DEVELOPMENT OF A NATIVE PLANT AGROFORESTRY SYSTEM TO RESTORE THE UNDERSTORY OF A LOWLAND WET FOREST IN HAWAI‘I

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ABSTRACT

Native plant agroforestry enrichment systems established in already degraded or altered environments have the potential to protect existing native habitat and provide plant material for cultural purposes while potentially favoring the reestablishment of other non-target native species. Limited information is available on the survival and growth of native Hawaiian plants planted in the understory of secondary forests dominated by nonnative species.

This study investigated an understory agroforestry system that utilized native plants with both economic and cultural value and was designed to provide desired plant material while also complementing restoration activities with the removal of invasive species. Research objectives were: 1) Measure establishment and growth response of three native species planted in removed or intact nonnative understory and determine to what extent light availability, soil moisture and nutrient availability influenced these responses; 2) evaluate the effects of understory nonnative species removal, particularly the dominant invasive species *Ardisia elliptica*, and the planting of native species on nonnative and native seedling recruitment; and 3) examine the photosynthetic light-response and functional differences of the native fern, *Microlepia strigosa*, planted in the two understory treatments.

Results of this research suggest that within lowland wet mesic forests dominated by nonnative species, light availability is the most critical resource limiting establishment and growth of understory native species. Successful and sustainable cultivation of these native species will require some level of canopy opening or manipulation to ensure adequate light levels. The relatively high survival of *M. strigosa* under varying understory light conditions suggests it is a good species for establishing an understory groundcover. Additionally, *M. strigosa* shows increases in photosynthetic capacity when planted within removed understory, but is photosynthetically limited to relatively low light and shaded environments. Results from this research also indicate that established native plantings may provide some resource competition for nonnative species but manipulation of environmental resources, such as decreasing available light, plus continued weeding is more effective at reducing nonnative species recruitment. Consequently, management for a more homogenous nonnative canopy cover can provide more uniform reductions in light transmittance to the understory and limit nonnative seedling recruitment.

TABLE OF CONTENTS

Chapter 5: Conclusion……………………..………………………………..106

LIST OF TABLES

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Chapter 2

Chapter 3

Chapter 4

CHAPTER 1:

INTRODUCTION AND LITERATURE REVIEW

1. Introduction

Tropical forests provide many goods and services for millions of rural and indigenous people around the world. They are resources for commodities such as fuel-wood and construction timber; fruits, nuts, oils, resins and other non-timber forest products (NTFPs), as well as a variety of botanical medicines and pharmaceutical compounds (Molina et al., 1997). Tropical forests also provide ecological services by protecting watersheds, are centers of biodiversity, and sequester atmospheric carbon, potentially slowing global climate change (McNeely and Scherr, 2003). A growing human population and expanding global trade have increased the pressure on tropical forests for resource extraction or conversion to crop and pasture land. Poorly managed forests are vulnerable to non-native species invasion, which can further reduce biodiversity and economic value of the forests (Hobbs and Humphries, 1995). Most forest restoration practices and conservation efforts involve some form of land protection, e.g. fencing, replanting with non-native or native species, and invasive weed control. Forest use by local people is often restricted to protect remaining intact forest and its related biodiversity, or for reforestation efforts (Lamb et al., 2005). In small tropical islands, where land is limited and highly valued, this approach becomes insufficient to incorporate cultural and economic uses of the forest. To address these issues, conservation models are needed that combine management practices that value natural processes of vegetation development with limited resource extraction from the forest (e.g. limited timber and/or NTFP harvesting) (Lamb et al., 2005). Effective ecosystem conservation programs will be those that can be managed to not only provide valuable environmental and biodiversity conservation gains but also cultural and economic benefits for communities.

2. Problem

In Hawaiʻi, as in many tropical areas, exploitation and development of native forests has led to extinctions and precipitous declines in populations of hundreds of native plant and animal species. Extensive clearing for fuel-wood and timber products, and land conversion to grazing and pasture resulted in deforestation of many of Hawaiʻi's watersheds by the late 1800's. Many of these watersheds were reforested in the early 20th century, but mostly with non-native tree species (Skolmen, 1980; Woodcock, 2003). In addition to reforestation activities, many non-native species have been brought to Hawai‘i as part of the botanical trade. Some have become naturalized or invasive by escaping from plantations, nurseries and gardens, spreading naturally from where they were initially planted via wind, birds and non-native mammals. Invasive species tend to grow rapidly, spread easily and are often resilient to disturbance, frequently out-competing native species for space and resources (NISC, 2006). They can adversely affect an ecosystem through changes in ecological processes that can limit survival of a native species as well as the overall composition and structure of native plant communities (NISC, 2006). Non-native species invasions in Hawai‘i have altered many forest ecosystems by impeding the reestablishment of native flora and fauna (Cabin et al., 2002; Litton et al., 2006; Mascaro et al., 2008). Habitat destruction and invasion of non-native species has contributed to the loss of almost half of Hawai’i’s native forests and left the remaining forests significantly altered. The understanding of impacts of non-native species on ecosystem functions, such as nutrient cycling and watershed attributes, can vary in scope and intensity (Gordon, 1998; Parker et al., 1999; Chapin III et al., 2000; Corbin and D'Antonio, 2004; Hobbs et al., 2006; Litton et al., 2006; Cole and Litton, 2014; Murphy et al., 2014).

Decline and degradation of Hawai‘i’s forests has made it increasingly difficult for local people to find and gather native plants for cultural and traditional practices (Timmons, 1996; Vieth et al., 1999; Anderson-Fung and Maly, 2002). Additionally, harvesting of native plants is often perceived to be an added pressure on already declining native populations. There are concerns that it may increase the potential for the spread of invasive species and/or exacerbate regeneration problems associated with invasive species (Dudley and Yamasaki, 2000; Ticktin et al., 2006a; Ticktin et al., 2006b).

Many native Hawaiian plant species are traditionally harvested from the forests and used for wood products, hula (chants and dance), lei (garlands), and healing remedies. These harvesting activities are ancient Hawaiian traditions that continue to hold great importance in present day Hawai’i. The harvesting of wood from the native tree *Acacia koa* was traditionally used for construction of Hawaiian voyaging canoes and now supplies a $35 million fine furniture and craft-wood industry (Friday et al., 2006). Hula, a sacred and ceremonial art composed of chants and dance, carries with it much of the oral history of the Hawaiian people and plays an important cultural role for many people living in Hawai‘i today (Josephson, 1998; Ticktin et al., 2006b). Lei, also used in hula, hold great spiritual value as they represent physical manifestations of Hawaiian deities (Ticktin et al., 2006b). They are also widely used by all segments of Hawai‘i’s multicultural society to celebrate special occasions, including birthdays, graduations and weddings.

3. Restoration Techniques and Approaches

3.1 Enrichment Plantings

In other tropical areas, cultivation and enrichment plantings in the forest understory have been implemented to increase the abundance of highly-valued non-timber forest product species (Sugandhi and Sugandhi, 1995; Carpentier *et al.*, 2000; Moegenburg and Weinstein, 2000; Wilkinson and Elevitch, 2000; Ticktin, 2005) as well as to assist reforestation and increase native plant diversity (Millet et al., 2013). In Hawai‘i, attempts have been made to grow culturally and economically valued understory crops in managed tree cropping systems to alleviate the pressure on wild populations (Dudley and Yamasaki, 2000). Another option, proposed by Ticktin et al. (2006a), is to increase the number of accessible populations of native species through outplantings into accessible forest areas. This could provide local cultural practitioners a way to continue a tradition of gathering while maintaining their own populations. Wilkinson and Elevitch (2000) also mention the potential of a native plant understory cropping system in which native forest areas are cultivated underneath with traditional medicinal or culturally valuable plants.

3.2 Managed Forests

Secondary forests could be used as a medium for this understory cropping system. Secondary forests are defined as forests regenerating largely through natural processes after significant disturbance of the original forest vegetation at a single point in time or over an extended period, and display a major difference in forest structure and or composition with respect to nearby primary forests on similar sites (FAO, 2003). Secondary forests when properly managed, restored or rehabilitated, have the potential to generate significant environmental and livelihood benefits. They can mitigate pressure on primary forests through their ability to produce both wood and non-wood forest products and provide environmental functions, such as protection from soil erosion, regulation of water loss, and fixation and storage of carbon (ITTO, 2002). Additionally, they can assist biodiversity conservation by conserving genetic resources, particularly in areas surrounded by agricultural or urban land and become templates for forest rehabilitation (ITTO, 2002). Restored and managed secondary forests can also become a part of larger mosaic of land-uses, whereby a range of secondary forest ages and stages coexist within landscapes that can support conservation efforts while also providing options for human utilization and provision of goods and services (Chazdon et al., 2009).

Many of the regenerating forests in Hawaiʻi, particularly those near urban or suburban areas have been altered and are considered degraded secondary forest due to the large dominance of non-native species. In these secondary forests, the diversity of native plants is reduced and the regeneration of native species is low (Drake, 1998). Integration of native enrichment plantings into non-native dominated secondary forests could assist it catalyzing native forest succession and increase native biodiversity (Chazdon et al., 2009).

In Hawaiʻi, regeneration of native understory species is more favorable under a native forest overstory than exotic tree plantations (Harrington and Ewel, 1997; Ostertag et al., 2008). However, manipulation of a non-native overstory at various stages of plant growth and restoration may also improve the growth and regeneration of planted native species (Loh and Daehler, 2007). The International Tropical Timber Organization (ITTO) (2002) recommends provisions of adequate light conditions and follow-up maintenance (especially canopy-opening treatments) to support successful enrichment planting. In a tropical secondary forest dominated by the invasive tree *Cinnamomum verum* on the oceanic island of Mahé (Seychelles), a study looking at different levels of canopy removal indicated that intermediate levels of canopy disturbance, i.e. those attained by felling one or a few trees, provided a combination of below- and aboveground resource limitation of seedling growth that could favor native species over invasive species (Kueffer et al., 2010). The authors proposed a strategy for restoring native vegetation that entailed making small gaps in the cinnamon-dominated forest and planting them with native tree species (Kueffer et al., 2010). Mueller-Dombois (2005) also emphasized several silvicultural techniques to achieve restoration success and recommended de-limbing branches from non-native trees and weed control. De-limbing can increase available light and provide substrates (decaying logs) for germination of native species. These recommendations were based on observations that in mature and senescing Hawaiian rainforests decaying logs were found to be the favored micro-habitats for native fern and woody plant establishment (Mueller-Dombois, 2005). Thus, restoration of forests and native biodiversity can be achieved through active management of forest structure and species composition (Daehler and Loh, 2007, Daehler and Loh, 2008).

3.3 Invasive Species Control

Forest restoration techniques, in Hawaiʻi, often include invasive species control. Research in different forest ecosystems in Hawaiʻi has shown that invasive species dominate resource capture and suppress the growth and regeneration of native species (Smith, 1985; Baruch and Goldstein, 1999; Stratton and Goldstein, 2001; Litton et al., 2006). Consequently, their removal generally results in higher resource availability and native plant growth and regeneration (D'Antonio et al., 1998; Cabin et al., 2002; McDaniel et al., 2011; Ammondt et al., 2013). However, since removal of invasive species often results in soil disturbance, lack of revegetation following removal can result in the same or other unwanted non-native species reestablishing. Extensive clearing of non-native species is now often accompanied by revegetation plans but they often utilize fast-growing non-native plants that are used to reforest degraded areas and compete against invasive species more effectively than native ones (Ewel et al., 1999; D'Antonio and Meyerson, 2002; Loh and Daehler, 2007; Ammondt and Litton, 2012). Research comparing a suite of native and non-native species in Costa Rica and Mexico has shown that some native tree species can perform as well or better than most non-native species commonly used for reforestation (Butterfield, 1995; Foroughbakhch et al., 2001). Restoration of degraded or invaded sites also can lead to increases in the natural colonization and regeneration of native species, especially where the forest overstory is restored (Fang and Peng, 1997; Loumeto and Huttel, 1997; Leopold et al., 2001).

In areas where invasive species dominate an extensive area and native plants are largely missing, it may not be possible to eradicate the invader completely. Instead, direct seeding and outplanting of native species could generate a community that, while different than what existed prior to the invasion, nevertheless supports an ecosystem with a substantial native plant composition (D'Antonio and Meyerson, 2002). Limited research has been conducted on the use of native plants to suppress regeneration of invasive species in Hawaiʻi (Ammondt and Litton, 2012). In other places, native species have been found to suppress invasive plants. For example, Perry et al. (2004) found that an invasive grass could be suppressed by a native sedge when nitrogen availability was reduced. Daehler (2003) found that invasive species in general are not statistically more likely to have higher growth rates, competitive ability, or fecundity than native species. Rather, the relative performance of invaders and co-occurring natives often depends on growing conditions. Most commonly, these conditions involve reduced resources (nutrients, light, water) and/or specific disturbance regimes. Ostertag et al. (2009) concluded that in a Hawaiian lowland wet forest, canopy opening will be critical to avoid complete conversion of these forests to non-native dominated systems. While the authors observed that adult native species responded slowly to removal and changes in resource availability, they concluded that native seedlings may be the strongest beneficiaries of removal as a management strategy. Another study in a Hawaiian dry forest restoration observed that native species showed increased productivity and resource acquisition with invasive grass removal (Thaxton et al., 2012). The authors concluded that the combination of grass removal and shading may be an effective approach to the restoration of degraded tropical dry forests in Hawaii (Thaxton et al., 2012). Consequently, manipulation of resources to improve growing conditions for out-planted native species could increase survival and establishment in environments dominated by non-native species.

3.3.1 Ardisia elliptica

The research sites for this project are dominated by the invasive tree *Ardisia elliptica*. *A. elliptica*, commonly known as shoebutton ardisia or inkberry, is an evergreen, small tree that can grow up to 6m in height. It is native to Sri Lanka, India, China, Taiwan, Malaysia, South East Asia, Indonesia, and the Philippines (Francis, 2003). While initially introduced as an ornamental plant to other tropical countries in the early 1900s, *A. elliptica* is now considered invasive and an environmental problem in many tropical areas around the world including the Cook Islands, French Polynesia, Australia, southern Florida, and Puerto Rico (Pascarella and Horvitz, 1999; McCormack, 2002; Space and Flynn, 2002; ISSG, 2014). In Hawaiʻi, *A. elliptica*, is listed as a noxious weed (DPI, 2003) and is found on four islands (Kauai, Oʻahu, Maui, and Hawaiʻi), with major infestations occurring on the islands of Oʻahu and Maui (Smith, 1985). This information comes from a survey conducted in 1984, and it is unclear how much the plant has spread since that time. Of particular concern are severe infestations occurring in Mānoa valley (R. Baker, personal communication).

Some of the characteristics that make *A. elliptica* invasive are its fast growth, ability to survive and reproduce in low light conditions, prolific fruiting, avian and mammalian seed dispersal, and high seed viability (Pascarella and Horvitz, 1999; Koop, 2004; Koop and Horvitz, 2005). The high reproductive output and high shade-tolerance, produces carpets of seedlings (>400 plants per square meter) underneath mature plants (Koop, 2004). *A. elliptica* can form dense thickets that reduce available space and light for other plants, especially understory native species. In addition, it does not require disturbance to become invasive and has been found in well-established forest understories in Florida (Koop, 2004).

While eradication of established *A. elliptica* populations is generally not feasible over large areas, restoration protocols that involve both removal of *A. elliptica* and revegetation could encourage establishment of target and non-target native species. Research on amur honeysuckle (*Lonicera maackii*), a shrub that can also form dense thickets, demonstrated that removal can have a positive influence on overall native plant establishment (Hartman and McCarthy, 2004). In Florida, control of *A. elliptica* significantly reduced cover by non-native vines and had a significant overall positive effect on recruitment of seedlings and saplings of native trees, shrubs and herbs (Horvitz and Koop, 2001).

4. Agroforestry Systems in Hawaiʻi

Using the above-mentioned restoration techniques and combining them with agronomic practices can create novel agroforestry systems that meet the needs of both the environment and the community. Traditional or indigenous agroforestry systems in the tropics, such as home gardens, which utilize the rich structural and species diversity of the forest to encourage the growth of desirable species and control the growth and spread of weeds, are often cited as examples of agronomic systems that are environmentally sustainable and support ecosystem function (Michon and De Foresta, 1997). It is unknown if native Hawaiians utilized specific agroforestry systems for conservation and cultivation of important native plant species, but they were certainly engaged in various degrees of forest management. Ticktin et al. (2006b) note that many of the traditional and customary protocols for gathering native plants have a strong conservation rationale that includes controls on the amount and means of gathering. Additionally, the authors state that “wild plants were not just gathered, but actively managed for increased propagation”, and provide examples such as maile (*Alyxia stellata*) seeds being strewn after gathering and propagation of mokihana (*Melicope anisata*) by planting cuttings in the forest (Ticktin et al., 2006b). Handy and Handy (1991) provide further examples of forest cultivation by native Hawaiians in their description of dry taro cultivation (*Colocasia esculenta*) within enclosed clearings of kukui (*Aleurites moluccana*) and tree-fern forests. Taro was planted in holes left by felled trees which were allowed to decompose on site and provided a means of weed control and fertilization through decaying leaves, trunks and branches. Handy and Handy (1991) also describe forest plantings on the banks of streams or in pockets above the streams, especially where valleys became narrow and were bordered by rain-forest. The authors note that native Hawaiian planters (farmers) cultivated flowering plants (e.g. ‘ilima (*Sida* spp.) and *Hibiscus* spp.) around houses in order to have flowers at hand for making lei (Handy and Handy, 1991). It seems probable that other useful plants could have been encouraged to grow around the dwelling either by weeding out other non-useful plants or by directly propagating or planting desired species.

4.1. Agroforestry and Restoration

Most modern agroforestry systems utilize a mixture of native and introduced plant species to maximize the growth of food or cash crops while providing a sustainable supply of fuel or construction wood. However, agroforestry systems with their numerous combinations of species compositions and management levels can be utilized to meet a variety of both human and ecological needs. Their ability to create a range of vegetation types and successional stages across the landscape promotes biological diversity, provides opportunities for growing and harvesting an array of products, and can promote active control of invasive species (Gillison, 2000; McNeely and Schroth, 2006). Agroforest plantations established on degraded land in Puerto Rico (Lugo, 1988; Parrotta, 1992; Lugo et al., 1993; Parrotta, 1993) and China (Brown and Lugo, 1994), have been shown to facilitate recolonization of native flora through their influence on understory microclimate and soil fertility, suppression of dominant grasses, and provision of habitat for seed-dispersing wildlife.

Agroforestry systems can also offer local people the opportunity to be involved with the management of their forest resources increasing their connection to and value of the forest. In Cameroon, the afforestation of *Imperata cylindrica* grasslands with a complex cocoa agroforestry system integrates empirical knowledge and practices derived from farmers' experience of cocoa cultivation while also increasing soil organic matter within the agroforestry system. Community-based forest management that can provide more favorable strategies to restore and manage forests can lead to local communities being more prepared to accept responsibility for sustainable forest management in exchange for socioeconomic development and forest-use benefits (Jagoret et al., 2012). In India and SE Asia, community-based reforestation projects have been successful in adapting traditional agroforestry practices to facilitate regeneration of locally valued native species in degraded secondary forests (Poffenberger and McGean, 1994). Agroforestry systems, thus, can easily be extrapolated to other areas where there is a need for rehabilitation of degraded lands caused by unsustainable agricultural practices, or to conserve fragile habitats against unsustainable exploitation or agricultural conversion. A combination of these approaches can produce innovative agroforestry systems that optimize the trade-off between maintaining the integrity of native forests and providing high yields of valuable products.

The management challenge for agroforestry systems with a restoration aim is to maintain certain species composition and structure in the long term, sustain regeneration of desired native species while also maintaining adequate resources to be able to support removal and harvesting of plant material. Management strategies should seek to regain and retain ecosystem integrity, i.e. the ability of an ecosystem to provide a certain set of goods and services for which the site is suited, and include the maintenance of native biological diversity, ecological processes and structure, and sustainable cultural practices.

5. Research goals

This research addresses the development of a novel agroforestry system in which the understory of secondary forests, dominated by nonnative species, is enriched with plantings of culturally and economically desired native plants. The goal is to be able to provide community groups and local organizations the opportunity to sustainably harvest desired plant material without negatively affecting wild declining populations. The system, therefore, serves a dual purpose of providing both desired plant material and complementing restoration activities with the removal of invasive species and the addition of native ones. Additionally, the system may potentially favor the regeneration of rare and/or declining non-target native species found within the area. The research will further knowledge and understanding of the selected native plant species in regards to their environmental requirements and potential for restoration while also exploring potential techniques and applications for understory restoration in Hawaiʻi .

6. Study objectives

The first objective was to measure establishment and growth response of native species outplanted within an intact non-native (uncleared) or where the non-native understory was removed (cleared). The research tested a mixture of three native species – a groundcover and two midstory shrubs – *Microlepia strigosa*, *Pipturus albidus*, and *Alyxia stellata* = *A. oliviformis,* cf. (Middleton, 2000). These plants were selected for their ecological, cultural, and economic values. The research was designed to provide desired plant material while also complementing restoration activities with the removal of invasive species and suppression of re-invasion through replacement with native species. In this study, we sought to answer the following questions: (1) how does establishment and growth response of selected outplanted understory native plants differ when grown in both existing and cleared forest non-native understory environments? And (2) to what extent do light availability, soil moisture and nutrient availability influence these responses?

The second objective evaluated the effects of both understory nonnative species removal and planting of native species on nonnative and native seedling recruitment. Contrasting forest structure and environmental conditions created by the dominant pioneer species may have an effect on the herbaceous trajectory of succession. Certain plants may not tolerate conditions created by dominant species, thereby the dominant species acts as an ecological filter permitting the regeneration of only certain species. Of particular interest in this objective was the effect of removing the dominant invasive species *A. elliptica* on community structure and composition, and native and nonnative seedling regeneration. Also of interest was the ability of native enrichment plantings to reduce nonnative seedling recruitment.

The third objective was to examine species-specific photosynthetic light-response to understory restoration. The native fern groundcover, *M. strigosa*, demonstrated the greatest survival and growth in both understory treatments. For this objective, attention was focused on the fern and understanding the functional differences between ferns grown in the two understory shaded environments. Light response curves of ferns in each treatment were measured and correlated those with selected frond traits; leaf mass per area (LMA), frond nitrogen per unit area (N_a), stomatal density (S_D), and stomatal guard cell length (S_L) to explain functional responses in the different understory light environments.

CHAPTER 2:

UNDERSTORY FOREST CULTIVATION OF THREE NATIVE PLANT SPECIES UNDER DIFFERENT LIGHT CONDITIONS IN A NON-NATIVE DOMINATED LOWLAND WET FOREST IN HAWAIʻI

1. Introduction

Habitat destruction and invasion of non-native species into Hawaiʻi's forests have made it increasingly difficult for local people to find and gather native plants for cultural and traditional practices (Vieth et al., 1999). Harvesting of native plants also comes into conflict with conservation and restoration goals as it is often perceived to be an added pressure on already declining native plant populations and can increase the spread of invasive species (Dudley and Yamasaki, 2000; Ticktin et al., 2006a; Ticktin et al., 2006b; Jakobs et al., 2010). There is a need to develop forest management strategies that can sustain the traditional harvesting needs of Hawaiʻi's local communities while also supporting ecosystem services and aiding in the restoration of Hawaiʻi's degraded forests.

In other tropical areas, forest farming systems, including understory enrichment plantings, have been implemented to increase the abundance of highly-valued non-timber forest products (NTFPs) and reduce collection pressure on plants and plant parts harvested from wild populations (Sugandhi and Sugandhi, 1995; Carpentier et al., 2000; Moegenburg and Weinstein, 2000; Wilkinson and Elevitch, 2000; Ticktin, 2005). Typically, forest farming systems are implemented to mitigate ecological degradation of intact forests and are viewed as a conservation strategy. Alternatively, in Hawaiʻi where native forest is relatively rare, forest enrichment plantings could be used as a restoration tool in which existing non-native forest is managed to enhance establishment and growth of native plants. A similar model has been put forth by Vieira et al. (2009) who propose complementing restoration practices with agricultural techniques. These mixed agricultural and restoration systems can create a range of vegetation types and successional stages across the landscape to support biological diversity, provide opportunities for growing and harvesting an array of products, and promote active control of invasive species (Gillison, 2000; McNeely and Schroth, 2006). Implementation of such agricultural-restoration systems in Hawaiʻi could be an additional conservation tool; however, there is limited research regarding forest cultivation of native plants in Hawaiʻi (Dudley and Yamasaki, 2000). In particular, little is known about the conditions that would optimize native understory species establishment and growth in forest areas now dominated by non-native species (Mascaro et al., 2008).

Successful re-vegetation of Hawaiian native species for restoration has included creating micro-environmental conditions conducive for outplanting survival and growth (Sailor, 2006). In general, it has been found that non-native invasive species, are not statistically more likely to have higher growth rates, competitive ability, or fecundity than native species (Daehler, 2003). Rather, the relative performance of invaders and co-occurring natives often depends on growing conditions; most commonly, availability of plant resources (e.g. light, water and nutrients) and/or specific disturbance regimes. Consequently, manipulation of micro-environmental resources to improve growing conditions for outplanted native species could increase survival and establishment in environments dominated by non-native species.

In invaded lowland wet-mesic forests in Hawaiʻi, light availability is likely the most limiting resource to understory species, particularly under stands of non-native dense canopy trees (Wong, 2007; Ostertag et al., 2009). Hence, active management of the light environment through the manipulation of the overstory to improve the establishment, growth and regeneration of outplanted native species has been considered a promising approach to create self-sustaining communities of native plants in Hawaiʻi (Loh and Daehler, 2007; McDaniel and Ostertag, 2010). However, questions remain as to how to best implement such manipulations and to what scale.

The creation of small gaps within the forest has been suggested as a means to afford understory species with improved light levels. In addition to increased light availability, microclimates within gaps are generally characterized by lower humidity, and higher soil moisture and temperature levels than the adjacent forest understory (Denslow et al., 1990). They can also allow for increased rainfall interception, and fewer plants can mean reduced transpiration losses. However, gaps can also promote establishment of undesirable species which then compete with desired understory plants. In Hawaiʻi, such gaps could exacerbate non-native species invasions which have been shown to impede the reestablishment of native flora and fauna by dominating resource capture in various forest ecosystems (Smith, 1985; Baruch and Goldstein, 1999; Stratton and Goldstein, 2001; Litton et al., 2006). The key is to find a balance between removing invasive species to facilitate establishment and growth of native species and avoiding disturbance of the forest canopy, which may allow other non-native species to invade the area (Kueffer et al., 2010).

In other tropical understory enrichment plantations, the forest canopy is left largely intact while much of the understory and midstory vegetation is cleared to decrease competition and increase light availability for cultivated species (Trauernicht and Ticktin, 2005). Similar forest management has been proposed in Hawaiʻi where partial removal of invasive species coupled with direct seeding and/or outplanting of native species has been proposed as a means to generate a community that while different than what existed prior to the invasion, nevertheless supports an ecosystem dominated by native species (D'Antonio and Meyerson, 2002). This type of invasive species management can be advantageous in areas of steep slopes where complete clearing can contribute to increased erosion. This also has the potential to reduce equipment and labor costs associated with invasive species removal.

Selection of native species appropriate for an agricultural-restoration system should be based on and prioritized by both the agricultural and restoration needs defined by the project and outplanting environment. In this study, the primary criterion was the need for species to have cultural, economic and/or restoration value in Hawaiʻi. A species’ cultural value was estimated by how much the species was currently utilized in Hawaiian culture. Economic value was evaluated based on price/monetary value of harvested plant material. Restoration value was determined by examining a species’ potential to compete with non-native invasive species. Desirable traits for restoration value include having relatively fast growth and spread and/or dense canopy that could shade out seedlings of non-native species. Secondly, species needed to be characterized as an understory plant and exist or have been documented to exist in the research area. Ideally, the source of plant material would come from local populations to maintain local gene pools and prevent the spread of plant diseases and insect pests (Sailor, 2006). Appropriate functional types of understory species include groundcovers, low lying herbaceous plants, and mid-story shrubs or small trees (Denslow, 1996). Desirable ground covers include those that can quickly establish and spread to reduce weed regeneration, soil erosion, and soil moisture evaporation. Mid-story species are desired that can grow in height relatively quickly, thereby filling the space occupied by invasive mid-story plants and that can provide shade to create a cooler and more humid microenvironment. A mixture of understory types is desired to increase efficiency of land use and exploit more environmental niches such as available light, space and nutrients (Wilkinson and Elevitch, 2000). Planting multiple species from an agricultural perspective also provides for a diversity of products, increased total yields over time, and a reduced risk of losing all outplantings from mortality, pests, and disease that may differentially affect species (Wilkinson and Elevitch, 2000). There is limited research on the effects of different plant combinations of both species and quantities, especially for native Hawaiian plants. Generally, the more complex the system the more difficult it is to discern the effects and interactions. The final criterion was that selected plant species would be available for purchase or easily propagated in large quantities so that they could be used by practitioners or restoration professionals for real-world projects.

