

**THE CURIOUS CASE OF MAILE: LESSONS IN
ECOTYPES, POPULATION VIABILITY AND RESTORATION**

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ABSTRACT

The harvest of non-timber forest products (NTFPs) is a major economic and cultural activity in many tropical forests. The continued availability of NTFPs is not only essential for conservation of the plant species, but also for the livelihoods of millions of people worldwide and accessibility of resources for cultural practices. Incorporating culturally significant plants in restoration may increase success rates through partnership with local communities.

The Hawaiian Islands are model study sites to examine the following key concerns in restoration: ecotypic variation, critical factors in establishment and survival, and population dynamics and persistence. Maile is a culturally prominent native Hawaiian NTFP liana with declining populations, and ideal species for addressing restoration concerns for other species in Hawai'i and elsewhere.

This study demonstrated significant differences in maile growth, survival, and seed germination rates between populations and in variable light, in a common garden experiment. These results support evidence of ecotypic variation in maile. Degree of climatic congruence between source and restoration sites appeared to be an important predictor of performance. The effects were physiologically and economically significant, and may have both short and long term effects on restoration success.

Substrate treatments used in maile reestablishment experiments showed significantly higher survival in soil than in coarse woody debris. Moisture and nitrogen availability were lower in coarse woody debris than in soil, and may be correlated with the drier than average annual precipitation study year. Coarse

woody debris may offer long-term benefits, such as safe sites, that deserve consideration.

Wild maile populations were projected to either remain stable or decline, and appeared to be sensitive to precipitation changes. Restored maile populations were projected to not persist in the long term, with the open canopy population having the lowest population growth rate. However, elasticity and life table response experiments analyses pinpointed key strategies, e.g., increasing juvenile and adult survival, to achieving success in restoration. This study emphasized the importance of demographic comparisons between wild and restored populations.

The results from these studies can serve to increase sustainability of NTFPs through guided restoration methodologies that can extend to other Hawaiian species and beyond.

LIST OF TABLES

Table 1. The value of ecosystem services and natural capital.....	1
Table 1.1. Characteristics of three source areas of maile seed and restoration site.....	13
Table 1.2. Cost benefit analysis of ecotype variation in lowland restoration.....	21
Table 2.1. Differences in substrate characteristics between terrestrial and advanced decay coarse woody debris.....	32
Table 2.2. Optimum foliar nutrient ratios compared with those found for terrestrial soil and advanced decay coarse woody debris at a lowland maile restoration site on Kaua'i island.....	32
Table 3.1. Characteristics of wild and restored maile population study sites.....	42
Table 3.2. Restored site status of total annual precipitation when compared with total annual precipitation 50 year mean \pm 1SD.....	59
Table 3.3. Wild site status of total annual precipitation when compared with total annual precipitation 50 year mean \pm 1SD.....	59

LIST OF FIGURES

Figure 1.1. Maile leaves and monoliform fruit.....	11
Figure 1.2. Study sites on the island of Kaua'i, Hawai'i, USA.....	12
Figure 1.3. Ecotype and light effects on maile seed germination.....	16
Figure 1.4. Effects of ecotype on growth of maile seedlings after two years in a lowland restoration site.....	17
Figure 1.5. Effects of ecotype on survival of maile seedlings after two years in a lowland restoration site.....	18
Figure 1.6. Population variation in wild maile leaf size appears to be retained in the common garden F ₁ plants, and correlated with elevation.....	21
Figure 2.1. Study site on the island of Kaua'i, Hawai'i, USA.....	27
Figure 2.2. Survival of maile seedlings in terrestrial soil versus coarse woody debris, outplanted in a a lowland restoration site on Kaua'i island.....	30
Figure 2.3. Growth of maile seedlings in terrestrial soil versus coarse woody debris, outplanted in a a lowland restoration site on Kaua'i island.....	31
Figure 2.4. Principal Components Analysis biplot of substrate bioavailable nutrients.....	33
Figure 2.5. Correlation between substrate moisture and Principal Component 1 axis.....	35
Figure 3.1. Maile lei.....	40
Figure 3.2. Study sites on the island of Kaua'i, Hawai'i, USA.....	42
Figure 3.3. Maile life cycle graph.....	44
Figure 3.4a. Summary of matrices population growth rate and 95% CI for wild and all canopy restored.....	46

Figure 3.4b. Summary of matrices population growth rate and 95% CI for closed and open canopy restored.....	47
Figure 3.5a-d. Elasticity values for wild maile populations at two sites, and over two years.....	47
Figure 3.6a-d. Life Table Response Experiments (LTRE) for wild maile populations.....	50
Figure 3.7a-d. Life Table Response Experiments for wild versus restored maile populations.....	52
Figure 3.8. Transient dynamics of restored maile populations under different management practices.....	55

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	iv
ABSTRACT.....	v
LIST OF TABLES	vii
LIST OF FIGURES	viii
 I. INTRODUCTION	 1
1. Justification.....	1
2. Restoration concerns.....	2
2.1. <i>Key questions</i>	2
2.2. <i>Do ecotypes matter?</i>	2
2.3. <i>What factors are critical for establishment and survival?</i>	3
2.4. <i>Will restoration populations persist in the long term?</i>	3
3. Model study site and species.....	4
3.1. <i>Hawaiian Islands</i>	4
3.2. <i>Maile</i>	5
 II. CHAPTER 1. ECOTYPE IMPLICATIONS FOR RESTORATION: A CASE STUDY OF THE HAWAIIAN NATIVE PLANT, <i>ALYXIA STELLATA</i>	 8
1. Introduction.....	8
2. Methods.....	11
2.1. <i>Habitat and species</i>	11
2.2. <i>Study sites</i>	13
2.3. <i>Seed germination, growth and survival</i>	14
2.4. <i>Data Analysis</i>	15
3. Results	15
4. Discussion.....	18
4.1. <i>Adaptive significance of ecotypic effects</i>	18
4.2. <i>Implications for restoration and cultural resource use</i>	19
ACKNOWLEDGEMENTS.....	23
 III. CHAPTER 2. NATIVE HAWAIIAN PLANT <i>ALYXIA STELLATA</i> SURVIVAL, MOISTURE AND NUTRIENT DIFFERENCES BETWEEN SOIL AND COARSE WOODY DEBRIS.....	 24
1. Introduction.....	24
2. Methods.....	26

2.1. <i>Habitat and species</i>	26
2.2. <i>Study sites</i>	27
2.3. <i>Maile growth and survivorship in soil and CWD</i>	27
2.4. <i>Comparison of substrate characteristics between soil and CWD</i>	28
2.5. <i>Data analysis</i>	29
3. Results.....	30
4. Discussion	33
5. Implications for restoration.....	36
ACKNOWLEDGEMENTS.....	38
IV. CHAPTER 3. POPULATION DYNAMICS OF WILD AND RESTORED ALYXIA STELLATA STANDS: IS RESTORATION VIABLE?	39
1. Introduction.....	39
2. Methods.....	41
2.1. <i>Habitat and species</i>	41
2.2. <i>Study sites</i>	41
2.3. <i>Reintroduction and monitoring</i>	43
2.4. <i>Wild population monitoring</i>	43
2.5. <i>Population projection matrices</i>	44
2.6. <i>Transient dynamics and assessing management for long-term viability</i>	45
3. Results	46
3.1. <i>Population growth rates and elasticity analysis</i>	46
3.2. <i>Life table response experiments</i>	49
3.3. <i>Restored populations transient dynamics</i>	49
4. Discussion.....	54
5. Recommendations for maile restoration and conservation.....	56
APPENDIX. ANNUAL PRECIPITATION STATUS.....	59
ACKNOWLEDGEMENTS.....	60
V. CONCLUSION.....	61
1. The importance of restoration with culturally prominent plants.....	61
2. Main lessons.....	61
REFERENCES.....	64

I. INTRODUCTION

1. Justification

We depend on the ecosystem for many essential services, including climate regulation, clean air and water, food production and material for cultural practices (Costanza et al. 1997, Daily et al. 1997, Millennium Ecosystem Assessment 2005). Valuation for natural capital services (Table 1) was estimated at US\$33 trillion per year (Costanza et al. 1997).

Table 1. The value of ecosystem services and natural capital

Ecosystem services	Annual value (trillion US\$)
Soil formation	17.1
Recreation	3.0
Nutrient recycling	2.3
Water regulation and supply	2.3
Climate regulation (temperature and precipitation)	1.8
Habitat	1.4
Flood and storm protection	1.1
Food and raw materials production	0.8
Genetic resources	0.8
Atmospheric gas balance	0.7
Pollination	0.4
Other services	1.6
Total value of ecosystem services	33.3

Source: Costanza et al. 1997, Maunder et al. 2002

A recent conservation paradigm promoting the commercial extraction of non-timber forest products (NTFPs) has been widely accepted (Ticktin 2004). This paradigm argues that economic incentives must be available to local communities to deter destructive land uses (Ticktin 2004). NTFPs represent an important source of income to millions of people worldwide and many species, while not globally threatened or endangered, have dwindling populations or have gone locally extinct (Ticktin 2004). Continued availability of NTFPs is not only essential for conservation of the plant species, but also for the livelihoods of many rural peoples and accessibility of resources for cultural practices. Using NTFP with cultural importance can serve a special role within this conservation paradigm. Recognizing and incorporating culturally prominent plants in restoration efforts may increase success rates through partnership with local communities (Garibaldi and Turner 2004). These actions may extend to ecosystem stewardship and conservation and can lead to enhancement of both social and ecological integrity (Garibaldi and Turner 2004).

2. Restoration concerns

2.1. Key questions

As human impacts on ecosystems increase, the restoration of plant populations becomes increasingly important (Colas et al. 2008). Restoration is commonly used to reestablish extinct populations or increase threatened populations (McKay et al. 2005). It can also play an integral role in the management of culturally or economically important wild plant resources such as NTFPs (Garibaldi and Turner 2004). There are several key questions in restoration that need to be addressed, ranging from small to large scale:

- (1) Do ecotypes matter?
- (2) What factors are critical for establishment and survival?
- (3) Will restoration populations persist in the long term?

2.2. Do ecotypes matter?

Ecotypic variation has typically been ignored (Rice and Emery 2003) but has recently been recognized as important in restoration (Hufford and Mazer 2003, Kauth et al. 2008). Ecotypes exhibit plant population differences in physiology, behavior, or structure adapted to particular environmental conditions. Ecotypic variation among populations of plant species has long been recognized (e.g., Clausen et al. 1940) and may allow species persistence across diverse habitats and environmental conditions (van Tienderen and van der Toorn 1991, Etterson 2004).

The few restoration studies that have examined ecotypic variation have illustrated that there can be important differences in seed germination and growth among ecotypes (Theunissen 1997, Hufford and Mazer 2003, Sanders and McGraw 2005, Herrera-C. et al. 2008, Kauth et al. 2008, Smith et al. 2009, Miller et al. 2011). Some studies have compared ecotype growth using reciprocal transplants, introducing plants from each environments into the other (Sanders and McGraw 2005) while others have examined growth differences in a single common environment that is most available for restoration purposes (Theunissen 1997).

Depending of the scale of local adaptation of a species, using local seed is advantageous in preserving genetic integrity and maximizing performance. Outplanting poorly adapted ecotypes can decrease plant fitness, threaten the success of restoration projects (Lesica and Allendorf 1999, Krauss and He 2006), and negatively affect adjacent locally adapted populations through gene flow (McKay et al. 2005). Recently, research has demonstrated the detrimental effects of restoration with maladapted ecotypes (Keller et al. 2000, Edmands and

Timmerman 2003, Hufford and Mazer 2003), emphasizing the need for further information on the scale of local adaptation (McKay et al. 2005).

2.3. What factors are critical for establishment and survival?

In many ecosystems, coarse woody debris (CWD) is important as seedbed and habitat providers (Thompson 1980, Harmon et al. 1986, Santiago 2000). The ecological value of CWD has been acknowledged (Harmon et al. 1986, Motta et al. 2006) and studied in many processes, including forest ecosystem function (Janisch and Harmon 2002, Spears et al. 2003, Laiho and Prescott 2004, Motta et al. 2006). Many studies have examined the relationship of CWD to biodiversity (Spies et al. 1988, Angelstam et al. 2003, Heilmann-Clausen and Christensen 2004, Motta et al. 2006). Research has also focused on long-term influence of CWD on nutrient cycles and species composition (Cohen et al. 1996, Harmon et al. 1996, Santiago 2000, Harmon et al. 2004, Motta et al. 2006).

The rate of CWD decomposition exerts considerable influence on the regeneration process of some plant species as not all the decay classes provide the same preferred habitat (Motta et al. 2006). Decay class can be an important predictor of seedling and sapling abundance in some studies (Santiago 2000, Takahashi et al. 2000), and advanced stages of decay are often correlated with higher establishment and abundance of seedlings and saplings.

Plant productivity and survival are greatly influenced by water availability (Wang and Klinka 1997, Carlos Lola da Costa et al. 2010), and nutrient availability is an important factor in determining ecosystem plant species composition (Roem and Berendse 2000, Bobbink et al. 2003). CWD is hypothesized to be a preferred establishment site for seedlings due to avoidance of competition, improved drainage in wet forests, safe sites and protection from feral ungulates and disturbance. However, there is a lack of data about the characteristics of CWD as a rooting medium and no studies have tested if outplanted seedlings fare better on soil or CWD in restoration efforts.

2.4. Will restoration populations persist in the long term?

To be effective, restoration of plant populations must address a host of imminent management questions related to habitat suitability, planting methods, and plant ecological requirements (Colas et al. 2008), and take into consideration environmental, genetic and demographic stochasticity. Restoration strategies must consider not only short-term goals of establishment, growth and survival, but also reproduction and long-term persistence within natural habitats (Menges 1991, Menges 1998, Bell et al. 2003).

Matrix projection models integrate individual vital rates (growth, reproduction and survival) into measures of long-term population growth and are powerful tools for assessing population status and comparing the demographic effects of different management practices (Crone et al. 2011). Although matrix population models are often used to generate recommendations for resource management (Schmidt et al. 2011), few studies have used matrix modeling to assess the viability of, or identify best management practices for, restored plant populations (Crone et al. 2011). In addition, few studies have compared the demography of wild and restored populations, even though this can reveal factors key to restoration success (Bell et al. 2003, Davelos and Jarosz 2004, Endels et al. 2005, Maschinski and Duquesnel 2007, Colas et al. 2008). For example, Colas et al. (2008) used life table response experiments (LTREs) to illustrate that higher survival of *Centaurea corymbosa* (Asteraceae) compensated for lower fecundity in restoration populations, so that wild and restored population growth rates were similar. Endels et al. (2005) used elasticity analysis to identify survival of reproductive adults and seedling recruitment as the life-history transitions to which long-term growth rates of restored populations *Primula veris* (Primulaceae) are most sensitive, and based management recommendations for on these results.

There are few demographic studies of vines in general (Kathriarachchi et al. 2004, Nabe-Nielsen 2004, Siebert 2004, McGeoch et al. 2008), and none comparing the demography of restoration and wild populations of vines.

3. Model study site and species

3.1. Hawaiian Islands

It is important to address the aforementioned questions in the Hawaiian Islands because degradation and loss of native habitat threaten the viability of many plant populations. Hawai'i has more endangered species per area than any other region on the globe, with close to one third of plant species (289) currently listed as threatened or endangered (Hawai'i biological survey 1995–2003) and over 90% of the native vascular are endemic (Goldman et al. 2008). Restoration of native plant communities is critical to conserve species and maintain ecosystem services, including resources important for cultural practices.

With its extreme isolation and the most topographic variation on earth, the Hawaiian Archipelago contains highly diverse habitats (Loope and Mueller-Dombois 1989) and many plant species exhibit strong phenotypic variation among and within islands (Raven et al. 2005). Ecotypic variation may be of special importance in Hawai'i, allowing species to survive across high topographic diversity (Raven et al. 2005). Indeed, genetic variation and phenotypic plasticity were demonstrated in highly variable Hawaiian endemic

tree species, *Metrosideros polymorpha* Gaud. (Cordell et al. 1998).

Despite the interest in restoration in Hawai'i (Goldman et al. 2008, Ostertag et al. 2009, Funk and McDaniel 2010) and the potential for ecotype variation, there are no published studies exploring these effects on physiological performance such as seed germination and survival, applied to restoration conditions.

Decaying logs have long been observed as the most common germination and establishment sites for many native woody plant species in Hawaiian montane forests (Coorey 1974, Scowcroft 1992, Santiago 2000) and many native species may start as seedlings on logs prior to establishing in the mineral soil (Coorey 1974, Mueller-Dombois 2005). However, all studies to date in Hawaiian forests have been observational; variation in nutrient bioavailability between soil and CWD, and differences in any plant species seedling growth and survival have not been experimentally tested. Understanding the role of CWD is critical for forest restoration efforts in Hawai'i and elsewhere.

Although recent studies have demonstrated the important role of vines in forest regeneration and ecosystem-level processes (Schnitzer and Bongers 2002), vine ecology is still poorly understood. A native Hawaiian vine, maile, plays a key role in some native Hawaiian forests, as a species whose population dynamics has a strong effect on the other species in the community (Mueller-Dombois 2005). However, there are no demographic studies on either wild or restored maile populations, nor any demographic studies comparing restored and wild populations for any plant species in Hawai'i.

3.2. Maile

I chose maile as a case study because it is a culturally important wild harvested NTFP, because I could sustainably collect sufficient numbers of propagules for experimentation and survey intact wild populations. Maile can be used as a model for other species, to address and examine key concerns in restoration.

Maile (*Alyxia stellata*) (J.R. & G. Forst.) Roem. & Schult. (Apocynaceae) (Middleton 2002) is an indigenous liana (woody vine) and one of the most culturally significant plants in Hawai'i. This favored species is harvested for lei (wreaths), where the stems and leaves are removed from the plant to twist together. Lei are used by all sectors of society for cultural events such as weddings, graduations, hula, and inaugurations (Abbott 1992, Mabberley 1998). It was mentioned in many chants including the Hawaiian Chant of Creation (Kumulipo) (Beckwith 1951, Queen Lili'uokalani 1978 [1897]), in place names, and is sacred to Laka, goddess of hula (Pukui and Elbert 1986).

The fragrance which emits from the stripped inner bark is prized, along with various leaf morphologies, named after five goddesses from the Hawaiian Romance of Lāʻieikawai (Beckwith 1940). Hawaiian maile forms were distinguished as: maile haʻi wale (brittle maile), maile lau liʻi (small leaf maile), maile lau nui (large leaf maile), maile pakaha (blunt leaf maile), and maile kaluhea (sweetly scented maile) (Wagner et al. 1990). The enormous variation in leaf shape and size has long been recognized both in Hawaiian traditional knowledge (Beckwith 1940) and by botanists (Hillebrand 1888, St. John 1975, Wagner et al. 1990, Mabberley 1998, Middleton 2002) to vary widely across sites, suggesting ecotypic variation.

