Impacts of introduced leaf-galling insects on reproduction and seedling survival of *Myoporum sandwicense*, a native Hawaiian tree

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By

Corie Melissa Yanger

Thesis Committee:
Rebecca Ostertag, Chairperson
Jonathan Price
M. Tracy Johnson
Elliott Parsons
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Dedicated to

My husband, Andrew, for starting and ending this journey with me
My parents, for always believing in what I can do
and
Sabana Lei, for being my reward
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Abstract

Insect herbivores released from biotic and abiotic controls of their native environment can have severe negative impacts on plant reproduction and survival in their introduced range. On Hawaiʻi Island, a recently introduced leaf-galling thrips species (*Klambothrips myopori*) has infested populations of an abundant native tree called naio (*Myoporum sandwicense*) causing widespread gall damage and foliage dieback. Mature trees show signs of infestation and have disappeared in some areas, yet the extent to which infestation affects naio reproduction has been unknown. Within two naio populations recently invaded by thrips, one in mesic forest and one in dry forest, I counted flowers and fruits and assessed gall damage and foliage dieback monthly for one year for naio trees with zero (0%), low (<33%), moderate (33%–66%), and high (>66%) initial gall damage. Gall damage was defined as the percentage of gall-deformed young leaf area. Foliage dieback was defined as the percentage of necrotic leaf tissue compared to total young leaf area. At these same sites, gall damage, foliage dieback and height were recorded for naturally occurring naio seedlings over one year to determine seedling survivorship. I found that naio reproduction decreased, particularly for trees with moderate and high initial gall damage, regardless of site. Reproduction also declined drastically for trees with zero to low initial gall damage at the dry site. I used generalized linear mixed models (glmm) to identify variables that best explained observed patterns in naio reproduction, including thrips-induced gall damage and foliage dieback, tree basal area, precipitation, temperature and humidity. Results from glmms indicated that tree foliage dieback, branch foliage dieback and branch death (precipitated by thrips gall damage) were the most significant variables for explaining naio reproductive decline over time. Thrips’ gall damage and foliage dieback increased for trees with zero to low initial gall damage at the mesic site, while gall damage remained extremely low and foliage dieback
was mostly low for trees with zero to low initial gall damage at the dry site. Gall damage and foliage dieback increased for trees with moderate initial gall damage at both mesic and dry sites, while gall damage and foliage dieback were high and then declined for trees with high initial foliage damage at both sites. Naio seedling survival was 34% at the mesic site and 88% at the dry site, but did not appear to be strongly related to thrips damage. At a third experimental site, I used pesticide to exclude thrips and evaluated reproductive differences in treated versus untreated naio trees of low and high initial gall damage classes. Reproduction decreased for all trees at the experimental site, and no significant difference was found in naio reproduction between treated and untreated trees. In the experiment, gall damage and foliage dieback increased for trees with low initial gall damage. Gall damage remained high and foliage dieback decreased for trees with high initial gall damage, but there was no difference in gall damage or foliage dieback between treated and untreated trees. Because I did not see a clear difference in gall damage and foliage dieback between treated and untreated trees, I think it unlikely that pesticide treatment was effective in excluding thrips. These results, taken as a whole across the three sites, indicate that introduced thrips have a notable negative impact on naio reproduction, and other factors are also negatively influencing naio reproduction and should be investigated. Also, further study is needed to understand dynamics of naio seedling recruitment and survival. These studies suggest that without management action, the potential for naio to replace itself through reproduction will decline.
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Introduction

Plant production of flowers, fruits and seeds or recruitment can be limited by many external biotic and abiotic factors, including: predation, herbivory, disease and extreme climatic conditions. Herbivory in particular plays a highly important role in terrestrial food webs and ecosystem processes, and can exert significant negative pressure on reproduction and seedling survival depending on the mode (Karban & Strauss 1993; Kettenring 2009), timing (Stanforth 1997), intensity or frequency (Doak 1992) of damage. Insects are a dominant though frequently overlooked herbivore group because visual evidence of plant-feeding insects is not often obvious (Schowalter 2011). These diminutive animals are generally thought to be more impacted by plants than vice versa (Crawley 1989) yet insect populations that are released from biotic and abiotic interactions can have dramatic effects on plant reproductive capacity and, in extreme cases, survival (Lovett Doust & Lovett Doust 1988; Crawley 1989). The impacts of such release are becoming more frequent as increasing numbers of insect herbivores are introduced to new locations and find new plant hosts.

Within the last century increasing attention has been given to cases of herbivory from introduced insects in temperate forests, where outbreaks and repeated defoliation events by multiple introduced insect species have led to high mortality rates in adult trees and dramatically reduced recruitment. In temperate forests of the United States, introduced hemlock woolly adelgids (*Adelges tsugae*) and gypsy moths (*Lymantria dispar*) have caused defoliation and mortality of hemlock (*Tsuga canadensis*) and oak (*Quercus* spp.) trees for decades (Asaro & Chamberlin 2015; Morin & Liebhold 2015). One study found that hemlock seedlings were completely absent in adelgid-infested forest sites showing 26% or higher hemlock mortality (Jenkins et al. 1999). Similarly, heavy (>60%) defoliation in oaks by gypsy moths was found to
cause premature acorn abscission, which decreased seed production by 98% (McConnell 1988). These examples illustrate how plant feeding by insects whose populations are no longer controlled by conditions of their native habitat can directly or indirectly influence reproduction or recruitment of new plant hosts, and thus holds the potential to reduce plant populations.

Compared to continental systems, islands are especially vulnerable to the establishment of introduced insects. Due to their isolation, islands tend to have fewer continental groups represented and smaller populations (Loope & Mueller-Dombois 1989) as well as high levels of endemism per unit area (Paulay 1994; Vitousek et al. 1997). Fewer continental counterparts and smaller populations create a simpler biological system with less overlap in species’ roles and higher niche availability. The Hawaiian Islands provide a fitting example, where a few founder species led to wide adaptive radiation in plants (e.g., silversword alliance and lobeliads) and animals (e.g., honeycreepers and Hawaiian Drosophila) (Wagner & Funk 1995). Nevertheless, only one third of insect orders are represented in native Hawaiian fauna (Loope 1989), a gap which may facilitate successful establishment by the other two thirds of orders. Indeed, today the Hawaiian Islands possess 25% more introduced insect species than the North American continent (Eldredge & Miller 1998; Pimentel et al. 2005). With less species diversity and complexity of interactions, islands serve as models of less complex systems where the likelihood of establishment and population expansion by introduced insects is high.

In the Hawaiian Islands, a recently introduced thrips species (*Klambothrips myopori*) has swept through populations of a native, dominant woody species, *Myoporum sandwicense* or naio. This particular case of thrips in Hawai‘i is unique because it is a rare instance where thrips, better known as agricultural pests, have become disturbers of a natural system, attacking a native forest tree as opposed to an ornamental plant. In their natural habitats, thrips serve important ecosystem
functions as pollinators (Sakai 2001), fungal feeders (Ananthakrishnan & Suresh 1983), or even predators (Trichilo & Leigh 1986) but they are less well known as herbivores. Thrips have developed a reputation as pests in the agricultural sector because they directly feed on or serve as disease vectors to plants and have caused significant losses of food and fiber crops (Lewis 1973; Childers & Achor 1995). Only recently have thrips gained attention for their impact on natural systems. Within the last decade, thrips have been reported as highly damaging to native tree species in other locations around the world, including Brazil (Thomazini & Lima 2014) and the French Antilles (Michel et al. 2008).

**Thrips and Myoporum**

Thrips that target *Myoporum* are members of the family Phlaeothripidae (order Thysanoptera, suborder Tubulifera) (Mound & Morris 2007), from which most gall-forming thrips species originate (Crespi et al. 1997). Gall-producing thrips are most common in Australia and the Indo-Malayan region (Lewis 1973). Adult thrips of this family use mouthparts to scrape leaf tissues and suck plant sap (Lewis 1973). In reaction to thrips feeding, leaf tissues thicken and curl, creating sheltered crevices where females lay their eggs (Lewis 1973). The thrips attacking *Myoporum sandwicense* in Hawai‘i, *Klambothrips myopori*, induce gall damage on naio leaves which has been observed to lead to foliage dieback (King et al. 2012). Because *K. myopori* were only recently discovered and identified as a new species little else is known about their biology (Mound & Morris 2007). Several entomological studies have identified native and non-native insect species associated with *M. sandwicense* in the Hawaiian Islands (e.g., Zimmerman 1948; Swezey 1954), including native thrips, but none have reported significant
herbivory levels prior to recent damage caused by *K. myopori*. The first record of these thrips came from Hawai‘i Island and currently no other islands have reported their presence.

Using molecular techniques, researchers determined that *K. myopori* in California and Hawai‘i are genetically identical and most likely originated from northern Tasmania (Cameron & Mound 2014), although the mechanism of thrips arrival at either location is unknown. *K. myopori* is one of a group of thrips species known to induce gall damage in native Australian *Myoporum* species, but not as acutely as what has been observed on plants growing in California and Hawai‘i (Mound & Morris 2007; Cameron & Mound 2014). The extensive leaf-deformation on *M. sandwicense* is similar to damage seen on ornamental *Myoporum laetum* (native to New Zealand) in California, where the insect was first identified (Mound & Morris 2007).

**Hawaiian Myoporum**

*Myoporum sandwicense* is an indigenous species that is part of a Pan-Pacific genus. *M. sandwicense* is found throughout the main Hawaiian Islands as well as Mangaia Island in the Cook archipelago (Wagner et al. 1990; Imada 2012). *M. sandwicense* is most abundant on the largest island, Hawai‘i, where the species has a wide elevational range, growing as a shrub at the coast to a tree at higher elevations (Wagner et al. 1990). Beyond the coastal strand, *M. sandwicense* is a common component of mesic and wet forest canopy or subcanopy (Wagner et al. 1990). In dry forest, the species reaches peak abundance as a codominant canopy tree in a broad saddle-shaped area located between the two largest volcanoes, Mauna Kea and Mauna Loa. The name “naio” is locally used to refer to *Myoporum* in Hawai‘i where two species are recognized: *M. sandwicense* and *M. stellata* (G.L. Webster) O. Deg. & I. Deg. (Imada 2012). Indigenous Hawaiians used naio wood to build house frames and the Hawaiian monarchy
exported logs to East Asia in the 1800s as a substitute for the diminishing native sandalwood supply (Kolb & Murakami 1994).

*Myoporum sandwicense* is an evergreen tree exhibiting continuous new leaf growth (Stratton et al. 2000). The plant has been described as highly variable in habit, but its variability has not been explicitly studied. Height of mature individuals varies from <2 m to greater than 10 m (Wagner et al. 1990), with taller individuals typically found in mesic and wet forests (C. Yanger, personal observation). Plants often have multiple main stems. Leaves are lanceolate and generally glabrous, although pubescence has been observed on plants growing in dry habitats (C. King, personal communication). Flowers (~1 cm wide and long) are borne along the stems of newer shoots and range in color from white to pale pink and occasionally have pink or purple markings toward the center of the corolla (Wagner et al. 1990). Tiny seeds (~5-12) are housed within a stony endocarp which is surrounded by fleshy white tissue when ripe (Wagner et al. 1990). An extinct endemic land bird, the Kona grosbeak (*Chloridops kona*), was a known predator of naio fruits, but likely also served as a disperser (Olson 2014).

Naio are generally considered to be abundant, year-round fruit-producers. A four-year study by Banko et al. (2010) reported that naio flowered and fruited heavily (>25% of branch tips per tree with ≥ 1 flower or fruit) and that fruit production was especially high (60-80% of trees) and constant over time. One study quantified naio flowers and fruits by area on trees at Pōhakuloa (saddle area between Mauna Kea and Mauna Loa), and found that naio flower production reached nearly 100,000 flowers per hectare and ranged between 100,000 and 400,000 fruits per hectare over one year (Tagawa 2013). Early studies of naio reproduction described naio reproduction patterns as subtly seasonal in flowering and fruiting. Lamoureux (1973) reported that naio within Hawai‘i Volcanoes National Park (HAVO), on the east side of Hawai‘i Island,
flowered from May to January, while trees bore fruits all year. On the west side of Mauna Kea, where naio are more abundant and codominate the forest canopy with the fabaceous tree, māmane (*Sophora chrysophylla*), Van Riper (1975) also observed seasonality in naio flowering that appeared to be highest from spring to early summer. Both Lamoureux (1973) and Van Riper (1975) reported a constant abundance of fruit despite periodic flowering, suggesting that fruits persist on branches for long periods of time.

It is challenging to predict the extent of reproductive impact from *Klambothrips* galling on naio because studies investigating the impact of insect gall damage on woody plant reproduction are scarce, and tend to be limited to stem, shoot or bud galling. However, the literature does have examples of the negative impacts of galling insects on reproduction. In a comparative observational study, Sacchi et al. 1988 found that stem galling sawflies (*Euura lasiolepis*) reduced flower buds of arroyo willow (*Salix lasiolepis*) by 43%. Another observational study found that the stem-galling insect *Reseliella clavula* caused a 46% decline in flowers and 79% decline in fruit production in flowering dogwood (*Cornus florida*) within the first year of attack (Sacchi & Connor 1999). A two-year chemical exclusion experiment found that buds of a native Chilean evergreen shrub (*Colliguaja integerrima*) attacked by a gall midge produced 59% less fruit than their ungalled counterparts (Gonzales et al. 2005). These studies suggest that thrips could potentially negatively impact naio reproduction in Hawai‘i. However, the extent of negative impact will likely be determined by the extent of damage caused to individual trees.
Study Purpose

My research goal was to expand understanding of the impact of introduced insect herbivores on newfound host plant reproduction by examining the interaction between *Klambothrips* and naio. By combining data from tree-damage monitoring with reproduction and recruitment impact data for mature trees and seedlings, managers and researchers can improve understanding of thrips’ population-level effects on naio.