The goal of this research was to address the challenges of forest enrichment in Hawaiʻi with the development of a novel agricultural-restoration system in which the understory of an existing forest, dominated by non-native species, was cultivated with plantings of culturally and economically desired native plants. The research tested a mixture of three native species – a groundcover and two midstory shrubs – to maintain a relatively simple design. The system was designed to provide desired plant material while also complementing restoration activities with the removal of invasive species and suppression of re-invasion through replacement with native species. In this study, we sought to answer the following questions: (1) how does establishment and growth response of selected outplanted understory native plants differ when grown in both uncleared and cleared forest understory environments? And (2) to what extent do light availability, soil moisture and nutrient availability influence these responses?

2. Materials and methods

2.1 Plant species

Three understory plant species native to Hawaiian wet-mesic forests were selected for this study: palapalai (*Microlepia strigosa* (Thunb.) Presl.), maile (*Alyxia stellata* (J. R. Forst. & G. Forst.) Roem. & Schult. = *A. oliviformis,* cf. (Middleton, 2000)), and māmaki (*Pipturus albidus* (Hook. &Arn.) A. Gray ex H. Mann). These species co-occur across a range of elevation and rainfall on many of the Hawaiian Islands (Krauss, 1993; Wagner et al., 1999). On the island of Oʻahu they have been historically found throughout wet-mesic forests in Mānoa Valley (MacCaughey, 1917). Palapalai is culturally important in Hawaiʻi, where it has been traditionally used to decorate hula altars and is currently woven into lei (Krauss, 1993). It is a relatively fast-growing understory fern, producing 6-10 new fronds per year depending upon site conditions (Ticktin et al., 2006a). Maile is a vining shrub. It is highly valued as a lei plant and shows high rates of seed germination and seedling survival under greenhouse conditions (Tanabe and Hirowatari, 1979; Tanabe and Smith, 1979; Tanabe, 1980). Māmaki is a tall, spreading shrub that casts moderate to heavy shade. It was traditionally used in making kapa cloth and as a medicinal plant. Today its leaves are sold as a popular herbal tea. Research has shown that its growth rate in partial shade is similar to that of several understory invasive weeds (Pattison et al., 1998). Consequently, it has the potential to maintain dominance over invasive herbs and shrubs that grow through a ground cover layer.

2.2 Study Sites

Two research sites were selected at the Harold L. Lyon Arboretum, located in Mānoa Valley on the leeward side of the island of Oʻahu, Hawaiʻi. These sites were selected because they are characteristic of wet-mesic forests dominated by non-native species found in the watersheds throughout Hawaiʻi. Additionally, the arboretum is owned and managed by the University of Hawaiʻi and has comprehensive records for outplanted trees and shrubs. The lower site (elevation 262 m) has a continuous overstory of various species of gymnosperms (e.g. *Juniperus* spp., *Aurocaria* spp. outplanted for reforestation ca. 1915) and other non-natives, such as *Schefflera actinophylla* (Endl.) Harms, *Aleurites moluccana* (L.) Willd., *Cinnamomum burmanni* (Nees & Th. Nees) Nees ex Blume., and *Rhus taitensis* Guill. The upper research site (elevation 290 m) has never been reforested, but it was subjected to deforestation and uncontrolled grazing in the 19th century. It has a non-continuous non-native overstory dominated by *S. actinophylla, C. burmanni*, and *R. taitensis* with no gymnosperms present. Some native mid- to upper-story species, such as kōpiko (*Psychotria* spp.) and lama (*Diospyros* spp.), and understory species, such as ʻieʻie (*Freycinetia arborea* Gaudich.), maile (*A. stellata*), māmaki (*P. albidus*), and palaʻā (*Sphenomeris chinensis* (L.) Maxon) are present. Both sites have a mid-story dominated by the invasive *Ardisia elliptica* Thunb. (Table 1).

The sites are located on steep terrain with slopes ranging from 50 to 80% and an annual mean rainfall of 3800 mm (WRCC, 2013) . The soil is part of the Tantalus Series and consists of shallow, well-drained silt loams developed from volcanic ash and material weathered from cinders (USDA, 1965). Under ideal conditions an area with lower slope would be more suitable for outplanting, since steep slopes can be difficult to access and increase erosion risks from trails and foot traffic. On O‘ahu, access to and availability of more suitable forested areas for research is limited. Nonetheless, slopes in this research area are representative of many invaded secondary forested areas throughout Hawai‘i’s various mountain ranges and are commonly encountered in restoration sites.

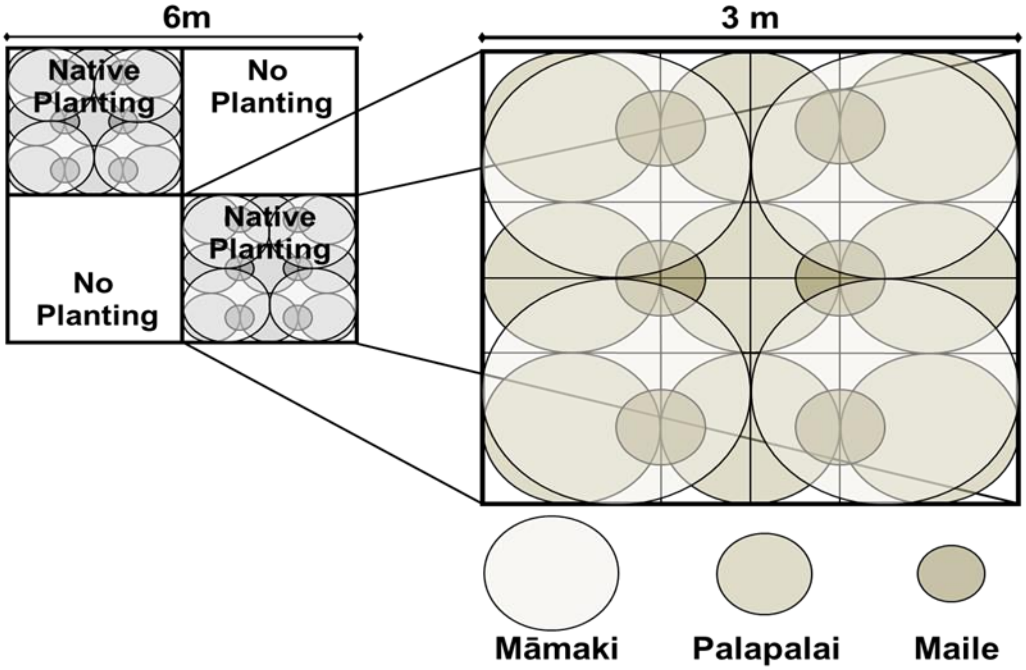
This experiment was laid out in the field in a randomized complete block, split-plot design with replications within blocks. Sites were designated as blocks and contained six plots, each measuring 6 x 6 m. All plots were orientated along a NW-SE aspect. A 1-m buffer zone surrounded each 6 x 6-m plot, with plots separated by at least 2 m. Each was divided into four 3 x 3-m quadrants. The experimental treatments consisted of understory removal and native species outplanting. The main-plot treatment, referred throughout the chapter as the “cleared treatment”, consisted of removal of non-native understory plants and included the removal of both stems and roots of all non-native species less than 10 cm dbh (diameter at breast height = 1.3 m). The split-plot treatment was outplanting of three native species. Native species were outplanted in two diagonally opposing quadrants (Figure 1), leaving a 0.5-m buffer unplanted at the edge of each quadrant. For this study, results are reported only for the planted split-plots.

Treatment application occurred during February and March of 2005 and involved removal of midstory and understory non-native plant species. The cleared treatment was manually weeded bi-annually. Non-native woody species were killed either by cutting to a stump or pollarding (partial trunk left rooted in ground – referred to as “living posts”), followed by treatment with an herbicide (8% triclopyr or GarlonA®) to eliminate re-sprouting. Understory herbaceous weeds were manually removed. Permit restrictions at Lyon Arboretum did not allow removal of trees ≥ 15cm DBH; hence, there was no overstory clearing.

Table 1. Plant species composition, stem density and basal area in study area prior to clearing.

	Upper Block			Lower Block		
DBH Size Class	**Woody Species**	**Stem Density (stems/ha)**	**Basal Area (m^2/ha)**	**Woody Species**	**Stem Density (stems/ha)**	**Basal Area (m^2/ha)**
>10cm	*A. elliptica*	46.30	0.51	*Juniperus spp.*	138.89	32.09
	C. burmanni	46.30	1.23	*R. taitensis*	46.30	1.56
	Citharexylum caudatum	46.30	0.41			
	Cordyline fruticosa	46.30	0.66			
	Diospyros spp.	46.30	0.43			
	Ilex paraguayensis	46.30	0.49			
	Macaranga mappa	46.30	0.48			
	S. actinophylla	92.59	2.10			
	Total	**416.67**	**6.31**	**Total**	**185.19**	**33.65**
5 - 9.9cm	*A. elliptica*	8703.70	28.12	*A. elliptica*	2083.33	5.57
	C. burmanni	138.89	1.08	*C. burmanni*	92.59	0.24
	C. caudatum	324.07	1.24	*C. caudatum*	46.30	0.18
	C. fruticosa	694.44	2.26	*C. fruticosa*	416.67	1.15
	M. mappa	46.30	0.14	*Heliocarpus popayanensis*	46.30	0.24
	P. cattleainum	138.89	0.52	*M. mappa*	555.56	1.82
	Psychotria spp.	277.78	1.17	*S. actinophylla*	185.19	0.85
	S. actinophylla	185.19	1.01			
	Total	**10509.26**	**35.55**	**Total**	**3425.93**	**10.06**
1 - 4.9cm	*A. elliptica*	10787.04	5.76	*Araucaria spp.*	46.30	0.01
	C. burmanni	92.59	0.07	*A. elliptica*	9398.15	0.09
	C. caudatum	185.19	0.04	*C. caudatum*	92.59	0.04
	C. fruticosa	2592.59	0.08	*C. fruticosa*	2037.04	0.06
	Costus spp.	1064.81	0.01	*M. mappa*	92.59	0.09
	F. arborea	92.59	0.03	*S. actinophylla*	138.89	0.06
	P. cattleainum	138.89	0.09			
	Psychotria spp.	185.19	0.09			
	S. actinophylla	92.59	0.02			
	Total	**15231.48**	**6.20**	**Total**	**11805.56**	**0.35**
<1cm	*A. elliptica*	15324.07	--	*A. elliptica*	4629.63	--
	C. burmanni	138.89	--	*C. fruticosa*	648.15	--
	Cinnamomum zelanicum	138.89	--			
	C. caudatum	138.89	--			
	C. fruticosa	231.48	--			
	S. actinophylla	46.30	--			
	Total	**16018.52**	--	**Total**	**5277.78**	--

Figure 1. Schematic diagram of original split-plot planting design. Low germination and slow growth limited actual number of maile plantings to three per quadrant for a total of six pants per plot.



2.3 Planting

The selected native species were planted in rows along the contour, following standard agroforestry designs (Clarke and Thaman, 1993; Nair, 1993; Elevitch and Wilkinson, 2000). Outplanting in rows allowed for ease of measurement, management, and harvesting, while planting along the contour reduces soil erosion. Plant spacing was 1.0 m for palapalai and 1.5 m for māmaki, based on personal observations of the average spread of mature plants found within the area (Figure 2). Maile was planted in between the palapalai and māmaki. Plants were outplanted 0.5 m inside the plot border to minimize edge effects. Plant density was based on potential inter-competition effects, expected growth-rate, and quantity of plants available. The focus of this study was on the survival and growth of native outplantings under different understory light conditions; consequently, planting density was not manipulated. Native species outplantings were planned to occur consecutively within a six- to eight-month period. Consecutive, as opposed to simultaneous, species outplanting was chosen due to difficulties in purchasing or propagating sufficient plants of each species at the same time. Palapalai was outplanted first in December 2005 and January 2006 to establish a ground cover that could reduce soil erosion and potentially minimize seedling regeneration of weedy species. Eighteen individuals per plot were outplanted. Māmaki was outplanted in late January and early February 2006 to establish a mid-story canopy capable of limiting growth of invasive herbs and shrubs that grow through the palapalai ground cover layer. Pest problems and high mortality within the greenhouse limited the number of māmaki outplanted to three per plot. Five additional plants per plot were added in October 2007 yielding a total of eight plants per plot. In June 2006 maile plants were added. Low germination rates and slow growth limited the number of maile plants to six plants per plot. Additional maile plants were later outplanted, but data from these plants were not included in this study.

2.4 Plant measurements

Survival and non-destructive growth measurements on outplanted species were taken every three months for two years except for the last measurement for maile and māmaki, which was taken after an interval of six months. Growth was measured by recording changes in plant dimensions and included:

- Palapalai – crown diameter (CD), length of longest frond (LF), number of fronds (NF), and number of fronds with spore development (FS). NF measurements began in April 2006. FS measurements began in January 2007 when spore development was first observed.
- Māmaki – height of main stem (SH). This species incurred loss of leaves and stem die-back due to herbivory, drought and falling debris. Additional growth measurements of leaf size are not included since they were highly variable and inconsistent.
- Maile – height of main stem (H), length of longest leaf (LL), number of leaves (NL), and number of stems (NS).

2.5 Light environment

To characterize the spatial and temporal distribution of photosynthetically active radiation (PAR) among understory treatments, LI-190SA line quantum sensors (LI-COR, Inc. Lincoln, NE) were randomly placed 1 meter above the soil surface and above the height of the outplanted species in each quadrant of the plot oriented along a North-South axis to prevent sunlight gradients along the length of the sensors. Sensors were attached to data loggers, and readings were taken every five minutes for 12 hours (7am to 7pm). An additional LI-90 point quantum sensor was placed in the closest open area (parking lot area of Lyon Arboretum, elev. 150m) to estimate incident PAR during the entire measurement period. Sensors were subsequently moved to the next plot and the above steps repeated for all twelve plots. Proportion of light transmitted was calculated as the ratio of below-canopy to above-canopy PAR.

Line quantum sensors are expensive, can be challenging to use in forest conditions, and are not conducive for obtaining a quick assessment of forest light conditions. More often an estimation of canopy cover is used for forest management recommendations. For comparison purposes, canopy cover was estimated using a hand-held concave spherical densiometer as described in Lemmon (1956).

2.6 Soil moisture and soil nutrient availability

Volumetric soil moisture content at the soil surface (sampling depth approx. 6 cm, sampling volume approx. 75 cm^3) was measured using a TH_2O Portable Moisture Probe (Dynamax, Inc., Houston, TX, USA). The probe sends a microwave signal and analyzes a reflected signal to measure the dieletric constant (theta) of the soil. The dielectric reading, expressed in millivolts, was then converted to volumetric water content after calibration with the soil type found within the research area. Three stratified sampling measurements per quadrant (upper, middle and lower) were taken twice a month for a year. Soil moisture measurements were graphed against monthly precipitation totals taken between June 2007 and May 2008 (Mānoa Lyon Arb. Station 785.2, Record of Climatological Observations, NCDC, NOAA). Total rainfall for June 2007 to May 2008 was 3937 mm.

An initial soil nutrient analysis was conducted in October 2005 prior to any treatment applications by collecting 10 random soil samples homogenized per plot and then analyzed for pH and major plant nutrients by the Agricultural Diagnostic Service Center at the University of Hawaiʻi at Mānoa. In August 2007 extractable soil nutrient concentrations were measured using PRS (Plant Root Simulator)™-probes (Western Ag Innovations, Inc., Saskatoon, Canada). Four sets of PRS-probes were placed in each plot (one set in each quadrant) for four weeks then removed and cleaned of soil with double distilled water. Probes were sent to Western Ag Innovations, Inc. for colorimetric analysis of major and minor nutrients.

2.7 Statistical Analyses

Exploratory data analysis revealed that palapalai survival count data did not fit either a normal or Poisson distribution and could not be normalized through transformation. Maile and māmaki survival count data followed a Poisson distribution but were positively skewed and could not be normalized through transformation. Additionally, maile and māmaki data sets contained a large number of zeros. Hence, survival count data for all three species was converted to a categorical format (i.e. survival = yes or no). Chi-square non-parametric tests were used to determine effects between treatment, block, and treatment by block interaction on survival. A third control variable of 'planting time' was added for māmaki. Fisher's exact test was reported since some plant species had cells with an expected frequency of less than five (SPSS, 2009).

Out of the three species only palapalai had an adequate number of surviving plants to compare plant measurement between treatments over time. Palapalai plant measurement data did not meet assumptions of sphericity; hence, MANOVA was used to analyze for treatment, block and interaction effects on repeated plant measurements over time. Except for the first measurement period, plant measurements did not meet assumptions of normality or homogeneity of variance-covariance matrices even when transformed. Variance tended to increase as plant measurements increased over time. Results from analysis were reported since MANOVA is robust to these violations when sample sizes are equal. Pillai's Trace was used as the multivariate significance test due to its robustness to violations of normality and homogeneity of dispersion (Field, 2009).

Maile and māmaki had low to zero survival in the uncleared treatment, respectively. Hence, ANOVA was used to analyze plant measurements for block effects over time within the cleared treatment. Two separate univariate tests on height measurements for māmaki were run to account for the two outplanting times and difference in number of individuals outplanted at each time. The first included all measurement dates (10) for plants outplanted in April 2006 (n = 36). The second included the last three measurement dates (Oct 2007, Feb 2008, and Jan 2008) for individuals outplanted in October 2007 (n = 60). All count data (NF, FS, NL and NS) were square root transformed prior to analysis to improve symmetry and spread within distribution.

Non-linear regression was used to predict species growth from percent light transmittance. Two plant growth measurement types were compared: plant measurement data collected during the same time period as light transmittance (7/1 – 7/31/2007) and relative growth rate (RGR) calculated as:

$$LN(T2 \text{ plant measurement}) - LN(T1 \text{ plant measurement}),$$

where LN is the natural log, T1 is plant measurement at outplanting and T2 is final plant measurement. Dates for T1 and T2 for each species are as follows: Palapalai (T1 = 12/28/2005; T2 = 2/18/2008), māmaki (T1 = 1/15/2006; T2 = 9/5/2008); maile (T1 = 6/21/2006; T2 = 9/5/2008). Plant measurements averaged per quadrant were compared with percent light transmittance per quadrant to improve accuracy. The following adapted Michaelis-Menten function was used to model effects of light on growth:

$$\mu = \frac{AL}{\frac{A}{S} + L}$$

where μ is the mean response of a species plant measurement per quadrant; L is percent light transmitted per quadrant; *A* and *S* are plant measurement specific parameters which represent asymptotic growth rate (*A*) and slope of growth response at low light (*S*). The Michaelis-Menten function has been commonly used as way to predict plant growth from light availability (Finzi and Canham, 2000; Lin et al., 2002). *A* and *S* parameters for July 2007 measurements were not compared to each other since they are unique for each plant measurement and reflect mean size or count values taken at a specific time. RGR values allowed us to evaluate across plant measurements within each species and compare their level of response to high (A) and low (S) light availability. Larger *A* values indicate that a plant measurement increases rapidly when light availability is high and conversely if values are small. Large *S* values indicate that when light is limited, a small increase in light availability leads to large increases in a plant measurement and conversely if values are small.

Proportion of light transmittance and overstory canopy cover data were arcsine square root transformed to improve normality and homogeneity of variance. Transformed data were analyzed using a two-way ANOVA. Proportion of light transmittance data was regressed against proportion of canopy cover data to determine effectiveness of canopy cover to predict light transmittance.

In this study, only soil moisture measurements taken in planted quadrants were analyzed. MANOVA was used to determine treatment and block effects over time.

For the initial soil nutrient analysis, T-tests were used to analyze differences in nutrient availability between blocks. Two-way ANOVA was used to analyze differences for each nutrient concentration using the PRS-probes. All statistical analyses were performed using PASW Statistics 18, Release Version 18.0.0. July 30, 2009 (SPSS, 2009).

3. Results

3.1 Environmental conditions

Percent light transmittance in the uncleared treatment varied between 0.62 and 1.93% (mean 1.11%) in the upper block and 0.34 and 1.16% (mean 0.65%) in the lower block (Figure 3). The cleared treatment ranged from 6.80 to 39.97% (mean 20.09) and 1.76 and 6.19% (mean 3.62%) in the upper and lower blocks, respectively. Percent canopy cover reflected the inverse of percent light transmittance with the uncleared treatment varying between 81.8 and 96.4% (mean 89.5%) in the upper block and 78.7 and 94.5% (mean 88.8%) in the lower block. Cleared treatment ranged from 18.9 to 73.74% (mean 45.6%) in the upper block and 51.6 and 88.3% (mean 71.9%) in lower block. Pearsons correlation analysis revealed a strong inverse relationship between canopy cover and light (-0.97). Linear regression analysis demonstrated that percent canopy cover was a good predictor of percent light transmittance in our plots, with an adjusted R^2 of 0.94 (Figure 4). Multivariate analysis of repeated soil moisture measurements from June 2007 to May 2008 revealed significantly higher soil moisture levels in the upper block (Table 3). No significant effects of treatment or treatment by block were found.

T-tests for differences in the initial soil nutrient availability survey showed that only zinc concentrations differed significantly between blocks (Table 6). Soil nutrient analysis of PRS^{TM} probes revealed no differences in nutrient availability between treatments (Table 7). Magnesium (Mg) concentrations were significantly higher in upper block; whereas, sulfur (S) concentrations were significantly higher in lower block. There was an interaction effect for Cu (F = 7.660, p = 0.024).

Table 2. Univariate analysis output for percent light transmittance and canopy cover.

Light Measurement Variable	**Mean Square**	***F***	***df***	***P* Value**
% Light Transmittance[a]				
Treatment	0.316	61.705	1	<0.001
Block	0.127	24.748	1	<0.001
Treatment x Block	0.087	17.084	1	0.001
% Canopy Cover[a]				
Treatment	1.583	111.312	1	<0.001
Block	0.221	15.557	1	<0.001
Treatment x Block	0.247	17.363	1	<0.001

a. Arcsine square root transformed data

Figure 2. Mean percent values for light transmittance and canopy cover.

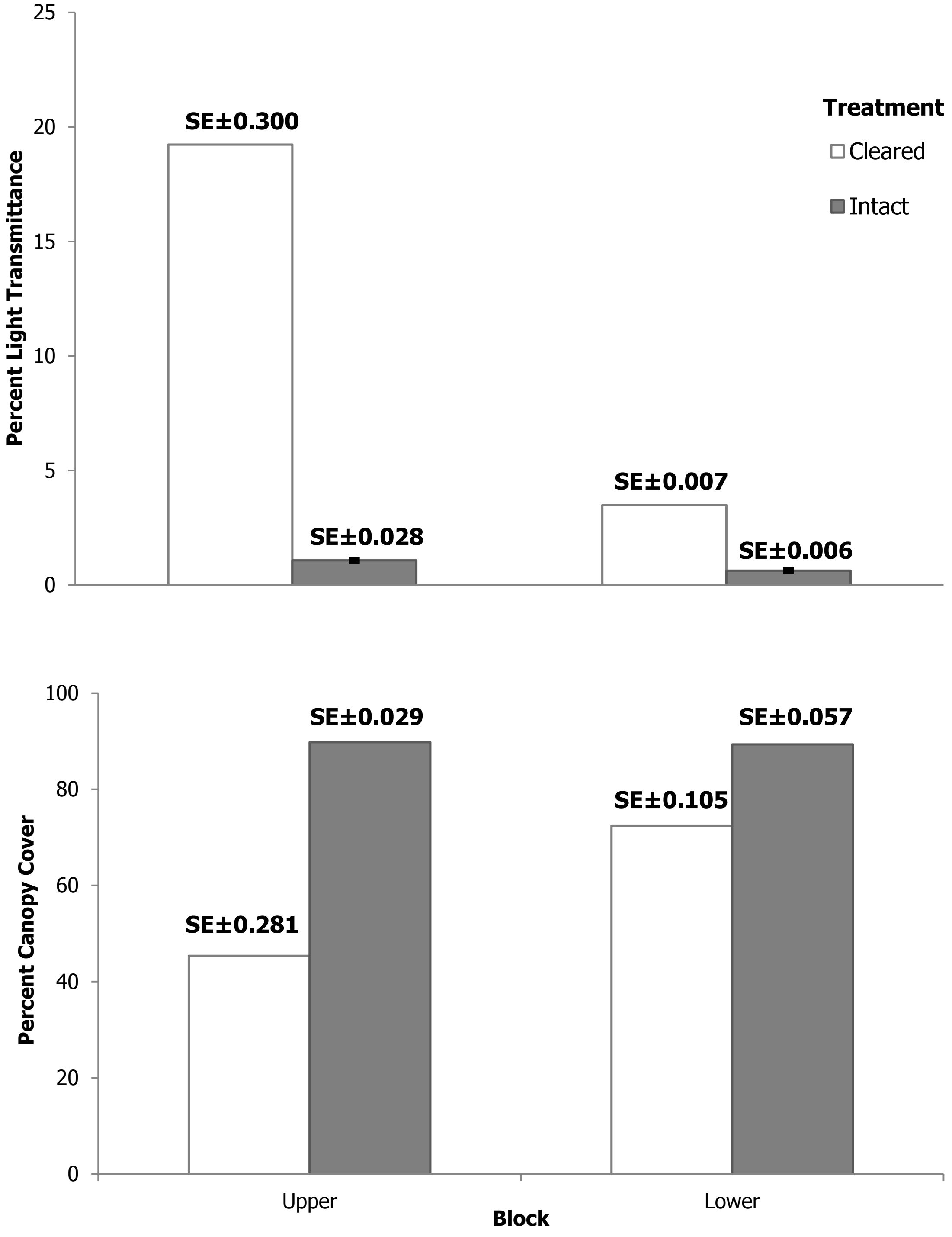


Figure 3. Percent light transmittance and percent canopy cover. Each datum represents one plot. The Pearson correlation coefficient is -0.97 (p = <0.001). Least-squares estimated fit for arcsine square root transformed data is $y = -0.7132x + 96.259$, adj. $R^2 = 0.936$.

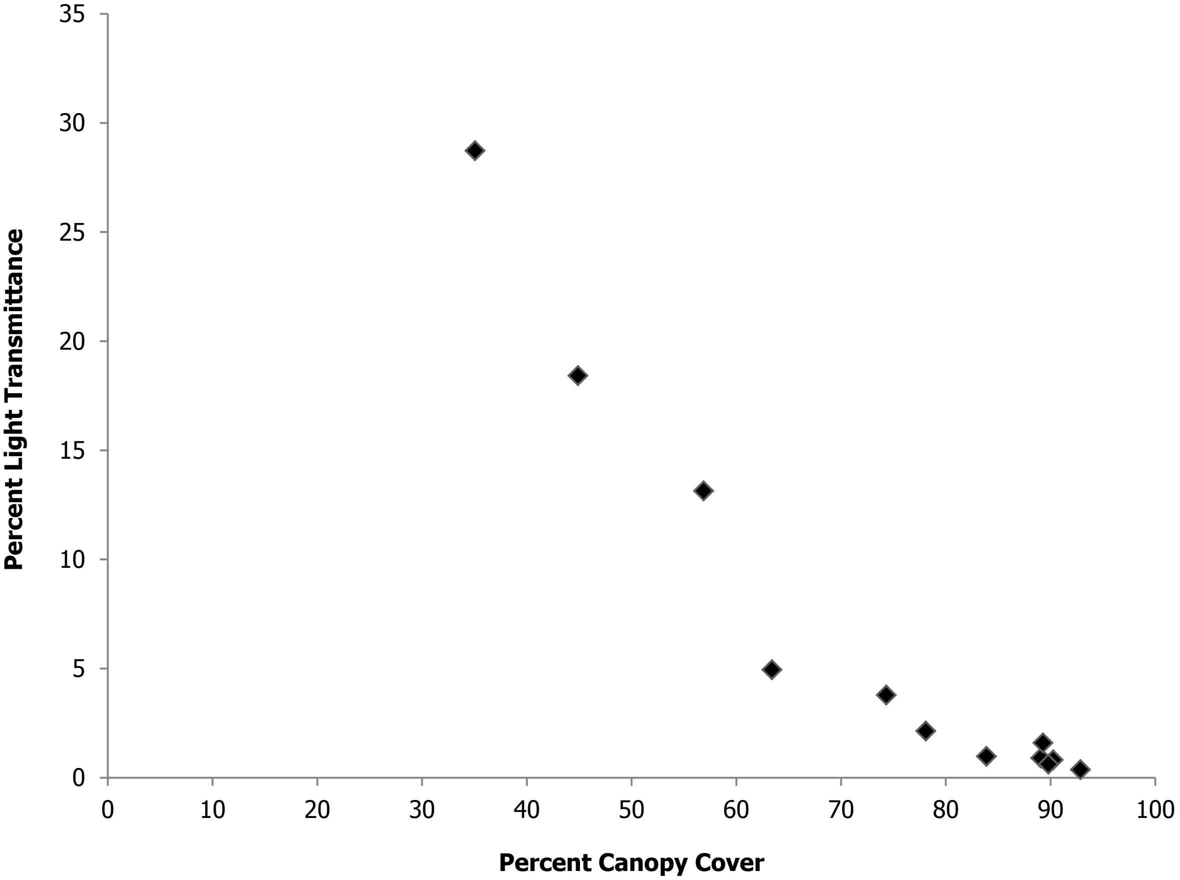


Table 3. Multivariate analysis of soil volumetric water content.

