ESTIMATING AND APPLYING BIOLOGICAL PARAMETERS

TO ENHANCE MANAGEMENT OF RAUVOLFIA VOMITORIA

AN INVASIVE TREE IN NORTH KOHALA, HAWAI‘I

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ABSTRACT

Introduced tree species can cause environmental harm through invasive traits like fast growth rates, long-term seed longevity, and long-distance seed dispersal. I estimated these rates for *Rauvolfia vomitoria*, a tree native to tropical Africa, which was introduced to Hawaii Island in the 1950's. I then compared these rates to other local trees species, both native and invasive, in order to understand *R. vomitoria's* relative invasive risk. It appears to be slow growing at ~1.4mm DBH growth annually, but its seeds can survive over 3 years and can be dispersed up to 1km. Managers have concluded *R. vomitoria* warrants control, and have decided to contain the invasion. Based on my estimates for growth and dispersal, I calculated the cost for a number of containment scenarios, which ranged from $36,000-$88,000 annually. Given that average annual funding for *R. vomitoria* control is ~$35,000, managers may need to request more funding or change management-tactics.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

DBH – Diameter of R. vomitoria trunk at basal height (~6cm above the ground) in centimeters

KWP – Kohala Watershed Partnership

BIISC – Big Island Invasive Species Committee

sUAS – Small (<50lbs) unmanned aerial system

Chapter 1:

Estimating Invasive Trait Parameters for R. vomitoria in North Kohala, Hawai‘i

1.1 Introduction

1.1.1 Invasive Plant Species

Alien species introduction is a main driver in human-caused global change (Vitousek et al. 1997). The federal government classifies the subset of alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health as invasive species (Executive Order 13112, 1999). The introduction of these species can result in biological invasions that may alter biogeochemical cycles (Mack et al. 2001; Atwood et al. 2010), disturbance regimes (Hughes et al. 1991; Mack & D'Antonio 1998), community assemblages (Simberloff & Von Holle 1999; Kourtev et al. 2002; Sanders et al. 2003), and ecosystem and evolutionary trajectories (Vitousek & Walker 1989; Mooney & Cleland 2001; Hughes & Denslow 2005).

Pacific island systems are known to be especially vulnerable to invasive species (Darwin Charles 1859; Elton 1958). The Hawaiian Islands have faced both the threat and effects of invasive species since the arrival of the first human (Kirch 1982), and given Hawai‘i’s extreme isolation—and consequential evolutionary uniqueness (D’antonio & Dudley 1995; Loope et al. 2013)—invasive species have been able to invade numerous, unoccupied ecosystem niches (MacDougall et al. 2009), while taking advantage of a generally, or at least respectively, depauperate predator system (DeWalt et al. 2004). Invasive plant species have been shown to affect native Hawaiian species composition (Ostertag & Verville 2002; Hughes & Denslow 2005) and extinction rates (Gurevitch & Padilla 2004), watershed health (Kaiser & Roumasset 2002), human health (https://hdoa.Hawai‘i.gov/pi/files/2013/01/poisonplantbrochure.pdf), civilian infrastructure (Hughes et al. 2011), and agricultural commerce (Newell & Haramoto 1968).

Plant species can be invasive in many ways (Van Kleunen et al. 2010). For example, the Hawai‘i Weed Risk Assessment—a program aimed at identifying potential invasive plant species before they become established in Hawai‘i—uses a list of 49 questions relating to plant traits in order to calculate an “invasiveness” score, including traits such as growth rate, seed longevity, and dispersal potential (Daehler et al. 2004). This score can then be used to quantify, compare, and understand an alien plant species’ invasive threat to Hawaiian natural systems. Furthermore, invasive plant species success’ can cause environmental harm to native plant systems through multiple mechanisms (Pyšek et al. 2012). For example, an invasive plant species like *Psidium cattleianum* (Strawberry guava) can inhibit native plant species germination and subsequent growth through altering light and water levels, potentially through faster growth rates and dense

canopies (Schulten et al. 2014), or increased vegetative competition via high levels of propagule pressures or seed viability (Cordell et al. 2009). Assessing through which mechanisms or traits invasive plant species specifically affect native vegetation is critical in estimating their potential invasiveness and associated environmental harm (Levine et al. 2003).

The rapid detection of newly arrived alien plant species paired with early assessments of its invasive traits is essential in estimating an alien species' potential invasive threat, accurately comparing this threat to other local invasive species, and forming appropriate management responses (Mack & Lonsdale 2002). The remainder of this work will deal with these actions against a somewhat-recently arrived, alien plant species in Hawai‘i, known as *Rauvolfia vomitoria* (Red-devil's pepper, Swizzle-stick tree).

1.1.2 Rauvolfia vomitoria

R. vomitoria is a flowering shrub or tree species in the Apocynaceae family, ranging between 0.5 and 20.0 meters tall. It is native to tropical Africa and has been documented in moist forest environments as far East as Sudan, West as Senegal, and South as Angola. *R. vomitoria* has been collected from an altitudinal range of 0 to 1750 meters above sea level (Missouri Botanical Garden 2014.) and on average, native *R. vomitoria* individuals experience a mean annual temperature of 26 degrees Celsius and mean annual rainfall of 1350 millimeters (Van Dilst & Leeuwenberg 1991; Orwa et al. 2016). Ecologically, *R. vomitoria* occurs in both gallery forest systems or areas of recent forest regrowth where fallow periods are prolonged and *R. vomitoria* is often one of the last species to disappear for this particular seral stage (Swaine & Hall 1983; Orwa et al. 2016). As an immigrant, *R. vomitoria* has naturalized throughout the globe, including parts of China, Bangladesh, Puerto Rico, and Hawai‘i.

R. vomitoria leaves are often elliptic and arranged in whorls of 3 to 5, with many pairs of ascending secondary veins. The inflorescence consist of 1 to 4 whorls, containing between 15 and 450 cymes. *R. vomitoria* flowers are five parted, colored greenish white to yellow, and fragrant. The flower tubes are glabrous outside. The fruit are globose to ellipsoid drupes, colored bright orange to red when ripe, and range from 8 to 14 millimeters in length and 3 to 9 millimeters in diameter (Li et al. 1995; Omino 2002). Reproductively, *R. vomitoria* is hermaphroditic (Orwa et al. 2016).

Traditionally, *R. vomitoria* has long been used for its medicinal properties by indigenous peoples (Cunningham 1993; Organization 2009), such as treating psychiatric patients in Nigeria (Obembe et al. 1994), leprosy in the Democratic Republic of Congo (Bokemo 1984), and arthritis is Ghana (Abbiw 1990). Additionally, it has been used as a numbing agent in drink mixing for the "Serpent Sect" of Ivory Coast peoples, which is the origin of its English common name "swizzle stick" (Burkill 1995).

Researchers have examined *R. vomitoria* for a number of potential medical benefits including its use as a tranquilizer and anti-hypertensive (Sofowora 1993), a antipsychotic (Obembe et al. 1994), an anti-carcinogen (Bemis et al. 2006), and as a treatment for sexual related infections (Ogunshe et al. 2008). Additionally, *R. vomitoria* has been examined for its emetic, purgative, and arbotifacient properties (Bemis et al. 2006), and for its reserpine and ajmaliune compounds (Hoareau & DaSilva 1999). Unfortunately, *R. vomitoria* appears to be somewhat endangered in its native ranges given people's desire for these apparent medicinal qualities, (Oni 1992; Ehiagbonare 2004; Gaoue et al. 2008; Mehrotra et al. 2012).

1.1.3 *Rauvolfia vomitoria* in North Kohala, Hawai'i

The North Kohala Sugar Company, Surety Inc. potentially introduced *R. vomitoria* to Hawai'i Island in the 1960's as an agricultural crop for medicinal properties (Antony et al. 2011). Given the general decline of the sugar plantation business throughout the 20th century, agricultural commodity exploration was common, and many of the previous cane fields were converted to both pastures and various orchard systems, including Macadamia Nut (Shigeura & Ooka 1984). *R. vomitoria* was seemingly abandoned after the failure of initial trials or due to lack of general interest, and was left to naturalize within the upland mesic forests, gulches, and pastures of the Makapala region of North Kohala. It was detected by conservation agencies in the early 2000's, collected by Melora Purrel of the Kohala Watershed Partnership, and subsequently identified by the Bishop Museum (Kennedy et al. 2010).

North Kohala land managers have pointed out many qualitative similarities between how *R. vomitoria* and the globally-notorious *P. cattleianum* invade forests in the invasion area (Lowe et al. 2000; Personal Correspondence). For example, *R. vomitoria* has been observed to grow into dense, mono-specific canopies (Personal Observation; Personal Correspondence with Surety Cooperation and Melora Purrel). This could suggest a fast level of growth which has the potential

to inhibit native and alien plant species growth through an increased shade environment, which has been observed for *P. cattleianum* (Schulten et al. 2014). Furthermore, the understories of some of these dense, mono-specific canopies have been observed to exclusively contain large numbers of *R. vomitoria* seedlings and saplings (Personal Observation; Personal Correspondence with Surety Cooperation and Melora Purrel). This suggests the potential for *R. vomitoria* to inhibit native and alien plant species' germination like *P. cattleianum* can, through high seed viability creating stronger levels propagule pressure and vegetative competition (Cordell et al. 2009). Additionally, like *P. cattleianum*'s dispersal ability (Seedling and clonal recruitment of the invasive tree *P. cattleianum*: implications for management of native Hawaiian forests), *R. vomitoria* has been seen by local land-managers to be viably dispersed across long distances either through endozoochary (seed carried in the gut of the dispersers such as birds -Personal observation), or epizoochary—seed carried on the outside of the disperser such as feral and domestic cattle or wild pigs (Personal correspondence with Cody Dwight).

Accordingly, multiple conservation agencies have been made aware of this assumed threat of *R. vomitoria* to Hawai'i's ecosystems and direct management has been initiated by the Kohala Watershed Partnership and subsequently joined by the Big Island Invasive Species Committee. Both agencies are additionally in partnership with The National Resource Conservation Service, The U.S. Forest Service, The University of Hawai'i College of Tropical Agriculture and Human Resources, and numerous local partners including land managers, ranchers, and concerned citizens.

However, beyond anecdotal evidence, there has been no direct scientific examination of invasive traits for *R. vomitoria* in North Kohala, or globally for that matter. Consequently, no comparisons of invasiveness can be made between *R. vomitoria* and other documented invasive plant species in Hawai'i, nor can *R. vomitoria*'s traits be compared with those of native plant species in Hawai'i. This inability to compare *R. vomitoria* to other local plants significantly hampers conservation agencies' ability to understand the threat of *R. vomitoria* to Hawaiian ecosystems, and subsequently create the appropriate management strategies respective to this threat.

For example, there are a number of documented invasive plant species that can potentially threaten Hawaiian native ecosystems through either their higher (1) growth rates, e.g., *Falcataria moluccana* (Albizia), (2) dispersal potential, e.g., *P, cattleianum*, or (3) seed longevity, e.g., *Ulex*

europeaus (Gorse). However, these same invasive plant species may at the same time represent lower levels of invasiveness in other characteristics, i.e., *U. europeaus* has poor dispersal potential (Clements et al. 2001) and *P. cattleianum* has poor seed longevity (Uowolo & Denslow 2008). Given these respective invasive trait differences, conservation agencies should understand the relative threat alien plant species pose through their unique set of invasive traits, and consequently manage them as different kinds of threats. For example, seed bank control could be the focus of *U. europeaus* management while immigration control could be the focus of *P. cattleianum* management.

1.1.4 Research Questions

In order to better understand the invasive threat of *R. vomitoria* for Hawai‘i—and the necessary management actions for the level and type of threat—I chose to examine three common parameters of invasive characteristics for *R. vomitoria* in North Kohala: (1) growth rate, (2) seed bank viability and lifespan, and (3) capacity for dispersal.

To understand *R. vomitoria*'s capacity for growth in different shade environments, I selected a number of *R. vomitoria* individuals of various sizes, assigned them one of two shade classes, and repeatedly measured them over time for their diameter at basal height. To understand *R. vomitoria*'s seed bank viability and lifespan, I collected a number of *R. vomitoria* fruit and buried them across the invasion site. I then systematically excavated the fruit over time and independently tested them for viability through laboratory and field experiments. Finally, to understand *R. vomitoria*'s capacity for dispersal, I conducted a number of foraging observations to evaluate which avian species are consuming *R. vomitoria* fruit. With this information, I then estimated potential dispersal distance through relevant works in Hawaiian natural systems pertaining to movement characteristics for a common *R. vomitoria*-foraging avian species of interest.

With these parameters estimated, I will quantitatively compare the invasive traits of *R. vomitoria* to other similar and common invasive tree species in Hawai‘i, and additionally to the dominant native tree species in North Kohala. The first hypothesis is that the growth rate of *R. vomitoria* is faster than that of other common non-native species that grow in the area. The second hypothesis is that seed viability is longer than those of other non-natives in the community. The third hypothesis is that dispersal rates are greater than key local native species. Specifically, I will

attempt to answer if *R. vomitoria* has on average a (1) faster or slower DBH growth rate, (2) a higher or lower initial and long-term seed viability, and (3) a shorter or longer dispersal distance than the invasive tree species: *P. cattlianum*, *Miconia calvescens* (Miconia), and *Schinus terebinthifolius* (Christmas berry), and the native tree species: *Metrosideros polymorpha* (‘Ōhi‘a), and *Acacia koa* (Koa). With the ability to create these comparisons, conservation agencies will have a more objective idea of whether *R. vomitoria* is invasive at all, and if so, what level of management *R. vomitoria* merits considering the other invasive plant threats currently detected in Hawai‘i and the limited funding afforded to their control.

1.2 Methods

1.2.1 Site

The *R. vomitoria* invasion area is located within the North-West portion of Hawai‘i island, approximately three kilometers south of the town of Kapa`au. It spans roughly a 4000-acre circular area, with its center approximately at 20.199031°, -155.763845° decimal degrees. The average annual rainfall for the area is 1866.1 mm (Giambelluca et al. 2013) and the average temperature is 65.9°F in January and 70.3°F in July (http://gis.ctahr.Hawai‘i.edu/SoilAtlas#map). The soil composition is wet, volcanic-ash, with high water holding capacity, fast permeability, and a pH range of 3.6 - 5.0 (CTAHR). The elevation ranges from 200 feet to 2000 feet above sea level (Google Earth) and the average slope for the area is 6-35% (CTAHR). Nearby natural resources to note are the Kohala-Hamakua Valley System which is to the West, and the Kohala Forest Reserve, which is the to the South, of the invasion area.

The history of land use in the area represents long-term agricultural practices, beginning with the Hawaiian field systems (Ladefoged et al. 2011). In the late 19th century sugar cane became the main commercial crop (MacLennan 1997), but by the mid-20th century these cane fields had been transformed into both pasture land and more boutique agricultural orchards, e.g., Macadamia Nuts (Shigeura & Ooka 1984). Very little native Hawaiian vegetation remains given this history of these extensive and intensive field systems, and instead the plant community is comprised of a majority of alien species, many of which are classified as invasive.