In 2010, researchers began to monitor thrips damage to *M. sandwicense* trees at nine sites spanning a portion of the plant’s dry forest range on leeward Hawai‘i Island (King et al. 2012). After two years, they reported that *Klambothrips* damage levels and *M. sandwicense* tree mortality increased at all nine study sites (King et al. 2012). The objective of my study was to answer the question about the consequences of this damage: Do gall damage and foliage dieback caused by introduced thrips negatively impact naio reproduction and seedling survival? Using this framework, I examined the system using four types of inquiry: (a) thrips presence/detection on plants (via visual gall damage), (b) foliage dieback due to thrips damage, (c) reproduction effects in relation to gall damage and foliage dieback, and (d) seedling survival in relation to gall damage and foliage dieback. To address these levels of investigation, I used both observational and experimental studies to test the following hypotheses at my chosen sites:

**H1a:** Gall damage caused by thrips will increase over time at all sites.

**H1b:** Increased gall damage will result in corresponding increased foliage dieback over time.

**H2a:** Assuming H1b is true, trees with high levels of gall damage and foliage dieback produce fewer flowers and fruits than trees with low levels of damage.

**H2b:** Experimentally reducing thrips on naio trees will reduce gall damage, which will lead to increased flower and fruit production.

**H3:** Seedlings with high levels of thrips damage display lower survivorship compared to seedlings with low levels of damage.
Methods

Study Sites

I conducted my research in two mesic forests and one dry forest location on the island of Hawai‘i (Fig. 1). I carried out observational studies at Kona Hema Preserve (KH)(dry-mesic) and Pu‘uwa‘awa‘a Forest Reserve (PW)(dry). I conducted an experimental study at Keauhou Ranch (mesic). Infestations at both Kona Hema Preserve and Keauhou Ranch were detected starting in late 2012 (M. Johansen & C. King, personal communication). State researchers first detected thrips at Pu‘uwa‘awa‘a Forest Reserve in 2010 (L. Kauffman, personal communication). When I began my study, Klambothrips infestation had not yet fully dispersed in the environment at Kona Hema, whereas the infestation seemed well-established at Pu‘uwa‘awa‘a Forest Reserve. Each of the study sites was relatively accessible for the extent and frequency of my planned data collection and both Kona Hema Preserve and Pu‘uwa‘awa‘a Forest Reserve had extensive areas of M. sandwicense trees showing some natural recruitment (C. Yanger, personal observation). Site characteristics are summarized in Table 1.

Kona Hema Preserve, owned by The Nature Conservancy, is located on the western slope of Mauna Loa. I conducted my study in the fenced northwestern Pāpā Unit, approximately 920 ha within the larger 3,238 ha preserve. The unit extends from 1000 to 1700 m in elevation and receives 1000 to 2000 mm in mean annual rainfall (Giambelluca et al. 2013). Soils of this unit are characterized as stony muck, and generally range in age from 1500 to 3000 years with a newer flow to the southeast (A.D. 1926) (Sato et al. 1973; Sherrod et al. 2007). Forest within the Unit is composed of ‘ōhi‘a (Metrosideros polymorpha) and koa (Acacia koa) as the canopy dominant species, with naio dominating the subcanopy and various native understory species.
below. In 1993, a fire spread through a portion of the forested northeast corner of the Unit, and
naio regeneration has been high in this area.

Pu‘uwa‘awa‘a Forest Reserve, part of the state Division of Forestry and Wildlife’s
Hawai‘i Experimental Tropical Forest network, is located on the northeast slope of Hualālai
volcano on the west side of Hawai‘i Island and extends from 1800 m to the coast. I conducted
my research on the east side of the Reserve’s unfenced Mauka Unit, where naio and māmane
create the dominant canopy type. The dry forest community type is located mostly on a
combination of worn ‘a‘ā and pāhoehoe lava flows dated at 1500 to 3000 BP (Sato et al. 1973;
Sherrod et al. 2007). Annual precipitation ranges from 500 to 750 mm (Giambelluca et al. 2013).

Keauhou Ranch, owned by Kamehameha Schools, is located on the southeastern slope of
Mauna Loa between 1200 and 3000 m in elevation. The property, encompassing roughly 13,163
ha, has been fenced since 2007 and cattle were removed from 2004 to 2005. Mean annual
precipitation in the study area is 2500 mm (Giambelluca et al. 2013). Substrate consists of mixed
pāhoehoe and ‘a‘ā flows between 1500 and 3000 years old (Sato et al. 1973; Sherrod et al. 2007).
Naio grow scattered in the lower pastures within kipuka (forested pockets) of mixed mesic forest
and sporadically within remnant pasture grasses. The dominant forest canopy and subcanopy
species include ‘ōhi‘a, koa, kolea (*Myrsine lessertiana*), and pilo (*Coprosma* sp.).

**Tree Selection and Physical Characters**

For observational studies, I examined trees across a landscape to identify ten trees in each
of four initial thrips gall damage classes (hereafter referred to as “initial gall damage classes”:
zero, low, moderate, and high). A tree in the zero initial gall damage class had 0% of its total live
branch tips showing gall damage. A tree in the low initial gall damage class had either <33% of
its total live branch tips displaying any level of gall damage (explained under the next section, Observational Study) or $\geq 33\%$ of its total live branch tips showing $<33\%$ gall damage. A tree with moderate gall damage had $33\%$ or more of its total live branch tips displaying mostly $33\%-<66\%$ gall damage on affected branch tips. A tree with high gall damage had $>66\%$ of its total live branches showing $>66\%$ of gall damage to its affected branch tips. To determine gall damage level of a tree, I visually assessed all live branch tips for the extent of gall damage and assigned trees to initial gall damage classes based on those estimates. I noted these initial gall damage classes during the first survey and used them as a reference point for data analysis. At KH, ten trees represented each initial gall damage class. At PW, trees were unevenly distributed: eight individuals represented the zero initial gall damage class and twelve represented the low initial gall damage class. Moderate and high initial gall damage classes at PW each had ten trees.

For the experimental study, trees included some individuals used in previous research and were randomly assigned to a treated (thrips-excluded) group and a untreated group. Experimental study trees represented only initial gall damage classes low and high for a total of 40 trees.

At all sites, trees were greater than $2\text{ m}$ in height, and located at least $10\text{ m}$ apart from each other. Tree size was approximated by calculating basal area ($\text{cm}^2$) using diameter at breast height (DBH) (1.3 m) measurements for each tree. I included live stems at least two centimeters in diameter in the basal area calculation. On each tree, I selected ten single branch tips by walking around the crown and marking branch tips between 1-2 m in height so that counts of reproductive units could be accomplished by an observer standing on level ground.
Tree Gall Damage, Foliage Dieback and Reproduction

Observational study

For each of the forty trees chosen (ten in each initial gall damage class) at each observational site, I monitored for three types of inquiry proposed for this study: thrips gall damage, foliage dieback and naio reproduction. Monitoring occurred from March 2014 to February 2015 for KH and from April 2014 to March 2015 for PW. Each month, I assessed naio for: 1) gall damage (first for the overall tree and then for each marked branch tip), 2) foliage dieback level (first for the overall tree and then for each marked branch tip) and 3) branch tip-level counts of reproduction. I made a distinction between tree- and branch tip-level gall damage and foliage dieback to account for differences in distribution of damage on trees and to examine the relative importance of tree- versus branch tip-level damage in relation to reproductive counts.

Gall damage levels for branch tips included: zero (no damage), low (<33% damage), moderate (33-66% damage) and high (>66% damage) (Figs. 2a-2d). I assessed visual gall damage based on the percentage of deformed young leaf area, which typically included leaves located within 3 cm of the shoot tip. I noted branch tips that died during the course of this study as “dead” and continued to record those branch tips for gall damage. I did not state that a branch tip was “dead” unless all foliage along the length of the branch tip was dead. When I did not see gall damage on branch tips that were dead or dying, I assigned a damage level for foliage dieback, and noted “not thrips.” I typically assumed that gall damage was high (>66% damage) for revisited dead branches, but had to correct gall damage readings if the data records showed any instance when I had noted “not thrips.”
Foliage dieback levels used the same classification system used for gall damage, but were applied to the observed necrotic leaf tissue (Figs 3a-3d). When evaluating foliage dieback, I included any brown leaf tissue associated with thrips damage. I assessed foliage dieback levels based on the percentage of necrotic tissue compared to total young leaf area. Therefore, if a branch tip contained leaves that were galled and completely brown one month, I recorded foliage dieback as high. If, in the following month, new leaves had sprouted from the same branch tip and sustained no gall damage or foliage dieback, I recorded foliage dieback as zero. If, for example, leaves of a branch tip were partially galled (e.g., 50% of leaf area) and foliage dieback had occurred for 40% of the total leaf area, I assessed foliage dieback as moderate (33%-66%).

Quantifying naio reproduction on branch tips involved counting flowers, young fruits (green), ripe fruits (white), and raisins (brown or shriveled flesh) (Fig. 4). I counted flower buds (corollas) if they were partially open and continued to count them as long as they were attached and retained some white tissue. I counted young fruits immediately after flower senescence and included them in the young fruits count until the flesh was completely white. I counted ripe fruits when flesh was white until all flesh had turned brown. I counted entirely brown or shriveled fruits as past-ripe or “raisins.” As mentioned earlier, naio can retain fruit on the stem for long periods of time. Therefore, I restricted raisin counts to those that were continuous from the distal end of the branch tip to at most 2.5 cm from the next most distal raisin(s) or the next most distal leaf (whichever was proximal to the base of the branch tip). I excluded aborted fruit from the counts, which I defined as fruit less than one half the size of a fully developed fruit.
Experimental study

I monitored trees for thrips gall damage, foliage dieback and reproduction at Keauhou Ranch in an experiment using pesticide treatment to exclude thrips. I did not encounter any trees for the zero gall damage class and found few trees for the moderate gall damage class. Therefore, I selected representative naio trees for only low initial gall damage (<33% gall damage) and high initial gall damage (>66% gall damage) classes. I randomly selected ten individuals per gall damage class for pesticide treatment and ten individuals per class for no treatment. I monitored trees seven times over eight months (September 2014-April 2015) according to the same gall damage, foliage dieback and reproductive count protocols used for the observational study. Three systemic pesticide treatments were applied. Staff from Forest Solutions, Inc. carried out the first treatment at the end of October 2014. Another licensed pesticide applicator conducted the second and third treatments, in mid-January 2015 and the beginning of March 2015. Forest Solutions, Inc. had tested the field efficacy of the systemic pesticide Safari® and reported that the chemical activity lasted no longer than two months. Therefore, I assumed that chemical activity from the first spray treatment was completed before the second treatment occurred. The active ingredient in the pesticide, dinotefuran, is a neonicotinoid, a chemical that is structured similarly to nicotine and is especially effective for piercing and sucking insects; the chemical kills the target insect by disrupting neural pathways (Tomizawa & Casida 2005).

Trees were sprayed with a 20% solution of chemical. One ounce of granular Safari® was dissolved in two liters of water and mixed with 5 mL of adjuvant in a 16 L backpack sprayer. Grass cover around the base of each tree was pulled back to expose the trunk and the chemical was applied to the full circumference of basal bark below one meter in a coating that wet the bark, but did not drip. Pesticide applicators completed treatments within 3-4 hours.
Additional biotic and abiotic variables

At all sites, I recorded non-thrips insect damage monthly for each monitored branch tip. Although I applied thrips gall damage ratings to newest growth, I evaluated “other insect damage” for all leaves on a branch tip, visually assessing damage to foliage in increments of 5%. I obtained temperature, precipitation and relative humidity data pertaining to Kona Hema and Puʻuwaʻawaʻa from the online MesoWest source for Remote Automated Weather Station (RAWS) records (accessed September 2015) (Horel et al. 2002). I identified maximum and minimum temperature (°C) and relative humidity (%) values for each day of each month of the study period. I then calculated the average maximum and minimum values for each month. I recorded canopy cover at Keauhou Ranch to account for variation in light reaching trees located at the edge of shaded forest patches or in pasture grasses. I assessed canopy cover above each naio tree in a single reading and recorded categories in four classes: 1 = 0-25% cover, 2 = 25-50% cover, 3 = 50-75% cover, 4 = 75-100% cover.

Seedling Gall Damage, Foliage Dieback and Survival

I located and marked natural seedlings at the main stem base with aluminum tags at both Kona Hema Preserve (KH) and Puʻuwaʻawaʻa Forest Reserve (PW). For this study, I included seedlings measuring 1-100 cm from the base of the longest growing tip to rooting point. I tagged a total sample size of 103 seedlings at KH and 127 seedlings at PW. At KH, seedlings were well-distributed throughout the study area and located mostly under parent trees. At PW, seedlings were scarce within the forested area and therefore seedlings were tagged along a recently bulldozed road. Each month, I revisited seedlings and assessed them for height (rounded to nearest 0.5 cm), thrips gall damage and foliage dieback class, and percentage of other insect
damage (rounded to nearest 5%). I used the same gall damage and foliage dieback class categories that I used in the tree study. I observed and recorded data for seedlings for thirteen months at KH, and eight months at PW (due to unexpected herbicide spraying of the roadside where most tagged seedlings were located). I counted seedlings as dead and removed the associated tag when all leaves and stem(s) were brown.