Variable	Pillai's Trace	*F*	*df*	Error *df*	*P* Value
Treatment	0.288	0.990	20	49	0.489
Block	0.617	3.952	20	49	<0.001
Treatment x Block	0.293	1.015	20	49	0.463

Figure 4. Mean soil volumetric water content (bars) and cumulative monthly precipitation (dashed line) over time by treatment and block. Error bars represent ±SE.

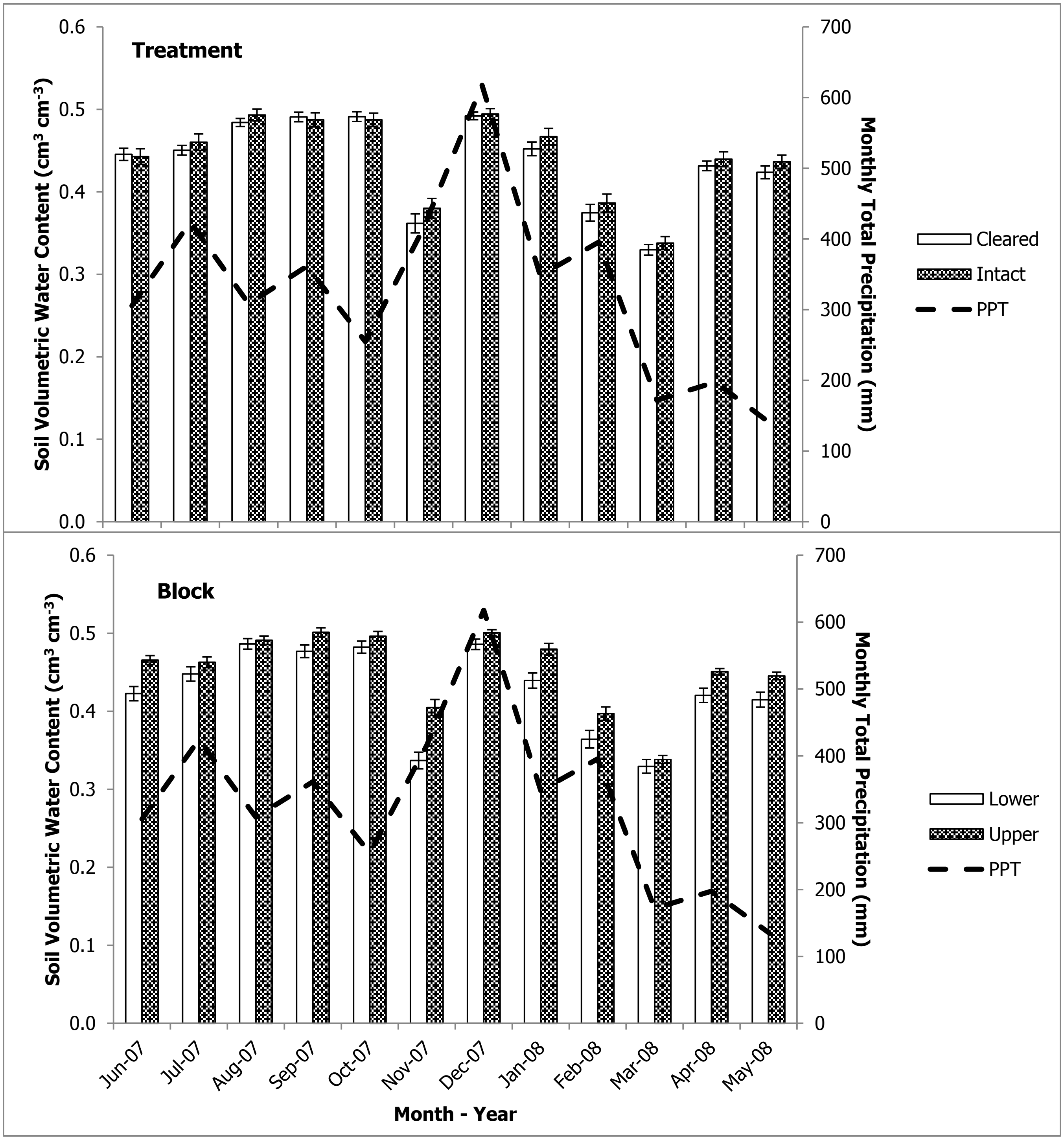


Table 4. Mean Initial Soil Nutrient Availability by Block (±SE).

Soil Nutrient Measure		Block	
		Upper	Lower
	pH	6.13 ± 0.05	6.18 ± 0.07
	%N	0.78 ± 0.03	0.80 ± 0.04
	%C	10.13 ± 0.72	10.38 ± 0.47
	C/N Ratio	13.05 ± 0.11	12.87 ± 0.35
μg/g	**P**	25.17 ± 3.25	18.83 ± 2.43
	K	135.33 ± 13.60	133.00 ± 7.74
	Ca	2072.33 ± 438.52	2632.50 ± 278.75
	Mg	1352.50 ± 159.40	1304.00 ± 76.65
mg/dm^3	**Mn**	17.17 ± 1.08	18.17 ± 0.60
	Fe	53.83 ± 4.38	50.33 ± 3.35
	Cu	5.18 ± 0.53	4.13 ± 0.52
	Zn	1.32 ± 0.24	0.79 ± 0.18

Table 5. Mean PRS^{TM}-probe Soil Nutrient Availability by Treatment and Block (±SE).

Treatment		Cleared		Uncleared	
Block		**Upper**	**Lower**	**Upper**	**Lower**
PRS^{TM}-probe supply rate (μg/10cm^2/burial length)	**Total N**	31.9 ± 0.1	60.3 ± 20.0	59.7 ± 27.0	99.6 ± 36.3
	NO_3^-	24.2 ± 3.6	54.2 ± 20.8	51.0 ± 27.4	91.3 ± 38.1
	NH_4^+	7.7 ± 3.6	6.1 ± 2.5	8.7 ± 1.3	8.3 ± 2.0
	Ca	960.9 ± 102.4	1384.3 ± 124.3	1372.4 ± 219.1	1465.5 ± 262.4
	Mg[a]	1175.9 ± 44.7	900.2 ± 33.9	1050.5 ± 107.6	978.3 ± 41.7
	K	15.3 ± 5.5	16.3 ± 2.0	19.6 ± 9.8	24.5 ± 8.5
	P	1.2 ± 0.2	1.4 ± 0.5	1.3 ± 0.1	0.9 ± 0.1
	Fe	31.4 ± 9.9	63.0 ± 2.6	50.0 ± 14.2	50.4 ± 14.2
	Mn	5.3 ± 2.5	6.6 ± 1.9	4.6 ± 1.0	8.7 ± 5.4
	Cu[b]	3.7 ± 0.8	6.7 ± 0.7	5.3 ± 0.9	3.9 ± 0.8
	Zn	1.6 ± 0.5	2.1 ± 0.3	3.1 ± 0.8	1.7 ± 0.3
	B	1.4 ± 0.3	2.3 ± 0.4	2.1 ± 0.5	2.5 ± 0.5
	S[c]	67.5 ± 7.3	114.9 ± 14.1	90.5 ± 9.2	98.5 ± 9.0

a. Block effect, *F*(1, 11) = 7.34, *p* = 0.03.
b. Treatment x Block effect, *F*(1, 11) = 7.66, *p* = 0.02.
c. Block effect, *F*(1, 11) = 7.39, *p* = 0.03.

3.2 Palapalai

Palapalai survival was greater in the cleared treatment across both blocks (Figure 6). All of the plants (*n* = 108) survived in the cleared treatment, and approx. 70% (*n* = 73) survived in the uncleared treatment. All plant measurements were significantly greater in the cleared treatment and continued to increase over time (Figure 7). Plant measurements in the uncleared treatment remained the same or decreased over time. Interaction effects were significant over time at $\alpha = 0.05$ for all plant measurements except CD (significant at $\alpha = 0.10$) (Table 7). Plant measurements within the cleared treatment were larger in the upper block, except LF which was larger in the lower block, but there was no significant difference between blocks in the uncleared treatment.

Overall, the Michaelis-Menten function was a good fit for modeling light as a predictor of palapalai growth. Light availability explained 71-81% of the variation in palapalai growth for measurements taken in July 2007 and 40-76% of the variation in growth for RGR (Table 8). R^2 values were higher using July 2007 measurements for CD and NF but lower for LF and FS. NF had the highest R^2 (0.807) using July 2007 measurements but the lowest R^2 (0.398) using RGR. Plant measurements differed in both their asymptotic growth rate (*A*) and their rate of growth under low light (*S*) (Table 8). Asymptotic growth was highest for NF (2.1) and lowest for LF (1.6). The sensitivity of growth under low light was highest for LF (105.1) and lowest for FS (14.4).

3.3 Maile

Survival counts of maile were greater in the cleared treatment, but treatment effects were only significant in the upper block (Upper block: Pearsons Chi Square = 10.286, df = 1, Fisher's Exact Test = 0.003). Survival percentages between treatments in the upper block were 44.4% in the cleared plots compared to 0% in the uncleared (Figure 6). For surviving plants within the cleared treatment, plant measurements H and LL significantly increased over time (Figure 8). LL was significantly greater in the lower block (Table 9). Generally, there was an increasing trend of NL and NS over time (Figure 8) but analysis found no significant effects (Table 9). Using the Michaelis-Menten model, light availability explained only 0.9 to 11% and 0 to 9% of the variation in maile growth for July 2007 and RGR plant measurements, respectively (Table 8).

3.4 Māmaki

Māmaki survived only in the cleared treatment for both planting times. In both the first and second plantings, survival counts were greatest in the cleared upper block. Height of surviving plants within cleared treatment increased significantly over time in both planting times (Table 10, Figure 9) with no block or block by time interaction effect. Application of the Michaelis-Menten function to both July 2007 or RGR measurements did not adequately predict stem height from light availability (Table 8).

Table 6. Chi-square of outplanting survival for each species.

Palapalai				
			Treatment x Block	
	Treatment	Block	Upper	Lower
Pearson χ-square	110.27	1.68	45.47	66.09
Fisher's Exact Test	<0.001	0.250	<0.001	<0.001

Maile				
			Treatment x Block	
	Treatment	Block	Upper	Lower
Pearson χ-square	10.67	0.30	10.29	2.22
Fisher's Exact Test	0.002	0.786	0.003	0.264

Māmaki								
	First Planting				Second Planting			
			Treatment x Block				Treatment x Block	
	Treatment	Block	Upper	Lower	Treatment	Block	Upper	Lower
Pearson χ-square	12.00	0.15	6.92	5.14	15.00	6.67	15.00	2.14
Fisher's Exact Test	0.001	1.000	0.029	0.082	<0.001	0.021	<0.001	0.483

Figure 5. Total survival counts and survival percentages for native plant species. Black bars = counts, open triangles = percentages. X-axis categories refer to treatment (C = cleared, I = uncleared) block (U = upper, L = lower) interaction. P1 and P2 refer to first and second outplanting of māmaki.

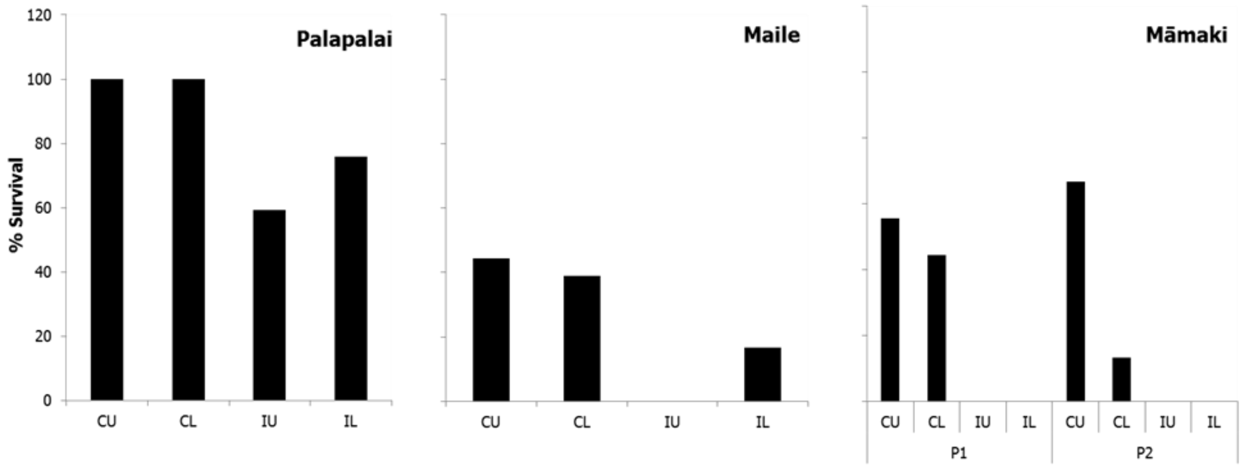


Table 7. Multivariate analysis of palapalai plant measurements over time

Plant Measurement Variable	Pillai's Trace	*F*	*df*	Error *df*	*P* Value
CD					
Treatment	0.700	43.741	9	169	0.000
Block	0.322	8.929	9	169	0.000
Treatment x Block	0.092	1.898	9	169	0.055
LF					
Treatment	0.710	46.018	9	169	0.000
Block	0.172	3.901	9	169	0.000
Treatment x Block	0.122	2.614	9	169	0.007
NF[a]					
Treatment	0.681	45.696	8	171	0.000
Block	0.222	6.098	8	171	0.000
Treatment x Block	0.155	3.921	8	171	0.000
FS[a]					
Treatment	0.467	30.358	5	173	0.000
Block	0.170	7.082	5	173	0.000
Treatment x Block	0.131	5.203	5	173	0.000

[a] Computed using square root transformed data

Figure 6. Mean (± 1 SE) palapalai plant measurements by treatment x block over time. Legend categories refer to treatment (C = cleared, I = uncleared) and block (U = upper, L = lower).

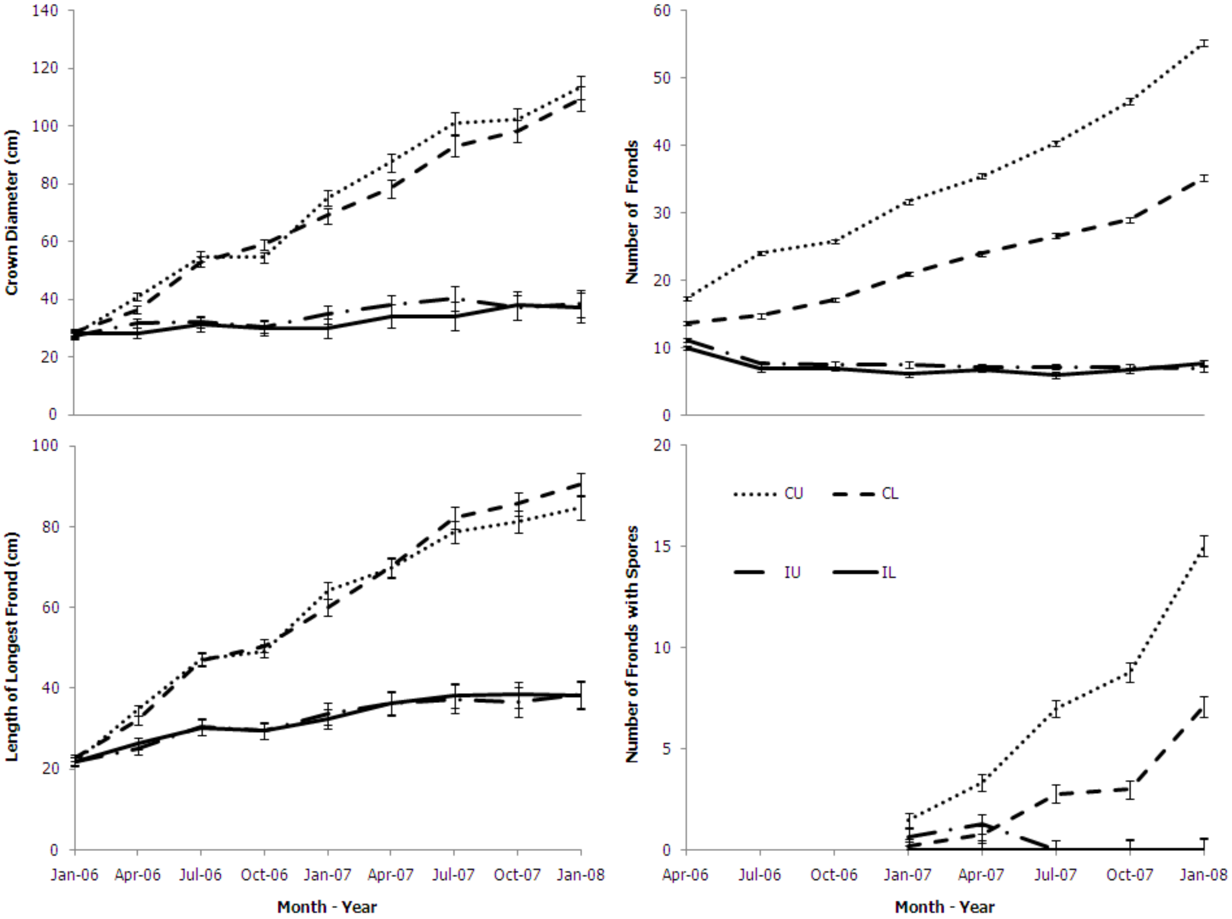


Table 8. Percent light transmittance as a predictor of plant growth measurements using the Michaelis-Menten function in nonlinear regression. *A* and *S* are parameters of the function and represent asymptotic growth (*A*) and slope of growth response at low light (*S*).

Species		**Parameter Estimates**			**Regression**		**Residual**	
Plant Measurement	**Growth Measurement**	***A* (SE)**	***S* (SE)**	**R^2**	**df**	**Mean Squares**	**df**	**Mean Squares**
Palapalai								
CD	Jul-07*	131.0 (10.6)	8264.1 (1704.6)	0.748	2	79332.9	22	432.9
	RGR**	1.7 (0.2)	62.5 (19.9)	0.667	2	10.1	22	0.2
LF	Jul-07	96.8 (6.9)	9368.2 (5344.9)	0.705	2	52431.1	22	236.7
	RGR	1.6 (0.1)	105.1 (24.0)	0.723	2	12.1	22	0.1
NF	Jul-07	80.4 (9.8)	1451.0 (321.3)	0.807	2	14892.7	22	119.8
	RGR	2.1 (1.4)	17.3 (14.2)	0.398	2	5.7	22	0.7
FS	Jul-07	52.5 (18.0)	240.2 (74.2)	0.752	2	2014.9	22	34.4
	RGR	1.9 (0.5)	14.4 (4.5)	0.761	2	4.4	22	0.1
Maile								
H	Jul-07	14.8 (2.6)	2523.5 (2199.4)	0.077	2	1126.3	13	32.5
	RGR	0.6 (0.1)	145.9 (208.5)	0.099	2	1.9	13	0.1
LL	Jul-07	6.1 (0.4)	12029.6 (17998.0)	0.038	2	265.2	13	1.2
	RGR	0.3 (0.1)	26.0 (31.4)	0.190	2	0.4	13	0.0
NL	Jul-07	14.4 (3.3)	1732.9 (1687.7)	0.108	2	974.8	13	45.7
	RGR	9292.7 (4.2E10)	0.1 (2.7)	0.000	2	0.0	13	0.3
NS	Jul-07	2.5 (0.6)	2969.2 (1236.4)	0.009	2	43.8	13	3.5
	RGR	0.3 (21.3)	0.2 (3.1)	0.000	2	0.0	13	0.2
Māmaki								
SH	Jul-07	45.5 (10.7)	2.1E10 (2.5E16)	0.000	2	11386.4	9	804.8
	RGR	0.4 (0.3)	1.5E8 (3.80E14)	0.000	2	0.8	9	0.4

*Plant growth measurements taken between 7/1 – 7/31/2007 and collected during the same time period as percent ambient light transmittance data.

**Relative growth rate calculated as LN (T2 plant measurement) – LN (T1 plant measurement) where LN is the natural log, T1 is plant measurement at planting and T2 is final plant measurement. Dates for T1 and T2 for each species are as follows: Palapalai (T1 = 12/28/2005; T2 = 2/18/2008), māmaki (T1 = 1/15/2006; T2 = 9/5/2008); maile (T1 = 6/21/2006; T2 = 9/5/2008).

Table 9. Univariate analysis of maile plant measurements within the cleared treatment over time.

Plant Measurement Variable	Mean Square	*F*	*df*	*P* Value
H				
Time	571.031	15.806	7	<0.001
Block	91.512	2.533	1	0.113
Time x Block	15.290	0.423	7	0.887
LL				
Time	15.218	7.340	7	<0.001
Block	20.413	9.847	1	0.002
Time x Block	1.159	0.559	7	0.789
NL[a]				
Time	1.636	1.405	7	0.204
Block	3.600	3.092	1	0.080
Time x Block	1.027	0.882	7	0.521
NS[a]				
Time	0.087	0.485	7	0.845
Block	0.445	2.490	1	0.116
Time x Block	0.121	0.679	7	0.690

[a] Square root transformed data

Figure 7. Maile plant measurements (mean ± 1 SE) per plot within cleared treatment by block over time.

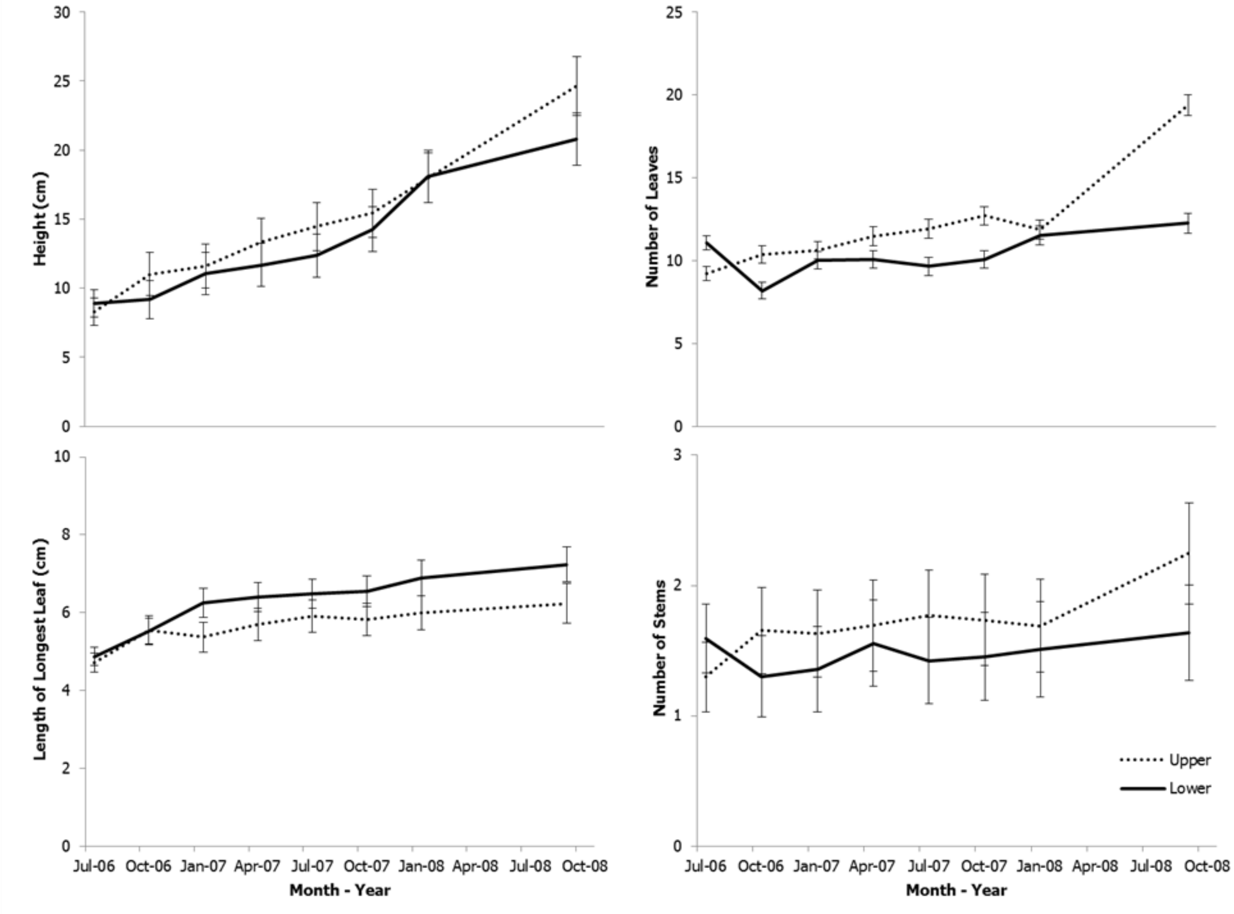
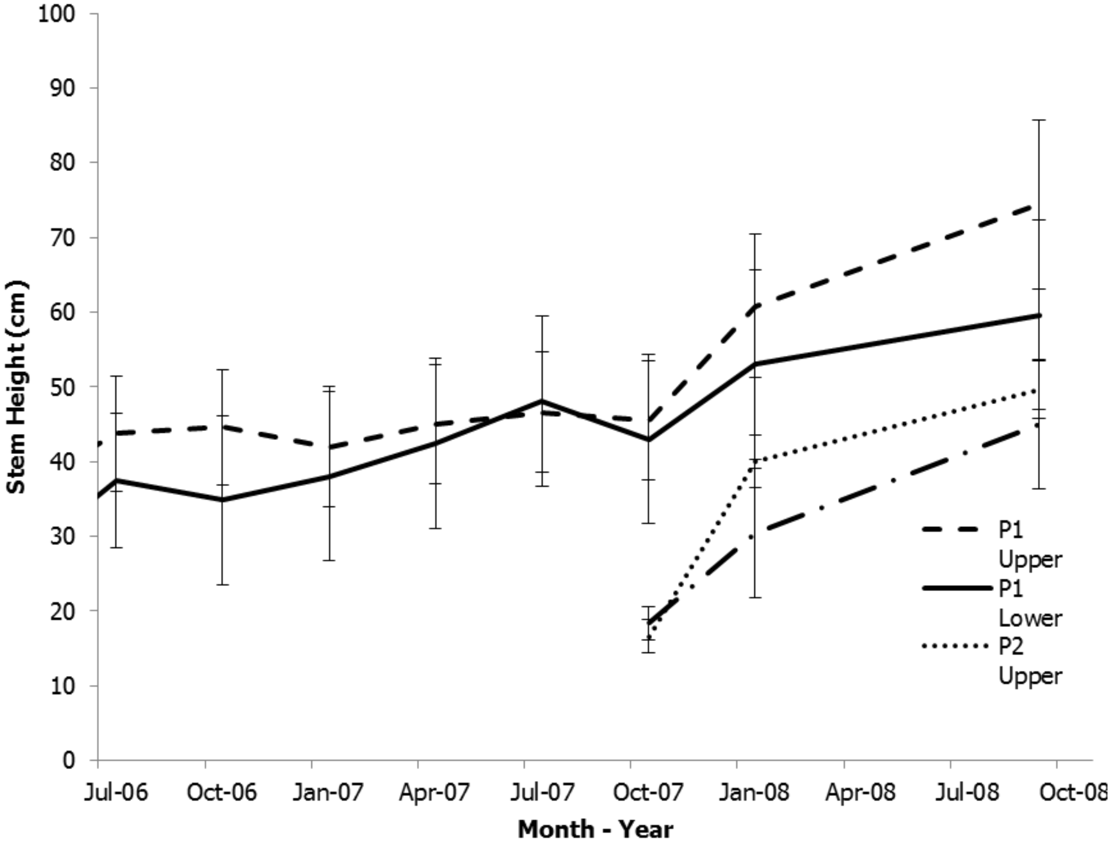


Table 10. Univariate analysis of māmaki stem height (SH) in cleared treatment for both outplanting times.

Outplanting Time Variable	Mean Square	*F*	*df*	*P* Value
First				
Time	2164.741	3.346	9	0.001
Block	1099.617	1.700	1	0.194
Time x Block	91.450	0.141	9	0.998
Second				
Time	3344.888	22.330	2	<0.001
Block	122.480	0.818	1	0.369
Time x Block	120.020	0.801	2	0.452

Figure 8: Mean stem height of māmaki (± 1 SE) per plot within cleared treatment in first and second plantings by block over time.



4. Discussion

4.1 Light effects

The clearing of understory and sub-canopy non-native species significantly increased percent light transmittance and decreased percent canopy cover above the outplanted species. Higher light availability in the upper block was most likely due to differences in species composition and basal area rather than stem density in the remaining overstory canopy (Table 1). Theoretically, increasing stem density within forests should lead to decreases in available understory light (Anderson, 1966; Campbell and Norman, 1989; Kuuluvainen and Pukkala, 1989); however, in our study, higher light availability was observed in the upper block with higher overstory (DBH ≥ 10 cm) stem density. Although the upper block had more overstory trees per area, the trees were relatively smaller and less uniform in size and composition. This created an overstory canopy cover that was more heterogeneous and open compared to the lower block, which consisted of fewer but larger trees, mostly of the same species. Montgomery and Chazdon (2001) found similar results in their study on the influence of forest structure and canopy architecture on understory light availability in a tropical rainforest. Their results showed that an inverse relationship between stem density and light availability only existed in old growth forests and not secondary forests. They concluded forest structure may be an important predictor of light availability at large scales, but at finer scales, more subtle factors such as tree architecture, species composition, and vertical distribution of foliage may be more influential. Sub-canopy species can also have a major influence on light availability. Several studies have shown that sub-canopy trees, saplings, palms, ferns, shrubs, and herbs can have a major influence on light availability within the understory (Denslow et al., 1991; Russell et al., 1998; George and Bazzaz, 1999). Hence, the manipulation of forest canopy layers to increase light availability to cultivated understory plants will most likely depend on the existing forest composition and structure, the size and amount of clearing, as well as the light requirements of desired understory species.