For alien tree species, the most common in the area are: *Casuarina equisetifolia* (Iron Wood); *Eucalyptus robusta* (Swamp Mahogany); *Ficus benghalensis* (Indian Banyan); *Macadamia integrifolia* (Macadamia Nut); *P. cattleianum*; *Psidium guajava* (Common Guava); *F. moluccana* and *S. terebinthifolius*. And for alien shrub and liana species, the most common in the area are: *Commelina diffusa* (Spreading Dayflower, Hono-hono Grass); *Passiflora spp*. (Passion Fruit Vine, Liliko`i); and *Rubus parviflorus* (Thimbleberry).

For native tree species, the most common in the area are: *M. polymorpha*; *Cheirodendron trigynum* (`Olapa); *Pandanus tectorius* (Hala); and *Psychotria hawaiiensis* (Kōpiko). And for native shrub and fern species, the most common in the area are: *Asplenium nidus* (Bird's Nest Fern, `Ekaha); *Dryopteris fusco-atra* (Laukahi); *Dryopteris wallichiana* (Shuttlecock Fern, `I`i); and *Osteomeles anthyllidifolia* (`Ūlei).

1.2.2 Growth Rate

All methods to estimate growth rate over time were based on the recommendations of Dr. Patrick J. Hart through personal correspondence as well as his work Hart (2010).

In the summer of 2012, I created a 100 x 100 meter grid system of 215 cells, totaling ~550 acres, and laid this across the approximate center of the invasion area, with ArcGIS (ESRI 2011). I ascribed the center of each of these cells a unique site I.D. and loaded its latitudinal position onto a handheld GPS unit.

In a random fashion, I visited ~100 of these sites and collected a number of categorical measurements. At each site, I estimated the center of the cell using the GPS unit and marked this point with the use of fluorescent plastic flagging. From this marked center position, I estimated a five-meter radius with measurement tape, and recorded the number of *R. vomitoria* individuals with heights of 0.1 - 0.5, 0.5 - 2, and > 2 meters into categorical bins of 0, < 5, 5-9.9, or ≥ 10 individuals. Additionally, I noted the presence of the following canopy tree species if I estimated the species to represent ≥25% of the canopy cover above the 5-meter radius site area: *Casuarina equisetifolia* (Iron Wood), *Macadamia integrifolia* (Macadamia Nut), *Falcataria moluccana* (Albizia), *P. guajava* (Common Guava), *P. cattleianum,* and *R. vomitoria*.

From the ~100 measured sites, I selected thirty-four based on the following criteria: (1) the site must be estimated to contain ≥5 *R. vomitoria* individuals for each 0.1 - 0.5, 0.5 - 2, and > 2 meter height group; and (2), the collection of sites should roughly represent an even distribution of the canopy tree species mentioned in the previous paragraph, when their presence covers at least 25% of the canopy above the 5-meter radius site.

Between June 10th and July 27th of 2013, I visited the above thirty-four sites and took the following steps. To represent different growth stages, I selected three *R. vomitoria* individuals within a five-meter radius of the site center from each of the following six size classes: 0-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-6 cm, and >6 cm, totaling 18 *R. vomitoria* individuals. I then measured each of these 18 *R. vomitoria* individuals for the diameter of their trunk at ~6 inches above the forest floor, i.e., diameter at ankle height (DBH). Additionally, I marked the exact site of the DBH measurement for each individual *R. vomitoria* trunk with either a piece of tied-off elastic banding for *R. vomitoria* individuals with <2 cm DBH, or a thumbtack pushed ~2cm into the bark for *R. vomitoria* individuals ≥2 cm DBH. I chose to record diameter at basal height instead of the more

traditional diameter at breast height metric because many *R. vomitoria* individuals were <1 meter in height.

Additionally, I categorically measured each *R. vomitoria* individual for its shade class in accordance with the modified methods of Smith et al. (1997). In this system, an individual plant is marked as representing one of the following two shade conditions: suppressed if the individual receives no or infrequent direct sunlight throughout the day, or dominant if the individual receives direct sunlight on the top or sides of its canopy crown throughout the day.

Between June 2nd and July 24th of 2014, I revisited the thirty-four field sites and again measured each *R. vomitoria* individual for DBH, using the last year's measurement site marker as a guide for where to re-measure. Additionally, I again assigned each *R. vomitoria* individual one of the possible two shade conditions, and noted them as either fruiting, i.e., either inflorescence or infructescence were present on the individual, or not fruiting, i.e., neither inflorescence nor infructescence were present on the individual. Finally, I marked each *R. vomitoria* individual as either as alive, i.e., green vegetation, presence of leaves, or dead, i.e., brown vegetation, absence of all leaves or individual. I again repeated these steps for each *R. vomitoria* individual at the thirty-four sites between June 14th and August 2nd of 2015.

1.2.3 Seed Viability

All the methods I used to estimate seed viability over time were based on the recommendations of Dr. Carol Baskin through personal correspondence.

Between June 2nd and 7th, I collected ~1100 *R. vomitoria* fruit that had fallen to the ground from across the invasion area. I selected the fruit if they showed signs of ripeness based on a fruit diameter >0.5 cm and a color range of yellowish-orange to light-red. I then mixed these ~1100 fruit together, and separated them into fourteen bunches of ~75 fruit each. I placed twelve of the fourteen bunches into nylon mesh stockings and buried them ~5cm underground at two sites within the invasion area, spaced ~1750 meters apart. I then tested the remaining two of fourteen bunches immediately for viability through the following two methods.

I conducted the first method, a Tetrazolium Chloride laboratory test (TZ Test), under the methods of Flemion and Poole (1948). Under these guidelines, I selected 50 of the ~75 *R. vomitoria* fruit randomly, and stripped the pericarp off to expose the seed. I then soaked these 50 *R. vomitoria* seeds for two hours in distilled water and cut them in half by the use of laboratory

forceps and scalpel to expose the embryo. I soaked the exposed embryo for 30 minutes in a 0.1% solution of tetrazolium chloride, and after 30 minutes, removed them from the solution and evaluated their color. A translucent or milky white embryo-color implied a non-viable embryo, while a pink to red embryo-color implied a viable embryo. I noted each embryo showing signs of viability, and then divided the number of viable seeds by the total number of seeds tested, i.e., 50, to estimate the percent of viable seed for each sample.

The second method, a sowed-tray field test (field-tray test), was conducted under the methods of (Hampton 1995). Under these guidelines, I selected 70 of the ~75 *R. vomitoria* fruit and separated them into two groups of 35 fruit, and evenly sowed them into two 20" x 10" common-germination trays filled with local soil, approximately 2-5 cm below the surface. I then placed these two trays at two sites within the invasion area, spaced ~1750 meters apart. I visited these trays approximately every two, six, and ten months afterwards, and noted any seed germination. After the last ~10 month observation, I divided the number of observed germinated seeds over the previous ~10 months by the total number of seeds sown, i.e., 70, to estimate the percent of viable seed.

Both these processes continued every six months, until the summer of 2015. And additionally, to estimate a more robust baseline for initial *R. vomitoria* seed viability, I randomly collected another ~300 *R. vomitoria* fruit between May 26th and June 1st of 2014. 50 of these seeds were then randomly selected and underwent the same type of TZ test described above. 70 of the remaining seeds were then randomly selected and underwent the same type of field-tray test described above.

1.2.4 Avian Dispersal Distance

To investigate the main sources of avian dispersal for *R. vomitoria* fruit, I conducted a number of field-observations between the hours of 8:30 am and 2:30 pm in June of 2013 and 2014. This involved myself sitting ~50 meters away from an unobstructed canopy of ≥8 viewable *R. vomitoria* panicles. With the aid of binoculars, I would view this *R. vomitoria* canopy for an hour per site, and record any instances of observed *R. vomitoria* fruit foraging by birds, noting the time of ingestion, the amount of fruit eaten, and the species of bird foraging. This procedure was conducted at 33 unique sites, spaced >100 meters from each other, representing 33 hours of total avian-foraging observations.

Based on these observations, I concluded that *Zosterops japonicus* (Japanese White-Eye) was the bird species eating the majority of the *R. vomitoria* fruit, and conducted a literature search regarding how far could *Z. japonicus* potentially disperse *R. vomitoria* seed. Unfortunately, there has been little to no work on estimating dispersal distances for any fruit ingested by *Z. japonicus*. However, a recent radio-telemetry tracking study conducted on Hawai‘i Island (Wu et al. 2014a) attempted to estimate the average distance travelled by *Z. japonicus* in relationship to how long the individual *Z. japonicus* was tracked.

Corresponding with the authors of this work, I was able to review their data set in order to better understand how far a *Z. japonicus* could potentially disperse *R. vomitoria* fruit. The data set was comprised of 1,741 observations of the distance travelled by *Z. japonicus* during three time-period categories, 30 minutes, 60 minutes, and 120 minutes. With these observations, I created a general linear model to estimate the distance *Z. japonicus* travels in a given time period. I then conducted an additionally literature search into how long *Z. japonicus* typically retains ingested seed. With this information, I estimated two time periods of gut retention time for *R. vomitoria* seed ingested by *Z. japonicus*, 30 and 60 minutes. By then using this general linear model for *Z. japonicus* movement, I created estimates for the average meters of distance travelled by *Z. japonicus* during these two times periods, and assumed that they represent potential distances that *Z. japonicus* would typically disperse *R. vomitoria* seed.

1.3 Statistical Analyses

To simplify the following explanations of my statistical methods, I will define the statistical terms used at the start of each section for *R. vomitoria* growth rate, seed viability, and dispersal distance.

1.3.1 Growth Rate Statistical Analyses

Terms:

- Growth rate is defined as the absolute centimeter diameter increase for a *R. vomitoria* individual over the course of ~365 days, averaged over the two measurement periods 2013-2014 and 2014-2015, for each *R. vomitoria* individual that survived across both measurement periods.
- DBH is defined as the diameter size in centimeters at basal height, measured in 2013, for each *R. vomitoria* individual that survived across both measurement periods.
- Shade class is defined as either two categorical variables suppressed or dominant, representing the amount of shade a *R. vomitoria* individual received over the course of ~365 days.

To investigate the distribution of growth rate observations for the years 2013-2014 and 2014-2015, I first conducted an Anderson-Darling test for normality to understand if the combined growth rate observations for the two measurement periods were distributed normally. To investigate the effects of measurement period on growth rate, I conducted a Mann-Whitney comparing growth rates between the years 2013-2014 and 2014-2015. To investigate the effects of DBH on growth rate, I conducted a linear regression analysis using DBH as a continuous predictor variable and growth rate as a continuous response variable. To investigate the effects of shade class on growth rate, I conducted a Kruskal-Wallis test using shade class as a categorical factor and growth rate as a continuous response variable. And to investigate the combined and interactive effects of shade class and DBH, I conducted a general linear model analysis using DBH as a continuous predictor variable, shade class as a categorical predictor variable, the interaction of DBH and shade class as a predictor variable, and growth rate as a continuous response variable.

1.3.2 Seed Viability Statistical Analyses

Terms:

- Months since burial is defined as roughly the number of months that have elapsed between the seed having been buried between June 2nd and 7th of 2013 and the time of the seed's excavation.
- Seed viability is defined as the amount of seeds determined to be viable—either through a TZ or field-tray test—divided by the total amount of seeds tested, per individual test.

To investigate the effects of months since burial on seed viability, I conducted a linear regression analysis using months since burial as a continuous predictor variable and seed viability as a continuous response variable. And I did this separately for both the TZ and field-tray test observations.

1.3.3 *Rauvolfia vomitoria* Fruit Dispersal Statistical Analysis

Terms:

- Flight time is defined as the number of minutes that had elapsed while the *Z. japonicus* individual was being tracked by telemetry.
- Flight distance is defined as the number of meters that had been travelled while the *Z. japonicus* individual was being tracked by telemetry, per flight observation.

To investigate the effects of flight time on flight distance, I conducted a linear regression analysis using flight time as a continuous predictor variable and flight distance as a continuous response variable. With this model, I then created two estimates for the average distance travelled during two time periods, 30 and 60 minutes.

1.4 Results

1.4.1 Growth Rate Sample Description

In 2013 a total of 520 *R. vomitoria* individuals were selected, marked, and measured using the methods described in the previous section. Sixty-six of the measured *R. vomitoria* individuals died between 2013 and 2014, representing 12.7% mortality for the observed population during this span—consequently 454 individual growth measurements were taken for *R. vomitoria* individuals for this span. Forty-six of the remaining measured *R. vomitoria* individuals then died between 2014 and 2015, representing 14.5% mortality for the observed population during this span—consequently, 388 individual growth measurements were taken for *R. vomitoria* individuals during this span (See Figure 1.1 and 1.2).

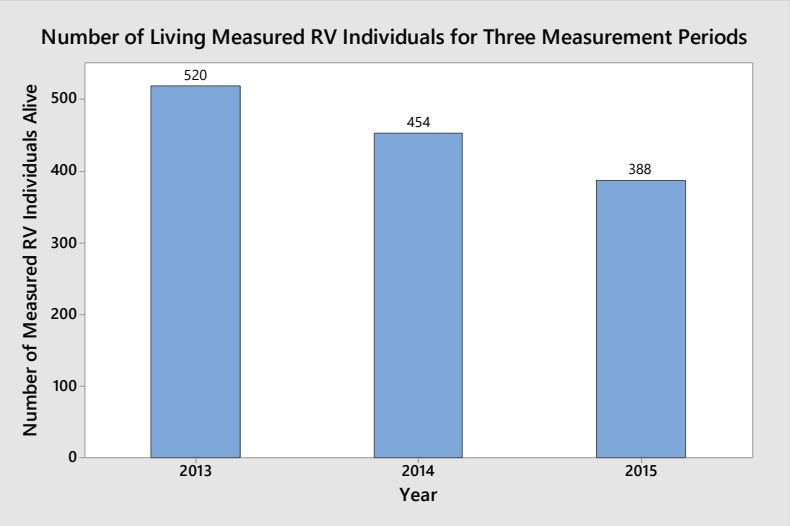

Figure 1.1 - Number of Measured R. vomitoria Individuals by Year

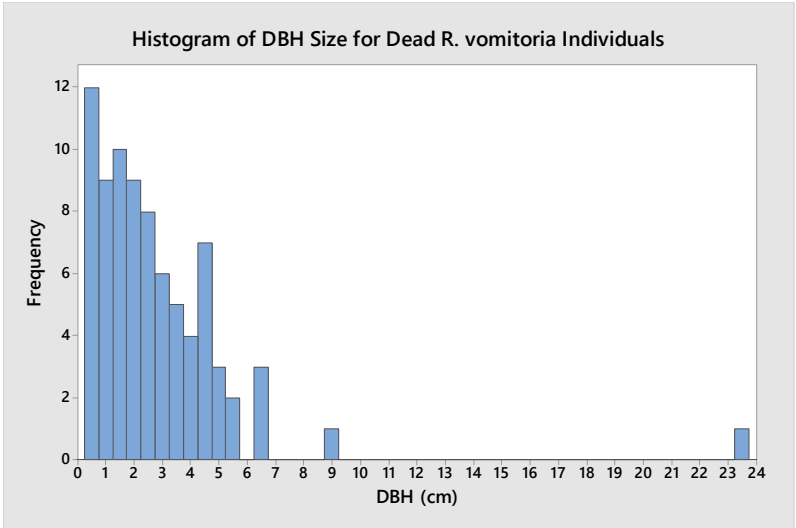

Figure 1.2 – Histogram of DBH Size (cm) for Dead R. vomitoria Individuals

The average DBH of this measured population was estimated to be 2.75 ± 1.424 cm and ranged between a minimum value of 0.1 and maximum value of 33.0 cm DBH, with a sample size of n = 520 and SE Mean = 0.158 cm (See Figure 1.3).