Maile has widespread distribution over the Pacific Islands, from Hawaiʻi to the Austral Islands, and Henderson Island to the Solomon Islands and the Caroline Islands (Middleton 2002). Human-assisted introduction, in part, was possibly involved in the widespread distribution, which may be indicated by the ceremonial use across many range places and synonymous names (maile or maire) (Middleton 2002). Hawaiian maile was originally classified as endemic *Alyxia oliviformis* but was recently lumped into *A. stellata* (Middleton 2002). *A. oliviformis* was thought as the most distinctive group within *A. stellata* and Middleton (2002) predicted that *A. oliviformis* will likely merit subspecific or varietal status after further investigation.

In Hawaiʻi, maile formerly grew across a range of habitats from 50–2000 m, from wet forest with closed canopy to dry open areas (Wagner et al. 1990). Maile commonly establishes on decaying logs in Hawaiʻi (personal observation, Mueller-Dombois 2005). Maile is currently found on all the main Hawaiian Islands except Kahoʻolawe and Niʻihau, and it is likely that the species grew on those islands as well, but has become extinct due to extensive habitat disturbance (Wagner et al. 1990).

Maile is still found in the wild, but it is becoming scarce. This may be due to habitat destruction, impacts of climate change, competition with invasive species, disturbance by feral ungulates, dispersal or pollination disruptions (Whitehead personal observation), seed predation by rats (Shiels and Drake 2011, Wong unpublished work), and unsustainable harvesting. As is the case for most native Hawaiian species, today the majority of remnant populations are found in upland forests (personal observation).

Many local community members on Kauaʻi island and Hawaiʻi island have stewardship of secret family patches. However, even though maile is one of the most popular lei plants, the majority of material used in Hawaiʻi has been imported from elsewhere (e.g., the Cook Islands, Tonga) due to our inability to meet our own demands. Maile shortage has induced some community members to take up arms, as reported in the Star-Bulletin (Tighe 1998): “marshals with guns guarded some areas of Kauaʻi from pickers when there was a drought-induced maile shortage caused by El Niño in 1998.” Understanding the ecology

of this species and how it pertains to harvest and restoration can serve to mitigate future potential community conflict, such as this.

There has been growing interest and investment in maile restoration by both conservation organizations and local communities. Restoring maile to its original range is an important conservation goal; however, most restoration projects take place in lowlands because these areas are often the most damaged habitats. Lowlands are also more accessible, an issue that is critical for a culturally important species.

To answer three key concerns in restoration, I designed the following studies:

- (1) Ecotype implications for restoration: a case study of the Hawaiian native plant, *Alyxia stellata*
- (2) Native Hawaiian plant *Alyxia stellata* survival, moisture and nutrient differences between soil and coarse woody debris
- (3) Population dynamics of wild and restored *Alyxia stellata* stands: is restoration viable?

We can use these results to gain better understanding of restoration practices for other species here in Hawai'i and elsewhere.

II. CHAPTER 1. ECOTYPE IMPLICATIONS FOR RESTORATION: A CASE STUDY OF THE HAWAIIAN NATIVE PLANT, *ALYXIA STELLATA*

1. Introduction

Restoration is commonly used to reestablish extinct populations or increase threatened populations (McKay et al. 2005). It can also play an integral role in the management of culturally or economically important wild plant resources such as non-timber forest products (NTFPs) (Garibaldi and Turner 2004). NTFPs represent an important source of income to millions of people worldwide. Many species, while not globally threatened or endangered, have dwindling populations or have gone locally extinct (Ticktin 2004).

One consideration that has typically been ignored (Rice and Emery 2003) but has recently been recognized as important in restoration (Hufford and Mazer 2003, Kauth et al. 2008) is ecotypic variation. Ecotypes exhibit plant population differences in physiology, behavior, or structure adapted to particular environmental conditions. These differences may be determined by genetic variation, phenotypic plasticity, or a combination of both (Jain and Martins 1979, Huenneke 1991).

Ecotypic variation among populations of plant species has long been recognized (e.g., Clausen et al. 1940) and may allow species persistence across diverse habitats and environmental conditions (van Tienderen and van der Toorn 1991, Etterson 2004). Some studies have compared ecotype growth using reciprocal transplants, introducing plants from each environments into the other (Sanders and McGraw 2005) while others examine growth differences in a single common environment that is most available for restoration purposes (Theunissen 1997).

The few restoration studies that have examined ecotypic variation have illustrated that there can be important differences in seed germination and growth among ecotypes (Theunissen 1997, Hufford and Mazer 2003, Sanders and McGraw 2005, Herrera-C. et al. 2008, Kauth et al. 2008, Smith et al. 2009, Miller et al. 2011). Seed dormancy and germination may vary among populations of a given species due to genetics, environment of the mother plant, or interactions between both (Baskin and Baskin 1998). Conditions required for germination can vary among populations of a species, possibly due to preconditioning (Baskin and Baskin 1998), whereby the environment of the immature and mature seed influences the germination process (Rowe 1964).

Depending of the scale of local adaptation of a species, using local seed is advantageous in preserving genetic integrity and maximizing performance. Some

research has recommended preserving a range of variability in the species especially in threatened and vulnerable plants, since diverse local genotypes exist and transplants often have low fitness (Huenneke 1991). Outplanting poorly adapted ecotypes can decrease plant fitness, threaten the success of restoration projects (Lesica and Allendorf 1999, Krauss and He 2006) and negatively affect adjacent locally adapted populations through gene flow (McKay et al. 2005). Recently, research has demonstrated the detrimental effects of restoration with maladapted ecotypes (Keller et al. 2000, Edmands and Timmerman 2003, Hufford and Mazer 2003), emphasizing the need for more information on the scale of local adaptation (McKay et al. 2005).

In the Hawaiian Islands, degradation and loss of native habitat threaten the viability of many plant populations. Hawai'i has more endangered species per area than any other region on the globe, with close to one third of plant species (289) currently listed as threatened or endangered (Hawai'i biological survey 1995–2003) and over 90% of the native vascular are endemic (Goldman et al. 2008). Restoration of native plant communities is critical to conserve species and maintain ecosystem services, including resources important for cultural practices.

With its extreme isolation and extensive topographic variation, the Hawaiian Archipelago contains highly diverse habitats (Loope and Mueller-Dombois 1989) and many plant species exhibit strong phenotypic variation among and within islands (Raven et al. 2005). Ecotypic variation may be of special importance in Hawai'i, allowing species to survive across high topographic diversity (Raven et al. 2005). Givnish et al. (2004) found that adaptive radiation in photosynthetic traits of six Hawaiian endemic genera of lobeliads (Campanulaceae) was strongly correlated with the diverse range of light conditions that each species occupied. Extremely variable Hawaiian tree species, *Metrosideros polymorpha* Gaud., has been found to exhibit phenotypic plasticity linked to leaf pubescence, and genetic variation in leaf size (Cordell et al. 1998). *M. polymorpha* leaf size appears to be highly correlated to elevation: leaf size decreased with increased maternal elevation, and these characteristics were retained in the common garden experiment (Cordell et al. 1998).

This research addresses the relevance of ecotypes for restoration, where functionally, population variation may affect the application of reestablishment. The common garden study is the classic method for determining if there is a genetic basis for observed differences among populations (Clausen et al. 1940, Hufford and Mazer 2003). Further distinction between divergence by drift or natural selection may be gained by reciprocal transplant experiments (Mazer and LeBuhn 1999, Hufford and Mazer 2003). The common garden can represent restoration, and support for ecotype relevance has been demonstrated by previous findings of source-site variability between populations (Theunissen 1997, Hufford and Mazer 2003, Miller et al. 2011).

Common garden experiments in Hawai'i have shown ecotype variations in plant water-use efficiency (*Acacia koa* Gray), N-fixation capacity (*A. koa*), and growth rates (*M. polymorpha*) are heritable (Pearson 1998, Ares et al. 2000, Treseder and Vitousek 2001a); whereas, other characteristics, such as specific leaf area and nutrient concentration appear to be influenced primarily by site conditions (Ares et al. 2000). Despite the interest in restoration in Hawai'i (Goldman et al. 2008, Ostertag et al. 2009, Funk and McDaniel 2010) and the potential for ecotype variation, there are no published studies exploring these effects on physiological performance such as seed germination and survival, applied to restoration conditions.

Maile (*Alyxia stellata*) (J.R. & G. Forst.) Roem. & Schult. (Apocynaceae) (Middleton 2002) is an indigenous liana and one of the most culturally important plants in Hawai'i. This species is prized for its fragrant leaves of various shapes and sizes, and whole stems with leaves are harvested for lei (wreaths). Lei are used by all sectors of society for cultural events such as weddings, graduations, hula, and inaugurations (Abbott 1992, Mabberley 1998). Maile is still found in the wild, but it is becoming scarce. This may be due to habitat destruction, impacts of climate change, competition with invasive species, disturbance by feral ungulates, dispersal or pollination disruptions (Whitehead personal observation), seed predation by rats (Shiels and Drake 2011, Wong unpublished work), and unsustainable harvesting. As a result, there has been growing interest and investment in maile restoration by both conservation organizations and local communities. Moreover, although recent studies have demonstrated the important role of vines in forest regeneration and ecosystem-level processes (Schnitzer and Bongers 2002), vine ecology is still poorly understood.

In Hawai'i, maile formerly grew across a range of habitats from 50–2000 m, from wet forest with closed canopy to dry open areas (Wagner et al. 1990). However, as is the case for most native Hawaiian species, today the majority of remnant populations are found in upland forests (personal observation). Restoring maile to its original range is an important goal for conservation; however, most restoration projects take place in lowlands because these areas are often the most damaged habitats. Lowlands are also more accessible, an issue that is critical for a culturally important species. If local lowland populations do not exist to provide progeny for restoration, which source populations best provide for restoration at low elevations? To address this, I focused my research on ecotypic physiological performance differences in lowland restoration sites.

Maile leaf size and shape has long been recognized both in Hawaiian traditional knowledge (Beckwith 1940) and by botanists (Hillebrand 1888, St. John 1975, Wagner et al. 1990, Mabberley 1998, Middleton 2002) to vary widely across sites, suggesting ecotypic variation. Maile appears to mirror the decreased leaf size with increased elevation pattern of *M. polymorpha* (personal observation),

but what does this mean for physiology? If variants of maile are better adapted to local conditions, this might affect success in restoring maile. Despite this and the growing number of restoration projects, there has been no research on ecotypic variation in maile and its consequences for restoration. I use Hawai'i and maile from different environments to test broader theories of ecotypes in determining whether physiological differences exist in maile, and if performance differences are related to degree of climatic congruence. My objectives were to determine if:

- (1) Maile seeds from three different forests have variable rates of germination, growth and survival in a lowland restoration site; and
- (2) Light level differentially affects seed germination rates of maile ecotypes.

I hypothesize that based on climatic similarities, ecotypes with the closest parameters will germinate, grow and survive at a higher rate. I discuss the implications of my results for success of maile restoration.

2. Methods

2.1. *Habitat and species*

Maile plants are twining lianas, and climbing or erect shrubs with milky sap. Leaves are lanceolate or ovate to elliptic, linear-lanceolate, or suborbicular in shape and arranged in whorls of three or opposite. Leaves are 0.7–9 cm long, 0.5–4.3 cm wide, smooth and hairless with entire margins (Wagner et al. 1990). Green to yellow-white corolla (4–5 mm long) flowers occur 2–5 in umbellate axillary cymes (Wagner et al. 1990). Floral syndromes along with field observations suggest the flowers may be pollinated, or at minimum visited by moths (Wong unpublished work). Maile produces ovoid drupes that resemble olives by shape with deep purple color when ripe. Often the fruits form end to end (monoliform), resembling a string of beads which consists of 2–4 one-seeded joints (Wagner et al. 1990) (Fig. 1.1).



Figure 1.1. Maile leaves and monoliform fruit

Maile has a widespread distribution across the Pacific Islands (Middleton 2002). Maile is currently found on all the main Hawaiian Islands except Kaho'olawe and Ni'ihau, and it is likely that the species grew on those islands as well, but has become extinct due to extensive habitat disturbance (Wagner et al. 1990).

Hawaiian maile was originally classified as endemic *Alyxia oliviformis* but was recently lumped into *A. stellata* (Middleton 2002). *A. oliviformis* was thought as the most distinctive group within *A. stellata* and Middleton (2002) predicted that *A. oliviformis* will likely merit subspecific or varietal status after further investigation. The distinguishing and consistent Hawaiian maile characters are found only rarely in *A. stellata*.

Up to five varieties are recognized by Hawaiian cultural experts, based on differing leaf morphologies and associated with maile forest goddess sisters (Beckwith 1940). Maile is connected to Laka, the Hawaiian goddess of hula, and is one of the five standard plants used in her altar (Pukui and Elbert 1986).

The enormous variation in the vegetative characters in previously designated *A. oliviformis* has been noted by many botanists (Hillebrand 1888, Wagner et al. 1990, Mabberley 1998), but most extensively by St. John (1975) in his designation of 10 infraspecific taxa (Middleton 2002).

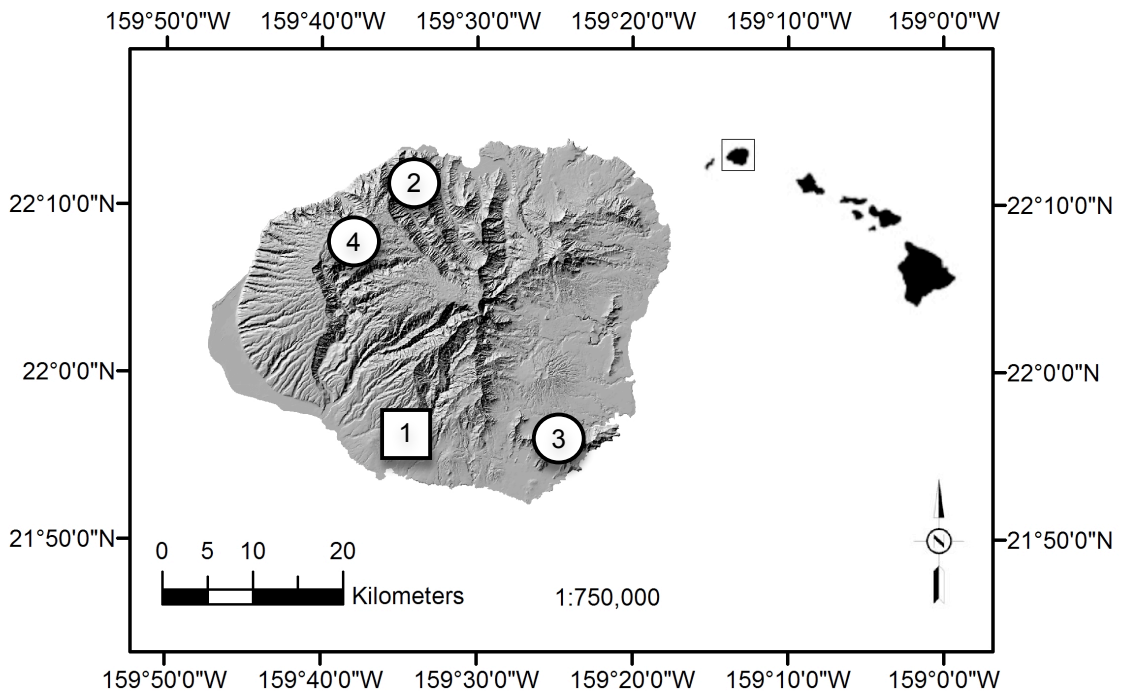


Figure 1.2. Study sites on the island of Kaua'i, Hawai'i, USA. (1) Lawa'i Valley NTBG, (2) Lower Limahuli Preserve NTBG, (3) Mt. Ha'upu, (4) Koke'e State Park.

2.2. Study sites

I conducted all germination, growth and survival experiments at the National Tropical Botanical Garden (NTBG) Lawa'i Valley Conservation and Horticulture Center on the island of Kaua'i, Hawai'i. I collected maile seeds from three forest sites that differed in elevation, precipitation and forest type (Table 1.1): the NTBG Lower Limahuli Preserve, Mt. Ha'upu, and Koke'e State Park (Fig. 1.2).

National Oceanic and Atmospheric Administration (NOAA) weather stations proximate to each site (51-9955, 51-8155, 53-0203, 51-3099) provided temperature and precipitation data.

Table 1.1. Characteristics of three source areas of maile seed and restoration site

Site	NTBG Lower Limahuli Preserve	Mt. Ha'upu	Koke'e State Park	NTBG Lawa'i Valley
Kaua'i orientation	North	Southeast	Northwest	South
Latitude / longitude	22°12'12"N, 159°36'32"W	21°55'41"N, 159°24' 15"W	22°7'49"N, 159°39'31"W	21°53'39"N, 159°39'38"W
Elevation	60–300 m	350–375 m	980–1100 m	25 m
Mean annual precipitation	305.1 cm	208.13 cm	168.3 cm	365 cm*
Mean annual temperature	22.13°C	22.57°C	15.16°C	24.37°C
Forest type	Remnant and restored native lowland to upland mesic and wet forest. Much of lower preserve is currently dominated by <i>Schefflera actinophylla</i>	Upland mesic forest with native and invasive canopy trees	Montane mesic forest dominated by native canopy trees <i>Metrosideros polymorpha</i> and <i>Acacia koa</i>	—
Degree of environmental similarity to restoration site	High	Medium	Low	—

*Approximate irrigation

2.3. Seed germination, growth and survival

In August 2008, I collected fruit from a minimum of 15 plants over a range of the populations at each of the three sites (Limahuli, Koke'e and Mt. Ha'upu) in order to reduce individual maternal effects as studies have shown that maternal effects may provide phenotypic adaptation to local environmental conditions (Galloway 2005). I soaked and depulped the fruits and excluded floating seeds due to potential inviability (personal observation). Dormancy-breaking treatments were not undertaken, as maile was classified as nondormant in some seeds but others exhibited physiological dormancy (Baskin et al. 2003).

To test the effects of ecotype and light on seed germination, for each of the three potential ecotypes I planted three replicates of 45 seeds in each of the two light treatments ($n = 810$ seeds). Seeds were planted at the NTBG Lawa'i Valley Conservation and Horticulture Center and watered once a day.

The two light treatments were 30% and 50% of incident solar radiation, using black woven shade cloth to reduce light intensity. These levels represent two ends of the range where maile is most commonly found in the wild: 30% represents deep shade and 50% represents the upper end of common light conditions in the understory. This range also represents typical light conditions for restoration of understory plants in general. I confirmed the reduction of photosynthetically active radiation (PAR) in the treatments measured as photosynthetic photon flux density (PPFD) by Licor LI-191 Line Quantum Sensors.

I placed the seeds on sterile cinder media in trays and covered with predator-proof wire. I rotated the trays each month to account for random variability between plots. I monitored seedling emergence and mortality over eight months. Germination was characterized as root breaking through the seed coat, visible to the naked eye. Although I did not further test viability of remaining ungerminated seeds, e.g., using 2,3,5-triphenyl tetrazolium chloride staining as outlined by Peters (2000), I estimated that an eight-month study period was sufficient to assess nondormant germination rates of this species based on preliminary propagation studies. In my experiment, all ecotypes stopped germinating prior to eight months.