Data Analysis

**Tree gall damage and foliage dieback**

I used bar-graphs to examine patterns in gall damage and foliage dieback over time at both the tree- and branch-levels. I developed transition matrices for each site to determine the probability of a tree within one of the initial gall damage classes progressing to another level of gall damage over one year. I calculated values per matrix cell using the formula \( F_t/F_i \), where \( F_i \) was the frequency of individuals in the initial state (i.e., gall damage level) and \( F_t \) was the frequency of individuals in the final state. I did not develop transition matrices for foliage dieback because initial foliage dieback was not used as a baseline factor for trees. For each month of monitoring, I added all instances of branch death associated with high gall damage and foliage dieback, and divided by 40 to obtain the mean number of dead branches per tree.

**Tree reproduction within and between initial gall damage classes**

I used non-parametric Spearman’s correlation tests to see if tree reproductive output changed significantly over time within initial gall damage classes. For each tree, I added counts of a reproductive type (e.g., flowers) for ten marked branch tips to yield a total number of units
for that type. I calculated the average of those total numbers for all trees within an initial gall damage class to obtain the mean total reproductive number per ten branch tips per tree. I also calculated mean total values for young fruits, ripe fruits, raisins and combined flowers and fruits (hereafter referred to as “combined reproduction”). I applied a post hoc Bonferroni correction for multiple comparisons to account for the five reproductive types examined, and determined significance at $p < 0.01$. I also checked whether mean flower and FYR (flowers plus young fruits and ripe fruits) reproduction were significantly different between thrips treated and control trees for the first and last months of monitoring at the experimental site using Mann-Whitney U tests.

**Tree reproduction in relation to gall damage and foliage dieback**

I analyzed repeated measures observations (4 classes x 10 trees x 10 branch tips x 12 months) for naio trees at Kona Hema (KH) and Puʻuwaʻawaʻa (PW). I examined relationships between tree reproduction and categorical gall damage and foliage dieback classes using generalized linear mixed-effects models (glmms) fit by maximum likelihood (Laplace Approximation). I incorporated additional biotic and abiotic factors that I thought might influence reproduction or thrips gall damage in the analyses, including tree size (basal area in cm$^2$), other insect and fungal damage (%), precipitation (mm), temperature (°C) and relative humidity (%). Analysis consisted of a two-part process to account for a large number of observed zero values in the dataset. First, I modeled reproductive data as presence/absence with all non-zero values of the response variable set to a value of one (binomial distribution). Second, I modeled count data excluding zero values to fit a gamma distribution, which was the best distribution for fitting determined by the Kolomogrov-Smirnov test.
I developed models in R (version 3.0.2; R Development Core Team 2013) using the glmer function in package lme4 (version 1.1-7; Bates et al. 2015) to examine significance of relationships between the independent variables mentioned previously and the single sum quantity of flowers, young fruits and ripe fruits (FYR). I excluded raisins (past ripe fruits) from this analysis because I was less certain that they accurately represented the most recent reproductive season. All models included time as a continuous random number and branch (branch tip) nested within tree as a random factor.

I followed several steps in order to fit mixed models for the binomial and gamma distributions. For initial data exploration, I fitted univariate models to determine if each independent variable was related to variation in the response. I culled individual variables that did not significantly relate to variation in the response from mixed modeling. Next, I examined correlation between variables, and excluded highly correlated variables ($r > 0.7$) from further modeling. If two variables were significant and highly correlated, I excluded the variable with the lower univariate corrected Akaike’s Information Criterion (AICc) value. Appendices A1-A2 contain the correlation matrices for each site. I created models using all logical combinations of the remaining independent variables and compared them using AICc values. Presence/absence (using binary values 1=presence, 0=absence) and count mixed models, null models, and AICc values are presented in Appendix B1 for KH and Appendix B2 for PW. I selected the final model according to the lowest AICc value (Zuur et al. 2009). I considered models with $\Delta$AICc $< 2$ as equally probable. Finally, I compared selected models to null models to determine the additional amount of reproductive variation explained by the best models.
Seedling growth & survival

I used Fisher’s exact tests to see if there was a significant difference in the proportion of live (versus dead) seedlings with zero-low (0% - <33% gall damage) versus moderate-high (>33% - >66% gall damage) levels of thrips gall damage. For KH and PW, I carried out separate Fisher’s exact tests for seedlings <10 cm and seedlings >10 cm. I arranged contingency tables according to each seedling’s last recorded gall damage level (either zero-low or moderate-high), and ensured each seedling was included only once as live or dead (by the end of the study).
Results

Tree Observational Study

Gall damage & foliage dieback: Kona Hema

The hypothesis that gall damage caused by thrips would increase over time (H1a) was supported by observed gall damage patterns and transition matrices at KH. Trees and branches in zero, low and moderate initial gall damage classes increased in gall damage over twelve months (Fig. 5). The incidence of high gall damage increased most for trees and branches in the low or moderate initial gall damage classes. Trees in the high initial gall damage class generally sustained high gall damage levels over 12 months, whereas branches showed variable damage levels. In both moderate and high initial gall damage classes, a subset of branches exhibited zero and low gall damage during the year. Transition probabilities reflected observed patterns, indicating that most trees at KH in the zero, low or moderate initial gall damage classes were likely to increase to the next level of gall damage over twelve months (Table 2).

The hypothesis that increased gall damage would result in increased foliage dieback over time (H1b) was also supported by data collected at KH. Trees and branches in the zero, low and moderate initial gall damage classes at KH displayed increased foliage dieback, supporting my hypothesis (Fig. 6). In contrast, trees in the high initial gall damage class showed an increase in foliage dieback for about seven months of the study and then a decline in foliage dieback due to flushes of new growth occurring on previously damaged branches. Branches in the same high initial gall damage class similarly displayed increased branch foliage dieback followed by a
decline. A subset of branches in both moderate and high initial gall damage classes displayed zero and low foliage dieback after readings of higher dieback.

All observational trees were alive at the conclusion of the study. The average number of dead branches per tree was low for the first six months of monitoring and then increased (Fig. 7a). Branch death corresponded to initial gall damage class, with mean branch death lowest for zero initial gall damage trees and highest for high initial gall damage trees. By the end of the study, 37% of 400 monitored branches had died at KH, with branch death almost exclusively (95%) observed for branches whose last gall damage assessment was “high.”

**Gall damage & foliage dieback: Puʻuwaʻawaʻa**

Patterns of damage observed in trees and branches at PW differed from my hypothesis that gall damage would increase (H1a). At PW, trees that began in the zero or low gall damage class maintained low gall damage over time (Fig. 8). Branches in the zero and low initial gall damage classes similarly maintained low gall damage. The incidence of high gall damage generally increased for trees and branches in the moderate initial gall damage class. In the high initial gall damage class at PW, gall damage ratings for trees declined for over the study period while branches in the high initial gall damage class maintained high gall damage levels over time. Similar to observations at KH, I found that several branches in the moderate and high initial gall damage classes displayed zero and low damage over the year. Transition probabilities at PW reflected observed patterns, showing that trees in zero and low initial gall damage classes were 100% likely to display low gall damage by the end of the study (Table 3). Trees in the moderate initial gall damage class were 40% likely to remain moderately gall-damaged and 40%
likely to transition to high gall damage. Trees in the high initial gall damage class were 20% more likely to exhibit moderate gall damage than remain highly gall damaged.

Throughout the study, I evaluated gall damage as the presence of galls, but made a new observation after the first month of data collection at PW: trees in the zero initial gall damage class were later found to have puncture or probing marks from thrips. After evaluating these findings, I stopped considering trees in the zero initial gall damage class at PW to be free of thrips damage. That change was reflected in gall damage assessments for the third month of monitoring. In the transition matrix for PW, I therefore combined values for trees in the zero and low initial gall damage classes to calculate changes in gall damage over time (Table 3).

Contrary to my hypothesis that foliage dieback would increase (H1b), at PW foliage dieback patterns varied among initial gall damage classes. In the zero initial gall damage class, most trees remained at zero foliage dieback, with some trees increasing to low foliage dieback (Fig. 9). Most branches of those zero initial gall damage trees maintained zero foliage dieback, and roughly 25% of branches fluctuated with low or high foliage dieback. In the low initial gall damage class, most trees started with zero foliage dieback and then increased to low foliage dieback. Corresponding branches of those low initial gall damage trees displayed a different pattern, with about 25% or less of branches maintaining low or high foliage dieback. Most trees with moderate initial gall damage had either low or moderate foliage dieback over time, while their branches showed a gradual increase in high foliage dieback. At PW foliage dieback associated with high initial gall damage trees declined over time from mostly high foliage dieback to mostly moderate foliage dieback due to flushing of new growth. About 60% of branches in the high initial gall damage class maintained high foliage dieback. A number of
branches in the high initial gall damage class were observed to have zero foliage dieback in each month of monitoring, although that number declined over time.

All observational trees were alive at the conclusion of the study. I observed dead branches in the third month of monitoring, after which the number of dead branches increased (Fig. 7b). The mean number of dead branches per tree remained low for zero and low initial gall damage trees, while branch death increased steadily in the moderate and high initial gall damage classes. At PW, 28% of 400 monitored branches died by the final reading, with most branch death occurring where high gall damage was the last observed damage.

**Relating reproduction to gall damage and foliage dieback: Kona Hema**

At Kona Hema, observations of naio reproduction supported my hypothesis that trees with high gall damage and foliage dieback produce fewer flowers and fruits than trees with low damage (H2a). As stated in the methods, I used “dieback” to refer to thrips-induced leaf tissue necrosis and visually estimated dieback for (a) an entire monitored tree and (b) ten individually marked branches on each monitored tree. Mixed modeling results for KH indicated that were different for each site in the type and direction of the relationship between thrips damage and reproduction presence and quantity.

Tree gall damage was significantly and positively related to the presence of flowers/young fruits/ripe fruits (FYR) at KH, where FYR presence increased by a factor of 3.8, 3.9 and 3.5 at low, moderate and high tree gall damage levels, respectively (Table 4). Basal area and minimum relative humidity were also positively related to the presence of FYR at KH. In contrast, FYR presence decreased by a factor of 6.5 for each per unit increase in dead branches. Quantity of FYR at KH was positively related to both dead branches and minimum temperature
by factors less than 0.5. The fitted generalized linear mixed model (glmm) for KH explained 15.8\% of variation in FYR presence and 0.01\% of variation in FYR quantity compared to null models. Tree gall damage and branch death accounted for almost all (98\%) explained variation in FYR presence data, with branch death explaining more than two thirds of data variation.

When the study began, mean combined reproduction (flowers plus young fruits, ripe fruits and raisins) was lowest in the zero initial gall damage class compared to other classes, with 100 reproductive units/10 branches/tree (Fig. 10). The moderate initial gall damage class had higher mean combined reproductive output at about 160 reproductive units/10 branches/tree. The low and high initial gall damage classes had the highest mean combined reproduction, more than two times the levels seen in zero initial gall damage trees, with greater than 200 reproductive units/10 branches/tree. Flower output was lowest in the zero initial gall damage class with an average 2.8 flowers/10 branches/tree. The highest average flower output occurred in the low initial gall damage class (6.4 flowers/10 branches/tree), followed by the moderate and high initial gall damage classes at 4.9 and 4.6 flowers/10 branches/tree, respectively.

Spearman correlations indicated that over one year at KH, mean combined reproduction did not change significantly within the zero initial gall damage class ($P=0.182$, Spearman’s Rho) nor within the low initial gall damage class ($P=0.074$, Spearman’s Rho). Separate counts of flowers, young fruits, ripe fruits or raisins for those same zero and low initial gall damage classes also showed no significant change. In the high initial gall damage class, mean combined reproduction declined by about 65\% from 263 to 92 reproductive units/10 branches/tree ($r_s = -0.391$, $P<0.001$) (Fig. 10). For the same high initial gall damage class, flower output declined by almost 94\% from 4.6 to 0.3 flowers/10 branches/tree ($r_s = -0.495$, $P<0.001$), young
fruits declined by 96% from 140 to 5 young fruits/10 branches/tree \( (r_s = -0.694, P<0.001) \) and ripe fruits declined by 95% from about 57 to 3 ripe fruits/10 branches/tree \( (r_s = -0.682, P<0.001) \).

**Relating reproduction to gall damage and foliage dieback: Pu‘uwa‘awa‘a**

At Pu‘uwa‘awa‘a, I observed that trees with high gall damage and foliage dieback produced fewer flowers and fruits than trees with low damage (H2a). At PW, tree foliage dieback, branch foliage dieback and dead branches were all negatively related to the presence of FYR (Table 5). At PW, FYR presence decreased by a factor of 0.6, 0.7 and 0.8 for low, moderate and high levels of tree foliage dieback, respectively. The presence of FYR decreased by a factor of 7.5 for every unit increase in dead branches. Quantity of FYR was positively related to branch foliage dieback level by a factor less than 0.05. The fitted glmm for PW explained 9.6% of variation in FYR presence and 0.1% of variation in FYR quantity compared to null models. For FYR presence at PW, tree foliage dieback and branch foliage dieback accounted for 98% of explained variation.

At the start of the study, naio trees in the zero and low initial gall damage classes had the highest level of mean combined reproduction at 278 and 300 reproductive units/10 branches/tree, respectively (Fig. 11). Those reproductive levels were more than three times what I found for the moderate and high initial gall damage classes, which both started with about 80 reproductive units/10 branches/tree. Flower numbers for zero and low initial gall damage classes were roughly two to three times greater (13 flowers/10 branches/tree) than flower numbers for moderate and high initial gall damage classes at 5 and 3 flowers/10 branches/tree, respectively. Young fruit levels were about two times greater for zero and low initial gall damage classes (roughly 100 young fruits/10 branches/tree) than for moderate and high initial gall damage classes.
(approximately 45 young fruits/10 branches/tree). Ripe fruits were four times higher in zero and low initial gall damage classes than in moderate and high initial gall damage classes. There were 51 and 57 ripe fruits/10 branches/tree in zero and low initial gall damage classes, and 8 and 13 ripe fruits/10 branches/tree in moderate and high initial gall damage classes.