Canopy cover estimates using the concave spherical densiometer were a good predictor for estimating understory light availability in the field. Other studies have shown mixed results. Bellow and Nair (2003) demonstrated that shade assessment using densiometers could provide an adequate, dependable guide for overstory management in multistrata systems, but they performed best when stand densities were greater than 500 trees per hectare and under closed canopy. However, the authors concluded that the use of densiometers was overall the best method in terms of accuracy over the range of conditions they studied. Ferment et al. (2001) found that densiometers were better at discriminating contrasting situations (gap versus intact canopy cover) but were less successful in discriminating intermediary situations. It is possible that the ability of densiometer canopy cover measurements to strongly predict understory percent light transmittance in our study may have been facilitated by the applied contrasting understory treatments (uncleared or cleared). Nonetheless, the ease of use and low cost of densiometers makes them a good tool for land resource managers and can provide an adequate baseline for determining amount of canopy removal. It is also important to note that light and canopy cover were measured once during the study, and hence, results can vary seasonally.

4.2 Soil moisture

Soil moisture levels can vary as a function of canopy structure and composition. In a mesic Hawaiian forest, Denslow et al. (2006) found that soil moisture levels were higher under open than closed koa (*Acacia koa*) canopy. In a tropical forest in Costa Rica, Vitousek and Denslow (1986) also found that soil moisture levels in the upper 10 cm of soil were consistently and significantly higher in forest gaps than in adjacent intact forest. These differences were present in small and large gaps that ranged in size from 116–600 m^2 and in both rainy and dry seasons. The authors concluded that the higher moisture levels were likely associated with a lower transpirational load on soils found within gaps. In this study, artificially created clearings were relatively small ($\approx 64m^2$) but similar reasoning was proposed and it was presumed that the cleared treatment would have higher soil moisture. While no treatment effect was detected, higher surface soil moisture levels were observed in the upper block of this study (Figure 5), where overstory canopy cover (DBH > 10cm) was more open (Table 1) and likely allowed more rainfall to reach the soil surface. Since there was no treatment effect, it is likely that within our study area surface soil moisture is driven more by rainfall interception through the remaining overstory canopy rather than by changes in transpiration loads and/or evaporative losses from the soil surface.

The study area is within a valley that receives a high amount of annual rainfall; hence it was presumed that soil moisture would not be a limiting resource for establishment and growth of outplantings. However, during the planting of palapalai and māmaki in late 2005 and early 2006 there were periods of up to three weeks with less than 5 mm of precipitation (WRCC, 2013; NWS, 2014). With well-drained soils and steep slopes, it is possible that soil moisture levels could have declined to levels that may have affected survival and growth of the outplanted native species. Recently transplanted plants were likely to be sensitive to drought since they were small in size and had limited root systems. Non-drought stressors (e.g. light and nutrient availability, pathogens and herbivore damage) and their interaction with drought stress can also influence plant survival during periods of drought (Augspurger, 1984a, b; Engelbrecht et al., 2005).

Many of the māmaki individuals in this study showed herbivory damage on the leaves ranging from <25% to >90% loss of leaf area (personal observation). Coupled with low light conditions, this may have led to low survival of this species. Additionally, no irrigation or manual watering was provided. To improve survival of recently outplanted species, even within mesic to wet forests, plants may need supplemental watering and should be outplanted during the rainy season.

4.3 Soil Nutrients

With fewer plants to take up nutrients it was expected that cleared plots would show higher concentrations of soil nutrients. However, in our study, while some nutrients differed across blocks, it does not appear that soil nutrient concentrations were affected by understory treatments. Similar results were found in a recent study in a Hawaiian lowland wet forest (Ostertag et al., 2009) where soil N and P were not found to be significantly different in 100 m^2-plots removed of non-native species compared to those left uncleared. The authors concluded that one-time sampling did not adequately capture soil nutrient trends. This may also have occurred in our study. Alternatively, it is possible that any differences in soil nutrient availability across treatments were buffered by surrounding forests due to the small size of plots ($\approx 64 m^2$) or the retention of the overstory trees, which likely dominate nutrient uptake. Denslow et al. (1990) proposed similar reasoning when they found that fertilization of forest gaps did not significantly affect plant growth rates in any light environment. The authors concluded that light appears to be the most critical resource limiting growth in forest gaps they studied and that the lack of a fertilization effect emphasizes the degree to which gap processes are commonly buffered by the surrounding forest. Previous research by Vitousek and Denslow (1986) also did not show differences in mobile nitrate-nitrogen within natural forest gaps. They suggested that within tree-fall gaps light availability is most likely the more limiting resource rather than any change in nutrient availability.

4.4 Plant survival

For all three species, the percent of surviving plants was greatest in the cleared treatment, indicating that the effects of understory removal (decline in plant competition and increase in light availability) allowed for increased survival across outplanted species. Maile and māmaki were further influenced by block effects. For both these species the effect of clearing on survival was strongest in the upper block where percent light transmittance was significantly higher than in the lower block. Previous greenhouse studies on growth requirements of selected native plant species found that māmaki survived in full or partial shade (100 and 31% light transmittance, respectively) with no survival at 5% (Pattison *et al.*, 1998). More recent research shows māmaki having relatively high survival under shade cloth treatments that limited light transmittance to 5% (McDaniel and Ostertag, 2010). Our research shows māmaki surviving at percent light transmittance levels ranging from 3.6 to 20.1%. Uncleared understory light levels of ≤ 1% light transmittance were not adequate for survival. However, even with adequate light levels in the cleared treatment, māmaki still had a low relative survival (13 to 55%) compared to palapalai. This may be due to its sensitivity to several factors, including periods of drought, herbivory and breaking of stems by falling branches (personal observation). Information regarding growth and light requirements of maile is limited (Wagner et al., 1999). Native plant nurseries in Hawaiʻi (Native Nursery and Hui Ku Maoli Ola) recommend planting maile in partial- to full-sun. Bornhorst (2005) states maile prefers shade to grow. In this study, the survival of maile could also have been affected by plot slope. Personal observation by the author noted some plants were buried by leaf litter and soil. Palapalai had the highest survival of all three plant species. Even in the uncleared treatment, survival was > 50%. Information on light and growth requirements for palapalai is also limited (Wagner et al., 1999). Native plant nurseries often recommend partial to full sun. Our study reveals that palapalai can be fairly shade-tolerant, demonstrating survival in uncleared understory treatments where light transmittance was less than 1%.

4.5 Plant Growth

Within the cleared treatment, plant measurements of all three species generally increased over time. Plant measurements of size and stem height (CD, H, and SH), and number of fronds or leaves (NF and NL) tended to be greater in the upper block where percent light transmittance was higher. This contrasts LF (palapalai) and LL (maile) plant measurements, which on average were larger in the lower block. Larger leaves or fronds in the lower block could be a response by the plants to increase light capture. For both LF (palapalai) and LL (maile) maximum growth was achieved under relatively low light conditions (3-5%). Increasing light levels above approx. 5% did not appear to cause an increase in either of these plant measurements.

Only palapalai had enough surviving individuals to compare treatment effects on changes in plant measurements. All palapalai plant measurements were greater in the cleared treatment. While palapalai plants survived in the uncleared treatment, their growth ranged from relatively minimal to not at all, suggesting that the light environment in the uncleared treatment is not adequate for sustained growth of plants, particularly if fronds are to be harvested. NF and FS maximized at approx. 20% light transmittance. Light may also play a role in spore development, since ferns in the upper block had twice as many fronds with spores (FS) than did those in the lower block. Although NF and FS showed higher *A* values when modeling growth as a function of light availability, the difference between the largest and smallest *A* value was 0.5, suggesting that all plant measurements will respond relatively similarly when light availability is high. Conversely, *S* values showed greater variability among plant measurements indicating that then when light is limited, a small increase in light will lead to larger increases in LF and CD than NF and FS. Hence, small increases in light availability may yield larger increases in frond length relative to number of fronds. Understanding these differences in response to changes in light availability will be critical to palapalai understory cultivation and can assist in determining appropriate light levels needed to achieve a sustainable harvestable yield of fronds.

Percent light transmittance was a poor predictor of growth rates for maile and māmaki surviving in the cleared treatment. This may have been due to several factors. Limited survival for both these species and thus, fewer data points, may have reduced the capacity of the function to fit the data. Maile plants were also planted among palapalai; hence individual plants may have experienced lower light levels than were measured at 1 m above the ground. Optimal light conditions for maile may be better determined by measuring light availability at the individual plant level as opposed to the plot level. Height of māmaki stems were also affected by stem die-back and being buried by soil (personal observation), variables that were not included in the current growth function. Māmaki clearly requires higher light than what was available in the uncleared treatment to survive and grow, but other factors including soil moisture, herbivory and damage from falling debris most likely also influenced establishment and growth.

5. Conclusion

This study sought to evaluate the establishment and growth response of three native plant species when planted and grown in both uncleared and cleared forest understory environments. Results suggest that within lowland wet mesic forests dominated by non-native species, light availability is the most critical resource limiting establishment and growth of understory native species. Successful and sustainable cultivation will require some level of canopy opening or manipulation to ensure adequate light levels. Regarding individual species, the relatively high survival of palapalai under varying understory light conditions, suggests it is a good species for establishing an understory groundcover in agricultural-restoration systems. Although able to survive in low light levels (1-5%) of an uncleared forest understory, higher light levels associated with understory clearing (15-20%) are most likely necessary to support palapalai harvesting for cultural uses. Previous research on frond harvest of palapalai from naturally occurring populations within non-native dominated forests on Oʻahu, suggest that annual harvesting of fronds may be sustainable when concurrent with weeding of non-native species (Ticktin et al., 2006a). Maile and māmaki did not establish well in the uncleared understory, and growth rates even with understory clearing were insufficient for harvesting after two years. If planting within an understory, both māmaki and maile will most likely have the highest chance of survival when outplanted into light gaps and areas cleared of non-native understory. Most native plants in Hawaiʻi have not been grown as crops and optimal planting conditions are unknown for many species. Better understanding of environmental conditions that favor native plant establishment and growth are important to improve understory cultivation efforts in Hawaiʻi. Additionally, further research on the effects of harvest, including determination of sustainable levels and frequency of plant or plant part removal, will be critical in evaluating the success of understory agroforestry systems.

This study also addressed the extent to which light availability, soil moisture and nutrient availability influenced establishment and growth of the outplanted native species. Increases in light availability via the cleared treatment appeared to be the most influential resource in increasing survival and growth of the outplanted native species compared to soil moisture and nutrient availability. Soil resources were most likely buffered by surrounding uncleared forest and may play a more prominent role in survival and growth response if clearing size is enlarged. From a cultivation perspective, positive survival and growth response in the cleared treatment despite the lack of soil effects is promising, since it is less variables to control or inputs to provide (i.e. via fertilizer and irrigation). However, the range of soil variables for this site was relatively narrow compared to what is found across Oʻahu and available soil nutrients should be assessed for other sites (Deenik and McClellan, 2007). Additionally, harvesting of plant parts will most likely add additional stresses to the plant and depending on the frequency and amount of harvest may require additional resource inputs.

Ultimately, the success of agroforestry-restoration type projects depends on the ability of cultural practitioners, scientists and land managers to work in partnership. Integration of traditional knowledge of native plants and harvesting protocols with research in agriculture and restoration ecology will provide an opportunity for participants to exchange ideas and potentially favor adoption and management of these projects by local community groups.

CHAPTER 3:

EFFECTS OF UNDERSTORY NATIVE PLANT CULTIVATION ON PLANT RECRUITMENT AND COMPOSITION IN A LOWLAND WET FOREST IN HAWAI‘I

1. Introduction

Many of Hawaiʻi's lowland wet mesic forests have been altered by a history of human disturbance, including over-grazing by ungulates and deforestation. These disturbances have encouraged the colonization and spread of non-native species, many of which have become invasive. In most of Hawaiʻi's lowland wet forests, native species have been replaced by non-native species that dominate forest composition, causing structural changes that favor higher densities of non-native species and lower light conditions (Wong, 2007; Zimmerman et al., 2008). Understory environments where non-native species dominate in density and cover, can alter the light environment and inhibit establishment and growth of native species (e.g. very low light at soil surface). In Hawaiʻi, less available light for the understory environment can inhibit recruitment and restoration of native species (Harrington and Ewel, 1997; Wong, 2007). Additionally, the ability of some non-native species to maintain relatively high growth despite low light conditions can result in these species securing a greater share of resources and becoming highly invasive even in undisturbed forests (Catford et al., 2012). Royo and Carson (2006) have called this type of non-native understory a recalcitrant understory layer since it can resist displacement by other species and remain intact for decades even beneath closed canopy forests. This can then lead to monotypic stands of a non-native species in the understory that can limit other species from growing and becoming established (e.g. kahili ginger in Minden et al., 2010b).

The creation of small gaps within the forest has been suggested as a means to afford understory native species with improved light levels. In addition to increased light availability, microclimates within gaps are generally characterized by lower humidity, and higher soil moisture and temperature levels than the adjacent forest understory (Denslow et al., 1990). Gaps can also allow for increased rainfall reaching the ground, and fewer plants can mean reduced transpiration losses. Ostertag et al. (2009) concluded that canopy opening is critical to restoration of Hawaiʻi's lowland mesic forests and suggests native seedlings may benefit from removal of invasive species as a management strategy. While canopy opening and gap creation provides benefits in the amount of increased resources to native plantings, it can also increase the spread of other non-native species (Zavaleta et al., 2001). In Hawaiʻi, such gaps could exacerbate non-native species invasions, which have been shown to impede the reestablishment of native flora and fauna by dominating resource capture in various forest ecosystems (Smith, 1985; Baruch and Goldstein, 1999; Stratton and Goldstein, 2001; Litton et al., 2006). Removal of all non-native species can also be costly, in turns of labor and time, and may not provide long-term benefits to native plantings if weed management is not maintained (Sailor, 2006). Additionally, removal of all non-native species may not be possible in certain areas, particularly if large trees are present or steep or rocky terrain makes it hard to access. In forests with mixed native and non-native species there are additional challenges to making sure native plants are not removed or harmed in the removal process.

Daehler (2003) found that invasive species in general are not statistically more likely to have higher growth rates, competitive ability, or fecundity than native species. Rather, the relative performance of invaders and co-occurring natives often depends on growing conditions. Most commonly, these conditions involve reduced resources (nutrients, light, water) and/or specific disturbance regimes. Perry et al. (2004) found that manipulating nitrogen availability allowed for a native sedge to competitively suppress an invasive perennial grass in prairie wetlands. Consequently, manipulation of resource availability to give native species a competitive advantage could increase survival and establishment in environments dominated by non-native species. In Hawaiʻi, manipulation of the microclimate can provoke different species response and has been used to design restoration strategies (e.g. Cabin et al., 2002). So what level of non-native species removal is best for creating understory light conditions conducive for native plant restoration? Small-scale management of the overstory, such as limited canopy opening through immediate removal of selected trees or slowly killing trees via girdling (Loh and Daehler, 2007), has been suggested by Ostertag et al. (2009) and Cordell et al. (2009). Loh and Daehler (2007) found that native seedling success was higher in plots where canopy trees were girdled rather than removed. Continued removal of non-native recruits will also be integral to maintaining restoration sites since reduction of non-native seedlings can create environments that are more favorable for native seedling survival. In Hawaiʻi, removal of *H. gardnerianum,* a major understory invader in native forests, resulted in regeneration of native species (Minden et al., 2010a).

In addition to small-scale canopy management and continued weed removal, supplemental planting has been recommended as an additional strategy to encourage native species regeneration (Sailor, 2006; Cordell et al., 2009). In areas where invasive species dominate an extensive area and native plants are largely missing, it may not be possible to eradicate the invader completely. Instead, direct seeding and outplanting of native species could generate a community that, while different than what existed prior to the invasion, nevertheless supports an ecosystem dominated by native species (D'Antonio and Meyerson, 2002). Understory enrichment with native plantings can be used to minimize effects of bare areas vulnerable to weed colonization and exclude more aggressive weeds via competition and shading (Sailor, 2006; Gomez-Aparicio, 2009; Ostertag et al., 2009; Vieira et al., 2009). Additionally, native plantings can also potentially supply more native propagules to the area and initiate an environmental trajectory that is more supportive to germination of native seedlings (Ammondt *et al*., 2013).

Hence, the key is to find a balance between removing invasive species to facilitate establishment and growth of native species and managing light availability to limit additional non-native species invasion (Kueffer *et al*., 2010). Understanding how the understory forest environment will respond to restoration activities is important for determining the appropriate level of invasive species removal and site management to support native plant establishment and growth. Mueller-Dombois (2005) argues that restoration of native Hawaiian rainforests should be based on silvicultural approaches that apply knowledge from forest ecological research and focuses on simulating and enhancing natural processes for “low input management”. However, in situations where the relative abundance of non-native species has increased following environmental modification, it may be more effective to target the cause of the problem (e.g. low light at the soil surface) rather than attempt to manage plant populations directly (Hulme, 2005; MacDougall and Turkington, 2005). Catford et al. (2012) argue that where management is committed and sustained, directly targeting the environmental factor that’s been modified by the non-native species may be a useful control technique. Similar forest management has been observed in understory plantations for non-timber forest products where most native canopy trees are kept for shade, but many of the smaller trees, shrubs and herbaceous plants are removed in order to increase light availability and reduce competition for cultivated species (Trauernicht and Ticktin, 2005). Removal is done prior to planting and periodically after, usually once every 6 months to a year. Similarly, initial and subsequent non-native species removal can also be implemented in restoration systems to enhance survival and growth of native plants.

The research area for this study is dominated by the invasive tree *Ardisia elliptica* Thunb. *A. elliptica*, commonly known as shoebutton ardisia or inkberry, is an evergreen, small tree that can grow up to 6m in height. It is native to Sri Lanka, India, China, Taiwan, Malaysia, South East Asia, Indonesia, and the Philippines (Francis, 2003). While initially introduced as an ornamental plant to other tropical countries in the early 1900s, *A. elliptica* is now considered invasive and an environmental problem in many tropical areas around the world including the Cook Islands, French Polynesia, Australia, southern Florida, and Puerto Rico (Pascarella and Horvitz, 1999; McCormack, 2002; Space and Flynn, 2002b, a; ISSG, 2014). In Hawaiʻi, *A. elliptica*, is listed as a noxious weed (DPI, 2003) and is found on four islands (Kauai, Oʻahu, Maui, and Hawaiʻi), with major infestations occurring on the islands of Oʻahu and Maui (Smith, 1985). This information comes from a survey conducted in 1984, and it is unclear how much the plant has spread since that time. Of particular concern are severe infestations occurring in Mānoa valley (R. Baker, personal communication).

Some of the characteristics that make *A. elliptica* particularly invasive are its fast growth, ability to survive and reproduce in low light conditions, prolific fruiting, avian and mammalian seed dispersal, and high seed viability (Pascarella and Horvitz, 1999; Koop, 2004; Koop and Horvitz, 2005). The high reproductive output and high shade-tolerance produces carpets of seedlings (>400 plants per square meter) underneath mature plants (Koop, 2004). *A. elliptica* can form dense mid-story thickets that reduce available space and light for understory native species. In addition, it does not require disturbance to become invasive and has been found in well-established forest understories (Koop, 2004). While eradication of established *A. elliptica* populations may not be feasible over large areas, restoration protocols that involve both removal of *A. elliptica* and revegetation could encourage establishment of target and non-target native species. Control of *A. elliptica* in Florida had a significant overall positive effect on recruitment of seedlings and saplings of native trees, shrubs and herbs (Horvitz and Koop, 2001).

This study was part of a larger research project that looks at the development of an *agroforestry restoration* system in which the understory of a non-native dominated forest was cultivated with culturally and economically desired native Hawaiian plants (see Chapter 2). In the current study, the effects of both understory non-native species removal and planting of native species on non-native and native seedling recruitment were evaluated, particularly the removal of the dominant invasive species *A. elliptica*. Of particular interest was how the loss of a dominant invasive species affected community structure and composition. Specifically, how does non-native species removal affect *A. elliptica* and other non-native seedling recruitment and how does this vary over time? Also of interest was the ability of native enrichment plantings to reduce non-native seedling recruitment. It was hypothesized that removal plots would contain fewer *A. elliptica* and other non-native seedlings and that it would continue to decrease over time as seed and seedling banks were exhausted. Relative increases in native seedling recruitment were expected over time as non-native seedlings were removed. It was predicted that native outplantings would provide resource competition for non-native seedlings and further reduce establishment of non-native seedlings in removed plots.

2. Materials and Methods

2.1 Site Description and Characterization

Two research sites were selected at the Harold L. Lyon Arboretum, located in Mānoa Valley on the leeward side of the island of Oʻahu, Hawaiʻi. The arboretum is owned and managed by the University of Hawaiʻi and has comprehensive records for outplanted trees and shrubs. The sites selected are characteristic of lowland wet-mesic forests dominated by non-native species found in watersheds throughout Hawaiʻi. The lower site (elevation 262 m) has a continuous overstory of various species of gymnosperms (e.g. *Juniperus* spp., *Aurocaria* spp. outplanted for reforestation ca. 1915) and other non-natives, such as *Schefflera actinophylla* (Endl.) Harms, *Aleurites moluccana* (L.) Wild., *Cinnamomum burmanni* (Nees & Th. Nees) Nees ex Blume., and *Rhus taitensis* Guill. The upper research site (elevation 290 m) has never been reforested, but it was subjected to deforestation and uncontrolled grazing in the 19th century. It has a non-continuous non-native overstory dominated by *S. actinophylla, C. burmanni,* and *R. taitensis* with no gymnosperms present. Some native mid- to upper-story species, such as kōpiko (*Psychotria* spp.) and lama (*Diospyros* spp.), and understory species, such as ʻieʻie (*Freycinetia arborea* Gaudich.), maile (*A. stellata*), māmaki (*P. albidus*), and palaʻā (*Sphenomeris chinensis* (L.) Maxon) are present. Both sites have a mid-story dominated by the invasive *A. elliptica*.

The sites are located on slopes ranging from 50 to 80 percent. The soil is part of the Tantalus Series and consists of shallow, well-drained silt loams developed from volcanic ash and material weathered from cinders (USDA, 1965). Mean annual rainfall is 3800 mm distributed evenly throughout the year (WRCC, 2013).

2.2 Study Design

The understory vegetation community was surveyed before treatment application in 2004 and two (2006), three (2007), and four (2008) years after to assess the effects of forest understory clearing and planting on seedling recruitment, structure and composition over time. Environmental variables, such as percent light transmittance, soil volumetric water content, and soil nutrient concentration were examined to explain potential treatment and site effects.

The experiment was laid out in the field in a randomized complete block, split-plot design with replications within blocks. Sites were designated as blocks and contained three replicates of the main treatment, for a total of six plots. Each plot measured 6 x 6 m with a 2-m buffer between adjacent plots. The main treatment is referred throughout the chapter as cleared or uncleared. The cleared treatment consisted of removal of both stems and roots of all non-native species less than 10 cm dbh (stem diameter at breast height at 1.3 m). Selected *A. elliptica* trees with a dbh >5cm, approximately 10 per plot, were not removed completely and were cut at a height of 1 m. These 1-m “living posts” were left along the contour of the plots to provide support for persons maneuvering through the steep terrain. The uncleared treatment was the control; non-native species were left intact with no removal of plant species. To maintain treatment design, every six months all non-native species in the cleared treatment were completely removed by hand, i.e. weeded, except *Cordyline fruticosa*. Any re-growth on *A. elliptica* posts were also removed. *Cordyline fruticosa* was not removed as it is culturally valued by Hawaiians and is used for food, fiber, and medicinal and ornamental purposes (Krauss, 1993). All plots were orientated along a NW-SE aspect. Each 6 x 6-m plot was divided into four 3 x 3-m quadrants for the split-plot planting treatment. The planting treatment consisted of three native species outplanted in two diagonally opposing quadrants (Figure 1), leaving two quadrants unplanted. A 0.5-m buffer was left unplanted at the edge of each quadrant.

Vegetation surveys were conducted in September or October of each respective year. The vegetation sampling design contained nested sub-plots with three different sizes. At the whole plot level (6 x 6 m) all woody species with a dbh of at least 5.0 cm were measured and identified. Within each plot, two 3 x 3-m quadrants were randomly selected for measuring and identifying woody species with a dbh between 1.0 and 4.9 cm. Stems less than 1.0 cm dbh but greater than 1.0 m in height were also counted and identified. A 1 x 1-m quadrat was randomly placed in each 3 x 3-m quadrant for a total of four 1-m^2 sub-plots for sampling both woody and herbaceous ground cover species. All ground cover plants between 5 and 100 cm in height were identified and measured for stem height. Seedlings less than 5 cm were counted and identified when possible. For this study, all species measured for dbh are defined as "woody species". All species measured within the 1 x 1-m quadrat are defined as "ground cover species" and "seedlings". In 2007, only ground cover species (those affected by planting treatment) were measured.

To further assess the effects of planting on seedling recruitment within the cleared treatment, at each biannual weeding from August 2005 through August 2008, weeded plants were collected from four randomly placed 1 x 1-m quadrats (one quadrat per 3 x 3-m quadrant). Weeded plants were sorted by species, oven-dried for 24 hours and weighed for dry biomass (g).

2.3 Statistical Analyses

2.3.1 Ground Cover Species Recruitment Measures

Repeated measures ANOVA was used to compare seedling height and density (number of individuals/m^2) across years (2004, 2006, 2007 and 2008), block, and clearing treatment. Analyses were made for (1) *A. elliptica* and (2) all species combined. A Greenhouse-Geisser corrected test was used for all repeated measures ANOVA if assumption of sphericity was violated. Data was log transformed if variance and normality needed improvement.

Survival of outplanted native species in the uncleared treatment was generally low (0-60%) and growth was minimal (Chapter 1). Hence, planting effects on recruitment measures were only analyzed for the cleared treatment. Analysis and variables compared between planting treatments were the same as the main clearing treatment with the addition of biomass values.

2.3.2 Community Composition and Structure Measures

Community composition and structure analyses were performed separately for woody species and ground cover species measurements. Woody species were assigned size classes based on nested sampling levels (dbh ≥ 5 cm, 1.0 to 4.9 cm, and ≤ 1.0 cm). To increase resolution, woody species at the plot level (≥ 5 cm dbh) were divided into two size classes, 5.0 to 9.9 cm and ≥ 10 cm dbh. Therefore, four size classes were used for woody species: (1) <1.0 cm, (2) 1.0-4.9 cm, (3) 5.0-9.9 cm and (4) ≥10 cm dbh.

Plant species richness and diversity and stem density (number of stems per hectare), were calculated by plot for each of the woody species size classes and all woody species size classes pooled together. All community composition variables for year 2004 were analyzed using ANOVA to provide an overview of plant community composition prior to treatment applications. The cleared treatment resulted in removal of all non-native species in three out of the four woody species size classes (<1.0 cm, 1.0-4.9 cm, and 5.0-9.9 cm). Hence, only the largest size class (≥10 cm), i.e. the remaining overstory, was analyzed using repeated measures ANOVA to determine any differences in species richness and diversity, and stem density over time.

Repeated measures ANOVA were used to compare ground cover community species richness and diversity (using Shannon-Weiner Diversity Index; $H = -\Sigma[(p_i) \times \ln(p_i)]$, where p_i = proportion of total sample represented by species *i*) across years (2004, 2006, 2007 and 2008), block, and treatment. Planting effects, as per seedling recruitment analyses, was analyzed only for the cleared treatment.

2.3.3 Environmental Variables

Percent light transmittance (%T), soil volumetric water content (cm^3cm^3) and soil nutrient concentration (µg/g or mg/dm^3 depending on soil nutrient) were measured and examined to provide a context within which effects of time, block or treatment on ground cover recruitment and community structure could be understood (see Chapter 2, section 2.7 Statistical Analyses).

3. Results

3.1. Ground Cover Species Recruitment

3.1.1. Seedling Density

Seedling density of all species in the cleared treatment showed a declining trend over time relative to the uncleared treatment (Fig. 1a) but the differences were not significant (Table 1). Analysis of *A. elliptica* seedlings showed significantly lower densities in the cleared treatment (Table 1) and densities across treatments responded differently over time (Fig. 1b). In the cleared treatment, *A. elliptica* seedling density showed a sharp decline from 2004 to 2007, whereas the uncleared treatment declined gradually. Between-subject block by treatment effects were significant for both all species and *A. elliptica*. Generally, lower seedling densities occurred in the cleared treatment at the lower block and differences between treatments were greater (Fig. 2).

Changes in seedling density due to treatment and time effects occurred exclusively in seedlings < 5 cm in height. For larger seedlings, density was uniformly low (~5/m^2). However, in the cleared treatment, density of seedlings in the smaller size class in 2008 was lower (2.8/m^2) than in the larger size class.

Planted sub-treatments did not show a significant effect on seedling density for either all species and *A. elliptica* (Table 2).