To test the effects of potential ecotype on seedling growth, in August 2008, samples of 200 seeds each were collected from Limahuli, Koke'e, and Mt. Ha'upu populations. The 600 seeds were sown on sterile cinder media, maintained by NTBG Lawa'i Valley Conservation and Horticulture Center and watered once a day. We transplanted seedlings into 21 cm deep dibble tubes in sterile cinder media at the appearance of true leaves and grew them in 50% available light. In August 2010, I randomly selected 50 juveniles from each ecotype ($n = 150$) and measured stem diameter by digital calipers with a resolution of 0.1 mm and accuracy of ± 0.3 mm. The diameter of the plant was

measured at the first point above the roots where the stem was standard (Nabe-Nielsen 2004). The largest point along the stem, lacking stem abnormalities such as knots, fissures, or wounds, is a commonly used measurement of growth in lianas (Gentry 1982, Gentry 1991, Dewalt et al. 2000, Burnham 2002). The largest point typically occurs close to the root system in many liana species (Schnitzer et al. 2006).

To test the effect of potential ecotype on seedling survivorship, another experiment was conducted where 4939 seeds from Limahuli (3250 seeds), Koke'e (569 seeds), and Mt. Ha'upu (1117 seeds) were sown in 2008 on sterile cinder media, watered once a day, and maintained by NTBG Lawa'i Valley Conservation and Horticulture Center. At the appearance of true leaves, emergent seedlings were transplanted into 10 x 10 x 10 cm pots with sterile cinder media and grown in 50% available light. Inspection of plants after 12 and 24 months showed that root spiraling was not an issue, due to the characteristic slow root growth of the species. The number of seedlings surviving was counted in August 2010.

2.4. Data Analysis

I used generalized linear models (glms) to test if seed germination, seedling growth and survival (response variables) varied among potential ecotypes (predictor variable). For germination and survival, I used glms with a binomial error structure. For seedling growth, I used log of final stem diameter as the response variable and log of initial stem diameter and potential ecotype as the explanatory variables. All analyses were carried out in 'R' version 2.13 statistical software (R development core team 2008).

Although there is likely a high level of phenotypic plasticity in maile populations, high numbers of sample size and replicates helped to overcome potentially high within population heterogeneity and reduced incidence of Type II error.

3. Results

Maile germination rate was significantly affected by potential ecotype, light and the interaction between them (Fig. 1.3). In both light conditions, seed germination was significantly lower for seeds from Koke'e (ranging from 34–39%), than from Limahuli (63–75%) and Mt. Ha'upu (68–78%). Seed germination increased significantly with higher light for both Koke'e (increase of 5%) and Mt. Ha'upu seeds (increase of 10%). In contrast, for Limahuli seeds, germination decreased significantly with higher light (decrease by 12%). Therefore under high light

conditions, germination was significantly higher in Mt. Ha'upu than in Limahuli but the reverse was true in low light.

Growth differences among all three sites were significant (Fig. 1.4), with Limahuli seedling growth highest after two years, followed by Mt. Ha'upu, and lowest in Koke'e seedlings. My study showed significant differences among ecotypes in seedling survival after two years (Fig. 1.5). Survival of Limahuli seedlings (64%) was nearly double that of Koke'e (38%).

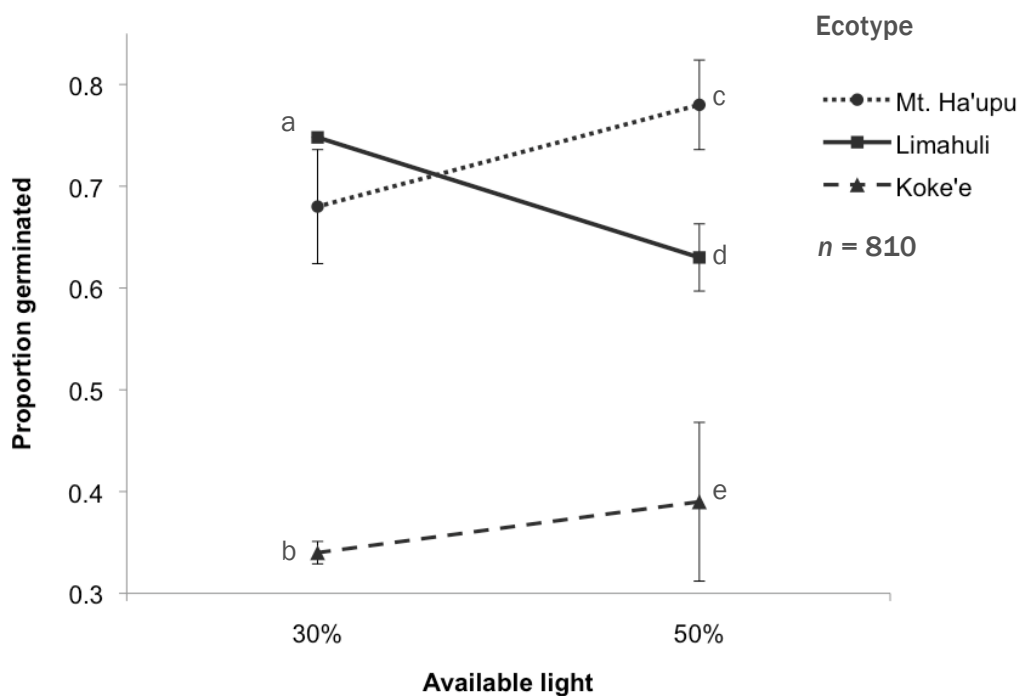


Figure 1.3. Ecotype and light effects on maile seed germination. Means \pm 1SE. Different letters represent significant differences ($P < 0.01$).

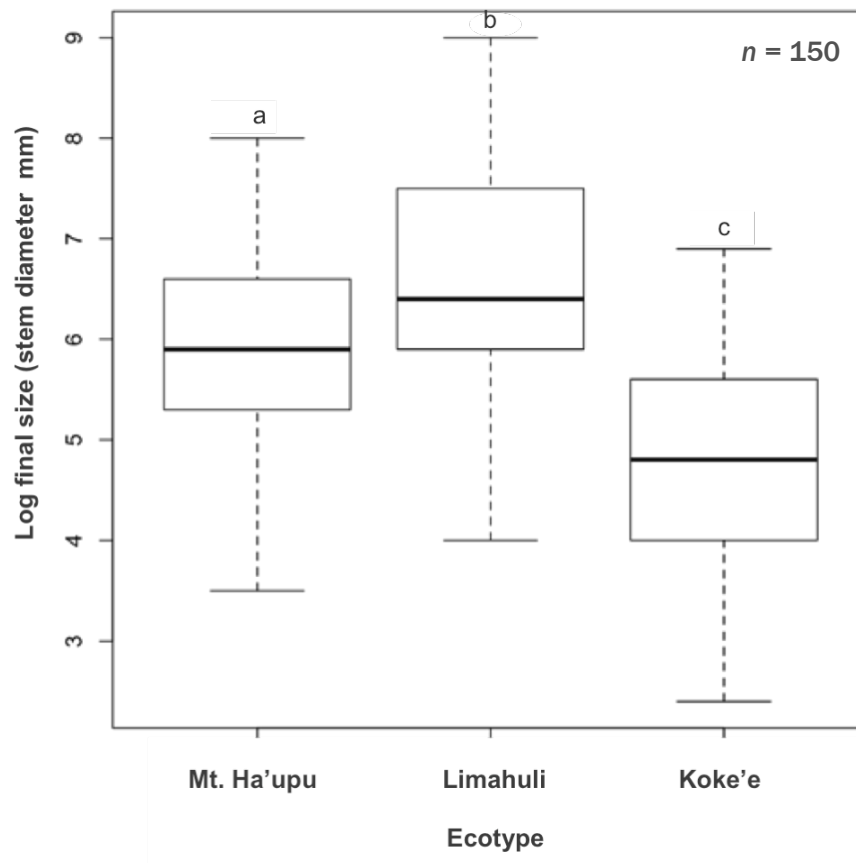


Figure 1.4. Effects of ecotype on growth of male seedlings after two years in a lowland restoration site. Mean \pm 1SE. Different letters represent significant differences ($P < 0.01$).

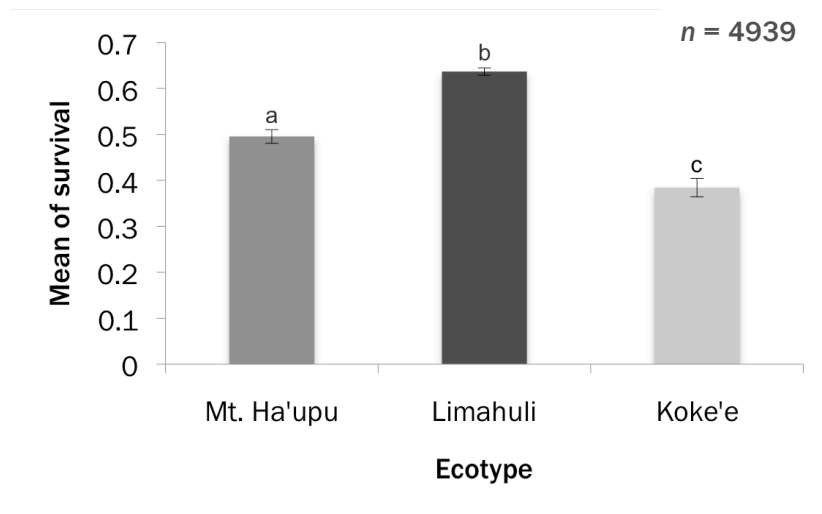


Figure 1.5. Effects of ecotype on survival of maile seedlings after two years in a lowland restoration site. Mean \pm 1SE. Different letters represent significant differences ($P < 0.01$).

4. Discussion

4.1. Adaptive significance of ecotypic effects

My results demonstrate that maile seeds from my three study sites exhibit consistent and significant differences in germination, seedling growth and survival in a lowland site. These results show important ecotypic differences are occurring among my study populations that could affect the success of lowland maile restoration projects.

Differences in seed germination rates could be based on genetic variation, a response to the environment or a combination of both (Baskin and Baskin 1998). There is some debate in the literature as to how many generations are needed before ecotype significance should be assigned to differences in performance of seeds from different populations of a species (Nelson et al. 1970, Quinn and Colosi 1977, Baskin and Baskin 1998). Differences in seed germination rates between populations in the common garden of my study may be due to maternal effects and preconditioning, but appear to be more likely caused by an interaction between genetics and environment rather than phenotypic plasticity.

The much lower germination rates of Koke'e seeds, regardless of light level, could be due the fact that Koke'e populations occur at a higher elevation and lower temperature than either Mt. Ha'upu or Limahuli populations and supports

my hypothesis of performance related to climate congruence. Multiple studies have shown that seeds produced at low temperatures commonly have lower germination rates than those produced by plants at high temperatures (Baskin and Baskin 1998).

In contrast to seeds from Koke'e and Mt. Ha'upu, Limahuli seed germination decreased significantly with increasing light. Within population seed germination variation with different available light treatments appears to be due either to phenotypic plasticity or genetic by environment interactions. More information regarding effects of preconditioning, genetic variation, phenotypic plasticity and interactions could be obtained by conducting experiments with seeds produced in reciprocal transplant gardens (Baskin and Baskin 1998).

The interpretation of this study is limited to differences in light quantity but not light quality (e.g., red: far-red ratio). My results are consistent with previous germination trials in 2006 that showed that Limahuli seeds had significantly higher germination rates than Koke'e in 30% and 100% PAR (Wong unpublished work). The consistency of my results over two different time periods indicates that my findings are not a result of conditions specific to the timing of my study.

The low growth and survival rate of Koke'e plants in comparison to those from Limahuli and Mt. Ha'upu seeds is likely because Koke'e is least ecologically similar to the restoration site. These results support my hypothesis. This site is at higher elevation and lower mean annual temperature and receives less mean annual precipitation; thus, plants from this site may have adopted a different strategy for growth and survival. Kauth et al. (2008) demonstrated that ecotypic differentiation affected seedling development of a widespread terrestrial orchid, *Calopogon tuberosus* var. *tuberosus*. Stem growth was decreased and inhibited by ethylene in an alpine ecotype of *Stellaria longipes* compared with the prairie ecotype (Emery et al. 1994).

4.2. Implications for restoration and cultural resource use

Do ecotypes matter in restoration? The results from my study show that they do. Significant differences in germination, growth and survival have important implications for the initial establishment and persistence of maile in low elevation restoration. It has become more common practice to select progeny from sites of high ecological similarity and adapted to local conditions in restoration (Erickson 2008, Miller et al. 2011). This research supports the argument for using local seed or seeds from similar habitats when possible. Maile is likely able to persist across highly variable Hawaiian habitats by performance adaptation to local conditions, and my results showed maximal functional advantages with climatic congruence.

Reciprocal transplant experiments could better determine whether local ecotypes are generally optimal for restoration or whether a smaller subset of ecotypes perform better, regardless of nursery or site conditions. There is evidence of functional adaptations to local conditions, e.g., temperature and rainfall, and support for maintaining local ecotypes (Heschel and Riginos 2005). Studies on drought stress tolerance in *Impatiens capensis* showed that in drought conditions, plants from dry-site populations exhibited higher water-use efficiency compared with wet-site populations (Heschel and Riginos 2005). Water-use efficiency has been linked to genetic differentiation in Hawaiian endemic tree species, *Acacia koa*, which has important implications for progeny selection and native forest restoration (Ares et al. 2000). Research showed that water-use efficiency was positively correlated to *A. koa* seed source elevation, which corresponded to a rainfall gradient (Ares et al. 2000).

The role of ecotypic variation in ecosystem function has been explored in *M. polymorpha* and *A. koa* (Treseder and Vitousek 2001a). Differential growth in *M. polymorpha* along a soil fertility gradient was demonstrated, and research suggests that slight genetic differentiation may influence plant nutrient cycling traits (Treseder and Vitousek 2001a).

Plants adapted to fertile versus infertile sites also appear to have different growth and nutrient-use strategies that can influence performance under differing site conditions (Chapin 1980, Treseder and Vitousek 2001a). For example, under high-nutrient conditions, plants from fertile sites tend to use nutrients to increase growth rates; whereas slow-growing plants from infertile sites store nutrients for growth in the future (Chapin 1980, Treseder and Vitousek 2001a). Under low-nutrient conditions, slow-growing ecotypes may be better adapted to sustain productivity due to this more conservative nutrient use strategy.

Ecotypic variation in maile seed germination rates, seedling survival and growth may affect the short- and long-term success of restoration projects. These results are both statistically, biologically and economically significant for restoration. Physiological performance comparisons with large disparities projected in survival and growth show that it is prudent for time and resource efficiency to collect from ecologically similar sites (e.g., Limahuli, Mt. Ha'upu) when restoring in lowlands, in order to maximize progeny (Table 1.2). Clearly, in similar restoration conditions, collecting seed stock largely from the least ecologically similar site populations (Koke'e) will adversely affect restoration in lowlands: whereas, the highest degree of congruence site (Limahuli) had both the greatest survival and growth of all three ecotypes. Decreased survival and growth would inhibit restoration success, and maladapted ecotypes may affect long-term plant fitness (Smith et al. 2009).

Table 1.2. Physiological performance comparison of ecotype variation in lowland restoration

Treatment with initial 1000 seeds	Koke'e	Mt. Ha'upu	Limahuli
Germination in 30% light	340	680	750*
Germination in 50% light	390	780*	630
Survival in 50% light	380	500	630*
Stem growth (mm) in 50% light	4.8	5.9	6.6*

* Leading performance

Nonetheless, there are other factors to consider for species like maile that have cultural value. Maile is valued for its leaf morphology and fragrance, both of which are highly variable. Some leaf morphological traits such as leaf size and shape appear to be passed down to some populations of first generation plants (F_1) and correlated to the elevation of the source population (personal observation). For example, leaves of maile from high elevation populations (e.g., Koke'e) are often generally smaller and strap-shaped compared to larger, elliptic leaves of plants from low elevation populations (e.g., Limahuli) (Fig. 1.6).

Maile plant tissues contain the volatile principle coumarin (1,2-benzopyrone), which is thought to be responsible for the fine fragrance (Dority 1965, Wagner et al. 1990, Tanabe 2009 personal communication). Coumarin has

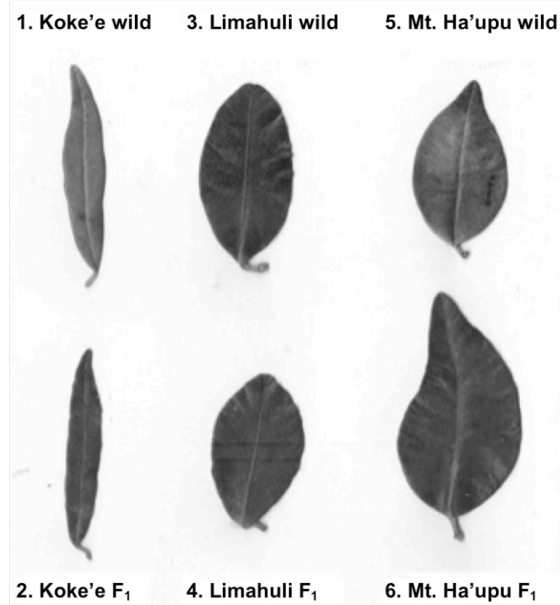


Figure 1.6. Population variation in wild maile leaf size appears to be retained in the common garden F_1 plants, and correlated with elevation.

a characteristically sweet herbaceous and strong vanilla scent. It may be produced by plants as a defense mechanism against herbivory. Coumarin release is dependent on tissue damage, e.g., herbivory or harvest, causing lactonisation and enzymatic hydrolysis (Dewich 2002, Yang et al. 2009). It is thought that maile from different locations varies greatly in fragrance intensity. Studies on the quantitative occurrence of coumarin in maile from different locations, and possible correlation with environmental conditions or genetic variation is underway (Wong unpublished work). Further research with reciprocal transplants, F_2 generations, and survival and growth in low-light conditions are needed.

Due to presence of local adaptation in some species, some researchers have advocated the exclusive use of local seed sources in restoration (Keller and Kollmann 1999, Mylecraine et al. 2005, Smith et al. 2009). However, consideration of potential ecotypes is also relevant when there is no local seed. This is often the case in Hawai'i and elsewhere, where restoration sites are in the lowlands but there is no surviving lowland seed sources. My study suggests that variation in important physiological aspects of maile obtained from different sites can indeed affect restoration success and thereby supports the argument for awareness and care in progeny selection.

Preserving genetic diversity within restored populations may be prudent for maximizing initial establishment and long-term persistence (McKay et al. 2005). Given the high morphological variability of many native Hawaiian species across the wide range of habitats they inhabit (Raven et al. 2005), I expect other species likely exhibit ecotypic differences that should be examined and considered in conservation and restoration ecology.

In Hawai'i and elsewhere, traditional ecological knowledge can play a valuable role in identification of potential ecotypes, as subtleties across populations of a species are often recognized by cultural experts. The findings from this study can help inform resource management of non-timber forest products and increase sustainable use.