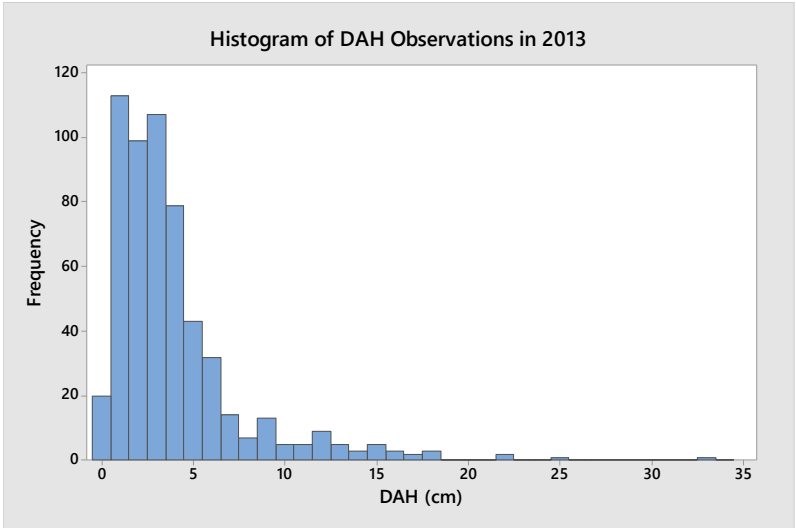

Figure 1.3 – Histogram of DBH Observations in 2013

465 of the measured *R. vomitoria* individuals were categorized as representing a shade class of suppressed. The remaining 55 *R. vomitoria* individuals were categorized as representing a shade class of dominant (See Figure 1.4). However, 30 of the *R. vomitoria* individuals categorized

originally as suppressed graduated to a dominant shade class during our observation time, while one unfortunate *R. vomitoria* individual switched from dominant to suppressed during the same time. These individuals that switched shade classes in this manner were removed from my growth analyses.

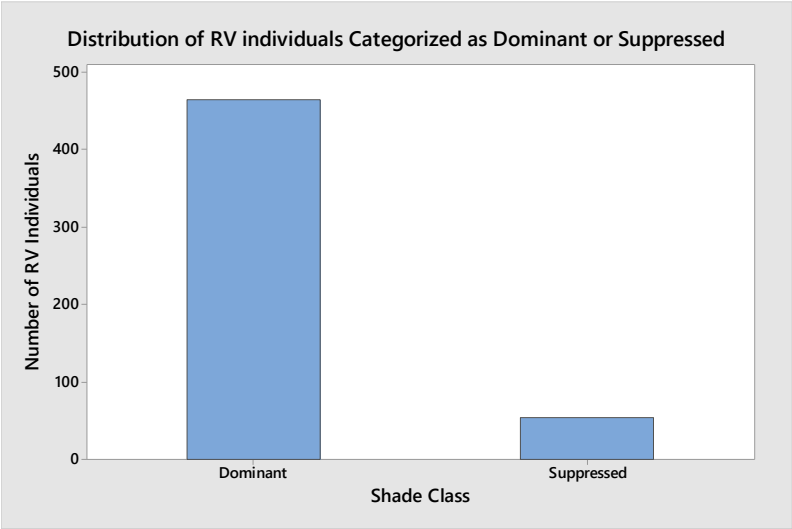

Figure 1.4 – Bar Graph for the number of R. vomitoria Individuals Measured per Shade Class

21 of the measured *R. vomitoria* individuals were categorized as fruiting in 2014, representing 4.6% of the observed population at this time. Remarkably, 21 of the measured *R. vomitoria* individuals were also categorized as fruiting in 2015, representing 5.4% of the observed population at this time. It should be noted that 66% of the total fruiting *R. vomitoria* individuals were categorized as fruiting in both 2014 and 2015.

Of the 21 fruiting *R. vomitoria* individuals in 2014, two were in the suppressed shade class and nineteen were in the dominant shade class. Of the 21 fruiting *R. vomitoria* individuals in 2015, one was in the suppressed shade class and twenty were in the dominant shade class.

Within the 5-meter radius area for each site, 348 of the measured *R. vomitoria* individuals were situated under of canopy of ≥25% *Falcataria moluccana* (Albizia), 291 under of canopy of ≥25% *R. vomitoria*, 264 under of canopy of ≥25% *Casuarina equisetifolia* (Iron Wood), 188 of under of canopy of ≥25% *P. guajava* (Common Guava), 58 under of canopy of ≥25% *P. cattleianum*, and 30 were not situated under any canopy with ≥25% canopy cover for any of the above-mentioned tree species (See Figure 1.5).

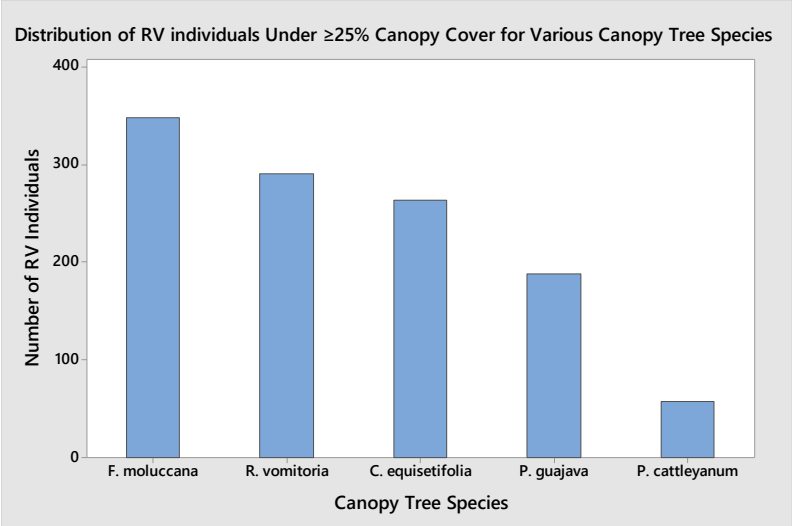

Figure 1.5 - Bar Graph for the number of R. vomitoria Individuals Measured per Canopy Species

In order to address the early life-stage characteristics for *R. vomitoria* growth, all observations for *R. vomitoria* individuals with a DBH ≥ 6 centimeters—179 in total—were removed from all the following growth rate statistical descriptions and analyses. I did this in order to focus my estimates on early life stages of *R. vomitoria* growth that pertain to its minimum generative time.

In order to estimate growth rate for this measured population, the average growth rate was calculated for each measured *R. vomitoria* individual from both the 2013 to 2014 and 2014 to 2015 measurement period, and then the average was calculated for these two periods.

The average annual DBH increase in centimeters for this measured population was estimated to be 0.143 ± 0.121, and ranged between a minimum value of 0.0 to a maximum value of 0.6, with a sample of n = 262 and SE Mean = 0.00749 (See Figure 1.6a and 1.6b).

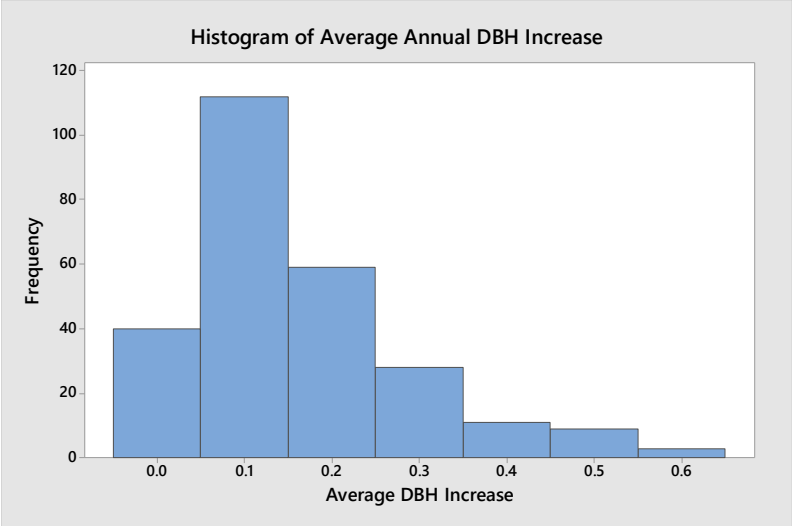

Figure 1.6a - Histogram for the number of R. vomitoria Individuals Measured per Annual DBH Increase

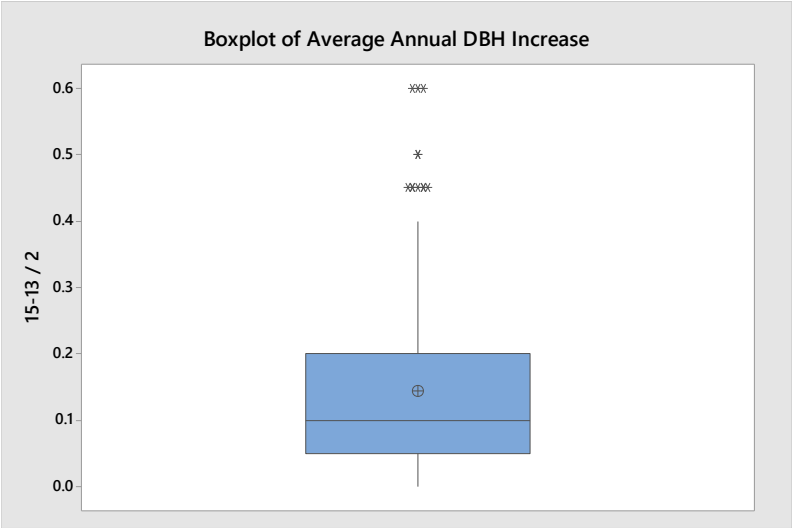

Figure 1.6b – Boxplot for R. vomitoria Annual DBH Growth, where the crossed-circle represents the median, the center box line is the mean, the top and bottom box line are the 2nd and 3rd quartile, the top and bottom of the center line are the 1st and 4th quartile, and the asterisks are the outlying observations.

1.4.1.1 Growth Rate Statistical Analyses Results

A Mann-Whitney test was conducted to investigate the effect of measurement period on growth rate**.** The average growth rate between 2013 and 2014 (0.146 ± 0.123 cm) was not found to be significantly different than the average growth rate between 2014 and 2015 (0.144 ± 0.153 cm): T-Value = 0.17, P-Value = 0.865, DF = 553 (See Figure 1.7)

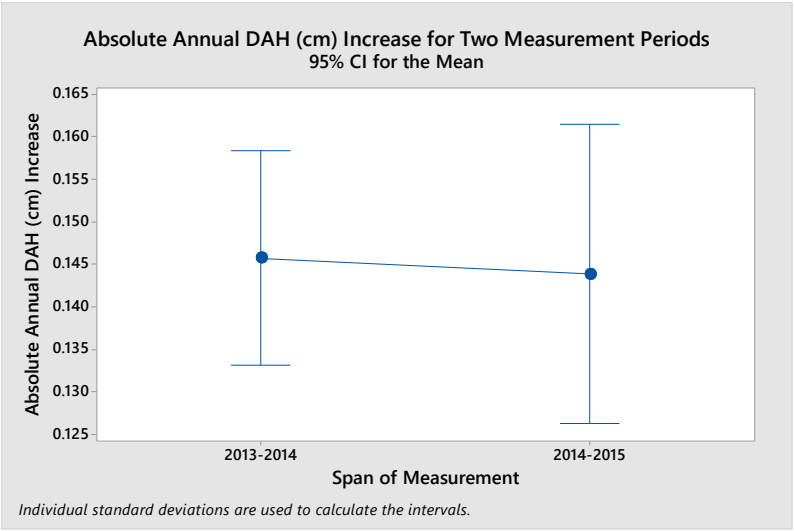

Figure 1.7 – Interval Plot for Average R. vomitoria Annual DBH Growth for Two Measurement Periods

A linear regression analysis was conducted to investigate the effects of DBH on growth rate. This analysis found that the continuous variable DBH was a significant predictor for growth rate: F-Value = 16.18, P-Value = < 0.000, DF = 261, R^2-Value = 5.86%. This significant relationship was found to be positive through the regression equation: growth rate = 0.0848 + 0.02137 DBH (Figure 1.8 and 1.9).

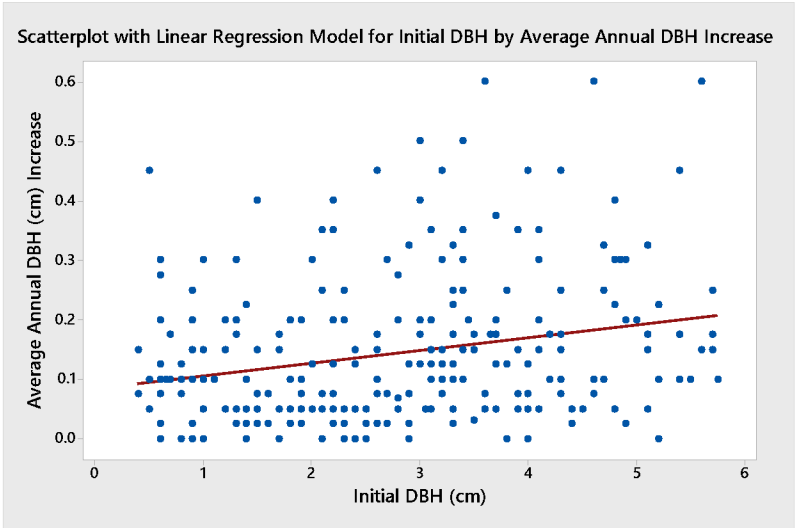

Figure 1.8 – Scatterplot with Linear Regression Model for Initial R. vomitoria DBH Size by Annual R. vomitoria DBH Growth

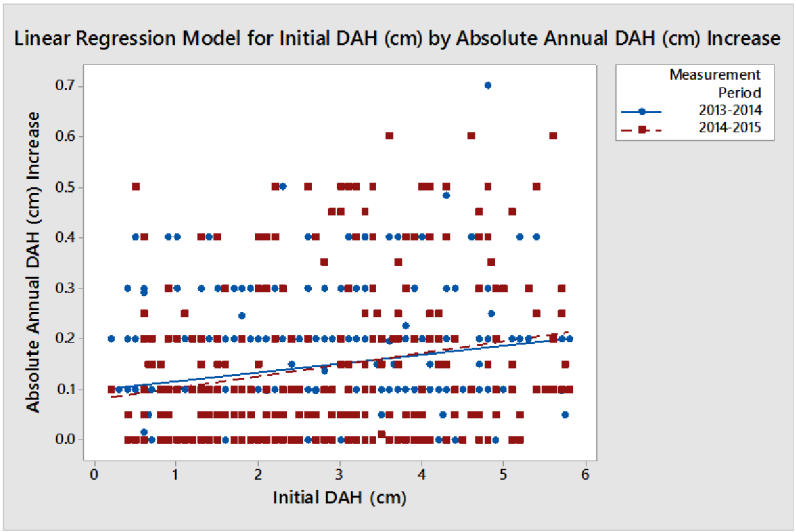

Figure 1.9 - Scatterplot with Linear Regression Model for Initial R. vomitoria DBH Size by Annual R. vomitoria DBH for Two Measurement Periods

A Mann-Whitney test was conducted to investigate the effects of shade class on growth rate. This analysis found that the average growth rate estimate for *R. vomitoria* individuals with a dominant shade class (0.4039 cm ± 0.14) was significantly larger than the average growth rate for *R. vomitoria* individuals with a suppressed shade class (0.1236 cm ± 0.097): F-Value = 137.91, P-Value = < 0.000, DF = 261, R^2-Value = 34.66% (See Figure 1.10).

