value of 2.8cm per meter (1981).

Basal diameter for each tree with dbh \geq 7cm was calculated by

$$b = d + (\text{taper} * 1.3\text{m to breast height})$$

$$b = d + (2.8\text{cm/m} * 1.3\text{m})$$

$$b = d + 3.64\text{cm}$$

d=diameter at breast height (cm)

Bole height to 7cm dob for each tree with dbh \geq 7cm was calculated by

$$h = t - h \quad \text{where:} \quad \frac{t}{b} = \frac{h}{7} \quad h = \frac{7 * t}{b} \quad h = t - (7 * t)/b$$

t= total tree height (cm)

h= height from the top of the tree down to 7cm diameter of bole (dob (cm))

Volume is calculated in cubic meters and converted to metric tons of heartwood according to the conversion factor $1\text{m}^3 = .85$ tons (Usumaki, 1981).

2.6 Results and Discussion

2.6.1 Distribution of *Santalum* species in Fiji, Tonga, Niue, and Neighboring Islands

Over the last several decades, there have been waves of sandalwood harvesting in both Fiji and Tonga, and an introduction of *Santalum album* with the subsequent *S. album* x *yasi* hybrids, which have resulted in significant changes in the distribution of sandalwood in Fiji and Tonga. Records of the historical distribution of sandalwood lack much detail, especially the records of its distribution before the latter end of the 19th century. Consequently, the historical distribution reported here may not be a complete representation of its past distribution. Some recent sources have reported detailed

descriptions of its distribution, though it is important to note that some of these more recent reports may be relying on distribution information that is long out-dated. Below is a summarized account of the historic distribution and an analysis of current distribution of sandalwood in Fiji, Tonga, and Niue according to the various sources as listed in the methodology section of this chapter (section 2.3.1). This only reports the naturalized populations of sandalwood and does not include sandalwood planted in village gardens. Forestry trial plots have been established in various locations in Fiji and Tonga and consist of both *S. album* and *S. yasi*, and some with *S. austrocaledonicum*. The location of these plots are included in this report on distribution as these may, over the coming years, be a source for dispersal of sandalwood into natural areas surrounding these plots. Place names below are reported from north to south, and west to east. Corresponding distribution maps are found in Figures 2.5 (Fiji) and 2.6 (Tonga and Niue).

Distribution of Sandalwood in Fiji

Rotuma

Although sandalwood is not native to Rotuma, an island lying 600km north of Viti Levu, the Fiji Ministry of Forestry established a mixed planting of *Santalum album*, *S. yasi*, and *S. album* x *yasi* onto the island more than 10 years ago. However, all of the *S. yasi* has died along with most of the pure *S. album*. The only trees that have become naturalized with good survival rates are the hybrids.

Vanua Levu Island

“Sandalwood Island”, historically documented to be the most plentiful area of yasi, has also been the most heavily yasi-exploited area, and now natural stands of yasi are all but non-existent. Yasi was once common on rocky slopes and lower hills of the Bua and Lekutu coasts (Parham, 1972) and most likely in other areas across the drier habitats of the island extending out to Udu point on the eastern tip of the island. Jiko (1991) states that “In earlier days, the wood was also obtainable in lesser quantities along the western and northern coast of Vanua Levu as far as Naduri, but as a result of heavy cutting and uncontrolled fire, yasi has disappeared along the Naduri coast.” Yasi has also been noted on the islands off the north coast of Vanua Levu, Galoa and Tavea, but now the only remaining sandalwood is that which is grown in the village yards. Smith (1985) mentions a fair population of yasi growing in the Bua and Macuata Provinces in Vanua Levu. Thomson et al. (2000) also mention yasi occurring in the Bua and Macuata Provinces, around the south-western corner of Galoa Island and Tavea Islands, and the north-eastern part of the island near Udu point. It has also been reported growing in the Cakaudrove provinces near Udu point. Personal observation of the western part of the island in December, 2006 revealed that the only sandalwood was within the village gardens. A small hill adjacent to Nawailevu village contained a very small but dense stand of naturalized sandalwood (it is unknown whether this was pure *Santalum yasi* or if it was *S. album* x *yasi* hybrid, but was most likely *S. yasi*). This young clump of sandalwood appeared to be less than five years old. The absence of natural stands of sandalwood in the Bua region was confirmed by all the mataqali leaders and occupants in

the four villages visited in the region in 2006. They also confirmed the lack of sandalwood regeneration there. With the burning of a large portion of natural forests in the area to accommodate pine plantations (*Pinus caribaea*), it is likely that most of the remaining regenerating sandalwood left after the harvesting would have been destroyed.

The absence of sandalwood in natural stands here was further confirmed by Rob McWilliam, the National Forest Inventory Coordinator for the Fiji Department of Forestry Management Services. After having performed a forest inventory in the area in April 2007, he reported that he and his crew never came across any sandalwood in the natural stands (personal correspondence, 2008). It was later confirmed that a sparse population was growing in open forest on hills around Navunievu village and a few on hills near Naicobocobo point in southwestern Vanua Levu. (personal correspondence with Marika Tuiwawa, 2009).

Viti Levu Island

The historical extent of sandalwood on Viti Levu is not well understood, but the last remaining natural stand of yasi on the island was reported in the Colo West Range of the Nausori Highlands, from Tubainasolo to Nasaucoko (Thomson et al. 2000). However, heavy harvesting has been occurring in this area recently and most sandalwood left has been destroyed by wild fires, except for a few sparse pockets towards Bukuya and Mt. Koroba in the Nausori Highland area. There may also be small amounts in the difficult-to-access cliffs in the region. *S. album* was introduced into the Nausori

Highland villages, presumably around 1990, and now hybrids are frequently found within village yards and surrounding areas.

Santalum album has also been introduced to the northern, eastern, and southern coasts of the island including the villages of Rakiraki, Tavua, Drasa, Lololo, along the Coral Coast (Lomawai, Tilivalevu, Cuvu, Sigatoka, Vatukarasa) and Galoa village. Some claim *S. album* was brought to the area from Lakeba in the Lau group (Fiji) and others claim it was brought from Nausori Highlands. *Santalum album* and *S. album x yasi* hybrids have become quite extensive, especially around Drasa and Lololo and down to Nadi. The Fiji Ministry of Forests and others consider them to be an environmental invasive (Personal communication with Sanjana Lal (2006) and Lex Thomson (2008)). Smith (1985) writes “*Santalum yasi* is by no means as depleted in Fiji as once believed, occurring in fair stands in parts of western Viti Levu between the Singatoka River and the river valleys inland from Nandi.” This is a surprising account as there have been no other records indicating *S. yasi* being so plentiful in this area. It is possible that what he was noticing was the early spreading of *S. album*, which, considering its present weediness, probably began being “plentiful” in 1985 in the area he described. Forestry trial plots including *S. album* and *S. yasi* have been established at Colo-i-suva and Nukurua, both north of Suva.

Kadavu

The historical distribution of *yasi* on Kadavu Island is not well documented, but its presence there has spanned at least five or six decades in the forests around

Muanisolo, Vunisei, Daku, and Naivakarauniniu villages. Yasi has also been documented in the forests around Nalotu, Naqalotu, Yakita, Korovou and Talaulia in the district of Yawe; Vukavu in the district of Naceva; and Naioti and Levuka in the district of Yale; and within village yards of several other villages (Duikoro & Tokariavua, 2002). As far as is presently known, *S. album* has not yet been introduced to Kadavu Island. Duikoro and Tokariavau (2002) also report that according to people from nearby Vunisei, sandalwood was brought to Kadavu from Bua at the end of the 19th century.

Lau Island Group

Samples of wild yasi were collected on Evuevu Islet in Quilqila Bay off of Vanua Balavu Island in 2007 by Marika Tuiwawa. On Lakeba, *Santalum yasi* and *S. album*, along with the spontaneous hybrids, are well distributed, though *S. yasi* is not as plentiful as the others. Ilisoni Tuiketei of Fiji Pine mentioned that *S. album* was introduced to Lakeba in 1980 from one tree from India. This may be the first place *S. album* was introduced into Fiji. Smith (1985) cites a collection of yasi from the central flat forest of Oneata and it is commonly known to be there presently, as well as on Komo island.

Ono-i-lau, geographically closer to Tonga than the main Fiji islands, is one of Fiji's most remote islands. Temo Gade Raravula, a forestry officer from Ono-i-lau, mentioned that in 1962, there was only one mature tree in Ono-i-lau, but by the 1980s it was growing on uninhabited islands around Ono-i-lau, even on the white sand. Temo's grandfathers said the yasi was brought there from Tonga and all the sandalwood there is regeneration from the single introduction from Tonga.

Distribution of Sandalwood in Tonga

Niuatoputapu

Niuatoputapu is the northern-most island in Tonga where yasi is known to occur, however it has become very scarce over the past several years due to extensive harvesting for export and only juvenile trees are currently present. Yuncker (1959) mentions a sample collection made on the volcanic soil on the mountain ridge above Vaipoa in 1951.

Vava'u Island Group

Yasi is found sporadically in Vava'u, which has recently been scoured by foreigners for harvesting. While visiting Vava'u in October 2006, the people in nearly every village with yasi mentioned that all their yasi was harvested just a few weeks or months prior. The densest population in the Vava'u group is on Hunga island, west of Vava'u where there is an effort by the local people to actively manage their wild yasi stands, marking them for protection from burning or felling (for agricultural purposes) by weaving coconut leaves around the base of the trunk. Yasi also occurs on Pangaimotu and Tapanā Islands south of Vava'u, and possibly infrequently on the other islands in the group. A forestry trial plot was established in the northwest highlands of Vava'u at Toafa including *S. album* which has not yet become naturalized.

Ha'apai Island Group

Yasi is found throughout many of the inhabited Ha'apai islands including Foa, Lifuka, Uiha, Uoleva, Lofanga, Ha'ano, Nukunamo, Ha'afeva, Nomuka, Tungua, and

Matuku. Yuncker (1959) noted a collection on Nomuka in a thicket along a road between the ocean and the central lake in 1953. *Santalum album* has been introduced to the forestry trial plot at Vaipoa on Foa Island, but has not become naturalized there.

Tongatapu Island Group

Yuncker (1959) mentioned several collections made in the 1950s in natural stands in Tongatapu near the villages of Fatai, Fu'amotu, Sopusu, and Niutoua. Thomson et al. (2000) mention that yasi is rarely found in the small areas of remaining natural forests of this heavily populated island. It seems that yasi is mainly restricted to 'api 'uta (agricultural land allotments) and in village yards where it has been planted, and is sometimes found to occur in nearby areas through natural regeneration. Forestry trial plots containing *Santalum album* and *S. yasi* have been established on Tokomololo and Sia'atoutai on Tongatapu, though *S. album* has not been naturalized yet.

'Eua clearly contains the densest populations of yasi in the world. The yasi here is also arguably the most morphologically diverse, though further morphological studies could confirm this. Yasi is most dense along the western coast and in the northern highlands north of Houma village. Thomson et al. (2000) note that yasi is very common on 'Eua especially in secondary forests. *Santalum album* was introduced to 'Eua 15-20 years ago near Pangai and Mata'aho. One forestry officer stationed in 'Eua noted that *S. album* is well adapted to the local environment and has already become naturalized and has even begun to be harvested along with yasi by the local people.

Yasi is very rare on 'Ata island, 145 km southwest of Tongatapu. 'Ata is currently uninhabited but has topography and vegetation similar to 'Eua.

Distribution of Sandalwood in Niue

There is currently a small (~1sq km) population of yasi just west of Hakupu village, in the southern part of Niue (~480 km west of Ha'apai, Tonga) (Thomson et al., 2005). It is very likely that yasi is of recent introduction to Niue. In 1902, Smith wrote that the "Tongan sandalwood" did not grow on Niue and he "doubted if it ever did so". Yasi was not included in Yunker's Flora of Niue in 1943, so it may be assumed that it was not introduced to Niue until after 1943. In 1965, Sykes (1972) made a collection on Niue from Hakupu among scrub on village outskirts and wrote "Sandalwood is very rare on Niue. The specimen cited was from the only tree known to be present on the island. Although the tree was close to the village, the owner of the scrub-covered land on which it was growing stated that it has not been cultivated." Sykes classified yasi as a probable introduction rather than an indigenous plant (1970). Lex Thomson interviewed residents living where yasi is found and they knew of no Tongan or Fijian who may have brought the plant to Niue and concluded that birds were the probable dispersal agents within the last few hundred years. The population was struggling until hurricane Heta hit Niue on January 1, 2004, causing significant breaks in the forest canopy, something which has not happened in possibly decades, providing an opportunity for regeneration in the population (Thomson et al., 2005).

Distribution of Yasi in Other Islands***Samoa***

Although prehistoric and historic trade with yasi occurred from Tonga and Fiji to neighboring Samoa, it seems to either never to have been established in Samoa, or has since become locally extinct. There is surprisingly only one record of its presence in the wild there near Falealupo (Brennan & Merlin, 1992). This tree has since died (Arthur Whistler, personal correspondence, 2006). Also, a forestry officer in the district where this sample was found said that he once, and only once, saw a tree come into the timber mill, perhaps in the 1970s (Arthur Whistler, personal correspondence, 2006). Talie Foliga, a forestry officer from Samoa, reported that forestry trial plots containing sandalwood from Fiji and Vanuatu (most likely *S. yasi* and *S. austrocaledonicum*, and possibly *S. album*) have been established in Samoa within the past five years. It is also interesting to note that Niuatoputapu, where yasi is known to occur, in the northern extreme of Tonga, is closer to Samoa than it is to the rest of Tonga, making the absence of yasi in Samoa even more puzzling. Given the extensive ethnobotanical uses of yasi in Samoa (see sections 1.8 and 1.10), it seems unlikely that this plant would have such cultural significance in Samoa if it was only obtainable through contact with Tonga, and perhaps hints towards either yasi being native to Samoa, or an aboriginal introduction, with subsequent local extinction.

Vanuatu

There is a yasi herbarium specimen deposited at Kew mentioned by Smith (1985) as having been collected from Vanuatu (previously known as New Hebrides), which is

where *Santalum austrocaledonicum* is native to. No other sources mention the occurrence of yasi in Vanuatu.

Discussion on the Distribution of Sandalwood

The distribution of wild *Santalum yasi* has clearly decreased over time, even to the point of local extinction or near extinction in certain areas, while the distribution of *S. album* and *S. album* x *yasi* appears to be increasing over time. In areas devoid of naturalized sandalwood populations, or with very sparse distribution, it is possible that seeds dispersed from village trees into the surrounding forests by birds could eventually lead to a restoration, or new introduction, of a natural population. The forestry trial plots established in various locations in Fiji and Tonga may also lead to natural dispersal of *S. album*, *S. yasi*, and possibly *S. austrocaledonicum* and hybrids. *Santalum yasi* and *S. austrocaledonicum* do not seem to be as easily naturalized as *S. album* and the *S. album* x *yasi* hybrids. *Santalum austrocaledonicum* has not been observed to hybridize as readily with *S. yasi* as does *S. album*, which is logical due to its more removed phylogenetic relationship within the genus (Harbaugh & Baldwin, 2007) It is interesting to note the history of sandalwood growth on Rotuma Island. The fact that the *S. album* x *yasi* out competed *S. yasi* and much of the *S. album* on this small isolated island may indicate a possible outcome of mixed stands in the future. This will be discussed more in sections 2.6.3 and 3.7.

The general lack of the presence of yasi on uninhabited islands is notable and explanations for this phenomenon may be complex. The presence of sandalwood on

inhabited islands may support the idea that human activities act as a mechanism for yasi population establishment, either through direct introduction by humans, or through human-induced environmental disturbances which create preferred habitat so that when seed dispersal occurs through natural means, regeneration is more successful, as sandalwood is an opportunistic, pioneer tree species in disturbed areas. While birds are known seed dispersers, the influence of birds for general dispersal may be minimized if suitable disturbed or open-canopy habitats are not available.

The distinctive distribution of sandalwood near inhabited areas is illustrated well when looking closer at the sandalwood populations in ‘Eua and ‘Ata in Tonga. The original inhabitants of ‘Ata island relocated to ‘Eua in 1863 and formed Ha’atu’a village. The coastal area between Ha’atu’a and Tufuvai (currently the most dense area of yasi) is where the village of Ha’atu’a was first located before it was relocated to the existing site further inland. The introduction of yasi by new villagers from ‘Ata, or the associated disturbance of the forest in this area may have promoted successful establishment. Yasi is currently found only sparsely on ‘Ata Island, a now uninhabited island 150 km southwest of ‘Eua.

Also, while yasi is common in the noted areas of ‘Eua, it is not found in the pristine, undisturbed forests of ‘Eua National Park along the eastern coast. This could be because, as mentioned before, sandalwood regenerates best in disturbed areas, or it could be due to the moist conditions along the eastern coast. The yasi population on Niue experienced noted regeneration after cyclonic disturbance. It is plausible that sandalwood could be found in sparse pockets on uninhabited islands throughout its range,

reseeded by birds after occasional natural disturbances such as tropical storms and hurricanes, or the natural felling of dead trees, but the occurrence of yasi on uninhabited islands has not been documented.

2.6.2 Size-class Structure

The results of the size-class analysis show that the 'Eua coastal population is the most dense of the three populations analyzed, followed by the 'Eua highland and then the Muanisolo Kadavu population (Figure 2.7). There was an estimated 401 total individuals/hectare (with 61 sexually mature trees/hectare (S5 and above)) in the 'Eua coastal population, 314 total individuals/hectare (with 52 sexually mature trees/hectare in the 'Eua highland population and 77 individuals/hectare (with 18 sexually mature trees/hectare)) in the Kadavu, Muanisolo population. The significantly lower population density of Muanisolo compared to the 'Eua populations may be due to significant topographical differences in habitat as transects spanned more stream ravines where yasi tends to avoid. Also, as suggested by Tevita Faka'osi, Head of Forestry in Tonga, the 'Eua coastal population is located over a relatively, recently disturbed, abandoned village locale, providing an opportunity for yasi proliferation.

The number of heartwood bearing trees per hectare is more evenly represented in all three populations. Although size is not necessarily an indicator of amount of heartwood, mature heartwood is generally found in trees 15cm dbh and larger, size-classes S7 and above, giving an average 1.7 heartwood bearing trees/hectare in the 'Eua coastal population, 1.3 heartwood bearing trees/hectare in the 'Eua highland population,

and 1.5 heartwood bearing trees/hectare in the Kadavu, Muanisolo population. Trees are often harvested, however, at smaller sizes in hopes of finding additional heartwood, even if heartwood content is minimal or non-existent. Individuals/hectare in S6 may be low for this reason. Yasi may potentially reach sizes over 40cm dbh (Thomson, 2006a; Usumaki, 1981), but no individuals greater than 23cm dbh were present in any population.

The resulting size class structures for the three populations analyzed contain substantial drops in numbers of individuals in S2 and S3 for all three populations. This size-class structure is typical of populations with discontinuous or periodic recruitment (Peters, 1996a). This structure is not surprising due to frequent cycles of harvesting which remove many of the mature fruit-bearing trees from the population.

Because the transect locations selected for this study were intentionally set in the densest continuous populations, these results show higher yasi densities than the previous studies discussed in section 2.3. The previous studies attempted to estimate yasi densities for significantly larger areas, which most likely included areas of population discontinuity included in their total hectare estimates. The transect data collected by Usumaki (1981) for populations in the ‘Bua region of Vanua Levu, Fiji calculates 3 individuals/hectare (76 individuals recorded over 26.7 hectares). Duikoro and Tokairavua’s (2002) enumeration of yasi in Kadavu, which was conducted using a “100% sampling” methodology, reports a total of less than 1 individual/hectare (835 individuals recorded over 1409 hectares) across all four study sites. Unfortunately, Duikoro and Tokairavua do not report population data specific to the Muanisolo area to

allow more close comparison. However, individuals/hectare values for Muanisolo may be presumed higher when considering that the Muanisolo population contained 78% of calculated yasi volume on 54% of the total land surveyed.

Note, these population data reported here represent values as of October of 2006 and do not reflect current levels due to subsequent, extensive harvesting in Muanisolo in 2007 and also in 'Eua between 2006 and 2008.

2.6.3 Observed Ecological Threats

The major ecological threat to yasi comes from unsustainable harvesting practices. Other ecological threats include damage to seedlings and saplings by feral pigs, and possibly include invasive plant species choking out potential regeneration, hybridization with other sandalwood species, and loss of habitat due to clearing of land for agricultural development and pine plantations.

Unsustainable Harvesting Practices

Early and Excessive Harvesting Patterns

Current harvest patterns such as the frequent and near complete harvest of all heartwood-bearing individuals in populations, including the frequent felling of young trees soon after, or even before, heartwood formation begins, limits the regenerative capabilities of populations due to the implicit, continued absence of large, seed-producing trees. Yasi trees are frequently harvested at an early age soon after the onset of heartwood formation at around 10 to 15yrs (Usumaki, 1981), which is only a few years after fruiting begins. Fruiting may begin as early as 3-4 years of age, but fruiting is not

reliable until 7 to 10 years of age (Smith, 1985; Bulai, 1995; Thomson, 2006a). The recurring and early removal of the main fruit-bearing trees from populations certainly reduces the number of seeds and seedlings, thereby lengthening the time for natural regeneration to occur.

The adverse ecological and economic consequences of early and excessive harvesting are obvious factors in the current lack of a wild-growing yasi population in Bua region, Vanua Levu, Fiji. The Fiji Forestry Department resource survey in 1981 by management officer Usumaki, conducted in this area of yasi habitat, which was the densest source of yasi in the country, reported populations smaller than desired and deemed below levels appropriate for commercial harvesting. While 50-61,000 individual trees were estimated across 15,000 hectares, almost 45% of recorded individuals were in the younger adult size of 10-15cm bdh, and very limited natural regeneration was identified with high mortality rates due to human factors. Nearly 82% of all recorded individuals were between 5 and 20cm dbh. Despite Usumaki's (1981) recommendations to continue the harvesting prohibition for another 10-20 years, and to withhold large scale harvesting until 30-40 years after plantations were established and yield predictions were reliable, harvesting of yasi resumed in 1984, and mainly from 1987 to 1990, which exhausted the supply of virtually all mature trees in the area (Jiko, 1991). The total tonnage of heartwood exported from Fiji between 1984 and 1993 was 1115 tons, a sum very close to the total national resource levels of 1090.5 tons heartwood estimated just a few years earlier (Usumaki, 1981; Tabunakawai & Chang, 1984). This near complete harvesting of all resources brought great initial financial reward but perhaps greater

ecological cost and significant future harvest yield loss. After 30 years, with minimal replanting efforts and fire damage, the Bua population has failed to regenerate in any significant way as observed in the findings of this research.

Furthermore, the frequent and near complete removal of fruit bearing individuals from populations reduces seeds available for collection for propagation programs. Replanting harvested or destroyed areas is currently uncommon, due in part because seedlings may not be available, (Wiser et al., 1999). A vital concern for the future of yasi is the availability of high quality seed for planting (Jiko, 1991). Collection of seeds for replanting and cultivation is becoming increasingly difficult due to the low number and far removed locations of remaining mother trees, and also due to occasional seed loss caused by cyclones which occur in untimely correspondence with the main fruiting season (Jiko, 2000; personal correspondence with Tevita Faka'osi, 2008).

“Checking” for heartwood formation

Because the size of a tree is not necessarily an indicator of the presence or amount of heartwood in a tree, the practice of “checking” the trees has become a way of determining whether or not a sandalwood tree is ready to harvest. To “check” a tree, a wedge of wood is cut from a living tree along the trunk until heartwood is found (Figure 2.8). Unfortunately, this greatly weakens the structural integrity of the tree, which is then more likely to fall down in strong winds, and also increases the susceptibility to termites and infections, which could lead to the death of the tree (Jiko, 1991).

Such destructive “checking” was found to occur in 22% of the mature (S5-S8) trees in the ‘Eua highland population with 79% of the “checked” trees occurring in the S5 size-class. This is one of the probable causes for the evident decrease in individuals in S6. Without the damaging effect of “checking”, more trees may be recruited from S5 into S6, and on into the harvestable size classes. Along with the evidence of early tree mortality due to “checking”, unfortunately, some trees were also completely cut down in S5 or S6 before heartwood formed and were found lying on the forest floor. As was soberly stated by one of the crewmembers upon seeing this, “*maumau ‘i ahi*”—“waste of sandalwood”.

Feral Pigs

The rooting habit of feral pigs wandering through the bush from neighboring villages, particularly along the portion of the coastal population near Tufuvai village, as well as wild pigs inhabiting the forest near Muanisolo, is destructive to the vulnerable, regenerative individuals, which are easily uprooted and trampled. In the ‘Eua coastal plots it was evident that pig rummaging was occurring. In plots where pig rummaging was evident there were 77% fewer seedlings (S1 individuals) per hectare, and 62% fewer S2 saplings (Figure 2.9). It appears that the incidence of pigs in the area has been relatively recent as the differences are less manifest as the size classes increase, though there are still distinct differences up until S6. The comparatively low number of seedlings in the “pigs present” plots will undoubtedly lead to fewer harvestable individuals being recruited in subsequent years in that area.

Introduced Plant Species

Tecoma stans

The introduced and invasive *Tecoma stans* known in Tongan as the “ti” plant, is likely another threat to yasi in the ‘Eua coastal population. *Tecoma stans*, which proliferates rapidly via wind dispersed seeds, was observed encroaching into portions of the western coastal areas of ‘Eua forming dense thickets. Further, populations of *T. stans* are sometimes introduced by humans through use of stems for living fence posts. It is also occasionally used by villagers as an agricultural species due to its reputedly positive benefits on soil texture and nitrogen content.

Psidium guajava

Of the introduced *Psidium guajava* (guava plant), Yuncker (1959) noted that “rather large colonies grow on ‘Eua” and that it “promises to become a pernicious weed”. Guava is still today the dominant vegetation in many of the highland areas in northern ‘Eua and presumably chokes out yasi regeneration. The yasi population there effectively stopped at the guava thickets.