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III. CHAPTER 2. NATIVE HAWAIIAN PLANT *ALYXIA STELLATA* SURVIVAL, MOISTURE AND NUTRIENT DIFFERENCES BETWEEN SOIL AND COARSE WOODY DEBRIS

1. Introduction

In many ecosystems, coarse woody debris (CWD) is important as seedbed and habitat providers (Thompson 1980, Harmon et al. 1986, Santiago 2000). The ecological value of CWD has been acknowledged (Harmon et al. 1986, Motta et al. 2006) and studied in many processes, including forest ecosystem function (Janisch and Harmon 2002, Spears et al. 2003, Laiho and Prescott 2004, Motta et al. 2006). Research has also focused on long-term influence of CWD on nutrient cycles and species composition (Cohen et al. 1996, Harmon et al. 1996, Santiago 2000, Harmon et al. 2004, Motta et al. 2006).

The rate of CWD decomposition exerts considerable influence on the regeneration process of some plant species as not all the decay classes provide the same preferred habitat (Motta et al. 2006). State of CWD decay may be evaluated and classified (three to five class systems) based on visual cues of decomposition (Thomas 1979, Muller and Liu 1991, Shifley et al. 1995, Jenkins and Parker 1997) and are useful though qualitative and subjective compared to nutrient immobilization or release assessments (Idol et al. 2001). Decay class can be an important predictor of seedling and sapling abundance in some studies (Santiago 2000, Takahashi et al. 2000), and advanced stages of decay are often correlated with higher establishment and abundance of seedlings and saplings.

Nutrients in decaying wood have been shown to be less concentrated than in fresh wood and losses of P, K, Mn, N, Ca and ash are general decomposition nutrient change patterns (Holub et al. 2001, Zalamea-Bustillo 2005). Zalamea-Bustillo (2005) showed that following fifteen years of decay, 5–95% of different nutrients were lost from CWD.

Plant productivity and survival are greatly influenced by water availability (Wang and Klinka 1997, Carlos Lola da Costa et al. 2010), and nutrient availability is an important factor in determining ecosystem plant species composition (Roem and Berendse 2000, Bobbink et al. 2003). Water availability and the processes that deliver nutrients to the root surface such as mass flow, diffusion, root interception, and saturated flow (Chapin et al. 2002) may vary greatly by substrate type. Linking soil and foliar nutrient concentrations has been a foundation of ecosystem science (Vitousek 1984, Townsend et al. 2007) with many studies demonstrating that nutrients in foliage reflect nutrient availability in proximate soil, especially N and P (Aerts and Chapin 2000, Vitousek 2004,

Townsend et al. 2007). Meta-analyses have revealed that terrestrial plants (conifers, deciduous species and herbaceous species) require nutrients in similar proportions (Knecht and Göransson 2004).

CWD is hypothesized to be a preferred establishment site for seedlings due to avoidance of competition, improved drainage in wet forests, safe sites and protection from feral ungulates and disturbance. However, there is a lack of data about the characteristics of CWD as a rooting medium and no studies have tested if outplanted seedlings fare better on soil or CWD in restoration efforts. Understanding the role of CWD is critical for forest restoration efforts in Hawai'i and elsewhere.

In the Hawaiian Islands, degradation and loss of native habitat threaten the viability of many plant populations. With 289 plant species listed as threatened or endangered (Hawai'i biological survey 1995–2003), restoration is a critically important management tool and more information is needed to identify best practices for restoration.

Decaying logs have been observed as the most common germination and establishment sites for many native woody plant species in Hawaiian montane forests (Coorey 1974, Scowcroft 1992, Santiago 2000). Many native species may start as seedlings on logs prior to establishing in the mineral soil (Coorey 1974, Mueller-Dombois 2005). One Hawai'i silvacultural restoration method recommends creating kipuka (patches) or light gaps by delimbing and inoculating late decay CWD with seeds and spores of selected native plants (Mueller-Dombois 2005). However, all studies to date in Hawaiian forests have been observational; variation in nutrient bioavailability between soil and CWD, and differences in seedling growth and survival have not been experimentally tested.

Maile (*Alyxia stellata*) (J.R. & G. Forst.) Roem. & Schult. (Apocynaceae) (Middleton 2002) is an indigenous liana and one of the most culturally important plants in Hawai'i. This species is prized for its fragrant leaves of various shapes and sizes, and whole stems with leaves are harvested for lei (wreaths). Lei are used by all sectors of society for cultural events such as weddings, graduations, hula, and inaugurations (Abbott 1992, Mabberley 1998).

Maile is still found in the wild, but it is becoming scarce. This may be due to habitat destruction, impacts of climate change, competition with invasive species, disturbance by feral ungulates, dispersal or pollination disruptions (Whitehead personal observation), seed predation by rats (Shiels and Drake 2011, Wong unpublished work), and unsustainable harvesting. As a result, there has been growing interest and investment in maile restoration by both conservation organizations and local communities, yet little is known about substrate preference and consequence. Maile plays a key role in some native Hawaiian

forests as a species whose population dynamics has a strong effect on the other species in the community (Mueller-Dombois 2005), and commonly establishes on CWD in Hawai'i (personal observation). Moreover, although recent studies have demonstrated the important role of vines in forest regeneration and ecosystem-level processes (Schnitzer and Bongers 2002), vine ecology is still poorly understood.

In this study I focus on a lowland restoration site for maile and address the following questions:

- (1) Do survival and growth of outplanted maile seedlings differ between CWD and soil?
- (2) How do CWD and soil differ in nutrient availability and substrate characteristics?

I hypothesized that survival and growth of outplanted maile seedlings would be higher in CWD than soil due to higher substrate moisture.

I discuss the implications of my results for success of maile restoration.

2. Methods

2.1. *Habitat and species*

Maile plants are twining lianas, and climbing or erect shrubs with milky sap. Leaves are lanceolate or ovate to elliptic, linear-lanceolate, or suborbicular in shape and arranged in whorls of three or opposite. Leaves are 0.7–9 cm long, 0.5–4.3 cm wide, smooth and hairless with entire margins (Wagner et al. 1990). Green to yellow-white corolla (4–5 mm long) flowers occur 2–5 in umbellate axillary cymes (Wagner et al. 1990). Floral syndromes along with field observations suggest the flowers may be pollinated, or at minimum visited by moths (Wong unpublished work). Maile produces ovoid drupes that resemble olives by shape with deep purple color when ripe. Often the fruits form end to end (monoliform), resembling a string of beads which consists of 2–3(4) 1-seeded joints (Wagner et al. 1990).

Maile has a widespread distribution over the Pacific Islands (Middleton 2002). In Hawai'i, maile grew across a range of habitats from 50–2000 m, in wet forest with closed canopy to dry open areas (Wagner et al. 1990). Maile is currently found on all the main Hawaiian Islands except Kaho'olawe and Ni'ihau, and it is likely that the species grew on those islands as well, but has become extinct due to extensive habitat disturbance (Wagner et al. 1990).

2.2. Study sites

This study took place in a remnant mesic-wet native forest in Ili'iili'ula at 350 m elevation (22°2'2"N, 159°27'50"W) on central Kaua'i island, Hawai'i (Fig. 2.1).

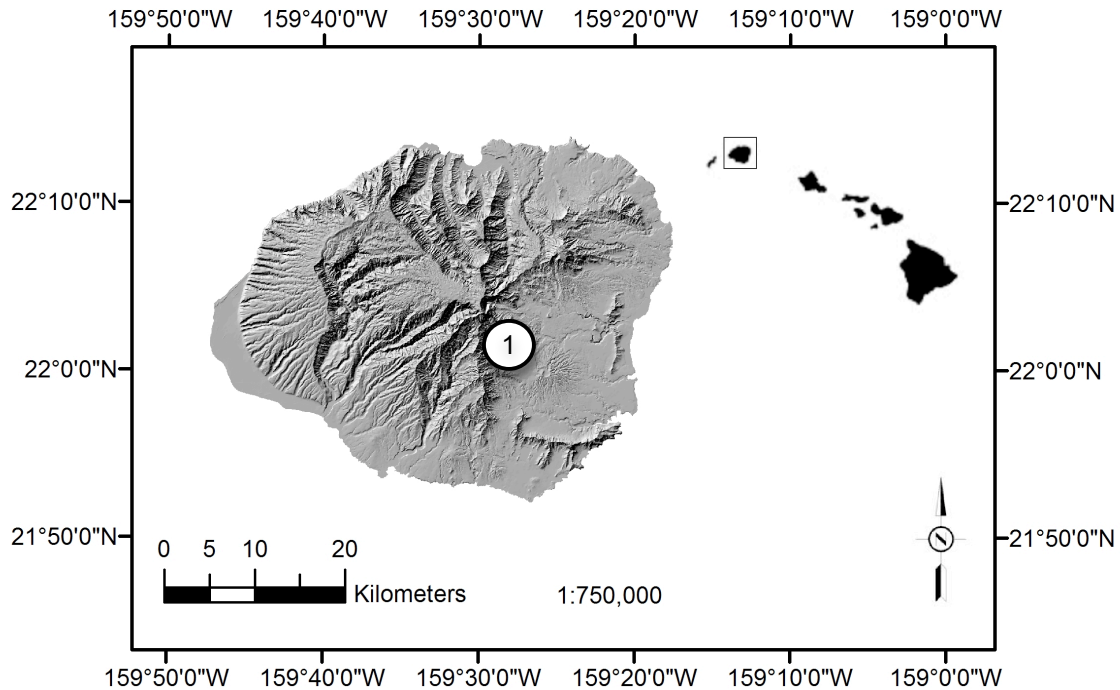


Figure 2.1. Study site on the island of Kaua'i, Hawai'i, USA. (1) Ili'iili'ula.

This site has a mean minimum–maximum annual temperature of 17.2–26.1°C and receives approximately 298 cm of rain annually (National Oceanic and Atmospheric Administration (NOAA) Waiahi Lower 1054 station).

2.3. Maile growth and survivorship in soil and CWD

In January 2010, we transplanted maile seedlings into plots in terrestrial soil and advanced stage of decay CWD (sapwood and heartwood mushy and rotten), class III from the three class system of Stewart and Burrows (1994). For each substrate, we planted ten seedlings into each of four 10 x 10 m plots (n total = 80 outplanted seedlings). Seedlings were approximately 16 months old and averaged $4.25 \text{ mm} \pm 1.75$ (mean \pm 1STD) in basal stem diameter. All seedlings were greenhouse grown from seed collected from wild maile populations in the National Tropical Botanical Garden Lower Limahuli Preserve on Kaua'i, in order to reduce potential confounding ecotypic effects (see Chapter 1). I measured

stem diameter at outplanting and six months later (July 2010) and recorded survivorship. Stem diameter was measured by digital calipers with a resolution of 0.1 mm and accuracy of ± 0.3 mm, and was measured at the first point above the roots where the stem was standard (Nabe-Nielsen 2004). The largest point along the stem, lacking stem abnormalities such as knots or wounds, is a commonly used measurement of growth in lianas (Gentry 1982, Gentry 1991, Dewalt et al. 2000, Burnham 2002), and the largest point typically occurs close to the root system in many liana species (Schnitzer et al. 2006).

Although moss coverage of CWD has been positively correlated with Hawaiian montane cloud forest seedling and sapling density and may help to preserve substrate moisture (Santiago 2000), I did not examine degree of moss coverage in my study.

2.4. Comparison of substrate characteristics between soil and CWD

I measured supply rate of 16 bioavailable nutrients in advanced decay CWD and terrestrial soil by installing Plant Root Simulator probes (PRSTM) which consist of ion exchange membranes embedded in a plastic stake. I buried four pairs of cation and anion probes in both treatment substrates in each of the four plots. The probes were left in the field for six weeks to ensure sufficient nutrient adsorption but also to prevent membrane saturation (Meason and Idol 2008). We included three pairs of cation and anion probes to use as blanks to verify absence of contamination. I washed PRSTM-probes with deionized water after removal. Washed probes were sent to the manufacturer for analysis (Western Ag Innovations, Saskatoon, Canada). Membrane ions were desorbed using a mild acid solution (HCl) and analyzed for nitrate (NO_3^- -N), ammonia (NH_4^+ -N) and phosphate (K^+) using colourimetric automated flow injection analysis. All other ion contents measured with inductively-coupled plasma spectrometry. Atomic absorption was used to measure the Ca, Mg, Fe, Zn, Mn, Cu, Al, Pb, and Cd contents, and flame emission used to measure K and Na (Szmigielska and Schoenau 1995, Szmigielska et al. 1998, Szmigielska et al. 2000). I report nutrient supply rates generated with the PRS-probes as the amount of nutrient adsorbed per amount of adsorbing surface area per time of burial in soil ($\mu\text{g}/10 \text{ cm}^2/6 \text{ weeks}$) (Qian and Schoenau 1995, Zalamea-Bustillo 2005). Generating nutrient supply rates through ion-exchange resin extraction, such as with PRSTM-probes, estimates available nutrients occurring for plant roots in the soil (Qian and Schoenau 1995, Zalamea-Bustillo 2005) in contrast with 'standard methods' of soil analysis that extract available and labile nutrients at a single point in time (Raij 1998).

I estimated percent organic matter by loss on ignition. Twenty samples of each substrate were dried to constant weight, placed in ceramic crucibles, and slowly

brought up to 450°C in a muffle furnace. Samples were cooled overnight in a drying oven and reweighed. Five samples of each substrate were submitted to the University of Hawai'i Agricultural Diagnostic Service Center (ADSC) for analysis of total carbon using a combustion furnace elemental analyzer with Hawaiian soils-specific standardized analytical methods (Hue et al. 2000).

I measured soil moisture to 12 cm depth as percent volumetric content (VWC %) by dielectric constant *in situ* using a soil moisture meter (Campbell Scientific HydroSense) and averaged five random readings per plot to account for heterogeneity. I measured soil temperature to 16 cm depth using a thermocouple thermometer probe (VWR International). The average of five random readings per plot was used to account for variability. I measured substrate pH of CWD and soil using a calibrated pH probe in a 2:1 substrate:distilled water mixture with ten samples of each substrate type.

2.5. Data analysis

To test if seedling survival differed between soil and CWD, I used a generalized linear model (glm) with a binomial error structure (Davies 1995). To test if seedling growth differed between the two substrates I used a multiple linear regression model where the log of the final diameter was the response variable and log (initial diameter) and substrate (CWD or soil) were the explanatory variables.

I tested if there were differences in nutrient availability, soil moisture and soil temperature between soil and CWD using Analysis of Variance (ANOVA). I also explored differences in patterns of nutrient availability based on standardized values (coefficient of variation) in soil and CWD using a Principal Components Analysis (PCA). I examined the relationship between soil moisture and nutrient content using a regression of soil moisture on PC1 axis. All analyses were carried out in 'R' version 2.13 statistical software (R development core team 2008).

I compiled optimum nutrient ratios in plant tissues based on a range of deciduous plant species (Knecht and Göransson 2004) and *Zea mays* (Rendig et al. 1976). Optimum nutrient ratios in plant tissues may indicate deficiencies for ratios occurring below. I calculated CWD and soil nutrient ratios ranges based on nutrient availability mean \pm 1SE.

Using National Oceanic and Atmospheric Administration (NOAA) weather station precipitation data, I compared study site total annual precipitation with site total annual precipitation 50 year mean \pm 1SD. Some studies have shown higher correlation between λ variation and previous year precipitation rather than same

year precipitation (Schmidt 2011). Higher rainfall in Hawai'i generally occurs in greater number of months in previous calendar years (3–4 months) than in same years (2–3 months) due to timing of the annual census. Due to the greater influence on total annual precipitation, I employed previous year precipitation in the site precipitation status analysis. Annual site precipitation status was categorized as dry (1) if total annual precipitation was $> 1SD$ below the 50 year mean, average (2) if in the range of the 50 year mean $\pm 1SD$, and wet (3) if it was $> 1SD$ above the 50 year mean.

3. Results

Survival of maile seedlings in soil (80%) was significantly higher than in CWD (50%) (Fig. 2.2). Growth of maile seedlings on CWD compared with terrestrial soil did not differ significantly over the study period (Fig. 2.3).

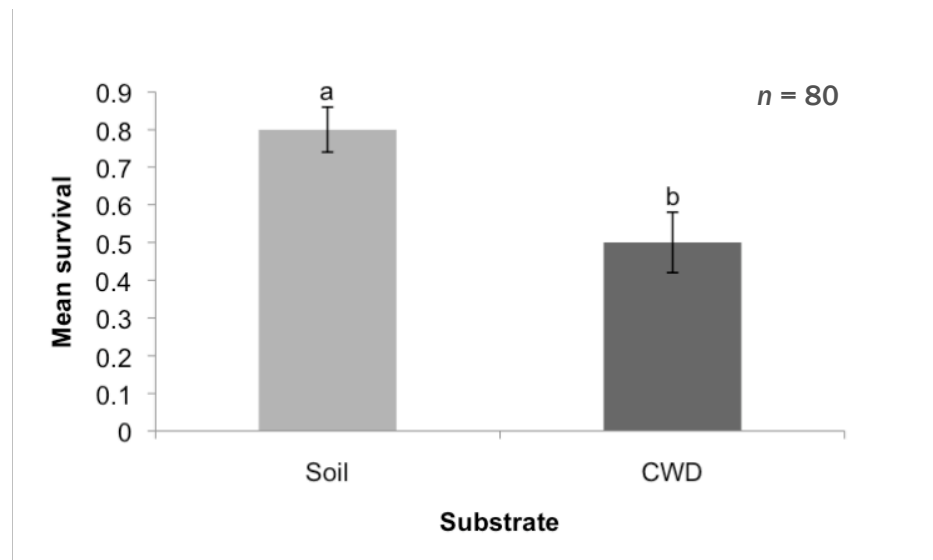


Figure 2.2. Survival of maile seedlings in terrestrial soil versus coarse woody debris, outplanted in a lowland restoration site on Kaua'i island. Mean $\pm 1SE$. Different letters represent significant differences ($P < 0.01$).

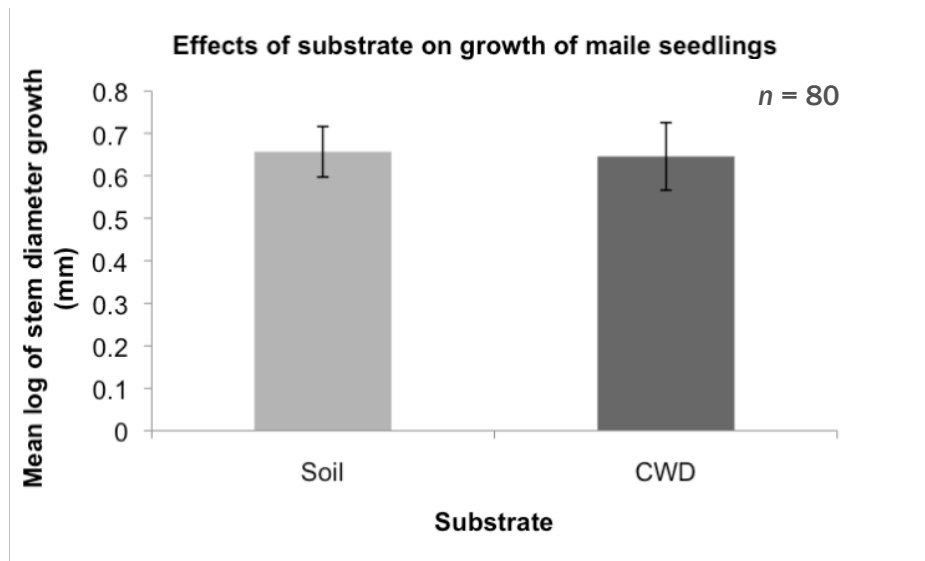


Figure 2.3. Growth of maile seedlings in terrestrial soil versus coarse woody debris, outplanted in a lowland restoration site on Kaua'i island. Mean \pm 1SE.