At PW, both zero and low initial gall damage classes reproduction declined significantly due to declines in flowers and raisins. In the zero initial gall damage class, mean combined reproduction declined by about 67% from 278 to 91 reproductive units/10 branches/tree ($r_s = -0.393$, $P<0.001$) (Fig. 11). In the low initial gall damage class, mean combined reproduction declined by 73% from 300 to 81 reproductive units/10 branches/tree ($r_s = -0.380$, $P<0.001$). Mean combined reproduction for the moderate initial gall damage class did not change significantly over time. In the same moderate initial gall damage class, mean flower quantity declined overall, although the twelfth month’s quantity was higher than the first month’s quantity: 5.3 versus 5.1 flowers/10 branches/tree ($r_s = -0.291$, $P=0.002$). In the high initial gall damage class mean combined reproduction declined by about 95% from 83 to 4 reproductive units/10 branches/tree ($r_s = -0.486$, $P<0.001$).

Tree Experimental Study

**Gall damage & foliage dieback: Keauhou Ranch**

The hypothesis that experimentally reducing thrips would reduce gall damage, and thereby lead to increased flower and fruit production (H2b) was inconclusive based on results from experimental chemical exclusion. Gall damage for pesticide treated and untreated trees with high initial gall damage did not show any noticeable difference over time. However, gall damage
in untreated trees with low initial gall damage appeared to be slightly higher than in treated trees (Figs. 12a-12d). Transition probabilities indicated that treated trees with low initial gall damage were slightly more likely to remain in the low gall damage class than untreated trees with the same initial damage (Table 6). Treated trees with high initial gall damage were more likely to sustain a moderate level of gall damage, while untreated trees were more likely to sustain a high level of gall damage.

Foliage dieback for treated trees declined slightly, while foliage dieback for untreated trees appeared to increase (Figs. 13a-13d). Foliage dieback appeared slightly higher in untreated trees with low initial gall damage than treated trees. Of the high initial gall damage trees, untreated trees had less foliage dieback than treated trees at the start of the monitoring period. However, by the end of the study, high initial gall damage trees that were treated showed lower foliage dieback than untreated trees.

One treated and one untreated tree died by the end of the study, and each tree had a high level of initial gall damage. Dead branches increased over time. However, there was no difference in the mean number of dead branches per tree between treated and untreated trees in either low or high initial gall damage classes (Fig. 16). Almost all dead branches in treated and untreated trees had high gall damage status in the month prior to death.

**Relating reproduction to gall damage and foliage dieback: Keauhou Ranch**

Mean combined reproduction was not significantly different between treated and untreated trees from the start of the study regardless of initial gall damage. Naio trees that received no treatment had similar mean combined reproductive output (about 30 reproductive units/10 branches/tree) whether they were in the low or high initial gall damage class (Figs. 17-
In contrast, low and high initial gall damage trees that received treatment began with mean combined reproduction of about 84 reproductive units/10 branches/tree.

Despite large differences in the starting point of same-class trees, Spearman correlations indicated that decreasing reproduction patterns over time were similar. Mean combined reproduction declined by almost 48% from 84 to 44 reproductive units/10 branches/tree for treated low initial gall damage trees ($r_s = -0.100$, $P<0.001$), and about 71% from 34 to 10 reproductive units/10 branches/tree for untreated low initial gall damage trees ($r_s = -1.000$, $P<0.001$). In treated high initial gall damage trees, mean combined reproduction declined roughly 49% from 84 to 43 reproductive units/10 branches/tree ($r_s = -1.000$, $P<0.001$). In untreated high initial gall damage trees, mean combined reproduction declined 61% from 31 to 12 reproductive units/10 branches/tree.

There was no significant difference in mean reproductive counts of FYR (combined flowers plus young fruits and ripe fruits) between treated and untreated trees in the low initial gall damage class (CI -38.9, 498.9, $W=131.0$, $P=0.0535$, Mann-Whitney U), or the high initial gall damage class (CI -99.1, 87.9, $W=108.0$, $P=0.8429$, Mann-Whitney U) when all sample times were combined. There was also no difference in mean reproductive counts of FYR for the first month of monitoring in low initial gall damage trees (CI -4.0, 134.0), $W=130.5$, $P=0.0577$, Mann-Whitney U) or the last month of monitoring (CI -0.00, 33.99, $W=122.0$, $P=0.1720$, Mann-Whitney U). There was also no difference in mean reproductive counts of FYR for the first and last months of monitoring in high initial gall damage trees (CI -21.0, 33.0, $W=112.0$, $P=0.5996$ and CI 0.000, 0.000, $W=99.0$, $P=0.5036$, Mann-Whitney U). Within classes, mean combined reproduction per tree declined, with the greatest declines in young fruits.
Seedling Study

Seedling gall damage and foliage dieback over time

At KH, I monitored 103 seedlings for 13 months (Table 7). Almost all seedlings were damage-free at the initial reading and by the final month of monitoring, 92% of seedlings had displayed some level of gall damage. At PW, I monitored 127 seedlings for seven months (Table 7). At PW most seedlings began with some gall damage and 88% of live seedlings had some level of gall damage by the last reading. At both KH and PW few seedlings displayed foliage dieback at the initial reading and roughly 10% showed no foliage dieback by the last reading.

Damage effect on seedling survival

I predicted that seedlings with high levels of thrips damage would display lower survivorship compared to seedlings with low levels of damage. Contrary to my hypothesis, seedling death was not strongly related to thrips gall damage.

At KH, 35% of seedlings survived until the last reading at 13 months (Table 7). Of the seedlings that died, I observed almost half sustained zero gall damage and 37% showed high gall damage in the month prior to death. At KH, seedlings <10 cm in height with zero to low gall damage were more likely to die than seedlings of the same height with moderate to high damage (Fig. 19, P=0.04, df=1, Fisher’s Exact Test). For seedlings >10 cm at KH, there was no difference in the likelihood of death for individuals sustaining zero-low gall damage versus moderate-high damage (P=1, df=1, Fisher’s Exact Test).

At PW, 88% of seedlings survived until the last reading at seven months (Table 7). Of the seedlings that died, more than half displayed zero gall damage and no seedlings sustained high
gall damage before dying. At PW, there was no difference in likelihood of death for seedlings <10 cm in height with zero-low gall damage versus seedlings of the same height with moderate-high damage (P=0.081, df=1, Fisher’s Exact Test). However, seedlings >10 cm with zero-low gall damage were more likely to die than seedlings with moderate-high damage (Fig. 20, P=0.002, df=1, Fisher’s Exact Test).
Discussion

Relating Reproduction to Thrips Gall Damage & Foliage Dieback

In this study, I found support for my overarching hypothesis that introduced *Klambothrips* negatively impact naio tree reproduction through two out of three levels of inquiry. Generalized linear mixed modeling provided compelling support for a negative impact, indicating that branch death (resulting from high gall damage) was the strongest explanatory variable for reproductive patterns at Kona Hema (KH), while branch death plus tree foliage dieback and branch foliage dieback were the strongest explanatory variables for reproductive patterns at Pu‘uwa‘awa‘a (PW). I found further evidence that thrips damage has a negative impact on naio reproduction using correlations between gall damage level and reproductive output. At KH and PW, reproductive declines occurred as predicted, with trees in moderate and high initial gall damage classes displaying significant negative trends. Still, the correlation I observed between increasing gall damage and declining reproductive output supports but does not confirm a direct connection between galling and naio reproduction. An experimental component would have solidified the connection between thrips and naio reproduction. However, in my third experimental level of inquiry, untreated trees did not differ in mean combined reproduction from treated trees. Thus, I found strong support for H1A and H1B, but weak support H2A. My findings were inconclusive for H2B and there was no support for H3.

At both KH and PW, reproduction levels in each of the four initial gall damage classes started at noticeably different points. Still, at KH, higher gall damage correlated with higher foliage dieback and larger declines in reproduction after twelve months as I expected. At KH, it was promising that there was no significant change in reproduction levels for the zero initial gall
damage class, despite about 10% of branches observed with a high level of foliage dieback in the last three months of monitoring. Reproduction in the low initial gall damage class, which was the highest among all classes in month one, also showed no significant change over twelve months. There was zero foliage dieback among all low initial gall damage class branches in the first month of monitoring, but from month nine to month twelve about 50% of those branches had high foliage dieback. Thus, with more time, it is likely that reproduction in the low initial gall damage class will decline significantly. Reproduction declined significantly in the moderate and high initial gall damage classes at KH, which generally correlated with a high incidence of tree and branch foliage dieback. Interestingly, I observed that tree foliage dieback levels in both the moderate and high initial gall damage classes were lower in the last two to three months of monitoring due to flushes of new growth. The occurrence of this new growth did not appear to influence reproduction during the course of this study. Both the moderate and high initial gall damage classes started with reproductive levels greater than the zero initial gall damage class, which at month one had the lowest reproductive output. Tree size seemed to be a factor in initial reproduction level differences at KH and should be studied. By the last reading, reproduction in both of the moderate and high initial gall damage classes had declined to levels lower than the zero initial gall damage class across all reproductive types except raisins.

At PW, higher gall damage was inconsistently correlated with high foliage dieback and large declines in reproduction. Reproduction was about three times greater for zero and low initial gall damage trees than for moderate and high initial gall damage trees in month one. By month twelve, reproductive levels for zero and low initial gall damage classes had fallen by 67% and 73%, respectively. The decline I observed in the zero and low initial gall damage classes is surprising because trees in both of those classes also sustained low levels of gall damage and
foliage dieback over time. Branch and tree level foliage dieback patterns in the moderate initial gall damage class at PW were unexpected. While tree foliage dieback changed little over time, branch foliage dieback increased, and still mean combined reproduction showed no significant change. Reproduction and foliage dieback levels in the high initial gall damage class displayed changes as I expected. Mean combined reproduction declined by 95% in the high initial gall damage class and was lowest among all other initial gall damage classes by month twelve. Overall, damage levels and reproduction declines were greater at PW than at KH.

Although statistical modeling provided strong support for the negative impact of thrips gall damage on naio reproduction, I identified an unexpected relationship at KH. Generalized linear mixed modeling for KH found that tree gall damage was positively related to the presence of flowers, young fruits and ripe fruits. This positive relationship between damage and the occurrence of reproduction was maintained for low (<33%), moderate (33%-66%) and high (>66%) levels of thrips damage. While herbivory is generally thought to have a negative impact on plants, there is a sizeable amount of evidence that some plants can respond positively to damage by compensating through growth or reproduction (Dangerfield & Modukanele 1996; Fang et al. 2006). Woody plants, in particular, have been found to compensate for tissue lost to herbivory by increasing growth (summarized in Hawkes & Sullivan 2001), but few studies have documented a compensatory reproductive response (but see Kaitaniemi et al. 1999; Sacchi & Connor 1999; Fang et al. 2006). Furthermore, there is strong evidence suggesting that woody plants sustaining high levels of herbivory (i.e., 50% or greater) show obvious reproductive declines (Obeso 1993; Kaitaniemi et al. 1999). In the current study, correlation data indicated significant reproductive declines for all of naio flowers, young fruits, and ripe fruits over time for trees in the moderate and high initial gall damage classes. Therefore, it seems unlikely that
reproductive compensation would be occurring. It is possible that the positive relationship between reproduction and gall damage found at KH was due to reproductive units that were present at the initiation of the study, particularly young and ripe fruits, that have a long retention time and therefore may also display a delayed response pattern to thrips damage. If data were collected today, with the thrips infestation having established, I would expect that generalized linear mixed models would reveal a negative relationship similar to what was observed at PW.

Another possible explanation for the positive relationship yielded by modeling, is that favorable rainfall in the year prior to my study could have promoted both naio reproduction and thrips damage. Previous studies have found strong lag patterns between wet season rains and flower and fruit production. Annual rainfall at KH is 1000-2000 mm, between dry and mesic rainfall amounts. A 26-month long study of flowering and fruiting in a dry forest system in Jamaica (receiving 600-900 mm of annual rainfall) found that tree phenology was strongly linked to rainfall and lagged behind the rainy season by as much as three to seven months (McLaren & McDonald 2005). In another study, researchers examining mesic savanna (receiving about 1600 mm of annual rainfall) in Australia over 30 months found that flower bud build-up for several tree species lagged behind the start of the rainy season by six to ten months (Williams et al. 1999). These previous studies suggest that rainfall that occurred before my study began could still have had an impact on reproductive patterns during the year of my data collection. If rainfall stimulated naio reproduction at KH, it likely also invigorated naio tree foliage. In a study of insect herbivory on oak species along an elevational gradient in California, researchers found that insect activity of specialists, like gall-makers, was both positively related to increased precipitation and particularly sensitive to changes in precipitation (Leckey et al. 2014). If the effect of favorable rainfall before the year of my study was increased reproduction levels and
higher quality leaves, the explanation of rainfall is plausible for explaining the positive relationship between reproduction and thrips damage. Still, evidence of longer-term growth and precipitation trends would help to better understand the possible impact of delayed responses.