Santalum album

An additional potential threat to *Santalum yasi* is *S. album*, an introduced species of sandalwood, particularly in certain islands in Fiji where *S. album* is widespread and readily hybridizes with *S. yasi*. *Santalum album* and particularly the *S. album* x *yasi*

hybrid show much more vigor than *S. yasi* and may present strong competition for available habitat and hosts. The F1 hybrids have been noted to grow 300% faster than *yasi* and 32% faster than *album* and also form heartwood 6-7 years earlier, making it a desirable introduction to the islands (Thomson, 2006b).

Furthermore, *Santalum album* is susceptible to the phytoplasmal sandal spike disease, which is currently threatening *S. album* populations in their natural extent in India. This disease causes “witches’ broom” symptoms including a severe reduction in leaf size and internode length, making the entire shoot appear like a spike inflorescence. The leaves and branches become dried out and the infected trees die one to two years after these symptoms appear. Because this phytoplasma has not been isolated and grown *in vitro*, it is very difficult to perform research on possible treatments for this disease (Thomas & Balasundaran, 2001; Khan et al, 2006), but methods have been developed to detect the presence of phytoplasmas in sandalwood (Hull et al, 1969); Khan et al, 2004). Currently sandal spike disease has not been identified in the Pacific Island populations of sandalwood and *yasi*’s susceptibility to the disease has not been established. However, even if *yasi* is not susceptible to the disease, in the event of an introduction of the phytoplasma, hybrids could act as a “bridge” allowing the disease to advance from *S. album* to *S. yasi* (Brigham & Schwartz, 2003). The genetic threat posed to *yasi* due to hybridization is discussed further in 3.6.3.

2.6.4 Growth Rates and Heartwood Yield Estimates

The recorded height and diameter of the 115 individual trees within the 'Eua coastal and highland populations with a diameter at breast height $\geq 5\text{cm}$ were plotted (Figure 2.10) and a regression line calculated as $y=24.318x + 430.4$ with an r^2 value of .2822. This figure illustrates the extensive variability of height within wild forest populations where host suitability and competition for resources vary by location.

The timeframe for advancement between size classes for an average individual tree gathered from the *S. austrocaledonicum* growth rates at differing ages (see section 2.3.3), combined with the regression line for height by diameter at breast height (dbh) illustrate a trend line for dbh according to tree age for an average yasi tree (Figure 2.11).

Using the height by dbh regression line of Figure 2.10, combined with dbh according to tree age trend line and with heartwood yield calculations (Figure 2.11), the heartwood yield of an average yasi tree by diameter (Figure 2.12) and according to tree age (Figure 2.13) can be illustrated. The values for heartwood yield presented are inline with Thomson's estimates that a 15-20 year-old tree appears to reach 8-12 m (26-40 ft) in height and 15 cm dbh and a 20-25 year old tree can produce 15-30kgs of heartwood (2006). Although the maximum diameter for yasi trees can reach over 50cm dbh, heartwood yield estimations were calculated only up to 41cm dbh because at these larger sizes and older ages, heartwood proportion continues to increase while height and diameter growth slow at rates that are less understood (Thomson, 2006a; Usumaki, 1981). Further study of heartwood yield for different tree sizes (preferably with known ages) would lend further insight to this calculation for an average tree at all sizes. Also, a

higher estimate may plausibly be expected than is presented if the trees are actively nurtured by promotion of suitable host, elimination of competing non-host trees, pruning low leaders to ensure one main bole, and other appropriate care.

While recognizing that real yield values for a given tree may be higher or lower than these average estimates due to variability in individual trees, these illustrations portray general trends informative for maximizing harvest value of intercropping yasi in pine plantations. Further, the trend lines represented by Figures 2.12 and 2.13 are informative of the significant percentage of yield lost when harvesting a smaller diameter, younger tree versus delaying harvest to allow for further growth.

The lack of trees above 23cm dbh found in the surveyed populations on 'Eua suggests that most yasi trees are harvested at less—probably much less—than 25cm dbh. As seen in Figure 2.12, harvesting a 25cm dbh tree would yield merely 30% of the potential heartwood if the tree is not harvested until 41cm dbh, representing a return of 1.5kg heartwood per year invested in growth. Harvesting of a 15 or 20cm dbh tree yields only 6-15% of the potential heartwood at 41cm dbh representing a return of .7 to 1.12kg/yr of tree growth. A single tree harvested at 35cm dbh, after approximately 43 years of growth, returns 2.7 kgs of heartwood per year invested in growth.

This loss in potential heartwood yield is significant when felling small trees especially across an entire population. According to Tongan forestry officer Heimuli Likiafu, the typical heartwood yield of most trees currently harvested in 'Eua ranges from 4 to 9kg per tree (personal correspondence, 2008). The generated yield table for an average yasi tree shows that this would represent trees harvested at 10 to 14cm dbh,

which therefore return only 3-6% of their potential yield at 41cm dbh. As per Tongan export records, 205 tons of heartwood were exported from Tonga in 2007. It is likely that, according to reported typical harvesting practices, a significant portion of that yield was collected from 15cm dbh trees or smaller representing a tragic 94-97% loss of potential heartwood yield from those trees and a return of only .7kg of heartwood per year invested in tree growth or less.

While the financial implication of early harvest of young trees is significant, the associated ecological loss in diminished regenerative capacity may be even more detrimental, especially in the long term (as discussed in 2.6.3, Observed Ecological Threats, Unsustainable Harvesting Practices). Conversely, by allowing mature trees to remain in the populations for an extended time, the genetic diversity within the older trees is retained in the population for longer periods, greater numbers of seeds are dispersed contributing to higher regenerative capacity and thus more future heartwood bearing trees. The exact impact early harvesting practices have on regenerative rates can be further understood by conducting surveys to determine fruit production levels of individuals in differing size classes.

2.7 Recommendations

Recommendation 1: Establish a regeneration initiative for *Santalum yasi*, proscribing harvesting to allow for growth and regeneration of remnant populations.

An initial harvesting ban should be placed on yasi until population numbers increase and a sustainable, enforceable management plan can be strictly implemented. Suggested principles to include in a sustainable management strategy will be discussed in Chapter 4.

Recommendation 2: Expand *Santalum yasi* resources through replanting post-harvesting and reintroduction of seedlings into previous, appropriate habitats currently devoid of *S. yasi*.

Expand programs for replanting of yasi post-harvesting (preferably using local germplasm) and reintroduction of seedlings into appropriate natural areas where yasi used to be prevalent to promote resource expansion. Seedlings may be protected from damage by placing simple stakes, made from nearby small poles, around the seedlings (Figure 2.14). Seedling cultivation can be conducted through forestry departments in collaboration with local communities and should include public education and awareness as well as production and distribution of relevant technical information.

Recommendation 3: Encourage noninvasive methods of checking for heartwood formation.

While there is some evidence that some wounding of hardwood trees may induce the production of heartwood (Shigo, 1989), the current practice of “checking” sandalwood trees for heartwood is beyond any beneficial level of wounding (see 2.6.3 Observed Ecological Threats). If resources and time allowed, a research program into discovering the effectiveness of different sustainable forms of wounding could be

conducted in a controlled environment. However, until the efficacy of wounding in sandalwood is established, and a correct methodology discovered, the practice of destructive “checking” should be strongly discouraged. To help identify harvestable trees, tree increment borers may be purchased and distributed. Increment borers extract a thin core of wood from the trunk allowing detection of heartwood while maintaining the structural integrity of developing trees. Due to the very dense wood of sandalwood, the cutting blades of tree borers would need to be maintained and proper methods of use would need to be followed, otherwise the obtaining of a core sample would prove too difficult as the drill may easily get stuck in the tree, thus professional training would need to take place. Another alternative would be to use a simple brace with a gas-powered drill using a small drill bit. Another option is to cut one of the larger side leader branches; if they show a small amount of heartwood, then that is generally a good indication that the bole has also developed heartwood. Possible funding to obtain increment borers or drills may be obtained through the Seacology Foundation or other sources.

Recommendation 4: Maintain current wild *Santalum yasi* stands through assisted natural regeneration, caretaking and harvest size/age limits.

Routine care of remnant populations, such as removing non-host competing species, protecting seedlings, replanting wildlings, and pruning to promote the formation of one strong leader can promote vigorous growth of extant adults and assist natural regeneration. Maintaining large, fruit-bearing adults in wild populations by only harvesting a portion of the largest/oldest trees in a stand further promotes natural

regeneration by greater continued seed production and maximizes harvest yields over time (see section 4.6 and Appendix 1).

Recommendation 5: Minimize the influence of introduced species, including feral pigs, in habitat areas.

Tecoma stans

The removal of present *Tecoma stans* thickets from the western coastal regions of ‘Eua in the prime yasi habitat areas could promote yasi regeneration and expand the current habitat. To further promote regeneration, following removal of *T. stans*, yasi seedlings could be planted, along with appropriate native hosts where the *T. stans* were removed. Also, further introductions and spread of *T. stans* should be minimized through discouragement of its use as fencing material.

Psidium guajava

Minimizing the effects of *Psidium guajava* could prove to be quite difficult, but it may be valuable to focus efforts on the possibility of preventing further encroachment of *P. guajava* into the key habitat areas in the ‘Eua highland population of yasi.

Feral Pigs

While completely eliminating the presence of feral pigs within yasi habitat could be problematic, a practical approach of fencing off or otherwise blocking main access

routes such as those near village roads and trails may be beneficial as well as building small barriers around young seedlings (Figure 2.14).

Pinus caribaea

While extensive pine plantations have replaced native forests where yasi was previously found (particularly in the Bua region of Vanua Levu, Lakeba of the Lau group, parts of Kadavu, and the highlands of ‘Eua), fortunately *Pinus caribaea* (Caribbean Pine) is an exceptional host species for yasi and the nearby plantations may be used to expand yasi habitat through carefully planned, simultaneous cultivation of yasi and pine. This practice is currently being conducted in some locations in Tonga, including Vava’u (Figure 2.15) and ‘Eua. Growth values estimated for yasi including heartwood formation suggest a harvest time frame of 30-40 years. Plausibility and practical concerns can be evaluated by forestry officers and plantation managers to discuss harvesting procedures that maximize the harvest value of both species, and resolve concerns regarding who will profit from the yasi in the pine plantations (i.e. involving nearby villages and sharing profits to replace harvesting yasi from its natural habitat). Although planting yasi within current pine plantations can be an economically opportune practice, expanding the current pine plantations into yasi habitat is not recommended. Also, the pine trees will, over time, acidify the soil, which may significantly inhibit the growth of yasi occurring with the pine trees.

2.8 Conclusions

While still fairly common in home gardens across Fiji and Tonga, wild growing populations of yasi have dwindled to local extinction in many areas, even where it was previously plentiful, as a result of the identified threats. For example, Vanua Levu, Fiji, named “sandalwood island” by the first European harvesters, is now almost devoid of wild growing sandalwood. At the time of data collection, the remaining wild stands had discontinuous size class structures typical of discontinuous recruitment, an evidence of regenerative stress, and covered a relatively small land area. The largest remaining wild population of yasi found in Fiji was near Muanisolo, Kadavu. Outside of Kadavu, wild growing yasi in Fiji is limited to scattered individuals. Tongan wild yasi populations are found mainly on ‘Eua Island and otherwise sparsely scattered elsewhere, mainly on the islands of Ha’apai and Vava’u. Regeneration rates may be sufficient to maintain the populations *in situ* if seed production continues by remaining adult trees and recruitment rates remain favorable. However, in the years following the data collection of this study, further harvesting has occurred in Muanisolo, Kadavu, Fiji, and ‘Eua, Tonga, and elsewhere in these countries making the current situation more depleted than reported here.

In contrast to *Santalum yasi*, the trend for the current distribution of naturalized *Santalum album* and *S. album* x *yasi* has increased, posing a potential ecological threat to the remaining stands of yasi due competition for resources, habitat, and hosts. While preliminary results of oil composition studies indicate that the heartwood oil of *S. album* x *yasi* may be comparable to market standards and limited sampling suggests heartwood

formation may occur earlier in hybrids (Doran, 2005), the introduction of *S. album* and the subsequent hybridization also creates a risk for sandal spike disease, a deadly phytoplasma which has severely damaged natural *S. album* populations in India. While currently the vulnerability of yasi and hybrids are unknown, hybrids could act as a bridge of susceptibility into yasi (Brigham & Schwartz, 2003). It is therefore recommended that the susceptibility of *S. yasi* and hybrids to sandal spike disease be determined before widespread introduction of *S. album* occurs.

The unsustainable practice of harvesting all heartwood bearing trees from a population, including even the young, small trees should be strongly discouraged due to the implicit negative effect on regeneration capacity from the removing fruit bearing trees, and the illustrated loss in heartwood yield potential of harvesting young trees. Maximized harvest values suggest delayed harvest until trees reach larger sizes, plausibly after 30-40 years.

Other observed ecological threats include competition with introduced species and destruction to regeneration by feral pigs. Recommendations revolve around efforts to reduce these threats by expanding replanting and maintenance initiatives and by placing an initial harvesting ban on yasi at least until a plausible community-mediated approach to the management of yasi can be established.

While the potential economic benefits of preserving yasi are great, the intrinsic value and cultural heritage of yasi also demand the attention and immediate action necessary to preserve this resource. The opportunity for immediate action is open now,

but management options may be greatly limited if action is delayed. The outlook for yasi can be positive if threats are minimized and proper management is implemented.

2.9 Future Research

Further research can benefit decision making for the management of yasi. Investigating seed production by tree age could help calculate the loss in regenerative capacity due to early harvest. Further investigation into growth rates, possibly with dendrometers, and heartwood production by tree age for yasi could further elucidate yield estimates useful for harvest planning. Based on the current sparse populations of yasi in Fiji and Tonga, further enumerations and resource surveys are not practical to conduct at this time. Rather, forestry and governmental efforts should focus on the promotion of local involvement in assisted regeneration and caretaking of wild stands, education regarding value lost with early harvest, and other similar endeavors.

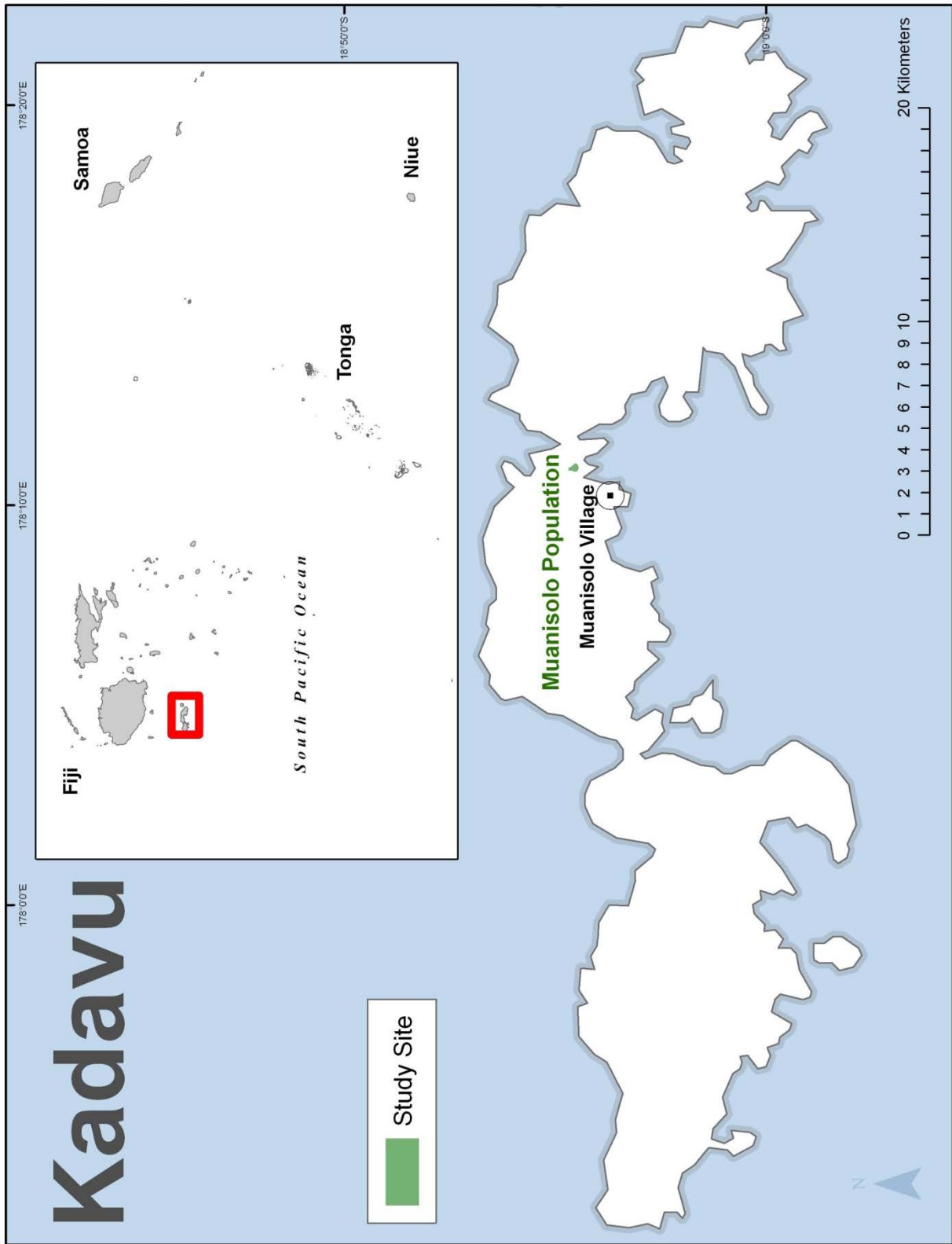


Figure 2.1 Kadavu, Fiji Study Site

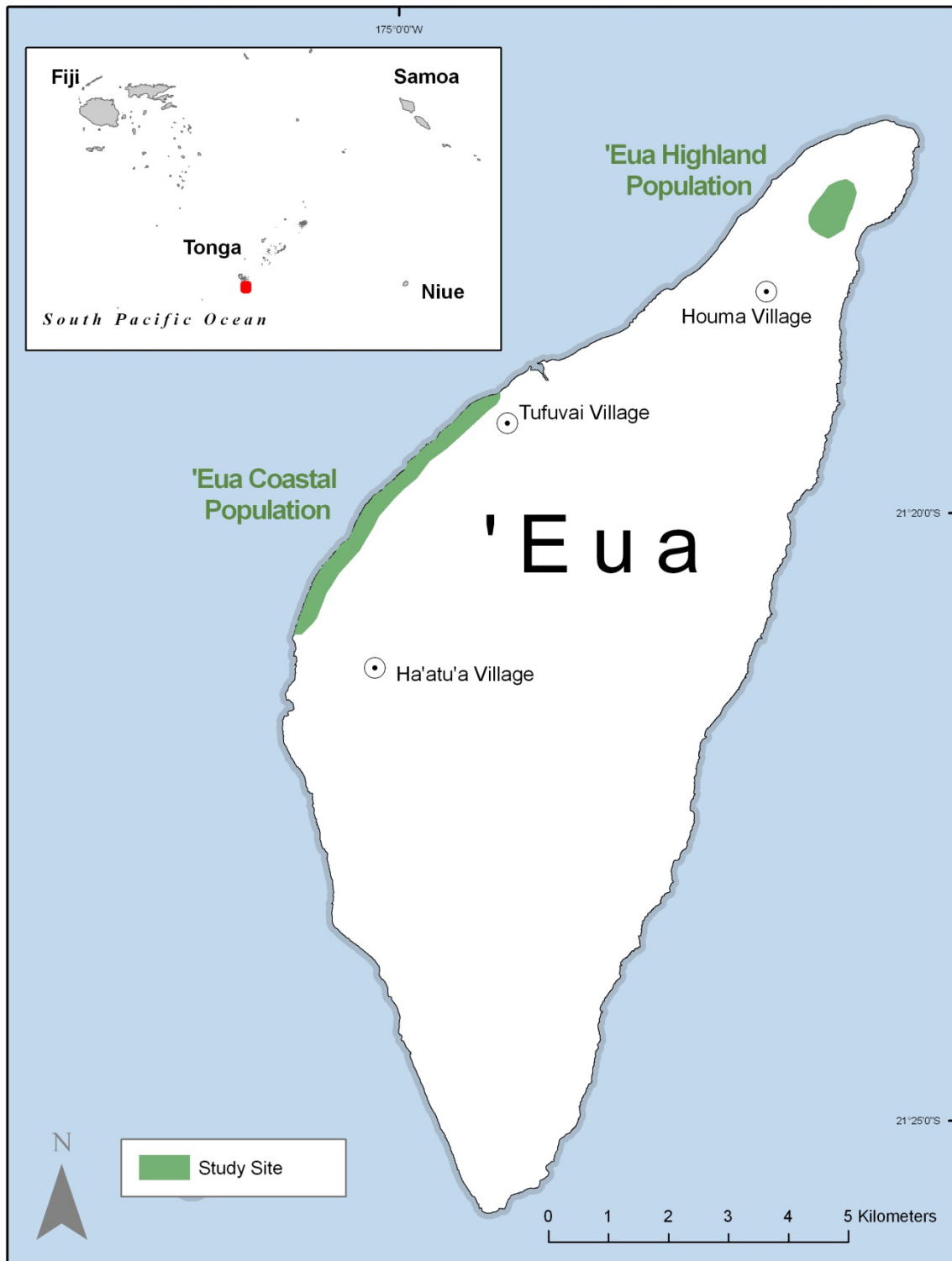


Figure 2.2 'Eua, Tonga Study Site

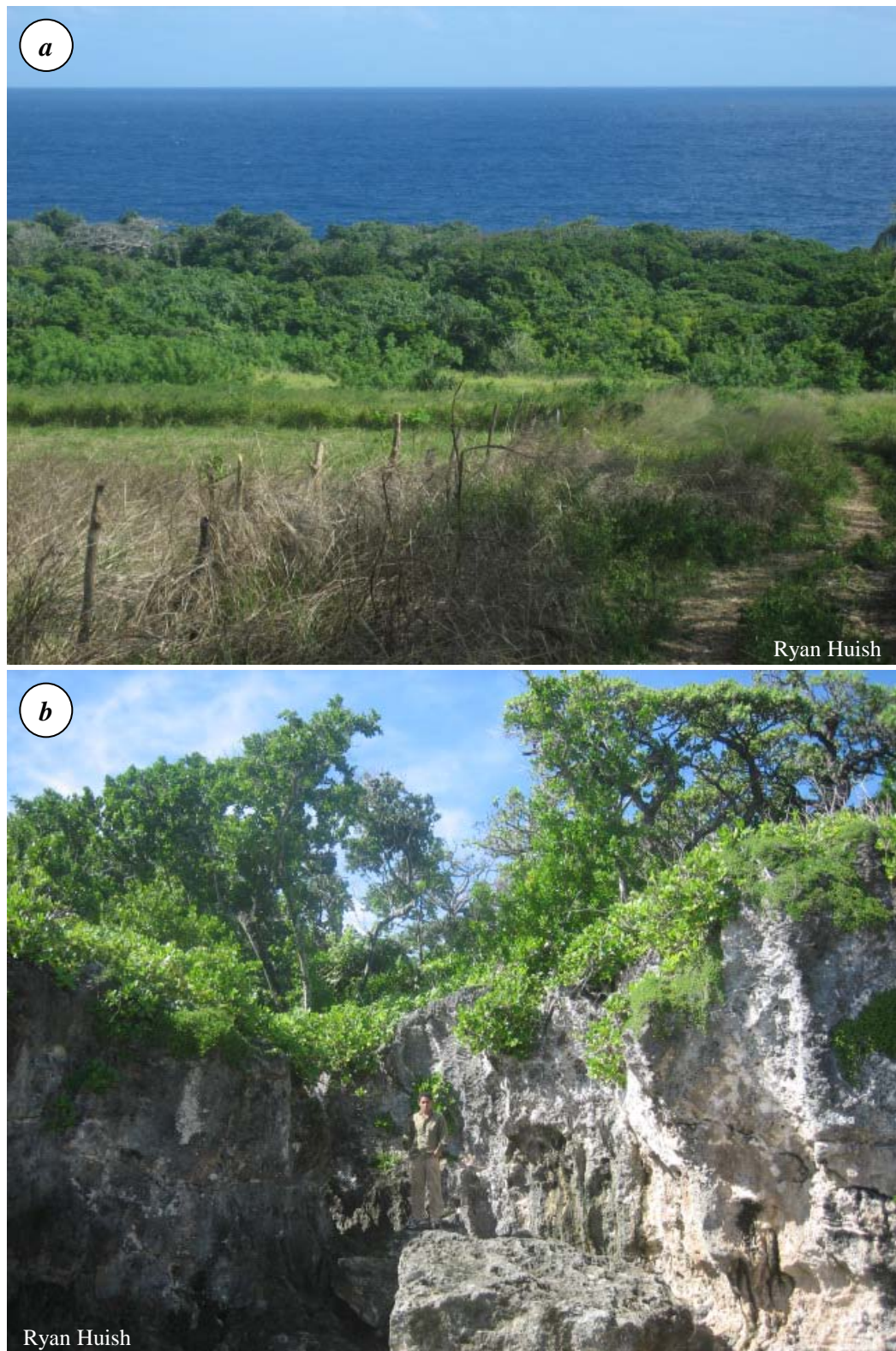


Figure 2.3 ‘Eua Coastal Population Habitat. Forest containing the densest population of yasi, ‘Eua Coastal Population as seen from inland (*a*) (photo credits: Ryan Huish), and from the coast (Heimuli Likiafu pictured at center) (*b*) (photo credits: Ryan Huish).



Figure 2.4 ‘Eua Highland Population Habitat and Data Collection.

a. Collecting ecological data with Heimuli Likiafu, top, and Tupou Fifita, bottom, in the highland population (photo credit: Ryan Huish). *b.* Transects ran to the edge of the cliff on the highland population. Yasi with stunted growth on right (photo credit: Ryan Huish).