Soil moisture to 12 cm depth was significantly higher (33.05% vs. 6.6%) in soil than CWD ($P < 0.01$). Substrate pH was much more acidic in CWD than in soil ($P < 0.01$). Percent organic matter (LOI) was 65.64% higher in CWD ($P < 0.01$) than in soil and thus carbon concentration was also significantly higher ($P < 0.001$) (Table 2.1).

Bioavailability of nutrients varied also greatly between the two substrates (Table 2.1, Fig. 2.4). The PCA and ANOVAs illustrated that CWD had much higher values of potassium and phosphorus, and much lower values of other nutrients, including total nitrogen, nitrate, calcium, magnesium. The PCA first principal component explained 61.1% of variation in the data and the second component explained 16.3%, so that together they explained 77.3% of the total variation. Nutrient ratios varied between soil and CWD and comparisons with optimum foliar nutrient ratios indicating possible nutrient deficiencies of both advanced decay CWD and soil (Table 2.2).

There was a significant, negative correlation ($R^2 = 0.523$, $P < 0.03$) between PC1 axis, representing variation in bioavailable nutrients, and substrate moisture (Fig. 2.5).

Table 2.1. Differences in substrate characteristics between terrestrial and advanced decay coarse woody debris. Mean \pm 1SE, *P*-values.

Characteristic	Terrestrial soil	CWD	ANOVA <i>P</i> -value
Organic matter %	28.09 \pm 0.62	93.73 \pm 0.47	**
Organic carbon %	5.01 \pm 0.25	16.84 \pm 0.73	***
pH	4.19 \pm 0.076	3.57 \pm 0.04	**
Moisture VWC %	33.05 \pm 0.39	6.60 \pm 0.21	***
Temperature °C	21.35 \pm 0.02	21.66 \pm 0.05	***
Total nitrogen	81.25 \pm 6.14	17.45 \pm 2.18	**
Nitrate	72.40 \pm 5.71	4.45 \pm 0.58	**
Ammonia	8.85 \pm 0.51	13.00 \pm 1.67	*
Calcium	783.40 \pm 26.90	207.55 \pm 3.11	****
Magnesium	651.60 \pm 6.88	233.05 \pm 20.91	****
Potassium	22.40 \pm 3.32	215.75 \pm 11.58	****
Phosphorus	1.10 \pm 0.053	4.00 \pm 0.38	****
Iron	37.60 \pm 0.76	3.05 \pm 0.36	****
Manganese	74.15 \pm 6.37	8.25 \pm 0.64	****
Copper	3.30 \pm 0.09	0.35 \pm 0.01	****
Zinc	1.90 \pm 0.36	0.65 \pm 0.35	****
Boron	1.05 \pm 0.04	1.00 \pm 0.02	n.s.
Sulfur	115.00 \pm 7.31	53.20 \pm 3.90	****
Aluminum	117.10 \pm 4.34	31.78 \pm 0.89	****
Cadmium	0.05 \pm 0.014	0.00 \pm 0.00	***
Lead	0.00 \pm 0.00	0.00 \pm 0.00	n.s.
Al:Ca	0.16 \pm 0.01	0.13 \pm 0.00	**

**** *P* < 0.0001

*** *P* < 0.001

** *P* < 0.01

* *P* < 0.05

n.s. not significant

Table 2.2. Optimum foliar nutrient ratios compared with those found for terrestrial soil and advanced decay coarse woody debris at a lowland maile restoration site on Kaua'i island (mean \pm 1SE). Asterisk * indicate potential nutrient deficiencies.

Nutrient ratio	N:P	N:K	N:Ca	N:Mg	N:S
Suggested optimum in plant tissues	12.5 ^a	1.55 ^a	14.29 ^a	10.64 ^a	22-50 ^b
Soil	65.14–83.47	2.92–4.58	0.09–0.12*	0.1–0.14*	0.61–0.81*
CWD	3.47–5.42*	0.07–0.1*	0.07–0.1*	0.06–0.09*	0.27–0.4*

^a Deciduous plant tissues, adapted from (Knecht and Göransson 2004)

^b *Zea mays* plant tissues, adapted from (Rendig et al. 1976)

4. Discussion

My studies illustrated that survival of outplanted maile seedlings was significantly lower on advanced decay CWD than in terrestrial soil, which did not support my hypothesis. This contrasts with observational studies that found higher densities of some native Hawaiian species on CWD than in soil (Coorey 1974, Scowcroft 1992, Santiago 2000, Mueller-Dombois 2005). I found no differences in maile growth, but this may also have been result of the short length (six months) of this study.

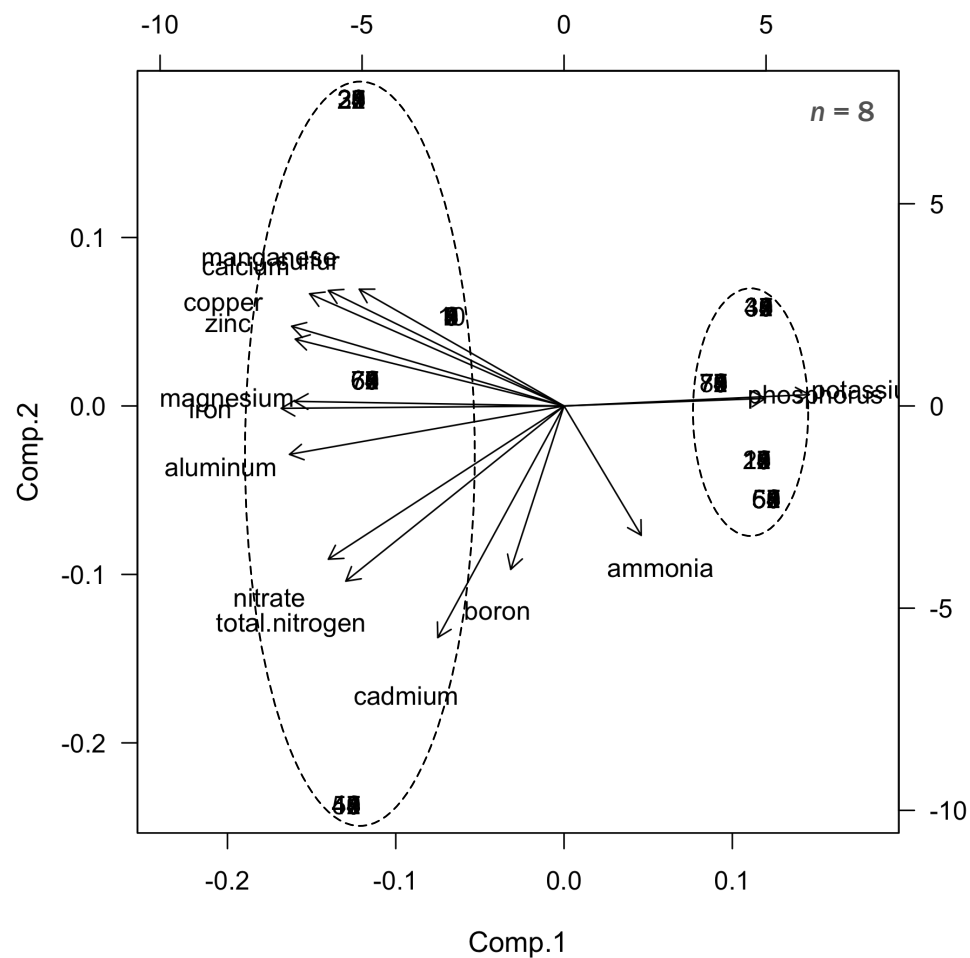


Figure 2.4. Principal Components Analysis biplot of substrate bioavailable nutrients. Soil samples are circled at left, CWD samples are circled at right. The first two axes explain 77.3% of the variation in the data.

The similarity in growth and differences in survival I documented may be a result of various factors. My estimation of potential nutrient deficiencies (Table 2.2) by comparing optimum foliar nutrient ratio ranges with substrate nutrient ratios (Methods 2.5) shows that advanced decay CWD was likely severely N-deficient related to P (Table 2.2). Tropical soils convert ammonia quickly to nitrate often due to a positive relationship with temperature (Marrs et al. 1988, Breuer et al. 2002), although limited by increased moisture (Breuer et al. 2002). Only twenty five percent of total nitrogen was nitrate in CWD as opposed to ninety percent in soil, and ammonia was higher in CWD than in soils (Table 2.1). This may indicate possible nitrification inhibition in CWD which may be due to low pH (Table 2.1) (Robertson 1982, Marrs et al. 1988, Zalamea-Bustillo 2005). The severity of CWD N-deficiency may have resulted in low survival, as nitrogen is often the most limiting plant nutrient in many natural ecosystems (Fisher and Binkley 2000).

In relation to foliar optimum nutrient ratios, the study soil was likely P-deficient related to N (Table 2.2). The low P:N ratio in the soil would be expected to lead to slow growth. Tropical forests have typically been characterized as P-limited (Vitousek et al. 2010) and in particular, P availability is low in 4,100,000 year old weathered soils of Kaua'i, which is the oldest of the Hawaiian Islands (Treseder and Vitousek 2001b). The low P yet high total N-availability in terrestrial soils of my study is consistent with previous research in a Hawaiian montane forests (Treseder and Vitousek 2001b). Other research has illustrated that phosphorus availability restricts the responses of plants to nitrogen in tundra habitats and polar deserts, indicating plant growth co-limitation by N and P (Gordon et al. 2001, Bobbink et al. 2003, Soudzilovskaia et al. 2005, Madan et al. 2007). Primary productivity in most terrestrial ecosystems is limited by either N and P or a combination of both (Treseder and Vitousek 2001b).

My results illustrate that a high percentage of organic matter is associated with high phosphorus, which is consistent with findings of other studies (Dalal 1977). Research has shown that pH is likely one of the most important properties that controls accumulation of organic matter and of inositol phosphates, the dominant class of organic P (Turner et al. 2002). My finding of higher acidity in CWD water extracts than in soil is consistent with a previous study (Takahashi et al. 2000). Often pH is a key indicator of potential availability, deficiency, and toxicity for micronutrient metals. Since acidic substrate pH values can alter cation availability (Paul and Clark 1989, Zalamea-Bustillo 2005) and some processes such as nitrification (Robertson 1982, Marrs et al. 1988, Zalamea-Bustillo 2005), the low pH of CWD may have contributed to slow growth of outplanted seedlings.

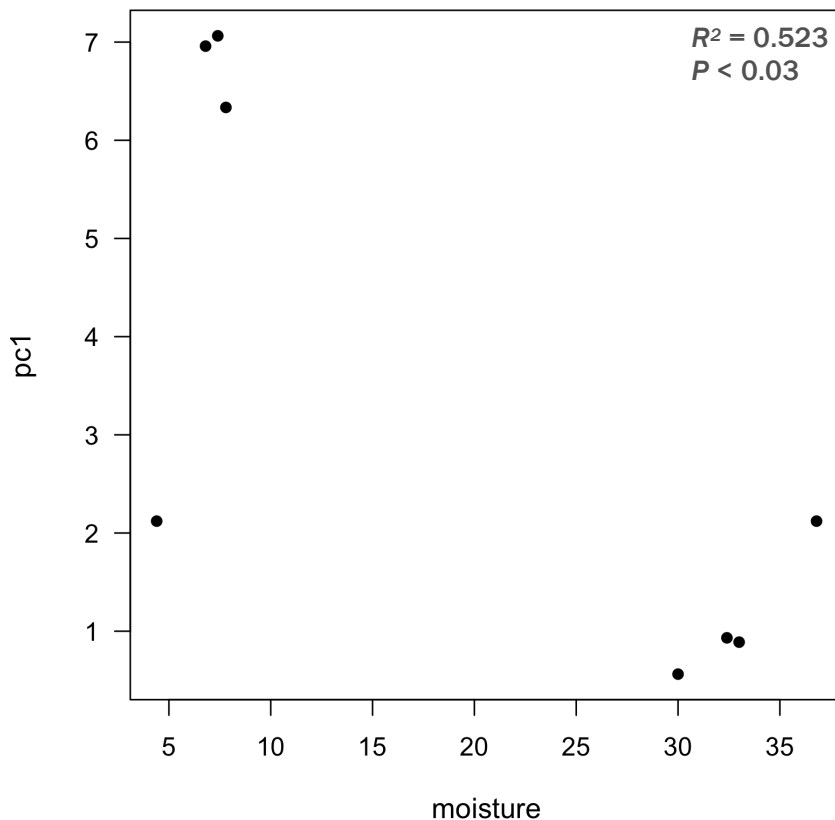


Figure 2.5. Correlation between substrate moisture and Principal Component 1 axis, representing variation in bioavailable nutrients ($R^2 = 0.523$, $P < 0.03$).

In other research where CWD functioned as a suitable seedbed, CWD was also found to have low mineral nutrient concentrations demonstrating that high levels of nutrients may not be essential to seedling establishment (Takahashi et al. 2000). Although the CWD in my study appears to be poorer in nutrients than soil as has been found in temperate ecosystems (Harmon et al. 1986), roots are likely able to access nutrients from CWD through mycorrhizal fungi association (Zalamea-Bustillo 2005).

The lower survival of maile outplants in CWD than in soil may be a result of the significantly lower soil moisture in CWD than soil. Research has shown that extended drought can lead to extensive plant mortality from water stress (Allen and Breshears 1998, Fensham and Holman 1999, Breshears et al. 2005).

The pattern of increased plant mortality following droughts linked with El Niño Southern Oscillation (ENSO) has been confirmed in many studies of other tropical rainforests (Leighton and Wirawan 1984, Condit et al. 1995, Van Nieuwstadt and Sheil 1995, Carlos Lola da Costa et al. 2010). Research has found that lianas were generally more susceptible to mortality due to drought, than either trees or palms (Nepstad et al. 2007). However, since substrate moisture is significantly correlated with differences in nutrient availability between soil and CWD (Fig. 2.5), it is not possible to separate the effects of moisture alone in my study. Moreover, soil moisture may significantly affect foliar nutrient concentrations, in addition to substrate nutrient availability (Wang and Klinka 1997). Some nutrient supply rates increase with substrate moisture, as ion mobility increases (Sulewski et al. 2002, Zalamea-Bustillo 2005). Research has shown that nutrient supply rates for Ca, Mg, K, Al, Fe, Mn, and Cu are higher with increased precipitation, but mobility of N and P are less related to substrate moisture and more connected to substrate biota-mediated processes (Zalamea-Bustillo 2005). Shade and drought lead to decreased root uptake nutrient capacity (Chapin et al. 2002).

The difference in substrate moisture between soil and CWD could also depend on climatic conditions. The superior water storing capacity of decomposing wood has been examined (Harmon and Sexton 1995, Durbak et al. 1998) reaching up to 250% of dry weight in advanced decay CWD (Maser et al. 1988). In other research, however, CWD did not preserve moisture in underneath soil (Zalamea-Bustillo 2005) and the water release characteristics of CWD under various levels of moisture stress resulting from drought are understudied. At least one study in the Pacific Northwest forests of the USA found higher average volumetric water content of CWD relative to soil over two dry summer periods (Hope and Li 1997), but this was not the case in my study.

Total annual precipitation at my study site was < 1 STD lower than the 50 yr mean, indicating a drier than average year. These drier conditions could have led to the much lower moisture in CWD than in soil, which in turn likely affected plant establishment and served as a barrier to survival. Lower moisture in CWD than in soil did not support my hypothesis.

5. Implications for restoration

Under some conditions, decaying logs were poorer substrates for transplanting than soil. These results showed that soil likely holds more moisture in the drier than average study year. This study shows that outplanting maile in soil compared to CWD is preferred, at least under the dry climatic conditions of my study. However, since transplant survivorship for CWD was still approximately 50%, planting a portion on CWD is likely beneficial due to potential rewards that might be observed over the long term but were not apparent in this short-term

study. An earlier study showed no significant difference in growth or survival of maile transplants, but was performed in an average precipitation year with a smaller sample size (Wong unpublished work).

Sowing seeds in CWD as an alternative to transplanting seedlings in restoration may yield different establishment and survival results (Mueller-Dombois 2005). Elevated organic substrates may offer safe sites that warrant consideration (Burton and Mueller-Dombois 1984, Ostertag 2002), especially if feral ungulates are present. However, the low moisture of CWD under dry climatic conditions that I found here may become a barrier for seedling establishment and survival on CWD in a climate that is predicted to become drier (Chu et al. 2010). Undertaking restoration efforts in predictably wetter years in Hawai'i, such as during La Niña years of El Niño Southern Oscillation (ENSO), may increase establishment success.

Clearly further studies that cover a longer time span and range of climatic conditions, with more species, CWD drying rates, and under different conditions, e.g., moss coverage, feral ungulate exclusion, are needed to better understand the role of coarse woody debris in forest dynamics and its potential role in plant restoration.

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IV. CHAPTER 3. POPULATION DYNAMICS OF WILD AND RESTORED *ALYXIA STELLATA* STANDS: IS RESTORATION VIABLE?

1. Introduction

As human impacts on ecosystems increase, the restoration of plant populations becomes increasingly important (Colas et al. 2008). Restoration is commonly used to reestablish extinct populations or increase threatened populations (McKay et al. 2005). It can also play an integral role in the management of culturally or economically important wild plant resources such as non-timber forest products (NTFPs) (Garibaldi and Turner 2004). NTFPs represent an important source of income to millions of people worldwide and many species, while not globally threatened or endangered, have dwindling populations or have gone locally extinct (Ticktin 2004). In addition, recognizing and incorporating culturally prominent plants in restoration efforts may increase success rates through partnership with local communities (Garibaldi and Turner 2004). Stakeholders in resource sustainability may have strong influence on associated habitats and community members may be more proactive in restoration if they connect through culturally significant species. These actions may extend to ecosystem stewardship and conservation and can lead to enhancement of both social and ecological integrity (Garibaldi and Turner 2004).

To be effective, restoration of plant populations must address a host of imminent management questions related to habitat suitability, planting methods, and plant ecological requirements (Colas et al. 2008), and take into consideration environmental, genetic and demographic stochasticity. Restoration strategies must consider not only short-term goals of establishment, growth and survival, but also reproduction and long-term persistence within natural habitats (Menges 1991, Menges 1998, Bell et al. 2003).