Table 1. Repeated measures analysis of clearing treatment on seedling density of all species and *A. elliptica* for years 2004, 2006, 2007 and 2008.

All Species

Variable^{a}	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	1.529	3.503	3	0.031
Year x Treatment	0.970	2.223	3	0.112
Year x Block	0.377	0.864	3	0.473
Year x Treatment x Block	0.404	0.927	3	0.443
Between-Subject Effects				
Treatment	6.203	3.167	1	0.113
Block	3.657	1.867	1	0.209
Treatment x Block	11.305	5.772	1	0.043

a. Natural log transformed data

A. elliptica

Variable^{a}	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	5.842	10.680	3	0.000
Year x Treatment	3.147	5.754	3	0.002
Year x Block	1.184	2.164	3	0.104
Year x Class	2.784	5.090	3	0.004
Year x Treatment x Block	0.249	0.455	3	0.715
Year x Block x Class	0.377	0.689	3	0.563
Year x Treatment x Class	3.453	6.312	3	0.001
Year x Treatment x Block x Class	0.446	0.815	3	0.492
Between-Subject Effects				
Treatment	34.011	23.531	1	0.000
Block	0.568	0.393	1	0.055
Class	54.558	37.747	1	0.000
Treatment x Block	11.773	8.145	1	0.011
Treatment x Class	1.772	1.226	1	0.285
Block x Class	0.611	0.423	1	0.525
Treatment x Block x Class	0.332	0.230	1	0.638

a. Natural log transformed data

Figure 1. Mean seedling density between clearing treatment in all species (A) and *A. elliptica* (B) from 2004 to 2008. Error bars indicate 95% confidence intervals.

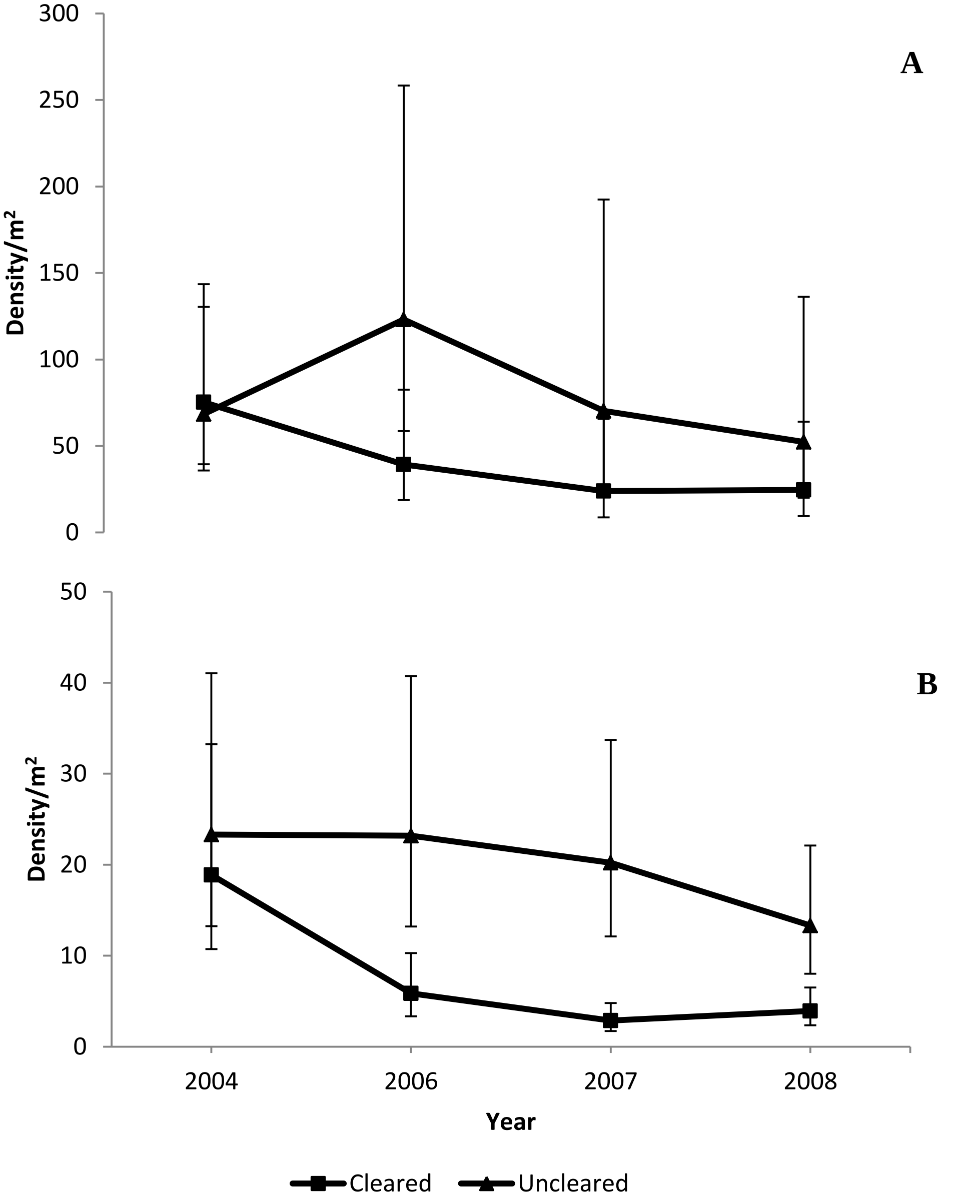


Table 2. Repeated measures analysis of planting treatment on seedling density of all species and *A. elliptica* within cleared treatment for post-treatment years 2006 to 2008.

All Species

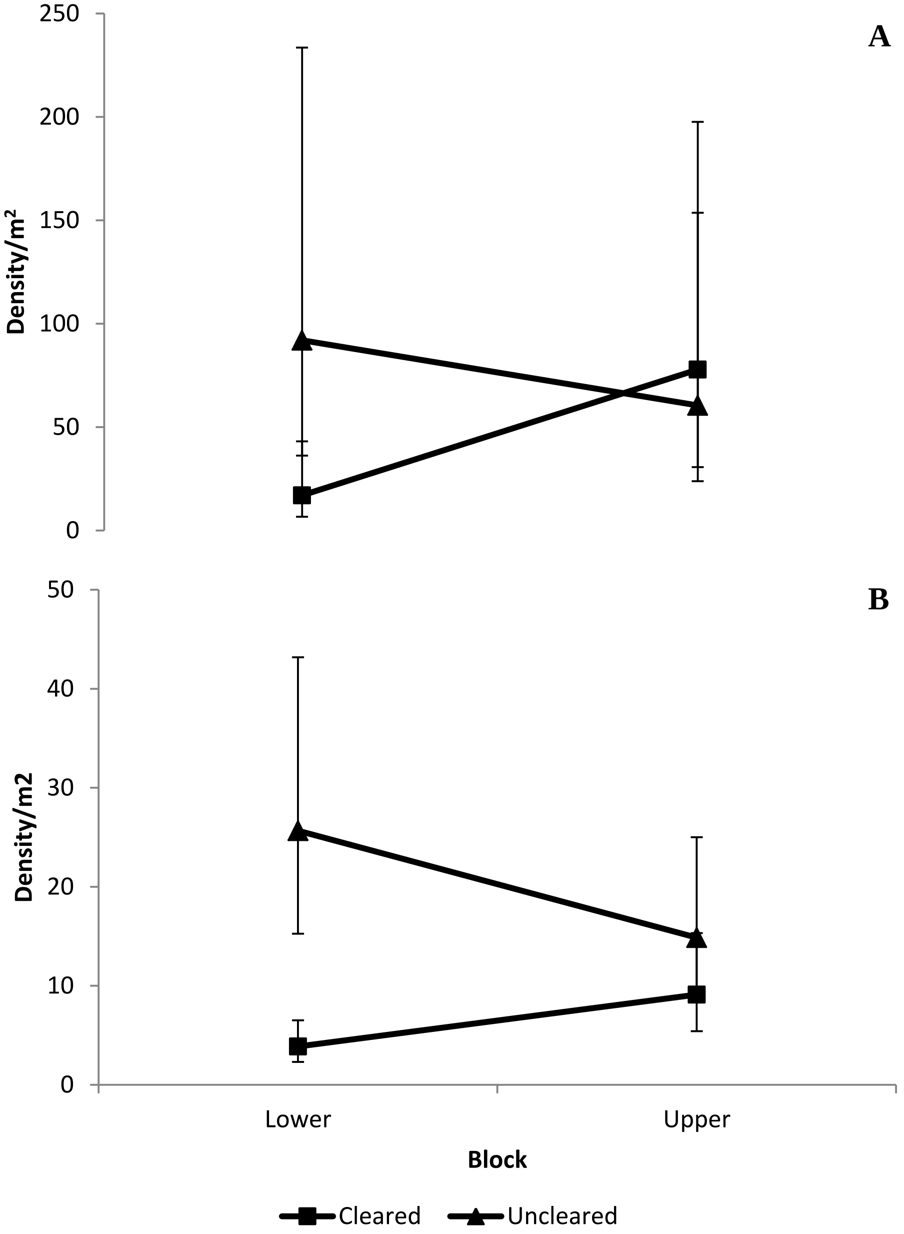
Variable^a	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	1.203	4.598	2	0.026
Year x PlantingTrtmt	0.269	1.027	2	0.381
Year x Block	0.874	3.342	2	0.061
Year x PlantingTrtmt x Block		0.702	2	0.510
Between-Subject Effects				
Planting Treatment	1.317	0.367	1	0.561
Block	21.237	5.928	1	0.041
Planting Trtmt x Block	0.142	0.367	1	0.847

a. Natural log transformed data

Variable^a	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	2.062	5.584	2	0.008
Year x PTreatment	0.566	1.533	2	0.231
Year x Block	0.381	1.031	2	0.368
Year x Class	5.401	14.629	2	0.000
Year x PTreatment x Block	0.100	0.271	2	0.764
Year x Block x Class	0.377	0.464	2	0.633
Year x PTreatment x Class	0.294	0.796	2	0.460
Year x PTreatment x Block x Class	0.211	0.571	2	0.571
Between-Subject Effects				
PTreatment	0.712	1.100	1	0.310
Block	3.476	5.373	1	0.034
Class	5.567	8.606	1	0.010
PTreatment x Block	0.062	0.096	1	0.760
PTreatment x Class	0.000	0.001	1	0.979
Block x Class	0.054	0.083	1	0.777
PTreatment x Block x Class	0.000	0.001	1	0.979

a. Natural log transformed data

Figure 2. Block by treatment interaction for seedling density of all species (A) and *A. elliptica* (B). Error bars indicate 95% confidence intervals.



3.1.2 Seedling Height

By 2008, seedling height for all species and *A. elliptica* was significantly lower in the cleared treatment (Table 3). Seedling height for all species in this treatment declined significantly from 30 cm in 2004 to 13 cm in 2006. From 2006 to 2008 additional declines in height were minimal (Fig. 3). Mean seedling height for all species and *A. elliptica* in the uncleared treatment remained relatively stable over time with an average height of 26 cm.

Mean seedling height was greater at the upper block for all species and *A. elliptica*. Height differences between blocks were 7.7 cm in 2007 and 3.8 cm in 2008. *A. elliptica* seedlings in the planted treatment were significantly shorter than those in the unplanted treatment. (Table 4). The height difference (~3 cm) was relatively consistent over time (Fig. 4).

Table 3. Repeated measures analysis of seedling height between clearing treatments from 2004 to 2008.

Seedling Height (cm)^a **Variable**	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	0.824	17.294	3	0.000
Year x Treatment	0.512	10.752	3	0.000
Year x Block	0.133	2.795	3	0.062
Year x Treatment x Block	0.129	2.709	3	0.068
Between-Subject Effects				
Treatment	3.028	44.279	1	0.000
Block	0.686	10.027	1	0.013
Treatment x Block	0.085	1.246	1	0.297

a. Natural log transformed data

***A. elliptica* Seedling Height (cm)^a** **Variable**	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	2.350	49.619	3	0.000
Year x Treatment	1.532	32.360	3	0.000
Year x Block	0.041	0.870	3	0.470
Year x Treatment x Block	0.092	1.951	3	0.148
Between-Subject Effects				
Treatment	9.778	255.311	1	0.000
Block	0.193	5.038	1	0.055
Treatment x Block	0.091	2.386	1	0.162

a. Natural log transformed data

Figure 3. Mean seedling height (cm^2) between clearing treatments for all species (A) and *A. elliptica* (B) 2004 to 2008. Error bars indicate 95% confidence intervals.

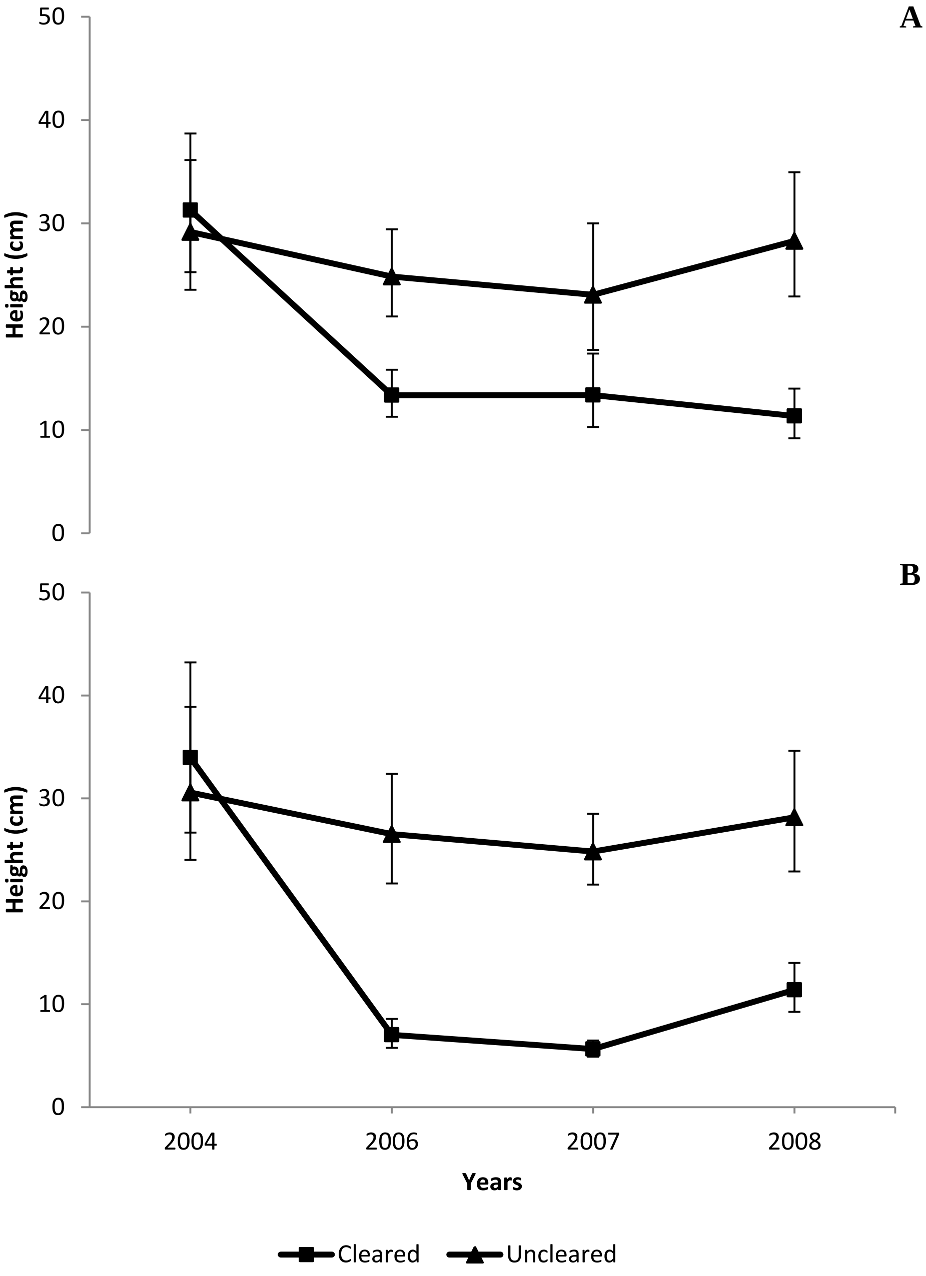


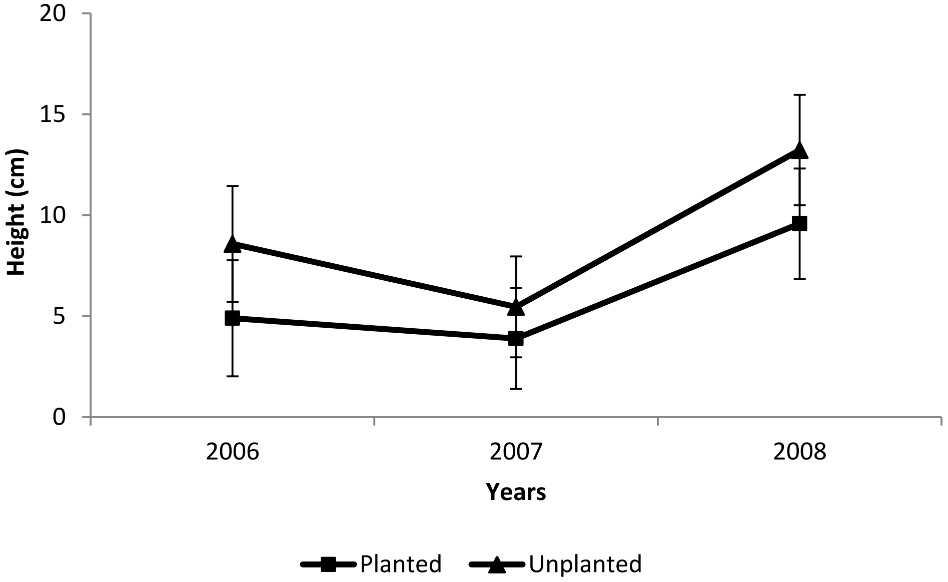
Table 4. Repeated measures analysis of seedling height for planting treatments within cleared treatment for post-treatment years 2006, 2007, 2008.

Seedling Height (cm)[a] Variable	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	0.134	1.078	2	0.364
Year x Planting Treatment	0.096	0.773	2	0.478
Year x Block	0.030	0.245	2	0.786
Year x Planting Treatment x Block	0.088	0.707	2	0.508
Between-Subject Effects				
Planting Treatment	0.200	0.805	1	0.396
Block	2.619	10.545	1	0.012
Planting Treatment x Block	0.010	0.042	1	0.843

***A. elliptica* Seedling Height (cm) Variable**	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	142.663	27.116	2	0.000
Year x Planting Treatment	4.399	0.836	2	0.451
Year x Block	12.405	2.358	2	0.127
Year x Planting Treatment x Block	0.845	0.161	2	0.853
Between-Subject Effects				0.046*
Planting Treatment	79.145	5.556	1	
Block	39.985	2.807	1	0.132
Planting Treatment x Block	0.741	0.052	1	0.162

* Significant at the 0.05 level

Figure 4. Mean *A. elliptica* seedling height (cm^2) between planting treatments within cleared treatment over post-treatment years 2006 to 2008. Error bars indicate 95% confidence intervals.



3.1.3 Seedling Biomass

Seedling biomass of all species and *A. elliptica* declined significantly over time in the cleared treatment (Table 5), especially with the initial 18 months post-treatment. Afterward, seedling biomass was relatively consistent at less than 2.3 g/m^2 for all species and 1.6 g/m^2 for *A. elliptica* (Fig. 5). Seedling biomass was greater at the upper block but as with treatment, biomass was uniformly low after 18 months. While biomass was generally lower in the planted sub-treatment, the differences were not significant.

Table 5. Repeated measure analysis of seedling biomass for all species and *A. elliptica* for planting sub-treatments over time.

All Species

Variable[a]	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects[b]				
Time	28.997	49.503	3.107	0.000
Time x Planting	0.914	1.560	3.107	0.207
Time x Block	0.920	1.571	3.107	0.204
Time x Planting x Block	0.799	1.364	3.107	0.257
Between-Subject Effects				
Planting	5.428	2.465	1	0.132
Block	62.318	28.301	1	0.000
Planting x Block	1.860	0.845	1	0.369

a.Natural log transformed data

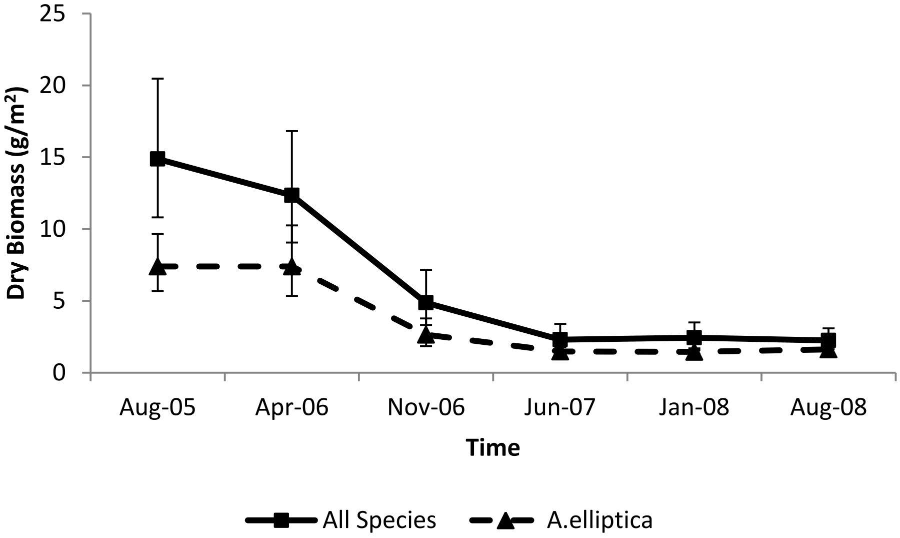
b. Greenhouse-Geisser Corrected Test (0.621) applied

Variable[a]	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects[b]				
Time	24.190	47.563	3.009	0.000
Time x Planting	0.154	0.303	3.009	0.823
Time x Block	0.249	0.490	3.009	0.691
Time x Planting x Block	0.218	0.429	3.009	0.734
Between-Subject Effects				
Planting	0.836	1.302	1	0.267
Block	7.762	12.079	1	0.002
Planting x Block	0.027	0.042	1	0.839

a. Natural log transformed data

b. Greenhouse-Geisser Corrected Test (0.602) applied

Figure 5. Seedling biomass over time for all species and *A. elliptica* within cleared treatment. Error bars indicate 95% confidence intervals.



3.2 Plant Community Descriptors

Before treatment application, the 2004 vegetation survey revealed higher woody species stem density and species richness at the upper site, but both sites had a mid-story dominated by *A. elliptica* and similar species diversity (Table 6). These characteristics were also reflected in the seedling community. Relative to the other woody species size classes, the largest trees had the lowest species richness and diversity. Highest species diversity and richness occurred in woody species with a dbh between 1.0 and 9.9 cm. Woody species with a dbh of <1.0 to 4.9 cm had the highest stem densities (Fig. 6). *A. elliptica* had the highest stem density among species in all size classes, except among trees with a dbh >10 cm (Table 7). After treatment application, surveys of the uncleared overstory canopy (dbh >10 cm) did not show any changes in stem density, species diversity or species richness (Table 8).

Species diversity and richness of seedlings were significantly higher in the cleared treatment throughout the post-treatment years 2006 to 2008 (Table 9). The greatest increase in diversity and richness within the cleared treatment occurred in 2006, one year post-treatment application (Fig. 7). After 2006, diversity and richness values gradually declined in the cleared treatment but never fell lower than pre-treatment levels. Block effects remained after treatment application, i.e. species richness and diversity were greater in the upper block.

The cleared treatment also responded differently within each block over time (Fig. 7). Species diversity in the upper block declined after 2006, but diversity continued to increase until 2007 in the lower block. Diversity values in the uncleared treatments across both blocks remained relatively stable over time. By 2008, the difference between treatments at the upper block was minimal; however, treatment differences in the lower block were sustained through 2008.

Generally, the effect of planting led to an initial decrease in species diversity, not including the planted native species themselves, but by 2008, planting effects were not significant (Table 10). Species richness in the planted treatment declined over time and was lowest in the lower block. The largest decrease occurred between 2006 and 2007.

Table 6. Univariate analysis of woody species diversity, species richness, and stem density before treatment application in 2004.

Species Diversity

Variable	**Mean Square**	***F***	***df***	***P* Value**
Between-Subject Effects				
Block	0.198	0.298	1	0.588
Class	2.840	4.283	3	0.010
Block x Class	0.599	0.903	3	0.448

Variable[a]	**Mean Square**	***F***	***df***	***P* Value**
Between-Subject Effects				
Block	1.319	6.286	1	0.016
Class	2.378	11.332	3	0.000
Block x Class	0.121	0.576	3	0.634

Variable[a]	**Mean Square**	***F***	***df***	***P* Value**
Between-Subject Effects				
Block	961.118	44.995	1	0.000
Class	2064.846	96.666	3	0.000
Block x Class	104.120	4.874	3	0.006

[a] Square root transformed

Figure 6. Woody species diversity (A), species richness (B), and stem density (C) between sites and size classes before treatment application in 2004. Error bars indicate 95% confidence intervals.

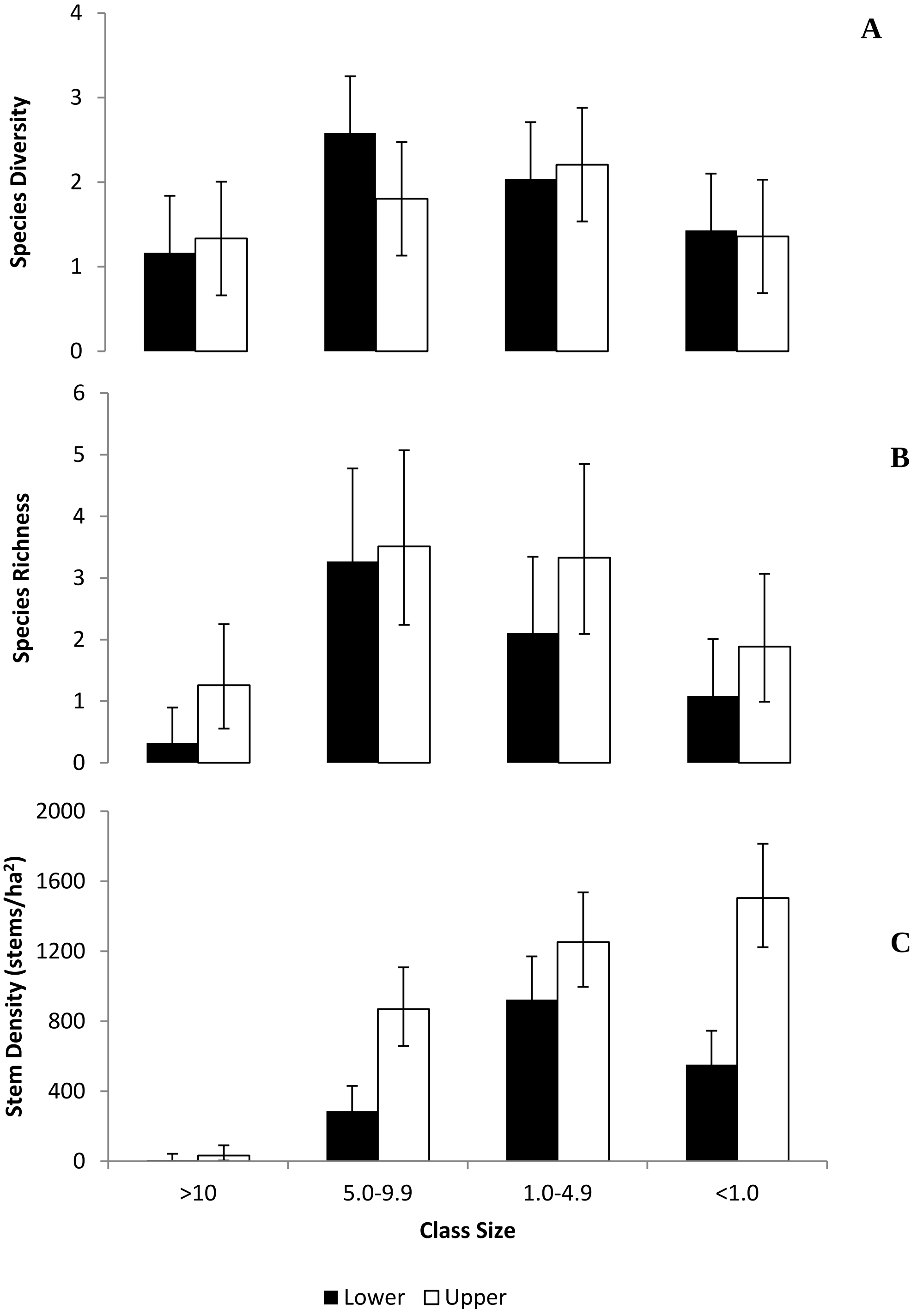


Table 7. Species stem density among all woody size classes in 2004. Species ranked by stem density per size class.

