PHENOLOGY, REPRODUCTIVE POTENTIAL, SEED DISPERSAL AND PREDATION, AND SEEDLING ESTABLISHMENT OF THREE INVASIVE PLANT SPECIES IN A HAWAIIAN RAIN FOREST

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BOTANY

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By
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We certify that we have read this dissertation and that, in our opinion, it is satisfactory in scope and quality as a dissertation for the degree of Doctor of Philosophy in Botany.

DISSERTATION COMMITTEE

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DEDICATION PAGE:

This work is dedicated to the memory of a brilliant and beloved mentor, Dr. Charles Lamoureux, a model teacher, a pioneering scientist in Hawai'i, and a great person.

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ABSTRACT

The objective of this study was to investigate phenology, reproductive potential, seed dispersal and predation, and seedling establishment of three important weed species (Clidemia hirta, Hedychium gardnerianum, Psidium cattleianum) of Hawaiian rain forests. The phenology results revealed that Clidemia ripe fruit production was highest from October through January, Hedychium from October through December, and Psidium in November. Compared to Psidium of similar sizes at lower elevations, the production of ripe fruit by Psidium at the study site appeared limited. Clidemia was estimated to produce more than four orders of magnitude more seeds than Hedychium and Psidium of equal cover. Individual Clidemia plants, which averaged 0.37 m^2 cover, produced an average of 3,815,552 seeds/yr. Birds, especially two common non-native species (Zosterops japonicus and Leiothrix lutea), are dispersing all three weed species as well as at least six native plant species, one non-native species, and four unidentified species. Under experimental conditions, the passage time for Clidemia seeds was as long as 210 minutes, for Hedychium seeds as long as 270 minutes, and with limited results, for Psidium seeds less than 60 minutes. Non-native rats (Rattus spp.) were discovered to be dispersing viable Clidemia seeds that did not differ significantly in germinability or germination rate from control seeds. Non-native rats were also discovered to have caused a 48.3% reduction in Hedychium seed production through flower bud, flower, and pre-dispersal seed predation. The final objective of this investigation was to determine which sites are suitable for germination and initial seedling growth of the study species. Results from Clidemia sites (but not Hedychium and Psidium) indicated a large, viable seed bank and/or substantial seed rain. Clidemia produced the greatest number and heights of seedlings in scalped and grassy sites. Hedychium produced the greatest number of seedlings in epiphytic sites and the least in grassy sites. Psidium were found in three site types, with the tallest seedlings being found in fernland sites. Data from the last part of this investigation suggest that Clidemia is disturbance-adapted and less adapted to protected, shaded sites, whereas Hedychium and Psidium are greater threats to recovering and intact rain forests.

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CHAPTER ONE:
INTRODUCTION

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ABSTRACT

Invasive, non-native plants have clearly emerged as one of the greatest threats to world biodiversity. On Maui island, Kīpahulu Valley, managed by Haleakalā National Park, contains some of the largest tracts of diverse koa (Acacia koa) and `ōhi`a lehua (Metrosideros polymorpha) rain forests in the state. Until recently, the primary threat to this forest was the effects of feral pigs (Sus scrofa). In the mid-1980s, the pigs were removed with a control program and a series of exclosure fences. Following the removal of pigs, native plant species increased and many non-native species decreased. However, the rapid spread rate and apparent ecosystem-modifying properties of three invasive plants began to alarm park resource managers; these include clidemia (Clidemia hirta (L.) D. Don, Melastomataceae), kahili ginger (Hedychium gardnerianum Ker. -Gawl., Zingiberaceae), and strawberry guava (Psidium cattleianum Sabine, Myrtaceae) (hereafter Clidemia, Hedychium, and Psidium). All three species are considered serious threats to wet forest in Hawai'i, on other oceanic islands, and elsewhere. I propose to investigate key life history attributes of these three species including phenology, seed dispersal, seed predation, and establishment sites. In the Hawaiian Islands and elsewhere, this study can provide important information for determining priorities and strategies for invasive plant control. On a theoretical level, it contributes to a more complete understanding of the life history attributes of invasive plants, which contributes to our developing model of invasive species ecology. Such a model has the potential to assess life history of non-native

species and to predict which have traits that indicate the potential to become serious invaders.

INTRODUCTION

I. GLOBAL OVERVIEW OF INVASIVE BIOTA

Introduced terrestrial biota are a growing problem that impacts human health, activities, and lifestyles, decreases agricultural productivity, and degrades native ecosystems. Increasingly, countries are linked by global trade and transport networks. Plant and animal species are inadvertently and intentionally introduced to new lands at an increasing rate. In the majority of cases, these species are completely dependent upon man for survival. A small percentage of species becomes naturalized, and a smaller subset has attributes which degrade native ecosystems. These relatively few species, however, are capable of serious and irreversible perturbations. In the U.S., fifteen serious invasive plant and animal species alone are estimated to cause future economic losses of 134 billion dollars (OTA 1993). The impacts of alien species are now widely recognized and few, if any, areas in the world appear free from their impacts (Vitousek et al. 1997).

Nonetheless, it is on isolated oceanic islands such as the Hawaiian Islands that invasive species pose the most serious threats to native ecosystems. The areas most prone to serious invasions of non-native species appear to be geographically isolated islands. Islands especially prone to problems with invasive species include Polynesia, especially New Zealand and the easternmost high islands of the Pacific, such as the Hawaiian, Marquesas, Society, Austral, and Galapagos Islands (Mueller-Dombois and Fosberg 1998), islands in the East Indian Ocean (Mauritius, Reunion, Madagascar, Rodrigues, Seychelles), and Saint Helena in the Atlantic Ocean. Other areas that also appear vulnerable to the impacts of invasions, but perhaps to a lessened degree, are volcanic and continental islands in the Pacific (e.g., Fiji, Tasmania, Juan Fernandez), the Atlantic (Madeira, Azores, Canary), as well as certain continental areas with Mediterranean or subtropical climates, such as Australia, California, Florida, and South Africa (Cronk and Fuller 1995; Groves and Di Castri 1991). Relatively invasion-free areas are the Arctic and Antarctica, northern boreal forests and tundra, the Neotropical forests, and to lesser degree Southeast Asian and African forests. Many islands of the Caribbean are relatively invasion-free in comparison with remote oceanic islands, perhaps because of lessened isolation and a native biota co-evolved with frequent hurricane impacts.

The most apparent common factor of invasion-prone areas is that they are all areas which are or have been geographically isolated. Generally, their biota are moderately speciose, largely endemic, and evolved from relatively few colonizing species. This last factor, the disharmonic nature of the biota, which is characteristic of isolated areas, is frequently cited as integral to the mechanisms of vulnerability to invasions (Loope and Mueller-Dombois 1989).