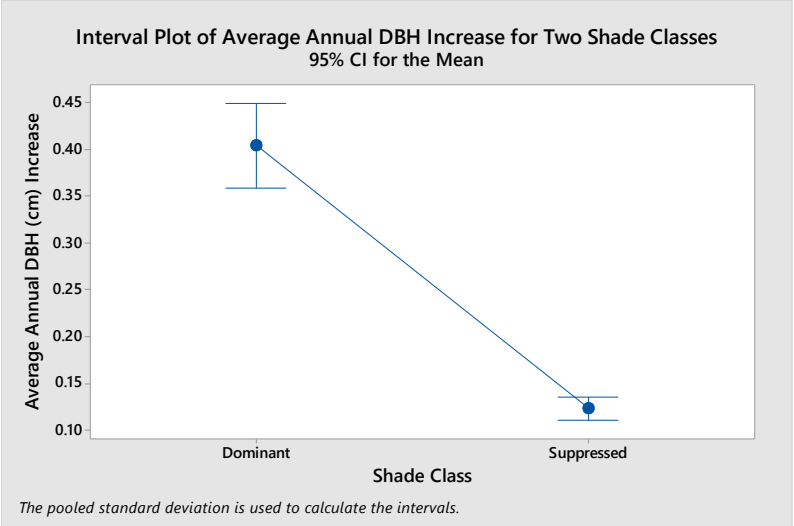

Figure 1.10 - Interval Plot for Average Annual R. vomitoria DBH Growth for Two Shade Classes

A general linear model analysis was conducted to investigate the combined and interactive effects of shade class and DBH on growth rate. This analysis found that both shade class and shade class * DBH were significant predictor variables for growth rate**:** F-Value = 30.20, P-Value = < 0.000, for the categorical variable shade class; and F-Value = 3.91, P-Value = 0.049, for the interactive effects between the categorical variable shade class and covariate DBH**.** However, the analysis found that DBH was not a significant predictor for growth rate**:** F-Value = 0.31, P-Value = 0.578. The entire model represented a R^2-Value of 37.10%, DFF = 261. The significant relationship was found to be negative for *R. vomitoria* individuals with a dominant shade class through the regression equation: growth rate = 0.4941 - 0.0237 DBH**.** The significant relationship was found to be positive for *R. vomitoria* individuals with a suppressed shade class through the regression equation: growth rate = 0.0879 + 0.0133 DBH (See Figure 1.11).

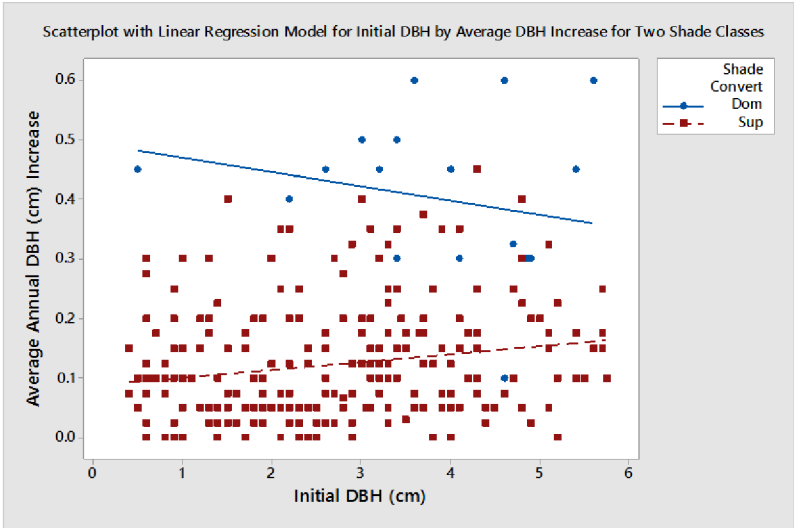

Figure 1.11 - Scatterplot with Linear Regression Model for Initial R. vomitoria DBH Size by Annual R. vomitoria DBH Growth for Two Shade Classes

1.4.2 Seed Viability Sample Description

In total 960 *R. vomitoria* seeds were tested for viability, 400 through a TZ test, and the remaining 560 through a field-tray test. This represented seven individual tests over time for both the TZ test and field-tray test methods. Observed viability estimates ranged between 32% and 9% for the TZ test method, and between 4.5% and 1.5% for the field-tray test method.

For the TZ test method, the average *R. vomitoria* seed viability at 0 months of burial was estimated to be 27.50 % ± 5.51 and ranged between a minimum value of 21% and maximum value of 33%, with n = 4 and SE Mean = 2.75. For the same TZ test method, the average *R. vomitoria* seed viability after 36 months of burial was estimated to be 10.0 % ± 1.41, and ranged between a minimum value of 9% and maximum value of 11%, with n = 2 and SE Mean = 1.0 (See Figure 1.12).

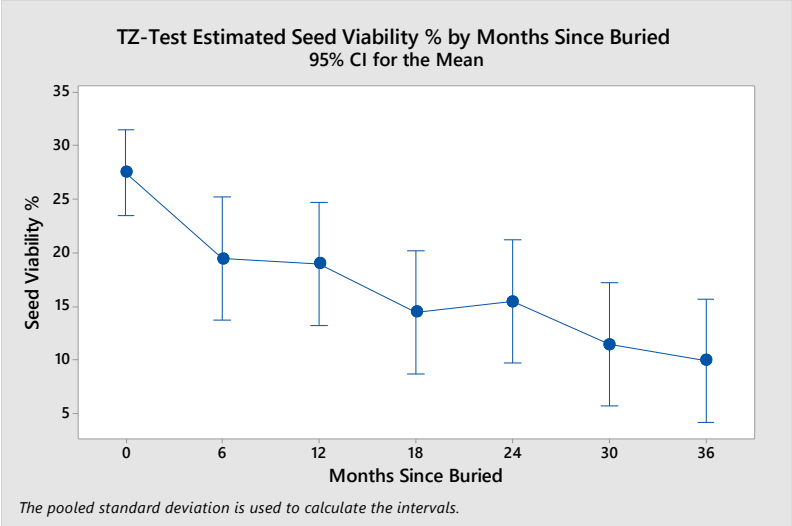

Figure 1.12 - Interval Plot for Average R. vomitoria Seed Viability Estimated from a TZ test by Months Since R. vomitoria Seed Burial

For the field-tray test method, the average *R. vomitoria* seed viability at 0 months of burial was estimated to be 4.0 % ± 1.82 and ranged between a minimum value of 2% and maximum value of 6%, with a sample size of $n = 4$ and SE Mean = 0.913. For the same field-tray test method, the average *R. vomitoria* seed viability after 36 months of burial was estimated to be 1.5 % ± 0.707, and ranged between a minimum value of 1% and maximum value of 2%, with a sample size of $n = 2$ and SE Mean = 0.5 (See Figure 1.13).

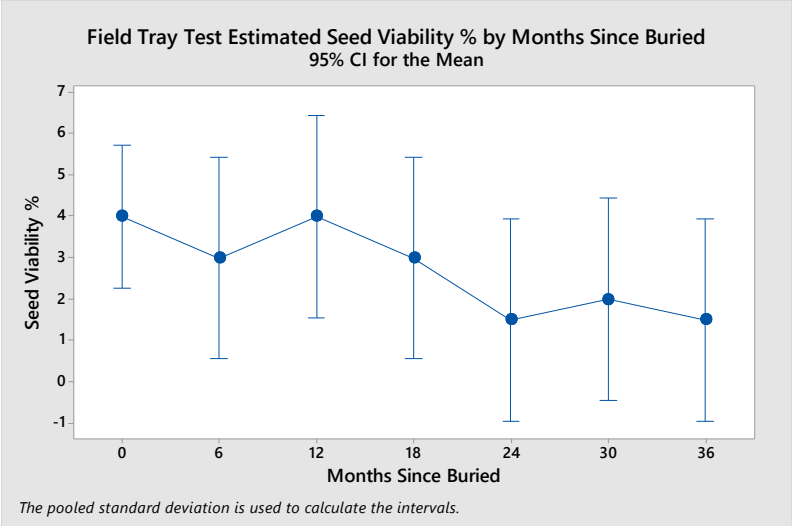

Figure 1.13 - Interval Plot for Average R. vomitoria Seed Viability Estimated from a field-tray test by Months since R. vomitoria Seed Burial

1.4.2.1 Seed Viability Statistical Analyses Results

For the TZ test observations, a linear regression analysis was conducted to investigate the effects of months since burial on seed viability. This analysis found that the continuous variable months since burial was a significant predictor for seed viability: F-Value = 56.97, P-Value = <0.000, DF = 1, R^2-Value = 88.9%. This significant relationship was found to be negative through the regression equation: seed viability = 25.45 - 0.465 months since burial (See Figure 1.14).

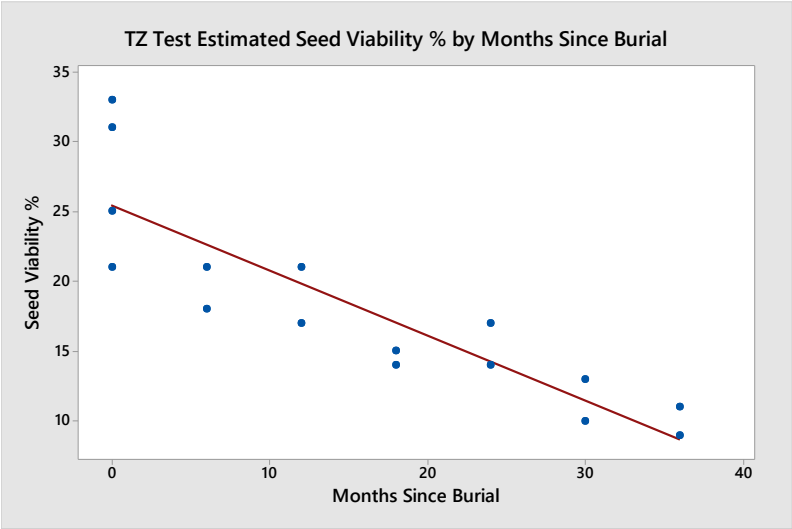

Figure 1.14 – Scatterplot with a Linear Regression Model for Average R. vomitoria Seed Viability by Months since R. vomitoria Seed Burial, Viability Estimated from a TZ test

For the field-tray test observations, a linear regression analysis was conducted to investigate the effects of months since burial on seed viability. This analysis found that the continuous variable months since burial was a significant predictor for seed viability: F-Value = 17.3, P-Value = 0.006, DF = 1, R^2-Value = 74.2%. This significant relationship was found to be negative through the regression equation: seed viability = 4.0 - 0.0714 months since burial (See Figure 1.15).

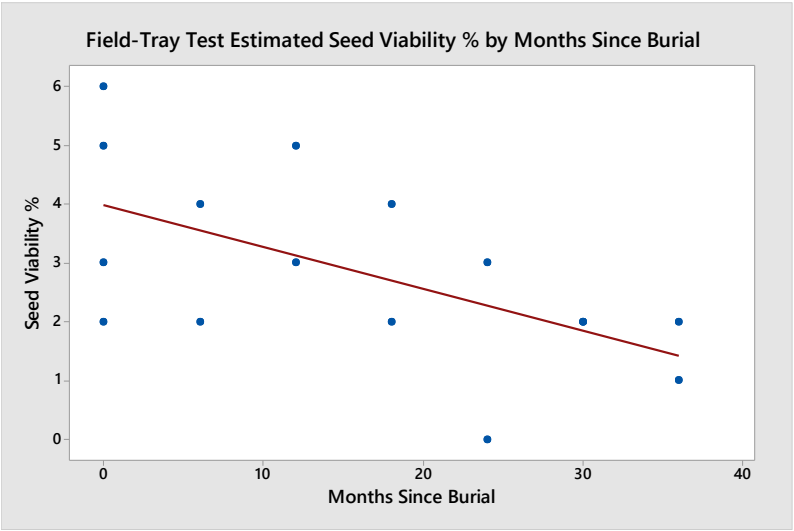

Figure 1.15 – Scatterplot with a Linear Regression Model for Average R. vomitoria Seed by Months since R. vomitoria Seed Burial, Viability Estimated from a TZ test

1.4.3 Dispersal Distance Statistical Sample Description

Over thirty-three hours of field observation, I noted 160 *R. vomitoria* fruit to be consumed by avifauna. The majority of these observations—153 or 95.6%—involved *Z. japonicus*, while the remaining 4.4% involved *Cardinalis cardinalis* (Northern Cardinal), *Serinus canaria* (Atlantic Canary), *Geopelia striata* (Zebra Dove) and *Leiothrix lutea* (Red-billed Leiothrix) (See Figure 1.16). Based on these observations, I concluded that *Z. japonicus* is the major dispersal vector for *R. vomitoria* fruit in respect to the concerns of this study.

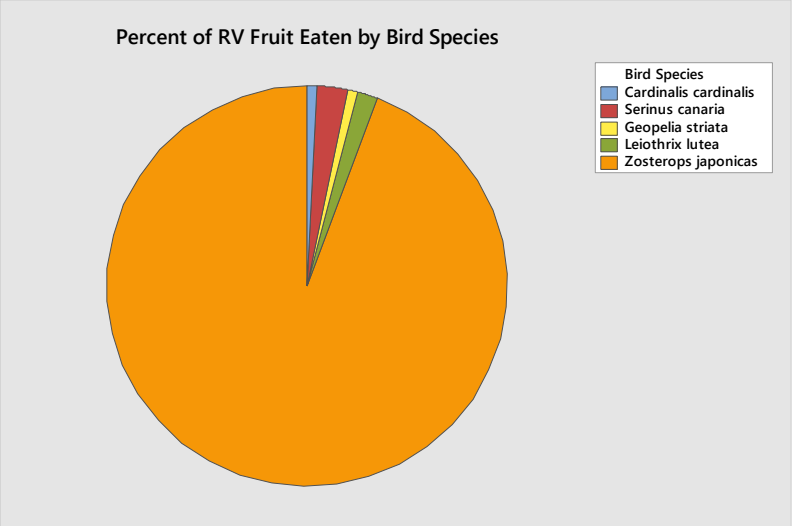

Figure 1.16 - Pie Chart for Percent of R. vomitoria Fruit Eaten by Bird Species

The data set I received from Wu et al. (2014a) contained 1741 unique samples for distance traveled across three time-period categories, 30 minutes, 60 minutes, and 120 minutes. However, due to telemetry methods limiting the ability of continuous tracking, these categorical periods contained samples that ranged from 22 to 38 minutes for the 30-minute category, 50 to 70 minutes for the 60-minute category, and 110 to 130 minutes for the 120-minute category.

For the entire data set and all time periods, the estimated average value for distance travelled was 207.04 ± 179.05 meters and ranged between a minimum value of 1.12 and maximum value of 1052.23, with a sample size of n = 520 and SE Mean = 4.29 meters (See Figure 1.17).