Matrix projection models integrate individual vital rates (growth, reproduction and survival) into measures of long-term population growth and are powerful tools for assessing population status, and comparing the demographic effects of different current or potential management practices (Crone et al. 2011). Although matrix population models are often used to generate recommendations for resource management (Schmidt et al. 2011), few studies have used matrix modeling to assess the viability of, or identify best management practices for, restored plant populations (Crone et al. 2011). In addition, few studies have compared the demographic of wild and restored populations, even though this can identify factors key to restoration success (Bell et al. 2003, Davelos and Jarosz 2004, Endels et al. 2005, Maschinski and Duquesnel 2007, Colas et al. 2008). For example, Colas et al. (2008) used life table response experiments (LTREs) to

illustrate that higher survival of *Centaurea corymbosa* (Asteraceae) compensated for lower fecundity in restoration populations, so that wild and restored population growth rates were similar. Endels et al. (2005) used elasticity analysis to identify survival of reproductive adults and seedling recruitment as the life-history transitions to which long-term growth rates of restored populations *Primula veris* (Primulaceae) are most sensitive, and based management recommendations for on these results.

In the Hawaiian Islands, degradation and loss of native habitat threaten the viability of many plant populations. Hawai'i has more endangered species per area than any other region on the globe, with close to one third of plant species (289) currently listed as threatened or endangered (Hawai'i biological survey 1995–2003) and over 90% of the native vascular are endemic (Goldman et al. 2008). Restoration of native plant communities is critical to conserve species and maintain ecosystem services, including resources important for cultural practices.



Figure 3.1. Maile lei

Maile (*Alyxia stellata*) (J.R. & G. Forst.) Roem. & Schult. (Apocynaceae) (Middleton 2002) is an indigenous liana and one of the most culturally important plants in Hawai'i. This species is prized for its fragrant leaves of various shapes and sizes, and whole stems with leaves are harvested for lei (wreaths) (Fig. 3.1). Lei are used by all sectors of society for cultural events such as weddings, graduations, hula, and inaugurations (Abbott 1992, Mabberley 1998). Maile is still found in the wild, but it is becoming scarce. This may be due to habitat destruction, impacts of climate change, competition with invasive species, disturbance by feral ungulates, dispersal or pollination disruptions (Whitehead personal observation), seed predation by rats (Shiels and Drake 2011,

Wong unpublished work), and unsustainable harvesting. As a result, there has been growing interest and investment in maile restoration by both conservation organizations and local communities. However, to date there have been no demographic studies on either wild or restored maile populations. Moreover, although recent studies have demonstrated the important role of vines in forest regeneration and ecosystem-level processes (Schnitzer and Bongers 2002), vine ecology is still poorly understood and there are few demographic studies of vines in general (Kathriarachchi et al. 2004, Nabe-Nielsen 2004, Siebert 2004, McGeoch et al. 2008). Some studies have shown that growth of lianas vary significantly with light, e.g., higher growth of *Calamus ovoideus* in high light conditions (Kathriarachchi et al. 2004).

I used matrix population models built from annual demographic data of one restored and two wild maile populations to address the following questions:

- (1) What are the projected long-term population growth rates of wild and restored populations?
- (2) What life-history transitions are most responsible for differences in projected growth rates between wild and restored populations ?
- (3) How does canopy cover affect long-term growth rates of restored population?
- (4) What management practices are needed for the long-term persistence of restored populations ?

I hypothesized that wild populations would have higher population growth rates than restored populations due to high mortality of seedlings and juveniles and, that closed canopies would increase population growth rates based on previous liana ecology studies (Kathriarachchi et al. 2004) and the understory habit of maile. I also hypothesized that, as has been found for other vines (Nabe-Nielsen 2004) long-term population growth rates would be most sensitive to changes in adult survival.

2. Methods

2.1. Habitat and species

Maile plants are twining lianas, and climbing or erect shrubs with milky sap. The flowers may be pollinated, or at minimum visited by moths (Wong unpublished work). Maile produces ovoid drupes that resemble olives by shape with deep purple color when ripe. Often the fruits form end to end (monoliform), resembling a string of beads (Wagner et al. 1990).

Maile has a widespread distribution across the Pacific Islands (Middleton 2002). In Hawai'i, maile formerly grew across a range of habitats from 50–2000 m, from wet forest with closed canopy to dry open areas (Wagner et al. 1990). Maile is currently found on all the main Hawaiian Islands except Kaho'olawe and Ni'ihau, and it is likely that the species grew on those islands as well, but has become extinct due to extensive habitat disturbance (Wagner et al. 1990).

2.2. Study sites

My study sites were located on the island of Kaua'i, Hawai'i. The restored maile population was located at the National Tropical Botanical Garden (NTBG) Lower

Limahuli Preserve and wild maile populations at Koke'e State Park and Limahuli (Fig. 3.2, Table 3.1).

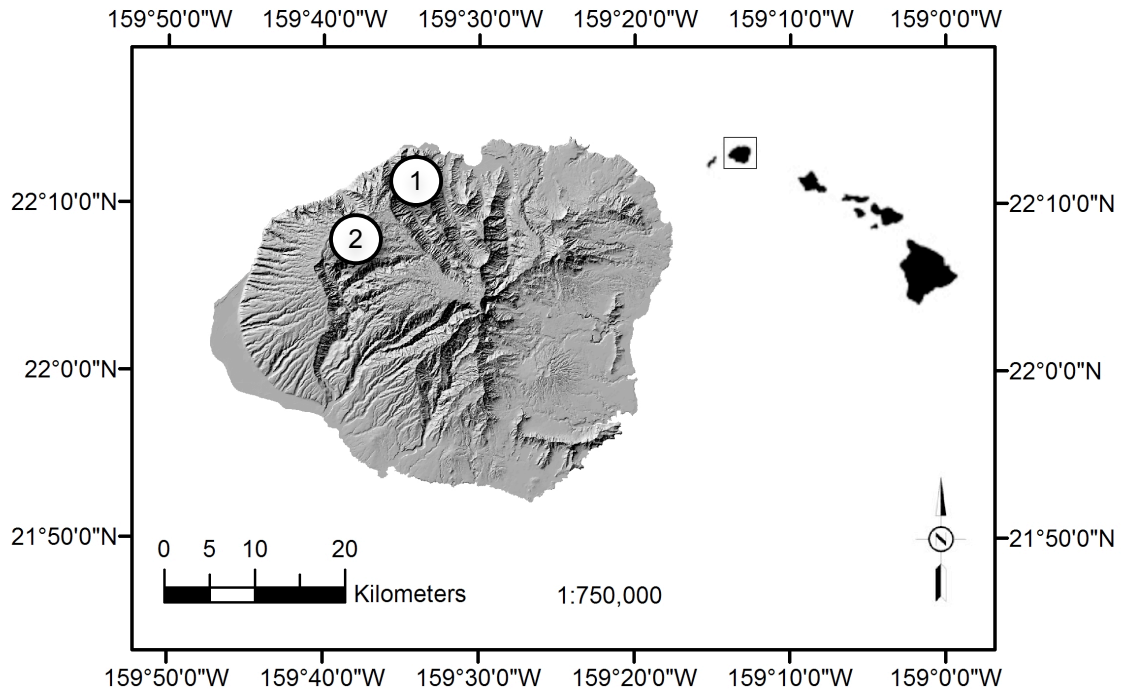


Figure 1.2. Study sites on the island of Kaua'i, Hawai'i, USA. (1) Lawa'i Valley NTBG, (2) Lower Limahuli Preserve NTBG, (3) Mt. Ha'upu, (4) Koke'e State Park.

Figure 3.2. Study sites on the island of Kaua'i, Hawai'i, USA. (1) Lower Limahuli Preserve NTBG, (2) Koke'e State Park.

Table 3.1. Characteristics of wild and restored maile population study sites

Site	NTBG Lower Limahuli Preserve	Koke'e State Park
Kaua'i orientation	North	Northwest
Latitude / longitude	22°12'12"N, 159°36'32"W	22°7'49"N, 159°39'31"W
Elevation	Natural population: 180–205 m Restoration population: 90–140 m	1060–1070 m
Mean annual precipitation	305.1 cm	168.3 cm
Mean annual temperature	22.13°C	15.16°C
Forest type	Remnant and restored native lowland to upland mesic and wet forest. Invasive species presence, e.g., <i>Schefflera actinophylla</i>	Montane mesic forest dominated by native canopy trees <i>Metrosideros polymorpha</i> and <i>Acacia koa</i>

2.3. Reintroduction and monitoring

In 2007, we transplanted 13 male individuals of multiple genotypes into each of ten 6 x 6 m plots ($n = 130$ transplanted individuals). Half of the plots were located under open canopy conditions (100% available light) and the other half under closed canopy conditions (22-50% approximate range of available light). Light levels were characterized as Photosynthetically Active Radiation (PAR) measured as Photosynthetic Photon Flux Density (PPFD) by Licor LI-191 Line Quantum Sensors. The size of all individuals was recorded at the time of outplanting, by measuring the diameter of each plant at the first point above the roots where the stem was standard (Nabe-Nielsen 2004), using digital calipers with a resolution of 0.1 mm and accuracy of ± 0.3 mm. The largest point along the stem lacking abnormalities such as knots or wounds, is a commonly used measurement of growth in lianas (Gentry 1982, Gentry 1991, Dewalt et al. 2000, Burnham 2002), and the largest point typically occurs close to the root system in many liana species (Schnitzer et al. 2006). Plots were remonitored for growth and survival every six months from 2007 to 2011. I also recorded the number of flowers and fruit at each census. At each census, all plots were hand weeded due to presence of alien invasive species such as *Panicum maximum* Jacq.

2.4. Wild population monitoring

In 2009, I tagged and measured 120 male individuals in each of two wild populations. I measured the diameter of each plant at the first point above the roots where the stem was standard, using digital calipers. The point of measurement was initially marked with paint to ensure stem measurement uniformity each time (Nabe-Nielsen 2004). I took annual surveys in 2010 and 2011, measuring growth, survival, and emergence of new seedlings. I monitored reproduction of adults biannually by randomly selecting five fruiting branches and counting and marking all fruits present. I counted total number of fruiting branches of the individual and multiplied by the average number of fruits per branch to estimate fruit production.

To determine if male maintains a seed bank, I buried 50 seeds in three wire baskets at three sites in Limahuli ($n = 450$) in 2009 and at Koke'e in 2010 ($n = 450$) under 10 cm of soil. One basket from each site of the three sites was recovered after one year and we counted the number of seeds that germinated *in situ* (as characterized by root breaking seed coat) and noted insect and fungal damage. In 2011, I tested viability of ungerminated seeds at Koke'e using tetrazolium seed viability testing (TZ). I used the TZ Apocynaceae protocol as outlined in Peters (2000). All seeds were preconditioned by imbibing on moist blotters overnight at 25°C. I prepared and stained seeds by longitudinal cut, leaving the seed intact at the top of the cotyledons. The seeds were placed in

petri dishes and covered with a 0.1% solution of 2,3,5-triphenyl tetrazolium chloride (TTC) and distilled water. I covered and placed the petri dishes in an oven at 35°C for 18 hours, and then evaluated seed viability based on stain pattern (Peters 2000).

2.5. Population projection matrices

I divided maile individuals into four stage classes based on size and morphology (Fig. 3.3). Adult stage classes reproduced sexually. I built 4 x 4 Lefkovich stage-structured transition matrices (Caswell 2001) directly from the annual census field data. Since maile was determined not to have a seedbank (see Methods 2.3), the number of seedlings produced per adult was calculated by multiplying number of new seedlings by number of fruit per adult divided by total number fruit of all adults.

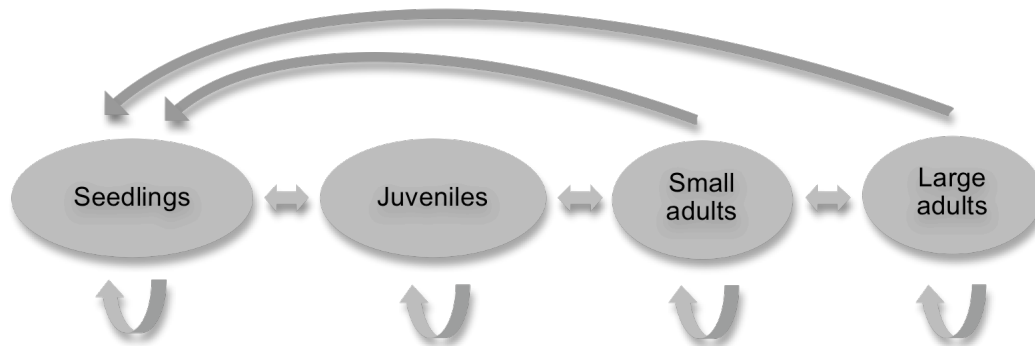


Figure 3.3. Maile life cycle graph. Seedlings have stem basal diameter < 2 mm, juveniles 2.1–8 mm, small adults 8.1–20 mm, large adults > 20 mm.

For each population, I used the matrix model:

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t)$$

where $\mathbf{n}(t)$ is a vector of stage abundances at year t , $\mathbf{n}(t + 1)$ is the population vector in the following year, and \mathbf{A} is the transition matrix for the population (Parker 2000, Davelos and Jarosz 2004). The dominant eigenvalue λ represents λ , the asymptotic finite rate of increase at the stable stage distribution.

Since maile is a relatively slow-growing species, for the restoration population I did not have representation of adult stages each year. I therefore built one mean matrix for the restored population where transition frequencies were calculated from the summation of transitions over the four year study period 2007–2011 (Bell et al. 2003, Maschinski and Duquesnel 2007, Colas et al. 2008). Transition rates for fecundity and stasis of large adults were estimated by taking the mean of those values from the two wild populations over two years.

For each matrix I calculated lambda (λ), the finite rate of population growth (the rate at which a population would grow over the long term under the parameterization conditions (Caswell 2001), elasticity values of the matrix elements and determined the 95% percent confidence intervals of λ with 2000 bootstrap runs (Caswell 2001).

I conducted life table response experiments (LTREs) to determine which stage classes and life-history transitions were most responsible for differences in lambda ($\Delta\lambda$) between restored and wild populations. For each wild population, I used a mean matrix of two study years. I also performed LTREs to determine which stage classes and life-history transitions were most responsible for differences in lambda ($\Delta\lambda$) between the wild populations at the two sites and the two years. All analyses were conducted in 'R' version 2.13 statistical software (R development core team 2008) with the 'popbio' package (Stubben and Milligan 2007).

2.6. Transient dynamics and assessing management for long-term viability

I examined transient dynamics of restored populations by numerical projection (Caswell 2001) in Microsoft Excel 2010. I examined six restoration scenarios: maile restored under a variety of canopy cover levels; maile restored only under closed canopy; maile restored only under open canopy; and three multiple year supplements of maile outplantings under closed canopy. Supplements were: increasing juvenile survival by 0.12 and multiple year supplement with 100 added juveniles in years 1–3 (JS); increasing adult survival by 0.12 and multiple-year supplement with 100 added small adults in years 1–3 (AS); and increasing both juvenile and small adult survival by 0.12 and multiple year supplement with 100 added juveniles and small adults in years 1–3 (AJS). I increased adult survival incrementally to identify what level is needed to have a long-term viable population. An increase of 0.12 small adult survival results in a projected stable population ($\lambda = 1$).

3. Results

3.1. Population growth rates and elasticity analysis

Projected growth rates (λ) of wild maile populations ranged between 0.893 for Limahuli in the first year to 1.046 for Koke'e in the second year. In both sites, projected growth rates changed from decreasing population rates in the first year to increasing ones in the second year, although confidence intervals overlapped 1 (Fig. 3.4a-b). The projected population growth rates for the restored population under the range of canopy cover was 0.938, indicating population decline over the long term. Although λ for populations under closed canopy was higher than that in open canopy, it was still less than 1 (Fig. 3.4b).

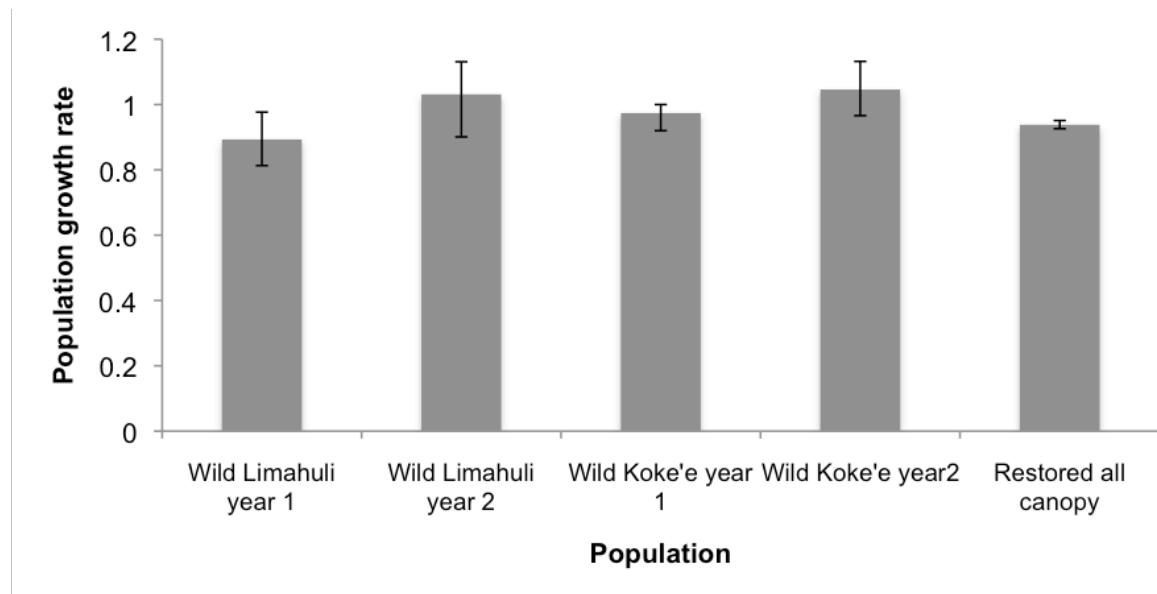


Figure 3.4a. Summary of matrices population growth rate and 95% CI for wild and all canopy restored