However, another factor in the susceptibility of these areas to invasions has been the increased disturbance that accompanies the habitation by humans. Chief among these has been the introduction of non-native ungulates that have caused large-scale destruction of native grasslands, shrublands, and forests. It is well documented that increased levels of disturbance facilitate invasions by non-native plant species. Perhaps the key attribute of insular biota that facilitates plant invasions is a greater vulnerability of island vegetation that has evolved without ungulates to mammalian herbivory and trampling. At some point however, ungulate-induced disturbance becomes so substantial that the “invader” plant species of the area could more accurately be described as “colonizing” species, becoming established in trampled and/or over browsed, highly disturbed areas (Bazzaz 1986). The role of ungulate-induced disturbance in ecosystem replacement by non-native species on islands has been considered but remains remarkably unexplored (Loope and Mueller-Dombois 1989; Merlin and Juvik 1992).

Invasive species are increasingly recognized as one of the most important and difficult factors that influence long-term conservation of native ecosystems. In restoration of degraded native ecosystems, invasive species may strongly affect recovery trajectories of individual native species and the long-term composition of restored ecosystems (Hobbs and Mooney 1993).

II. BIOLOGICAL INVASIONS IN HAWAI'I

Hawaiian biota provide a unique contribution to the world's natural heritage. Because of the volcanic origin and extreme geographic isolation of Hawai'i, the native biota is derived from few founder species, many of which have undergone spectacular adaptive radiations. These species-clusters, scattered across a diverse assortment of plant and animal groups, serve as invaluable sources of knowledge of evolutionary processes. The islands, for their small land area, have impressive diversity of endemic species. With only 0.18 % of the land area of the U.S., the Hawaiian Islands has 6.6% of the country's vascular plant species, 7.2% of bird species, 5.5% of insect species, and 51% of terrestrial mollusk species (Appendix I). Locally, native biota provides context for Hawaiian cultural activities, serve as effective watersheds, and provide unique landscapes for visitors.

The history of invasive species in the Hawaiian Islands began with the arrival of the first humans, colonizing Polynesians in the 5th century A.D. Based on the first European collections and archaeological evidence, it is likely that, along with plant and animal species intentionally introduced for agriculture and utility, voyaging Polynesians inadvertently imported several gecko and skink species, and at least three snail species and ten plant species (Kirch 1982). The Polynesian rat, <u>Rattus</u> <u>exulans</u>, may represent an inadvertent (Kirch 1982) or intentional introduction (Watling 1986). Based on existing evidence, the plant species introduced by Polynesians appear to have had negligible impact on native Hawaiian ecosystems.

First contact with Europeans in the late 18th century was quickly followed by the introduction of cattle, goats, sheep, European stocks of pigs as well as many non-native plant species, resulting in catastrophic losses of native Hawaiian plants and animals (Loope and Mueller-Dombois 1989). In leeward areas, browsing by introduced ungulates and invasions by non-native grasses have caused wholesale landscape changes involving greatly increased wildfire frequency and the loss of native species (D'Antonio and Vitousek 1992).

Of Hawaiian plants currently considered by the U.S. Fish and Wildlife Service as Endangered, Threatened, Candidate, and Proposed, invasive plant species are, by far, the most common reported threat (90.2%, 303/336 species) (Hawai'i and Pacific Plant Recovery Coordinating Committee 1998). A recent evaluation of invasive species in the Hawaiian Islands described the situation as one of crisis proportions (Holt 1996).

Over the past two hundred years, approximately 13,000-15,000 non-native plant species have been introduced to Hawai'i (George Staples pers. comm.), outnumbering native vascular plant species (1200 species) at an 11:1 ratio. Of non-native plants, 870 species have become naturalized, roughly 6% of the total (Wagner, Herbst, and Sohmer 1990). Of naturalized plants, about 100 species are considered to be a serious concern to natural area management (Smith 1985b; C.W. Smith pers. comm., 1998). Hence, of non-native plants in Hawai'i, one in 130-150 species has become a threat to native species (0.7% of all introduced plant species and 11.5% of naturalized species).

The first serious conservation efforts to curb this loss of Hawaiian plants and animals were undertaken in the 1970s and 1980s at Hawai'i Volcanoes and Haleakalā National Parks. These first attempts were focused primarily on the formidable task of removing non-native ungulates, mostly feral pigs and goats. After ungulate exclusion, the resurgence of both introduced and native vegetation was overwhelming. Other public and private land managers began ungulate exclusion programs to restore native ecosystems.

On the heels of this recovery from ungulate damage arose questions regarding the trajectories of invasive plants and outcome scenarios of these recovering ecosystems. Ecosystem restoration in Hawai'i is in its founding stages and lacks completed role model projects. One of the earliest and most important of restoration efforts in Hawai'i is focused on rain forests of Kīpahulu Valley in eastern Maui by Haleakalā National Park.

III. PROPERTIES OF INVASIVE PLANT SPECIES

The term invasive is used to describe species that are effective at naturalizing, dispersing, and modifying ecosystems. Cronk and Fuller (1995) distinguish “invasive plants” from “ruderals and weeds” that characteristically are “invading highly disturbed man-made or agricultural habitats”. They define an “invasive plant” as “an alien plant spreading naturally (without the direct assistance of people) in natural or semi natural habitats, to produce a significant change in terms of composition, structure or ecosystem processes.”

Two apparently independent characteristics are described here. The first is the ability without human assistance to disperse and become established in native ecosystems; the second is the ability to develop dense stand structure that modifies native ecosystems, leading to the loss and/or reduction of native species. To some extent, the traits that facilitate invasion (effective establishment, rapid maturation, high reproductive capacity, and effective dispersal) also contribute to development of the dense stand structure responsible for the decline of native species. However, in reality, this is not always the case. In Hawaiian rain forests, some species (e.g., the introduced fern, Deparia petersenii) are very effective at dispersing and becoming established over relatively long distances, yet does not develop the densities that substantially modify the invaded habitat. Other invasive species have relatively limited dispersal abilities yet once at a suitable site can come to dominate and displace native species. One example is the mat-forming grass Pennisetum clandestinum that on Maui produces no seeds, yet by vigorous vegetative production of stolons and rhizomes is a destructive and overwhelming invader of dryland forests. The most serious concerns to Hawaiian natural areas involve those species that spread rapidly and degrade invaded systems profoundly. One of the most impressive examples to date of such an invader is Miconia calvescens (Melastomataceae). Introduced to the island of Tahiti in the Society Islands in 1937 into a local botanical garden, this quick-growing tree spread rapidly. By the 1980s, extensive, very dense stands of this species had replaced much of the native rain forest of that island, directly threatening 40-50 endemic plant species with extinction (Meyer 1994; Meyer 1996; Meyer and Florence 1996).

Based on recent literature, predicted life history characteristics of highly invasive plants include:

- Rapid growth rate from seedling to first and full reproductive efforts
- Unusually effective capture and utilization of resources
- Self-compatible breeding system requiring either no pollinating agents or generalized ones
- Small seed size
- High reproductive output
- Effective dispersal mechanism
- Ability to establish in low-disturbance areas of native vegetation
- Ability to develop closed stands and suppress native species

The capability to produce large numbers of seeds annually with minimum duration between episodes of fruit production is cited as a characteristic of invasive plant species (Rejmanek and Richardson 1996). Quantitative estimations of numbers of seeds produced are difficult to record and rarely are done, especially for those species with exceptionally high reproductive output. Quantitative phenology of marked individuals can offer important insights into plant reproductive strategies (Wheelwright 1986).