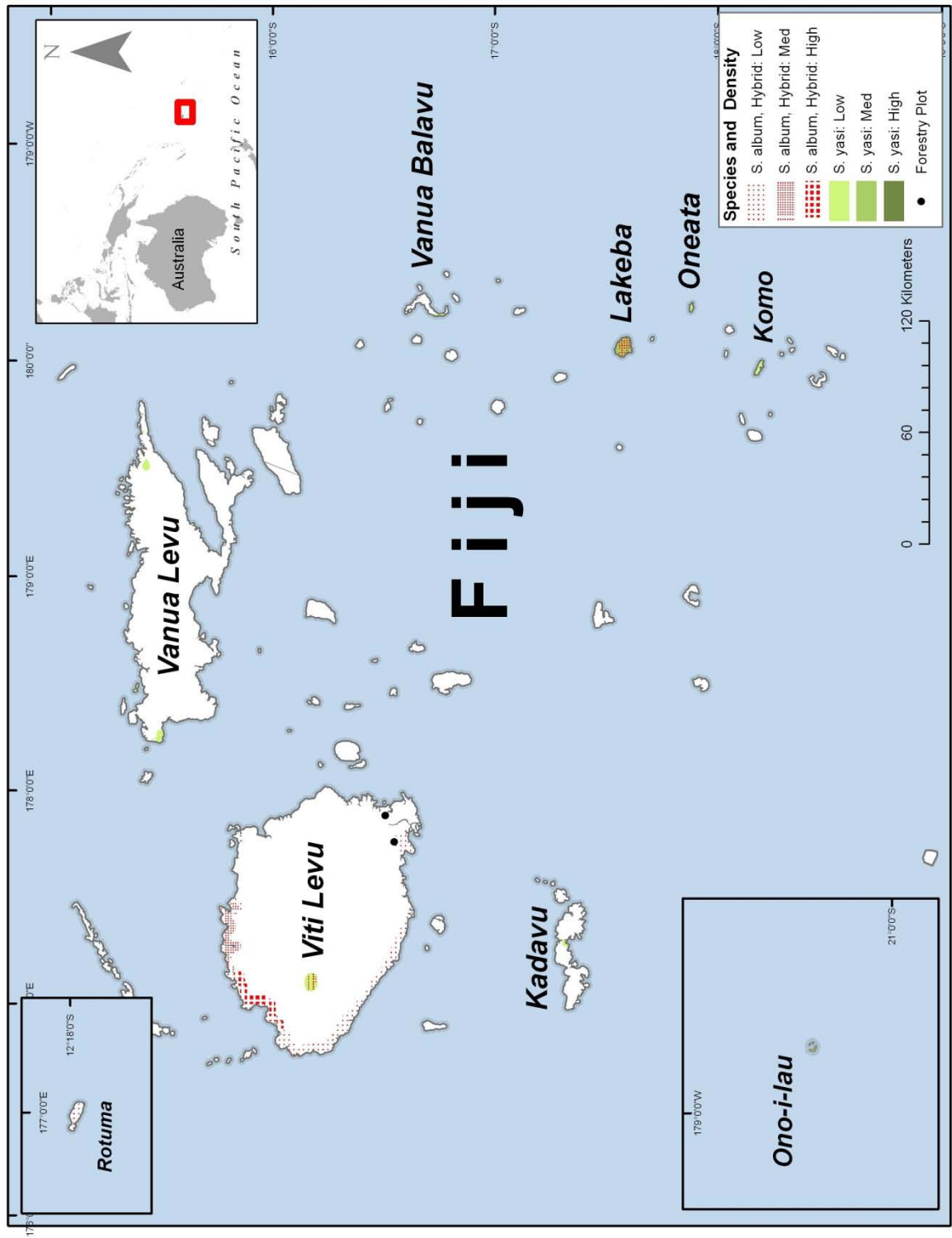


Figure 2.5 Natural Distribution of *Santalum* Species in Fiji.

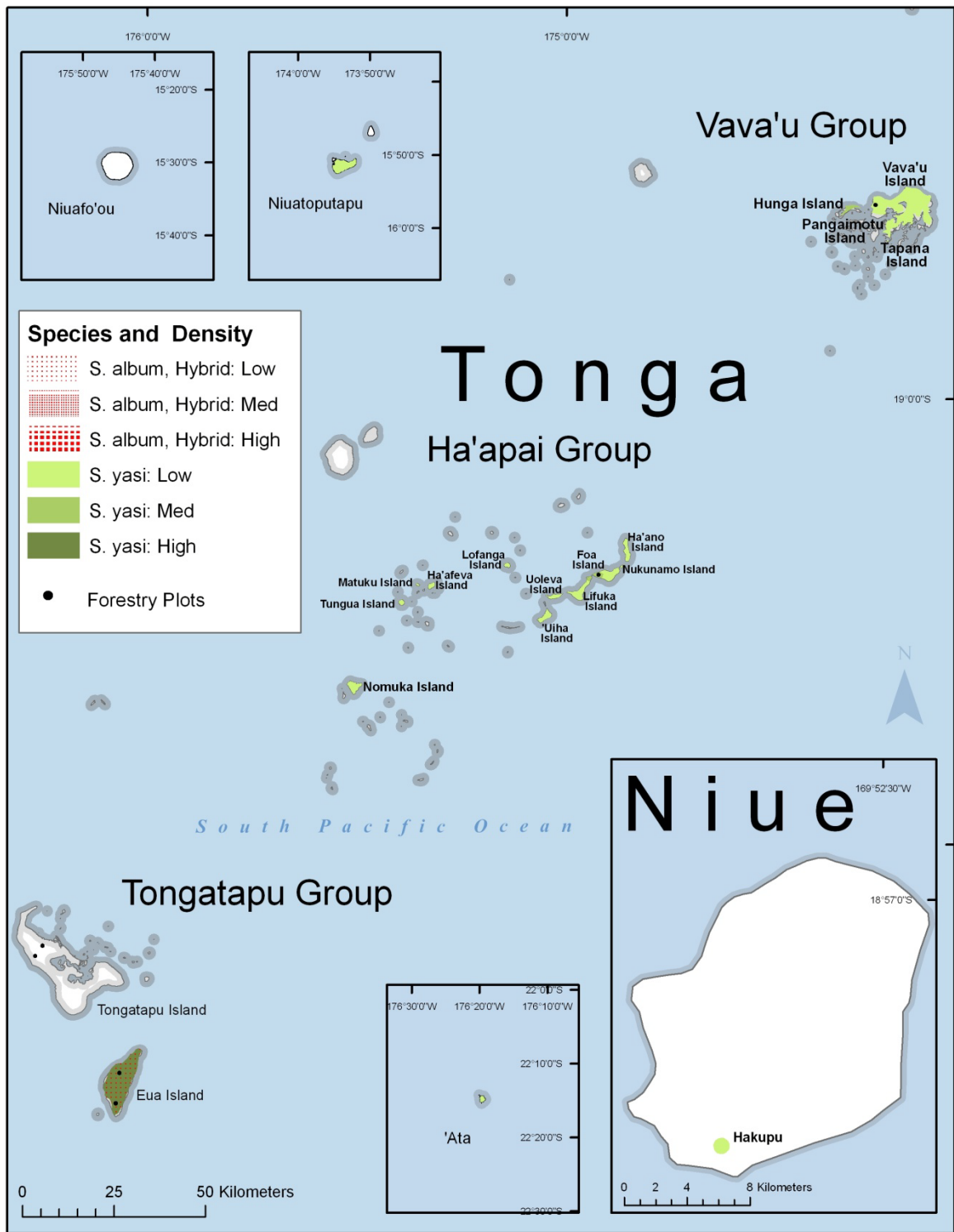


Figure 2.6 Natural Distribution of *Santalum* Species in Tonga and Niue.

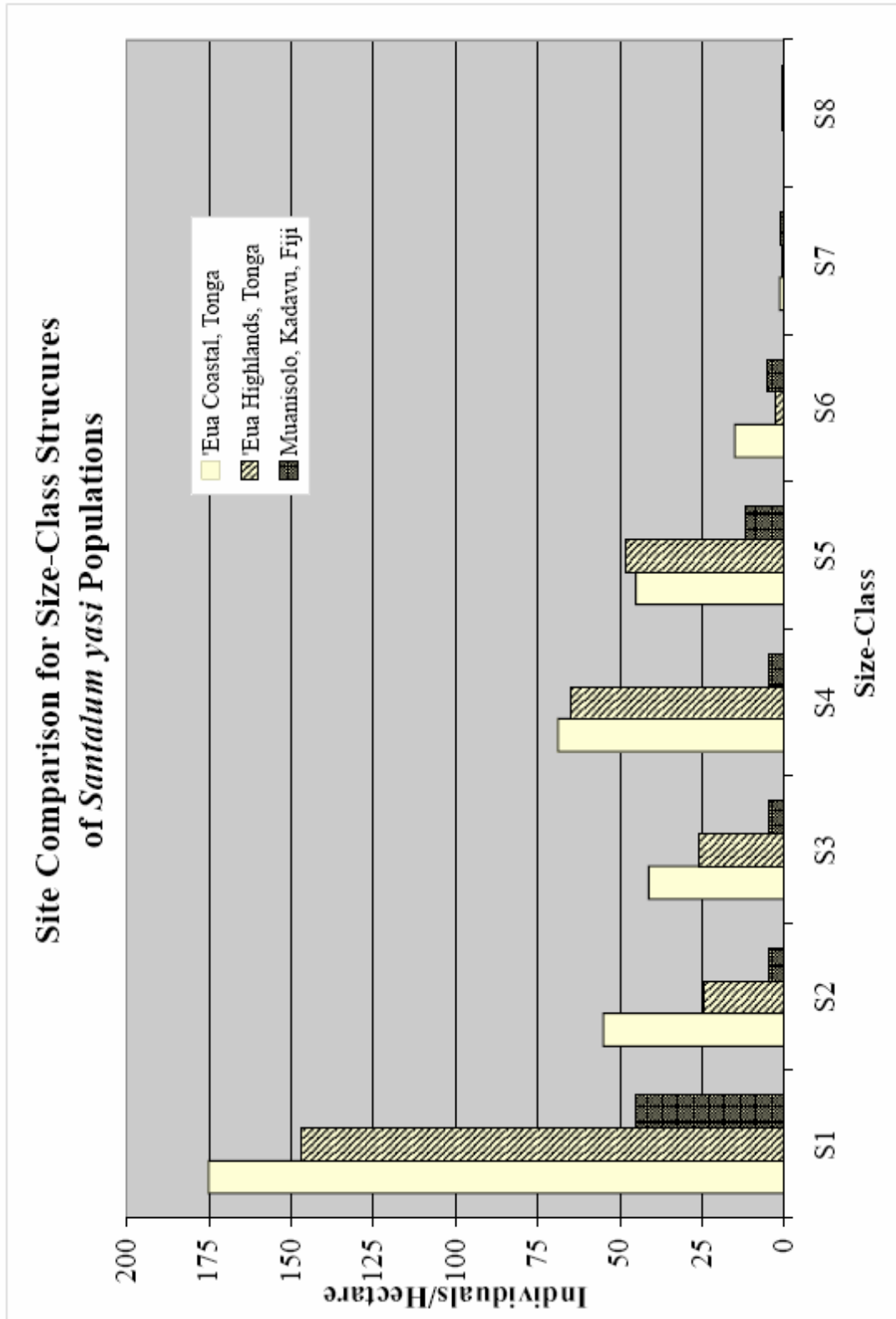


Figure 2.7 Site Comparison for Size-Class Structures of *Santalum yasi*.



Figure 2.8 Damaging Effects of “Checking” Yasi Trees for Heartwood. (Photo credits: R. Huish)

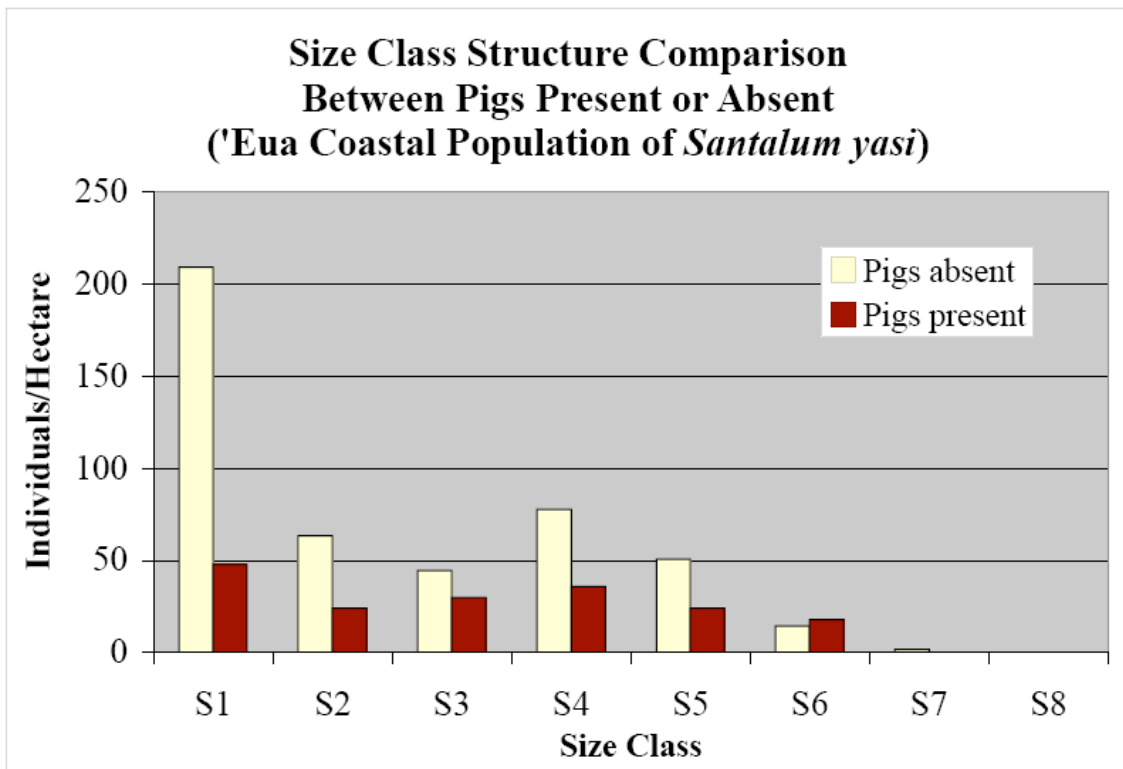


Figure 2.9 The Effect of Feral Pigs on *Santalum yasi* Regeneration.

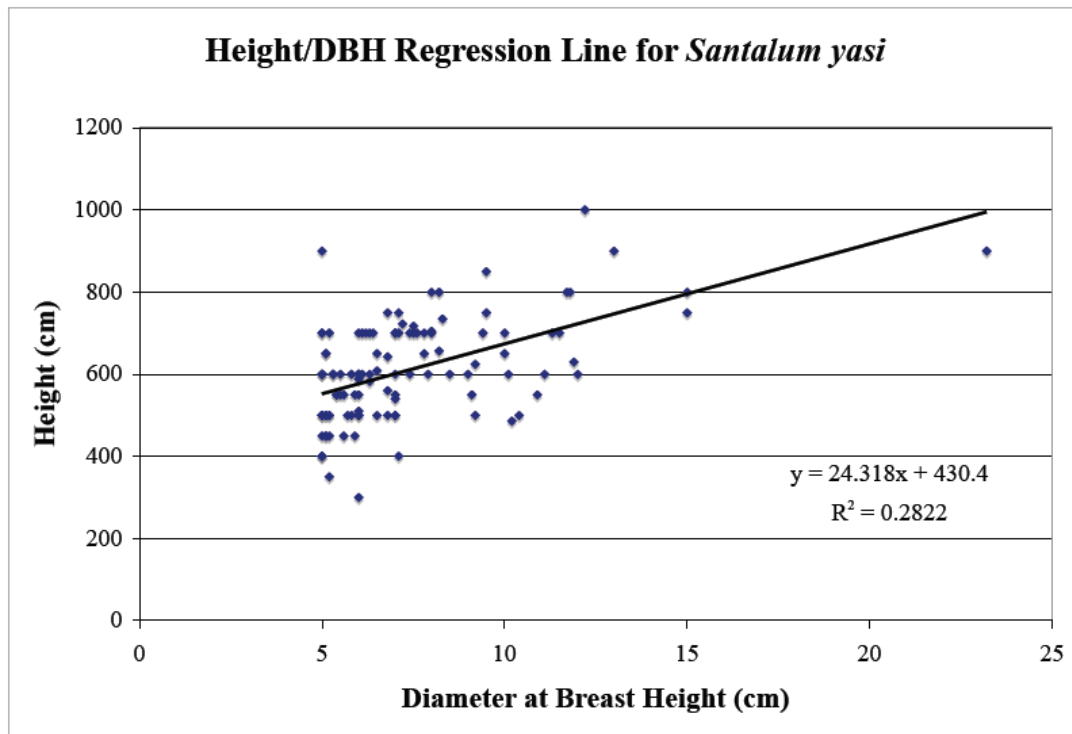


Figure 2.10 Height/Diameter at Breast Height Regression line for *Santalum yasi*.

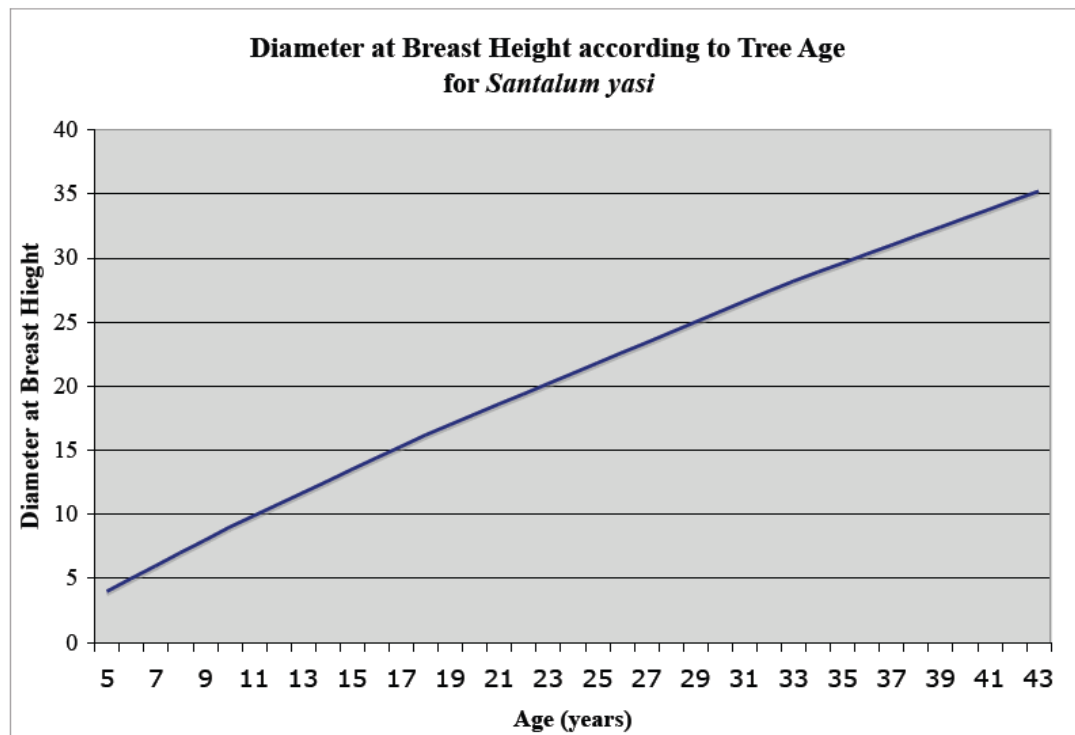


Figure 2.11 Extrapolation of Diameter at Breast Height of *Santalum yasi* According to Tree Age.

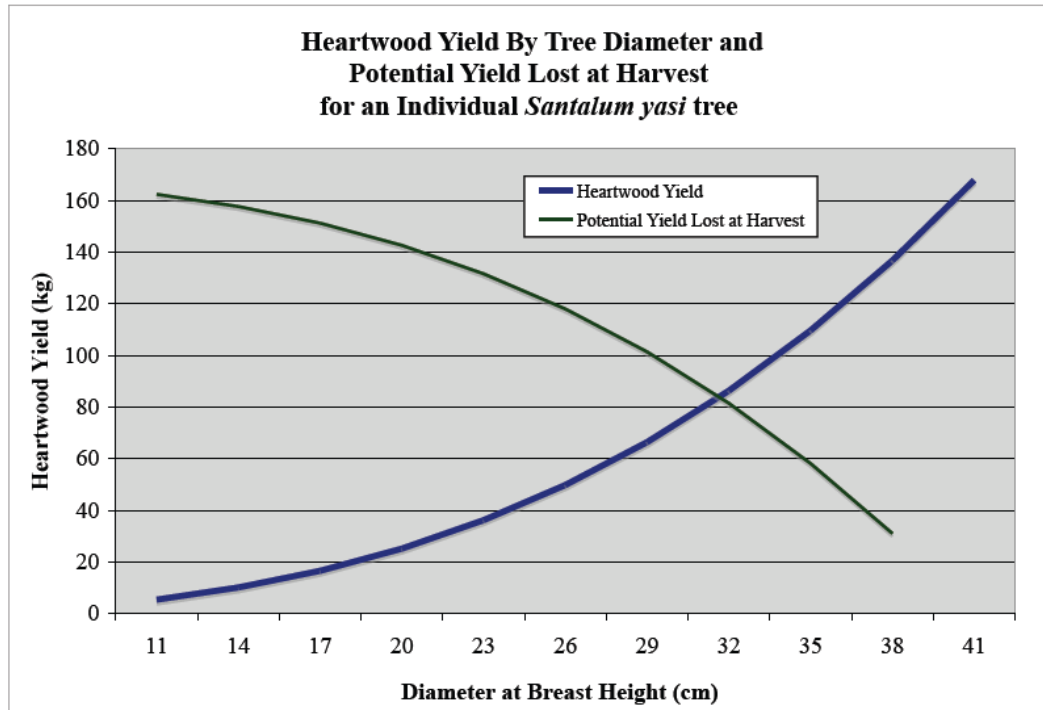


Figure 2.12 Illustration of Individual *Santalum yasi* tree Heartwood Yield by Diameter and Potential Yield Lost if Harvested Early.

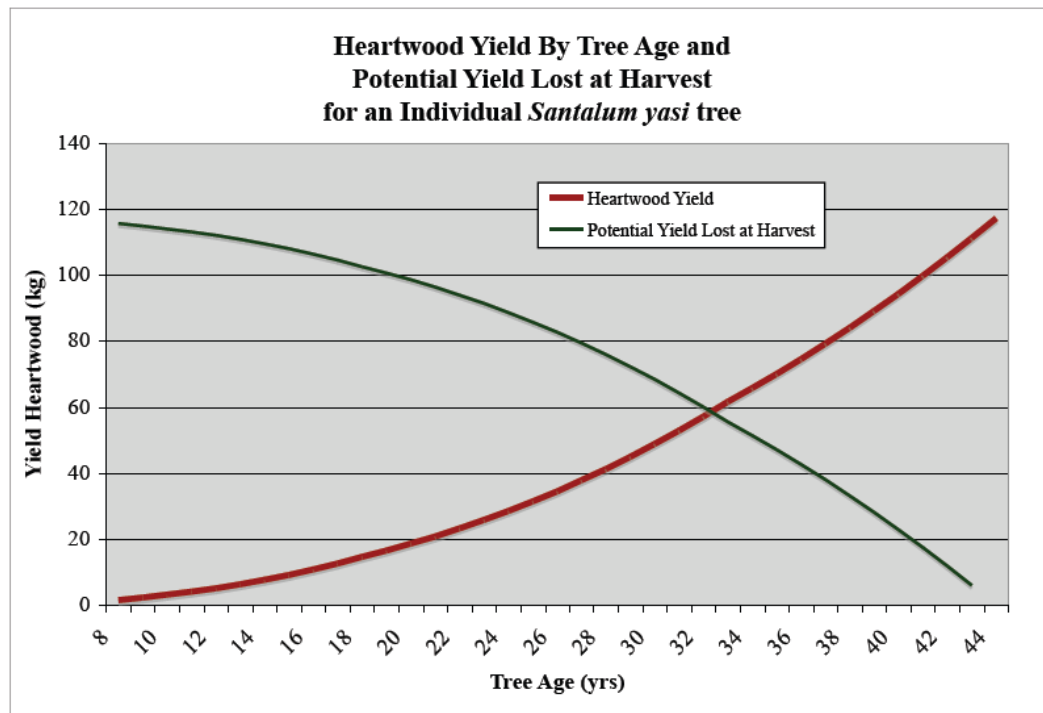


Figure 2.13 Illustration of Individual *Santalum yasi* Tree Heartwood Yield by Tree Age and Potential Yield Lost if Harvested Early.



Lex Thomson

Figure 2.14 Protecting young seedlings. *Santalum yasi* seedling protected from damage by stakes, Tonga (Photo credit: Lex Thomson).



Ryan Huish

Figure 2.15 *Santalum yasi* intercropped with *Pinus caribaea*, one of its host species, in Vava'u Tonga (Photo credit: Ryan Huish).

CHAPTER 3

POPULATION GENETICS OF *SANTALUM YASI*

3.1 Introduction

Chapter 3 reports on an analysis of the population genetics of yasi and its relation to species conservation and biogeography. The chapter begins with a discussion on the significance of population genetics to the conservation management of yasi followed by a summary of previous studies on yasi genetics. The methods section of this chapter will include information on sample collection criteria, including sampling sites, on DNA extraction, and on selection of microsatellites. Further methods and results for analysis of genetic diversity, departure from random mating, population differentiation, and historical biogeography will be noted. A discussion will consider the results each of these analyses, make recommendations, and draw conclusions on the implications for conservation management, comparisons with other sandalwood species, and future research directions.

3.2 Significance of Population Genetics in Yasi Conservation Management

A foundational concept in population genetics is that the loss of genetic diversity in a species diminishes the probability of species survival (Brush, 2000). Island systems are particularly susceptible to factors, such as strong insularity, that decrease genetic diversity in plants, making them more vulnerable to extinction (Bottin et al., 2005b). The genetic diversity of remaining yasi therefore is an important indicator for species health and an important consideration in developing a sustainable management strategy. In the

absence of any previous study on genetic variation of this species [beyond Harbaugh & Baldwin's work on phylogenetic relationships of the *Santalum* genus (2007)], this study will elucidate current diversity values, establish a baseline for future comparative work, and provide a glimpse into the biogeographic history of the species.