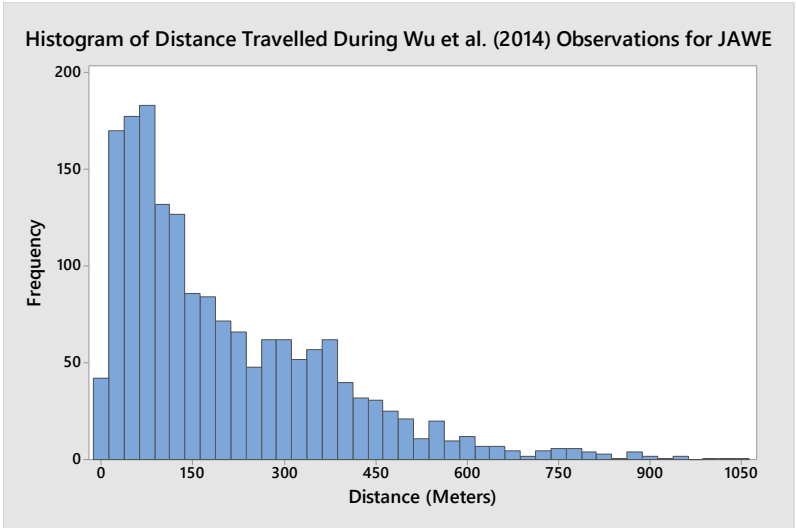

Figure 1.17 – Histogram of Distance Travelled in Meters during Unique Observations for Z. japonicus Movement, from Wu et al. 2014

For individual birds across all time periods, the lowest average value for distance travelled was estimated to be 72.6 ± 60.1 meters, the highest average value for was estimated to be 290.58 ± 187.5 meters, the lowest maximum value was estimated to be 148.2 meters, and the highest maximum value was estimated to be 1053.23 meters (See Figure 1.18).

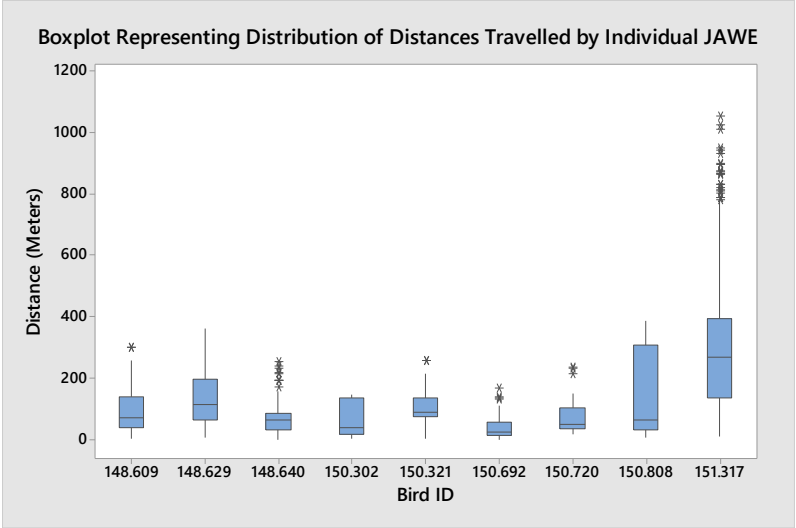

Figure 1.18 – Boxplot for Distribution of Distance Traveled in Meters by Individual Z. japonicus Birds

1.4.3.1 Dispersal Distance Statistical Analyses Results

This linear regression analysis found that the continuous variable flight time was a significant predictor for flight distance: F-Value = 21.7, P-Value = < 0.000, DF = 1741, R^2-Value = 1.23%. This significant relationship was found to be positive through the regression equation: flight distance = 170.52 + 0.581 flight time (See Figure 1.19).

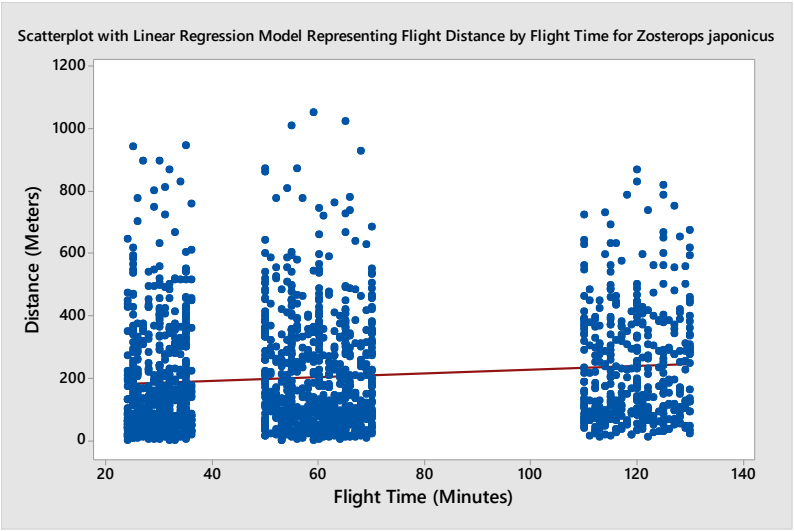

Figure 1.19 - Scatterplot with a Linear Regression Model for Distance Travelled by Z. japonicus by Flight Time

My literature search to determine typical gut retention times for *Z. japonicus* found only one work, Medeiros (2004), a doctoral thesis which observed gut retention times of 60 to 210 minutes across three different seed species. However, peer-reviewed studies for gut retention times associated with bird species similar to *Z. japonicus* in size and habit found retention times of 3 to 80 minutes (Herrera 1984; Levey & Karasov 1989; Stanley & Lill 2002; Brown & Downs 2003; Logan & Xu 2006; Wu et al. 2014). Based on this evidence, and through personal correspondence with the authors of Medeiros (2004) and Wu et al. (2014), I decided to use two estimates for *Z. japonicus* gut retention time, 30 and 60 minutes. And through the above linear regression model, I estimate that during this 30-minute period *Z. japonicus* will travel an average of 184.1 meters and maximum of 947.5 meters, and during this 60-minute period, an average of 209.4 meters and maximum of 1,052.23 meters.

1.5 Discussion

1.5.1 Growth Rate

For all observed *R. vomitoria* individuals, 46.7% grew approximately 0.1 to 0.2 cm in diameter a year, while 10.4% were found to have not grown at all. On average, a *R. vomitoria* individual receiving little to no direct sunlight—i.e., a shade suppressed individual—grew 0.124 cm in diameter a year, while a *R. vomitoria* individual receiving direct sunlight throughout the day—i.e., a shade dominant individual—grew 0.404 cm in diameter a year. The maximum observed growth rate for a suppressed *R. vomitoria* individual was 0.5 cm diameter growth a year and the minimum was zero. The maximum observed growth rate for a dominant *R. vomitoria* individual was 0.7 cm diameter growth a year and the minimum was zero.

For suppressed *R. vomitoria* individuals, I observed a significant positive relationship between DBH size and diameter growth, where diameter growth increased by 0.0133 centimeters for every 1 cm of DBH size increase. However, for dominant *R. vomitoria* individuals, I observed a marginally significant negative relationship between DBH size and diameter growth, where diameter growth decreased by 0.0237 centimeters for every 1 cm of DBH size increase. This may be explained by some tropical tree species' tendency to divert resources away from DBH growth and towards other goals such as fruiting or developing a dense foliar canopy when reaching a full light status in their environment (Amaral et al. 2001), or once beyond a certain DBH size (Le Bec et al. 2015). Additionally the amount of light received by the *R. vomitoria* individuals could play a part, e.g., this pattern was somewhat observed for a *R. vomitoria* growth study pertaining to reserpine concentration in Yunnan, SW China, where average total-biomass growth was highest for *R. vomitoria* individuals with 75% light irradiance levels, followed by *R. vomitoria* individuals with 100%, then 50%, and then 25% levels irradiance levels (Cai et al. 2009).

To compare these growth estimates to other invasion tree species in the North Kohala area, *Falcataria moluccana*, one of the fasted growing trees in the world (Walters 1971) has been observed in state-owned plantations in East Java to reach a mean diameter of 11.3–18.7 cm, and a maximum diameter of 25.8 cm, in 3 to 5 years (Kurinobu et al. 2007). Furthermore, a study of tree growth in secondary tropical forests in Puerto Rico observed an average diameter at breast height growth of 2.1 centimeters and a maximum of 12.4 centimeters over a 10-year period for a group of fourteen shade tolerant small trees including *P. guajava*. For their entire study pool of 81 tree species, they observed an average annual DBH growth of 0.37 centimeters, ranging from a

minimum of 0.01 cm for *Persea americana* to a maximum of 0.92 cm in *Spathodea campanulate* (Adame et al. 2014), a known invasive tree in Hawai`i. In Florida, *S. terebinthifolius* has been observed to grow an average of 0.41 cm DBH per year, and *M. calvescens* can grow an average of ~1 cm DBH a year (Loope 1997 - HNIS Report for Miconia Calvescens). And to compare these growth estimates to dominant native Hawaiian trees, *M. polymorpha* can grow an average of ~0.13 cm DBH a year (Hart 2010), and *A. koa* can grow an average of ~0.5 cm and maximum of ~1 cm DBH a year (Scowcroft et al. 2007).

Finally, given that these estimates are based on only two measurement periods, 2013-2014 and 2014-2015, the potential exists for these observations to be dependent on a certain set of climatic or other unknown variables that existed during my observation periods. Furthermore, my growth estimates may be somewhat restrained by not encompassing the potential growth of larger, more dominant R. *vomitoria* individuals because all the *R. vomitoria* individuals observed were of a generally small stature, i.e., 0-6 cm DBH, and because of the large discrepancy in sample sizes between *R. vomitoria* individuals with a suppressed shade class (*n*=205) and those of a dominant shade class (*n*=56). However, smaller sized *P. cattleianum* individuals of <1.0 cm DBH were observed to grow an average of 0.3 cm DBH over a year period in Hawai‘i Volcanos National Park, which is still larger than my average estimate for all observed *R. vomitoria* growth, suggesting that *R. vomitoria* may simply be a slower growing species than other common invasive trees in Hawai‘i (Huenneke & Vitousek 1990)

1.5.2 Seed Viability

The TZ test and field tray test produced large differences in estimates for viability of *R. vomitoria* seeds, both initially and over time. For example, the initial average germination rate was 27.25% and 4.0% for the TZ and Field tray tests respectively. However, this was to be expected somewhat given the nature of the tests, i.e., the TZ method can detect any remaining viability in a seed, while the field tray method can only detect viability in seeds that complete their entire germination cycle (Freeland 1976). Nevertheless, the average germination rate at the end of my observations—36 months since burial—was 10% and 1.5% for the TZ and Field tray tests respectively, representing a declining trend for both methods, and a level of significant difference for the TZ test observations. Furthermore, both regression models found that *R. vomitoria* seed viability had a significant negative relationship with months since burial, where percent viability

decreased 0.5% and 0.07% per month for the TZ and Field tray tests respectively. However, my observations cannot demonstrate unequivocally that *R. vomitoria* seeds reach a viability of 0% after a certain amount of time.

To compare these estimates to other invasion tree species in the North Kohala area, *P. cattleianum* has been observed in lowland wet forests of Hawai‘i Island to have a seed viability of 22.3% at one month since burial, and 0% at 6.5 months since burial (Uowolo & Denslow 2008), and *S. terebinthifolius* has been observed in Florida to have a seed viability of 30-60% at 2 months since burial, and 0.05% at 5 months (Gioeli & Langeland 1997). For native tree species, *M. polymorpha* seed under ideal experimental conditions represents an average viability of ~15.5% after 30 days in storage conditions (Burton 1982). *A. koa* in general laboratory conditions represents an average viability of ~66% (Gardner 1980).

In general, tropical rain forests seeds have the shortest ecological longevity of seeds of any plant community, with a tendency for rapid germination immediately after dispersal (Vázquez-Yanes & Orozco-Segovia 1993). This assessment corresponds well with the above-mentioned observations for *P. cattleianum* and *S. terebinthifolius*, and my findings for *R. vomitoria* adhere to this trend somewhat as well. However, given that over the course of 36 months of burial some *R. vomitoria* seeds were still found to be viable for both test methods, *R. vomitoria* may represent a longer than average seed longevity for tropical tree species. Furthermore, some tropical tree species in Hawai‘i have been observed to have seed longevity lengths far beyond 1-2 years, e.g., Meyer (1994) has verified *M. calvescens* seed life in soil samples of more than 2 years—and later in time—up to 15 years or more (Meyer pers. comm., in Hester et al. 2010). However, given that seed size and time of fruiting can have an effect on both germination rates and seed longevity in the tropics, where smaller seeds may tend to germinate faster than large seeds (Leishman et al. 2000) and plant species that fruit during a rainy season can have heavier seeds and shorter viability than plant species that fruit during a dry season (Murali 1997), inter-specific comparisons for seed longevity can be difficult and confounded.

Finally, to address the effect of experimental burying on seed viability compared to a more natural deposition mechanism, studies have shown no indication that burial conditions enforced or induced any artificial dormancy in the seeds of primary forest trees (Hopkins & Graham 1987).

1.5.3 Dispersal Distance

I estimated that *Z. japonicus* could disperse a *R. vomitoria* seed an average of 184 meters, and a maximum of 947.5 meters during a 30-minute gut retention period, and an average of 209.4 meters and a maximum of 1,053.2 meters during a 60-minute gut retention period. Furthermore, I estimated that for the entire data set, with time periods ranging from 22-130 minutes, an average dispersal distance of 207.04 meters and maximum of 1052.23 meters. The estimates for the two times periods and the entire data set were relatively similar in both the average and maximum dispersal distances. This could suggest that *Z. japonicus* would disperse *R. vomitoria* seed relatively the same distance, both typically and rarely, if gut retention time was either 30, 60, and up to 120 minutes. However, the standard errors associated with the average estimates were quite large, e.g., 179.05 for the entire data set average of 207.04 meters, and should be taken into account when considering these dispersal estimates.

My linear regression analysis for dispersal distance did find a significant positive relationship between flight time and flight distance, suggesting that as gut retention time potentially increases for *Z. japonicus*, so could the distance the *R. vomitoria* seed is dispersed. This increase was at a small rate of 0.581 meters of distance for every minute of travel, and the constant, or y-intercept for this regression model was 170.52, which quite above the 0 meters of distance one would expect for 0 minutes of flight time. This could imply that this method may not yield practical estimates for dispersal distance in the lower bounds of flight time.

To compare these dispersal distance estimates for *R. vomitoria* to local native tree species, *A. koa* seeds are large and dispersed largely by gravity and somewhat by wind, and consequently limited to about 50 meters of distance (Brewbaker 1972). *M. polymoprha* seeds are quite small and can be dispersed by wind currents across very large distances under certain weather conditions, but the density of seed can decrease by 95% once 250 meters away from the source tree (Corn 1972; Drake 1992; Hatfield 1996).

To compare these dispersal distance estimates to three other invasive tree species in Hawai‘i, *P. cattlianum*, *M. calvescens,* and *S. terebinthifolius* all have fleshy fruit or seed similar in size to *R. vomitoria's* (Pannetta 1997; Meyer 1998; Shiels 2011), and generally are browsed upon by the same bird species I observed foraging on *R. vomitoria* fruit, e.g., *Z. japonicus, C. cardinalis, G. striata,* and *L. lutea* (LaRosa 1985; Chimera 2010; Medeiros 2004; Wu et al. 2014a).

This suggests that *R. vomitoria* fruit is likely dispersed by the same pool of bird species as these three invasive trees, and therefore should be dispersed relatively the same distances.