Invasive plant species characteristically have an effective seed dispersal system suitable to allow the non-native species to first reach the new habitat, then to spread it throughout its potential range (Baker 1986; Rejmanek and Richardson 1996). Seed dispersal by vertebrates is an important trait associated with invasive woody plant species (Rejmanek 1996). Fleshy fruits and seed dispersal by non-native fruit eating birds are traits associated with invasive plant species on remote oceanic islands (Mueller-Dombois and Fosberg 1998).

Some have suggested that freedom from predators is one of the primary reasons certain non-native species are so competitive when released into new habitats. Seed predators are among the most important predators limiting plants (Harper 1977; Louda 1989).

Establishment of each species is dependent upon “safe sites” where dispersed seeds find the proper microhabitats for successful germination and growth (Harper 1977). This concept is especially important in evaluating the trajectories of invasive plant species in a given environment. A chief concern in this evaluation is assessing the role of disturbance in facilitating invasion. In terms of management of protected natural areas, the most problematic invasive plants are those that can become established in shaded sites or those of limited disturbance regimes.

Prior to control of feral pigs in Kīpahulu Valley, bare ground, caused by rooting, was very prevalent. Since feral pigs were controlled in the mid 1980s, however, bare ground in the valley has substantially decreased. Currently bare ground is only present due to water and human movements, and is now restricted to trails, fence routes, and eroding sides of watercourses. Many non-native plant species that proliferated in pig-disturbed clearings declined after pigs were eliminated. Areas that were formerly bare ground became colonized by extensive growth of the non-native grass Paspalum conjugatum. Based on field observations and semi-permanent plots, the general trend appears to indicate that the sites dominated by alien grasses are slowly being replaced by a native matted fern community, composed primarily of Diplazium sandwichianum. In pig-free Kīpahulu Valley, information is needed as to which of these vegetation communities provide “safe sites” that facilitate the spread of invasive species. Prior to fencing, feral pig rooting and traffic reduced many areas of rain forest understory to bare ground. Mechanically scalped plots can be used to experimentally model the impact of pig-disturbed sites on the germination and establishment of the three study species. I hope to make predictions regarding the trend of invasion potential for the three study species in pig-free Kīpahulu

Valley by determining the establishment response of each species in four sites characteristic of Kīpahulu rain forests (sites dominated by alien grasses, native Diplazium matted fern thickets, disturbed sites, epiphytic sites).

STUDY SYSTEM

I. STUDY AREA

The primary study site is Kīpahulu Valley within Haleakalā National Park. Due to the difficulty of access into Kīpahulu Valley (necessitating helicopter transport), Makawao Forest Reserve (hereafter Makawao F.R.), accessible by 4-wheel drive, were used for one of the study species, Hedychium, for certain work (seed dispersal, seed predation, and seed set). The State of Hawai'i Division of Forestry and Wildlife manage Makawao F.R. Invasive populations of all three study species are found in Kīpahulu; only Hedychium is common in upper Makawao F.R.

Windward Haleakalā Volcano contains some of the largest tracts of biologically diverse rain forest remaining in the Hawaiian Islands (Meyers 1997). This remote montane rain forest provides habitat for five federally Endangered bird species, 12 Endangered, 13 Proposed, and 24 “Species of Concern” plant species, as well as numerous unlisted, locally endemic invertebrate species. The rain forest vegetation of both Kīpahulu and upper Makawao F.R. is similar, the canopy being dominated by the trees \`ōhi\`a lehua (Metrosideros polymorpha) and koa

(Acacia koa), with diverse shrub, vine, and herb layers with the understory of many areas dominated by matted native ferns.

Currently, the greatest threat to Maui rain forests appears to be European stock domestic pigs that have become feral. These pigs first appeared in Kīpahulu Valley in the 1960s, becoming more common and eventually spreading to all parts of the valley and adjacent headlands by the 1980s (Diong 1982; Loope et al. 1991). Digging by pigs caused substantial ground disturbance facilitating the spread of many non-native plant species. Pigs also act as highly effective dispersal agents for the seeds of one of the areas important invasive plants, strawberry guava, transporting large numbers of seeds in droppings (Diong 1982). Selective herbivory by feral pigs virtually eliminated certain plant species from terrestrial habitats. Some native species survived locally in highly impacted forests as epiphytes. It is likely that feral pigs caused the regional extirpation of a number of endemic plant species (e.g., Cyanea grimesiana, Solanum incompletum). By the 1980s, an effort was launched by the National Park Service to protect this forest. A series of woven wire fences were constructed in the extremely rugged landscape and an intensive pig control program initiated. As a result, within much of Kīpahulu Valley, feral pigs have been excluded for about a decade (Anderson and Stone 1993).

The elimination of ungulates in natural areas has had profound ecological consequences. The removal of such an important source of disturbance caused two general responses in non-native plant species. One group of species was apparently dependent on ungulate disturbance; in ungulate-free areas, these species began to decline immediately. One example in Kīpahulu rain forests was thimbleberry (*Rubus rosifolius*), whose local dominance was largely replaced by native ferns following ungulate removal. The other group of species, problematic for land managers, was those that did not decline following ungulate removal but continued to spread.

After protection from feral pigs, native plant species in Kīpahulu have become increasingly more dominant as indicated by the increasing cover of native herbaceous species and increasing occurrence of younger size classes of shrubs and trees. In many areas within Kīpahulu Valley, recovery of native vegetation has restored an apparently intact native ecosystem. Though over 100 non-native naturalized plant species have been recorded in Kīpahulu Valley (Medeiros *et al*. 1998), only a few species continue to pose a significant threat to the long-term conservation of this area. Three of them have been identified as among the most invasive and modifying of invasive plant species: *Clidemia*, *Hedychium*, and *Psidium* (Anderson *et al*. 1992; Medeiros *et al*. 1995).

II. STUDY SPECIES

Clidemia hirta is native to Mexico, the West Indies, Central America and northern South America to Bolivia and southern Brazil (Gleason 1939; Smith 1992) (Figure 1). In its native range in Trinidad and Jamaica, *C*. *hirta* is a species of secondary succession, characteristically found in moist, shaded localities, on the edges of clearings and stream-banks, in ditches, along paths and roadways and in moist pastures and thickets from 30-900 m elevation (Cronk and Fuller 1995). Inadvertently introduced throughout much of its non-native range, presumably with seed-infested soil, it has become widely naturalized and, in many areas, is considered to be a threat to native vegetation (Table 1, Figure 1).