	Lower Block		**Upper Block**	
Class (cm)	**Species Name**	**Stem Density (# ha^{-2})**	**Species Name**	**Stem Density (# ha^{-2})**
>10	*Ardisia elliptica*	2315	*Ardisia elliptica*	7662
	Cordyline fruticosa	324	*Cordyline fruticosa*	116
			Cinnamomum burmanni	69
			Cinnamomum zelanicum	69
			Citharexylum caudatum	69
			Schefflera actinophylla	23
5.0-9.9	*Ardisia elliptica*	4699	*Ardisia elliptica*	5394
	Cordyline fruticosa	694	*Cordyline fruticosa*	1296
	Schefflera actinophylla	69	*Costus spp.*	532
	Citharexylum caudatum	46	*Citharexylum caudatum*	93
	Macaranga mappa	46	*Psychotria spp.*	93
	Araucaria spp.	23	*Psidium cattleainum*	69
			Cinnamomum burmanni	46
			Freycinetia arborea	46
			Schefflera actinophylla	46
1.0-4.9	*Ardisia elliptica*	1042	*Ardisia elliptica*	4352
	Macaranga mappa	278	*Cordyline fruticosa*	347
	Cordyline fruticosa	232	*Citharexylum caudatum*	185
	Schefflera actinophylla	93	*Psychotria spp.*	139
	Cinnamomum burmanni	46	*Schefflera actinophylla*	93
	Citharexylum caudatum	23	*Cinnamomum burmanni*	69
	Heliocarpus popayanensis	23	*Psidium cattleainum*	69
			Macaranga mappa	23
<1.0	*Juniperus spp.*	69	*Schefflera actinophylla*	46
	Rhus taitensis	23	*Ardisia elliptica*	23
			Cinnamomum burmanni	23
			Citharexylum caudatum	23
			Cordyline fruticosa	23
			Diospyros spp.	23
			Ilex paraguayensis	23
			Macaranga mappa	23

Table 8. Repeated measures analysis of species diversity, species richness, and stem density of overstory trees (dbh >10 cm) over post-treatment years 2006 to 2008.

Species Diversity

Variable	Mean Square	*F*	*df*	*P* Value
Within-Subject Effects				
Year	0.312	1.297	2	0.301
Year x Treatment	0.377	1.569	2	0.239
Year x Block	0.058	0.242	2	0.788
Year x Treatment x Site	0.198	0.824	2	0.457
Between-Subject Effects				
Treatment	0.469	0.836	1	0.387
Site	0.825	1.470	1	0.260
Treatment x Site	0.420	0.749	1	0.412

Variable	Mean Square	*F*	*df*	*P* Value
Within-Subject Effects				
Year	0.361	1.444	2	0.265
Year x Treatment	0.361	1.444	2	0.265
Year x Block	0.083	0.333	2	0.721
Year x Treatment x Block	0.194	0.778	2	0.476
Between-Subject Effect				
Treatment	1.361	0.961	1	0.356
Site	6.250	4.412	1	0.069
Treatment x Site	1.361	0.961	1	0.356

Variable	Mean Square	*F*	*df*	*P* Value
Within-Subject Effects				
Year	282.799	2.111	2	0.154
Year x Treatment	312.567	2.333	2	0.129
Year x Block	104.189	0.778	2	0.476
Year x Treatment x Block	193.494	1.444	2	0.265
Between-Subject Effects				
Treatment	535.830	0.364	1	0.563
Block	5953.666	4.040	1	0.079
Treatment x Block	952.586	0.646	1	0.445

Table 9. Repeated measures analysis of clearing treatment on seedling species diversity and richness from 2004 to 2008.

Species Diversity

Variable^a	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	1.428	20.432	3	0.000
Year x Treatment	0.615	8.794	3	0.000
Year x Block	0.042	0.599	3	0.622
Year x Treatment x Block	0.218	3.124	3	0.045
Between-Subject Effects				
Treatment	4.449	16.438	1	0.004
Block	1.070	3.955	1	0.082
Treatment x Block	0.411	1.519	1	0.253

a. Natural log transformed data

Species Richness

Variable	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	42.188	11.728	3	0.000
Year x Treatment	17.688	4.917	3	0.008
Year x Block	1.465	0.407	3	0.749
Year x Treatment x Block	8.632	2.400	3	0.093
Between-Subject Effects				
Treatment	180.188	15.281	1	0.004
Block	212.521	18.023	1	0.003
Treatment x Block	22.688	1.924	1	0.203

Figure 7. Clearing treatment and block effects on seedling species diversity and richness over time. Error bars indicate 95% confidence intervals. Scale on the y-axis differs between blocks.

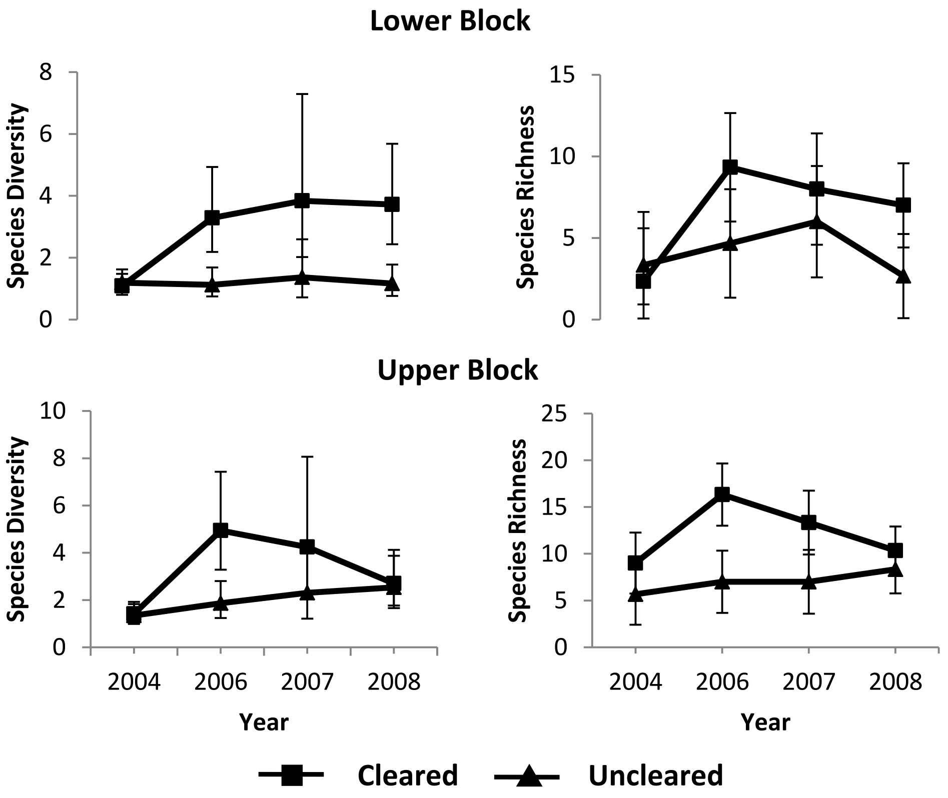


Table 10. Repeated measures analysis of planting treatments on seedling species diversity and richness from 2006 to 2008.

Species Diversity

Variable[a]	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	1.238	0.948	2	0.408
Year x Planting	1.076	0.825	2	0.456
Year x Block	1.348	1.033	2	0.379
Year x Planting x Block	3.997	3.062	2	0.075
Between-Subject Effects				
Planting	1.662	0.492	1	0.503
Block	4.076	1.207	1	0.304
Planting x Block	0.214	0.063	1	0.807

a. Natural log transformed data

Species Richness

Variable	**Mean Square**	***F***	***df***	***P* Value**
Within-Subject Effects				
Year	7.861	7.327	2	0.006
Year x Planting	7.444	6.939	2	0.007
Year x Block	2.194	2.045	2	0.162
Year x Planting x Block	0.750	0.699	2	0.512
Between-Subject Effects				
Planting	1.174	0.301	1	0.598
Block	98.340	25.242	1	0.001
Planting x Block	3.896	0.786	1	0.401

3.2.1 Plant Species Composition

A total of 32 species were observed in the understory over the four years of the study; 13 of these were found consistently in each of the four years (Table 11). Only two out of the 32 understory species were native, *Freycinetia arborea* and *Psychotria* spp. Regeneration of these species was limited and regeneration of other native species present within the research area (e.g. *Diospyros* spp., *Alyxia stellata*, and *Pipturus albidus*) was not observed in any of the post-treatment years. Eleven species were unique to the cleared treatment, and two species were unique to the uncleared. Among blocks, 13 species were found only in the upper block and two species only in the lower block. Seven species were observed only in the post-treatment years

(2006-2008). While these species were not observed in the plots prior to treatment application, they were present within the research area outside of the plots (personal observation) and many have been documented as naturalized within Lyon Arboretum (Daehler and Baker, 2006) and the greater Mānoa Valley (MacCaughey, 1917; Wagner *et al.*, 1999). All of these colonizing species were non-native, including five herbaceous ground cover species, a shrub (*Rubus rosaefolius*), and a tree (*Trema orientals*). Most of these species are categorized as ruderal or pioneering species, taking advantage of disturbed areas.

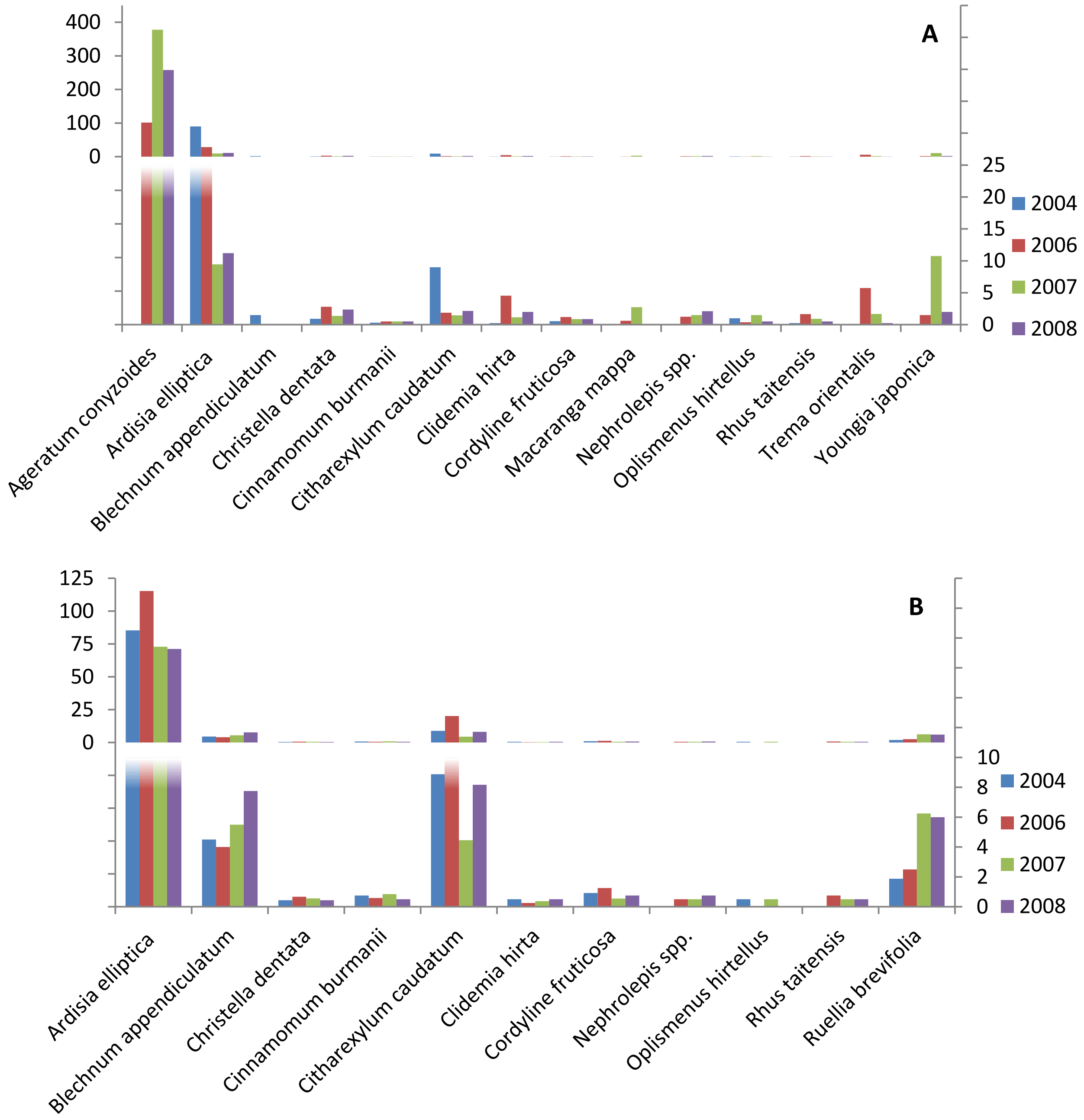
Although seedling density of *A. elliptica* declined over time in the cleared treatment, it remained one of the most abundant species in the understory across treatments and was present in all plots for all four years (Figure 8). Within the uncleared treatment, the species with the second highest seedling density after *A. elliptica* was *Citharaxylum caudatum* with a five- to eight-fold mean difference in density depending on year. Although, *Ageratum conyzoides* ranked above *A. elliptica* in seedling density in the cleared treatment, it was only present within one plot.

Table 11. Understory species observed within research area.

	Year 20-				Trtmt		Block				
Species Name	**04**	**06**	**07**	**08**	**C**	**UC**	**U**	**L**	**Functional Type**	**Native**	**Family**
Ageratina riparia		x	x	x	x		x		Forb		Asteraceae
Ageratum conyzoides		x	x	x	x		x		Forb		Asteraceae
Araucaria spp.	x			x		x		x	Tree		Araucareacea
Ardisia crenata	x	x		x	x	x	x		Shrub		Myrsinaceae
Ardisia elliptica	x		x	x	x	x	x	x	Tree		Myrsinaceae
Blechnum appendiculatum	x	x	x	x	x	x	x		Pteridophyte		Blechnaceae
Cecropia obtusifolia	x	x	x		x		x	x	Tree		Urticaceae
Christella dentata	x	x	x	x	x	x	x	x	Pteridophyte		Thelypteridaceae
Cinnamomum burmanii	x	x	x	x	x	x	x	x	Tree		Lauraceae
Citharexylum caudatum	x	x	x	x	x	x	x	x	Tree		Verbaneacea
Clidemia hirta	x	x	x	x	x	x	x	x	Shrub		Melastomataceae
Cordyline fruticosa	x	x	x	x	x	x	x	x	Tree/shrub		Asparagaceae
Costus scaber	x	x	x	x	x	x	x	x	Shrub		Costaceae
Elaeocarpus grandis		x			x		x		Tree		Elaeocarpaceae
Emilia sonchifolia		x	x	x	x		x		Forb		Asteraceae
Falcataria moluccana		x	x		x	x	x	x	Tree		Fabeaceae
Filicium decipiens	x	x	x		x	x	x		Tree		Sapindaceae
Freycinetia arborea				x	x		x		Shrub	x	Pandanaceae
Juniperus spp.		x	x		x	x		x	Tree		Cupressaceae
Macaranga mappa		x	x		x		x	x	Tree		Euphorbiaceae
Nephrolepis spp.		x	x	x	x	x	x		Pteridophyte		Nephrolepidaceae
Oplismenus hirtellus	x	x	x	x	x	x	x	x	Graminoid		Poaceae
Paederia scandens	x	x	x	x	x	x	x	x	Vine		Rubiaceae
Psidium cattleianum	x	x	x	x	x	x	x		Tree		Myrtaceae
Psychotria spp.		x	x		x		x		Tree	x	Rubiaceae
Rhus taitensis	x	x	x	x	x	x	x	x	Tree		Anacardiaceae
Rubus rosaefolius		x	x	x	x		x	x	Shrub		Rosaceae
Ruellia brevifolia	x	x	x	x		x		x	Forb		Acanthaceae
Schefflera actinophylla	x		x	x	x	x	x	x	Tree		Araliaceae

Setaria palmifolia	x	x		x		x		Graminoid		Poaceae
Trema orientalis	x	x	x	x		x	x	Tree		Cannabaceae
Youngia japonica	x	x	x	x		x		Forb		Asteraceae

Figure 8. Seedling density by species across years for cleared (A) and uncleared (B) treatment. Upper panel shows all data; lower panel shows smaller values. Scale on the y-axis differs between A and B.



3.3 Environmental Conditions

Most of the treatment effects for seedling recruitment and community descriptors appear to be driven by the repeated biannual removal of non-native species in the cleared plots. However, for many of the recruitment and community descriptors there were also block and treatment by block effects. The only two environmental variables to show an associated block effect were percent light transmittance and soil moisture (Table 12 and 13, respectively). More open canopy cover at the upper site is most likely allowing for more light and precipitation to reach the forest floor (Chapter 2). Higher percent light transmittance and soil moisture at the upper block could explain block effects in recruitment measurements of seedling height and biomass; and treatment by block interactions for seedling densities, particularly in the cleared treatment.

Table 12. Univariate analysis for percent light transmittance and canopy cover.

Variable	**Mean Square**	***F***	***df***	***P* Value**
% Light Transmittance[a]				
Treatment	0.316	61.705	1	<0.001
Block	0.127	24.748	1	<0.001
Treatment x Block	0.087	17.084	1	0.001
% Canopy Cover[a]				
Treatment	1.583	111.312	1	<0.001
Block	0.221	15.557	1	<0.001
Treatment x Block	0.247	17.363	1	<0.001

a. Arcsine square root transformed data

Table 13. Multivariate analysis of soil volumetric water content

Variable	**Pillai's Trace**	***F***	***df***	**Error *df***	***P* Value**
Treatment	0.288	0.990	20	49	0.489
Block	0.617	3.952	20	49	<0.001
Treatment x Block	0.293	1.015	20	49	0.463

4. Discussion

4.1. Removal and Planting Effects

Removal of non-native species is often the first step in preparing a site for restoration of native plant species (e.g. a subtractive-approach Sailor, 2006). In areas where non-native species dominate forest composition, removal can create areas more susceptible to non-native species recruitment due to increases in light availability and other resources. Hence, follow-up non-native species removal becomes important for limiting their spread and increasing chances for survival and growth of outplanted or regenerating native species. Understanding effects of quantity and frequency of non-native species removal, as well as native plant enrichment (additive-approach) can assist land managers in administering more efficient weed management strategies and potentially reduce associated costs. This study sought to improve that understanding by examining the effects of removal of non-native understory plant species and outplanting of native species, on seedling recruitment and community composition.

4.1.1 Removal Frequency Effects on Non-native Seedling Recruitment

In any type of cultivation system, there will be a need to control undesired plant species, i.e. weeds. It was expected that repeated removal of non-native species would reduce non-native seedling density but unknown was which and in what quantities non-native species would grow back within the six-month removal frequency.

Species diversity and richness values were highest in the first year following clearing but declined and leveled off in the second and third years. Following initial clearing, resources were more available and seedling competition from *A. elliptica* was reduced allowing for more species to establish; however, by 2008 the repeated removal limited the introduction of new species. A difference in seedling density between blocks suggests the importance of available understory light on the amount of seedling recruitment. At the upper block seedling density was not as reduced as in the lower block, suggesting the higher light environment was enough to sustain greater seedling densities in the cleared treatment despite repeated removals. In particular, it was observed that within one cleared plot at the upper block, *A. conyzoides*, an herbaceous ruderal species, became more dominant than *A. elliptica* seedlings with densities approximately 400/m^2 (Fig. 8). This particular plot also had the highest light transmittance (40%), and since *A.*

conyzoides was absent from all other plots it is likely that it benefited from the increased light. Greater species richness at the upper block also is most likely a response to increases in available light due to a more open and mixed forest canopy cover.

It was expected that seedling density in the uncleared treatment would remain relatively stable over time since there was no removal of plant material from these plots. A difference in seedling density between years was not significant but there was downward trend. Disturbance from planting native species in 2005 and inadvertent trampling from subsequent measurements of native plants and vegetation could have contributed to slight declines in seedling density in uncleared plots.

Higher percent light transmittance and a more open canopy cover in the upper block could also explain block effects for seedling height within the cleared treatment where seedlings grew taller between weeding events than their more shaded counterparts in the lower block. In uncleared plots, where weeding was not occurring and light transmittance was approximately 1%, seedlings were taller than in the cleared treatment. Additionally, these seedlings were predominantly *A. elliptica* (Fig.8) and may have been several years old since *A. elliptica* has recalcitrant seeds and is known to maintain seedling banks (Koop, 2004). Hence, without weeding, forests dominated by *A. elliptica* and other shade-tolerant species, can continue to sustain their respective seedling populations even in relatively low percent light transmittance. Differences in density between *A. elliptica* seedlings ≤ 5 cm and those > 5 cm, also suggests clearing effects on seedling growth. If seedlings ≤5 cm are considered recently emerged seedlings, successive weeding is essentially removing more seedlings than are being replaced by the annual seed rain. Larger seedlings become more present over time since there is less competition for resources and can grow larger in the six-month time frame between removals.

Hence, removal of non-native understory species every six months was more effective at reducing non-native seedling recruitment, particularly of the targeted non-native species *A. elliptica*, when remaining canopy cover was more uniform and light transmittance ranged from 2 to 6 percent. Consequently, available light will determine how much and how often non-native plant removal will be required. Differences in seedling recruitment response between blocks, suggests that in higher light conditions (6 to 40% light transmittance), weeding efforts will need to be more frequent and will be critical for keeping target non-native species recruitment low as well as preventing another undesirable species from taking advantage of released resources. McDaniel and Ostertag (2010) determined that 5% light transmittance reduced non-native grass biomass but was sufficient for survival and growth of Hawaiian native woody species. These findings coincide with understory light availability levels for a native *Metrosideros*-dominated wet forest on the island of Hawai‘i which ranged from 5–10% (Burton and Mueller-Dombois, 1984; Pattison *et al.*, 1998), compared to a lowland wet forest, also on the island of Hawai‘i, which had a predominance of non-native species and whose understory available light levels averaged 2% (Wong, 2007). Understory light levels at around 5%, like those found at the lower block in this study, are more conducive for a less-managed approach where weeding could most likely be reduced to an annual effort. Removal frequency is also critical. In this study, an increase in species diversity and richness was observed in the first year post-treatment, suggesting that weeding efforts should be concentrated in the time immediately following clearing and for at least a year. Reductions in biomass from repeated removals were also most apparent in the initial 18 months post-treatment but then leveled off; suggesting that after two years weeding frequency can most likely be reduced. Available understory light and frequency of removal are important considerations for restoration management strategies aiming to minimize non-native recruitment and support native species growth.

4.1.2 Planting Effects on Non-native Species Recruitment

Control of weedy species via competition and shading from other plants has been proposed as a means to make restoration more effective and reduce costs associated with repeated weeding (Gomez-Aparicio, 2009; Vieira *et al.*, 2009). In this study, mean values for recruitment measures tended to be greater in the unplanted treatment; however, significant declines in seedling height for *A. elliptica* and reduced species richness over time, along with possible declines in seedling biomass for all species in the planting treatment (p = 0.132), suggests planting may have a negative effect on seedling recruitment. Hence, planting of native species may not directly reduce the capacity for non-native seedling germination (e.g. many seedlings can germinate in shade) but could potentially reduce capacities for seedling growth, as measured by seedling height, via shading and resource competition.

More conclusive planting effects may have been observed if more time had been allowed between weeding events. It's possible that the six-month weeding frequency did not allow enough time for differences in growth of seedlings to be observed between planting treatments. Repeated weeding could also have obscured planting effects by reducing the seedling population enough so that no treatment effect could be detected. In other words, the overall negative effect of repeated weeding on seedling recruitment could have been greater than any potential negative effects of planting. Lastly, slope and soil erosion may also have confounded planting effects and seedling height measurements by burying seedlings (personal observation).

It was expected that planting would reduce species diversity and richness values by reducing the number of seedlings and, hence available species, capable of germinating among and competing with planted species even with repeated weeding. While this was observed within species richness, planting effects on species diversity were less clear.

While this study did not conclusively isolate the effect of planting on seedling recruitment, there is evidence that competition and shading can negatively affect non-native seedling growth, even for species adapted to low-light conditions. Significant declines in seedling height for *A. elliptica* suggest that the outplanted native species have the potential to reduce the ability of *A. elliptica* seedlings to reach maturity. Results from Chapter 2, show that *M. strigosa*, did establish and reach sizes capable of providing ground cover and shade to emerging seedlings. Another potential benefit of the plantings once established is that they can limit soil erosion, particularly if clearing is conducted on steep slopes.

Ultimately, seedling recruitment is dynamic, and short-term and long-term factors (e.g. removal and developed overstory, respectively) can affect seedling quantities and qualities. The ability for a plant species to regenerate in continually cleared plots will depend on its life cycle (perennial vs. annual), seed rain, seed bank and seed germination. Since *A. elliptica* seeds are recalcitrant, semi-annual weeding intervals were selected to occur after fruiting and hence capture emerging seedlings. However, most of the other non-native species found within the area have orthodox seeds (Hong et al., 1996), and it was unknown if this type of "seedling bank exhaustion" would result in another species dominating the area. Other than the specific response of *A. conyzoide*s in one particular plot, no other species came to dominate species composition, as did *A. elliptica*. However, seedling recruitment of existing native species or outplanted native species within the research area was not observed. Other studies in Hawai‘i have also observed an insufficient native seed bank to support natural regeneration and/or environmental conditions have changed sufficiently to no longer support germination (Drake, 1998; Mascaro *et al.*, 2008; Cordell *et al.*, 2009; Ostertag *et al.*, 2009). Cordell *et al.* (2009) suggests that native seedling establishment may depend on the nature of the post-disturbance environment in which case further research is needed into what post-disturbance environments are most conducive for native seed germination. It is possible that more time is required to observe native species germination in the cleared areas.

4.2 Experimental Design Limitations

The split-plot experimental design with repeated weeding had limitations. While the planted and unplanted sub-treatments were equally represented in the cleared and uncleared treatments, nesting the planting sub-treatment within the main clearing treatment reduced the experimental area by half and may have had a confounding effect on planting. Ideally, the clearing treatment and planting treatment would have used a complete factorial requiring 12 plots for each block (n = 3) to more clearly determine which factor (clearing or planting or combination) were driving declines in all species as well as *A. elliptica* seedlings. Imposing different levels of removal occurrences could also have provided additional information, e.g. single weeding versus different frequencies of repeated weeding. For this study, limited land was available for research within Lyon Arboretum and elsewhere. The research area was highly variable in aspect, slope, rockiness, and plant cover. Thus, when installing the experiment, it was determined that increases in plot numbers, size or replicates would introduce more variables that would confound treatment effects.

5. Conclusion and Implications for management

There is no single management strategy to restore non-native dominated forests in Hawai‘i. Studies have shown that removal of invasive species is needed to support restoration of native species in Hawai‘i (Cabin *et al.*, 2002; Mascaro *et al.*, 2008; Ostertag *et al.*, 2009; Ammondt *et al.*, 2013). Removal provides benefits in the amount of increased resources to native plantings but can also increase the spread of other non-native species. Hence, level of removal should correspond with management that is feasible both economically and ecologically. Some managers have recommended removing no more than 10% of the canopy in one year as a general rule of thumb (Sailor, 2006).

Removal of all non-native species can be costly and may not provide long-term benefits to native plantings if weed management is not maintained. Additionally, removal of all non-native species may not be possible in certain areas, particularly if large trees are present or steep or rocky terrain makes it hard to access. In forests with mixed native and non-native species there are additional challenges to making sure native plants are not removed or harmed in the removal process.

Kirkman et al. (2007) suggest using undesirable species as a structural or functional bridge to foster ecological processes during restoration. In other words, selecting existing non-invasive, non-native species to maintain forest structure and function during the restoration process and sustain important ecological processes until native plants can fulfill those roles. In Hawaiʻi, there is ongoing research on the potential for using non-invasive, non-native species in conjunction with native species plantings to create novel plant communities that can more effectively suppress invasive species recruitment than just native species alone and in the long-term require less management (Ostertag et al., 2014). Since many of Hawaiʻi's lowland forests have become dominated by non-native species, these non-native species could be managed to support restoration goals. The results of this study indicate that management for a more uniform non-native homogenous canopy cover can provide more uniform light transmittance to the understory and decrease seedling recruitment. It can also allow for further expansion of the removed understory once seedling recruitment levels off (e.g. 18 months in this study). This can become the basis of a weed management plan where there is a sequential alteration between clearing undesired species and planting native ones. For example, after an initial clearing of understory invasive species where an overstory canopy is left intact, shade-tolerant native species such as ferns can be planted, e.g. palapalai and maile. Subsequent ground cover weeding can limit invasive species recruitment while supporting growth of native species. Once weeding efforts plateau, further removal of the understory could then be undertaken if the area needed to be expanded or partial canopy openings could be created to support growth of native understory plants requiring more light (e.g. Māmaki). It is important to note that the success of manipulating resources as a restoration strategy could also be influenced by other abiotic factors (e.g., precipitation, temperature, soil fertility). For example, the ability of a plant to establish in decreased light availability may be facilitated by the lack of competition for soil moisture or soil fertility (Wright, 1992).

This study aimed to shed light on this non-native species utility by evaluating removal and planting strategies that can support native plant restoration while minimizing recruitment of non-native species. While established native outplantings may provide some resource competition for non-native species, the results of this study indicate that manipulation of environmental resources, such as light, plus continued weeding will be more effective in reducing non-native species recruitment.