There are a number of differences in landscape characteristics between the North Kohala *R. vomitoria* invasion site and the kipuka system—a once contiguous forest of 3000-5000 year old substrate currently fragmented by volcanic lava flows—where Wu et al. (2014a) conducted their research. The elevation is higher at 4900-5700 feet above sea level, receives more rain with 2000-3000 millimeters of rainfall per year (Giambelluca et al. 2013), and represents slightly lower temperatures ranging from 50 to 70 °F. However, given the fragmented agricultural landscape of the North Kohala *R. vomitoria* invasion site—where pastures, orchards and timber plantings in various states of abandonment, abut gulches, developing alien forests, and remnant native forest—the area may also resemble a number of kipuka characteristics. For example, the sixteen fragmented forests in Wu et al. (2014a) ranged in size from 0.25 to 25 acres, with a mean size of 4.2 to 6.1 acres, dimensions that could well represent the heterogeneous forest stands of the North Kohala *R. vomitoria* invasion site.

This can be important because landscape characteristics can have an effect on seed dispersal distance by birds. For example, in central Germany dispersal distances the blackbird species *Turdus merula* were observed to be larger within farmland environments, when compared to within forest stands (Breitbach et al. 2012).This type of habitat effect has been observed in disposal behavior for *Z. japonicus* as well, where in the dryland forests of East Maui Island, 96.9 percent of all avian dispersed seeds were deposited beneath trees, which represented only 15.2% of the study area (Chimera & Drake 2010).

Wu et al. (2014a) did not incorporate gut retention times into their observations for *Z. japonicus* movement, and consequently, the data set and my analysis specifically represents movement, not dispersal behavior over time. However, given that bird behavior involves constant feeding (Howe 1977), and that the maximum observed period of 120 minutes is a fair over-estimate of potential gut retention times for *Z. japonicus* (Herrera 1984; Levey & Karasov 1989; Stanley & Lill 2002; Brown & Downs 2003; Logan & Xu 2006; Wu et al. 2014a), I assume that *Z. japonicus* dispersal behavior was observed inherently in their movement, and therefore my estimates relevant for *R. vomitoria* dispersal potential.

Wu et al. (2014a) did conduct fecal sample analyses upon *Z. japonicus* within this kipuka system, and found some types of fruit species similar in form to *R. vomitoria* fruit. For example,

153 of the 160 seeds collected were from the two *Vacciumium* species *reticulatum* and *calycinum*, which share a similar red to orange color and size, 6-13 mm, with *R. vomitoria*. This can also be an important consideration given that dispersal distance has been shown to negatively correlate with seed mass in tropical forests (Muller-Landau et al. 2008).

To compare my estimates to other tropical frugivorous dispersal distances in respect to gut retention time, (Weir & Corlett 2007) Chinese birds observed in the fragmented forest landscapes upland of Hong Kong with median gut retention times of 42 and 77 minutes, were observed to have median dispersal distances of 40 to 131 meters and maximum dispersal distances of 1,005 to 1,124 meters. Larger birds with maximum gut retention times ranging from 100 to 159 minutes, were observed to have maximum dispersal distances of 348 to 803 meters. However, all these birds tend to be much larger than *Z. japonicus*, which can also effect dispersal distances (Wotton & Kelly 2012), with average grams of body mass ranging from 7 to 8 grams for *Z. japonicus*, and 26 to 100 grams for the observed Chinese birds (Su et al. 2012; Wu et al. 2014b; Wu et al. 2015).

1.6 Conclusion

My estimates for three invasive trait parameters, growth rate, seed viability, and dispersal distance, will facilitate an evaluation for the invasiveness of *R. vomitoria* relative to those of other invasive tree species in the North Kohala region and Hawai‘i Island.

For example, *R. vomitoria* DBH was observed to grow at an average of ~0.15 cm across all shade classes, ~0.4 cm across the dominant shade class, and a maximum of ~0.7 cm a year. This is lower than *F. moluccana*'s, *M. calvescens',* and *A. koa*'s ability to respectively grow at an average of ~3, ~1, and ~0.5 cm DBH a year and is only slightly faster than the dominant native tree species in the area, *M. polymorpha*, which can grow an average of ~0.13 cm DBH a year. Other tropical, shade tolerant trees including *P. guajava* can grow at an average of ~0.2 cm and maximum of ~1.2 cm a year, and a larger pool of tropical trees including Hawai‘i invaders like *Spathodea campanulata* can grow at an average of ~0.4 cm a year. Finally, *P. cattleianum* individuals less than one DBH in size have been observed to grow faster than my total observations for *R. vomitoria*, with an annual DBH increase of 0.3 cm. And in the same study, mortality rates for these small *P. cattleianum* individuals was ~5.5%, which is lower than my observation of 14.5% for all observed *R. vomitoria* individuals. This suggests that in general, *R. vomitoria* can grow comparably in speed to some tropical tree species both native and invasive, e.g., *M. polymorpha* and *P. guajava,* but also dramatically slower than some of the more notorious invasive species, e.g., *F. moluccana*'s and *M. calvescens*.

The average initial seed viability of *R. vomitoria* was observed to range from ~4% when tested in the field, to ~27% when tested in a laboratory, which is higher than laboratory observations of ~15% for *M. polymorpha* (Burton 1982), but lower than general observations of 66% for *A. koa* (Gardner 1980). The TZ test value of 27% seed viability is comparable to *P. cattleianum*—which has been observed after one month of fruit-burial to represent an average germination rate of 22.3% (Uowolo & Denslow 2008)—but lower than observations for *S. terebinthifolius* which can represent a 30-60% germination rate after two-months of burial (Gioeli & Langeland 1997). And while both *P. cattleianum* and *S. terebinthifolius* seeds have been observed to respectively reach 0% and 0.05% viability after 6.5 and 5 months of burial, I was not able to observe *R. vomitoria* fruit reach a viability of 0% over my three years of observation. This is important to note because other tropical fruit seeds have much longer lifespans, e.g., 15 years and counting for *M. calvescens* (Meyer pers. comm., in Hester et al. 2010), and this could be true

as well for *R. vomitoria*. Given this, and local land managers reports of very dense, monotypic understories of *R. vomitoria* juveniles, ranging between 50 to 300 individuals in one square meter, *R. vomitoria* appears to possess a comparatively average to high level of seed viability, which can translate into strong propagule pressure (Personal Observation, Personal Correspondence with Cody Dwight).

The ability to be dispersed by frugivores is a common high-risk invasive trait (Pyšek & Richardson 2008), and one that comparatively elevates *R. vomitoria* dispersal abilities above other local tree species with shorter dispersal methods, e.g., gravity for *A. koa*, or a maximum wind dispersal distance of ~80 meters for *Albizia julibrissin* seed (Pardini & Hamrick 2008)—which has similar seed to *F. moluccana* (Little & Skolmen 1989). Therefore, my observations of avian endozoochory associated with *R. vomitoria*—paired with the chance for random long distance dispersal events through the epizoochary of wide ranging animals such as wild pigs (Personal Observation, Personal Correspondence with Cody Dwight)—suggest that *R. vomitoria* possesses a comparatively high level of dispersal ability.

Overall, *R. vomitoria* appears to grow slower than locally-notorious invasive trees, and only slightly faster than the dominant native tree species *M. polymorpha*. However, its seeds are just as initially viable, may last longer than most tropical invasive species, and share the same long distance dispersal vectors. This, along with widely reported observations of its apparently shade tolerant, mono-specific stands, suggests that *R. vomitoria* may not reach a dominant position quickly in a Hawaiian forest, but can nonetheless. Given that its introduction was likely less than 60 years ago, and the somewhat common phenomenon of "lag-time" observed in some invasive species invasions (Crooks et al. 1999), *R. vomitoria* could express a greater level of invasiveness over time. For example, North Kohala may represent only a portion or edge of *R. vomitoria*'s potential habitat, and perhaps other areas of Hawai'i more similar to its native climate could facilitate a greater invasive potential. Additionally, the DBH distribution for my total *R. vomitoria* observations was skewed to the left (See figure 1.3), with the average DBH size of 2.75 cm being much lower than the maximum observed value of 33 cm. This could suggest that *R. vomitoria* population may still be developing in forest stature, and the form of its climax community, or at least a more advanced state, may yet be unobservable. Finally, there is the chance that these three parameters do not cover the more important, or threatening invasive traits for *R. vomitoria*, for example, its suggested extreme shade tolerance. Tests that analyze a greater number of invasive

traits may help to address this kind of omission, and the Hawai‘i-Pacific Weed Risk Assessment, which covers 49 questions for invasive traits, ranks *R. vomitoria* into the ~97 percentile of invasive threat for plant species in Hawai‘i (Daehler et al. 2004; www.hpwra.org 2017).

With these comparisons, managers concerned with the potential threat for *R. vomitoria* now have better information regarding its risk priority compared to the other myriad problems most natural resources face in Hawai`i. This can lead to better decision making, agency and community involvement, and funding requests for concerned parties (Hiebert 1997; Anderson 2005; Mehta et al. 2007; Keller et al. 2009). Furthermore, through the estimates and statistical models created for these comparisons, managers can quantitatively scale their management efforts towards certain aspects of *R. vomitoria* control. For example, this study has helped determine the time period that managers will have to wait until a *R. vomitoria* seed bank is depleted to a certain level of viability or how long it takes for an *R. vomitoria* individual to reach a certain size. The next chapter will deal with how to better answer these questions, and how the different scales of those answers, e.g., considering average or maximum dispersal distance, can accumulate to different management costs.

Chapter 2:

Utilizing Biological Parameters to Estimate the Management Cost of *R. vomitoria* Containment in North Kohala, Hawai‘i

2.1 Introduction

2.1.1 Invasive Species Management

In chapter one, I examined the growth rate, seed viability, and dispersal potential of *R. vomitoria* on the island of Hawai‘i. This work suggested that *R. vomitoria*, even in the best conditions, is slow in increasing its diameter over time when compared to other invasive trees and therefore may not have the capacity for rapid growth. However, my comparisons also suggest that its seeds can have a relatively long lifespan and long-distance dispersal potential. Although only three invasive trait estimates are not enough to understand a species' overall invasive threat, other studies concluded *R. vomitoria* represents the potential to be a high-risk invasive species (Daehler et al. 2004; Chimera 2012). Finally, those most involved with *R. vomitoria* invasion in Hawai‘i—Kohala Watershed Partnership (KWP) and the Big Island Invasive Species Committee (BIISC)—the land-managers currently dealing with its presence, commonly observe *R. vomitoria* becoming the dominant tree species within numerous native and alien forest environments (Personal Correspondence with KWP and BIISC).

Given all this, *R. vomitoria* may not represent an invasive threat to Hawai‘i on the same level as *M. calvenscens* or *P. cattleianum* (Lowe et al. 2000), but it may still have a strong potential to displace native systems through high levels of propagule pressure and shade tolerance, albeit only over large periods of time due to its slow growth. Fortunately, *R. vomitoria* is currently found in one limited area in Hawai‘i, its borders have been delineated, and local stakeholders are interested and engaged in attempting to manage its presence. Therefore, this potentially manageable current distribution, paired with my results, suggest that management of the *R. vomitoria* as an invasive threat to North Kohala is the correct response from natural resource agencies in Hawai‘i. However, the strategies and costs associated with this management should be developed through the above understandings for *R. vomitoria*'s relative invasive risk as well as conservation agencies' current and future capacities to deal with this relative risk compared to the other myriad—and potentially more dangerous—threats facing Hawai‘i's natural systems.

In general, management of invasive species is a difficult process (Simberloff 2003), taking the form of various strategies (Carlton 2003). Eradication, the destruction of all individuals in a new range, is the clearest and most direct strategy in invasive species management (Vitousek et al. 1997). However, the success of an eradication-campaign largely depends on the detectability of the invasive species (Clout & Veitch 2002), while its cost largely depends on the invasion's

establishment (Mack & Lonsdale 2002). Due to the lag time between first detection of the invasion and subsequent management actions, eradication is not often feasible (Rejmánek & Pitcairn 2002; Panetta & Lawes 2005) because established invasions require enormous and expensive eradication campaigns, often taking decades to achieve (Panetta 2009).

Currently, the population of *R. vomitoria* in North Kohala, Hawai‘i, represents a management area of approximately 8,000 acres. On average, it costs approximately $300 dollars for active managers to remove all detected *R. vomitoria* individuals from an acre of land in North Kohala (Personal Correspondence with KWP and BIISC). Since active management of *R. vomitoria* began in 2008, the average funding for *R. vomitoria* management is approximately $35,000 annually, and therefore is far below the ~$2,400,000 needed to conduct just the first sweep in a successful eradication campaign (Personal Correspondence with KWP and BIISC). Given this, the managers of the *R. vomitoria* invasion have decided that the eradication of *R. vomitoria* from North Kohala is currently not feasible, (Personal Correspondence with KWP and BIISC; Moore et al. 2011b). This decision is supported by my findings in chapter one, in that *R. vomitoria's* relative invasive risk may not represent a threat worthy of large and upfront sums of money and labor, nor do conservation agencies associated with *R. vomitoria* management currently have the means to provide these funds.

Biological research into the population ecology of invasive species can provide useful insight into creating procedures, not only for risk assessment, but also for effective management strategies (Simberloff 2003). Comprehensive research into the population ecology of both an invasive species, and its respectively invaded habitat, can be used as parameters for population modeling, projecting possible patterns of dispersal, rate of spread, and decision analysis (Maguire 2004). Furthermore, through estimating an invasion's key demographic parameters—such as its capacity for dispersal and growth (Harris et al. 2009)—an integrated management campaign can model, evaluate, and implement the best practices for critical maintenance inputs, e.g., the required area and frequency of surveillance and control (Buckley et al. 2001; Buckley et al. 2003). This type of interdisciplinary collaboration between academics and managers is essential for improving future invasive species management strategies (Sheley & Krueger-Mangold 2003).

Containment, the deliberate and perpetual prevention of emigration beyond a predefined area (Grice et al. 2012), is often presented as the second option when eradication is deemed unrealistic (Moore et al. 2011b; Grice et al. 2013). The agencies managing *R. vomitoria* on Hawai‘i

Island, Kohala Watershed Partnership (KWP) and the Big Island Invasive Species Committee (BIISC), have chosen containment as the management strategy towards the North Kohala *R. vomitoria* population (Personal Correspondence with KWP and BIISC). My findings in chapter one support this decision in that while *R. vomitoria's* relative invasive risk may not warrant the costs of an eradication campaign, it nonetheless is an invasive risk and should be managed as one—as far as conservation agencies can relatively afford too. Given that the necessary upfront costs involved in a containment campaign are typically below that needed for eradication (Sharov 2004; Burnett et al. 2006; Cacho et al. 2008; Rout et al. 2011; Fletcher et al. 2015), it is possible that conservation agencies can better afford to implement this type of practice.