In the Hawaiian Islands, Clidemia was first reported in 1941 (on O'ahu) and on Maui on Haleakalā (East Maui) in 1976 and West Maui in 1982. On O'ahu where the species has had the longest tenure, Clidemia is ubiquitous in wet areas and in many places comprises the dominant vegetation. Populations increased dramatically on Kaua'i following hurricane-induced canopy disturbance. In areas such as Lumahuli, increases in Clidemia after Hurricane Iwa (1992) were estimated as fifty-fold within a few years (S. Perlman and K. Wood pers. comm.).

Eleven years after the first report of Clidemia on Maui in 1977, the area of its occupation in wet windward forests was estimated at 1200 ha (Medeiros et al. 1989). In 1988, Clidemia was first discovered in Kīpahulu Valley at 855 m

Table 1. Naturalized range of Clidemia hirta. In areas indicated by an asterisk, the species is considered to be a threat to native vegetation.

Area	Reference
Africa:	
*Tanzania	(“On the African continent, the unique Eastern Usambara mountain range of Tanzania is under threat from alien vines and shrubs, including Clidemia hirta and Lantana camara” Murphy 1998); Sheil 1994
Asia:	
Borneo (Brunei, Sabah)	Cronk and Fuller 1995; pers. obs.
Java	Cronk and Fuller 1995
India	Cronk and Fuller 1995
*Peninsular Malaysia	Peters 2001; Wee 1970
*Singapore	(“…only a tropical American, bird-dispersed shrub Clidemia hirta (L.) D. Don…(occurs) in primary and tall secondary forest patches” Teo et al. 2003) also Turner and Tan 1992
*Southeast Asia	Weber 2003; Cronk and Fuller 1995
Sri Lanka	Ashton et al. 2001
Taiwan	Yang 2001
Eastern Australia:	
*northern Queensland	(This species, first discovered in 2001 at a former tropical palm nursery site, has apparently been present since at least 1996. Based on field observations, local dispersal of seeds by birds (possibly fruit-eating doves and pigeons) appears very likely. An early eradication program is underway.) Smith 2002; F.D. Panetta pers. comm.; G. Werren pers. comm.

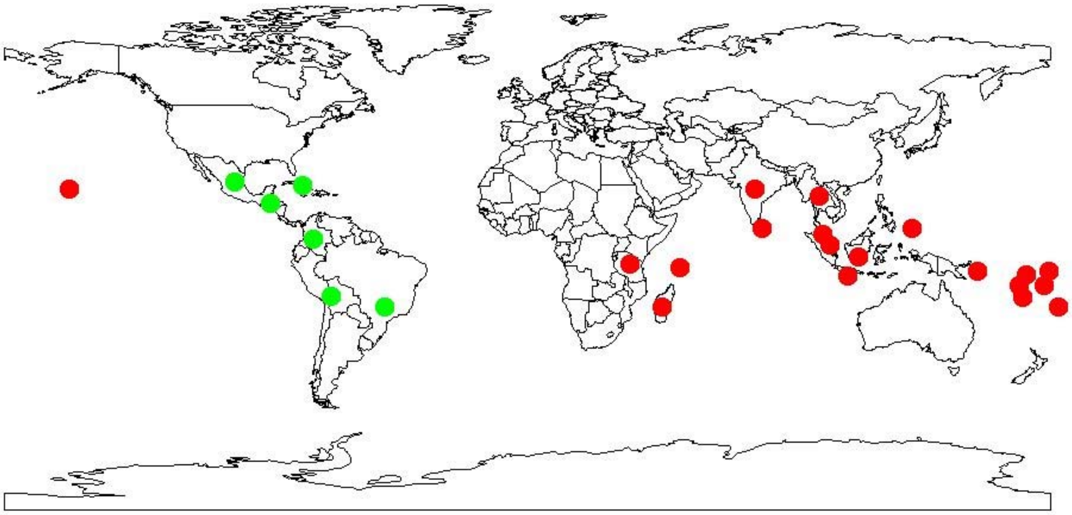
Indian Ocean islands:

Comores	Cronk and Fuller 1995
*La Reunion	Strasberg 1994; S. Baret pers. comm..
Madagascar	Binggeli 2003
*Seychelles (Silhouette and Mahe islands. Control and restoration program ongoing in Morne Seychelles National Park.)	Weber 2003; Gerlach 1993; Friedmann 1994; Cronk and Fuller 1995

Pacific Ocean islands:

*American Samoa (Tutuila, Ta’u, Ofu, and Olosega islands)	T. Togia pers. comm.; Whistler 1983
*British Solomon Islands	Weber 2003; Cronk and Fuller 1995
*Fiji (Viti Levu, Vanua Levu, Taveuni, Kandavu, Yasawas islands)	Smith 1985a; Meyer 2000
*Futuna	Cronk and Fuller 1995; Meyer 2000
Guam	Cronk and Fuller 1995
*Hawaiian Islands (Kaua’i, O’ahu, Moloka’i, Lānaʼi, Maui, and Hawai’i islands)	Smith 1992
Palau (Belau)	Whistler 1995
*Solomon Islands	Weber 2003; Swarbrick 1997; J. Space pers. comm.
Tonga (reported by Cronk and Fuller 1995 but not seen in recent survey – possible mistaken report)	Space and Flynn 2001
*Vanuatu	Weber 2003; Swarbrick 1997; J. Space pers. comm.
*Wallis	Cronk and Fuller 1995; Meyer 2000
*Western Samoa (Upolu and Savai’i islands)	Meyer 2000; Whistler 1983

Figure 1. Native and naturalized range of Clidemia hirta (green dots are native range; red dots are invasive range).



elevation (Medeiros et al. 1998). Despite substantial control efforts by management since that time, well-established populations of Clidemia persist in the valley and continue to spread at 825-1040 m elevation.

Hedychium gardnerianum is a cold tolerant, large (to 2 m height) ginger, native to the Himalayas and adjacent regions (Nagata 1990) (Figure 2), where it occurs at least up to 2500 m elevation (Graf 1992). The species was first collected by Dr. Nathaniel Wallich in Katmandu in the early 1800s, cultivated at the botanical gardens at Calcutta, India, and introduced to England in 1823 (Clay and Hubbard 1987). Widely cultivated in the tropics for its attractive, fragrant flowers, it has become widely naturalized and is considered to be a threat to native vegetation (Table 2, Figure 2).

In Hawai'i, Hedychium was introduced relatively recently (before 1943), yet is widely cultivated and considered one of the most attractive and desirable gingers for home gardens (Kuck and Tongg 1943; Neal 1965). It is well known as kahili ginger or `awapuhi kāhili for the similarity of the yellow and red inflorescences to Hawaiian feather staffs, the kāhili (Kuck and Tongg 1943). The Hawaiian name, kahili ginger, is now used worldwide as the common English name for this species (Graf 1992); the local Creole name on Reunion island is longose (Strahm 1999).

Table 2. Naturalized range of *Hedychium gardnerianum*. In areas indicated by an asterisk, the species is considered to be a threat to native vegetation.