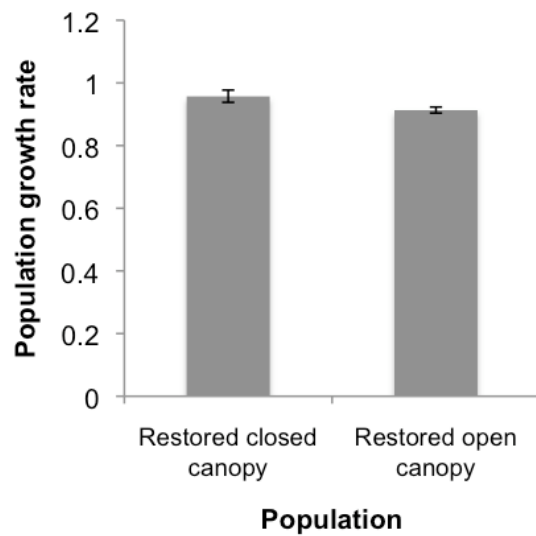
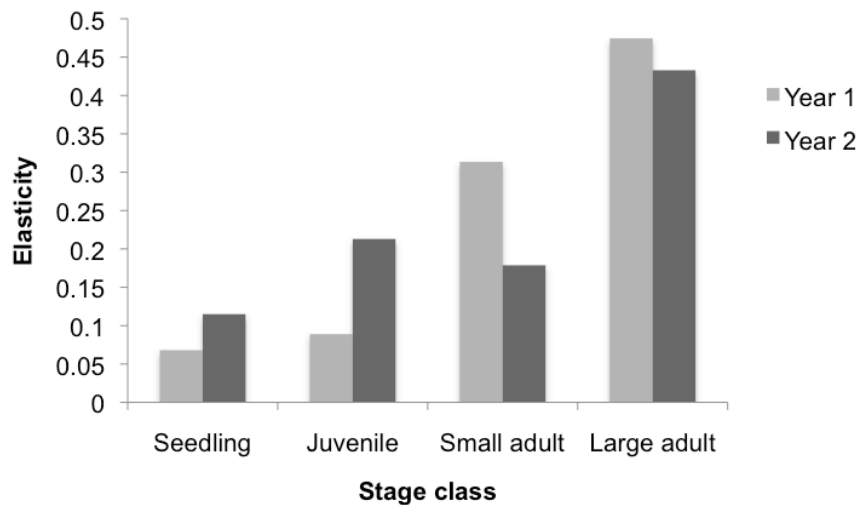
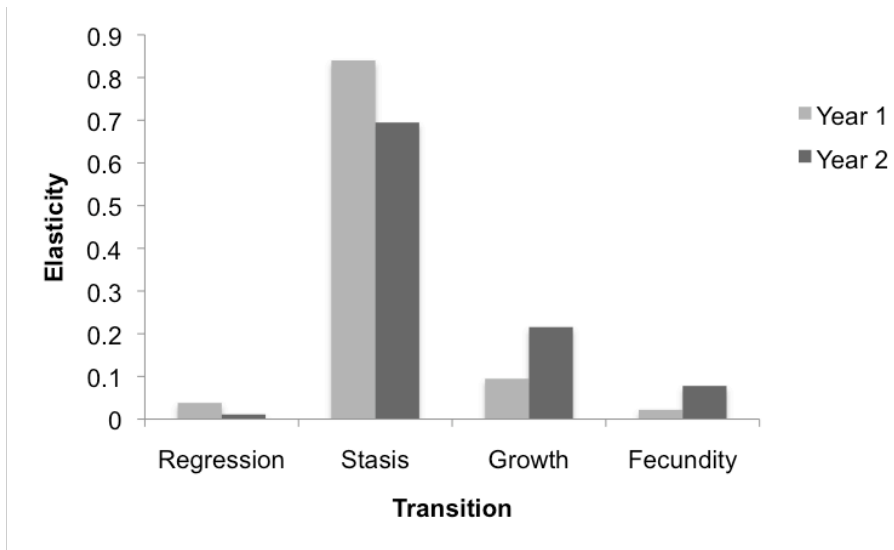


Figure 3.4b. Summary of matrices population growth rate and 95% CI for closed and open canopy restored

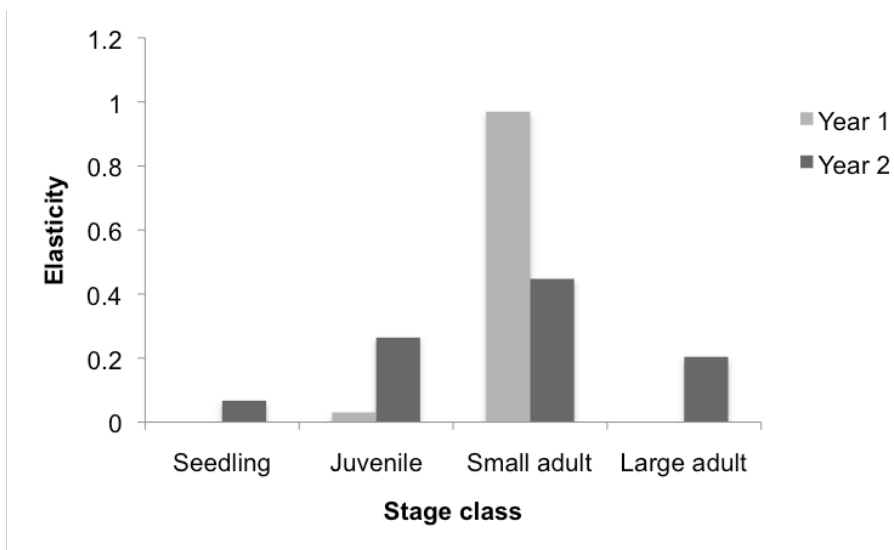
Elasticity values varied between populations and years (Fig. 3.5). For Limahuli, stasis of large adults had the highest elasticity, but, depending on the year, stasis of juveniles and small adults also had high values (Fig. 3.5a-b). For Koke'e elasticity was dominated by stasis of small adults (Fig. 3.5c-d).



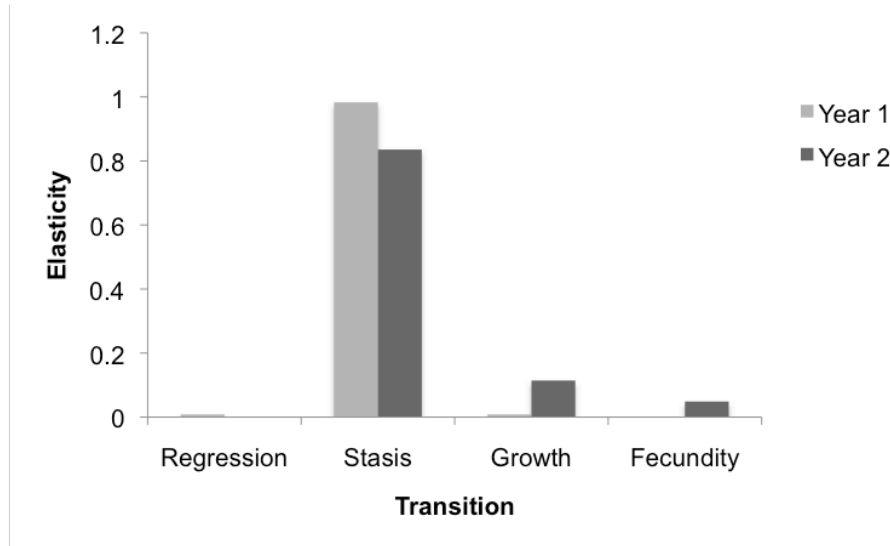
Figures 3.5a–d. Elasticity values for wild maile populations at two sites, and over two years. Fig. 3.5a. Limahuli site.



Figures 3.5a–d. Elasticity values for wild maile populations at two sites, and over two years. Fig. 3.5b. Limahuli site.



Figures 3.5a–d. Elasticity values for wild maile populations at two sites, and over two years. Fig. 3.5c. Koke'e site.



Figures 3.5a–d. Elasticity values for wild maile populations at two sites, and over two years. Fig. 3.5d. Koke'e site.

3.2. Life table response experiments

Higher growth of seedlings and juveniles made the biggest contributions to the higher lambda values observed in wild populations the second year versus the first year (Fig. 3.6a-b). The largest contributor to the higher growth rate in Koke'e versus Limahuli was higher survival of small adults (Fig. 3.6c-d).

Lower adult stasis was the biggest contributor to the lower lambda observed in restored population under closed canopy versus the Koke'e population (Fig. 3.7a-b). Growth of seedlings in the restored population made positive LTRE contributions (Fig. 3.7a-b). The largest contributors to the lower lambda values in the open canopy restored population were lower survival of adults compared to Koke'e (Fig. 3.7c-d) and lower values of all vital rates for seedlings, juveniles and small adults compared to Limahuli (Fig. 3.7c-d).

3.3. Restored populations transient dynamics

The short-term dynamics of restored maile population vary widely depending on the overstory canopy openness and on how populations are supplemented over time with outplants (Fig. 3.8). Under open canopy, only 1 individual of the 130 planted remained after 20 years; under closed canopy this value was 10. If closed canopy populations are supplemented during each of the first three years

with 100 juveniles (JS), 190 individuals remained after 20 years. With increased juvenile survival of 0.12, the population continued decreasing ($\lambda = 0.982$). In the second supplement (AS) where populations received 100 small adults during each of the first three years, 544 individuals remained after 20 years. With small adult survival increased by 0.12, the restoration population was stable ($\lambda = 1.002$). In the third supplement (AJS) where populations received 100 juveniles and 100 small adults during each of the first three years, 1134 individuals persisted after 20 years ($\lambda = 1.027$). With a survival increase of 0.12 in both juveniles and adults, the population increased ($\lambda = 1.027$). Although the younger supplement (JS) had the same number of added individuals as the older supplement (AS), the population was estimated to be less than half the size in 20 years (Fig. 3.8). Using both juveniles and small adults increased the 20 year projected population size exponentially (Fig. 3.8).

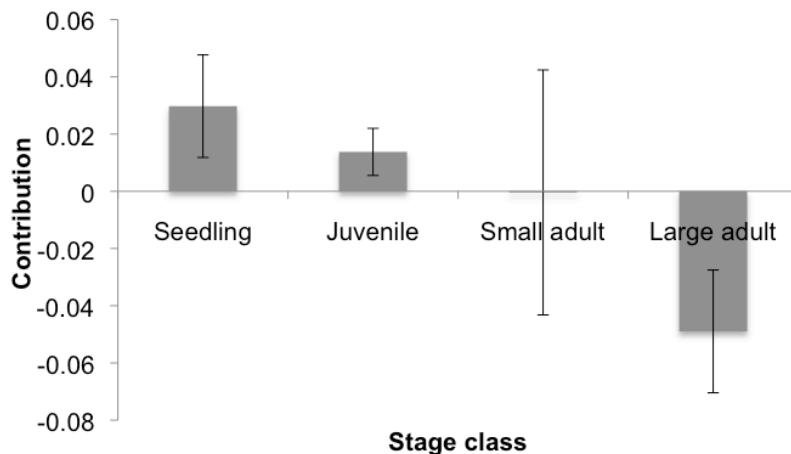


Figure 3.6a–d. Life Table Response Experiments (LTRE) for wild maile populations. Fig. 3.6a. Year 1 vs year 2. Value represent the mean between sites, \pm 1SD. Positive values represent contributions to higher long-term population growth rates (λ) observed in year 2.

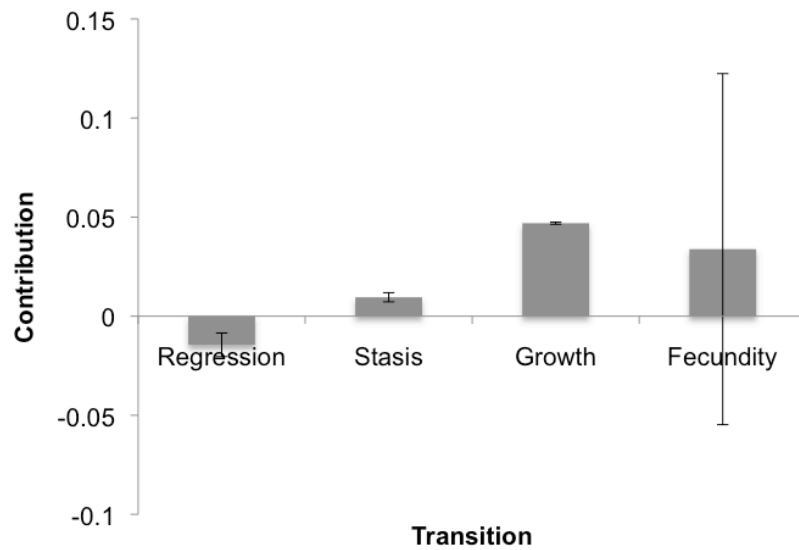


Figure 3.6a–d. Life Table Response Experiments (LTRE) for wild maile populations. Fig. 3.6b. Year 1 vs year 2. Value represent the mean between sites, \pm 1SD. Positive values represent contributions to higher long-term population growth rates (λ) observed in year 2.

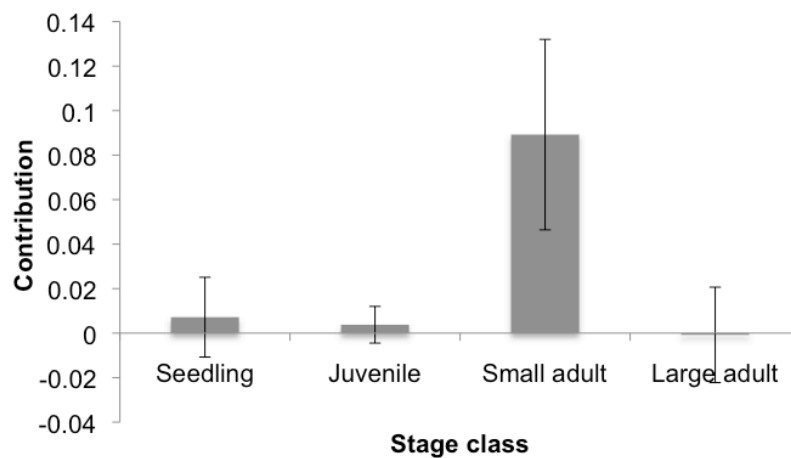


Figure 3.6a–d. Life Table Response Experiments (LTRE) for wild maile populations. Fig. 3.6c. Limahuli vs Koke'e. Values represent the mean between years \pm 1SD. Positive values represent contributions to higher long-term population growth rates (λ) observed in Koke'e.

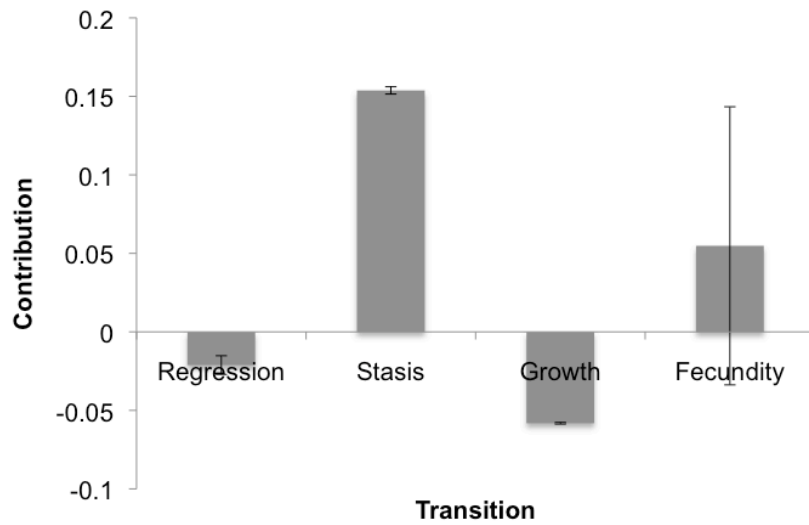


Figure 3.6a–d. Life Table Response Experiments (LTRE) for wild maile populations. Fig. 3.6d. Limahuli vs Koke'e. Values represent the mean between years \pm 1SD. Positive values represent contributions to higher long-term population growth rates (λ) observed in Koke'e.

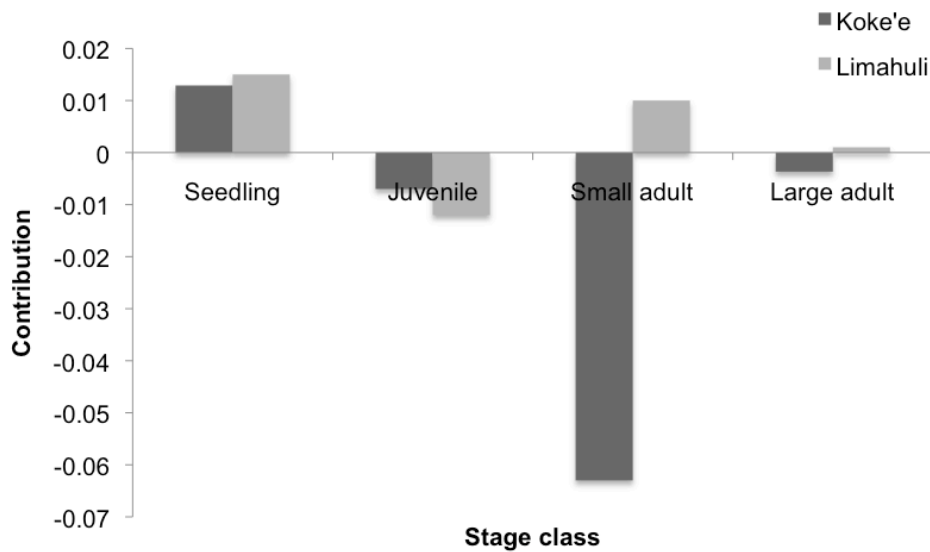


Figure 3.7a–d. Life Table Response Experiments for wild versus restored maile populations. Fig. 3.7a. Closed canopy restored population vs mean of wild populations over two years. Positive values represent contributions to higher long-term population growth rates (λ) observed in the wild populations.

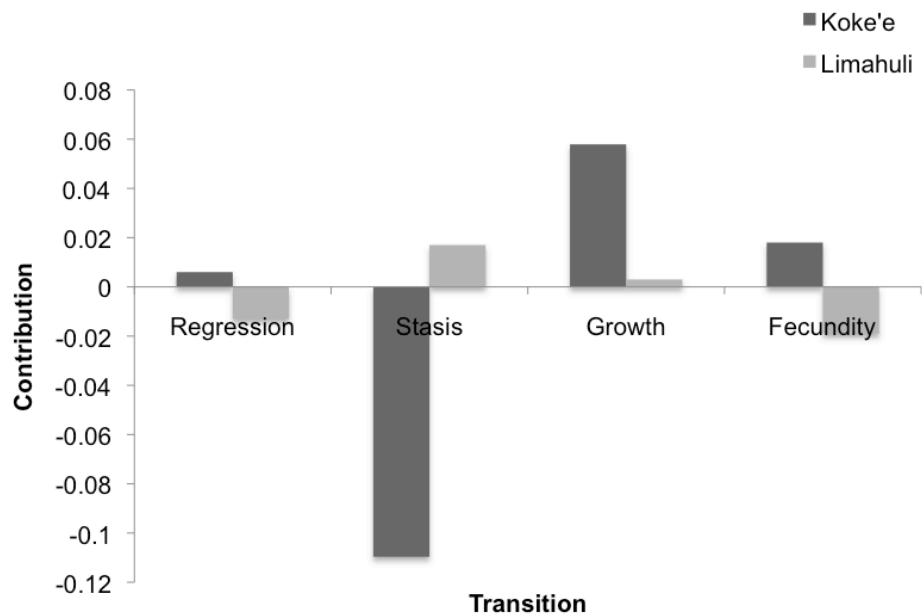


Figure 3.7a–d. Life Table Response Experiments for wild versus restored maile populations. Fig. 3.7b. Closed canopy restored population vs mean of wild populations over two years. Positive values represent contributions to higher long-term population growth rates (λ) observed in the wild populations.