However, containment will require similar needs for detection and removal as eradication, and although this is may be on a smaller and therefore more practical spatial-scale, it will also be on a far larger temporal-scale (Panetta 2007). For example, in order to maintain containment, all *R. vomitoria* individuals dispersing outside the contained area must be removed before they reach maturity and extended the dispersal range of the invasion, and this must be done in perpetuity. Due to this temporal increase, the costs associated with containment can accumulate, rival, and eventually exceed those of an eradication-campaign over time (Cacho et al. 2008; Moore et al. 2011b). Therefore, feasible, sustainable containment programs must be built around clearly defined containment units—consisting of both an invaded zone, the core, and the surrounding zone of surveillance and control, the buffer zone. This buffer zone must not only be scaled spatially to account for *R. vomitoria*'s capacity for dispersal, but also temporally to account for *R. vomitoria*'s capacity for growth, e.g., how quickly a *R. vomitoria* individual can reach maturity (Grice et al. 2013). Over time, a buffer zone properly calibrated to account for *R. vomitoria*'s invasion potential should be able to successfully contain *R. vomitoria* while potentially maximizing cost-savings by lowering management buffer sizes and frequencies to their required levels and promoting the efficient use of limited resources (Panetta & Cacho 2014).

2.1.2 Research Questions

I will use the parameter estimates derived in chapter one for *R. vomitoria* growth rate and dispersal distance to estimate two basic management parameters: (1) frequency rate, or how often management needs to be conducted in order to prevent any *R. vomitoria* seedling from reaching maturity. and (2) buffer size, or how far from the core management needs to survey in order to

account for any *R. vomitoria* individuals that may have been dispersed from the core into the buffer zone. With these management parameters, I will can then estimate the dollar costs of these management actions by multiplying the cost of *R. vomitoria* control per acre, by the size of the buffer zone and rate of management frequency.

Furthermore, I use will predicative intervals to estimate how these two management parameters can vary across different levels of statistical, and thus management, confidence. For example, a buffer zone size that accounts for 95% of all possible dispersal distances will be smaller than a buffer zone accounting for 99.9% of all dispersal possibilities, and therefore cost less, but also with a higher risk of containment loss. And unlike a confidence interval which predicts the range that the mean value could fall within the statistical model, a predictive interval predicts range that *any* future data point could fall within the statistical model. This is important, because invasive species managers must account for rare or outlier events, e.g., a prodigiously fast growing *R. vomitoria* individual, or a rare long distance dispersal event, and not just average trends.

I will estimate this level of difference in predictive interval confidence—95% and 99.9%—in order to create two different management scenarios for the two management parameters, and calculate and compare their respective costs. This can provide managers more information regarding the cost of *R. vomitoria* containment as well as the ability to understand how these costs vary for different levels of management certainty or risk, potentially leading to better decision making and funding requests. Additionally, I will compare the costs of these management scenarios to the current average funding for *R. vomitoria* control. And if these cost estimates exceed current funding levels, I hope that these different scenarios can help managers more accurately request for funding, better focus on particular threats, e.g., buffer zone size is increased to the diminishment of management frequency, or spur changes in management tactics, e.g., aerial surveillance as opposed to ground surveillance.

2.2 Methods

2.2.1 Estimating Management Frequency Rate

In order to understand how quickly a *R. vomitoria* individual can grow from seedling to fruiting size, I will first estimate two variables, annual growth rate and minimum size at fruiting. My observations for fruiting *R. vomitoria* individuals found a mean DBH of 8.29 ± 3.3 centimeters, and a maximum and minimum DBH of 16.2 and 4.0 centimeters, discussed in chapter one. Since it is essential for successful containment to prevent any *R. vomitoria* individual in the buffer zone from reaching maturity, *R. vomitoria*'s potential for smallest fruiting size must be addressed by management. Consequently, I choose this minimum value of 4.0 centimeters, which I observed across 388 potential *R. vomitoria* individuals and other haphazard surveys, to be the minimum size that a *R. vomitoria* individual can fruit.

In regard to how fast *R. vomitoria* grows, I will use the general linear model for *R. vomitoria* growth calculated in chapter one (growth rate = DBH + shade class + DBH * shade class) to estimate annual growth across various life stages. Again, since it is essential for successful containment to prevent any *R. vomitoria* individual in the buffer zone from reaching maturity, *R. vomitoria*'s maximum growth potential must be addressed by management. Therefore, I will use the growth model to estimate how quickly a *R. vomitoria* individual with a DBH starting size of 0.01 centimeters will reach a DBH of 4.0 centimeters. I will accomplish this by determining the upper bound of the model's predictive interval throughout life stage sizes, i.e., what is the maximum growth that *R. vomitoria* can accomplish annually for an individual of X size, where X is an accumulating DBH value as the years increase from a time of zero and a DBH size of 0.01 centimeters. Once this X value has progressed through multiple iterations and become ≥ 4.0 centimeters, I will note the number of years that it took to grow from 0.001 centimeters to ≥ 4.0 cm as the minimum time needed for a *R. vomitoria* seedling to reach maturity—for both 95% and 99.9% predicative interval confidences.

2.2.2 Estimating Management Buffer Size

In order to best understand how far a *R. vomitoria* fruit can be dispersed from its source, I will determine both the main dispersal vector for *R. vomitoria* fruit, and how far this vector can disperse *R. vomitoria* fruit during its gut retention time. As discussed in chapter one, *Z. japonicus*

is the major dispersal vector for *R. vomitoria* fruit, and thus will be used as the model species for the following estimates.

To estimate how far *Z. japonicus* can disperse *R. vomitoria* fruit, I will use the linear regression model for *Z. japonicus* movement calculated in chapter one to estimate dispersal distance. Again, since it is essential for successful containment to prevent any invasive plant species from being dispersed beyond the buffer zone, *R. vomitoria*'s maximum dispersal potential must be addressed by management. Consequently, I will calculate a predictive interval for this linear regression model and the upper bound values will be used to estimate the maximum dispersal distance that can be expected for *R. vomitoria* by *Z. japonicus*.

I will use a flight time of 120 minutes as the X value for this linear regression model because I estimate this 120-minute value to be the maximum retention time that a *R. vomitoria* seed is likely to stay within a *Z. japonicus* gut. This estimate was based on a number of sources, including previous work for *Z. japonicus* (Herrera 1984; Levey & Karasov 1989; Stanley & Lill 2002; Brown & Downs 2003; Logan & Xu 2006; Wu et al. 2014) as well as personal correspondence with local avian dispersal experts (Personal correspondence with Dr. Art Medeiros). Therefore, the upper bounded value that the predictive interval produces for a flight time of 120 minutes will be taken as the typical maximum dispersal distance that a *Z. japonicus* could disperse *R. vomitoria* seed, for both 95% and 99.9% predictive interval confidences.

2.2.3 Estimating Management Costs for Containment

Currently, *R. vomitoria* managers in North Kohala have decided to only contain the Eastern and Southern borders of the *R. vomitoria* invasion site because they assume that the factors such as agricultural land-use or coastline will contain the Western and Northern borders (Personal Correspondence with KWP and BIISC). The length of this containment border is ~8,000 meters in length, and roughly delineates the shift from alien forest to pastureland across the Eastern border, and the shift from alien to native forest across the Southern border (See Figure 2.1).

Figure 2.1 – Map representing the Southern and Eastern containment boundaries for the R. vomitoria invasion area in North Kohala, HI

The costs associated with *R. vomitoria* containment in North Kohala will depend on the size of buffer zone, and the frequency of management control within the buffer zone (Moore et al. 2011b; Grice et al. 2013). Therefore, once I estimate the buffer size and management frequency necessary to contain *R. vomitoria* in North Kohala, I will then be able to calculate the associated management costs of these estimates, and for both predictive interval confidence levels of 95% and 99.9%. I will do so by multiplying the cost of *R. vomitoria* detection and control per acre ($300), by my estimates for the required size of the buffer zone and the annual management frequency. I have chosen to estimate the cost of *R. vomitoria* detection and control at $300 per acre through correspondence with the agencies managing *R. vomitoria*, (Personal Correspondence with KWP and BIISC).

Additionally, given that my estimates for management frequency will differ between shade dominant *R. vomitoria* individuals—those growing in an open light environment—and shade suppressed individuals—those growing in closed light environment—I will adjust the required management frequency based on the landscape characteristics of the buffer zone. For example, given the history of land use in the area, the environment surrounding the Eastern and Southern borders of the *R. vomitoria* invasion containment line is generally either a closed forest stand or

an open pasture. Therefore, through analysis of satellite imagery, I will divide the estimated buffer zone into two landscape types, forest or pasture. I will then estimate the management frequency and associated costs required for these two landscape types by using my estimates for growth with respect to *R. vomitoria* individuals with either a dominant shade status, (i.e., those in a pasture), or suppressed shade status, (i.e., those in a forest).

Finally, I will provide another cost estimate for *R. vomitoria* containment that compares the price of surveillance for *R. vomitoria* individuals within pasture landscapes by a ground crew, with the price of aerial surveillance through the use of a small unmanned aerial system (sUAS). The Big Island Invasive Species Committee has conducted research into both the efficacy and efficiency in using a sUAS to both detect *R. vomitoria* individuals and direct ground crews to them within a pasture landscape. Through this work, we estimate that a sUAS can save up to 72% in costs, by replacing ground crew surveillance with the one-person crew associated with sUAS aerial reconnaissance (Unpublished Data BIISC 2016). With this research, I will then calculate the cost of *R. vomitoria* containment when sUAS vs. ground crews are used to survey the pasture landscape types within the buffer zone.

2.3 Results

2.3.1 Required Management Frequency Rate

Using a predictive interval with 95% confidence based off the general linear model growth rate = DBH + shade class + DBH * shade class, I estimated that a *R. vomitoria* individual with a dominant shade class can reach fruiting size—i.e., a DBH >4.0 centimeters—within ~6 years, while a suppressed *R. vomitoria* individual can reach fruiting size within as quickly as ~13 years. Using a predictive interval with 99.9% confidence for the same model, I estimated that a *R. vomitoria* individual with a shade class of dominant can reach fruiting size within ~5 years, while a suppressed *R. vomitoria* individual can reach fruiting size within as quickly as ~9 years (See Figure 2.2, Table 2.1).

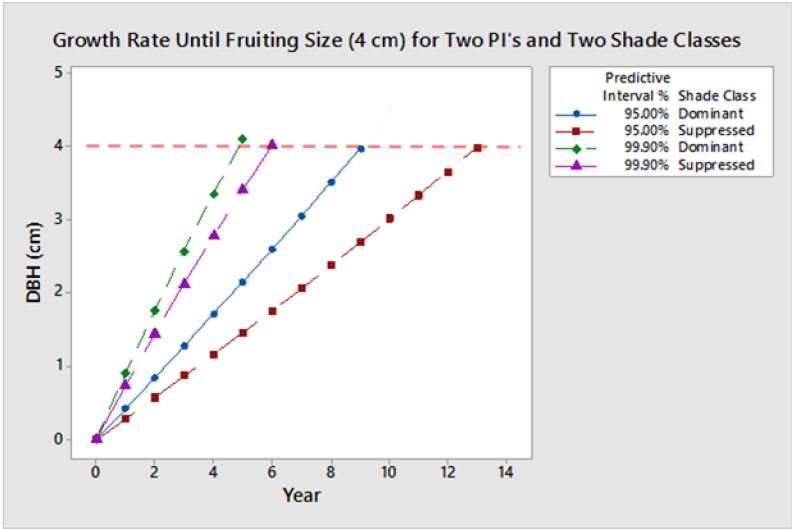

Figure 2.2 –R. vomitoria Growth Potential Estimated through the Upper Bound of a Predictive Interval for Two Shade Classes. The red line represents the estimated minimum DBH size at which fruiting can occur for R. vomitoria.

Individual RV Age (Years)	95% Predictive Interval				99.9% Predictive Interval			
	Suppressed Shade Class		Dominant Shade Class		Suppressed Shade Class		Dominant Shade Class	
	Predicted Annual Growth (cm)	Total Size (cm)	Predicted Annual Growth (cm)	Total Size (cm)	Predicted Annual Growth (cm)	Total Size (cm)	Predicted Annual Growth (cm)	Total Size (cm)
0	0.28	0.00	0.74	0.00	0.42	0.00	0.90	0.00
1	0.29	0.28	0.70	0.74	0.42	0.42	0.85	0.90
2	0.29	0.57	0.68	1.44	0.43	0.84	0.81	1.75
3	0.29	0.86	0.65	2.12	0.43	1.27	0.78	2.57
4	0.30	1.16	0.63	2.77	0.44	1.71	0.75	3.34
5	0.30	1.46	0.61	3.40	0.45	2.15	0.73	**4.10**
6	0.31	1.76	0.60	**4.01**	0.45	2.59	0.72	4.83
7	0.31	2.07	0.59	4.61	0.46	3.05	0.72	5.56
8	0.31	2.38	0.58	5.20	0.46	3.50	0.71	6.27
9	0.32	2.69	0.57	5.78	0.47	**3.97**	0.72	6.99
10	0.32	3.01	0.56	6.34	0.48	4.44	0.72	7.70
11	0.33	3.33	0.56	6.91	**N.A.**			
12	0.33	3.66	0.56	7.47				
13	0.34	**3.99**	0.55	8.02				
14	0.34	4.33	0.55	8.58				
15	0.35	4.67	0.55	9.13				

Table 2.1 R. vomitoria Growth Potential Estimated through the Upper Bound of a Predictive Interval for Two Shade Classes and Two Predictive Interval Confidence Levels

2.3.2 Required Management Buffer Size

Using a predictive interval with 95% confidence based off the linear regression model flight distance = flight time, and a maximum retention time of 120 minutes, I estimated that a *Z. japonicus* individual can disperse a *R. vomitoria* seed up to 589.69 meters from the seed source. And using a predictive interval with 99.9% confidence, I estimated that a *Z. japonicus* individual can disperse a *R. vomitoria* seed up to 827.53 meters from the seed source.

2.3.3 Required Management Costs for Containment

Based on my estimates, if 95% of all possibilities for *R. vomitoria* seed dispersal by *Z. japonicus* are accounted for by management, the area of the buffer zone will be ~1,300 acres, comprising ~800 acres of pasture, and ~500 acres of forest. However, if 99.9% of all possibilities for *R. vomitoria* seed dispersal by *Z. japonicus* is accounted for, the area will be ~1,750 acres, comprising ~1,100 acres of pasture, and ~650 acres of forest. Furthermore, if *R. vomitoria* growth is accounted for at the 95% confidence level by management, *R. vomitoria* individuals in open canopy areas will have to be controlled at a maximum of every 6 years, and *R. vomitoria* individuals in closed canopy areas will have to be controlled at a maximum of every 13 years. However, if *R. vomitoria* growth is accounted for at the 99.9 confidence level, *R. vomitoria* individuals in open canopy areas will have to be controlled at a maximum of every 5 years, and *R. vomitoria* individuals in closed canopy areas will have to be controlled at a maximum of every 9 years (See Table 2.2; Figures 2.3, 2.4).

Estimates for Required Management Actions for *R. vomitoria* Containment, for Two Predictive Interval Confidences					
Predictive Interval (Percent)	**Buffer Zone Estimate (Acres)**			**Management Frequency (Years)**	
Confidence	**Forest**	**Pasture**	**Total**	**Forest**	**Pasture**
95%	500	800	1,300	~6	~13
99.99%	650	1,100	1,750	~5	~9

Table 2.2 – Table representing estimates for containment of R. vomitoria in North Kohala in regard to two buffer size and management frequency required for two different predictive interval confidences.