Area Reference

Africa:

*South Africa (Natal; declared Category 1 Weed by the National Botanical Institute of South Africa http://www.plantzafrica.com/miscell/aliens2.htm) Weber 2003; Henderson 1995; Cronk and Fuller 1995

Australia (northern New South Wales and southern Queensland) Weber 2003; Lazarides, Cowley, and Hohnen 1997

Atlantic Ocean islands:

*Azores (Sao Miguel, Pico, Flores, and Terceira islands) Weber 2003; Cronk and Fuller 1995; C.W. Smith pers. comm.

Madeira Cronk and Fuller 1995

Caribbean islands:

*Jamaica (e.g., Blue Mountain National Park)
("The gradual change of the floristic composition of the forests due to invasion by aggressive alien species in underway in some parts. Particularly troublesome in the Blue Mountains are *Pittosporum undulatum* and *Hedychium gardnerianum*" http://www.nmnh.si.edu/botany/projects/cpd/ma/cb10.htm) Weber 2003; Grubb and Tanner 1976.

Indian Ocean islands:

*La Reunion (In 2000-2001, this species eradicated from Les Makes Biological Reserve, C. Lavergne *in litt*.) Strahm 1999; Macdonald *et al*. 1991; Cronk and Fuller 1995

Pacific Ocean islands:

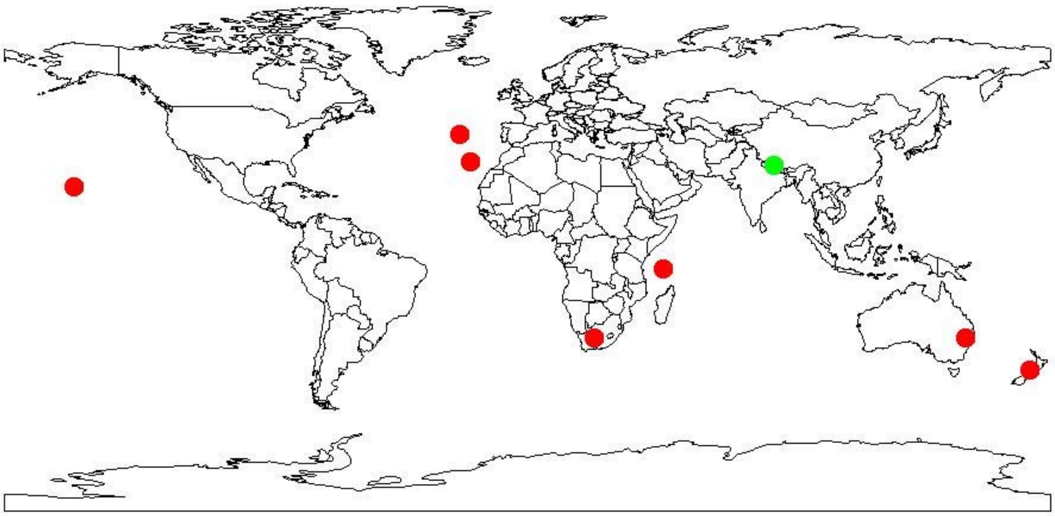
*Hawaiian Islands (Kaua'i, Lāna'i, Maui, and Hawai'i islands)
Nagata 1990; Wagner, Herbst, and Sohmer 1990

*New Zealand (North Island and the north and west portions of South Island including Adele and Mercury islands) Weber 2003; M. Newfield pers. comm.; C. Buddenhagen pers. comm.

South America:

Brazil	C. Smith pers. comm.

Figure 2. Native and naturalized range of Hedychium gardnerianum (green dot is native range; red dots are invasive range).



In Hawaiian wet forests, this ginger forms dense thickets and is now recognized as one of the worst invasive plants of that community on the islands of Lāna'i, Maui, and Hawai'i (Wagner et al. 1990). In rain forests of the Kīlauea district of Hawai'i island, near Hawai'i Volcanoes National Park, this species has reached such densities in the understory of Metrosideros-dominated rain forest that it apparently threatens the long-term survival of that ecosystem

On Maui, Hedychium was introduced as an ornamental to the Nāhiku and Hāna districts of windward East Maui (Haleakalā) in the 1950s (L. Oliveira pers. comm.). Currently, at least three major naturalized Hedychium populations are known from Maui: upper Makawao F.R., Nāhiku- Hāna, and Kīpahulu Valley. In Kīpahulu Valley, Hedychium was first recorded in 1988 (Higashino et al. 1988). Currently, four primary populations and numerous satellite populations of this species are known in the valley at 730-1160 m elevation.

Psidium is native from Brazil to Uruguay in South America (Wagner et al. 1990) (Figure 3). Common English names include strawberry guava (used in Hawai'i), Chinese guava (Indian Ocean islands), cherry guava (Australia), and purple guava (Caribbean, New Zealand) (Owen 1997; Tankard 1987; Wagner et al. 1990). Introduced and cultivated worldwide in tropical and subtropical areas by humans for its edible fruit, Psidium has become widely naturalized (see below) and, it has become widely naturalized and is considered to be a threat to native vegetation (Table 3, Figure 3).

Figure 3. Native and naturalized range of Psidium cattleianum (green dot is native range; red dots are invasive range).

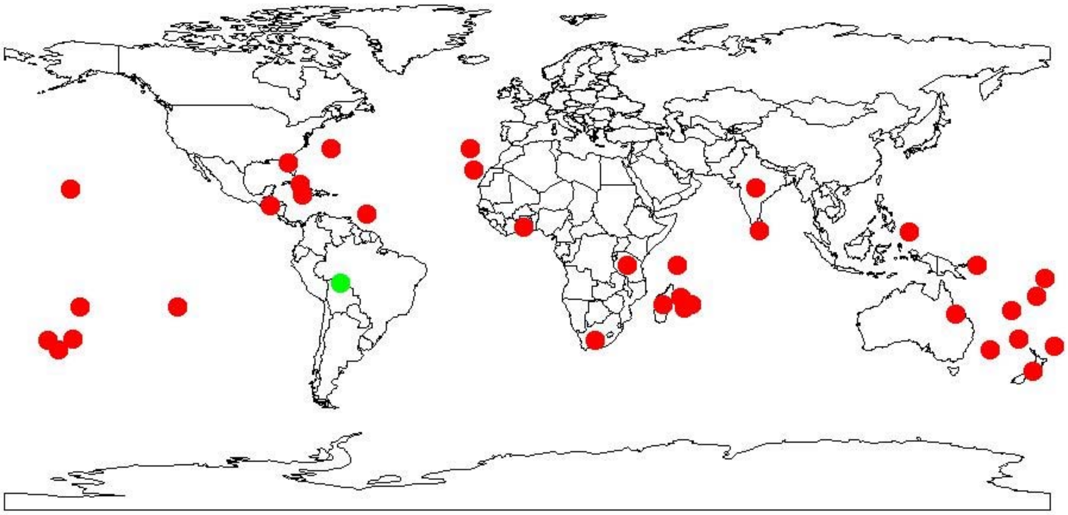


Table 3. Naturalized range of _Psidium_ _cattleianum_. In areas indicated by an asterisk, the species is considered to be a threat to native vegetation.