**Gall Damage and Foliage Dieback at Observational Sites**

More patterns surfaced from gall damage and foliage dieback levels than the expected increase in severity over time. First, at PW, most trees and branches in the zero and low initial gall damage and foliage dieback classes maintained low gall damage and foliage dieback throughout the study. Second, at both KH and PW, trees in the high initial gall damage class were assessed at lower gall damage and foliage dieback levels over time. And third, at both sites, trees with moderate and high gall damage and foliage dieback possessed individual branches that displayed zero and low damage and dieback levels through the study period.

At PW, the occurrence of trees which maintained low gall damage and foliage dieback levels over time suggests that naio trees somehow escaped detection or, “avoided” thrips. In the current study, there were no substantial barriers to thrips movement between naio trees, low-damage trees were interspersed within the larger forest matrix, and thrips were well-established at PW. These conditions make it highly unlikely that thrips failed to locate trees that seemingly avoided attack. During data collection tiny pit marks were observed on leaves of all naio with zero-low damage (noted on datasheets as “probing”) indicating that thrips had indeed found and even sampled plants. This finding is what one would expect to see as an insect differentiates among its suitable host plants. An insect will test plant tissues searching for nutritional composition according to its needs (Schowalter 2011). Because most insects must balance between searching and host suitability, they may avoid feeding if the plant is less nutritious or
requires too much work to feed on, especially if other suitable hosts can be found nearby (Schowalter 2011). It is possible that thrips may have preferred feeding on some naio individuals versus others for nutritional reasons. Studies comparing nutrient availability in naio leaves and nutrient requirements of introduced *Klambothrips* would be needed to lend support to this hypothesis.

Other mechanisms helping naio plants to avoid thrips attack could be physical or chemical defense. Leaf toughness (caused by high lignin) was not considered in this study, but is known to deter insects from feeding or ovipositing because it increases time and energy spent to obtain the desired plant resource (Gatehouse 2002). Also, it has been observed that naio foliage, especially in dry habitats, sometimes possess fine hairs (C. King, *personal communication*). Presence of leaf hairs can be a strong physical barrier to insect feeding or ovipositing (Schillinger & Gallun 1968; Levin 1973). However, in my casual observations of low-damage naio at PW I found that trees lacked leaf hairs, which lessens the weight of hair presence as a defense mechanism for those trees. Chemical defense is another way that naio trees at PW may have sustained low gall damage and foliage dieback levels. Many plants of the genus *Eremophila*, closely related to *Myoporum*, produce resins, so it is possible that naio exhibit this trait too (Dell 1975). There is some evidence that alkaloids, a chemical group generally known to have insect-deterring effects (Levinson 1976), may be an important factor influencing thrips attack in naio. Previous studies have found alkaloids in *Myoporum* species in Australia (Aplin & Cannon 1971), and specifically in *Myoporum sandwicense* (Swanholm et al. 1959). Furthermore, other studies have found that alkaloids can strongly reduce survival of insect herbivores (Davidson 1929; Macel et al. 2005; Cheng et al. 2011), suggesting that naio resistance of thrips attack via chemical means is a reasonable hypothesis. Long-term monitoring, experimentation
and further investigations will be needed to identify the mechanisms facilitating sustained low-damage on some naio trees at PW, and if and how alkaloids or other phytochemicals produced by naio impact *Klambothrips* preference.

Over the monitoring year, I observed that naio trees and branches in the high initial gall damage class at KH and PW displayed lower levels of gall damage and foliage dieback. At both sites, I recorded individual branches with zero and low gall damage and dieback status. Trees that I had rated as high gall damage and foliage dieback were rated as moderate gall damage and foliage dieback in the last few months of monitoring. Similar patterns in data were observed by King et al. (2012), who found a declining trend in gall damage levels particularly at the study site of earliest thrips detection. In this study and the study by King and others lower ratings were caused by resprouted foliage that occurred after thrips attack (Figs. 21-22). Because foliage damage and dieback levels were assessed for the newest leaf growth, resprouted leaves lowered recorded damage levels giving the impression that damage levels were improving (Fig. 23).

Resprouting is a well-documented response seen in woody plants as a reaction to disturbance of many forms, including fire, herbivory, frost or other injury (Belsky et al. 1993). A plant’s dormant meristematic tissue can be activated to compensate for injury, and stimulated regrowth may result in a net gain in biomass for the affected plant. In a study of simulated herbivory, researchers examined the growth response of an arid-growing fabaceous shrub (*Caragana korshinskii*) in China to above-ground shoot removal (Fang et al. 2006). They found that *C. korshinskii* biomass was greater than in control plants when 30% of the main shoot length was removed and when 25% or 50% of the main shoot number were removed. Although the study of this particular shrub species demonstrates the capacity for woody plants to compensate for damage, the study findings only apply to the single “herbivory” event. Other researchers have
contended that activation of the plant’s dormant meristematic buds uses carbohydrate reserves such that the plant’s ability to respond to future attack episodes is lowered, especially if attacks are recurring (Belsky et al. 1993). This hypothesis is illustrated in an eight-year study of mountain birch (*Betula pubescens* ssp. *czerepanovii*) in Sweden, where researchers observed a three-fold increase in long shoots of defoliated versus non-defoliated trees in the first year (Karlsson & Weih 2003). After that first year of vigorous growth response to herbivory, leaf area of defoliated mountain birch trees declined in the following years. Similar to previous research on woody plant growth in response to herbivory, naio trees in the current study exhibited some ability to tolerate foliage damage from thrips by resprouting. Based on field observations of naio tree mortality since the thrips infestation began, it seems that stimulated regrowth may prolong tree life, but not ultimately guarantee survival.

**Reproduction at Observational Sites**

While reproductive decline at KH seemed to correspond to increased damage levels, reproductive decrease at PW was puzzling. At PW, trees with high gall damage showed significant decline in reproduction, as expected. However, trees with sustained low gall damage levels surprisingly also displayed a large decline in reproductive output. The significant decline in reproduction observed in trees with very little thrips gall damage alludes to some other strong influence on naio at PW. As year-long observations at this site do not point to any externally obvious effect, I hypothesize that environmental stress may have caused reduced reproduction.

Combined reproductive decline displayed by trees in the zero and low initial gall damage classes at PW was greater than decline seen for the same classes of trees at KH, and despite the fact that damage to KH trees increased over time. Yet generalized linear mixed modeling did not
reveal an environmental factor important in explaining variability in reproduction. Considering factors included for my study, water stress is a strong candidate for influencing reproductive declines seen at PW. Plants that are water stressed may allocate fewer resources to reproduction. In a study of a tropical dry forest tree, *Tabebuia neochrysantha*, researchers compared soil moisture between the tree’s dry and wet habitats (Reich & Borchert1982). They found a strong negative correlation between the rate of leaf fall of this deciduous tree and both soil moisture in early drought conditions, and tree water stress (indicated by reduction in trunk circumference). Using rainfall data and irrigation experiments, the authors found that *Tabebuia* trees would only flower after adequate rainfall or irrigation had occurred. In the current study, precipitation records from PW (presented as average accumulated precipitation (mm/day)) indicate that there were three occasions during the year of monitoring where average accumulated precipitation was less than 0.5 mm per day for two consecutive months (Fig. 24). In that light, naio trees may have endured compounding water stress, which in turn limited resource allocation to reproduction. However, multi-year precipitation data for PW and measurements of soil moisture, and plant water potential would be needed to strengthen this hypothesis.

Damage is another possible explanation for the decline in reproduction observed at PW. Damage caused by insects other than thrips could have an important influence on reproduction. However, data collected on other insect damage showed that average damage levels per ten branches per tree were <5%, providing weak support for a major influence from other insects. This study did not examine potential below-ground influences on reproduction such as root-feeding insects, but they could also negatively influence naio health and therefore naio reproduction. In a meta-analysis examining effects of root-feeding insects in 85 experimental studies, researchers found that belowground herbivory led to reductions in root biomass,
aboveground plant growth, photosynthesis and reproduction (Zrereva & Kozlov 2012). While the meta-analysis was not limited to woody species, it does demonstrate the great potential for root-feeding to negatively impact plant health and fitness. There are many variables to consider in gaining a better understanding of naio reproductive patterns. The variables discussed here illustrate the complexity of this system and the challenge in teasing out the exact strength of impact that thrips have on naio reproduction. It is likely that there are multiple influences contributing to the strong decline in naio reproduction observed at PW.

Evaluating Naio Response to Pesticide Treatment

At Keauhou Ranch, reproduction declined in a similar manner across low and high initial gall damage trees despite differences in starting reproduction levels. Whether trees were treated or untreated, or in low or high initial gall damage classes, reproduction declined to roughly half of the initial reading levels. Tree gall damage patterns, foliage dieback patterns, and branch death were similar between treated and untreated trees in both low and high initial gall damage classes. I observed a steady increase of galling of branches in treated trees, which can be interpreted as fresh galling over the course of the experiment in spite of treatment. There was no significant relationship between experimental exclusion of thrips and naio reproduction, nor was there a significant difference in reproduction between pesticide-treated and untreated trees. Assuming that treatment was effective, I offer several explanations for these findings.

One potential explanation for no significant difference in reproduction between treated and untreated naio trees is that the data were too variable to statistically detect a difference. The data were highly variable, especially for reproduction within and among trees. High variability was a characteristic of data at all of my study sites, so it would not be surprising if that character
was responsible for lack of significant statistical findings. An alternative hypothesis is that the impact of chemical exclusion of thrips was negligible for trees in the low initial gall damage class, yet not strong enough to stimulate growth and reproduction for trees in the high initial gall damage class. Inclusion of trees at the zero and moderate initial gall damage levels might help to determine if there is a threshold of damage, whereby chemical treatment is least effective if damage is low and not effective enough if damage is too high. Identifying such a threshold might help future managers or researchers to focus chemical treatment on trees that are more likely to show improvement.

Considering logistical factors can also provide alternate explanations for no significant findings in the experimental component of this project. Naio is a continuously flowering tree and its fruits generally remain attached through successive seasons, therefore a longer time period of herbivore exclusion using pesticides could improve the chance of detecting differences in treated and untreated trees. Previous studies using chemical exclusion to elucidate reproductive impact of an insect have taken multiple years. In one study, researchers applied a chemical pesticide to branches of the shrub *Colliguaja integrerrima* (Euphorbiaceae) for two years before detecting a response in reproduction (Gonzalez et al. 2005). In another study, researchers devoted ten years of chemical exclusion before determining that chronic herbivory reduced seed yields in the shrub *Sarothamnus scoparius* (Fabaceae) by 75% (Waloff & Richards 1977). Because naio is a woody plant, it is reasonable to suppose that reproductive response to chemical exclusion, as seen in the previous examples, takes longer than six months. In the future, effectiveness of chemical treatment can be checked by comparing samples of thrips' populations on treated and untreated trees. Also, a larger sample size could increase the statistical power to detect change.
Impact of Gall Damage on Natural Seedlings

For seedlings, this study found no effect of thrips gall damage on the likelihood of death. At KH, seedlings less than 10 cm in height were generally less likely to survive despite thrips gall damage, while seedlings greater than 10 cm were equally likely to survive with or without thrips damage. At PW, seedlings were likely to survive regardless of height or gall damage level. Thus, there did not appear to be a strong relationship between galling and naio seedling survival based on this study.

At KH, small seedlings (<10 cm) had a low likelihood of survival despite low thrips gall damage. There are several potential explanations for this finding. Thrips gall damage (even low damage) might weaken small seedlings. Very young, small seedlings are highly vulnerable and it is possible that even small amounts of gall damage could lower a seedling’s chance of survival by exposing leaf tissue to pathogens or other herbivores. Another explanation for low survival likelihood is that seedlings are dying from pathogen attack. Previous seedling studies in the tropics have found that seedlings have higher pathogen avoidance if located farther from parent plants and thus tend to exhibit greater survivorship and growth (Augspurger 1983; Augspurger & Kelly 1984). In one of those studies, most seedlings of the tree Platypodium elegans were located close to the parent plant and were attacked by and succumbed to fungal pathogens within the first three months after germination (Augspurger 1983). In a follow-up study of the same tree species, researchers experimentally manipulated seedlings and found that greater dispersal distance from parent plants and lower density of seedlings were significant factors in higher seedling survivorship (Augspurger & Kelly 1984). Thus, pathogen-induced mortality for seedlings <10 cm may reasonably explain low seedling survival at KH. Most seedlings observed at KH were located directly under the canopy of parent trees and tended to be clustered, and my
study did not control for seedling density and proximity to parent plants. Therefore, future studies could better elucidate the impact of density and proximity on seedling survival by mapping and monitoring individual seedlings. These potential influences on natural naio seedlings require further study to determine what limits survival of small seedlings and would be very useful for understanding the future of naio populations.

High likelihood of survival in >10 cm seedlings at KH and all seedlings at PW regardless of thrips gall damage suggests that thrips were not a serious limiting factor over the course of study for natural naio seedlings at these sites. This finding is surprising considering that planted, greenhouse-raised naio seedlings have been reported to sustain high levels of thrips gall damage and consequently high mortality rates (S. McDaniel, L. Dement, personal communication). An obvious difference between greenhouse-raised plants and natural seedlings is that greenhouse plants are fertilized. Considering that insects respond to nutrient levels of their hosts (Schowalter 2011), *Klambothrips* may have been strongly attracted to the nutritious content of planted seedlings. Perhaps natural naio seedlings have certain chemical protections that enable them to effectively deter thrips after they reach a certain size. Earlier in the discussion, it was stated that alkaloids, chemical compounds known to be toxic to thrips have been detected in *Myoporum sandwicense* (Swanholm et al. 1959). Therefore, naio seedlings might be producing such herbivore-deterring chemicals. In terms of the observational study, seedlings at PW were monitored for half a year and perhaps would have shown higher mortality if monitored for an entire year. Monitoring for multiple years and comparing data from natural and planted seedlings would help to truly determine how thrips gall damage impacts naio seedling survival.