Threats leading to extinction can come from both deterministic and stochastic elements such as habitat destruction, overexploitation, species translocation, as well as random changes in environment or demographics, genetic drift and inbreeding. Events or forces that diminish genetic diversity, removing beneficial alleles from a population or increasing the number of harmful alleles, threaten the survival of the species. While threats may be controllable or uncontrollable, a population becomes increasingly susceptible to these threats as the size of the population decreases (Allendorf, 2007).

The effects of genetic stochasticity are particularly strong in small populations and when combined with other threats can lead to an "extinction vortex" (Allendorf & Luikart, 2007). The inbreeding that occurs in some small populations leads to a reduction in fecundity, which in turn decreases population size, compromising long term survivability (Frankel & Soulé, 1981; Gilpin & Soule, 1986). The lack of genetic variation, due most likely to inbreeding, in remnant populations of *Santalum lanceolatum* is the reputed cause of reproductive problems as serious as pollen sterility, self-incompatibility, and pistil dysfunction (Warburton et al., 2000). A high level of inbreeding, and subsequently high potential for genetic stochasticity, occurs in "bottleneck" scenarios when a significant and rapid reduction in population occurs (Allendorf & Luikart, 2007).

Island systems are also particularly susceptible to stochastic forces due to oceanic barriers and isolation and are also strongly affected by human activities both directly through overexploitation and indirectly through habitat changes or pollution (Bottin et al., 2005b). These forces on island populations, particularly small islands, can create low genetic variation within an island, though evident low genetic variation may also be due to the recency of introduction or isolation from the mother population (Kwon & Morden, 2002). Ocean barriers between island populations, conversely, may create a strong increase in variation, comparatively, due to the same isolative factors (Bottin et al., 2005b).

Understanding the remaining levels and kinds of genetic diversity in and between yasi populations will be important in developing propagation and management programs that will maintain and improve the fecundity and vigor of yasi stands. Currently seed lots and woodlots are being formed in both Fiji and Tonga to create sources for high quality seedlings for plantation establishment and also to preserve the genetic heritage of the species (Thomson et al., 2000). Present efforts have aimed at utilizing local seeds and genetic material for use in local seed lot and woodlot establishment in hopes of maintaining and promoting local adaptations. A possible negative result of using genetic stock only from local populations is inbreeding depression whereby there is an increase in expression of negative alleles and subsequent decrease in population fitness (Petersen & McCracken, 2005). These possible deleterious effects are particularly dangerous to small populations with low genetic variation (Petersen & McCracken, 2005).

Conversely, the crossing of individuals from separate populations which normally do not cross, can introduce outbreeding depression where introduced genes are less adapted to local conditions and resulting offspring are less suited to the habitat (Petersen & McCracken, 2005). Further, outbreeding depression can be dangerous if positive alleles once extant in the population are lost. The extreme case of outbreeding depression comes with hybridization between normally disjointed species where all individuals of the rare species become extinct and only hybrids remain (Petersen & McCracken, 2005).

Current efforts in the production of seedlots and woodlots have faced challenges in finding propagation materials due to the shortage of sources for seeds, seedlings, and scions. Materials, therefore, have generally included individuals from across island groups within each country (Wainiqolo, 2004; Likiafu & Robson, 2005). The introduction of *Santalum album* seeds and seedlings into many propagation programs is also particularly significant to efforts in managing yasi (Wainiqolo, 2004; Likiafu & Robson, 2005). *Santalum yasi* and *S. album* readily hybridize into vigorous quick growing trees. The genetic implications of these practices have not been investigated.

The lack of information on the genetic variation distribution within and between remnant populations of yasi is noted as a major constraint to the development of a successful management program for yasi (Thomson et al., 2000). This chapter reports the attempts to ascertain this needed data on yasi population genetic structure through a microsatellite analysis of several populations of yasi in Fiji and Tonga by addressing the following questions:

3.3 Research Questions

1. What are the patterns and distribution of genetic variation within and between remnant populations of yasi in Fiji and Tonga?
2. Does intraspecific genetic data shed light on the historical migrations of yasi? Is yasi originally native to Fiji or Tonga?

3.4 Previous Genetic Studies

Harbaugh and Baldwin (2007) performed a genus-wide phylogenetic analysis for *Santalum* using a combination of 18S-26S nuclear ribosomal (ITS, ETS) and chloroplast (3' *trnK* intron) DNA sequences. In this analysis, multiple exemplars of yasi (two from Tonga and six from Fiji) were analyzed representing different populations and no genetic variability was shown using the gene regions sequenced. Harbaugh suggested that perhaps with microsatellites, more significant variation could be determined (personal communication, 2006). Harbaugh (2008) also showed several ploidy levels in *Santlum*. *Santalum yasi* as well as *S. album* and *S. austrocaledonicum* are all diploid ($n=10$); other *Santalum* species were found to be tetraploid, hexaploid, and octoploid.

3.5 Methods and Materials

3.5.1 Sampling methods and DNA extraction

DNA samples were collected from 76 yasi individuals from Fiji (30 samples) and Tonga (46 samples) (see Appendix 1). In Fiji, samples were collected from four different islands. In Tonga, samples were collected from five different islands. Because

of the small population sizes, sampling was limited, particularly in the Bua region, Nausori Highlands, and Vava'u. The samples from Bua and Nausori Highlands were taken from trees growing within the villages, due to the lack of wild populations in the area. Village leaders confirmed that the samples collected were pure yasi from mother trees that were once wild in the same region of the respective islands. The remaining samples were all collected from wild yasi stands. Additionally, three samples of *S. album* were collected (one from the Colo-i-suva forestry plot on Viti Levu, and two from Lakeba), and two known *S. album* x *yasi* samples were collected (both from Colo-i-suva forestry plot) for comparison purposes. Except for the samples from Colo-i-suva forestry plots, collections were made from individuals that were at least 50 meters apart to avoid sampling clones due to possible root suckers.

For each specimen, five young leaves were collected and sealed in plastic bags containing silica gel, and stored therein at room temperature until DNA extraction. Total DNA was extracted from dry leaf material using CTAB protocol (Doyle & Doyle, 1987) as modified by Little & Barrington (2003).

3.5.2 Microsatellite Selection and Amplification and Visualization of Microsatellites

Eight nuclear microsatellites have been developed for *Santalum austrocaledonicum* (Bottin et al., 2005a) and eight for *S. insulare* (Lhullier et al., 2006a). After a trial on 6 representative samples, 12 of these 16 loci were found to be cross reactive and appear to be one locus for yasi, showing specific amplicons: *mSaCIRE09*, *mSaCIRH09*, *mSaCIRG01*, *mSaCIRG10*, *mSaCIRF04*, *mSaCIRF10*, and *mSaCIRH10*

Table 3.1. Characteristics of 12 nuclear microsatellites used in the analysis of *Santalum yasi*, originally developed for *S. austrocaledonicum* (Bottin et al, 2005a) (locus 1-7), and *S. insulare* (Lhullier et al. 2006a) (locus 8-12).

Locus	Repeat motif	Annealing temp.	Allele size range (nt)	No. of alleles	H_O	H_E	X square	P value
1. <i>mSaCIRE09</i>	(CT) _x	50°C	178	1			N/A	N/A
2. <i>mSaCIRH09</i>	(GA) _x	55°C	100-106	3	0.2368421	0.27835007	7.8067	0.1126
3. <i>mSaCIRG01</i>	(CA) _x	50°C	284	1			N/A	N/A
4. <i>mSaCIRG10</i>	(AG) _x GG(AG) _x	55°C	243, 247	2	0.02631579	0.02562327	0.0555	1
5. <i>mSaCIRF04</i>	(GT) _x (GA) _x	50°C	242, 244	2	0.2039474	0.2402614	1.7362	1.7362
6. <i>mSaCIRF10</i>	(GA) _x	50°C	163-183	6	0.21710526	0.37093144	99.0295	0.0003
7. <i>mSaCIRH10</i>	(GA) _x	50°C	244-248	3	0.24342105	0.2408241	0.1662	1
8. <i>mSiCIR33</i>	(TC) _x	50°C	246-254	5	0.5	0.49575831	13.2689	0.7411
9. <i>mSiCIR42</i>	(GA) _x	50°C	236	1			N/A	N/A
10. <i>mSiCIR44</i>	(TG) _x	50°C	134-139	3	0.22368421	0.28202909	7.6663	0.1035
11. <i>mSiCIR148</i>	(TG) _x CG (TG) _x ... (AT) _x	48°C	211, 214	2	0.07894737	0.15027701	17.1226	0.0003
12. <i>mSiCIR153</i>	(CA) _x GA (CA) _x	50°C	302, 310	2	0.05263158	0.06146122	1.5685	0.298

originally designed for *Santalum austrocaledonicum* (Bottin et al., 2005a), and *mSiCIR33*, *mSiCIR42*, *mSiCIR44*, *mSiCIR148*, *mSiCIR153*, and *mSiCIR185* originally designed for *Santalum insulare* (Lhullier et al., 2006a) (Table 3.1).

Polymerase chain reaction (PCR) amplifications were performed in 10 μ l total reaction volume containing 1 μ l 10x buffer (with 200mM Tris-HCl pH 8.8 (25C), 100mM KCl, 100mM (NH₄)₂ SO₄, 20mM MgSO₄ · 7H₂O, 1% (v/v) Triton X-100, 50% (w/v) sucrose, 20 μ g/mL bovine serum albumin (BSA)), 0.8 μ l dNTP (0.2 mM final concentration) (equimolar of 4, New England Biolabs NO447L), 2 μ l betaine (280 mM betaine final concentration) (Q-solution (Qiagen)), 0.2 μ l forward primer, 0.2 μ l reverse primer (though for *mSaCIRE09*, *mSiCIR42*, and *mSiCIR148*, 0.8 μ l of forward and reverse primer were used), 0.08 μ l *Taq* DNA polymerase, and 0.5 μ l genomic DNA template, with the remaining volume being H₂O. The amplifications were carried out on a thermocycler with an initial 2.5 minute denaturing step at 95°C followed by 30 cycles consisting of 30 seconds at 95°C, 30 seconds at the annealing temperature (Table 3.1), 30 seconds at 72°C; then a final 30 second extension step was set at 72°C. After initial amplification, the product was diluted 1:100 μ l in H₂O whereupon a second PCR was performed using the same conditions as described above, except for the labeled M13 dye primer replaced the forward primer in the reaction (same volume). The same thermocycler programs were used for the second PCR. Microsatellite visualization and fragment analysis were then performed with a capillary electrophoresis machine (CEQ 8800 Genetic Analysis System, Beckman Coulter). At least five samples were repeated for each locus to determine the scoring error rate.

3.5.3 Data Analyses

The statistical program R (R development core team, 2009) was used to estimate genetic diversity and departure from Hardy-Weinberg equilibrium, calculating observed heterozygosity (H_o), and expected heterozygosity (H_E) (Edwards, 2008) per locus with the associated Pearson's Chi-square test (based on 10,000 replicates). Wright's F-statistics, F_{ST} , (Wright, 1951) were estimated for all populations to determine departure from Hardy-Weinberg equilibrium.

Analysis of population differentiation by AMOVA (Analysis of Molecular Variance) (Excoffier et al., 1992) was also performed in R. This determines molecular variation within a species in order to measure the genetic structure of the population. Three kinds of structure were tested: Variation between Fiji and Tonga, Variation between islands within Fiji and Tonga, and variation between individuals within islands. Pairwise genetic distances were also computed using R software. To help visualize population structure and patterns of differentiation, results were represented as a spanning tree, a pairwise distribution matrix, and the geographic mapping of allele distribution across Fiji and Tonga.

3.6 Results and Discussion

3.6.1 Results

Of the 12 microsatellite loci tested, nine were polymorphic. The number of alleles per polymorphic locus ranged from two to six. Observed and expected (in parentheses) heterozygosity values ranged from 0.05 (0.06) to 0.50 (0.49). The three

monomorphic loci as well as the two most allele-rich loci departed from Hardy-Weinberg equilibrium, the latter possibly only due to small sample size combined with high levels of alleles in those particular loci. Results regarding the Hardy-Weinberg equilibrium are given in Table 3.1. After repeating at least five samples for each locus, it was determined that the scoring error rate was negligible as each repeat was scored identically to the original.

The results of the AMOVA showed that of the total variance in the data set, 1.75% came from variation between Fiji and Tonga populations (P value = 0.1647, showing no significant variation between Fiji and Tonga populations), 14.72% came from variation between islands/subpopulations (P value = 0.1499, showing no significant variation between islands/subpopulations), and 83.53% came from variation within islands/subpopulations (P value = 0.0175, showing significant variation within islands/subpopulations), suggesting that there is more variation within islands than between (Table 3.2).

Table 3.2 AMOVA Results

Source of Variation	% of Total Variance in Data Set	P value
Variation between Fiji & Tonga	1.75%	0.1647
Variation between Islands/Subpopulations	14.72%	0.1499
Variation within Islands/Subpopulations	83.53%	0.0175

The mean genetic distance between all the samples is 0.27682, showing that there is a 28% dissimilarity between the samples. There was a slight difference in the mean

distances between Fiji (0.3545) and Tonga (0.2028). The mean differences for the presumed sub-populations were made into a minimum spanning tree without geographic referencing (Figure 2.1) and with geographic referencing (Figure 2.2). These results suggest that there has been notable, and perhaps continual, gene flow between Fiji and Tonga.

The population assignment analysis (K-means clustering) categorized the 76 individual samples into 29 genetically similar clusters. These clusters each contained one to five individuals, with an average of 2.62 individuals per cluster. Five of the 29 clusters contained one individual, nine clusters contained two individuals, eight clusters contained three individuals, six clusters contained four individuals, and one cluster contained five individuals. These clusters contained individuals from various subpopulations of both Fiji and Tonga. Of the 29 clusters, only three (excluding the clusters with only one individual) were composed solely of individuals from the same island (four of the Lifuka samples, two of the Bua samples, and three of the Tufuvai samples). Of the 29 clusters, 10 were composed of uniquely Tongan individuals, seven composed of uniquely Fijian individuals, and the remaining 12 clusters were of mixed nationality. The resulting pairwise distribution matrix from this analysis represents these results visually (Figure 3.3). The results from the F_{ST} attribute 12% ($P=0.0066$) of the variation to deviations from Hardy Weinberg equilibrium (i.e. migrations, mutations, and non-random mating).

Although very little differentiation was observed between the Fiji and Tonga yasi populations when considering all the loci together, some trends were noticed when considering the geographic distribution of alleles, locus by locus (Figures 3.4-3.12). For

example in Figure 3.9 the allelic diversity is higher in Tonga than in Fiji for that particular locus (*mSaCIRG10*).

3.6.2 Discussion

The yasi of Fiji and Tonga exhibit allelic variation within populations but overall genetic structure between the populations is absent when all the loci are considered together. These results agree with previous observations of the widespread morphological variation (folk varieties) of yasi within each population (as opposed to these variants being isolated from each other), and the variation in yasi oil quality across populations (Doran, 2005). In effect, this diversity pattern suggests that “populations” across the islands of Tonga and Fiji may more accurately be considered as effective subpopulations of one large population.

The isolation of genetic and morphological varieties and insularity expected in the ecology of island systems, and as observed in the population genetics of *Santalum austrocaledonicum* and *S. insulare* (Bottin et al., 2005a, 2005b, 2007a, 2007b; Lhuillier et al., 2006a, 2006b; Butaud et al., 2005), are not apparent in the analyses of this dissertation. Rather, the geographically dispersed yasi folk varieties together with the widespread variation in oil quality (Doran, 2005) and the similar high levels of genetic variation between sub-populations, as seen in the population assignment analysis (showing 29 clusters, each with an average of 2.62 individuals), and pairwise distribution matrix (Figure 3.3) suggest significant migratory events. Possible migration patterns explaining these results could include several or many incidents of migrations long ago

either before humans arrived in the islands (ca. 3000 years ago (Franklin et al., 1999)) or after, or possibly by numerous recent migration occurrences, or any combination of these three. Given the geographic ocean barriers, these gene flow events would all presumably be human and/or bird/bat mediated. This apparent high level of gene flow between populations has masked evolutionary patterns suggesting the origination of yasi to Fiji or Tonga. Rather, these findings support the ethnobotanical role yasi has held within and between these countries. The cultural importance of this plant and inter-island and international patterns of trade in yasi, as documented by early Western visitors (Labillardiere, 1800; Vason, 1810; Martin, 1817), which presumably had been occurring before Western contact, may be reflected by the observed genetic variation.

So why might the distribution of *Santalum yasi* folk varieties and population genetics depart from the expected insular pattern as found in *S. insulare* (French Polynesia) and *S. austrocaledonicum* (New Caledonia and Vanuatu)? The bird and bat species that are suspected to disperse the sandalwood seeds in the Pacific Islands occur in the geographical areas where these three sandalwood species occur, so if it were the birds or bats that were acting as vectors for the gene flow between islands in Fiji and Tonga, one would suspect that the other insular sandalwood species would follow similar patterns of wide-spread folk varieties and genetic variation. If it is not the birds and bats that are acting as agents of seed dispersers, the next logical dispersers of genetic material are humans. These genetic results may provide molecular evidence confirming the Western and traditional documentation/folklore of extensive interaction between Fiji and

Tonga and their trade of plants and culture (Labillardiere, 1800; Vason, 1810; Martin, 1817).

While high heterozygosity is generally an indicator of genetic health and the ability to recover from the immediate effects of bottlenecks, allelic diversity is an indicator of the ability of a population to overcome the long-term effects of bottlenecks over many generations, thereby suggesting conditions for the ultimate survival of a population or species (Allendorf, 1986). When compared to similar microsatellite analyses in other Pacific sandalwood species, allelic richness seems low. *Santalum austrocaledonicum* had three to 33 alleles per locus for eight selected microsatellites (Bottin et al., 2005a, 2005b), *S. insulare* had three to 15 alleles per locus for eight selected microsatellites (Lhuillier et al., 2006a, 2006b), and *S. yasi* only had one to six alleles per locus for the 12 microsatellites selected. Perhaps if more microsatellites were developed specifically for yasi, a greater amount of allelic richness would be found. Greater differentiation between the populations at the allelic level is seen when considering the data locus-by-locus (Figures 3.4-3.12), suggesting possible unique alleles in certain groups of sub-populations. While microsatellite alleles are usually non-coding, the presence of unique non-coding DNA may reflect the presence of similarly unique genotypes for active alleles. Thus, while the low allelic diversity in yasi compared to other *Santalum* species may just reflect the loci selected for this study or the limited sample size, as an indicator of long-term survival, it obliges the preservation of local genotypes through minimization of germplasm movement between islands.

3.7 Recommendation

Recommendation 6: Maintain allelic diversity of local *Santalum yasi* populations by minimizing unnecessary transfer of germplasm between islands and prohibiting all transfer of sandalwood germplasm from islands with *S. album* and/or *S. album* x *yasi* to those islands without *S. album* and/or *S. album* x *yasi*.

The comparatively, low allelic richness in extant *yasi* populations, and the associated negative implications for long-term survival, necessitate that management endeavors seek to maintain allelic diversity of local populations by minimizing unnecessary transfer of germplasm, and promoting measures to increase extant population size. Furthermore, the introduction of *Santalum album* into propagation programs and native habitat present an immediate genetic threat to *S. yasi* due to rapid hybridization with *S. album*. The introduction of *S. album* and *S. album* x *yasi* germplasm to islands without these species should be prevented to preserve the genetic integrity of remaining pure *S. yasi* stands. The idea of keeping certain islands free of *Santalum album* and hybrids is not new to Forestry officers in Fiji and Tonga.

3.8 Conclusions

While variation is evident within populations of *yasi* in Fiji and Tonga, genetic structure between the populations is absent. These results agree with previous observations of the high morphological variation (folk varieties) of *yasi* within each

population and suggest significant gene flow either as ancient or numerous recent migratory events from diverse localities in Fiji and Tonga, or both. These gene flow events are all assumedly human and/or bird/bat mediated due to oceanic barriers. While these genetic migrations mask evolutionary patterns suggesting the origination of yasi to Fiji or Tonga, these findings support the ethnobotanical role yasi has held within and between these countries and reflect the cultural importance of yasi and the inter-island and international patterns of trade, possibly even in prehistoric times.

The allelic richness of yasi populations sampled here was low compared to other Pacific sandalwoods despite the use of more microsatellites in this study. Greater differentiation between the populations at the allelic level is seen when considering the data locus-by-locus, suggesting possible unique alleles in certain groups of sub-populations (islands). While the comparative lack of allelic diversity may reflect locus selection and/or limited sample size, measures should be taken to maintain the remaining allelic diversity of local populations, which allelic diversity is an indicator of ability for long-term survival of genetic bottlenecks, such as that occurring from overexploitation. Furthermore, given the rapid hybridization of *Santalum yasi* with *S. album*, and the noted, changing trends in their distribution (Figure 2.5 and 2.6), the introduction of *Santalum album* and *S. album* x *yasi* germplasm to islands without these species should be immediately discontinued to preserve the genetic integrity of remaining pure *S yasi* stands.

3.9 Future Research

Further microsatellite analyses on yasi, including more individual samples (i.e. ~ 200-400 samples) from more populations, may improve the clarity of results presented here. Also, to gain more insights into the diversity of *Santalum yasi*, morphological studies could be carried out to determine areas of high morphological variation, especially in 'Eua, Tonga, before *S. album* and hybrids become more prevalent, masking original morphological variation of the natural *S. yasi*.

A controlled experiment to test the effect of Sandal Spike Disease on *Santalum album*, *S. yasi*, and *S. album* x *yasi* would be valuable in identifying differences in susceptibility to the disease. Because this phytoplasma has not been isolated and grown *in vitro*, it is very difficult to perform research on possible treatments for this disease (Thomas & Balasundaran, 2001; Khan et al, 2006), but methods have been developed to detect the presence of phytoplasmas in sandalwood (Hull et al, 1969); Khan et al, 2004). The results of this study would help direct decisions as to the expansion of hybrid plantations, particularly if hybrids are shown to be more susceptible to the disease than yasi. This study should not be performed in the Pacific, but in a location where the Sandal Spike Disease already occurs, to avoid introducing the phytoplasma into the region.

Research to help determine whether early and significant heartwood production has any genetic connections would also be beneficial in managing productive yasi trees. If early heartwood development, as well as high heartwood to sapwood ratio, has a genetic basis then harvesters are selecting *against* this desirable trait by harvesting these

trees early, thus preventing higher levels of regeneration from these individuals, and negatively impacting heartwood production over time (Nasi & Ehrhart, 1996).

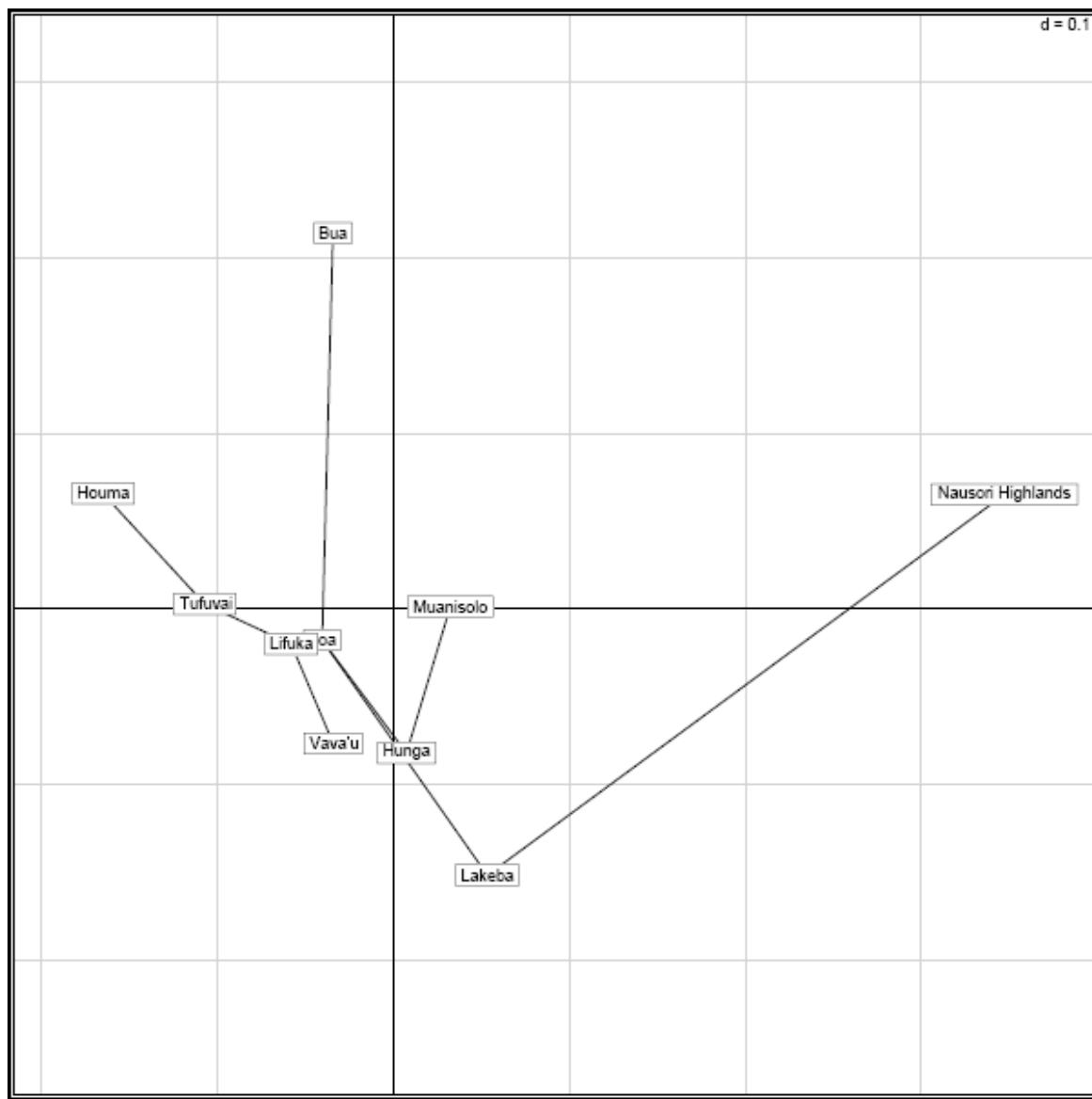


Figure 3.1 Minimum spanning tree without geographic referencing.