Area	Reference
East and West Africa:	
Ghana	Sem 1984
*South Africa	Weber 2003; Henderson 1995
Tanzania	Sem 1984
Northeastern Australia:	
*Queensland	Weber 2003; Lazarides, Cowley, and Hohnen 1997
Southern Asia:	
India	Sem 1984
Sri Lanka	Adams 1972
Caribbean islands:	
Bermuda	Sem 1984
Cuba	Sem 1984
Jamaica	Adams 1972
Trinidad	Sem 1984
Central America:	
Guatamala	Sem 1984
Indian Ocean islands:	
*Comores (Grand Comore and Anjouan islands)	J. Mauremootoo pers. comm.

*La Reunion Strahm 1999; Macdonald et al. 1991

*Madagascar Cronk and Fuller 1995

*Mauritius Strahm 1999; Lorence and Sussman 1986; Cronk and Fuller 1995

*Rodrigues W. Strahm pers. comm.

*Seychelles (common by 1870s; currently found in most habitat types)
Friedmann 1994; W. Strahm pers. comm.

Southeastern North America:

*Florida (approximately southern half of the state)
Weber 2003; Sem 1984

Pacific Ocean islands:

*American Samoa (Western Tutuila island. Two trees in Pavai'ai village, one tree in Leone village; and 27 individuals in small naturalized population near Afau village, all sites discovered from 2003-2004)
T. Togia pers. comm.

*Austral Islands (Rapa, Tubuai, and Rurutu islands)
Meyer 2004; J.-Y. Meyer pers. comm.

*Cook Islands (Rarotonga, Mangaia, and Miti'aro islands)
Meyer 2004; Meyer 2000; Merlin 1985; Smith 1985a; J. Space pers. comm.

*Fiji (Viti Levu) Smith 1985a; J. Space pers. comm.

*Hawaiian Islands (Kaua'i, O'ahu, Moloka'i, Lāna'i, Maui, and Hawai'i islands)

Wagner, Herbst, and Sohmer 1990

*Kermadec Islands (Raoul island)
Webb, Sykes, and Garnock-Jones 1988;
M. Newfield pers. comm.

*Lord Howe Island Pickard 1984; 1994<http://www.deh.gov.au/biodiversity/threatened/recovery/lord-howe-wood-hen/previous.html>

*Marquesas (Hiva Oa and Fatu Hiva islands)	Meyer 2004; J.-Y. Meyer pers. comm.
New Caledonia	Sem 1984
*New Zealand (North Island north of Auckland)	Webb, Sykes, and Garnock-Jones 1988; M. Newfield pers. comm.
*Norfolk Island	T. Rodd pers. comm.; N.E. Gillett, pers. comm.; Mueller-Dombois and Fosberg 1998
*Palau (Belau)	Meyer 2000; Whistler 1995
Pitcairn	Meyer 2004; P. Binggeli pers. comm.
*Society Islands (Tahiti, Moorea, and Raiatea islands)	Meyer 2004; J.-Y. Meyer pers. comm.
*Solomon Islands	Weber 2003; Sem 1984
Western Samoa (e.g., Malololelei forest, ‘Upolu island)	T. Togia pers. comm.

Psidium, first introduced in 1825 to the Hawaiian Islands, is now widely naturalized in wetter regions to 1220 m elevation and is one of the most serious plant pests (Smith 1985b; Wagner *et al*. 1990). In Hawai’i, feral pigs disperse viable *Psidium* seed (Diong 1982). Fruit eating birds are also presumed to disperse *Psidium* seed (Anderson *et al*. 1992; Huenneke and Vitousek 1990; Wagner *et al*. (1990). LaRosa *et al*. (1987) demonstrated that, in captivity, mynah birds (*Acridotheros tristis*) and Japanese white-eyes (*Zosterops japonica*) consume and pass viable seeds of *Psidium*. This aggressive tree displaces native wet forests with dense, monospecific thickets that may possess allelopathic properties (Wagner et al. 1990).

OBJECTIVES

I. GENERAL OBJECTIVES

The general objective of this research is to examine key life history characteristics of Clidemia hirta, Hedychium gardnerianum, and Psidium cattleianum, three problematic plant invaders of Hawaiian rain forests. Regionally, the data are intended to provide information pertinent to a more accurate assessment and prioritization for land managers leading to better informed control strategies for these invasive plants. At a broader level, this research is intended to provide information on critical junctures (fruit production, dispersal, and establishment) of the life histories of the three study species. This information may assist in predicting which non-native species have the potential of becoming problematic plant invaders.

II. SPECIFIC HYPOTHESES

The four specific hypotheses of the proposed research are:

1. H_O: there is no annual pattern of ripe fruit production in the study species (to quantitatively assess the phenology of study species, focusing on the timing of the production of ripe fruits).

2. H_O: seeds of the study species are not dispersed by resident vertebrate species (to identify methods of seed dispersal and assess them in terms of importance for the study species).

3. H_O: the reproductive potential of the study species is not substantially reduced by seed predators (to determine if seed predators are present, and if so, to quantitatively determine their overall impact on seed production of the study species).

4. H_O: establishment of the study species is not affected by microhabitat type (to determine the establishment response of each study species in four sites characteristic of Kīpahulu rain forests i.e., alien grassland, native matted fern, mechanically scalped areas, and epiphytic sites).

METHODS

I. Reproductive phenology and quantitative assessment of reproductive potential: This work was conducted within invasive populations of the study species in Kīpahulu rain forest in areas approved by Haleakalā National Park Resource Management personnel. Ten to twenty-five reproductively mature individuals/units of the study species were located and tagged. Within the population, study individuals were selected non-randomly based on ease of access and on having achieved sufficient size as to be reproductive. At monthly intervals for a year, the reproductive units on each tagged plant were counted and recorded. Reproductive units included flower buds, open flowers, immature fruits, and mature fruits (Kearns and Inouye 1993).

II. Seed dispersal: Observations of visiting birds were made at fruiting patches of study species. The date, time of day, bird species, plant species, and bird behavior was entered in field notebooks. Mist nets were set up within and at the periphery of fruiting patches of the study species. These nets were extended during periods of high bird activity (e.g., morning) and monitored closely for captures. Captured non-native birds were held in cloth bags for 20 minutes. After the holding period, all birds were banded and released. With each capture, the holding bag was tagged and the bird species, date of capture, location, study species fruiting nearby, and presence of juvenile plumage were recorded. Later, the dropping was removed from the bag by scraping or by washing with water. Extracted seeds of all plant species were identified and counted. Invertebrate parts were pooled per site and per bird species and preserved in 90% ethanol.

In a second component of this study, rain forest passerine birds that have been identified as important frugivores were captured and offered study plant seeds. By periodically removing the uppermost cage papers, droppings were chronologically segregated and seed passage time estimated. Study plant seeds were extracted from droppings and washed. The seeds were counted and placed on paper discs in Petri dishes to test viability. By regularly monitoring the Petri dishes, the rate and final percentage of germination was determined.