Experiments comparing survival of damaged and undamaged seedlings would provide the clearest support for a relationship between thrips gall damage and seedling survival. A
seedling component for this project was pursued, but was unsuccessful. Over 120 naio seedlings from three locations were raised in a greenhouse setting. Each naio plant was caged with a sleeve of polyester mesh. Thrips were harvested, sorted based on sex, and were applied to plants within 48 hours of capture. Although the most active thrips were preferentially chosen for the experiment, none of the individuals applied to naio plants survived after 48 hours of application. Time and materials limited further development of this project component.

**How Does Klambothrips Leaf-Galling Compare to Similar Damage?**

Previous studies of stem, shoot and bud-galling insect damage had found a range of reproductive impact from roughly 40% to 80% decline (Sacchi et al. 1988; Sacchi & Connor 1999; Gonzalez et al. 2005). At KH, negative change in mean combined reproduction per 10 branches per tree from the first to last month of monitoring was 62% and 65% for trees in moderate and high initial gall damage classes, respectively. At PW, reproductive output of trees in the high initial gall damage class exhibited a decline of 95% over twelve months. Of the two sites, data from KH are likely closer to what might be found by an experimental study because trees at that site were captured at the beginning of thrips expansion through the area. The range of reproductive decline observed in the current study appears to be similar to findings from previous studies of gall-type damage, but experimental exclusion of thrips would better define the relationship between gall damage and naio reproduction.

Within the broad context of herbivory, naio foliage dieback caused by thrips’ feeding is similar to defoliation. Typically, defoliation is described as the result of chewing animals, such as mammals or insects, consuming plant foliage (Gurevitch et al. 2002). Yet it can be argued that functional defoliation of naio occurs because branches eventually die from leaf tissue necrosis.
that is brought about by thrips’ galling. Within one year, moderate and high initial gall damage trees at KH declined from 10 to 5.3 and 6.6 mean number of surviving branches per tree, respectively. In other words, live branches declined by 47% and 34% from the first to last months of monitoring. Naio branch mortality can result in long-term loss of reproduction that is functionally similar to effects observed in sustained defoliation events. A study of successional impacts of hemlock woolly adelgid across the eastern United States examined multi-decadal forest plot data from 22 states and found that hemlock seedling density declined and hemlock tree mortality increased as years of adelgid infestation increased (Morin & Liebhold 2015). In contrast, defoliation events that last for shorter time periods, such as a year, can severely reduce reproduction without causing long-term reproductive loss. In Panama, for example, noctuid moths (*Eulepidotis* spp.) caused a year-long defoliation of a locally common tropical forest tree, *Quararibea asterolepis* (Wong et al. 1990). Comparison of heavily (80-100%) and lightly (0-30%) defoliated trees revealed a nearly 100% reproductive decline in heavily defoliated trees, but declines lasted only for the year of the event. In the short-term of this study *Klambothrips* did not cause utter defoliation of naio. However, previous research findings that gall damage tends to increase over multiple years suggest that thrips feeding is likely to continue (King et al. 2012). If, as seen in my study, branch mortality also increases, then I suspect longer-term effects of defoliation, such as reproductive cessation and tree mortality, will occur.

**Impacts of Introduced Insects on Islands**

Because islands have high endemism levels and relatively small plant populations, invasive insect herbivores are especially problematic. Many plant groups in these systems have evolved in isolation long enough for chemical or physical protections to diminish or be lost. Such
changes yield unique species, but also leave island plants more vulnerable to introduced insect herbivores. For example, on St. Helena Island an endemic tree of the sunflower family, *Commidendrum robustum*, nearly went extinct due to attack by an introduced scale insect (*Orthezia insignis*) (Fowler 2003). In the Galápagos Islands, another invasive scale, *Iceria purchasi*, threatened survival of endangered plants (Kenis et al. 2009). Plants native to the Hawaiian Islands have been bombarded with invasive insects as well. Currently, some of the rarest endemic Hawaiian trees are being targeted by the introduced black twig borer (*Xylosandrus compactus*), and preventive measures for protecting trees have not been effective (Wagner et al. 1990). In the last decade, an introduced gall wasp (*Quadratichus erythrinae*) caused defoliation and almost irreversible decline of the culturally and biologically important native wiliwili tree (*Erythrina sandwicensis*) (Gramling 2005). In the St. Helena, Galápagos Islands and Hawaiian wiliwili tree cases, loss of the native species was curbed because biocontrols were identified and used. Although those stories are cited as successes, the already small native plant populations were reduced to an even smaller number. Thus, progeny of surviving plants will be genetically poorer. Significant loss of genetic diversity is a major impact of introduced insect herbivores, and that loss seems to be playing out in the case of naio studied in this project. The situations described here illustrate the real threat that introduced insects pose to island systems. If accidental introductions are not prevented through improved biosecurity measures, managers and researchers may have to spend more time on saving native plant genetic stock and identifying biocontrols to prevent the loss or genetic impoverishment of native species.
Potential Influence of Climate Change

Global climate change will likely mediate long-term Hawaiian *Myoporum* reproductive patterns but the direction of that influence is unclear. Studies of plant reproductive response to climate change report conflicting results. A meta-analysis of 79 domesticated and undomesticated plants found that reproduction was generally enhanced by increased temperature and carbon dioxide (Jablonski et al. 2002). Similarly, an 18-year study of reproduction in a wet old growth forest of Panama reported that reproduction for 48 tree species increased significantly with El Niño events that brought higher temperatures and lower rainfall (Wright & Calderón 2006). In contrast, others have noted increased mortality, especially during El Niño drought events. For example, in a comparison of tree mortality in a tropical wet forest of Sarawak before and during the 1997-1998 El Niño, researchers found more than a 4-fold increase in tree deaths in a 1.38 ha plot (Nakagawa et al. 2000). These studies illustrate the variety of plant reproductive responses connected to climate change, and therefore the challenge in predicting how naio reproduction might be affected. Still, it seems most likely that water stress will be a strong influence on naio reproduction. Increase in the frequency of El Niño/Southern Oscillation events are forecasted to cause more frequent winter droughts (Chu 1989), and will likely exacerbate existing stressors for naio located in dry areas such as PW and thus lead to lower reproduction.

Global warming and climate change may also affect Hawaiian *Myoporum* reproduction by impacting the interaction between naio trees and introduced thrips. A study comparing leaf fossils from before, during and after the Paleocene-Eocene Thermal Maximum (55.8 Ma) found that the frequency of insect herbivory increased by ~20% or more, when atmospheric carbon dioxide levels spiked (Currano et al. 2008). The same study found that diversity of insect herbivores also increased. These findings suggest that as human-driven global temperature rises,
and greenhouse gas concentrations, particularly carbon dioxide, elevate to levels comparable to those of the Paleocene-Eocene Thermal Maximum, *Klambothrips* gall damage to naio could increase in virulence and also be compounded by damage from other herbivorous insects. The consequence of such damage could be lowered reproduction or, if naio responds positively to warming, an offsetting effect where increased naio reproduction is countered by increasing damage from *Klambothrips* and other insects.

**Concluding Thoughts & Recommendations**

Results of this study indicate that *Klambothrips* gall damage increases over time, while naio reproduction decreases over time, and suggest that these introduced thrips have an important influence on naio reproduction. Large reproductive declines in naio can be expected where thrips gall damage is greater than 33%. Over one year at KH, reproduction was reduced, though not significantly, for trees in the zero and low initial gall damage classes. However, the increasing trend of gall damage and foliage dieback in those trees portends an eventual detectable reproductive decline. At PW, trees that sustained low gall damage and foliage dieback over the entire monitoring period gave hope that naio have some ability to resist thrips attack. Yet the marked decline in reproduction in those trees despite low damage is highly concerning and requires further study. The outcome of increased branch death over time at all sites will likely be drastic loss of reproduction and recruitment potential for naio trees.

Without some management action taken to protect naio on Hawai‘i Island, it is highly possible that naio will be severely depleted from its existing dry forest range. While there are many possible actions, I propose three, possibly most effective, actions for large-scale naio preservation: preserve naio habitat, create a naio seed bank and invest time and resources needed
to identify a suitable biocontrol for thrips. Dry forests constitute the largest areas of naio habitat, but have mostly been lost or degraded due to human and ungulate activity. Ungulate browsing and damage was obvious and common for naio trees and seedlings at Pu‘uwa‘awa‘a, where naio habitat was unfenced. Protected habitat (i.e., habitat absent of ungulates) will ensure the greatest level of genetic diversity in naio populations, which in turn will increase the probability of identifying resistant individuals. If fencing a population is impractical, then individual trees should, at least, be protected. In the event that naio reproduction continues to decline, seed collection and long-term storage will be imperative to maintaining genetic diversity of naio trees if restoration is one day possible. There are several groups currently storing naio seeds that could collaborate to develop and share protocols for long-term storage so that the highest percentage of viable seeds can be preserved. The widespread distribution of thrips populations and virulence of their herbivory are reminiscent of the better-known case of Erythrina gall wasp and its attack of endangered wiliwili (Erythrina sandwicensis) trees. In that situation, biocontrol was the foremost recommendation to prevent the loss of wiliwili (Gramling 2005) and the same recommendation is applicable for naio. To date, the search for a suitable biocontrol species for thrips has been hindered because the species is newly identified, thrips are extremely small and very hard-bodied, and the shelters created by their leaf-galling provide a substantial barrier to any predatory organism (T. Johnson, personal communication). While there is no certainty that a biocontrol agent exists, efforts should continue in case a biocontrol species can be found.

There are several avenues of research to pursue given the findings of this project. These broadly include exploring Myoporum population genetic diversity, genetic resistance, and potential reproductive limitations (e.g., successful pollination, nutrient deficiency). No genetic studies for Myoporum have been published to-date. Known species descriptions, respective
locations and characteristics (e.g., Webster 1951, Wagner et al. 1990, Chinnock 2007, Imada 2012) could be used as a stepping stone from which to explore genetic differences among populations. Better understanding of the abundance and incidence of naio populations (e.g., coastal variety versus dry and wet forest varieties) can guide targeted efforts to preserve genetic materials from those populations. Genetic resistance or resilience must be examined as trees that remain undamaged by thrips or sustain very low damage could be the best source of natural naio recruitment. To some extent, resilience may have been identified in this study. However, the story is still incomplete. Experiments can determine if seedlings from resilient trees have greater viability than seedlings from gall damaged trees, or if they are more resilient to thrips gall damage than seedlings from damaged trees. Pollination studies would be useful to determine if fertilization is occurring successfully and to verify the quality of naio seeds within fruits. Examination of nutrient uptake and allocation would help to determine if and how naio trees are nutrient limited. If naio are found to be nutrient limited, then experiments could be done to see if fertilization stimulates reproduction.

Dry forests have undergone dramatic changes in vegetation composition and structure and are considered to be one of the most highly threatened biological systems in the world (Janzen 1986; Murphy & Lugo 1986). In Hawaiian dry forests, where naio are most abundant, intensive grazing by introduced ungulates has degraded these systems and changed plant composition (Cuddihy & Stone 1990; Cabin et al. 2000). Dry forests that once covered more than 100,000 ha of land (Cuddihy & Stone 1990) have been reduced by at least 90% (Bruegmann 1996). The largest expanse of this forest type is located on Hawai‘i Island. One of the canopy dominant species, sandalwood, was logged in the late 1800s for export to East Asia. On Mauna Kea, naio and māmane are now the most abundant canopy species in the dry forest and together
provide food for the endangered palila (*Loxioides bailleui*) forest birds (Banko et al. 2010). If naio decline drastically, palila may lose an important food and shelter option. Endemic Hawaiian yellow-faced bees would also be seriously impacted by naio declines. Yellow-faced bees are known to feed on naio pollen have been declining throughout the Islands, and specifically within the Pu‘uwa‘awa‘a dry forest on Hualalai for decades (Magnacca & King 2013; K. Magnacca, personal communication). Despite these negative possibilities, through my study, I found that there is some hope for dry forests because of the presence of apparently resilient reproductive individuals. Naio are highly variable in both their habitat and morphology, so it possible that that variability along with their genetic variation may provide a key to their long-term survival.

Within mesic forests naio is not considered a dominant canopy tree although it is common and provides important food and habitat resources for native animals. The effects of naio decline within this system may be subtler. Similar to dry forests, mesic forests have a history of degradation in the Hawaiian Islands through intensive cattle ranching (Cuddihy & Stone 1990). Large tracts of mesic forest were cleared for ranch activity in the early 1900s and today are dominated by introduced pasture grasses (Cuddihy & Stone 1990; McDaniel et al. 2011). Naio grow naturally as an understory tree scattered through forest remnants in those pasture areas (personal observation). With its former predator, the Kona grosbeak, extinct, naio may be a potential food source for the Hawaiian crow, which is extinct in the wild but planned for release in 2017. There are various other native animals such as native insects that may be negatively impacted by naio decline, especially host-specific leafminers, leafhoppers and longhorned beetles. Still, there is hope in these mesic forests because naio are more widely spaced and than in dry forests. In mesic forests, the distance between existing plants may prevent *Klambothrips* from finding all potential naio hosts. In that way, naio might escape infestation.
As introduced *Klambothrips* continue to spread throughout Hawai‘i Island, the impact of these insects on *Myoporum sandwicense* population size will likely be severe, especially in dry forests where this plant is most abundant. Still, my research has found that resistant or resilient individuals may exist, and further investigations should tease apart the mechanism for that finding. Another logical next step would involve studying *Klambothrips* impact on naio growing in wetter habitats as the thrips might have a lesser impact where water availability is greater. This study has reported on examinations of this system at the levels of gall damage, foliage dieback and the impact of both gall damage and foliage dieback on reproduction. I hope that managers and researchers can now move forward with a better understanding of thrips’ impacts on naio populations. It is likely that gall damage and foliage dieback will show an increasing trend wherever thrips become established. In response, naio reproduction will decline, and cease when entire trees die. Action should be taken to identify resilient individuals on the landscape and to reduce biotic and abiotic stressors for those trees where possible. Broader landscape study of naio recruitment is needed as thrips gall damage may be of lesser importance for seedling survival than factors such as dispersal, pathogens or predators. My final hope is that the impact of introduced thrips on naio reproduction I have found through this study provides motivation to prevent the spread of thrips to other Hawaiian Islands as well as to find practical solutions to slow decline of naio as an important native tree.
Tables and Figures

Tables

Table 1. Site characteristics for two observational sites (KH and PW) and one experimental site (KR).