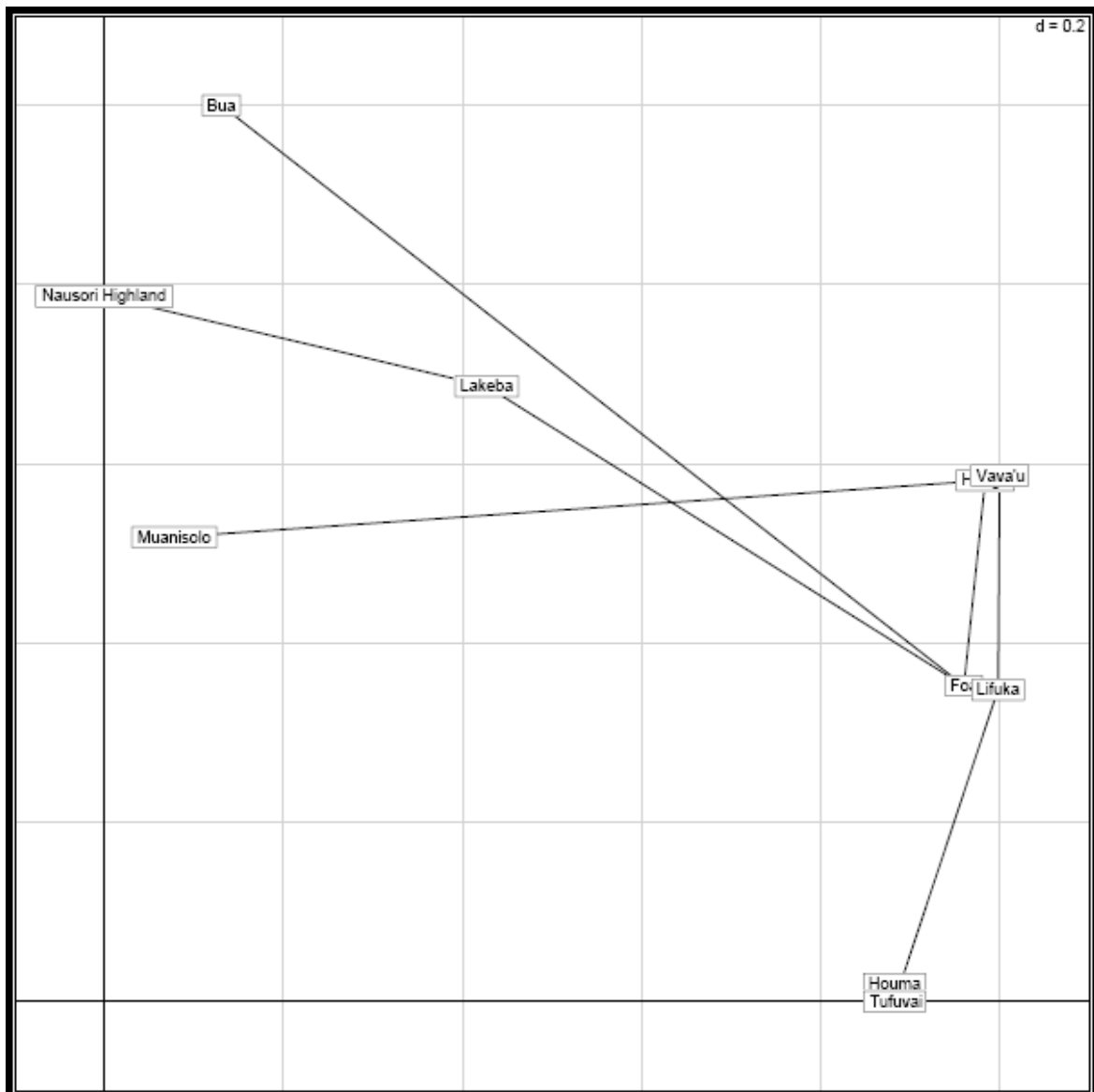


Figure 3.2 Minimum spanning tree with geographic ordination.

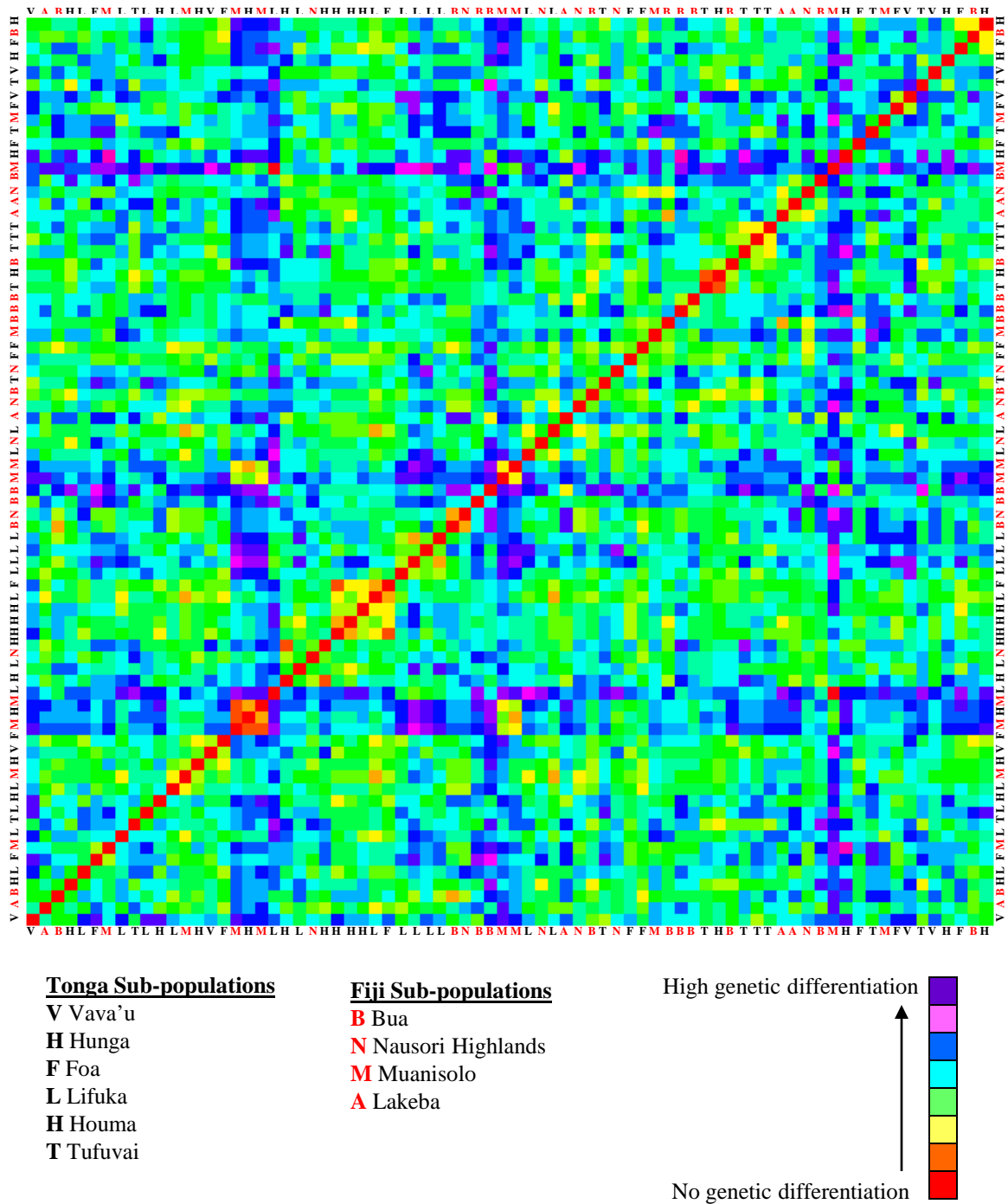


Figure 3.3 Pairwise similarity matrix organized by the 29 K-means clusters.

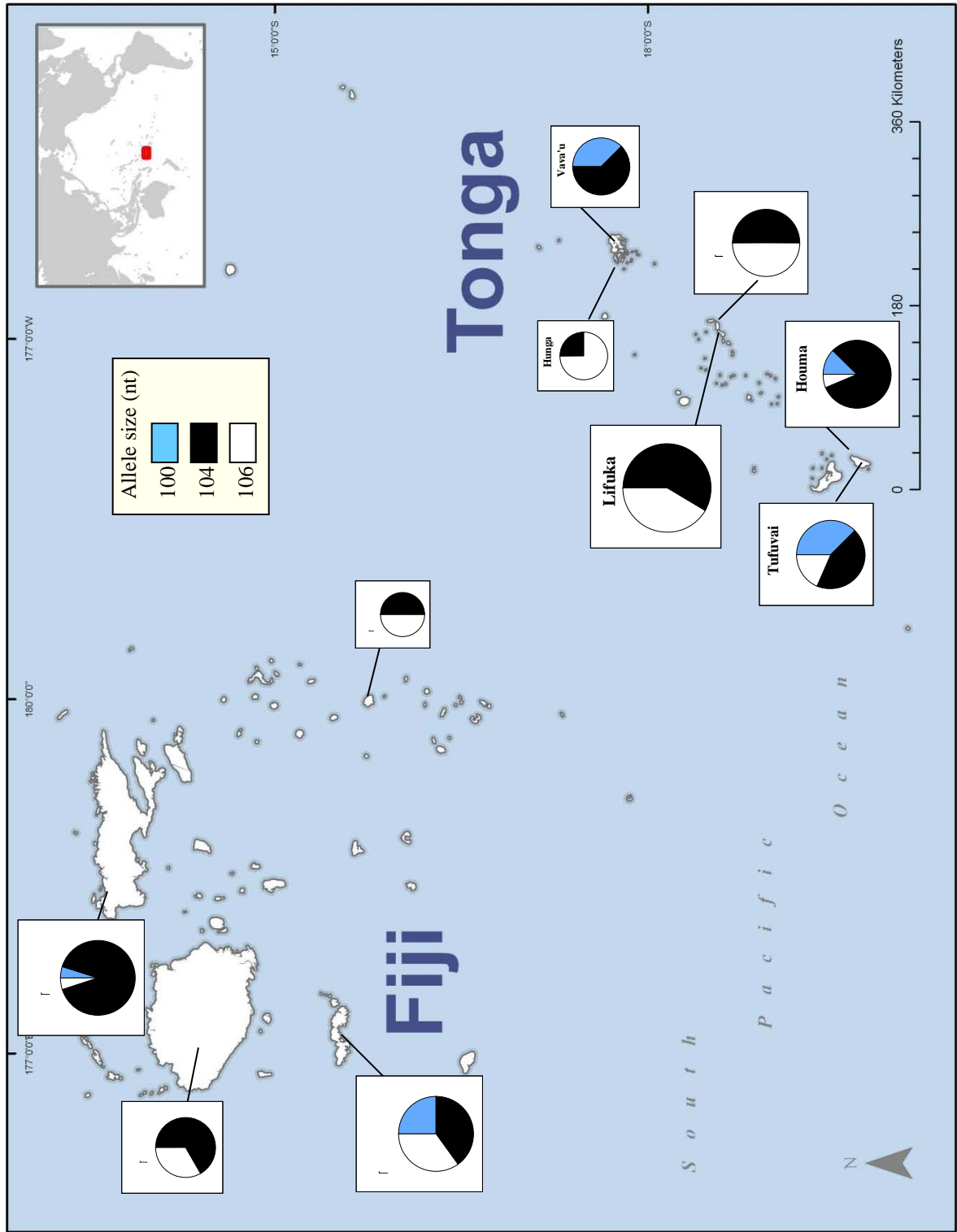


Figure 3.4 Geographic distribution of alleles for *mSaCIRH09*. (Pie charts are proportional to sample size.)

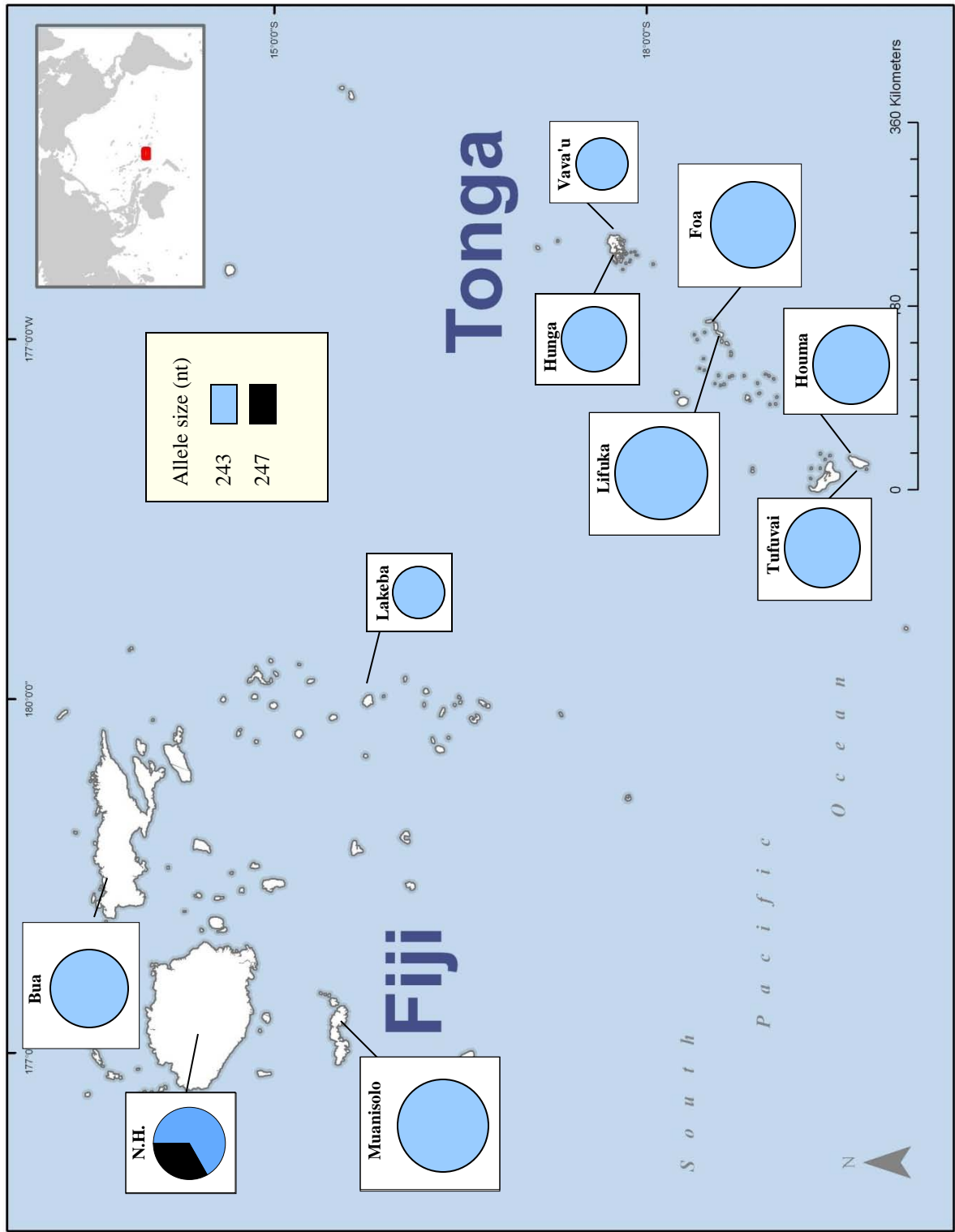


Figure 3.5 Geographic distribution of alleles for *mSaCIRG10*. (Pie charts are proportional to sample size.)

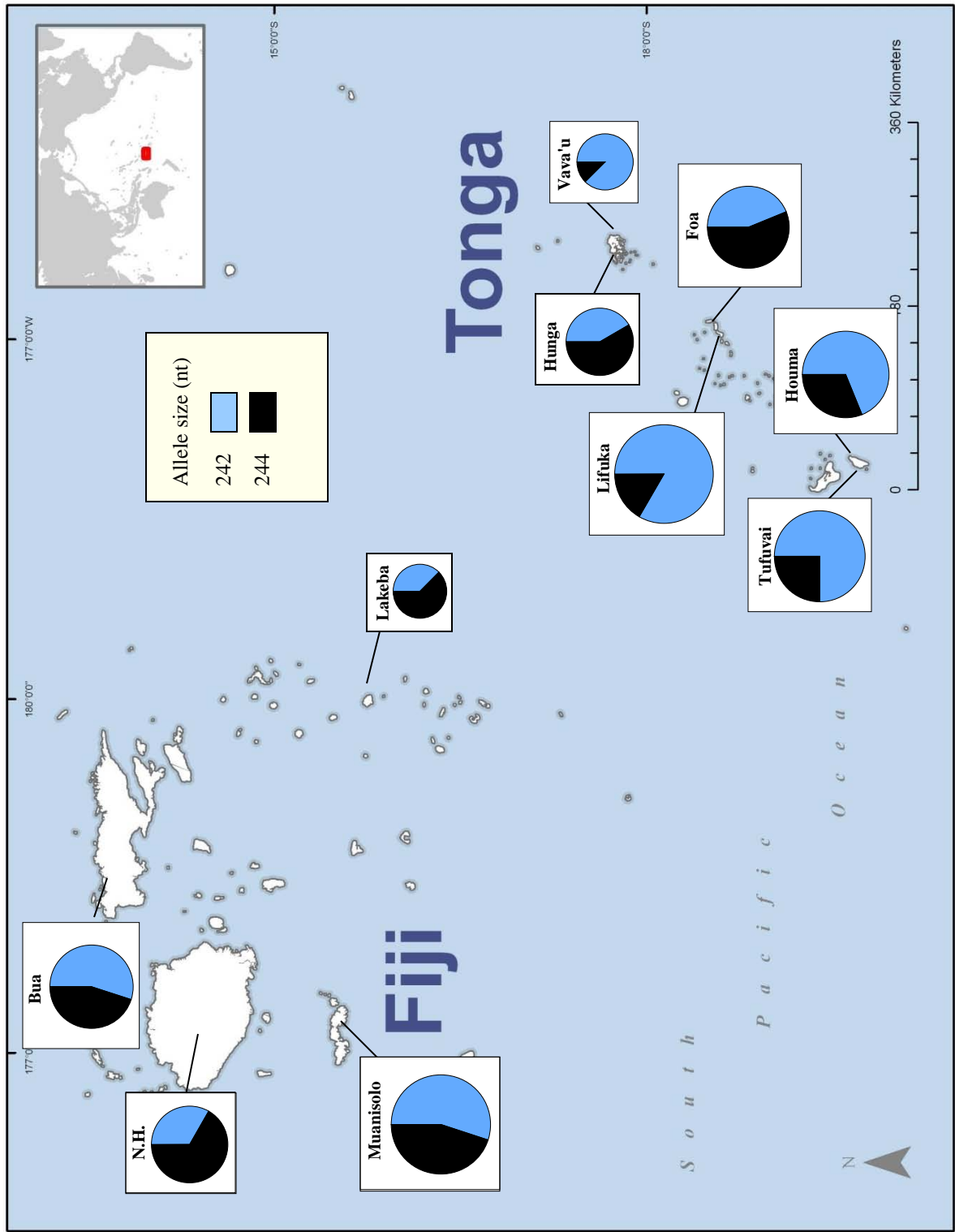


Figure 3.6 Geographic distribution of alleles for *mSaCIRF04*. (Pie charts are proportional to sample size.)

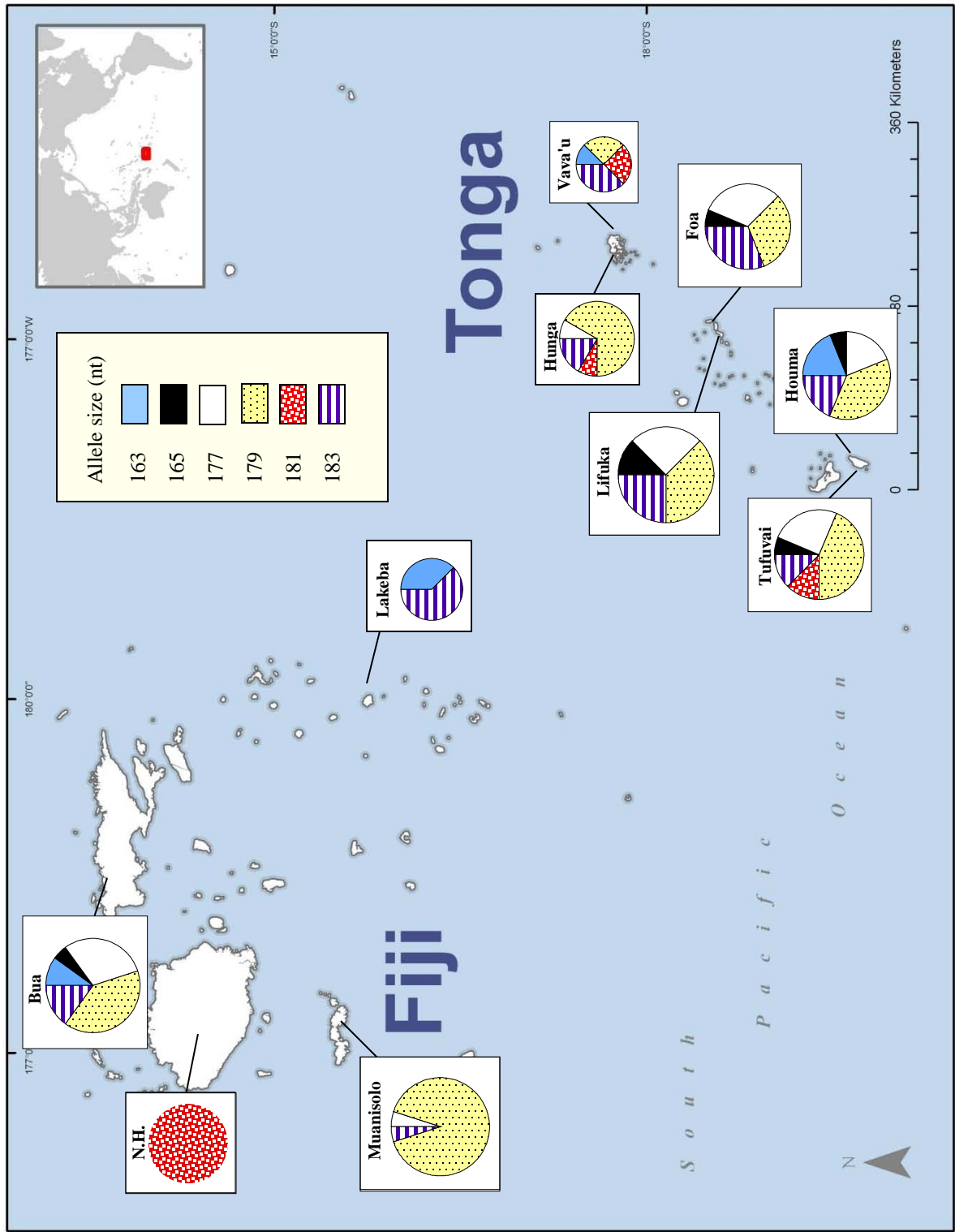


Figure 3.7 Geographic distribution of alleles for *mSaCIRF10*. (Pie charts are proportional to sample size.)

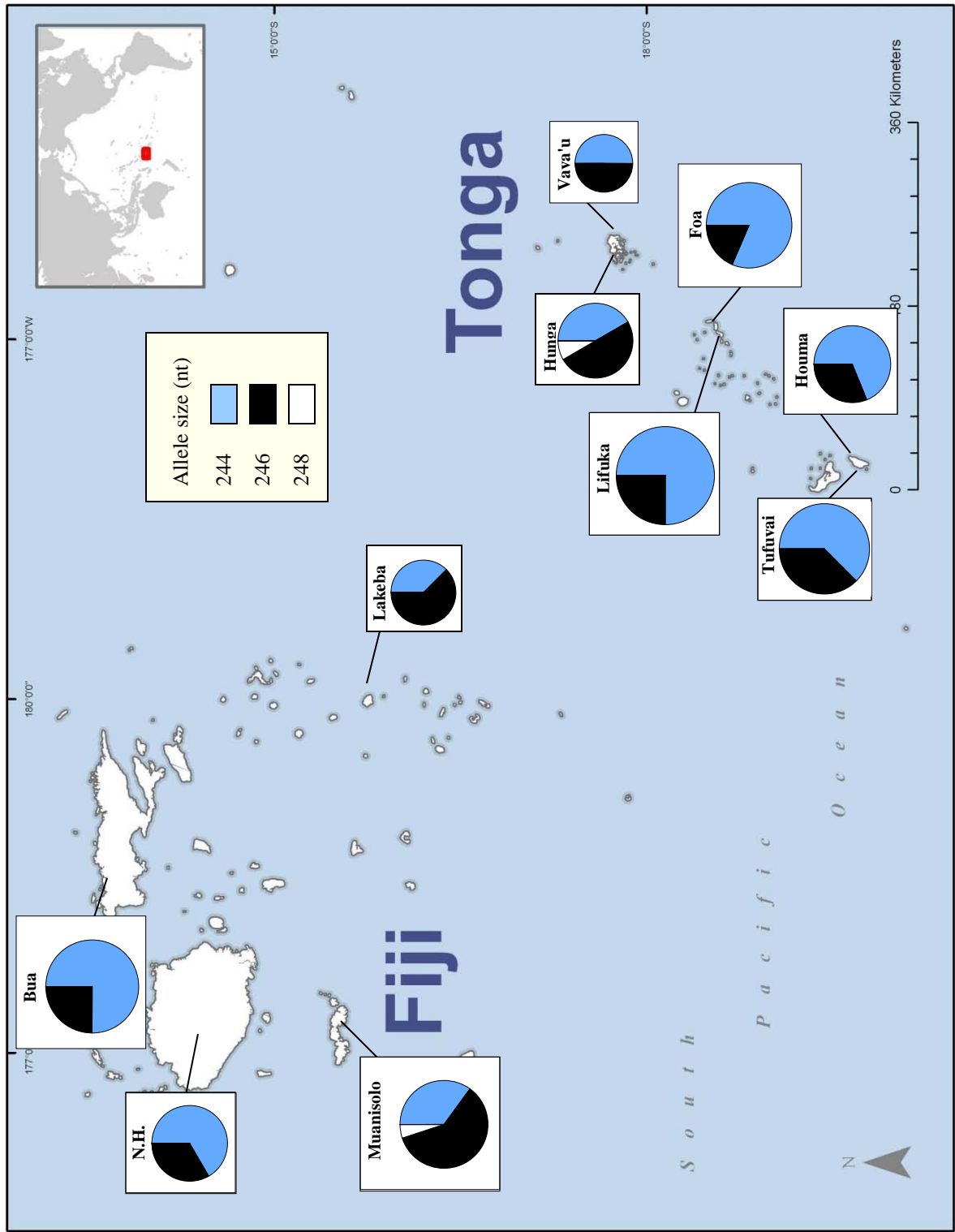


Figure 3.8 Geographic distribution of alleles for *mSaCIRH10*. (Pie charts are proportional to sample size.)