Fresh droppings of other vertebrates were opportunistically collected at rain forest study sites and later examined under a dissecting microscope. If intact seeds of the study plant species were obtained, the study plant seeds were extracted and washed. The seeds were counted and placed on paper discs in Petri dishes to test viability. The Petri dishes were monitored regularly and the germination rates of seeds extracted from droppings of vertebrates, such as rodents, were compared with germination rates of seeds dissected from fresh fruit.

III. Seed predation: Fruits of study plants were examined and held in rearing out jars to determine if insect seed predators were present. Observations were made in rain forest conditions of fruits of study species and the surrounding area for evidence indicating vertebrate seed predation, such as gnawed fruit fragments and rodent feces with seeds, seed fragments or fruit pulp.

Where there was evidence of seed predation by rodents, 50-100 individuals of the study species that were beginning to flower were non-randomly selected and marked. These sequentially numbered individuals were quantitatively assessed periodically throughout the flowering and fruiting period to assess seed predation by rodents. Determination that flower and fruit damage was due to rodents versus that by birds were based on the presence of discernible gnaw grooves and of rodent droppings on flowering plants. Trapping was done near fruiting plants to determine specific identification of rodents as one of three locally common species: black rat (Rattus rattus), Polynesian rat (Rattus exulans), and house mouse (Mus domesticus).

IV. Seedling establishment sites: Within invasive populations of the study species in Kīpahulu rain forest, a number of transects were established in two dominant groundcover vegetation types. In areas dominated by alien grasses, transects totaling 60 meters were laid out. In adjacent areas dominated by native matted ferns, transects totaling 30 meters were laid out. Transect locations were determined non-randomly primarily to facilitate maximum site utilization without crossing existing trail networks. Along these transects, 0.25 m^2 plots (0.5 m x 0.5 m) were located and marked with 1 meter spacing between them as a buffer between plots. This arrangement yielded 40 quarter-meter plots in alien grass areas and 20 quarter-meter plots in native fern areas.

To evaluate the response of the study species to disturbed sites (simulating pig diggings), half of the 0.25 m^2 plots (i.e., 20 plots) in areas dominated by alien grasses were mechanically scalped of all living vegetation and leaf litter and scraped down to mineral soil. Selection of which sites in alien grass areas were to be scalped was random. As a result, sixty quarter-meter plots were randomly selected, 20 scalped to mineral soil, 20 in sites dominated by alien grasses, and

20 in sites dominated by native ferns. To consider epiphytic sites for suitability to establishment, 20 sections of elevated moss-covered living tree branches were identified and marked.

Because of ethics associated with distributing seeds of invasive plant species in a nature reserve such as Kīpahulu and as stipulated by Haleakalā National Park Service personnel, these experiments were conducted within known populations of the study species being considered. As a result, three separate experimental areas (one for each study species in a preexisting population) must be used. Control plots were needed in which study species seed are not added to account for seedlings produced from stored seed bank and seed rain of the study species.

Ten of 20 plots of each of four potential establishment sites (grass-dominated areas, fern-dominated areas, bare ground, and epiphytic sites) were randomly selected to add seed of the study species. Where assigned, seed were added at the center of the plot, crushed and incorporated into a small amount of mud to reduce its attractiveness to vertebrates. Copious seed were added to help assure that the effects of stochastic events were minimized. For the large-seeded species (Hedychium and Psidium), 25 seeds were added per plot; for the very small-seeded Clidemia, three fruits were added per plot (approximately 1800 seeds). One year after the experiments start, all plots were examined and the number and size (height and basal diameter) of all emergent seedlings of the study species recorded. By comparing numbers of seedlings present in plots where seed had (treatment) and has not been added (control), the number of seedlings contributed by the stored seed bank was roughly estimated. By comparing the number and size of seedlings found in the four establishment sites (grass-dominated areas, fern-dominated areas, bare ground, and epiphytic sites), suitable establishment sites can be identified for each study species.

DISCUSSION

Though trends are changing, remarkably little research is ongoing regarding understanding the biology or control of invasive species considering their global impacts. The magnitude of the problem of invasive plant species in the long term conservation of Hawaiian ecosystems suggests that unless more information becomes available and effective prevention and control strategies are forthcoming, other threats to Hawaiian forest and their denizens may become irrelevant.

Even otherwise knowledgeable scientists and managers seem to have developed an unrealistic ideological dependence on biological control to implement a long-term solution to problems posed by invasive plants. Yet for each non-native plant targeted, a biological control program costs on average approximately one to two million US dollars (Andres 1977). Biological control has a record of successes that averages between one in two (Markin et al. 1992) to one in six cases (Hobbs and Humphries 1995). Biological control has been a critical factor in control programs for a few selected invasive plant species, but on the whole, is not considered to constitute an important factor in the control strategies of the majority of invasive plant species (Hobbs and Humphries 1995). It must be noted that valiant efforts to find and screen biological control agents are underway for all three of this study’s target weeds with some hopeful progress (R.C. Anderson, P. Conant, and C.W. Smith pers. comm.).

In dealing with the number of serious invasive plant species that threaten Hawaiian ecosystems, the critical phases of an effective management strategy appear to be public education, the implementation of legal restrictions, early detection and control, and in some cases, effective population containment and eradication. The success of each of these phases is greatly benefited by information provided by focused investigations into the biology of invasive plants.

In a practical sense, the results of this research may be most useful in developing realistic management strategies for these three invasive species in protected rain forest tracts in Hawai’i. Recently a project was initiated by a coalition of private and public land agencies to exclude feral pigs from an additional 9,788 acres (3961 ha) of upper elevation native rain forest, adjacent to Kīpahulu Valley on Haleakalā with exclosure fences (East Maui Watershed Partnership 1996). When completed and the fences joined, this management effort will exclude feral pigs from much of the middle to upper elevation windward rain forest on Haleakalā, the largest ungulate-free rain forest in the state.

Information such as this study provides will likely aid in the timing and methods of management implemented in this rain forest reserve. Land managers will have more refined answers for key questions such as, ‘which invasive plant species are likely to spread faster?’ ‘which invasive plant species are likely to survive in areas with disturbed ground and pig populations, and which are likely to continue to spread even after primary vegetation recovery following pig removal?’ Better information will inevitably lead to better decisions in determining priorities and strategies for invasive plant control.

On other oceanic islands where these invasive species also occur, this research can assist in many of the same ways. For oceanic islands without these species, the greatest benefit is the documentation of the invasive potential of these important invasive plant species that may act to increase awareness which leads to the implementation of measures designed to prevent their inadvertent or intentional import. The three study species are most invasive in medium to relatively high elevation wet forests (150-1500 m elevation). Tropical oceanic high islands that appear particularly vulnerable to invasion by the study species include the Society Islands, the Marquesas, the Austral islands, New Zealand, the Cook Islands (Rarotonga), Madagascar, and Mascarene Islands. Other areas that may also be susceptible to invasion by the study species include the island groups of Fiji, Tonga, American and Western Samoa, Tasmania, Galapagos, Juan Fernandez, Madeira, Azores, Canary, Saint Helena, and continental areas such as Australia, Florida, and South Africa.