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<th></th>
<th>Kona Hema (KH)</th>
<th>Pu’uwa’awa’a (PW)</th>
<th>Keauhou Ranch (KR)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start of infestation</td>
<td>2012</td>
<td>2010</td>
<td>2012</td>
</tr>
<tr>
<td>Substrate</td>
<td>Stony muck</td>
<td>Worn ‘a’ā/pāhoehoe</td>
<td>Worn ‘a’ā/pāhoehoe</td>
</tr>
<tr>
<td>Substrate origin</td>
<td>Mauna Loa</td>
<td>Hualālai</td>
<td>Mauna Loa</td>
</tr>
<tr>
<td>Substrate age (years)</td>
<td>1500-3000</td>
<td>1500-3000</td>
<td>1500-3000</td>
</tr>
<tr>
<td>Site elevation (m)</td>
<td>1600-1700</td>
<td>1500-1600</td>
<td>1500-1600</td>
</tr>
<tr>
<td>Annual rainfall (mm)</td>
<td>1000-2000</td>
<td>500-750</td>
<td>2500</td>
</tr>
<tr>
<td>Fenced</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Experimental</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Table 2. Transition matrix for gall damage level of trees at Kona Hema. Values indicate ratio of a tree changing from its initial gall damage level (zero, low, moderate, or high) to another gall damage level (zero, low, moderate or high) over the course of one year. Values were calculated using the formula $F_f/F_i$, where $F_i$ was the frequency of individuals in the initial state (i.e., gall damage level) and $F_f$ was the frequency of individuals in the final state. Damage assessment could move in both directions (get better or worse), but once a tree had some damage, it did not return to zero damage.

<table>
<thead>
<tr>
<th></th>
<th>Zero</th>
<th>Low</th>
<th>Moderate</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zero</td>
<td>0.0</td>
<td>0.8</td>
<td>0.2</td>
<td>0.0</td>
</tr>
<tr>
<td>Low</td>
<td>--</td>
<td>0.2</td>
<td>0.5</td>
<td>0.3</td>
</tr>
<tr>
<td>Moderate</td>
<td>--</td>
<td>0.0</td>
<td>0.1</td>
<td>0.9</td>
</tr>
<tr>
<td>High</td>
<td>--</td>
<td>0.0</td>
<td>0.2</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Table 3. Transition matrix for gall damage level of trees at Pu’uwa’awa’a. Values indicate ratio of a tree changing from one gall damage level (zero/low, moderate or high) to another gall damage level (zero/low, moderate or high) over the course of one year. Values were calculated using the formula $F_f/F_i$, where $F_i$ was the frequency of individuals in the initial state (i.e., gall damage level) and $F_f$ was the frequency of individuals in the final state. Damage assessment could move in both directions (get better or worse), but once a tree had some damage, it did not return to zero damage. Trees in classes zero and low were found to have no significant difference in damage level and were therefore combined into one class.

<table>
<thead>
<tr>
<th></th>
<th>Zero</th>
<th>Low</th>
<th>Moderate</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zero/Low</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Moderate</td>
<td>--</td>
<td>0.2</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>High</td>
<td>--</td>
<td>0.0</td>
<td>0.6</td>
<td>0.4</td>
</tr>
</tbody>
</table>
Table 4. Independent variable estimates, standard error and P-values for generalized linear mixed models of the response variable flowers/young fruits/ripe fruits for presence and quantity with the lowest AICc values for Kona Hema. Tree gall damage is the damage level assessed for an entire tree. Humidity and temperature parameters were monthly averages. Significance indicated with * at P < 0.05, ** at P < 0.01, and *** at P < 0.001.

<table>
<thead>
<tr>
<th>Presence/Absence</th>
<th>Quantity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
</tr>
<tr>
<td>Tree gall damage-low</td>
<td>3.799</td>
</tr>
<tr>
<td>Tree gall damage-moderate</td>
<td>3.850</td>
</tr>
<tr>
<td>Tree gall damage-high</td>
<td>3.491</td>
</tr>
<tr>
<td>Branch dead</td>
<td>-6.538</td>
</tr>
<tr>
<td>Basal area</td>
<td>1.326</td>
</tr>
<tr>
<td>Minimum relative humidity</td>
<td>1.035</td>
</tr>
<tr>
<td>Minimum temperature</td>
<td>--</td>
</tr>
</tbody>
</table>

Table 5. Independent variable estimates, standard error and P-values for generalized linear mixed models of the response variable flowers/young fruits/ripe fruits for presence and quantity with the lowest AICc values for Pu'uwaʻawaʻa. Tree dieback is the foliage dieback level for an entire tree, whereas branch dieback is the foliage dieback level of an individual branch. Significance indicated with * at P < 0.05, ** at P < 0.01, and *** at P < 0.001. No significance abbreviated as N.S.

<table>
<thead>
<tr>
<th>Presence/Absence</th>
<th>Quantity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
</tr>
<tr>
<td>Tree dieback-low</td>
<td>-0.563</td>
</tr>
<tr>
<td>Tree dieback-moderate</td>
<td>-0.731</td>
</tr>
<tr>
<td>Tree dieback-high</td>
<td>-0.761</td>
</tr>
<tr>
<td>Branch dieback-low</td>
<td>-0.564</td>
</tr>
<tr>
<td>Branch dieback-moderate</td>
<td>-0.378</td>
</tr>
<tr>
<td>Branch dieback-high</td>
<td>-0.141</td>
</tr>
<tr>
<td>Branch dead</td>
<td>-7.536</td>
</tr>
</tbody>
</table>
Table 6. Transition matrix for treated and untreated trees at Keauhou Ranch. Values indicate probability of a tree changing from one gall damage level (low or high) to another gall damage level (low, moderate, or high) over the course of seven months. Damage assessment could move in both directions (get better or worse), but once a tree had some damage, it did not return to zero damage.

<table>
<thead>
<tr>
<th>TREATED</th>
<th>( \text{Low}_t )</th>
<th>( \text{Moderate}_t )</th>
<th>( \text{High}_t )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \text{Low}_i )</td>
<td>0.9</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>( \text{High}_i )</td>
<td>0.0</td>
<td>0.4</td>
<td>0.6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>UNTREATED</th>
<th>( \text{Low}_t )</th>
<th>( \text{Moderate}_t )</th>
<th>( \text{High}_t )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \text{Low}_i )</td>
<td>0.7</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>( \text{High}_i )</td>
<td>0.0</td>
<td>0.2</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Table 7. Summary table for naio seedlings at Kona Hema and Pu‘uwa‘awa‘a. Percentage of seedlings with thrips gall damage calculated by dividing total number of seedlings showing gall damage at any point by the total number of seedlings.

<table>
<thead>
<tr>
<th></th>
<th>Kona Hema</th>
<th>Pu‘uwa‘awa‘a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monitoring period</td>
<td>13 months</td>
<td>7 months</td>
</tr>
<tr>
<td>Total seedlings</td>
<td>103</td>
<td>127</td>
</tr>
<tr>
<td>Height range</td>
<td>1.5 cm -83.0 cm</td>
<td>3.5 cm-45.0 cm</td>
</tr>
<tr>
<td>Average height</td>
<td>10.6</td>
<td>14.9</td>
</tr>
<tr>
<td>% Thrips gall damage</td>
<td>92%</td>
<td>88%</td>
</tr>
<tr>
<td>% Seedling survival</td>
<td>34% (78% @ 7 months)</td>
<td>88%</td>
</tr>
<tr>
<td>High gall damage before death</td>
<td>37%</td>
<td>0%</td>
</tr>
<tr>
<td>Zero gall damage before death</td>
<td>~50%</td>
<td>&gt;50%</td>
</tr>
</tbody>
</table>
Figure 1. Study locations on Hawai‘i Island, Hawai‘i, USA. Map shown with 500 m contours.
Figure 2. Thrips gall damage on Myoporum sandwicense branch tips. Four gall damage assessment levels for this study included: zero gall damage (a), low (<33%) gall damage (b), moderate (33-<66%) gall damage (c) and high (> 66%) gall damage (d).
Figure 3. Thrips foliage dieback on *Myoporum sandwicense* branch tips. Four foliage dieback assessment levels for this study included: zero foliage dieback (a), low (<33%) foliage dieback (b), moderate (33-<66%) foliage dieback (c) and high (> 66%) foliage dieback (d).

Figure 4. *Myoporum sandwicense* branch with (left to right) flowers, young fruits (green), ripe fruits (white) and “raisins” (brown/shriveled).
Figure 5. Change in thrips gall damage for naio trees (across top) and branches (across bottom) over time according to initial damage level at Kona Hema. Entire months with no data indicate data removed due to recording error. Within a given month, “no data” values were due to missing or broken branches. Branches that were considered dead continued to be evaluated for gall damage and were recorded as “high gall damage” when associated with thrips galling.
Figure 6. Change in foliage dieback for naio trees (across top) and branches (across bottom) over time according to initial gall damage level at Kona Hema. Entire months with no data indicate data removed due to recording error. Within a given month, “no data” values were due to missing or broken branches. Branches that were considered dead continued to be evaluated for foliage dieback and were recorded as “high foliage dieback” when associated with thrips galling.
Figure 7. Average number of dead branches per tree (+/-SE) over time (2014-2015) according to initial gall damage class at Kona Hema (a) and Pu’uwa’awa’a (b).
**Figure 8.** Change in thrips gall damage for naio trees (across top) and branches (across bottom) over time according to initial gall damage level at Pu‘u‘awa‘awa‘a. Entire months with no data indicate data removed due to recording error. Within a given month, “no data” values were due to missing, broken, or browsed branches. Branches that were considered dead continued to be evaluated for gall damage and were recorded as “high gall damage” when associated with thrips galling.
Figure 9. Change in foliage dieback for naio trees (across top) and branches (across bottom) over time according to initial gall damage level at Pu'uwa'awa'a. Entire months with “no data” indicate data removed due to recording error. All other cases of “no data” values were due to missing, broken, or browsed branches. Branches that were considered dead continued to be evaluated for foliage dieback and were recorded as “high foliage dieback” when associated with thrips galling.
Figure 10. Mean number of flower and fruit types per ten branches per month for naio trees at Kona Hema according to initial gall damage. Spearman’s correlation coefficient and P-value listed. Significance (box) taken at 0.01 after Bonferroni adjustment for multiple comparisons.
Figure 11. Mean number of flower and fruit types per ten branches per month for naio trees at Pu‘uwa‘awa‘a according to initial gall damage class. Spearman’s correlation coefficient and P-value listed. Significance (box) taken at 0.01 after Bonferroni adjustment for multiple comparisons.
Figure 12. Change in gall damage for treated (a) and untreated (b) naio trees and branches over time in the low initial gall damage class at Keauhou Ranch. Data collection was not done for month of October. Within a given month, “no data” values were due to missing or broken branches. Dashed lines indicate treatment.
Figure 13. Change in gall damage for treated (a) and untreated (b) naio trees and branches over time in the high initial gall damage class at Keauhou Ranch. Data collection was not done for month of October. Within a given month, “no data” values were due to missing or broken branches. Dashed lines indicate treatment.
Figure 14. Change in foliage dieback for treated (a) and untreated (b) naio trees and branches over time in the low initial gall damage class at Keauhou Ranch. Data collection was not done for month of October. Within a given month, “no data” values were due to missing or broken branches. Dashed lines indicate treatment.
Figure 15. Change in foliage dieback for treated (a) and untreated (b) naio trees and branches over time in the high initial gall damage class at Keauhou Ranch. Data collection was not done for month of October. Within a given month, “no data” values were due to missing or broken branches. Dashed lines indicate treatment.
**Figure 16.** Average number of dead branches per tree (+/-SE) over time (2014-2015) at Keauhou Ranch according to initial gall damage class (Low or High) and treatment (T-treated or U-untreated/control).
Figure 17. Mean reproduction per tree over time for thrips treated and control trees with low initial gall damage levels at Keauhou Ranch, September 2014-April 2015. Spearman’s correlation coefficient and P-value listed. Significance (box) taken at 0.01 after Bonferroni adjustment for multiple comparisons.
Figure 18. Mean reproduction per tree over time for thrips treated and control trees with high initial gall damage levels at Keauhou Ranch, September 2014 - April 2015. Spearman’s correlation coefficient and P-value listed. Significance (box) taken at 0.01 after Bonferroni adjustment for multiple comparisons.
Figure 19. Fisher’s exact test for seedling survival based on initial height ($H_t < 10$ cm (a) or $> 10$ cm (b) and last assessed damage class (Zero-Low or Moderate-High) at Kona Hema. Seedlings (103 total) were observed for thirteen months. P-values and degrees of freedom (df) given, and significance indicated with *.
Figure 20. Fisher’s exact test for seedling survival based on initial height ($H_t < 10$ cm (a) or $>10$ cm (b) and last assessed damage class (Zero-Low or Moderate-High) at Pu‘uwa‘awa‘a. Seedlings (127 total) were observed for seven months. For each test, there were two cells with expected values < 5. P-values and degrees of freedom (df) given, and significance indicated with *. 
Figure 21. A resprouted naio branch tip showing the dead original terminal shoot (a) and a new un-galled shoot that has emerged (b). In this case, the new shoot would be assessed for thrips gall damage and dieback, and any remaining flowers and fruits on the original stem would be counted.