CHAPTER 4:

PHOTOSYNTHETIC LIGHT RESPONSE OF AN OUTPLANTED NATIVE FERN, *MICROLEPIA STRIGOSA* (THUNB.) K. PRESL, TO VARYING UNDERSTORY LIGHT CONDITIONS

1. Introduction

In Hawai‘i, habitat destruction and invasion of non-native species have contributed to the loss of almost half of its native forests and left the remaining forests significantly altered (Cuddihy and Stone, 1993). Successful restoration of these altered forests often requires outplanting and seeding of native plants since native seed sources are often limited (Drake, 1998; Denslow *et al.*, 2006; Mascaro *et al.*, 2008; Cordell *et al.*, 2009). Invasion of non-native tree species can contribute to a decline in light availability due to increased leaf area associated with increased tree density or through changes in canopy structure, e.g. greater light absorption per unit leaf area index (Wong, 2007). Light is considered one of the most important factors influencing species recruitment and deep shade can limit growth and survival of understory species (Bazzaz and Pickett, 1980). However, light is the main resource that can easily be manipulated by land managers through selective thinning of canopy species or removal of non-native species. In restoration projects where light conditions may be changing over time, the ability for an understory outplanted species to survive and grow under a range of light conditions may prove critical to restoration success and its ability to compete with non-native species introductions. A better understanding of the ecophysiological responses of native species to invaded understory is needed to improve their survival and growth, as well as determine whether these invaded understories are amenable to native plant restoration through light management.

This study relates the photosynthetic response of an outplanted native, understory fern, *Microlepia strigosa* (Thunb.) K. Presl, to differences in the understory light environment of a non-native dominated forest in which the understory was either cleared or not cleared of an invasive species, *Ardisia elliptica* Thunb. Measurement of photosynthetic responses to varying light levels can determine whether these ferns are restricted to shade or whether they can tolerate a wider range of light availability. If light-saturated net photosynthesis rates [$P_N(I_{max})$] do not increase over a certain threshold of percent light transmittance (% LT) then the optimal light level for the fern lies below that threshold. Indeed, higher light levels may incur negative effects, through an associated increase in temperature, increase in evaporative demand, or photoinhibition (Vincent, 2001).

In general, research on the photosynthetic capacity of plants in response to light focuses on the response of species in existing or naturally regenerated populations growing under different light regimes, e.g. forest gaps, understory, or clearings. In Hawai‘i, it has largely centered on the impact of invasive species on the photosynthetic response of existing native plant populations (Pearcy and Calkin, 1983; Pearcy and Ehleringer, 1984) or directly compares photosynthetic responses of native versus invasive species (Pattison *et al.*, 1998; Baruch and Goldstein, 1999; Durand and Goldstein, 2001). However, research into the photosynthetic capacity of outplanted native Hawaiian species for restoration could not be found. Photosynthetic responses of ferns vary by geographic location, climate and ecological function (Choy-Sin and Wong, 1974; Ludlow and Wolf, 1975; Hollinger, 1987; Brach *et al.*, 1993; Noodén and Wagner Jr., 1997; Saldaña *et al.*, 2005). There is limited information on native Hawaiian ferns (Durand and Goldstein, 2001). A study in New Zealand (Hollinger, 1987) found that the photosynthetic responses of two fern species matched their different understory light environments, with the fern species growing under higher light conditions also showing a higher light-saturated rate of photosynthesis. Another study compared three existing populations of *Blechnum* species growing under different light environments to determine whether magnitude of phenotypic plasticity to light availability was matched to their ecological breadth (Saldaña *et al.*, 2005). This research demonstrated that ferns with a greater photosynthetic capacity under increasing available light also had wider ecological distributions (i.e. occurred in a range of understory light environments). Research on a single fern species, *Oleandra pistallaris*, also showed capacity for ferns to adapt to varying light conditions (Takahashi and Mikami, 2006).

This study was sought to understand the functional differences between ferns grown in two understory shaded environments. Light response curves of ferns were measured in each treatment and correlated those with selected frond traits; leaf mass per area (LMA), frond nitrogen per unit area (N_a), stomatal density (S_D), and stomatal guard cell length (S_L) to explain functional responses in the different understory light environments.

2. Materials and Methods

2.1. Site Description

The study was conducted at the Harold L. Lyon Arboretum in Mānoa Valley, O‘ahu, Hawai‘i. The research area consists of a lower and upper site where the lower site (elevation 262 m) has a continuous overstory of various species of gymnosperms (e.g. *Juniperus* spp., *Araucaria* spp. outplanted for reforestation ca. 1915) and other non-natives such as *Schefflera actinophylla*, *Aleurites moluccana*, *Cinnamomum burmanni* and *Rhus taitensis*. The upper research site (elevation 290 m) has never been reforested, but was subjected to deforestation and uncontrolled grazing in the 19th century. It has a non-continuous overstory dominated by *Schefflera actinophylla*, *Cinnamomum burmanni*, and *Rhus taitensis* with no gymnosperms present. Some native mid- to upperstory species (e.g. *Psychotria* spp., *Diospyros* spp. and *Pipturus albidus*) and understory species (e.g. *Freycinetia arborea*, *Alyxia stellata*, and *Sphenomeris chinensis*) are present. Both sites have a mid-story dominated by the invasive *A. elliptica*. The sites are located on steep terrain with slopes ranging from 50% to 80%. Mean annual rainfall ranges from 2000-3000 mm (WRCC, 2013). The soil is part of the Tantalus Series and consists of shallow, well-drained silt loams developed from volcanic ash and material weathered from cinders (USDA, 1965).

2.2. Photosynthetic Measurements

Young *M. strigosa* sporophytes were outplanted in January 2006 in six replicate 6 x 6 m plots at each site. Half of the plots were cleared of nonnative mid-story and half were left uncleared. Percent light transmittance (% LT) for each understory treatment was calculated from photosynthetically active radiation (PAR) measured using LI-190SA line quantum sensors and an LI-90 point quantum sensor (LI-COR, Inc. Lincoln, NE) in July 2007 (for method details please see Chapter 1, section 2.5).

The uncleared treatment had mean values from 0.7 to 1.1%, the cleared treatment 3.6 to 20.1 % (Table 1). Net CO_2 assimilation (P_N) and stomatal conductance (g_s) of *M. strigosa* to changes in photosynthetic photon flux density (PPFD) were measured in September through October 2007 using a portable photosynthesis system (CIRAS-1, PP Systems, Amesbury, MA, USA). One fully mature, recently expanded frond from one fern in each plot was selected for photosynthetic measurement at each site. Fern selection was based on average size found within each plot and accessibility. A portion of the frond without spores was enclosed in a 2.5 cm^2-diameter cuvette, with a 12-V quartz-iodide lamp connected to an external battery. Photosynthetic gas exchange was measured at nine light levels ranging from 0 to 800 $\mu mol\ m^{-2}\ s^{-1}$. Fronds were allowed to acclimate to each light level for five minutes under ambient CO_2

concentration and temperature before gas exchange was measured. Measurements of gas exchange were used to generate light response curves of P_N to PPFD for clearing treatments at each site. Air temperature within leaf cuvette ranged from 20 to 25°C and relative humidity ranged from 57 to 93%.

Net photosynthetic light-response curves (P_N/I curves) were fitted by the Solver function of *Microsoft Excel* for each treatment and block combination as provided by and described in Lobo *et al*. (2013). The function requires inputs of measurements of P_N and I as well as estimates of the sensitivity of the equipment used to obtain these measurements since the fitting process is iterative. For this study, default regression parameters and instrumental information was used except for the minimum limit imposed for the light compensation parameter which was decreased from 5.0 (photons) m^{-2} $s^{-1}$to 3.0 µmol (photons) m^{-2} s^{-1}, and cuvette leaf area, which was changed to 2.5 cm^2. The minimum limit for the light compensation parameter was lowered to reflect the potential of ferns grown in shade to have relatively lower light compensation points than seed plants (Bannister and Wildish, 1982). The best P_N/I curve fit was selected based on the model with the lowest sum of the square of the errors (SSE) for a majority of the treatment/block combinations. For this study the best fit model for all treatment combinations was that developed by Ye, (2007):

$$P_N = \varphi\,(I_0\_I_{comp}) \text{ x } [(1 - b \text{ x } I)/(1 + g \text{ x } I)] \text{ x } (I - I_{comp})$$

Where: P_N = net photosynthesis rate [µmol (CO^2) m^{-2} s^{-1}]

$\varphi(I_0\_I_{comp})$ = apparent quantum yield at the range between $I = 0$ µmol (photon) m^{-2} s^{-1} and I_{comp}

β = adjusting factor

γ = adjusting factor

I = photosynthetic photon flux density [µmol (photons) m^{-2} s^{-1}]

I_{comp} = light compensation point [µmol (photons) m^{-2} s^{-1}]

The Solver function of *Microsoft Excel* generates a range of variable estimates for the various photosynthetic parameters, e.g. light saturation points, light-saturated net CO^2, and quantum yield of specific I (Lobo *et al.*, 2013). For this study, specific variable estimates in each photosynthetic parameter were selected *a priori* to provide more precise contrasts and included: light-saturated net CO^2 uptake [$P_N(I_{max})$], light saturation point beyond which there is no significant change in net CO^2 uptake (I_{max}), light compensation point (I_{comp}), dark respiration (R_D), and quantum yield in the range of I_{comp} to I_{50} [φ ($I_{comp\_}I_{50}$)]. Parameters were compared across treatments and sites using multiple ANOVA tests ($\alpha = 0.5$, $n = 3$).

Table 1. Light environment of studied *M. strigosa* ferns averaged over a 12 hour period. Values are %LT or PPFD ± SE of three replicates per treatment (Cleared/Uncleared) within blocks (Lower/Upper), where %LT = ambient percent light transmittance; PPFD = photosynthetic photon flux density (μmol (photons) m^{-2} s^{-1}).

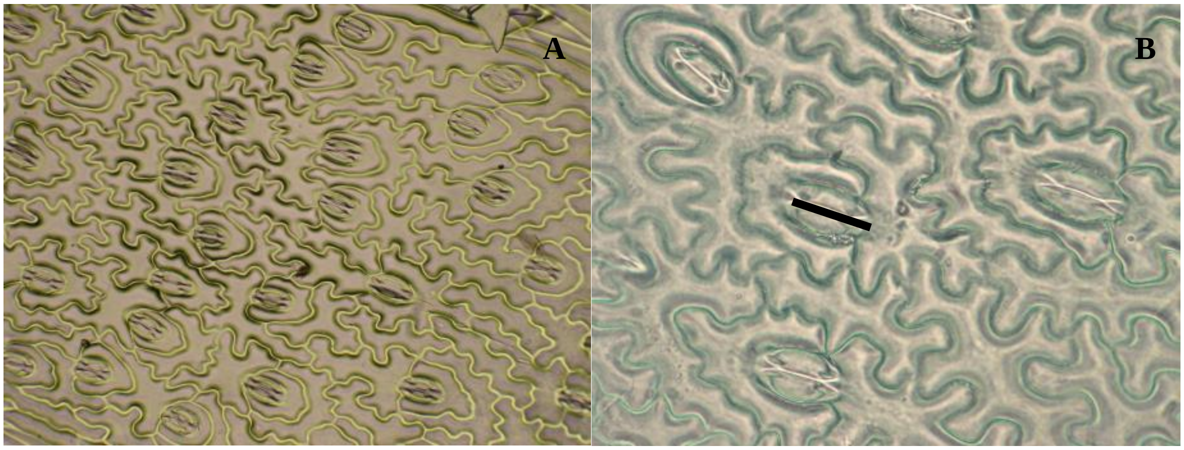
	Cleared		**Uncleared**	
Light Variable	**Lower**	**Upper**	**Lower**	**Upper**
% LT	3.62 ± 0.82	20.09 ± 4.58	0.65 ± 0.18	1.11± 0.25
PPFD	3832 ± 836	14955 ± 3302	855 ± 275	899 ± 228

2.3 Frond Traits

Fresh whole fronds were collected in the field and placed on ice within plastic bags for dry mass measurements and leaf nitrogen content. Frond area was measured using a LI-3000A leaf area meter (LI-COR Biosciences, Lincoln, NE). Fronds were dried at 70°C for 48 hours and weighed to determine dry mass (g) which was used to determine leaf mass per area [LMA (g m^{-2})]. Fronds were then ground in a ball grinder to obtain a minimum 5 mg sample for total nitrogen content (mg g^{-1}) analysis at University of Hawai‘i at Mānoa Agriculture Diagnostic Service Center (ADSC). Nitrogen content was converted to an area-based parameter N_a since physiochemical processes related to photosynthesis, such as light interception, diffusion of CO_2 and transpiration occur as a flux per unit leaf surface area (Hikosaka, 2004). Fresh whole fronds were also collected to measure stomatal density [S_D (number/cm^2)] and stomatal guard cell length [S_L (μm)]. Stomatal traits were estimated from nail varnish replicas of the abaxial surface at three points (lower, mid, and upper portions of the frond) for fronds taken in each plot. Varnish replicas were mounted on slides and digitally photographed at 20x and 40x through a microscope. Analysis of pictures using a lattice micrometer and X software (Publisher, City, State) was used to identify and count stomata (20x) and measure length of stomatal guard cells (40x) (Figure 1). The lengths of five stomata at each point on the frond were measured. Length measurements were taken on the bottom guard cell along the edge of the inner wall.

To explain differences in functional response of *M. strigosa* to varying amounts of PPFD, frond traits LMA, $N_{a,}$ $S_{D,}$ and S_L were correlated with each other and significant photosynthetic parameters. Positive correlations were further analyzed with regression. Frond traits and significant photosynthetic parameters were also plotted against % LT to understand correlations within the context of available light. Non-parametric Spearman correlation coefficient and Kendall's tau-b was used to correlate frond traits and photosynthetic parameters since relationships with %LT were non-linear. All statistical analyses were analyzed using PASW Statistics 18, Release Version 18.0.0. July 30, 2009 (SPSS, 2009).

Figure 1. Digital photographs of abaxial nail varnish replicas of *M. strigosa* at (A) 20x, and (B) 40x. Line in (B) shows location of stomatal guard cell length measurement.



3. Results

3.1 Photosynthetic Parameters

Figure 2 shows the light response curves of net photosynthesis for fronds growing in the different clearing conditions. Net photosynthesis was light saturated (I_{max}) at 196 and 187 µmol (photons) m^{-2} s^{-1} for fronds grown in cleared conditions at the upper and lower site, respectively, compared with 91 and 89 µmol (photons) m^{-2} s^{-1} for the uncleared treatment at the upper and lower site (Table 2). Light-saturated net photosynthesis rates [$P_N(I_{max})$] for the fronds in the cleared treatment were also significantly higher at 4.5 and 4.3 µmol CO_2 m^{-2} s^{-1} in the upper and lower blocks, respectively, relative to the uncleared treatment at 2.5 and 2.0 µmol CO_2 m^{-2} s^{-1}. Mean I_{comp} at 4 µmol (photons) m^{-2} s^{-1}, and dark respiration values between 6-7 µmol CO_2 m^{-2} s^{-1} did not significantly differ across treatments or blocks. Quantum yield values in the range of I_{comp} to I_{50} were greater in the cleared treatment. $P_N(I_{max})$, (I_{max}), were positively correlated with %LT, r_s (10) = 0.878, $p < 0.001$ and $t_b(10) = 0.719$, $p = 0.001$; r_s (10) = 0.744, $p = 0.006$ and $t_b(10) = 0.523$, $p = 0.019$, respectively (Table 6). Both demonstrated an asymptotic relationship that shows no additional increase in photosynthetic capacity above 4% LT (Figure 3).

Stomatal conductance (g_s) values (27 to 4450 mol m^{-2} s^{-1}) were relatively high and highly variable when compared to other ferns (Hollinger, 1987; Brodribb *et al.*, 2005) and data should be interpreted with caution. High relative humidity and heavy precipitation experienced in the field when measuring photosynthesis could have contributed to these values. Stomatal conductance values were most variable at low PPFD and did not show a response to increasing PPFD (Figure 4).

Figure 2. Response of net photosynthesis (P_N) to varying photosynthetically active photon flux density (PPFD) for blocks (◆ upper and ■ lower) within each treatment (A) = cleared and (B) = uncleared.

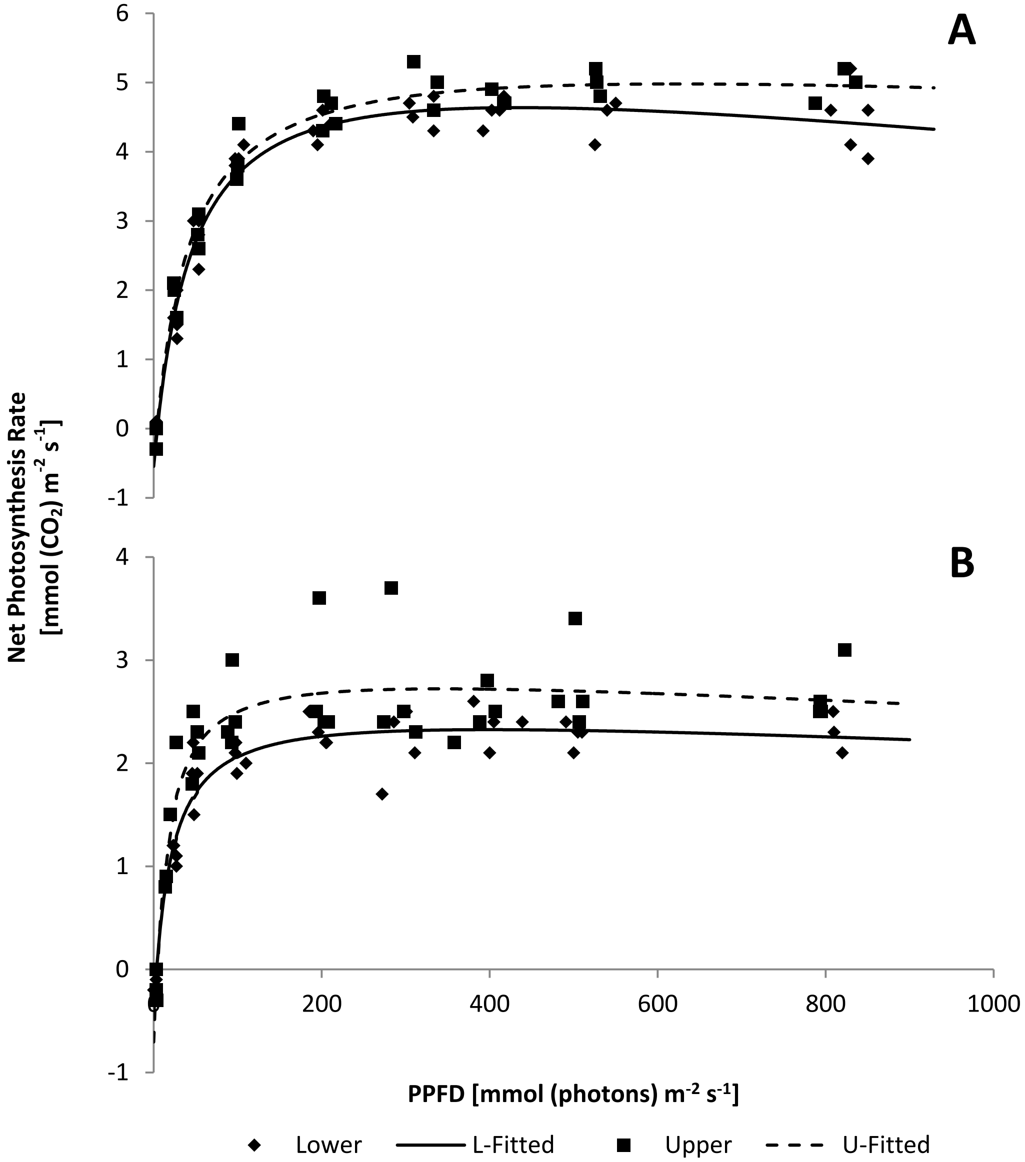


Table 2. Photosynthetic characteristics of *M. strigosa* calculated from light-curve estimation following methodologies proposed by Lobo *et al.* (2013). Values are means ± SE of three replicates per treatment within each block.

Photosynthetic Parameter	**Cleared**		**Uncleared**	
	Lower	**Upper**	**Lower**	**Upper**
I_{comp}	4.29±0.85	3.73±1.70	4.07±0.27	3.55±0.86
I_{max}	186.67± 9.77	195.67±10.48	89.33±8.50	91.00±2.67
$P_N(I_{max})$ µmol (CO^2) m^{-2} s^{-1}	4.33±0.11	4.53±0.07	2.00±0.31	2.57±0.09
R_D	0.60±0.10	0.57±0.21	0.57±0.07	0.70±0.10
φ ($I_{comp\_}I_{50}$)	0.057±0.002	0.060±0.001	0.033±0.006	0.046±0.001

Table 3. Analysis of variance of *a priori* selected photosynthetic parameters.

Photosynthetic Parameter	MS	df	F	*P*-value
I_{comp}[a]				
Treatment	0.008	1	0.057	0.818
Block	0.057	1	0.394	0.548
Treatment x Block	0.000	1	0.000	0.999
I_{max}				
Treatment	30603.000	1	143.340	0.000
Block	85.333	1	0.400	0.545
Treatment x Block	40.333	1	0.189	0.675
$P_N(I_{\mathrm{max}})$				
Treatment	13.868	1	132.071	0.000
Block	0.441	1	4.198	0.075
Treatment x Block	0.101	1	0.960	0.356
R_D				
Treatment	0.008	1	0.153	0.706
Block	0.007	1	0.153	0.706
Treatment x Block	0.021	1	0.424	0.533
$\varphi\ (I_{\mathrm{comp}}\_I_{50})$[b]				
Treatment	2.38E-10	1	47.971	0.000
Block	2.21E-11	1	4.453	0.068
Treatment x Block	0.000	1	0.000	1.000

[a] Computed using natural log transformed data

[b] Computed using $\varphi\ (I_{\mathrm{comp}}\_I_{50})^4$ transformed data

Figure 3. Relationship of photosynthetic parameters (A) $P_N(I_{max})$, (B) I_{max} and (C) φ ($I_{comp\_}I_{50}$) to percent ambient light transmittance values.

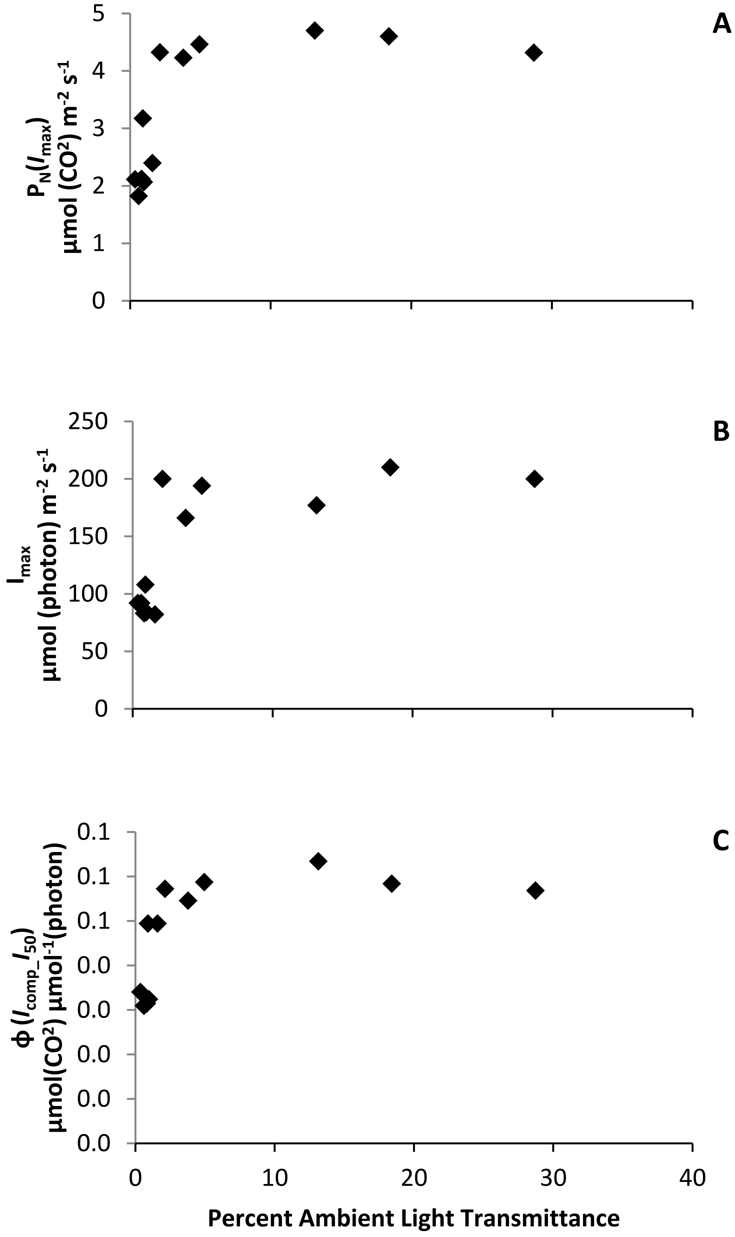
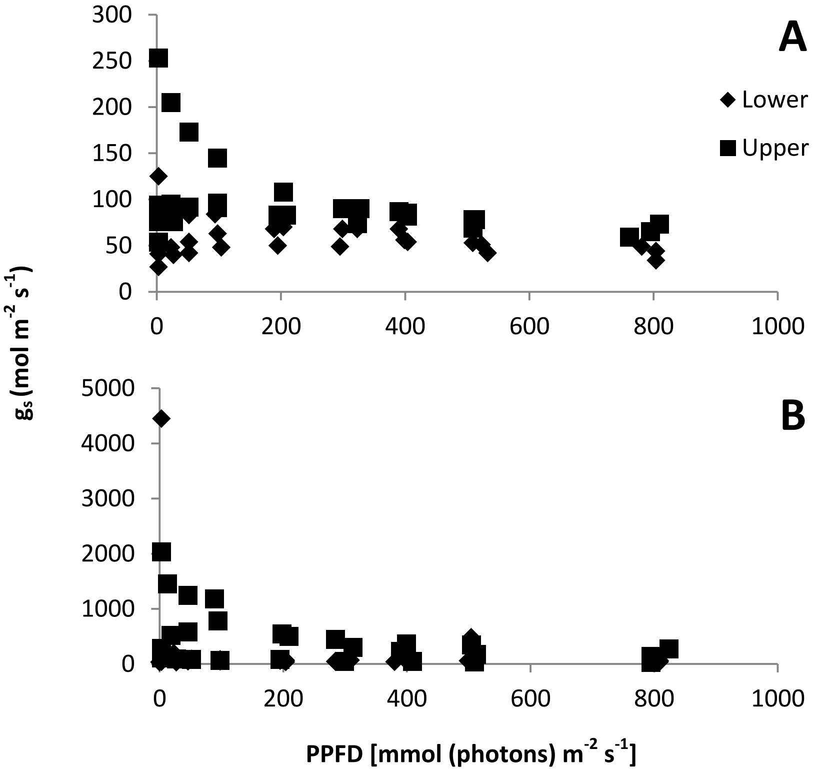


Figure 4. Response of g_s to PPFD in (A) cleared and (B) uncleared treatment



3.2 Frond Traits

Fronds were generally larger in area (cm^2), dry mass (g) and LMA (g m^{-1}) in the cleared treatment (Table 4). Photosynthetic parameters $P_N(I_{max})$, I_{max} and φ ($I_{comp}\_I_{50}$) were positively correlated with frond traits LMA, $N_{a,}$ and $S_{D,}$ and showed no correlation with S_L (Table 5). When plotted against $P_N(I_{max})$, LMA, $N_{a,}$ and S_D reach their highest values between 4.2 and 4.6 µmol (CO^2) m^{-2} s^{-1}. Above these values increases in LMA, $N_{a,}$ and S_D do not contribute to increases in $P_N(I_{max})$ (Figure 5). PNUE (photosynthetic nitrogen use efficiency [ratio between $P_N(I_{max})$ and N_{area}]) also did not correlate with % LT (Table 6). Stepwise regression of $P_N(I_{max})$ versus LMA, S_D and N_{area} revealed S_D and LMA were highly correlated ($r(10) = 0.892$, $p < 0.001$). When the model was adjusted to only include LMA and N_{area} as predictors, the model explained approximately 90% of the variation in $P_N(I_{max})$ (Table 7).

Table 4. Mean values (±SE) for *M. strigosa* frond traits in blocks within treatments.

Treatment	**Cleared**		**Uncleared**	
Block	**Lower**	**Upper**	**Lower**	**Upper**
Frond Area (cm^2)	697.4±27.2	498.2±15.9	189±40.6	171.5±31.1
Dry Mass (g)	3.1±0.1	3.5±0.2	0.6±0.2	0.6±0.1
LMA (g m^{-2})	0.219±0.015	0.174±0.017	0.011±0.003	0.012±0.005
N_{area} (g m^{-2})	9.22E-04±6.16E-05	4.08E-04±1.89E-05	3.14E04±5.68E-05	2.32E04±5.94E-05
PNUE (µmol mol^{-1} s^{-1})	4735±234	11193±735	6885±1436	11979±1997
S_D (# cm^{-2})	3497±261	4595±267	2589±120	2406±194
S_L (µm)	36.2± 0.8	37.4± 1.8	37.1± 1.8	39.7± 0.2

Table 5. Pearson correlation coefficients between photosynthetic parameters and selected frond traits ($df = 10$). Values in bold indicate correlations significant at $\alpha = 0.05$.