Figure 2.3 – Map representing Two Different Landscape Types, Forest or Pasture, Outside the R. vomitoria Invasion Area in North Kohala, Hawai'i

Figure 2.4 – Map representing different buffer zone sizes for two different predictive interval confidences for R. vomitoria Containment in North Kohala, Hawai'i

Assuming that it costs roughly ~$300 to survey for and control one acre of *R. vomitoria*, the estimated annual costs for the above management interpretations are as follows: ~$51,540 for a buffer zone size and management frequency accounting for 95% of possibilities, ~$64,670 for a

buffer zone size and management frequency accounting for 95% and 99.9% of possibilities respectively, $70,000 for a buffer zone size and management frequency accounting for 99.9% and 95% of possibilities respectively, and ~$87,670.00 for a buffer zone size and management frequency accounting for 99.9% of possibilities (See Figure 2.4).

However, if I replace the cost of *R. vomitoria* detection in pasture environments by ground crews with that of sUAS reconnaissance instead, the estimated annual costs for the above management interpretations are lowered as follows: ~$35,540 for a buffer zone size and management frequency accounting for 95% of possibilities, ~$45,470 for a buffer zone size and management frequency accounting for 95% and 99.9% of possibilities respectively, $48,000 for a buffer zone size and management frequency accounting for 99.9% and 95% of possibilities respectively, and ~$61,270 for a buffer zone size and management frequency accounting for 99.9% of possibilities (See Table 2.3).

Survey Method	**Buffer Zone PI%**	**Management Frequency PI%**	**Annual Cost**
Ground	99.9%	99.9%	$ 87,666.67
sUAS + Ground	99.9%	99.9%	$ 61,266.67
Ground	99.9%	95%	$ 70,000.00
sUAS + Ground	99.9%	95%	$ 48,000.00
Ground	95%	99.9%	$ 64,666.67
sUAS + Ground	95%	99.9%	$ 45,466.67
Ground	95%	95%	$ 51,538.46
sUAS + Ground	95%	95%	$ 35,538.46

Table 2.3 – Estimated annual costs for R. vomitoria containment in North Kohala for eight different combinations of management scenarios—including sUAS reconnaissance—based upon the upper bound values of a predictive interval for their respective model

2.4 Discussion

2.4.1 Estimating Management Frequency in Relation to Minimum Generative Time

Altering the predictive confidence interval percentage between 95 and 99.9% resulted in two different estimated minimum generative times for *R. vomitoria* individuals; 5 versus 6 years for *R. vomitoria* individuals receiving direct sunlight, and 9 and 13 years for *R. vomitoria* individuals receiving only intermittent direct sunlight, throughout the day. It can be difficult understanding how these different estimates, and their associated empirical risks, can be interpreted by managers (Simberloff 2003; Maguire 2004). However, one could frame it as 95% of all *R. vomitoria* can reach maturity at 6 years of age (i.e., 95% confidence) but an additional 4.9% can reach maturity by 5 years of age (i.e., 99.9% confidence). Ideally management would always operate at 99.9% confidence, but given budgetary restraints this is often unfeasible. Therefore, by altering confidence levels—and comparing the associated management consequences—managers can better work with the resources currently available and understand what said resources are capable of accomplishing.

I assume through my observations that the minimum fruiting size of *R. vomitoria* is 4 centimeters at basal diameter, and this is likely the largest caveat regarding my minimum generative estimates. While I observed over 520 *R. vomitoria* individuals, only 33 *R. vomitoria* individuals were noted as fruiting. However, a large number haphazard DBH observations of fruiting *R. vomitoria* individuals of smaller size were also conducted during my field collections, yielding a similar conclusion. Nevertheless, a number of variables regarding these observed fruiting *R. vomitoria* trees were not possible to collect, including individual historical shade class or climatic characteristics, conditions which could have affected growth and fruiting behavior (Gregoriou et al. 2007). Finally, the assumption that fruiting is dependent on size for tropical tree species can be species dependent (Thomas 2011).

To compare my minimum generative estimates for *R. vomitoria* in North Kohala to elsewhere, Swaine and Hall (1983) haphazardly observed the early succession of tropical tree species within cleared land in Ghana, and found individual *R. vomitoria* trees flowering at only 2 years of age and 2 meters in height. It is interesting to note that the other pioneer species observed in the work represented either similar or faster generative times, e.g., flowers were observed on *Tetrorchidium didymosemon* at 2 years of age, on *Harungana madagascariensis* at 2 years for a 7.8 meter tall tree, and on *Trema orientalis*—a known invasive tree on Hawai‘i Island (Motooka

et al. 2003)—at 6 months for a 3 meter tall tree. Additionally, Swaine and Hall (1983) reported a observed mortality rate of 23%, which is higher than my observations of 12.7 and 14.5%.

Clearly this observed minimum generative time is much lower than my estimate. To compare, the study site for Swaine and Hall (1983) was the Atewa Range Forest Reseve in Ghana, representing an elevation of ~775 meters above sea level, a mean annual temperature of 22°C, and mean annual rainfall of ~2200 millimeters (Swain & Hall 1977). Before observations began, the site had been entirely cleared by the use of bulldozers, and consequently may have provided a more open environment encouraging *R. vomitoria* growth and maturation than a more natural setting. Finally, *R. vomitoria* was not the focus of the Swaine and Hall (1983) work, and observations for its generative time were byproducts of data collection, which may have impaired their accuracy.

However, large differences in growth characteristics between invasive plant species in their native and alien ranges have been observed before, and can be the result of different environmental (DeWalt et al. 2004) and genetic conditions (Willis et al. 2000). For example, Benitez and Ostertag (2010) compared growth characteristics between native and Hawaiian invasive varieties of *P. cattleianum*, *Clidemia hirta*, and *Tibouchina herbacea* in common garden, quarantine plots in East Hawai‘i Island, and found all invasive varieties to differ significantly from their native range counterparts.

Finally, to compare my minimum generative estimates for *R. vomitoria* in North Kohala to other invasive tree species in Hawai‘i, *M. calvescens* has been observed to fruit at 4 years of age (Medeiros et al. 1997), *P. guajava*, *P. cattleianum*, and *S. terebinthifoliuss* at 3 years (Yadava 1996), and *T. herbacea* at 2 years (Almasi 2000).

With these caveats stated, managers seeking to account for all potentials of *R. vomitoria* growth should assume a minimum generative time of approximately five years. As an example of how to apply this estimate to management actions, managers must ensure that in no *R. vomitoria* sprouted after control efforts will reach maturity, and therefore could conduct control efforts every: (a) five years to maximize cost savings by increasing time between management actions; (b) four years to better ensure that high growth rates for *R. vomitoria* potentially missed in my observation could better be accounted for; or (c) 2 years to account for the fact that management detection is imperfect and some *R. vomitoria* individuals may be missed during control efforts (Moore et al. 2011a).

2.4.2 Estimating Buffer Zone Size in Relation to Maximum Dispersal Distance

Altering the predictive interval confidence percentage between 95 and 99.9% resulted in two different estimated maximum dispersal distances for *R. vomitoria* seed by *Z. japonicus*, ~590 meters versus ~825 meters. Again, interpreting the level of management importance between different predictive interval confidences can be difficult, and in this case one could frame it as 95% of all *R. vomitoria* seeds are dispersed within ~600 meters—i.e., 95% confidence—but an additional 4.9% of *R. vomitoria* seeds can be dispersed up to ~830 meters, i.e., 99.9% confidence.

As stated, the maximum gut retention time of *R. vomitoria* seeds within *Z. japonicus* was assumed to be 120 minutes, and all dispersal distance estimates are based on this constant. And while the majority of literature reviewed and local researchers consulted agree that this is a fair or over-estimate for gut retention times (Herrera 1984; Levey & Karasov 1989; Stanley & Lill 2002; Brown & Downs 2003; Logan & Xu 2006; Wu et al. 2014), Medeiros (2004) did observe in East Maui a maximum gut retention time of 220 minutes for *Z. japonicus*, with a sample size of $n = 9$. However, through personal correspondence, this value was explained to most likely represent a sampling method error rather than accurate value (Personal correspondence with Dr. Medeiros). Additionally, this gut retention time value was in respect to invasive shrub *C. hirta*, whose seed is significantly smaller than *R. vomitoria*'s, a difference that can affect gut retention time (Figuerola et al. 2010).

No direct evidence is available concluding that *R. vomitoria* seed is viable after gut passage through a *Z. japonicus*, however many other seeds of tropical tree species have been proven viable after *Z. japonicus* gut passage (Medeiros 2004), and *R. vomitoria* seed has also been observed to be viable after dispersal by other animal species (Poulsen et al. 2001). Nevertheless, the assumption of 120 minutes of gut retention time for *R. vomitoria* seed in *Z. japonicus* is clearly a parameter that could be better understood in future analyses for potential *R. vomitoria* dispersal distance by *Z. japonicus*.

Furthermore, *Z. japonicus* is not the only vector for *R. vomitoria* seed dispersal in North Kohala. Approximately 4.5% of the observed foraged *R. vomitoria* fruit were ingested by non-*Z. japonicus* bird species. Additionally, KWP has observed *R. vomitoria* juveniles associated with known cattle trails, suggesting that epizoochary—e.g., seeds attached to animal fur or appendages—may be an additional dispersal vector for *R. vomitoria* (Personal correspondence with KWP). Differences in dispersal distance regarding epizoochory and endozoochory—seeds

ingested and deposited by animals—are dependent upon a number of variables, but a large study of dispersal distances for global temperate regions found that mean and maximum values for dispersal distance were generally the same at ~400 and ~1,500 meters for both epizoochory and endozoochory vectors (Vittoz & Engler 2007).

With these caveats stated, I estimate that for managers seeking to account for all potentials of *R. vomitoria* dispersal by *Z. japonicus*, the minimum buffer zone radius should be ~830 meters. As an example of how to apply this estimate to management actions, managers must ensure that no *R. vomitoria* individual is allowed to immigrate beyond the buffer zone from the core. Therefore, managers could draw a buffer zone radius of: (a) 830 meters to maximize cost savings by scaling the buffer radius to my estimates for *Z. japonicus* dispersal behavior; (b) ~1,000 meters to better ensure that dispersal distances for *R. vomitoria* by *Z. japonicus* potentially missed in my observation could better be accounted for; or (c) ~1,500 meters to account for the fact that other species may be dispersing *R. vomitoria* seed beyond my estimates for *Z. japonicus* (Vittoz & Engler 2007). Finally, it should be noted that dispersal distances can reach unprecedented levels—e.g., >6,000 meters—when accounting for agochory, the movement of seed by human actions (Vittoz & Engler 2007).

2.4.3 Estimating Costs for Different Management Scenarios of *R. vomitoria* Containment

Altering the predictive interval confidence percentage between 95 and 99.9% for growth and dispersal potential resulted in different management costs associated with the different combined management scenarios. The management scenario most avoiding the risk of containment loss, a buffer zone and management frequency accounting for 99.9% of growth and dispersal possibilities, had the highest annual cost of ~$87,700. If managers choose to instead account for only 95% of growth and dispersal possibilities—and consequently increase the potential for containment loss—they would then spend only ~$48,000 annually, saving about 45% in costs. This level of cost difference is significant especially considering containment's perpetual nature, and the actual management consequences associated with its increased risk should be better understood in order to compare its cost-benefit relationship and strategic implications. For example, how many *R. vomitoria* seeds could actually be dispersed within the additional ~140-meter buffer extension associated with the 95% and 99.9% predictive interval, and what chance

would they have to reach mature status and compromise containment given their seed viability, survivability, etc.

My cost estimates assume that a single field action by management would both detect and control 100% of all *R. vomitoria* individuals. However, given that all detection and control efforts are imperfect and multiple field actions may be necessary to ensure complete detection and removal all *R. vomitoria* individuals (Moore et al. 2011a), my cost estimates for management frequency may be significantly understated. Additionally, my cost estimates could also be greatly exaggerated due to my use of the upper bound, i.e., maximum value, of the predictive interval as opposed to the mean for my potential growth and dispersal estimates. For example, if all *R. vomitoria* individuals grew at my average estimate of 0.15 cm in DBH a year—as opposed to the maximum of ~0.6—then the management frequency necessary for containment would be over 25 years and the required management costs significantly lowered. Finally, assuming a cost of $300 per acre to survey for and control all *R. vomitoria* individuals is a very rough estimate at best, given the vast differences in difficulty that various landscapes can pose to management efforts, e.g., remote gulches versus roadside pastures.

Nevertheless, all my cost estimates for the different management scenarios are at least ~$13,000 higher than average funding levels for *R. vomitoria* management. This suggests that without enhanced funding or capacities increasing the risk of containment loss may be necessary in order to attempt containment at all, e.g., a buffer zone and management frequency accounting for only 90% of growth and dispersal possibilities. However, by replacing the cost of ground based detection actions with that of the increased capacity of sUAS reconnaissance, management costs are significantly lowered, and could account for 95% of growth and dispersal possibilities at ~$35,700 annually—a value within the range of average funding levels.

In general, sUAS technology used in this manner is relatively new, but a number of studies have proven its capabilities to detect invasive species targets in Hawai‘i (Perroy et al. 2017), and at a high level of accuracy in open field systems (Rango et al. 2009; Peña et al. 2013; Torres-Sánchez et al. 2013). This type of new technology could be essential is providing conservation agencies the cost-savings necessary to address a greater number of threats, and my cost estimates here, as well as my own field-studies for sUAS detection of *R. vomitoria* in North Kohala, help to support this notion. Furthermore, given my observations in chapter one regarding how *R. vomitoria* are much more likely to fruit only within a canopy or open-light position—i.e., 93% of all fruiting

trees were marked as shade dominant—aerial surveillance could also play a large part in search for fruiting *R. vomitoria* in forest environments, potentially extending the length of the required management frequency for those areas.

2.5 Conclusion

It seems that containment of *R. vomitoria* in North Kohala may be possible with the current level of average funding, at ~$35,700 annually for the cheapest management scenario. However, my estimates suggest that this containment would account for only 95% of growth and dispersal possibilities, and would additionally require enhanced surveillance capacities like sUAS reconnaissance. Ultimately, it is up to land managers to decide if this level of risk and technological investment is worth in attempting to contain *R. vomitoria* to its current boundaries. In addition, these managers could use this work to better request funding to improve this containment effort, or to compare the estimated costs of containment—up front and over time—with that of other management strategies, e.g., exclusion or biocontrol.

Much research has been done on evaluating the relationship between the cost of invasive species impact and the cost of their management, and how this changes in respect to the population's presence and growth over time (Leung et al. 2002; Yokomizo et al. 2009; Moore et al. 2010). Nevertheless, studies mostly agree that these costs will only increase—and at times exponentially—with the expanding size of the invasive population. Therefore, if the funding and feasibility exist to limit the size of invasive population to its current distribution, then conservation agencies associated with the invasion should strongly consider doing so, given that the problem will likely grow only larger in time (Naylor 2000; Sharov 2004; Buhle et al. 2005; Rout et al. 2011). However, this decision must be made in respect to current levels of funding for natural resource management in Hawai‘i, and what level of threat the invasive species poses to Hawai‘i.

My comparisons of *R. vomitoria* invasive threat to other invasive tree species suggest that *R. vomitoria* is certainly not the worst invasive threat currently within Hawai‘i, but given its potential to succeed in other habitat types and proximity to native forest systems, *R. vomitoria* is still likely to displace native species as its population grows. These comparisons in conjunction with my cost estimates can now provide decision makers with a better understanding of the threat that *R. vomitoria* poses and the cost of its containment. With these crucial estimates, the involved stakeholders can better make the right decisions in prioritizing how *R. vomitoria*'s invasive risk and management cost should be managed alongside Hawai‘i's other myriad natural resource threats.

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