Figure 22. A naio tree displaying severe foliage dieback. This resprouted tree has some of its original leaves, which have turned brown and shriveled, but most have been lost.
Figure 23. Epicormic resprouts on a thrips-galled naio tree.

Figure 24. Average daily accumulated precipitation at Pu‘uwa‘awa‘a for the months of April 2014 to March 2015.
Appendices

Appendix A1. Multivariate mixed models considered at Kona Hema (KH). Models listed include the null and three models with the lowest corrected AIC (AICc) values. The model with the best fit is summarized last.

a. R-code for KH binomial mixed models for flowers +young fruits (green)+ripe fruits (white) (FLGRWH=FYR in thesis text). Other variables include: tree gall damage (TRGALL), dead branch (BRDEAD), basal area (BA), and minimum average relative humidity (RHMIN).

```r
> mod.null<-glmer(FLGRWH~(1)+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=binomial)
> AICc(mod.null, return.K = FALSE, second.ord = TRUE)
[1] 3402.022
> mod1<-glmer(FLGRWH~TRGALL+BRDEAD+scale(BA)+scale(RHMIN)+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=binomial)
> AICc(mod1, return.K = FALSE, second.ord = TRUE)
[1] 2865.393
> mod2<-glmer(FLGRWH~TRGALL+BRDEAD+scale(BA)+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=binomial)
> AICc(mod2, return.K = FALSE, second.ord = TRUE)
[1] 2869.363
> mod3<-glmer(FLGRWH~TRGALL+BRDEAD+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=binomial)
> AICc(mod3, return.K = FALSE, second.ord = TRUE)
[1] 2874.673
> summary(mod1)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
Family: binomial  ( logit )
Formula: FLGRWH ~ TRGALL + BRDEAD + scale(BA) + scale(RHMIN) + (1 | TREE/BRANCH) + (1 | JDAY)
Data: kh
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+05))

AIC   BIC  logLik deviance df.resid
2865.3 2930.1 -1422.7  2845.3     4770

Scaled residuals:
        Min      1Q  Median      3Q     Max
-12.913  -0.109   0.041   0.185  32.328

Random effects:
  Groups     Name        Variance Std.Dev.
  BRANCH:TREE (Intercept) 13.665   3.697
  TREE        (Intercept)  6.559   2.561
  JDAY        (Intercept)  1.610   1.269
Number of obs: 4780, groups:  BRANCH:TREE, 400; TREE, 40; JDAY, 12

Fixed effects:
Estimate  Std. Error  z value  Pr(>|z|)
(Intercept)  -1.7715     0.6858  -2.583   0.00979 **
TRGALL1      3.7990     0.3339  11.379  < 2e-16 ***
TRGALL2      3.8498     0.4324   8.904  < 2e-16 ***
TRGALL3      3.4910     0.4737   7.370   1.7e-13 ***
BRDEAD1      -6.5377     0.5566 -11.746  < 2e-16 ***
scale(BA)     1.3261     0.4729   2.804   0.00504 **
scale(RHMIN)  1.0352     0.3750   2.760   0.00577 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
  (Intr) TRGALL1 TRGALL2 TRGALL3 BRDEAD scale(BA)
TRGALL1      -0.450
TRGALL2      -0.484  0.825  0.907
TRGALL3      -0.490  0.791  0.907 -0.072 -0.054 -0.047 -0.035
BRDEAD1      -0.024  0.067  0.088  0.097 -0.042
scale(BA)    -0.052  0.090  0.101  0.107  0.014  0.017

b. R-code for KH count mixed models for flowers + young fruits (green) + ripe fruits (white) (FLGRWH=FYR in thesis text). Other variables include: branch gall damage (BRGALL), dead branch (BRDEAD), and minimum average temperature (TPMIN).

```r
> m.null<-glmer(FLGRWH~(1)+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=Gamma)
> AICc(m.null, return.K = FALSE, second.ord = TRUE)
[1] 19000.71
> m4<-glmer(FLGRWH~BRGALL+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000000)),family=Gamma)
> AICc(m4, return.K = FALSE, second.ord = TRUE)
[1] 18960.31
> m5<-glmer(FLGRWH~BRDEAD+scale(TPMIN)+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000000)),family=Gamma)
> AICc(m5, return.K = FALSE, second.ord = TRUE)
[1] 18932.36
> m6<-glmer(FLGRWH~BRDEAD+(1|TREE/BRANCH)+(1|JDAY),data=kh,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000000)),family=Gamma)
> AICc(m6, return.K = FALSE, second.ord = TRUE)
[1] 18936.36
> summary(m5)
```

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
Family: Gamma ( inverse )
Formula: FLGRWH ~ BRDEAD + scale(TPMIN) + (1 | TREE/BRANCH) + (1 | JDAY)
Data: kh
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+08))
AIC   BIC   logLik deviance df.resid
18932.3  18973.8  -9459.2  18918.3    2772

Scaled residuals:
     Min      1Q  Median      3Q     Max
-1.7281 -0.7730 -0.0813  0.5675  6.0987

Random effects:
Groups   Name        Variance Std.Dev.
BRANCH:TREE (Intercept) 2.649e-03 0.051472
TREE       (Intercept) 6.224e-04 0.024948
JDAY       (Intercept) 1.205e-05 0.003471
Residual             3.125e-01 0.558975
Number of obs: 2779, groups: BRANCH:TREE, 334; TREE, 40; JDAY, 12

Fixed effects:
             Estimate Std. Error t value Pr(>|z|)
(Intercept)  0.143860   0.009317  15.440  < 2e-16 ***
BRDEAD1      0.267817   0.052236   5.127 2.94e-07 ***
scale(TPMIN) 0.004980   0.001714   2.906  0.00366 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
             (Intr) BRDEAD
BRDEAD1    -0.003
scale(TPMIN) -0.002  0.001
Appendix A2. Multivariate mixed models considered at Pu‘uwa‘awa‘a (PW). Models listed include the null and three models with the lowest corrected AIC (AICc) values. The model with the best fit is summarized last.

a. R-code for PW binomial mixed models for flowers + young fruits (green) + ripe fruits (white) (FLGRWH=FYR in thesis text). Other variables include: tree foliage dieback (TRDIEB), branch foliage dieback (BRDIEB), and dead branch (BRDEAD).

```r
> mod.null <- glmer(FLGRWH~(1)+(1|TREE/BRANCH)+(1|JDAY), data=pw, family=binomial)
> AICc(mod.null, return.K = FALSE, second.ord = TRUE)  
[1] 2855.659
> mod1 <- glmer(FLGRWH~TRDIEB+BRDIEB+BRDEAD+(1|TREE/BRANCH)+(1|JDAY), data=pw,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=binomial)
> AICc(mod1, return.K = FALSE, second.ord = TRUE)  
[1] 2582.478
> mod4 <- glmer(FLGRWH~TRDIEB+BRDEAD+(1|TREE/BRANCH)+(1|JDAY), data=pw,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=binomial)
> AICc(mod4, return.K = FALSE, second.ord = TRUE)  
> mod5 <- glmer(FLGRWH~BRDIEB+BRDEAD+(1|TREE/BRANCH)+(1|JDAY), data=pw,control=glmerControl(optimizer="bobyqa",optCtrl=list(maxfun=100000)),family=binomial)
> AICc(mod5, return.K = FALSE, second.ord = TRUE)  
[1] 2584.783
```

> summary(mod1)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
Family: binomial  ( logit )
Formula: FLGRWH ~ TRDIEB + BRDIEB + BRDEAD + (1 | TREE/BRANCH) + (1 | JDAY)
Data: pw
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+05))

AIC  BIC logLik deviance df.resid
2582.4 2653.3 -1280.2 2560.4  4625

Scaled residuals:
     Min      1Q  Median       3Q      Max
-12.1985 -0.1267  0.0473  0.1875 10.5967

Random effects:
Groups       Name        Variance Std.Dev.
BRANCH:TREE (Intercept) 6.1214  2.4742
TREE       (Intercept) 12.5136  3.5375
JDAY       (Intercept)  0.9948  0.9974
Number of obs: 4636, groups: BRANCH:TREE, 400; TREE, 40; JDAY, 12

Fixed effects:
(Intercept)  1.7531    0.6799   2.579  0.00992 **
TRDIEB      -0.5629    0.2096  -2.685  0.00725 **
|                | Estimate | Std. Error | z value | Pr(>|z|) |
|----------------|----------|------------|---------|---------|
| TRDIEB2        | -0.7305  | 0.3072     | -2.378  | 0.01739 *|
| TRDIEB3        | -0.7609  | 0.3427     | -2.220  | 0.02643 *|
| BRDIEB1        | -0.5643  | 0.1924     | -2.933  | 0.00336 **|
| BRDIEB2        | -0.3784  | 0.3193     | -1.185  | 0.23597  |
| BRDIEB3        | -0.1413  | 0.2725     | -0.519  | 0.60406  |
| BRDEAD1        | -7.5358  | 0.9005     | -8.369  | < 2e-16 ***|

---

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

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<th>TRDIEB2</th>
<th>TRDIEB3</th>
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<th>BRDIEB2</th>
<th>BRDIEB3</th>
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b. R-code for KH count mixed models for flowers + young fruits (green) + ripe fruits (white) (FLGRWH=FYL in thesis text). Only one model converged for the PW count dataset, and the only variable included in that model was branch foliage dieback (BRDIEB).

```r
m.null <- glmer(FLGRWH~(1)+(1|TREE/BRANCH)+(1|JDAY), data=pw, family=Gamma)
m1 <- glmer(FLGRWH~BRDIEB+(1|TREE/BRANCH)+(1|JDAY), data=pw, family=Gamma)
summary(m1)
```

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']

Family: Gamma  ( inverse )
Formula: FLGRWH ~ BRDIEB + (1 | TREE/BRANCH) + (1 | JDAY)
Data: pw

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Scaled residuals:

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Random effects:

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Number of obs: 2564, groups: BRANCH:TREE, 313; TREE, 40; JDAY, 12
Fixed effects:
\[
\begin{array}{cccc}
\text{Estimate} & \text{Std. Error} & t \text{ value} & \text{Pr(>|z|)} \\
(\text{Intercept}) & 0.166005 & 0.014034 & 11.829 < 2e-16^{***} \\
\text{BRDIEB1} & 0.008127 & 0.002378 & 3.418 0.000631^{***} \\
\text{BRDIEB2} & 0.005525 & 0.007459 & 0.741 0.458908 \\
\text{BRDIEB3} & 0.019134 & 0.005891 & 3.248 0.001163^{**} \\
\end{array}
\]

---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
\[
\begin{array}{cccc}
(\text{Intr}) & \text{BRDIEB1} & \text{BRDIEB2} \\
\text{BRDIEB1} & -0.065 \\
\text{BRDIEB2} & -0.062 & 0.196 \\
\text{BRDIEB3} & -0.100 & 0.256 & 0.275 \\
\end{array}
\]
### Appendix B1

Correlation matrix for categorical and continuous biotic and abiotic independent variables considered for mixed modeling of the response FYR (flowers, young fruits, ripe fruits) at Kona Hema. Two variables were considered to be highly correlated when $r > 0.7$ (values underlined). Variables from left to right include: tree gall damage (TRGALL), tree foliage dieback (TRDIEB), branch gall damage (BRGALL), branch foliage dieback (BRDIEB), dead branch (BRDEAD), basal area (BA), maximum average temperature (TPMAX), minimum average temperature (TPMIN), maximum average relative humidity (RHMAX), minimum average relative humidity (RHMIN), and average precipitation (PRECIP).

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<th>BRGALL</th>
<th>BRDIEB</th>
<th>BRDEAD</th>
<th>BA</th>
<th>TMAX</th>
<th>TMIN</th>
<th>PRECIP</th>
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<td>1.000</td>
<td>0.781</td>
<td>0.793</td>
<td>0.738</td>
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<td>-0.074</td>
<td>0.176</td>
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<td>0.015</td>
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<tr>
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<td>0.692</td>
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<td>-0.218</td>
<td>0.158</td>
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<td>0.086</td>
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<td>0.167</td>
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<td>0.024</td>
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<td>0.858</td>
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<td>0.186</td>
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<td>0.556</td>
<td>0.820</td>
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<td>RHMIN</td>
<td>-0.209</td>
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Appendix B2. Correlation matrix for categorical and continuous biotic and abiotic independent variables considered for mixed modeling of the response FYR (flowers, young fruits, ripe fruits) at Puʻuwaʻawaʻa. Two variables were considered to be highly correlated when $r >0.7$ (values underlined). Variables from left to right include: tree gall damage (TRGALL), tree foliage dieback (TRDIEB), branch gall damage (BRGALL), branch foliage dieback (BRDIEB), dead branch (BRDEAD), basal area (BA) maximum average temperature (TPMAX), minimum average temperature (TPMIN), maximum average relative humidity (RHMAX), minimum average relative humidity (RHMIN), habitat suitability (HABSUIT), and average precipitation (PRECIP).

<table>
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