Photosynthetic Parameters	**LMA**	**N_{area}**	**S_D**	**S_L**
$P_N(I_{max})$	**0.833**	**0.639**	**0.814**	-0.125
I_{comp}	-0.043	0.269	0.128	0.152
I_{max}	**0.808**	**0.669**	**0.846**	-0.187
R_D	-0.059	-0.049	-0.015	0.497
$\varphi\ (I_{comp}\_I_{50})$	**0.800**	**0.563**	**0.692**	0.028

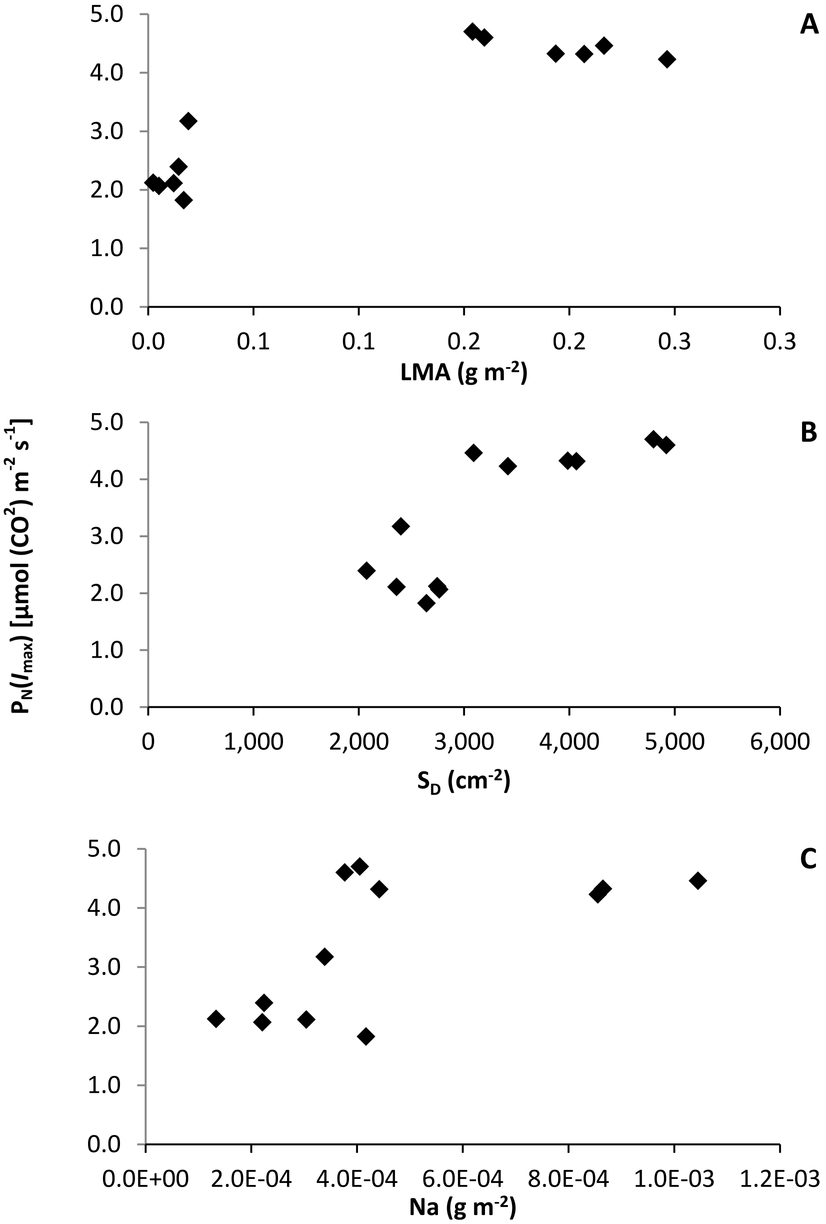
Table 6. Spearman correlation coefficient and Kendall’s tau-b between percent ambient light transmittance (%LT) and $P_N(I_{max})$, I_{max}, $\varphi\ (I_{comp}\_I_{50})$, LMA, N_a, and S_D ($df = 10$). Values in bold indicate correlation values significant at $\alpha = 0.05$. *P*-values are in parentheses.

	%LT	
	Spearman Correlation	**Kendall's Tau-b**
$P_N(I_{max})$	**0.878 (<0.001)**	**0.719 (0.001)**
I_{max}	**0.744 (0.006)**	**0.523 (0.019)**
$\varphi\ (I_{comp}\_I_{50})$	-0.145 (0.654)	-0.156 (0.488)
LMA	**0.895 (<0.001)**	**0.727 (0.001)**
S_D	**0.825 (0.001)**	**0.636 (0.004)**
N_a	0.333 (0.090)	0.333 (0.131)
PNUE	0.196 (0.542)	0.091 (0.681)

Table 7. Regression analysis and values for the dependent variable $P_N(I_{max})$ and predictor variables LMA and N_a.

	SS	df	F	*p*-value
Regression	14.202	2	61.011	<0.001
Residual	1.047	9		
Total	15.249	11		
r^2	0.931			
Intercept	0.061			
LMA	0.737			
N_a	0.496			

Figure 5. Response of LMA (A), S_D (B), and N_a (C) to $P_N(I_{max})$.



4.0 Discussion

4.1 Photosynthetic Responses

M. strigosa photosynthetically adapted to the different understory light environments. Higher values for $P_N(I_{max})$, I_{max}, φ ($I_{comp}\_I_{50}$), demonstrate that ferns in the cleared understory showed higher photosynthetic capacity than ferns in the uncleared understory. Typically plants acclimated to low light environments have low dark respiration rates when expressed on a unit leaf area basis (Bazzaz and Pickett, 1980). In this study, *M. strigosa* did not show differences in light compensation and dark respiration values between the two understory light environments. This coupled with higher quantum yield efficiency values between 0-50 µmol m^{-2} s^{-1} in the cleared understory treatment suggests that while *M. strigosa* in the uncleared understory environment acclimated to lower light conditions they are not photosynthetically more efficient at the lower PPFDs and hence, do not respond to increases in light quicker than their cleared understory counterparts. When related to the % LT, maximum values for $P_N(I_{max})$ and φ ($I_{comp}\_I_{50}$) were highest at 13%, and I_{max} at 18%. This suggests that the light transmittance range needed to optimize photosynthetic capacity in *M. strigosa* is between 2 and 13% LT.

LMA, S_D and N_a all positively correlated strongly with $P_N(I_{max})$ and φ ($I_{comp}\_I_{50}$). Increases in LMA in response to increasing light availability have been shown to be important mechanisms of acclimation in other fern species (Saldaña *et al.*, 2005). By increasing the area of a given unit of leaf biomass, the interception of light is increased under low light conditions and photosynthetic capacity is improved in higher light conditions due to increases in photosynthetic biomass per unit leaf area. A positive $P_N(I_{max})$-LMA relationship was observed in *M. strigosa* but saturated at 4.6 µmol CO_2 m^{-2} s^{-1}. Differences in photosynthetic capacity of leaves exposed to different light levels may also arise from variation in nitrogen content per leaf area. Higher leaf nitrogen content is usually associated with greater photosynthetic rates and there is a consistent relationship between leaf nitrogen content and maximum net photosynthesis that holds across species and across habitats (Field and Mooney, 1986; Evans, 1989; Reich *et al.*, 1994; Hikosaka, 2004). Similar to LMA, N_a shows a positive relationship with $P_N(I_{max})$ but saturated around 4.3 µmol CO_2 m^{-2} s^{-1}. Although LMA, S_D and N_a all contribute to increased photosynthetic capacity in *M. strigosa* within the cleared understory, $P_N(I_{max})$ saturates around 4.6 µmol CO_2 m^{-2} s^{-1} regardless of additional increases in any of the frond traits.

4.2 Stomatal affects

Stomatal conductance should increase with increasing maximum net photosynthesis since resistance to diffusion of water vapor from inside the leaf to the air stream passing over the leaf, will decrease with increasing stomatal aperture opening. Stomatal conductance measured in this study was quite higher than observed for other ferns (Hollinger, 1987; Brodribb *et al.*, 2005) and did not show increasing levels with increasing PPFD. The high relative humidity and rainfall that occurred while measurements were being taken most likely contributed to the very high stomatal conductance values where high air moisture and adequate soil moisture could allow the ferns to keep stomata open. The lack of a response to increasing PPFD is typical of ferns (Hollinger, 1987; Hunt *et al.*, 2002; Gago *et al.*, 2013). Ferns have been described as having less sensitive stomatal control relative to seed plants (Brodribb *et al.*, 2005). Ferns may not close their stomata in cases where seed plants would and can remain open even under conditions not favoring photosynthesis, such as low light (Flexas *et al.*, 2012).

For *M. strigosa*, stomatal density was correlated with increased photosynthetic capacity rather than stomatal guard length. Increases in stomatal density were expected since plants make more stomata on leaf surface under higher light, lower atmospheric CO_2 concentrations and moist environments (Franks and Beerling, 2009). Increases in S_D also led to greater photosynthetic capacity since the more frequent stomata can provide greater CO_2 diffusion per unit leaf area but S_D values saturated at 4.5 µmol CO_2 m^{-2} $s^{-}1$ with no additional increase in $P_N(I_{max})$ with greater S_D. Hence, S_D shows some contribution to increases in photosynthetic capacity but only up to a certain point. An increase in S_D can optimize the physiological control of CO_2 diffusion and loss of water, and assist in regulating frond temperature, which will be important for fronds that are more exposed to increases in wind and light (Doria *et al.*, 2010). S_D values may have continued to increase even after $P_N(I_{max})$ values leveled off due to higher light and air turbulence exposure in the cleared understory without necessarily conferring an associated increase in photosynthetic capacity.

Stomatal diffusion resistance is directly related to size of stomata and generally there is a negative correlation between guard cell length and stomatal density (Franks and Beerling, 2009; Doria *et al.*, 2010). In this study, that relationship was very weak (Pearson’s Coefficient = -

0.326, *p*-value = 0.301) and stomatal guard cell length did not contribute to increases in photosynthetic capacity. Similar guard cell lengths have been observed in shade leaves (Sack *et al.*, 2003). It is possible that in a shaded understory environment where water is not limiting there is no conferred advantage to decreasing stomatal guard cell length to increase conductance of water vapor.

M. strigosa shows increases in photosynthetic capacity when planted within cleared understory, but this study suggests that they are photosynthetically limited to relatively low light and shaded environments. Ferns generally show low photosynthetic capacity and LMA relative to seed plants (Wright *et al.*, 2004; Karst and Lechowicz, 2007). *M. strigosa* has been found to survive at irradiance levels below 1% LT but the fronds do not grow very large (Chapter 1) and their photosynthetic capacity is reduced. Its optimal light conditions appear to be from 4 to 13% LT. *M. strigosa* is therefore a good candidate for understory restoration plantings and is amenable to thinning or removal of non-native understory or in areas where non-native canopies may have reduced available light to 2-4% but not be as well suited to open environments where % LT is greater than 30%.

5. Conclusion

This study highlights the importance of understanding mechanisms influencing the growth and survival of seedlings planted as part of reforestation efforts. Beyond recording morphological measures, understanding the physiological responses to microhabitat should help to design cost-effective planting strategies. Species-specific differences in responses to varying light environments of forest understory may be an important consideration in choosing species for reforestation or restoration. More research is needed on the ability of native species to grow under a range of light, soil nutrient, and soil moisture conditions and the importance of understanding the level of canopy cover and the direct effect of light intensity and transmittance on planted seedlings.

CHAPTER 5:

CONCLUSION

1. Introduction

This study sought to explore the potential for a native plant agroforestry system whereby the understory of non-native dominated secondary forest in Hawaii was enriched with selected native plants. The system utilized native plants with both economic and cultural value and was designed to provide desired plant material while also complementing restoration activities with the removal of invasive species.

Changes in land-tenure and habitat destruction have reduced forest cover and degraded existing native forests, limiting areas where local people can collect native plant material for cultural and traditional practices. There is a need to provide alternatives to collecting wild plants and reduce pressure on declining populations. Native plant agroforestry and forestry enrichment systems established in already degraded or altered environments can help protect existing native habitat and provide for continuation of cultural traditions. Additionally, they may potentially favor the reestablishment of other non-target native species.

Much of forest restoration has focused on planting trees and shrubs with less attention toward establishing understory vegetation. However, understory plants contribute more than 80% of the overall species richness in some forests and play critical roles in nutrient cycling (Gilliam, 2007; McClain *et al.*, 2011) and are increasingly becoming recognized as an important part of forest restoration designs (Koch, 2007; McClain *et al.*, 2011; Gould *et al.*, 2013). Limited information is available on the survival and growth of native plants outplanted in the understory of secondary forests dominated by non-native species and there is a need to better understand the response of native species to these novel ecosystems. By combining native species restoration, invasive species control and culturally valuable forest products, native plant agroforestry systems also provide an incentive for local people to get involved with restoration and land management.

To evaluate the success of the native plant agroforestry system it is important to identify key indicators that can be tracked in order to determine how outplantings are doing and whether the agroforestry system is having its intended results (O'Connor et al., 2005). For this research, indicators for success included:

- Establishment and growth of native outplanted species with survival greater than 60% and adequate size for harvesting plant material.

- Significant reduction in non-native species, both in number of species and quantity of biomass.
- Regeneration of non-target native species (especially of those native species already found within the area).
- Improved environmental conditions for further restoration and agroforestry activities.
- Production of harvestable plant material for all outplanted species and positive returns after subtraction of costs (e.g. plants, labor and maintenance).

2. Research findings

2.1 Establishment and Growth of Native Plants

For all three species, the percent of surviving plants was greatest in the cleared treatment, indicating that the effects of understory removal (decline in plant competition and increase in light availability) allowed for increased survival across outplanted species. Regarding individual species, maile and māmaki did not establish well in the uncleared understory, and growth rates even with understory clearing were insufficient for harvesting after two years. If planting within an understory, both māmaki and maile will most likely have the highest chance of survival when outplanted into light gaps and areas cleared of non-native understory.

This contrasted with the relatively high survival of palapalai under varying understory light conditions, suggesting it is a good species for establishing an understory groundcover in agroforestry restoration systems. Although able to survive in low light levels (1-5%) of an uncleared forest understory, higher light levels associated with understory clearing (15-20%) are most likely necessary to support palapalai harvesting for cultural uses. Measured photosynthetic parameters also demonstrated that ferns in the cleared understory showed higher photosynthetic capacity than ferns in the uncleared understory. Available light may also play a role in spore development, since ferns growing in 15% light transmittance or greater had twice as many fronds with spores than those growing in lower light levels. Understanding light availability needs for palapalai cultivation will be critical to determining harvestable yield of fronds, since higher light conditions may be needed to support the frequency and amount of harvesting.

2.2 Seedling Recruitment of Native and Non-native Species

Overall, the initial clearing of non-native understory followed by subsequent semi-annual weeding had a negative impact on recruitment of non-native seedlings, particularly the invasive *A. elliptica*. Seedling density showed strongest declines where mean light transmittance was four percent and mean canopy cover was 77 percent. Seedling density did not appear to be strongly affected by clearing at higher light transmittance, suggesting the higher light environment was enough to sustain greater seedling densities in cleared plots despite repeated removals.

Seedling recruitment of existing native species or outplanted native species within the research area was not observed. This is line with other studies, where it was observed that there was not a sufficient native seed bank to support natural regeneration and/or environmental conditions had changed sufficiently to no longer support germination (Drake, 1998; Mascaro *et al.*, 2008; Cordell *et al.*, 2009; Ostertag *et al.*, 2009).

While this study did not conclusively isolate the effect of planting on seedling recruitment, there is evidence that competition and shading can negatively affect nonnative seedling growth, even for species adapted to low-light conditions. Significant declines in seedling height for *A. elliptica* suggest that the outplanted native species have the potential to reduce the ability of *A. elliptica* seedlings to reach maturity. Native plantings, once established, can also limit soil erosion, particularly if clearing is conducted on steep slopes.

2.3 Effects of Environmental Condition

This study suggests that within lowland wet mesic forests dominated by non-native species, light availability is the most critical resource limiting establishment and growth of understory native species. Increases in light availability via the cleared treatment appeared to be the most influential resource in increasing survival and growth of the outplanted native species compared to soil moisture and nutrient availability. The study area is within a valley that receives a high amount of annual rainfall; hence it is likely soil moisture was not a limiting resource to establishment and growth of outplantings. However, it was observed that within the research time period, there were often 2-3 weeks with less than 5 mm of precipitation. During these drier periods, well-drained soils and steep slopes could have lead to a rapid decline in soil moisture and may have affected establishment of māmaki. Recently transplanted māmaki plants were likely sensitive to drought since they were small in size and had limited root systems. Soil nutrient resources did not differ between understory clearing treatments and were most likely buffered by surrounding uncleared forest. Removal of nonnative plants may have a stronger effect on soil nutrient levels if the clearing size is enlarged.

2.4 Production of Harvestable Material

Palapalai was the only native plant out of the three native plants selected for outplanting that grew large enough to support harvesting within the cleared treatment. Low survival and smaller sized plants among all three native species within the uncleared treatment made them unsuitable for harvesting. Understanding light availability needs for palapalai cultivation will be critical to determining harvestable yield of fronds, since higher light conditions may be needed to support the frequency and amount of harvesting. Due to time constraints, experiments investigating different levels of harvestable amounts and frequency were not conducted. At the end of the data collection period, one hula halau was allowed access to the plots to harvest for one performance. There were 108 harvestable mature palapalai plants with an average of 50 fronds per plant. Two fronds from each plant were harvested to supply 52 students with lei. Based on observed lei making (personal observation) one lei took 3-8 fronds depending on length of lei required. This study was unable to measure regeneration of fronds after harvest, however, for palapalai harvested in the wild, Ticktin *et al*. (2006) found that frond regeneration was on average 3.8 fronds per year with removal of no more than two fronds per year.

Removal of non-native species can be costly and yield only distant future returns. However, it is important in the initial stage to demonstrate measurable effects from forest restoration, management and rehabilitation efforts and can reduce the time in which a forest crop will become available. In this study, initial clearing took approximately 6 hours per 6x6-m plot for three people. This removal included all non-native species under 15.5 cm in diameter. For continued removal of non-native seedling regeneration, it took one person approximately 30-45 minutes to weed a 6x6-m plot every six months. Amount of time to weed declined after 18 months to about 15-20 minutes per plot with greatest reduction in time in plots where percent light transmittance was ≤ 5%.

3. Management Implications

3.1 Removal of Non-native Species

Non-native species can further inhibit native understory recruitment by establishing persistent communities, altering habitat quality and outcompeting natives. Successional trajectories dominated by non-native species are becoming increasingly common in areas where non-natives are prevalent. In this study the forest is dominated by *A. elliptica* and shows evidence of sustaining its respective seedling populations even in relatively low percent light transmittance, unless repeatedly removed. To prevent an alternative stable state dominated by non-natives it will be important to apply restoration management strategies that incorporate strategies for removal of non-native species and suppression of non-native seedling recruitment.

Removal of non-native species is often the first step in preparing a site for restoration of native plant species. In areas where non-native species dominate forest composition, removal provides benefits in the amount of increased resources to native plantings but can also create areas more susceptible to non-native species recruitment due to increases in light availability and other resources. Hence, follow-up non-native species removal becomes important for limiting their spread and increasing chances for survival and growth of outplanted or regenerating native species. Removal of all non-native species can be costly and may not provide long-term benefits to native plantings if removal is not maintained. Level of removal should correspond with management that is feasible and removal of all non-native species may not be possible in certain areas particularly if large trees are present or steep or rocky terrain makes it hard to access. Non-native species can serve as structural or functional bridges to support ecological processes during restoration. Since many of Hawaiʻi's lowland forests have become dominated by non-native species, these species should be managed to support restoration goals. Understanding how much and when to remove non-native species as well as plant native species can assist land managers in administering more efficient weed management strategies and potentially reduce associated costs.

The results of this study indicate that management for a more uniform nonnative homogenous canopy cover can provide more uniform light transmittance to the understory and decrease seedling recruitment. In higher light conditions (6 to 40% light transmittance), removal efforts will need to be more frequent and will be critical for keeping target non-native species recruitment low as well as preventing another undesirable species from taking advantage of released resources. Light levels at around 5% appear to be more conducive for a less-managed approach where removal could most likely be reduced to an annual effort. While established native outplantings may provide some resource competition for non-native species, the results of this study indicate that manipulation of environmental resources, such as light, plus continued removal will be more effective in reducing non-native species recruitment.

3.2 Restoration of Native Plant Species

This study highlights the importance of understanding mechanisms influencing the growth and survival of native seedlings planted as part of reforestation efforts. Beyond recording morphological measures, understanding the physiological responses to microhabitat should help to design cost-effective planting strategies. Species-specific differences in responses to varying light environments of forest understory may be an important consideration in choosing species for restoration.

In addition to managing for specific native plant requirements, the restoration of native forest species should consider how to complement or work within existing non-native forests. Complete recovery to the “original” forest composition does not have to be the only goal (Lugo and Helmer, 2004). Generalist tree species, whether native or non-native, can serve as “nurse” species or as food sources, nest sites, and roosting sites for pollinators and seed dispersers (Mueller-Dombois, 2005; Padilla and Pugnaire, 2006). In Hawaii, the use of a fern as a nurse plant has been shown to facilitate seedling survival and growth of outplanted native seedlings (Gould *et al.*, 2013). Management strategies to support establishment and growth of native species can include introducing lightly managed plantings, involving a variable number of nurse or facilitative species intended to catalyze natural forest succession and ecosystem restoration primarily for environmental benefits (such as soil conservation and watershed stabilization) in the near term but offering multiple economic, social and ecological benefits in the longer term. Retaining large non-native trees can also ameliorate microclimatic conditions, reduction of soil water loss, changes in light intensity for seedlings (ITTO, 2002).

To reintroduce a full-complement of native understory species it will most likely be necessary to introduce species over time as conditions become appropriate or as resources are managed to support more species. In this study, retention of the non-native canopy allowed for establishment and survival of a shade-tolerant understory fern. Further expansion of the removed understory can occur once non-native seedling recruitment plateaus and a sequential alteration between removal of undesired species and planting of native ones can become the basis of a restoration management plan. With expanded removal of the non-native understory and potential removal of selected large non-native trees, associated increases in light availability can support the addition of more light-demanding native plants. This contrasts with typical restoration management that starts with a large amount of removal more conducive for outplanting of light-demanding plants with the addition of shade-tolerant understory species planted later after the forest canopy has developed. The manipulation of forest canopy layers to increase light availability to cultivated understory plants will most likely depend on the existing forest composition and structure, the size and amount of clearing, as well as the light requirements of desired understory species. Successful and sustainable cultivation will require some level of canopy opening or manipulation to ensure adequate light levels. It is important to note that the success of manipulating resources as a restoration strategy could also be influenced by other abiotic factors (e.g., precipitation, temperature, soil fertility). For example, the ability for māmaki to establish may have been reduced due to water stress during an unanticipated dry period. To improve survival of recently outplanted species, even within mesic to wet forests, plants may need supplemental watering and should be outplanted during the rainy season. However, harvesting of plant parts will most likely add additional stresses to the plant and depending on the frequency and amount of harvest may require additional resource inputs.

4. Future Research

4.1. Sustainable Harvesting of Plant Material

Further research is needed on effects of harvesting native plant material and determining the sustainable amount and frequency of removal that can be supported by the system, particularly if nutrient and water additions are limited. This information will be critical in evaluating the success of an agroforestry-restoration system and determining how many cultural practitioners it can support. Ticktin *et al.*’s (2006) study did not show a significant effect of frond-harvesting on palapalai frond density, plant density, size-class structure, mortality rates or frond production and suggest that plants were able to recover to pre-harvest levels after three months. However, this only measured response after one harvest and it is unclear how the plants would respond to continued harvesting.

A cost-benefit analysis for the system should also be conducted after harvesting levels have been determined. This will provide an additional tool in evaluating both the economic and ecological success of the system.

4.2 Additional Native Plantings

More research is needed to better understand successional targets for outplanting native species and identify appropriate sequences and timing for outplanting of different functional species or species requiring different amount of resources, e.g. light. Selection for native plants with positive attributes for restoration would also assist in increasing survival and growth of outplanted seedlings. This can include traits such as high fecundity, drought tolerance, relatively faster growth.

In restoration projects where light conditions may be changing over time, the ability for an understory outplanted species to survive and grow under a range of light conditions may prove critical to restoration success and its ability to compete with non-native species introductions. A better understanding of the ecophysiological responses of native species to invaded understory is needed to improve their survival and growth, as well as determine whether these invaded understories are amenable to native plant restoration through light management. Additionally, most native plants in Hawaiʻi have not been grown as a crop and optimal planting conditions are unknown for many species. Better understanding of environmental conditions that favor native plant establishment and growth are important to improve native plant agroforestry efforts in Hawaiʻi.

4.3 Native Species Regeneration

In this study area, regeneration of native species was absent. Cordell *et al.* (2009) suggests that native seedling establishment may depend on the nature of the post-disturbance environment in which case further research is needed into what post-disturbance environments are most conducive for native seed germination. It may be that these removal areas need more time to record native species germination. It’s also possible that seed viability may be affected and further tests of the viability of pollen and seeds for native species found within the area should be conducted.

4.4 Community Participation

Ultimately, the success of an agroforestry-restoration system depends on the ability of cultural practitioners, scientists and land managers to work in partnership. Integration of traditional knowledge of native plants and harvesting protocols with research in agriculture and restoration ecology will provide an opportunity for participants to exchange ideas. Participation and inclusion of cultural practitioners in the development and experimental process can then favor implementation and management of agro-restoration projects by local community groups.

5. Limitations

5.1 Native Plant Survival and Growth

Both maile and māmaki had low survival in the cleared treatment and did not show a strong relationship between plant growth and increasing light transmittance. This may have been due to several factors.

For maile, low survival may have been due to initial seedlings size (≤10 cm) not being adequate to survive without irrigation and being buried by soil moving down slopes (personal observation). Survival of a second planting of maile within the research area but not included in this study was more successful when outplantings were 15-20cm in height. Size of plants can be an issue in restoration projects where plants need to be transported long distances, often through steep terrain. There is a trade-off between size and amount of plants that can be transported. Larger quantities of smaller plants can be transported than larger plants but smaller plants with smaller developed root systems may suffer higher mortality rates than larger ones.

For māmaki, low survival may have been associated with transplant shock. Māmaki are known to have fragile root systems and are not always amenable to transplanting (cite). Better transplanting success occurred during the second outplanting when māmaki plants were propagated in peat pots that could then be directly planted into the soil without disturbing the root systems. Planting was timed to correspond with the winter rains but, as mentioned earlier, māmaki survival may also have been affected by declines in soil moisture due to a three week period where there was little precipitation.

Limited survival for both these species and thus, fewer data points, may have also reduced the capacity of the growth function to fit the data. Additionally, maile plants were planted among palapalai and individual maile plants may have experienced lower light levels than were measured at 1 m above the ground. Optimal light conditions for maile may be better determined by measuring light availability at the individual plant level as opposed to the plot level. Height of māmaki stems were also affected by stem die-back and being buried by soil (personal observation), variables that were not included in the current growth function. Māmaki clearly requires higher light than what was available in the uncleared treatment to survive and grow, but other factors including soil moisture, herbivory and damage from falling debris most likely also influenced establishment and growth.

5.2 Planting Effects

More conclusive planting effects may have been observed if more time had been allowed between weeding events. It's possible that the six-month weeding frequency did not allow enough time for differences in growth of seedlings to be observed between planting treatments. Additionally, repeated weeding could have obscured planting effects by reducing the seedling population enough so that no treatment effect could be detected. Lastly, slope and soil erosion may also have confounded planting effects (e.g. buried seedlings from eroding bare soil were observed).

The split-plot experimental design with repeated weeding also had limitations. While the planted and unplanted sub-treatments were equally represented in the cleared and uncleared treatments, nesting the sub-treatment within the treatment reduced the experimental area by half and may have had a confounding effect on planting. Ideally, the clearing treatment and planting treatment would have used a complete factorial requiring 12 plots for each block (n = 3) to more clearly determine which factor (clearing or planting or combination) were driving declines in non-native seedlings. Imposing different levels of removal occurrences could also have provided additional information, e.g. single weeding versus different frequencies of repeated weeding. For this study, limited land was available for research within Lyon Arboretum and elsewhere. The research area was highly variable in aspect, slope, rockiness, and plant cover. Thus, when installing the experiment, it was determined that increases in plot numbers, size or replicates would introduce more variables that would confound treatment effects.

6. Conclusion

This research addresses the development of a novel agroforestry system in which the understory of secondary forests, dominated by non-native species, is enriched with plantings of culturally and economically desired native plants. It has sought to identify a forest management system that can meet both conservation and cultural needs particularly as more forests in Hawaiʻi are becoming altered by development and/or the introduction of new species. From an ecological perspective, this study has furthered knowledge and understanding of the selected native plant species in regards to their environmental requirements and potential for restoration while also exploring potential tools and techniques, such as light manipulation, for understory restoration in Hawaiʻi. This research shows that a variety of silvicultural techniques can be successful and increase the forest management options available to both restoration and cultural practitioners.

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