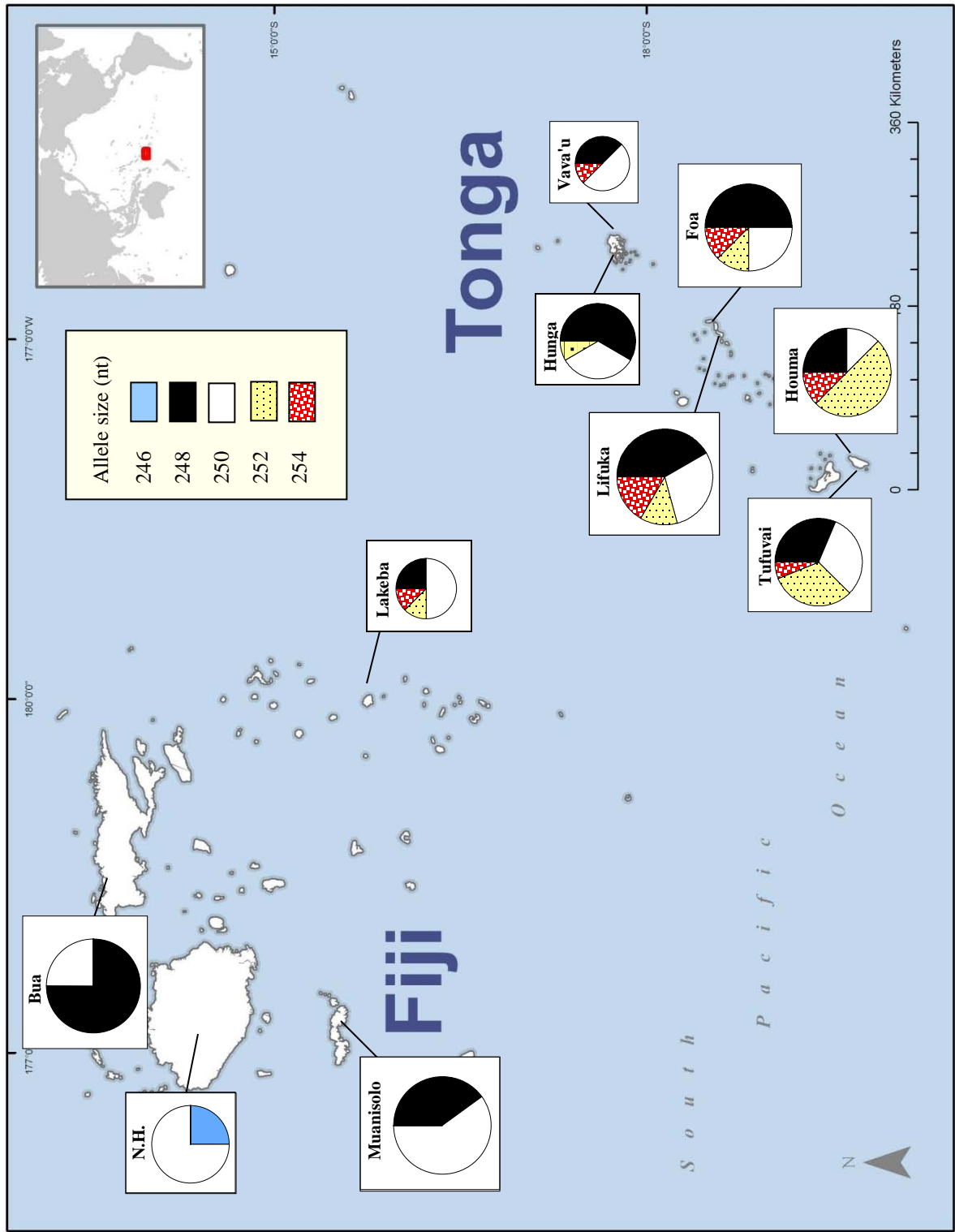


Figure 3.9 Geographic distribution of alleles for *mSiCIR33*. (Pie charts are proportional to sample size.)

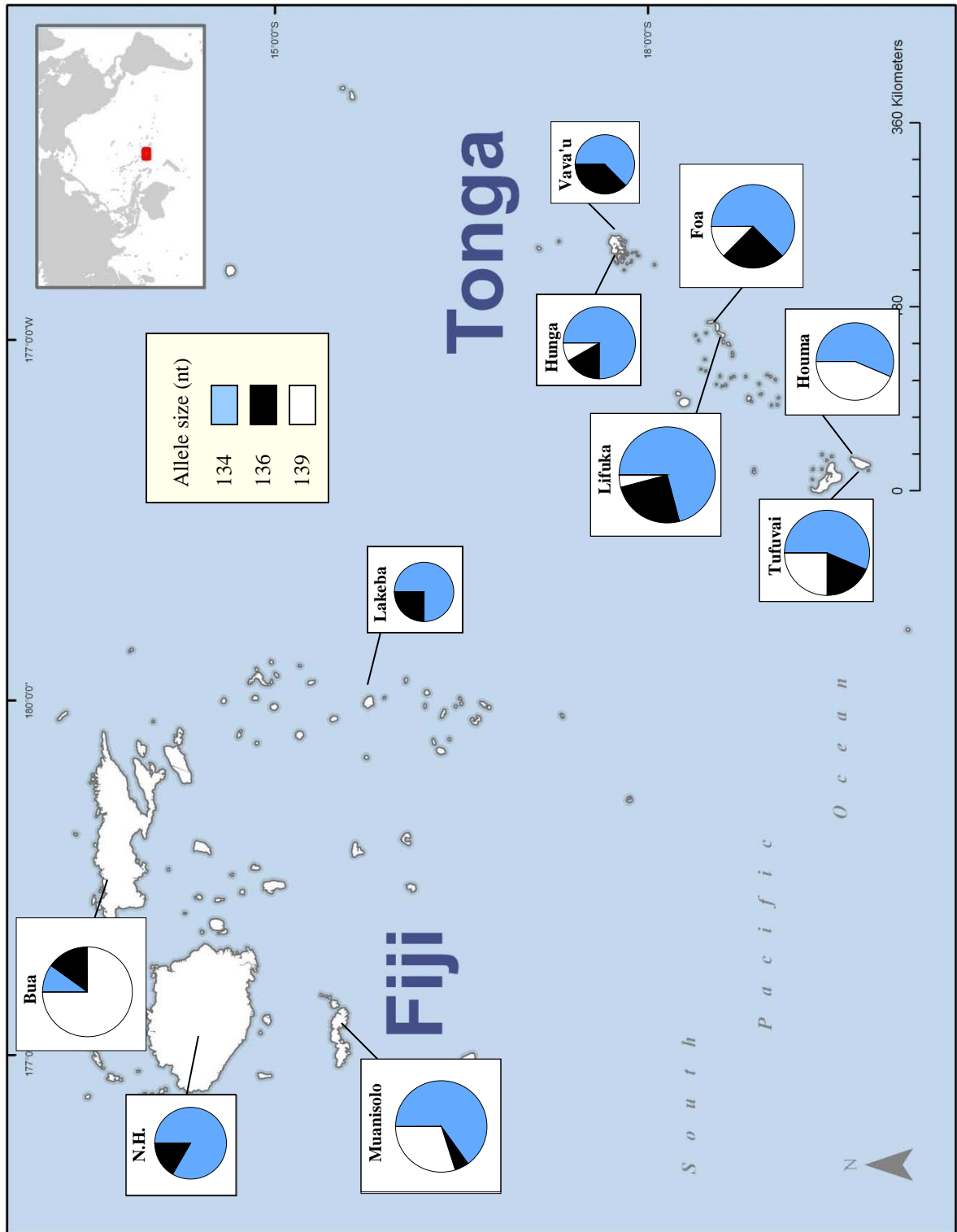


Figure 3.10 Geographic distribution of alleles for *mSiCIR44*. (Pie charts are proportional to sample size.)

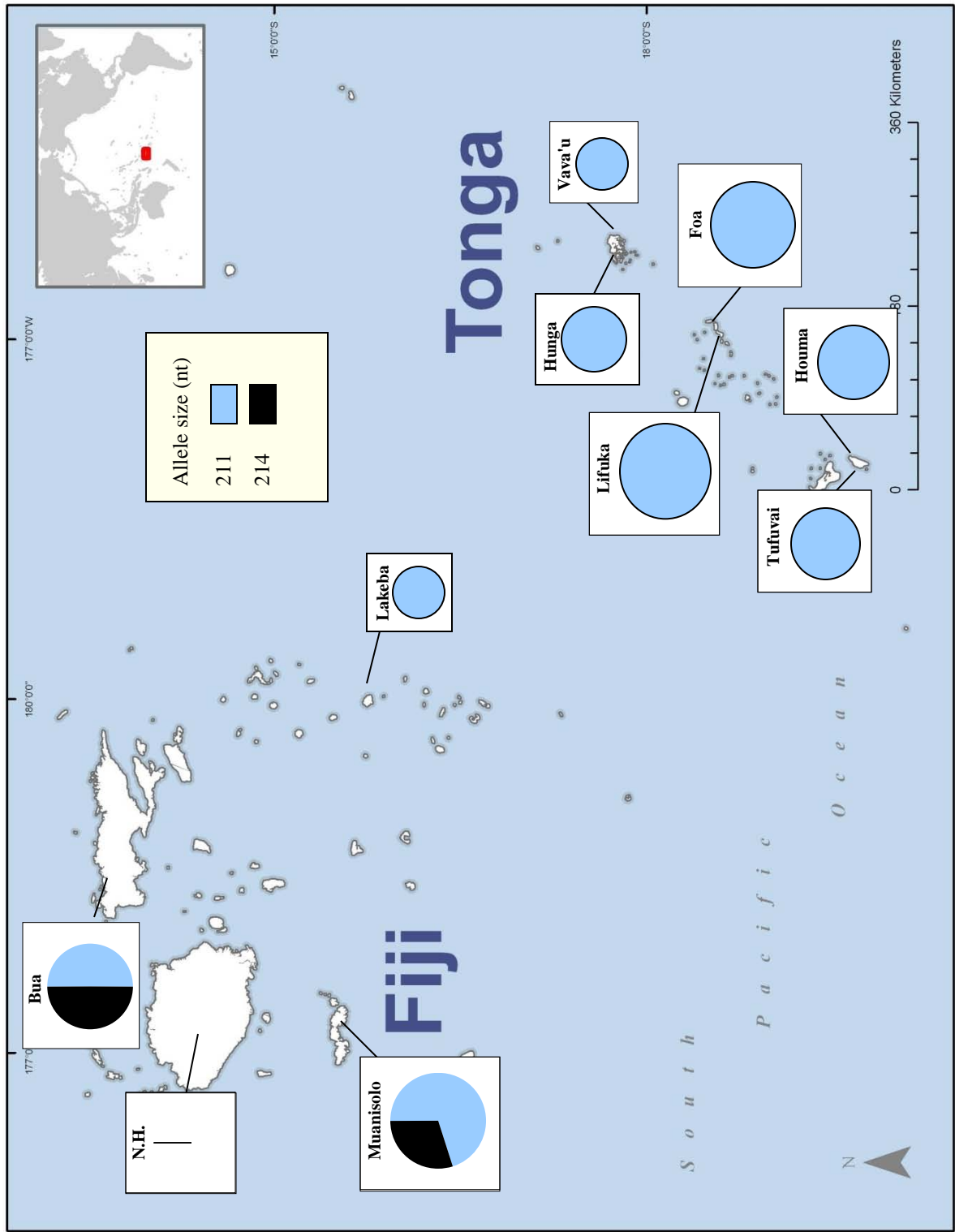


Figure 3.11 Geographic distribution of alleles for *mSiCIRI48*. (Pie charts are proportional to sample size.)

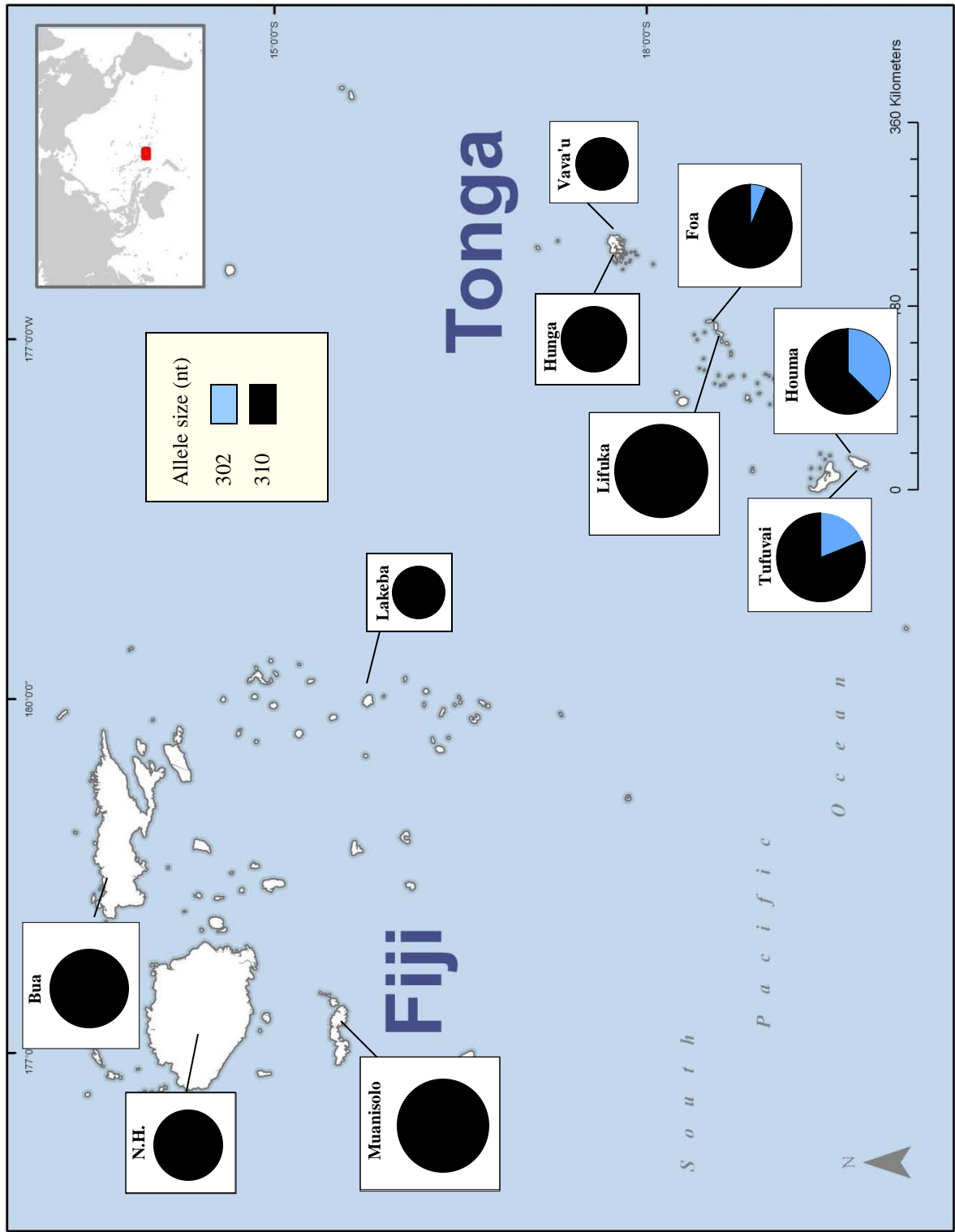


Figure 3.12 Geographic distribution of alleles for *mSiCIR153*. (Pie charts are proportional to sample size.)

CHAPTER 4

DISCUSSION AND CONCLUSIONS ON THE SUSTAINABLE MANAGEMENT AND CONSERVATION OF *SANTALUM YASI*

4.1 Introduction

This chapter focuses on the past and present efforts towards the conservation and sustainable management of yasi and builds on the recommendations of Chapter 2 and Chapter 3 within the context of conservation strategies. The chapter begins with a summary of the history of conservation legislative efforts in Fiji and Tonga, and then a review of previous management recommendations and strategies for yasi in Fiji and Tonga. An investigation into the challenges posed to the successful implementation of management strategies includes a discussion of environmental factors, replanting and land ownership issues, premature and excessive harvesting patterns, legislative and enforcement issues, and financial pressures. Further discussion speaks of the need for local villages to become key partners and benefactors of conservation and recommends the formation of a sandalwood conservancy operated and maintained at the local level to provide both a viable strategy for yasi utilization and needed financial opportunities for community development. This chapter concludes with a complete list of the integrated recommendations from all chapters, conclusions regarding the current and future outlook for yasi in Fiji and Tonga, and a summary of future research areas.

4.2 History of Legislative Efforts towards Yasi Conservation

Environmental and land use issues are becoming a prominent concern and a top priority of the Fijian and Tongan governments (Masikerei et al., 1996). Population growth and changes in land use have caused increasing pressure on land resources. While boosting the economy, the advent of large-scale coconut plantations at the turn of the 20th century, pine plantations, and the cash cropping developments of squash, kava, watermelon, and vanilla cultivation have replaced much of the traditional subsistence farmland and nearly all of the indigenous forestland in Tonga due to extensive land clearing (Masikerei et al., 1996). Legislative decisions by both countries have sought to maintain the balance between utilization and conservation of natural resources. The conservation efforts specific to yasi are discussed in the following sections.

4.2.1 Fijian Legislation

As early as 1930, an “Order in Council” prohibited export of sandalwood from Fiji except under permit, though some harvesting still occurred for local consumption (Jiko, 1991). Later the Bua Provincial Council, recognizing the shortage of sandalwood even for traditional uses, sent a resolution to the Secretary of Fijian Affairs recommending the termination of all harvesting. In July 1950 a prohibition on sandalwood harvesting was declared except with the written consent of the Conservators of Forests (Jiko, 1991), allowing limited harvesting for ceremonial purposes (Usumaki, 1981).

Licensed harvesting began in the mid-to-late 1980s soon after resource surveys were conducted by the Department of Forestry in Bua in 1981 (Usumaki), and in Ono-i-lau in 1984 (Tabunakawai & Chang). These surveys are summarized in Chapter 2. Harvesting was justified based on the understanding that a significant number of sandalwood trees were of harvestable size, plans had been made by the Department of Forestry for replanting, and financial resources were needed to promote community development (Jiko, 1981). At that time a 10% regeneration levy, beyond the 2.55% government fees and 5% royalty, was also instigated, administered jointly by the Native Lands Trust Board and the Ministry of Forests (Jiko, 1991; Thomson et al., 2000).

Also, yasi is listed in Schedule 1 of Section 3 of the Endangered and Protected Species Act of 2002 (Enacted 23 December 2002 by the Parliament of the Fiji Islands), which was drafted for Fiji's annual CITES report. Schedule 1 to this Act lists all species indigenous to the Fiji Islands that are "believed to be threatened with extinction", and can not be exported except with an export permit. A person who exports any specimen mentioned in section 3 without an export permit commits an offence and is liable on conviction, in the case of a first offence, to a fine of FD\$20,000; and in the case of a second or subsequent offence, to a fine of FD\$100,000 or to imprisonment for five years (Uluivuda, 2002).

4.2.2 Tongan Legislation

The major yasi harvesting from Tonga during the 1960s and 1970s, caused the disappearance of nearly all mature trees, as well as immature trees, on Tongatapu and

‘Eua, spurred the Tongan Government to implement the Forest Act of 1979, banning all yasi harvesting. The harvest ban in Tonga was lifted in the 1990s and export was approved under permission granted by the Director of Agriculture and Food with licensing issued from the Ministry of Labor Commerce and Industries (MAFF, 2005). Harvesting was conducted through the 1990s and into the 21st century.

In 1992, Mount Talau National Park in Vava’u (~ 80 hectares) and ‘Eua National Park (449 hectares) were established to help protect remaining indigenous vegetation in Tonga and promote public awareness for conservation. Yasi grows sparsely in Mount Talau National Park. National parks are an important designation for public awareness, but legal enforcement is imperative for these forests to remain protected where anthropomorphic activity is noted as the greatest current threat (Wiser et al., 1999).

Based on the recommendations of forestry officers and the preliminary findings of this dissertation (personal correspondence with Tevita Fakaosi & Heimuli Likiafu, 2008), Tonga instated a “Code of Practices for Sandalwood Harvesting in Tonga” in 2007 with provisions regarding harvesting conditions and volumes, permit fees, applications, reforestation and evaluation (MAFFF, 2007b). Training and full compliance with the code was to ensue by the end of 2008. Harvesting stipulations include periods of harvest and regeneration determined by Ministry of Agriculture, Fisheries, Food and Forests, and a minimum harvest size (15cm dbh, as determined by distributed diameter strings). An investment into replanting by landowners and private investors, and establishment of seed banks and research were also a desired outcome of the code. A period of regeneration

(harvesting ban) began in late 2008 and was announced repeatedly over Tongan national television and radio in late.

4.3 History of Management Recommendations and Strategies

In the history of yasi utilization, various strategies have been employed to manage populations and harvesting. Early management of yasi resources has been primarily through periodic bans on harvesting to allow for regeneration of natural stands and licensure programs. Usumaki recommended a more involved approach to yasi management in Fiji in 1981. Most recently, “A Strategy for Conserving, Managing and Better Utilizing the Genetic Resources of *Santalum yasi* in the Kingdom of Tonga and Republic of Fiji” was produced in 2000 through the combined efforts of Fiji’s Department of Forestry, the Tongan Ministry of Agriculture and Forestry, CSIRO Forestry and Forest Products with support from Australian Aid (Thomsons et al., 2000). The recommendations of each document are summarized below.

4.3.1 Usumaki’s Recommendations, 1981

The Fiji Forestry Department resource survey and population inventory conducted by Usumaki (1981) makes several recommendations regarding yasi management. His survey was conducted in 1981 on yasi in the Bua region of Vanua Levu. Though his recommendations have only been partially realized, they are well-substantiated. His survey reports poor ecological conditions, an absence of local replanting plans and capabilities, and notes the dearth of available ecological, silviculture and biological

information on yasi. His findings are discussed in more detail in section 2.4.1. These findings present significant cause for Usumaki's recommendation to extend harvesting prohibition for another 10-20 years. He further recommended no large-scale harvesting until 30-40 years after plantations were established and yield predictions were reliable.

Usumaki also recommended beginning a replanting program in cooperation with local village members and trained forestry officers. This endeavor could have produced a host of young seedlings for immediate planting, and continual seedling production for replanting when future harvesting began. The promotion of natural reseeding and also replanting could have helped to maintain a healthy genetic heritage of the population.

Usumaki's 1981 survey further suggested a 6,000 to 12,000 ha of marginal, unutilized land be placed under sandalwood plantation before any commercial exploitation of extant populations occur. Usumaki also advocated that forest reserves be established to conserve the species' genetic vitality, and provide locale and populations for seed reserves and future research.

Since 1981, Usumaki's recommendations have been partially realized. His suggested 10-20 year harvest ban was maintained for only 3 years when harvesting resumed in 1984 and continued from 1987 to 1990 (Jiko, 1991). Some efforts in research and seedling production have been made in the establishment of the Nawailevu Yasi Project in Nawailevu Village in the Bua region of Vanau Levu Island with funding from the Fiji German Forestry Project. The Nawailevu Yasi Project commenced in the early 1990s, establishing a yasi nursery using seed collected from mother trees growing within the village. The objectives of this establishment include conducting research into

germination, outplanting and host requirements, and spacing and cultural treatment for use in large-scale yasi production. The nursery experienced very low germination rates in initial trials, and young seedlings suffered losses from cyclones (Seruwaqa, 1993). The nursery was in limited operation, at the time of data collection for this research, in hopes of continuing production for large-scale plantations.

More recently, other villages have also attempted plantation establishment with varying degrees of success in cooperation with international organizations such as Australian Aid and SPRIG as recommended in the AusAid Strategy and discussed below.

4.3.2 AusAid Strategy

In a collaborative effort, Fiji's Department of Forestry, the Tongan Ministry of Agriculture and Forestry, and Australian Aid put forward a report in 2000 (hereafter referred to as the AusAid Strategy) called "A Strategy for Conserving, Managing and Better Utilizing the Genetic Resources of *Santalum yasi* in the Kingdom of Tonga and Republic of Fiji", which gives four major recommendations (Thomson et al. 2000). Three of the recommendations focus on establishing seed and gene conservation stands of yasi in areas where it has naturally grown using local seed germplasm. This entails collecting seed and wildlings from remaining native stands of yasi and developing high quality seedlings. This is proposed to occur as a coordinated effort between forestry officers and extension offices, and also interested local landowners. The fourth recommendation specifies the need for ongoing research into population dynamics,

genetic structure of the species, the biology and ecology involved in genetic maintenance, and the best silvicultural methods for yasi.

A major aspect of the recommendations is the promotion of education, training and encouragement for dedicated landowners in native sandalwood habitat areas who commit to developing, nurturing, and keeping detailed records and history of woodlot stands. Woodlots would be one hectare in size and contain around 400 trees, grown from the locally collected seeds of at least 25 different mother plants. The use of locally collected seed was recommended towards the maintenance and of the genetic heritage and the continued genetic adaptation of the species to local conditions.

The proposed creation of these seed and gene conservation stands was also aimed at eventually returning financial rewards to the committed landowners when the trees reach harvestable size (after 25 to 30 years) and after a second woodlot has been established to replace the first. Data recorded on heartwood quality and quantity at harvesting times would be used to help identify superior trees from which collected seeds could be used for future plantings.