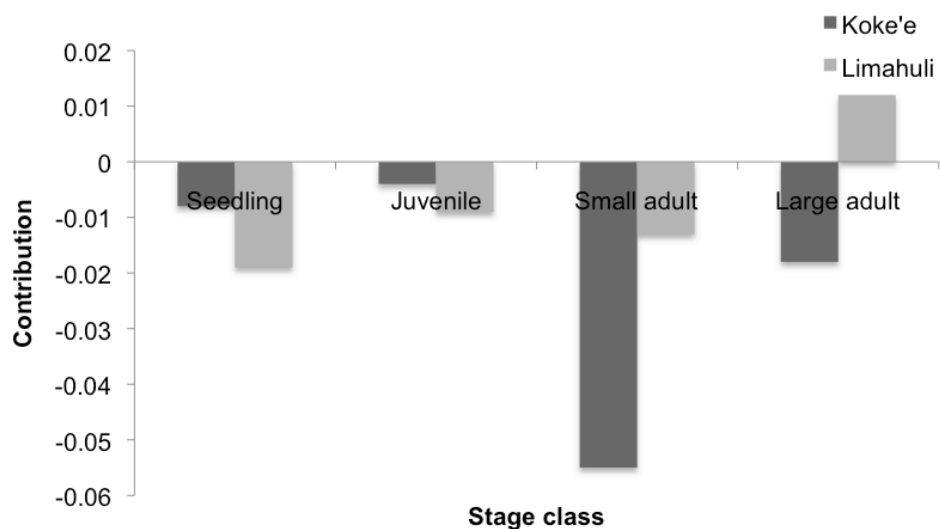


Figure 3.7a–d. Life Table Response Experiments for wild versus restored maile populations. Fig. 3.7c. Open canopy restored population vs mean of wild population. Positive values represent contributions to higher long-term population growth rates (λ) observed in wild population.

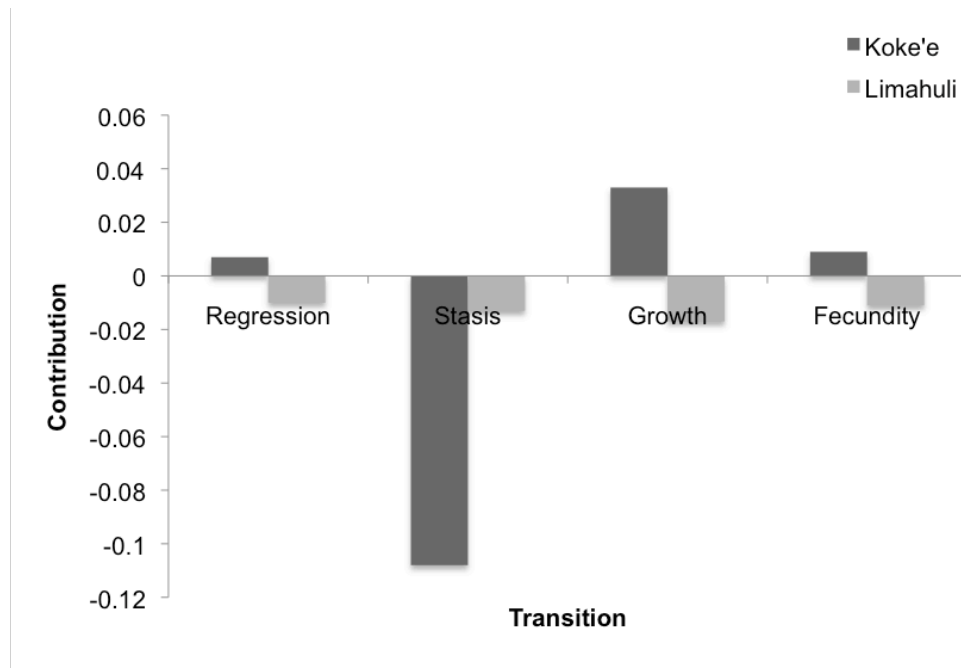


Figure 3.7a–d. Life Table Response Experiments for wild versus restored maile populations. Fig. 3.7d. Open canopy restored population vs mean of wild population. Positive values represent contributions to higher long-term population growth rates (λ) observed in wild population.

4. Discussion

My results illustrate that, although there was variation across sites and over time, three out of four λ I obtained for wild maile populations did not differ significantly from one, and one was significantly lower. This suggests that the wild maile populations I monitored are projected to either remain stable or decline over time, if conditions remained similar to those of the study. The only other published study to assess the long-term population growth rate of a liana showed that the shade-tolerant neotropical species, *Machaerium cuspidatum*, had a slightly increasing population ($\lambda = 1.033$) in shaded understory (Nabe-Nielsen 2004).

In contrast, my analyses revealed that my restored populations were not viable, with $\lambda < 1$ for populations under both open and closed canopies if vital rates remained unchanged. Of the few other studies to assess long-term population growth rates of restored populations, two have also found decreasing populations. In a 10-year demographic comparison between restored and wild populations of *Centaurea corymbos* in Southern France, Colas et al. (2008) found

that both restored and wild λ were < 1 . Similarly, restored populations of *Asclepias meadii* in midwestern USA all decreased, with λ ranging from 0.85 to 0.874 (Bell et al. 2003).

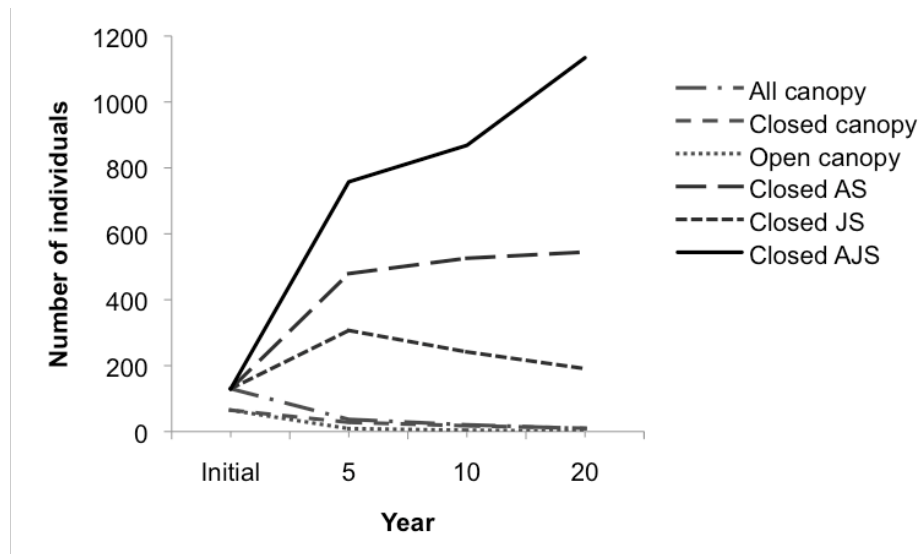


Figure 3.8. Transient dynamics of restored maile populations under different management practices. Projections: increasing juvenile survival by 0.12 and multi-year supplement with 100 added juveniles in years 1–3 (JS); increasing adult survival by 0.12 and multi-year supplement with 100 added small adults in years 1–3 (AS); and increasing both juvenile and small adult survival by 0.12 and multi-year supplement with 100 added juveniles and small adults in years 1–3 (AJS).

The lowest λ I found was for a restored population in open canopy conditions. Maile seedlings and juveniles in open canopy had elevated mortality, likely due to dessication. The low survival of maile in high light conditions is consistent with findings from other liana research (Nabe-Nielsen 2004). Demography studies of the liana *Machaerium cuspidatum* showed that understory plants in high light did not contribute positively to the population growth rate, comprised of plants in various light conditions (Nabe-Nielsen 2004).

I found that the main contributor to higher growth rates in wild Koke'e maile populations, compared with the restored population, was higher adult survival. Lower survival in the restored populations may be a result of various factors. One is that survival may increase with size, and there were fewer large individuals within the small adult class in these early stages of restoration. Nonetheless,

survival of small adults was similar in the restoration site and in the wild Limahuli population. Another reason may be that the two years in which there were adults in the restored populations were also very dry years (< 1 STD from the 50 year mean, Appendix, Table 3.2), and this may have led to higher mortality. The low λ values for restored populations of some other species, e.g., *Cirsium pitcheri*, *Asclepias meadii*, are also thought to be a result of low annual precipitation (Menges 1998, Bell et al. 2003).

The higher growth rates in the wild maile populations during the second year may be a result of differences in climatic conditions. For Koke'e at least, the first year of the study was especially dry while the second year was average (Appendix, Table 3.3). For Limahuli, both study years were dry (< 1 STD from the 50 year mean, Appendix, Table 3.3). However, both Koke'e and Limahuli sites received higher total annual precipitation in year two compared with year one. These findings, combined with the poor performance of maile under drier, open canopy conditions, suggest that maile populations may be quite sensitive to decreases in precipitation. The pattern of increased plant mortality following droughts linked with ENSO has been confirmed in many studies of other tropical rainforests (Leighton and Wirawan 1984, Condit et al. 1995, Van Nieuwstadt and Sheil 1995, Carlos Lola da Costa et al. 2010). Research has found that lianas were generally more susceptible to mortality due to drought, than either trees or palms (Nepstad et al. 2007). Maile population growth rates appear to fluctuate with El Niño Southern Oscillation (ENSO), and this may point to cyclic recruitment. Restrospective analysis of climate trends from 1955–2010 show Koke'e with mostly average precipitation years with intermittent wet and dry years. Limahuli, however, trends from a past majority in average with intermittent wet years to predominantly dry years (Wong unpublished work). Maile populations may be at risk if there are increasing drought years in the future, as predicted for Kaua'i and O'ahu islands (Chu et al. 2010).

5. Recommendations for maile restoration and conservation

My elasticity analyses and LTRE results suggest that the most effective way to increase maile populations is to increase survival of large (reproductive) individuals, as well as juveniles. High elasticity values for adult stages is typical for slow-growing woody species and has been found for other vines (Escalante et al. 2004, Nabe-Nielsen 2004, Kouassi et al. 2008).

Increasing adult survival could potentially be achieved using various approaches. Since maile appears vulnerable to drought, irrigation during dry periods or years may be necessary. Treefall may be another major cause of adult mortality in maile (personal observation), and when this occurs extra outplantings to replace the adults may be necessary, as well as removal of alien invasive species. Reintroduction with juveniles and adults over seedlings may be more

efficient for species such as maile with slow maturation (Bell et al. 2003, Guerrant and Fiedler 2003). However, outplanting large individuals could result in decreased fecundity due to lower fitness of greenhouse plants (Bell et al. 2003).

For my restored population, I estimated survival of the largest adults from wild maile populations as my restored plants did not reach that size. Since survival of small adults was lower in restored populations, the same could be true for the larger individuals. In this case λ would be even lower. On the other hand, if the incidence of tree fall was lower, survival could be higher in restored populations. Clarity on this must await further work (Bell et al. 2003).

My transient analyses suggest that with the starting population size that I used (130 outplants), which is within the typical range of many restoration programs, and under a management scenario of increased survival of juvenile and small adult under closed canopy with multi-year supplements (AJS), maile would be harvestable after a short time period. Fifty eight large adults of harvestable size would exist in five years. Since maile stems are generally harvested from adult individuals, it is also imperative to ensure that harvest does not decrease adult survival. Further studies on this topic are needed.

Small restoration populations are highly vulnerable to environmental, demographic and genetic stochasticity (Lande 1988, Menges 1991, Bell et al. 2003); therefore, increasing initial population size is recommended, especially if increasing drought predictions are realized. To buffer against stochastic losses, other studies (Maschinski and Duquesnel 2007) recommend restoration approaches that involve multiple years paired with multiple sites.

This study illustrates the importance of demographic monitoring of restored populations, even for those like maile which have been assumed to have relatively good chances of success in restoration. As my results illustrate, populations that increase over short periods still may not be viable over the long term (Fig. 3.8). In Hawai'i, multiple maile restoration programs have been initiated to address concerns of decreasing populations, and some of them occur in open canopy or other unsuitable conditions. My results suggest that many of these may not be viable over the long term. This represents loss in population propagules, economic costs, time and effort. This study projected maile restoration populations as not viable but identified measures to achieve persistence. Elasticity and LTRE analyses pinpointed key strategies that were not obvious, e.g., increasing seedling survival would not be enough to allow restoration populations to persist, instead we must focus on juvenile and adult survival to achieve success.

This study highlights the importance of demographic comparisons between restored and wild plant populations. More detailed demographic studies of wild and restored populations are needed to improve the success of restoration projects for maile and other native species. It also emphasizes the need to make long-term commitments to increase survival of outplants until they become mature individuals to ensure restoration of viable populations. For maile and other NTFP species, this also increases the compatibility of harvesting plant material with restoration goals.

APPENDIX

ANNUAL PRECIPITATION STATUS

Using National Oceanic and Atmospheric Administration (NOAA) weather station precipitation data, I compared study site total annual precipitation with site total annual precipitation 50 year mean \pm 1SD. Some studies have shown higher correlation between λ variation and previous year precipitation rather than same year precipitation (Schmidt 2011). Higher rainfall in Hawai'i generally occurs in greater number of months in previous calendar years (3–4 months) than in same years (2–3 months) due to timing of the annual census. Due to the greater influence on total annual precipitation, I employed previous year precipitation in the site precipitation status analysis. Annual site precipitation status was categorized as dry (1) if total annual precipitation was $> 1SD$ below the 50 year mean, average (2) if in the range of the 50 year mean $\pm 1SD$, and wet (3) if it was $> 1SD$ above the 50 year mean. Tables 3.2 and 3.3. summarize the total annual precipitation status by population site and year.

Table 3.2. Restored site status of total annual precipitation when compared with total annual precipitation 50 year mean $\pm 1SD$

Site status of total annual precipitation (cm)	Year 1	Year 2	Year 3	Year 4	Year 5
Restored	average	dry	average	dry	dry

Table 3.3. Wild site status of total annual precipitation when compared with total annual precipitation 50 year mean $\pm 1SD$

Site status of total annual precipitation (cm)	Year 1	Year 2
Limahuli	dry	dry
Koke'e	dry	average

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V. CONCLUSION

1. The importance of restoration with culturally prominent plants

Integrating culturally prominent plants when appropriate may increase success of restoration projects through collaboration with local communities (Garibaldi and Turner 2004). This has been confirmed in my personal experience hosting many local community conservation outreach programs with Grove Farm on Kaua'i island. I have witnessed the excitement in and dedication to restoration that is generated by incorporating native plants of cultural significance, while fortunate to work with over 400 Kaua'i community members. These community members included: middle school students, Boy Scouts, hunters, wild plant harvesters, University of Hawai'i Botany professors, international university field school students, Hawai'i Youth Conservation Corps, State of Hawai'i Department of Land and Natural Resources, Natural Area Reserves System, and Kaua'i Invasive Species Committee.

2. Main lessons

We all depend on ecosystem services for our basic needs to survive and to improve our quality of life. The harvest of non-timber forest products (NTFPs) is a major cultural and economic activity in many native tropical forests and represent an important source of income to millions of people worldwide (Ticktin 2004). The true value of NTFPs is underestimated due to missing data and limitations of subsistence use valuation; therefore, the reported value of US\$18.5 billion for 2005 likely covers but a portion of the total (Food and Agriculture Organization of the United Nations (FAO) 2010). Continued availability of NTFPs is not only essential for conservation of the plant species, but also for the livelihoods of many rural peoples and accessibility of resources for cultural practices. Using culturally prominent plants such as maile can play a special role in conservation.

I used maile as a model species to examine various key principles in restoration, lessons from which can be applied to other native plant restoration projects.

The three main lessons from this research are:

(1) Ecotypes matter in restoration.

Significant differences in germination, survival and growth have important implications for the initial establishment and persistence of maile in low elevation restoration. This research supports the argument for using local seed or seeds

from similar habitats when possible. Maile is likely able to persist across highly variable Hawaiian habitats by performance adaptation to local conditions, and my results showed maximal functional advantages with climatic congruence.

Ecotypic variation in seed germination rates, seedling survival and growth may affect the short- and long-term success of restoration projects. These results are both statistically, biologically and economically significant for restoration. Decreased survival and growth would inhibit restoration success, and maladapted ecotypes may affect long-term plant fitness (Smith et al. 2009).

Due to presence of local adaptation in some species, some researchers have advocated the exclusive use of local seed sources in restoration (Keller and Kollmann 1999, Mylecraine et al. 2005, Smith et al. 2009). However, consideration of potential ecotypes is also relevant when there is no local seed. This is often the case in Hawai'i and elsewhere, where restoration sites are in the lowlands but there is no surviving lowland seed sources. My study suggests that variation in important physiological aspects of maile obtained from different sites can indeed affect restoration success and thereby supports the argument for awareness and care in progeny selection. Nonetheless, preserving genetic diversity within restored populations may be prudent for maximizing initial establishment and long-term persistence (McKay et al. 2005).

Given the high morphological variability of many native Hawaiian species across the wide range of habitats they inhabit (Raven et al. 2005), I expect other species likely exhibit ecotypic differences that should be examined and considered in conservation and restoration ecology.

In Hawai'i and elsewhere, traditional ecological knowledge can play a valuable role in identification of potential ecotypes, as subtleties across populations of a species are often recognized by cultural experts. The findings from this study can help inform resource management of non-timber forest products and increase sustainable use.

(2) Substrate characters greatly affect establishment and survival.

Under some conditions, decaying logs were poorer substrates for transplanting than soil. These results showed that soil likely holds more moisture in the drier than average study year. This study shows that outplanting maile in soil compared to CWD is preferred, at least under the dry climatic conditions of my study. However, since transplant survivorship for CWD was still relatively high, planting a portion on CWD is likely beneficial due to potential rewards that might be observed over the long term but were not apparent in this short-term study. Elevated organic substrates may offer safe sites that warrant consideration (Burton and Mueller-Dombois 1984, Ostertag 2002), especially if feral ungulates are present. However, the low moisture of CWD under dry climatic conditions

that I found may become a barrier for seedling establishment and survival on CWD in a climate that is predicted to become drier (Chu et al. 2010). Undertaking restoration efforts in predictably wetter years, such as during La Niña years of El Niño Southern Oscillation (ENSO), may decrease nutrient limitations and increase establishment success.

Clearly further studies that cover a longer time span and range of climatic conditions, with more species, CWD drying rates, and under different conditions, e.g., moss coverage, feral ungulate exclusion, are needed to better understand the role of coarse woody debris in forest dynamics and its potential role in plant restoration.

(3) Do not assume long-term persistence in restoration populations.

This research illustrates the importance of demographic monitoring of restored plant populations, even for those like maile which have been assumed to have relatively good chances of success in restoration. As my results illustrate, populations that increase over short periods still may not be viable over the long term. In Hawai'i, multiple maile restoration programs have been initiated to address concerns of decreasing populations, and some of them occur in open canopy or other unsuitable conditions. My results suggest that many of these may not be viable over the long term. This represents loss in population propagules, economic costs, efficiency and effort.

This study projected maile restoration populations as not viable but showed measures to achieve persistence. Elasticity and LTRE analyses pinpointed key strategies that were not obvious, e.g., increasing seedling survival would not be enough to allow restoration populations to persist, instead we must focus on juvenile and adult survival to achieve success. This study highlights the importance of demographic comparisons between restored and wild plant populations. More detailed demographic studies of wild and restored populations are needed to improve the success of restoration projects for maile and other native species.

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