Initial funds and support for woodlot establishment is suggested to be facilitated through regeneration funds collected from previous sandalwood export fees by the Fiji Native Lands and Trust Board and Tongan Ministry of Lands, Surveys, and Natural Resources. The recommended, extensive training of local growers by forestry officers would be imperative and include the distribution of a detailed planting guide printed in both English and Fijian or Tongan. Ideally two years of on the job training would allow landowners to become proficient and eventually self sufficient in maintaining woodlots

with minor assistance and ongoing advice from forestry officials. The guidebook would outline proper cultivation techniques including host selection and use. A draft of the guidebook is included as an appendix to the AusAid Strategy (Thomson et al., 2000).

Implementation of these recommendations has started as part of the South Pacific Regional Initiative on Forest Genetic Resources (SPRIG) to better utilize and conserve the genetic resources of priority tree species as a way to enhance environmental protection and promote opportunities for sustainable rural development (Wainiqolo et al., 2004). *Santalum yasi* was the priority species selected for Fiji and Tonga for this initiative. Wainiqolo et al. (2004) noted the maintenance of seed production areas for sandalwood at the villages of Lololo (0.24 ha in December 2003) and Vunimaqo (0.5 ha in September 2002) on the main island Viti Levu, and seed stands in the villages of Lekutu (0.29 ha in February 2003) and Nawailevu (0.31 ha in Feb 2003) in the Bua region of Vanua Levu Island. The SPRIG Phase 2 Progress Report 1 also notes the translation of a sandalwood manual into the Fijian language and a potted grafted seed orchard at Colo-i-suva near Suva, SE Viti-Levu (SPRIG, 2005).

Tongan efforts have included a potted and grafted gene conservation/seed stand at Tokomalolo, Tongatapu, and seed plots established on Tongatapu and 'Eua totaling 1.6 hectares (Likiafu & Robson, 2005). Over 4,200 wildlings were collected from 'Eua for planting programs and were used as stock for grafting of 150 scions collected from Ha'apai, 'Eua, and Tongatapu with a 74% initial success rate after one month, but final success rate of only 3.3%, or 5 of 150 individuals (Likiafu & Robson, 2005).

Multiple regional workshops on sandalwood have been organized including a seed, nursery, and planting technology training workshop in Noumea, New Caledonia in 1994 organized through the South Pacific Forestry Development Program (SPFDP). In 2005 a “Regional Workshop on Sandalwood Research, Development and Extension in the Pacific and Asia” was conducted in Nadi, Fiji to discuss current research and future prospects, with the support of multiple organizations and 45 participants from across the Asia-Pacific region (Bulai, 2005). A training workshop, including training in silviculture methods, was also held at the end of 2005 at the Forestry offices in Colo-i-Suva, Fiji with 14 participants from across Fiji, one from Rotuma, and one from Tonga (Bulai et al., 2005). In conjunction with these meetings, the Fiji Forestry Department formulated a strategic development plan for 2005-2007 with a goal of 150 ha of yasi planted by 2007, and future planting schemes of 200 ha per year (Bulai et al., 2005).

4.4 Challenges of Conservation Management

Enforcing harvesting bans and limiting harvest levels by licensure has proved difficult (Kaufusi, 1995; personal conversations with Tevita Faka’osi and Heimuli Likiafu, 2006-2009, and Sanjana Lal, 2006) and the implementation of other management recommendations has often been neglected, unsuccessful, complicated, and expensive (Jiko, 1991; Seruwaqa, 1993; Thomson et al., 2000). Many issues, outside of ecological and genetic factors, play a role in the complexities of managing wild yasi resources in Fiji and Tonga, which merit attention and require some degree of resolution.

Replanting harvested or destroyed areas is currently uncommon, due in part because seedlings may not be available (Wiser et al., 1999). Even when yasi seeds are available in abundance, replanting programs may be inhibited due to land ownership issues. The location of yasi populations can complicate population management, replanting and caretaking. This is a key issue in Tonga where some wild, naturally growing yasi trees are harvested from the forested areas of royal estate and government land. The initial time and energy invested in replanting and continued caretaking, long before harvesting, would be an improbable endeavor for individuals with no ownership or jurisdiction over the land or resources and, therefore, with no guaranteed reward. The lack of clear ownership or jurisdiction by harvesters over wild growing populations further encourages premature harvesting due to the scenario of gleaning on a first-come-first-served basis.

Furthermore, social obligations, such as those associated with the *fahu* system (superordinate kin) in Tonga can play both a deleterious and beneficial effect on yasi, and general conservation as discussed by Evans (2007) in his paper “Property, Propriety, and Ecology in Contemporary Tonga”, which considers the ecological consequences of privatization versus common property laws and customs in Tonga. While the political significance of the *fahu* system has diminished in modern times and land ownership in Tonga is legally private, the role of the *fahu* system in social practice is pervasive and compelling (see Bott, 1981 & 1982 for further discussion of the *fahu* system). Thus, yasi growing on private land may be demanded under these social obligations. This social pressure was a major factor in the defensive, widespread and near complete harvest of

yasi from Ha'ano Island, Ha'apai over a period of two years in the early 1980s (Evans, 2007). In this case, the consequence of social pressures was deleterious to yasi, but the long term, historical and present effects of these social obligations have also been beneficial in that they allowed for the "interregional movement of plants... by the dispersion of people with overlapping customary rights to one another" (Evans, 2007). This interregional movement of yasi is reflected in the genetic findings of this dissertation discussed in Chapter 3.

The necessary obligation of governments to provide financial opportunities for community development can appear at odds with conservation strategies in locations and situations where other sources for income are minimal. The notable disconnect between Forestry Department recommendations and governmental legislative initiatives, as evident in the timeline of forestry surveys and harvesting allowances in Bua, Fiji (discussed in 4.3.1 of this chapter), has had a detrimental affect on the preservation of the wild yasi stands in Bua. The further difficulties with legislation enforcement, due to lack of man power, funding, and other factors have created a large gap between the volume of export under permit, and actual export values in Tonga (Likiafu, 2008). The Ministry of Agriculture, Fisheries, Food and Forests (MAFFF) Quarantine Division Annual Reports show a large discrepancy between the values exported and the permitted. In 2004, 140 tons were permitted but 257 tons were exported. In 2005, 32 tons were permitted but 52 tons were exported. In 2006, 0 tons were permitted but 50 tons were exported. In 2007, 26 tons were permitted but 205 tons were exported. The remote locations of populations make regulation of harvesting by removed forces nearly impossible, while the high value

of yasi attracts poachers. These statistics suggest that a permit system alone is not sufficient to maintain sustainable harvest levels.

Notably, a great force undermining the sustainable use of yasi populations, and causing the disappearance of wild yasi habitat, comes from the lack of alternative financial resources for individual and community development in the remote locations near wild yasi habitat. This financial pressure fosters illegal harvesting and premature harvesting of young yasi trees, further encouraging owners to defensively harvest their trees before others take them (Evans, 2007). This premature removal of trees diminishes the regeneration capabilities of wild populations and lengthens regeneration times significantly. The need for financial resources for community development was reported as a main impetus for the beginning of modern harvesting and exports from Fiji (Jiko, 1991), despite forestry recommendations against harvesting (Usumaki, 1981; Tabunakawai & Chang, 1984). This fundamental financial need is therefore a major factor demanding attention within an effective management strategy.

4.5 Community-Mediated Approach for the Management of Wild Yasi

The recommendations of Usumaki (1981) and AusAid Strategy (Thomson et al., 2000) can potentially benefit greatly the continued genetic integrity of yasi as a viable species and help increase numbers of harvestable trees. The research and recommendations of Chapters 2 and 3 of this dissertation support these well-formulated recommendations. However, these strategies and current conservation actions in Fiji and Tonga do not attend to the maintenance of remnant wild yasi populations and habitat,

though the formation of sandalwood seed lots, or even intercropped plantations, could indirectly benefit wild populations through incidental reseeding by birds. Furthermore, the underlying factors hindering successful implementation of management strategies need to be addressed more fully. A community-mediated management strategy to improve and utilize the remaining wild yasi populations in a sustainable manner is put forth in this section. This section will discuss the benefits and importance of maintaining wild yasi populations and habitat, establish the significance of a community-mediated approach, and detail the principles behind this recommended management approach.

4.5.1 Benefits and Importance of Maintaining Wild Yasi Populations and Habitat

Maintenance of wild yasi populations is prudent and imperative to the success of any yasi management strategy. A focus on improving the yields of extant wild stands avoids the initial costly and complicated development of nurseries (though the future development of nurseries could be funded later through the profits of the wild harvested heartwood according to village goals). Wild yasi cultivation also has low maintenance to high harvest value compared to nurseries and alternative high input/low output crops with uncertain market value (Barrett & Fox, 1994). Furthermore, the maintenance and care of wild yasi populations and habitat also help ensure the preservation of the many other native forest plants and products for continued traditional use. This point is of particular concern to yasi populations and habitat in Tonga where pressure on land resources is increasing and cash-cropping developments have replaced much of the traditional subsistence farmland and nearly all indigenous forestland (Masikerei et al., 1996).

Moreover, a conservation management strategy relying solely on seedlots, to the neglect of wild populations, is insufficient and tenuous. The preservation of wild populations is vital to maintain a source for the initial and future high quality seed collection essential to the seed and woodlot formation recommended by the AusAid Strategy. As noted by Jiko (2000) and the Director of Forestry and Conservation Division of the Tongan MAFFF, Tevita Faka'osi (personal correspondence, 2008), the current shortage of available seed is one of the greatest constraints to management strategies. Outbreeding preference is requisite for successful breeding by seedlots (Hosius et al., 2000). While the strength of outbreeding preference has not been thoroughly examined for yasi, preferential outcrossing is suggested by the results of the population genetics analysis of this dissertation. The efficacy of seedlots at preserving genetic structure, however, has been questioned in breeding systems with phenological variation in flowering (Gomory et al., 2003). In a study on outcrossing levels in *Santalum spicatum* the general preference for outbreeding was absent in one population due to desynchronized flowering, which induced higher rates of inbreeding (Muir et al., 2006). Yasi also has noted variation in floral phenology (Bulai, 1995; Thomson, 2006a). Seedlot design must, therefore, attempt to account for variation in flowering patterns to promote prolonged maintenance of allelic structure from parental stock to progeny (Muir et al. 2006). The difficulty of seedlot design for such circumstances, where panmixis in seedlots cannot readily be assumed, is ominous and genetic drift is a likely, and documented, outcome (Muir et al. 2006). Preservation of large, wild stands of yasi, as an

open breeding system, is therefore fundamentally important in ensuring continual genetic variation, the survival of the species, and resource sustainability.

4.5.2 Significance of a Community-Mediated Strategy

While human needs and activities present the biggest threat to wild yasi populations, human prudence can also, therefore, become the biggest factor supporting yasi's recovery. The excellent market value of yasi, once the cause of its decline, can potentially play a positive part in its own preservation and help to meet the needs of communities. A logical and prudent answer to sustainable management obstacles may lie in the creation of a community-mediated sandalwood conservancy trust for each of the main villages neighboring extant yasi habitat, which is fundamentally operated and maintained by the local, extant leadership and organization of neighboring villages, and the support of the forestry department as needed. Such a conservancy over wild yasi populations can be effectively and economically implemented and provides necessary funds for community development in a more ecologically, and culturally advantageous alternative to the influx of pine plantations or other cash crops.

This type of community-based, coordinated management effort has been discussed by leaders of villages in Tonga and operated successfully in a simple form in Muanisolo, Fiji. The available information on the harvests and regeneration of yasi near Muanisolo village on Kadavu Island in Fiji is positive and enlightening, in contrast to the story of early, near complete harvest and lack of regeneration of yasi in Bua. While the population is still very small and harvesting has been extensive, yasi growing wild around

the village of Muanisolo, compared to equally habitable areas surrounding other villages of the same region, showed a significantly higher level of regeneration and larger population size according to an enumeration of resources for four yasi populations on Kadavu Island in 2002 (Duikoro & Tokairavua, 2002). Plausible factors for the comparatively positive dynamics of the Muanisolo yasi population may be the ongoing care and maintenance of wild yasi trees by village members and their understanding of the tremendous value of the population. Villagers visit yasi trees regularly and remove competing non-host species, prune leaders to form one straight bole, and prevent damage by wild pigs. The village benefited enormously from the profits of the 1988 harvest (earning over \$100,000), which paid for the building of a new village church and community building. The wild stand may have also benefited from the expertise of village member, Joseva Mateboto, a retired forestry officer.

The AusAid Strategy's promotion of education and local involvement of landowners and interested individuals in woodlot and seedlot creation to help promote economic development for local communities is noteworthy. Reports on the progress of these initiatives in June 2005 showed increasing interest in participation by rural communities across Fiji. The aim of self-sufficiency in yasi population management occurring at the local level in each area where it is naturally found is important for preserving local genetic diversity and the long term success of a management program. Also important is providing the members of villages neighboring habitat areas with an opportunity for community development inline with both village needs and conservation initiatives. McNeely's injunction (1993), concerning indigenous people and protected

areas, gives useful insight. “It is usually better to strengthen local institutions than to create new ones,” and “a key point is that local responsibility should follow local institutional patterns” (McNeely, 1993). This principle has been successfully implemented in forest conservation in Samoa when initiatives were built on the foundation of local culture, and when responsibility and at least partial ownership of protected areas were given to the indigenous people neighboring the areas (Cox & Elmqvist, 1997). Conservation efforts, however, were ineffective and harmful in similar attempts when the involvement of outside authorities became excessive and inattentive to local needs (Cox & Elmqvist, 1997).

Rohadi (2000) reports similar findings in his paper discussing the negative impacts of attempts at resource control and regulations on populations of *Santalum album* in East Nusa Tenggara. The production of sandalwood in East Nusa Tenggara is based on natural regeneration. Rohadi mentions intensive attempts at plantation establishment but reports that, due to lack of silviculture techniques, poor management systems, and limited facilities, the over 2400 ha planted were unsuccessful. He further notes that while illegal harvesting, low natural regeneration rates, uncontrolled burning, wild grazing and inventory complications are factors undermining government attempts to manage sandalwood resources, the root of these problems stem from the neglect of community rights, lack of real community incentives and minimal community participation in the maintenance of natural regeneration. Rohadi notes the need for local involvement and jurisdiction over sandalwood resources and recommends a management approach where the government focuses on investment into populations rather than centralized regulation.

Decentralization also encourages local involvement in population maintenance and regeneration through the transfer of management authority to a local level.

Similarly, in Tonga and Fiji, plausible solutions to the complex concerns and issues associated with sustainable management of wild yasi populations may be found in the explicit creation of a sandalwood conservancy trust, which is operated and maintained at the community level.

4.6 Recommendation

Recommendation 7: Implement management strategies to improve and utilize wild *Santalum yasi* populations through the formation of a community-mediated sandalwood conservancy trust for each village neighboring extant, wild *S. yasi* populations, which is fundamentally operated and maintained by local leadership and organizations with the technical support of forestry officers as needed.

Key aspects of a community-mediated sandalwood conservancy trust would include: (1) legal tenure of and stewardship over yasi populations granted to neighboring villages and caretaking responsibilities mediated through extant village leadership and organization; (2) a sustainable, maximized harvesting schedule cooperatively developed by village leaders and forestry officers, which includes an initial regenerative period followed by incremental, periodic harvesting with preference given to the largest

diameter trees; and could also include (3) contracted sales and optional formation of a trust fund. Details of implementation, contract specifics, and harvest schedules (Appendix 2) would be adapted to local needs and circumstances, but the essential principles and advantages of a locally-operated sandalwood conservancy trust are outlined here.

Legal tenure and stewardship

Under the conservancy trust, villages neighboring wild yasi populations become full-fledged partners in conservation and each village as a collective receives legal tenure and stewardship over populations within a specified area, thereby holding the greatest responsibility for caretaking and management. This division of responsibility is practical and advantageous because nearby villagers are the most knowledgeable about the specifics of local forest dynamics and regularly visit and inspect the forest areas. Caretaking responsibilities could include assisted natural regeneration, such as removing competing, non-host species (i.e. lianas) and protecting young seedlings (i.e. erecting fences to prevent herbivory), as well as pruning side leaders to promote the formation of one main bole, collecting basic inventory, and performing other prudent responsibilities. The existing local leadership within communities and villages is a proven organization to oversee caretaking responsibilities and ensure contract guidelines are followed and compensation is appropriately allocated towards a common interest (such as village improvements like a new school, church, community building, or road, or education fund). The local land tenure system of mataqali in Fiji and the social obligations of *fahu*

in Tonga should be upheld in such systems and concerns and issues considered and resolved locally on a community level. Forestry officers would work with village members to provide appropriate silviculture training and help in establishing nurseries to further promote regeneration and plantation establishment beyond the maintenance of wild yasi stands as desired.

Conservancy trust contracts would include caretaker responsibilities of the village, designation of poaching intervention rights and responsibilities to village members (such as rights to confiscate poached wood, and fine poachers for damages and harvest value lost), and a budget for financial compensation to all involved parties. While a portion of harvest profits would return to any applicable landowners, support the assistance of forestry officers, and pay for appropriate government fees, conservancy villages would receive the greatest financial compensation from yasi harvest profits. This recurring financial compensation to conservancy villages and the contracted involvement will encourage and ensure proactive caretaking and management and provide a unique opportunity for economic growth for the community. The inclusion of all members of each village community in the benefits and responsibilities of yasi tenure and stewardship will improve the prevention of poaching by outsiders or insiders due to maximized monitoring abilities and financial interests.

Sustainable, Maximized Harvest Schedule

Fundamental to the success of a sandalwood conservancy is the use of a sustainable, maximized harvesting schedule. The damaging effects of the harvesting of

all mature heartwood bearing individuals in a population can be greatly reduced, while regular harvest profits can be gained and continually increased if harvesting occurs in a systematic, incremental manner. The management of *Santalum austrocaledonicum* populations in Vanuatu involves restrictions on size-cutting limits, and harvesting bans according to the specifics of each population (Channel & Thomson, 1999). The “Code of Practices for Sandalwood Harvesting in Tonga” also seeks to implement harvest size limits (MAFFF, 2007b). A similar tactic underlies the establishment of a sustainable harvesting schedule for each wild growing population of yasi based on the initial dynamics of each population.

All yasi harvesting would be predetermined according to a schedule developed cooperatively by village leaders and forestry officers. Forestry officers would provide technical information regarding the effects of invasive species, heartwood yield potential over time, yield lost due to immature harvesting, and so forth. Figures 2.12 and 2.13 may be a useful resource to illustrate value lost due to premature harvest, and value added by an incremental harvesting schedule. Village leaders would determine how to apply the information and principles in creating a harvest schedule best suited to the current and future needs of their community.

The finalized harvesting schedules would include a timeline for cycles of regeneration and harvesting periods and stipulations on size limits and harvest percentages per size class per harvesting cycle. Harvest preference at each cycle would be for individuals in the largest size class, or classes, currently available in the population, however only a small portion of these largest individuals would be harvested

at each cycle. A percentage of these individuals from the largest size classes would be left to produce seeds (promoting regeneration) and to continue forming heartwood (increasing future harvest profits and yields). Maintaining such a harvest schedule specific to each population would increase regeneration and recruitment, thereby increasing harvest profits with each cycle through the steady increase in extant tree size within the population. Several sample harvest schedules and associated heartwood yield graphs have been constructed in Appendix 2 for reference and use to illustrate the different yield capacities of each harvest schedule.

Beyond the routine care and management of populations, more thorough surveys would be conducted by village leaders periodically, and ideally early within each harvesting year, to measure population dynamics and regeneration levels, to finalize regenerative periods and allotted harvesting levels, and to identify poaching. Surveys could involve the assistance of forestry officers and may include checking for heartwood formation in individual trees, which would be conducted in a nondestructive manner, such as by removing a smaller side branch to check for the beginnings of heartwood formation. Conservancy members will in this way ensure the population health and positive growth in yasi stands are maintained, while also maximizing the harvest value available.

Contracted Sales and Optional Conservancy Trust Fund

Historically, the value returned for yasi heartwood has been highly variable (anecdotal reports recount prices ranging from several cents/kg to over US\$25/kg to the

exporter, and significantly more to the final consumer). Also, the tenuous state of infrastructure associated with cash cropping sometimes discourages the investment into the production of export commodities in remote locations (Evans, 2007). Contracted sales are recommended to help ensure timely sales and fair prices. This may be of particular concern in Tonga where harvesters are frequently offered lower prices than received in Fiji. Further, a conservancy trust fund may be established with a bank for the benefit of a village, saving and dispensing harvest profits on a regular basis, according to an agreeable schedule.

4.7 Complete List of Recommendations

Recommendation 1: Establish a regeneration initiative for *Santalum yasi*, proscribing harvesting to allow for growth and regeneration of remnant populations.

Recommendation 2: Expand *Santalum yasi* resources through replanting post-harvesting and reintroduction of seedlings into previous, appropriate habitats currently devoid of *S. yasi*.

Recommendation 3: Encourage noninvasive methods of checking for heartwood formation.

Recommendation 4: Maintain current wild *Santalum yasi* stands through assisted natural regeneration, caretaking, and harvest size/age limits.

Recommendation 5: Minimize the influence of introduced species, including feral pigs, in habitat areas.

Recommendation 6: Maintain allelic diversity of local *Santalum yasi* populations by minimizing unnecessary transfer of germplasm between islands and prohibiting all transfer of sandalwood germplasm from islands with *S. album* and *S. album* x *yasi* to those islands without *S. album* and *S. album* x *yasi*.

Recommendation 7: Implement management strategies to improve and utilize wild *Santalum yasi* populations through the formation of a community-mediated sandalwood conservancy trust for each village neighboring extant, wild *S. yasi* populations, which is fundamentally operated and maintained by local leadership and organizations with the technical support of forestry officers as needed.

4.8 Summarized Findings and Conclusions

The findings of this dissertation are, for the most part, in support of, and inline with the ongoing, meritorious efforts of various organizations to sustainably manage yasi resources. The current distribution of wild/naturalized yasi in Fiji, Tonga, and Niue has been that of decrease, even to the point of local extinction in several areas of Fiji. In contrast, the trend for the distribution of naturalized *Santalum album* and *S. album* x *yasi* has been that of increase, posing a potential ecological threat to the remaining stands of yasi due to competition for resources, habitat, and hosts. The three, densest, remaining populations covered a relatively small area and showed size-class structure patterns of discontinuous recruitment, an evidence of regenerative stress. Regeneration rates may be sufficient to maintain the populations *in situ* if seed production continues by extant adult trees and recruitment rates remain favorable. However, since this study, a major wave of harvesting has taken nearly all adult trees from each of the study sites making the current situation more depleted than reported here.

The practice of harvesting all heartwood-bearing trees from populations leads to an implicitly negative effect on regeneration capacity due to the early removal of main fruit-bearing trees. Also, early harvesting of young trees results in an illustrated loss in heartwood yield potential. Maximized harvest values suggest delayed harvest until trees reach larger sizes, plausibly after 30-40 years. Furthermore, harvesting young trees soon after the development of heartwood, rather than allowing fuller development and seed production, also limits the genetic variation maintained in the population over time. If early development of heartwood is genetic, and if the trees forming heartwood early are

prematurely taken out of the gene pool, over many years, the population trends for heartwood development could change towards lower-heartwood-producing trees.

Establishment of seed and gene conservation stands and seedling production has begun in several locations in Fiji and Tonga with some success, though frequent mortality has occurred in some areas due to fungal infections, cyclone, and other causes.

Currently, production stands, particularly those in Tonga, utilize seeds and materials collected from various populations across island groups combined into one stand due to the lack of locally available propagation materials, forming an *ex situ* conservation site. While allelic richness is relatively low compared to other insular sandalwood species, allelic diversity is evident among remaining yasi populations suggesting that there may be potentially beneficial alleles in certain sets of populations that play important roles in local adaptations through resistance to environmental stresses such as disease and pests. Conservation of the genetic integrity of yasi would preferentially include minimizing germplasm transfer between islands to maintain local differentiation and maintaining larger extant population sizes to decrease genetic drift due to induced inbreeding.

Furthermore, many of the seed and gene conservation stands include individuals of the introduced *Santalum album*, which poses a significant and immediate threat to the genetic integrity of yasi through rapid hybridization. Given the rapid hybridization of yasi with *Santalum album*, as noted above, the introduction of *Santalum album* and *S. album* x *yasi* germplasm to islands where they have not yet been introduced should be prohibited in order to preserve the genetic integrity of remaining pure yasi stands.

The introduction of *Santalum album* and the subsequent hybridization creates a further risk for sandal spike disease, a deadly phytoplasma which has severely damaged natural *S. album* populations in India. While preliminary results of oil composition studies indicate that the heartwood oil of *S. album* x *yasi* hybrids may be comparable to market standards and limited sampling suggests heartwood formation may occur earlier in hybrids (Doran, 2005), it is recommended that the susceptibility of *yasi* and hybrids to sandalwood spike disease be determined before widespread introduction of *S. album* occurs in areas because hybrids could act as a bridge of susceptibility into *yasi* (Brigham & Schwartz, 2003).

Overall genetic structure between *yasi* populations is absent when all studied loci are considered together. This suggests significant gene flow between populations either as ancient or numerous recent migratory events from diverse localities in Fiji and Tonga, all assumedly human and/or bird/bat mediated. The apparent high level of gene flow between populations has masked evolutionary patterns suggesting the origination of *yasi* to Fiji or Tonga. Rather, findings support the ethnobotanical role *yasi* has held within and between these countries and may provide molecular evidence for extensive interaction between Fiji and Tonga before European contact. The cultural importance of the plant as well as the interisland and international patterns of trade in *yasi*, even in prehistoric times, may be reflected by the noted widespread genetic variation. Further, the distinctive ecological distribution of *yasi* on inhabited islands and near inhabited areas may also be indicative of the importance human-induced events and circumstances have played in *yasi* dispersal and continuation. These positive effects of human influence on

yasi distribution and establishment is in pleasant contrast to the frequently noted ill effects of human exploitation. Furthermore, the positive role of human influence is insightful in considering the human role in the future of sustainable management of yasi.

Currently, there are few mature sandalwood trees in Fiji and Tonga and the trade of yasi is minimal, but over the last decade there have been sporadic export surges associated with increases in heartwood supply (Thomson et al., 2000). These market surges and historic patterns suggest that the demand for yasi is limited only by supply, and thus the potential for continual economic gain is similarly fundamentally dependant on continual, sustainable management of populations and harvesting levels. Past and present efforts to manage yasi resources have been undermined by various factors, as discussed, but fundamentally by the need for financial resources for rural villages neighboring wild yasi habitat and the associated practices of frequent, extensive and premature harvesting of wild growing populations. The resources for harvesting regulation enforcement and *in situ* nursery establishment are currently insufficient.

While the potential economic benefits of preserving the species are great, the intrinsic value and cultural heritage of yasi and associated natural forest habitat also demand the attention and immediate action necessary for the preservation of this species. With the maintenance and care of wild yasi populations and habitat, many other forest plants and products are also preserved for continued traditional use. A suggested management strategy for wild populations lies in the creation of a community-mediated sandalwood conservancy trust operated by local villages and existing customary village leadership and organizations. Such a conservancy would mutually benefit the wild

growing yasi populations and provide the funds for community development in a more ecologically advantageous and culturally acceptable approach.

4.9 Future Research

Further research can benefit decision making for the management of yasi. Investigating seed production by tree age could help calculate the loss in regenerative capacity due to early harvest. Further investigation into growth rates, possibly with dendrometers, and heartwood production by tree age for yasi could further elucidate yield estimates useful for harvest planning. Further microsatellite analyses on yasi, including more individual samples (i.e. ~ 200-400 samples) and/or more populations, may improve understanding of the extent and nature of genetic variation and evolutionary origin. Also, to gain more insights into the diversity of yasi, morphological studies could be carried out to determine areas of high morphological variation, especially in 'Eua, Tonga, before *S. album* and hybrids become more prevalent, masking original morphological variation of the natural yasi.

A controlled experiment to test the effect of sandal spike disease on *S. album*, *S. yasi*, and the hybrid *S. album* x *yasi* would be valuable in identifying differences in susceptibility to the disease. The results of this study would help inform wise decisions as to the expansion of hybrid plantations, particularly if hybrids are shown to be more susceptible to the disease than yasi. This study should not be performed in the Pacific, but in a location where the Sandalwood Spike Disease already occurs, to avoid introducing the phytoplasm into the area.

Based on the current sparse populations of yasi in Fiji and Tonga, further enumerations and resource surveys are not practical to conduct at this time. Rather, forestry and governmental efforts may be best spent focused on promotion of local involvement in assisted regeneration, caretaking of wild stands, education regarding value lost with early harvest, and other similar endeavors.

APPENDIX 1. DNA Samples and Voucher Specimens

Taxon	Country	Location	Subpopulation Coordinates	Voucher
<i>Santalum yasi</i>	Tonga	'Utulei, Vava'u	18°39'89"S 173°59'62"W	RH111, NY
<i>Santalum yasi</i>	Tonga	'Utulei, Vava'u		RH112, NY
<i>Santalum yasi</i>	Tonga	'Utulei, Vava'u		RH113, NY
<i>Santalum yasi</i>	Tonga	'Utulei, Vava'u		RH114, NY
<i>Santalum yasi</i>	Tonga	Hunga, Vava'u Group	18°41'14"S 174°07'13"W	RH115, NY
<i>Santalum yasi</i>	Tonga	Hunga, Vava'u Group		RH116, NY
<i>Santalum yasi</i>	Tonga	Hunga, Vava'u Group		RH117, NY
<i>Santalum yasi</i>	Tonga	Hunga, Vava'u Group		RH118, NY
<i>Santalum yasi</i>	Tonga	Hunga, Vava'u Group		RH119, NY
<i>Santalum yasi</i>	Tonga	Hunga, Vava'u Group		RH120, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua	21°21'37"S 174°58'06"W	RH121, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua		RH142, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua		RH122, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua		RH123, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua		RH124, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua		RH125, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua		RH126, NY
<i>Santalum yasi</i>	Tonga	Tufuvai, 'Eua		RH127, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua	21°18'12"S 174°55'19"W	RH128, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua		RH129, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua		RH130, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua		RH131, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua		RH132, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua		RH133, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua		RH134, NY
<i>Santalum yasi</i>	Tonga	Houma, Eua		RH135, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai	19°46'14"S 174°20'21"W	RH144, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH145, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH146, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH147, NY

<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH148, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH149, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH150, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH151, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH152, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH153, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH154, NY
<i>Santalum yasi</i>	Tonga	Lifuka, Ha'apai		RH155, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai	19°45'11"S 174°19'09"W	RH156, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai		RH157, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai		RH158, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai		RH159, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai		RH160, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai		RH161, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai		RH162, NY
<i>Santalum yasi</i>	Tonga	Foa, Ha'apai		RH163, NY
<i>Santalum yasi</i>	Fiji	"Bua" Nawailevu, Vanua Levu	16°44'52"S 178°34'24"E	RH175, NY
<i>Santalum yasi</i>	Fiji	"Bua" Nawailevu, Vanua Levu		RH176, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH178, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH179, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH180, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH181, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH182, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH183, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH184, NY
<i>Santalum yasi</i>	Fiji	"Bua" Lekutu, Vanua Levu		RH177, NY
<i>Santalum yasi</i>	Fiji	Nausori Highlands, Viti Levu	17°49'33"S 177°37'05"E	RH185, NY
<i>Santalum yasi</i>	Fiji	Nausori Highlands, Viti Levu		RH186, NY
<i>Santalum yasi</i>	Fiji	Nausori Highlands, Viti Levu		RH187, NY
<i>Santalum yasi</i>	Fiji	Nausori Highlands, Viti Levu		RH188, NY
<i>Santalum yasi</i>	Fiji	Nausori Highlands, Viti Levu		RH189, NY
<i>Santalum yasi</i>	Fiji	Nausori Highlands, Viti Levu		RH190, NY
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu	19°00'40"S 178°15'34"E	RH138, NY

<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		RH139, NY
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		RH140, NY
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		No voucher
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		No voucher
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		No voucher
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		No voucher
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		No voucher
<i>Santalum yasi</i>	Fiji	Muanisolo, Kadavu		No voucher
<i>Santalum album</i>	Fiji	Colo-i-suva, Viti Levu	18°03'45"S 178°27'14"E	RH166, NY
<i>S. album x yasi</i>	Fiji	Colo-i-suva, Viti Levu		RH167, NY
<i>S. album x yasi</i>	Fiji	Colo-i-suva, Viti Levu		RH168, NY
<i>Santalum yasi</i>	Fiji	Lakeba, Lau Group	18°12'00"S 178°47'00"W	RH169, NY
<i>Santalum yasi</i>	Fiji	Lakeba, Lau Group		RH170, NY
<i>Santalum yasi</i>	Fiji	Lakeba, Lau Group		RH171, NY
<i>Santalum yasi</i>	Fiji	Lakeba, Lau Group		RH172, NY
<i>Santalum album</i>	Fiji	Lakeba, Lau Group		RH173, NY
<i>Santalum album</i>	Fiji	Lakeba, Lau Group		RH174, NY

APPENDIX 2. Sample of a Maximized Harvesting Schedule***Introduction***

The financial benefits of a carefully developed, incremental harvesting schedule have been alluded to in Figures 2.12 and 2.13, which show harvest yield lost if harvest occurs early versus the potential heartwood yield of a larger, older tree. This harvesting principle is fundamental to a sandalwood conservancy trust operated and maintained by local villages neighboring wild yasi populations. The long-term implications of carefully selecting tree sizes to be harvested can be seen through a progressive simulation of the growth and yield of a hypothetical stand of *Santalum yasi* (Schedules 1-3 below). This simulation is based on a hypothetical wild stand of *S. yasi* trees containing initially 100 size-class 7 (S7) individuals (15-19.9cm dbh) as the largest trees in the population. This starting figure is considered reasonable in view of actual numbers and sizes of trees remaining in the wild coastal and highland populations, covering an area of 40 hectares, surveyed on 'Eua in 2006. However, these wild populations on 'Eua have since undergone harvesting, therefore this hypothetical simulation can not readily be applied to the actual or potential yield capacity of the 'Eua populations, though general yield trends and principles identified through the simulation will be informative and applicable to any yasi stand.

Methods

The three harvesting schedules simulated follow a six-year harvesting cycle according to the six years required to advance between each size class from S7-S9 with 7

years required for advancement between each class from S9-S11 (see Table 2.2). Thus with each cycle, with a presumed negligible level of mortality at these size classes due to forces other than harvesting, it is assumed that 100% of individual trees will advance one size class from S7 to S8 and S8 to S9 while 85% of individual trees will advance one size class from S9 to S10 and S10 to S11. Initially, each six years 100 new S7 trees enter the simulation population. A regeneration increase is gradually added to the simulation (from 100 new S7 trees per cycle to 200 trees per cycle over a 4 cycle (24 year) period) as mature trees are left in the population for greater periods of time and thereby contribute a greater number of seeds, leading to higher regeneration rates. While *S. yasi* could have a potentially high regeneration rate almost to the point of invasiveness (Thomson, 2006), for the purpose of this simulation, and due to unknown levels of competition with other forest species, a cap at regenerative capacity is hypothetically placed at 200 incoming S7 trees per 6 year harvesting cycle. These recruitment rates assume a 0% mortality level between all size classes, which is considered reasonable due to the assumed lack of competition, diseases, or other factors causing death at these size classes, beyond hurricanes and harvesting.

The harvesting simulation illustrates three possible harvesting schedules, explicating lengths of initial harvesting bans, and sizes and percentages of trees that can be felled during harvest years. The detailed sustainable harvesting schedule with harvesting percentages and values is fully described in Schedules 1-3 below, while key aspects are summarized here. Figure A1 presents the three harvesting schedules graphically.

Schedule 1

Schedule 1 begins with a six-year harvesting ban. Upon the sixth year, one third of the S8 individuals (20-24.9 cm dbh) are harvested to begin the flow of money into the management system. All S7 trees and two-thirds of the S8 trees remain for future growth, and to continue producing seeds. After 12 years, another one-third of the S8 trees are harvested and half of the S9 trees (25-29.9 cm dbh), to further boost the monetary yield while maintaining a growing cohort of larger size-class trees. By 18 years, harvesting of S8 trees is terminated in favor of higher future yields and only 50% of S9 and 100% of S10 trees (30-34.9 cm dbh) are harvested and this rate continues until year 54. From 54 to 66 years, fewer and fewer S9 trees are harvested at each cycle until year 72, when the stabilized harvesting rate becomes 35% of S9 and 100% of S10 trees at each cycle. With a maximal harvest size of S10 (30-34.9 cm dbh), Schedule 1 returns over 42% of the estimated potential heartwood yield (see Figure 2.12 and 2.13 and Figure A1) (see Schedule 1 table below).

Schedule 2

Schedule 2 also begins with a six-year harvesting ban and follows a similar pattern, in the beginning, as schedule 1. Upon the sixth year, one third of the S8 individuals are harvested to begin the flow of money into the management system. All S7 trees and two-thirds of the S8 trees remain for future growth, and to continue producing seeds. After 12 years, another one-third of the S8 trees are harvested and half of the S9 trees, to further boost the monetary yield while maintaining a growing cohort of

larger size-class trees. By 18 years, harvesting of S8 trees is terminated in favor of higher future yields and only 50% of S9 trees and 100% of S10 trees are harvested. At year 24, schedule 2 changes from schedule 1 whereupon the harvesting rates change to 50% of S9, 80% of S10, and 100% of S11 trees (35-39.9 cm dbh). Between years 24 and 96, the harvesting rates gradually change in preference of the larger size classes, ending with a stabilized rate of 35% of S10 and 100% of S11 trees. By 96 years, a constant harvesting level has been reached for schedule 2, with a harvest return accounting for over 65% of the estimated potential heartwood yield (see Figures 2.12 and 2.13) (see Schedule 2 table below). The main difference between schedule 1 and 2 is the maximal harvest size, S10 in Schedule 1 and S11 in Schedule 2, which increases the heartwood yield after 80 years (see Figure A1).

Schedule 3

Schedule 3 begins with an 18 year harvesting ban. This allows the cohort of 100 initial S7 trees to grow to size S10 before harvesting begins. Beginning in year 18, 60% of the S10 trees are harvested. In year 24, 50% of S10 and 100% of S11 trees are harvested. Between years 24 and 42, the harvesting rates gradually change in preference for the larger size classes, ending with a stabilized rate of 35% of S10 and 100% of S11. By year 66, a constant harvesting level has been reached for schedule 3, with a harvest return accounting for over 65% of the estimated potential heartwood yield see Figures 2.12 and 2.13) (see Schedule 3 table below). The main difference between schedule 2

and 3 is an addition of 12 years to the initial harvesting ban, which in turn causes the maximal heartwood yield to be reached 30 years earlier (see Figure A1).

Santalum yasi trees can actually reach a maximal diameter at breast height of up to 50cm dbh. When the tree attains to this size, though growth in height and girth may slow, the heartwood percentage may actually increase (Thomson, 2006 & Usumaki 1981)).

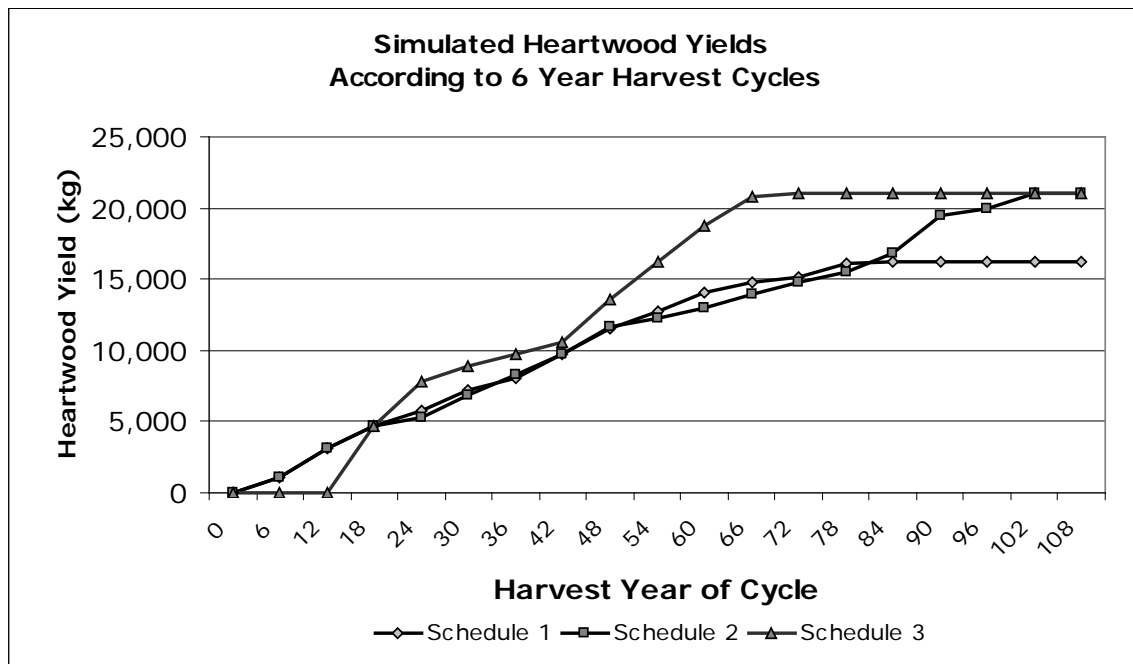


Figure A1. Simulated Heartwood Yields According to Six-Year Harvest Cycles

Discussion

By 24 yrs, a regeneration increase is evident in all schedules, due to the extended time mature trees are fruiting in the population before harvesting, and can be seen in the increased numbers of incoming S7 size class trees from 100 new individuals per cycle to 125 individuals. By 42 years the regeneration boost has stabilized at an influx of 200

new S7 trees per cycle. By 60 to 66 years the full strength of regeneration boost is felt at the highest size classes (S10 or S11) in all schedules.

In contrast to early and near complete harvesting practices, as noted in Bua, Fiji, and elsewhere where regeneration is slow, the heartwood yield per harvest cycle of each harvesting schedule, shown in Figure 11, is seen to increase steadily even with regular harvesting. The maximal harvest yield difference is significant between schedule 1, which holds a maximal harvest size at S10, and schedules 2 and 3, which gradually increase harvest size limits towards S11 (35 or > cm dbh) or larger trees. Even greater heartwood yields per cycles could potentially occur if maximal harvest sizes were extended to S12 (40 to <45cm dbh) or S13 (45cm dbh +). Yasi trees are noted to reach a maximal diameter at breast height of up to 50cm dbh (Usumaki, 1981). When a tree attains to this size growth in height and girth may slow while the heartwood percentage may actually increase (Thomson, 2006 & Usumaki 1981)). Because growth and yield rates are less understood at these levels, the harvest simulations did not extend to include trees of these sizes.

Conclusions

While a longer initial ban creates greater initial harvest yields, as seen in Schedule 3, the ability to begin selective, incremental harvesting even after a short harvesting ban and still maintain and increase population size and future yields with each harvest cycle is significant. The specifics of harvesting levels and times are highly adaptable to the local needs and desires. As long as populations are cared for and maintained such that

harvesting preferences gradually select for a portion of only the largest trees and a large portion of mature trees remain to produce seeds for regeneration, then the positive effects of the selective harvesting schedule, namely increasing and steady heartwood yield, will also continue. The mutual advantage of both strengthening yasi populations and increasing financial profits is one of the most attractive features of the sandalwood conservancy trust and a core component leading to its potential success. The increasing financial returns to the participating villages will help fuel the needed continual management of sandalwood populations essential for continued success of this plan.

Schedule 1					
YEAR 0	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	0
S8	0	33%	0	0	0
S9	0	50%	0	0	0
S10	0	100%	0	0	0
					Total: 0

YEAR 6	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	33%	33	67	1,122
S9	0	50%	0	0	0
S10	0	100%	0	0	0
					Total: 1,122 TOP\$54,978

YEAR 12	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	33%	33	67	1,122
S9	67	50%	34	34	1,943
S10	0	100%	0	0	0
					Total: 3,065 TOP\$150,185

YEAR 18	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	0%	0	100	0
S9	72	50%	36	36	2,079
S10	29	100%	29	0	2,593
					Total: 4,672 TOP\$228,928

YEAR 24	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	125	0%	0	125	
S8	100	0%	0	100	0
S9	105	50%	53	53	3,046

S10	31	100%	31	0	2,774
					Total: 5,820
					TOP\$285,180
YEAR 30	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	150	0%	0	150	
S8	125	0%	0	125	0
S9	107	50%	54	54	3,113
S10	45	100%	45	0	4,064
					7,177
					TOP\$351,673
YEAR 36	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	175	0%	0	175	
S8	150	0%	0	150	0
S9	133	50%	66	66	3,843
S10	46	100%	46	0	4,154
					Total: 7,997
					TOP\$391,853
YEAR 42	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	175	0%	0	175	0
S9	159	50%	80	80	4,619
S10	57	100%	57	0	5,128
					Total: 9,747
					TOP\$477,603
YEAR 48	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	186	50%	93	93	5,398
S10	68	100%	68	0	6,164
					Total: 11,562
					TOP\$566,538
YEAR 54	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	

S8	200	0%	0	200	0
S9	213	45%	96	117	5,560
S10	80	100%	80	0	7,204
					Total: 12,764
					TOP\$625,436

YEAR 60	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	216	40%	87	130	5,021
S10	101	100%	101	0	9,069
					Total: 14,089
					TOP\$690,361

YEAR 66	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	218	37%	81	137	4,682
S10	112	100%	112	0	10,050
					Total: 14,732
					TOP\$721,868

YEAR 72	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	219	35%	77	143	4,451
S10	118	100%	118	0	10,639
					Total: 15,089
					TOP\$739,361

YEAR 78	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	220	35%	77	143	4,465
S10	123	100%	130	0	11,700
					Total: 16,165
					TOP\$792,085

YEAR 84	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
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S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	220	35%	77	143	4,466
S10	123	100%	130	0	11,700
					Total: 16,166
					TOP\$792,134

Schedule 2					
Year 0	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	0	33%	0	0	0
S9	0	50%	0	0	0
S10	0	100%	0	0	0
0					
Year 6	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	33%	33	67	1,122
S9	0	50%	0	0	0
S10	0	100%	0	0	0
					Total: 1,122 TOP\$54,978
Year 12	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	33%	33	67	1,122
S9	67	50%	34	34	1,943
S10	0	100%	0	0	0
					Total: 3,065 TOP\$150,158
Year 18	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	0%	0	100	0
S9	72	50%	36	36	2,079
S10	29	100%	29	0	2,593
					Total: 4,672 TOP\$228,928
Year 24	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	125	0%	0	125	
S8	100	0%	0	100	0
S9	105	50%	53	53	3,046

S10	31	80%	25	6	2,220
S11	0	100%	0	0	0
					Total: 5,265
					TOP\$257,985
Year 30	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	150	0%	0	150	
S8	125	0%	0	125	0
S9	107	50%	54	54	3,113
S10	45	75%	34	11	3,058
S11	5	100%	5	0	700
					Total: 6,871
					TOP\$336,679
Year 36	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	175	0%	0	175	
S8	150	0%	0	150	0
S9	133	50%	66	66	3,843
S10	46	75%	35	12	3,125
S11	10	100%	10	0	1,286
					Total: 8,254
					\$404,446
Year 42	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	175	0%	0	175	0
S9	159	50%	80	80	4,619
S10	57	75%	43	14	3,856
S11	10	100%	10	0	1,314
					Total: 9,789
					TOP\$479,661
Year 48	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	186	50%	93	93	5,398
S10	69	75%	51	17	4,632
S11	12	100%	12	0	1,621
					Total: 11,652
					\$570,948
Year 54	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	

S8	200	0%	0	200	0
S9	213	40%	85	128	4,942
S10	80	75%	60	20	5,412
S11	15	100%	15	0	1,948
					Total:12,302
					TOP\$570,948
Year 60	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	218	30%	65	153	3,791
S10	110	70%	77	33	6,934
S11	17	100%	17	0	2,276
					Total:13,001
					TOP\$637,049
Year 66	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	221	20%	44	177	2,568
S10	131	65%	85	46	7,682
S11	28	100%	28	0	3,748
					Total: 13,998
					TOP\$685,902
Year 72	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	225	10%	22	202	1,304
S10	152	60%	91	61	8,231
S11	40	100%	40	0	5,217
					Total: 14,752
					TOP\$722,848
Year 78	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	228	0%	0	228	0
S10	174	55%	96	78	8,619
S11	52	100%	52	0	6,922
					Total:15,541
					TOP\$761,509
Year 84	Total	% Harvested	Harvested	Remaining	Heartwood

	Individuals		Individuals	Individuals	Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	232	0%	0	232	0
S10	196	45%	88	108	7,958
S11	67	100%	67	0	8,895
					Total:16,853
					\$825,797
Year 90	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	232	0%	0	232	0
S10	200	40%	80	120	7,187
S11	93	100%	93	0	12,269
					Total:19,455
					\$953,295
Year 96	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	233	0%	0	233	0
S10	200	35%	70	130	6,302
S11	103	100%	103	0	13,597
					Total:19,899
					\$975,051
Year 102	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	233	0%	0	233	0
S10	200	35%	70	130	6,304
S11	112	100%	112	0	14,763
					Total:21,067
					\$1,032,283
Year 108	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	233	0%	0	233	0
S10	200	35%	70	130	6,304
S11	112	100%	112	0	14,767
					Total:21,072

Year 114	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	233	0%	0	233	0
S10	200	35%	70	130	6,304
S11	112	100%	112	0	14,768
					Total:21,072
					\$1,032,528

Schedule 3

Year 0	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	0	0%	0	0	0
S9	0	0%	0	0	0
S10	0	100%	0	0	0

Year 6	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	0%	0	100	0
S9	0	0%	0	0	0
S10	0	100%	0	0	0

Year 12	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	0%	0	100	0
S9	100	0%	0	100	0
S10	0	100%	0	0	0

Year 18	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	100	0%	0	100	
S8	100	0%	0	100	0
S9	100	0%	0	100	0
S10	86	60%	52	34	4,644
					Total:4,644
					\$227,556

Year 24	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	125	0%	0	125	
S8	100	0%	0	100	0
S9	114	0%	0	114	0

S10	86	50%	43	43	3,870
S11	30	100%	30	0	3,905
					Total:7,775
					\$380,975

Year 30	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	150	0%	0	150	
S8	125	0%	0	125	0
S9	116	0%	0	116	0
S10	98	45%	44	54	3,976
S11	37	100%	37	0	4,881
					Total:8,858
					\$434,042

Year 36	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	175	0%	0	175	
S8	150	0%	0	150	0
S9	141	0%	0	141	0
S10	100	40%	40	60	3,595
S11	46	100%	46	0	6,130
					Total:9,725
					\$476,525

Year 42	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	175	0%	0	175	0
S9	170	0%	0	170	0
S10	122	35%	43	79	3,830
S11	52	100%	52	0	6,802
					Total:10,632
					\$520,968

Year 48	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	199	0%	0	199	0
S10	146	35%	51	95	4,604
S11	68	100%	68	0	8,973
					Total:13,576

\$665,224

Year 54	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	228	0%	0	228	0
S10	171	35%	60	111	5,389
S11	82	100%	82	0	10,784
					Total: 16,173
					\$792,477

Year 60	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	232	0%	0	232	0
S10	196	35%	69	127	6,176
S11	96	100%	96	0	12,624
					Total: 18,800
					\$921,200

Year 66	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	232	0%	0	232	0
S10	200	35%	70	130	6,286
S11	110	100%	110	0	14,468
					Total: 20,754
					\$1,016,946

Year 72	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	233	0%	0	233	0
S10	200	35%	70	130	6,302
S11	112	100%	112	0	14,726
					Total: 21,028
					\$1,030,372

Year 78	Total Individuals	% Harvested	Harvested Individuals	Remaining Individuals	Heartwood Yield (kg)
S7	200	0%	0	200	
S8	200	0%	0	200	0
S9	233	0%	0	233	0
S10	200	35%	70	130	6,304
S11	112	100%	112	0	14,762
					Total:21,066
					\$1,032,234

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