By continuing to refine our knowledge of life history stages of invasive species, it is hoped progress can be made toward creating a model of invasive species biology and ecology. Such a model has the potential to assess key life history traits of non-native species and predict which have traits that indicate the potential to become serious invaders. The ultimate criterion which defines success in these ventures, however, were whether real progress can be made in preventing new invaders from becoming established, and managing the worst of the extant invasive species threatening natural ecosystems in Hawai’i, on other oceanic islands, and elsewhere.

CHAPTER TWO:

PHENOLOGY AND REPRODUCTIVE POTENTIAL ESTIMATES FOR THREE IMPORTANT INVASIVE PLANT SPECIES OF NATIVE RAIN FOREST AT KĪPAHULU, MAUI, HAWAIIAN ISLANDS

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ABSTRACT

The objective of this investigation was to quantitatively determine the reproductive phenology of three important weed species (Clidemia hirta, Hedychium gardnerianum, Psidium cattleianum) of Hawaiian rain forests and to provide an estimate of the total reproductive potential of the species. At twelve consecutive monthly intervals, reproductive units (flower buds, open flowers, immature fruits, and mature fruits) of tagged plants/units of the three study species were counted and recorded. The results revealed that Clidemia ripe fruit production was highest from October through January, Hedychium from October through December, and Psidium in November. Compared to Psidium of similar sizes at lower elevations, the production of ripe fruit by Psidium at the study site appeared limited. Among likely explanations are the suppression of ripe fruit production at higher elevations and the smaller sizes and lower densities of Psidium at the upper elevational limit of its invasion. Clidemia was estimated to produce more than four orders of magnitude more seeds than Hedychium and Psidium of equal cover. Individual Clidemia plants, which averaged 0.37 m^2 cover, produced an average of 3,815,552 seeds/yr. Determination of phenological patterns and reproductive potential should assist managers in prioritization and timing of control efforts and in fine-tuning trait assessment used to screen non-native species for importation restrictions.

INTRODUCTION

Virtually every native Hawaiian ecosystem is imperiled by non-native plant species (Stone et al. 1985; Hawai’i and Pacific Plant Recovery Coordinating Committee 1998), yet relatively little is known about the biology of most of these invaders. Since European contact over two hundred years ago, more than 13,000 non-native plant species have been introduced by humans to Hawai’i (George Staples pers. comm.), outnumbering native plant species (ca. 1,200 species) eleven to one. Of introduced plant species, 1,148 flowering plant species have become naturalized (Evenhuis and Eldredge 2002) (roughly 8.8% of all non-native plant species present), of which about 100 species are considered to be a serious concern to natural area management (Smith 1985; C.W. Smith pers. comm.). Hence, despite the fact that Hawaiian ecosystems are being rapidly displaced, only one in 130 non-native plant species has become a threat to native species in the Hawaiian Islands (0.8% of all introduced plant species and 8.7% of naturalized species).

Are there discernable traits that predispose some species to have an increased risk of naturalizing in and threatening areas of native vegetation? One important trait of invasive plant species critical to successful colonization of new areas is reproductive strategy (Bazzaz 1986). The ability to produce large numbers of seeds with minimal duration between episodes of fruit production has been associated with invasive plant species (Rejmanek and Richardson 1996).

In this study, reproductive phenology (i.e., production of flower buds, flowers, immature and ripe fruits) was quantitatively assessed for three invasive and habitat-modifying plant species of Hawaiian rain forests: Clidemia hirta (L.) D. Don, Hedychium gardnerianum Ker.-Gawl., and Psidium cattleianum Sabine (hereafter Clidemia, Hedychium, and Psidium). Based on this assessment, annual reproductive potential of the study weeds in the study area was estimated. Detailed phenology of marked individuals such as in this investigation offer insights into plant reproductive strategies such as the numbers of seed produced and their timing relative to maximizing utilization of seed dispersers or avoiding seed predators (Wheelwright 1986).

Windward Haleakalā (East Maui) Volcano contains some of the largest tracts of biologically diverse rain forest remaining in the Hawaiian Islands (Medeiros et al. 1995). Beginning in the 1930s, escaped domestic pigs began to become feral over broad expanses of Haleakalā and facilitating the invasion of regional rain forests by a variety of non-native plant species (Diong 1982; Medeiros et al. 1998). With its protection from feral pigs beginning in the mid-1980s, the rain forest of Kīpahulu Valley (SE Haleakalā) at 245-2135 m elevation is one of the largest and most diverse protected rain forest units in the state. The canopy is composed largely of two dominant canopy trees, koa (Acacia koa) in the lower to middle reaches (25-1680 m) and `ōhi`a lehua (Metrosideros polymorpha) throughout with native shrub, vine, herb and matted fern layers (Medeiros et al. 1998). After protection from feral pigs, three weeds continued to spread and gain local dominance. One species (Psidium) had been present in Kīpahulu for at least 50 years, but the other two (Hedychium and Clidemia) were first noted in Kīpahulu only in the late 1980s (Anderson and Stone 1993; Higashino et al. 1988; Medeiros et al. 1998).

Psidium, first introduced into Hawai'i in 1825, had become naturalized by the early 1900s (Diong 1982). In Kīpahulu, it became established in pastures and lower elevation forests by the 1950s and by the early 1960s began to spread upslope, possibly aided by the upland spread of feral pigs (Diong 1982). By 1967, Psidium was observed up to 670 m elevation (Lamoureux 1968); by 1980, to 1170 m elevation (Yoshinaga 1980); and by 1998, to 1400 m elevation (Medeiros et al. 1998). Currently, from 490-915 m, Psidium forms very dense, monospecific stands with a darkened understory that excludes nearly all native plant species, perhaps by allelopathy (Loope et al. 1985).

Hedychium gardnerianum was first collected in the Hawaiian Islands around 1940 (Wagner et al. 1990). Currently, this species has become naturalized in native rain forest on several islands. It forms dense and extensive thickets that displace native understory species in some areas, most notably on Hawai'i island at its original site of naturalization near Hawai'i Volcanoes National Park (Stone and Pratt 1994). The species was first recorded in the study area of Kīpahulu in 1987 (Higashino et al. 1988) and elsewhere on Maui has substantial populations in native rain forest in Makawao Forest Reserve and above Hāna. Currently, Hedychium populations in Kīpahulu are still fairly extensive, despite intensive management efforts by Haleakalā National Park staff. In its native Himalayan range, this species occurs at high elevations up to 1900 m (Stainton 1997). Based on this, it seems likely that the range of Hedychium could expand from lower elevations into cooler upper elevation forests of Kīpahulu Valley and elsewhere on East Maui where the tree line is approximately 1950-2070 m.

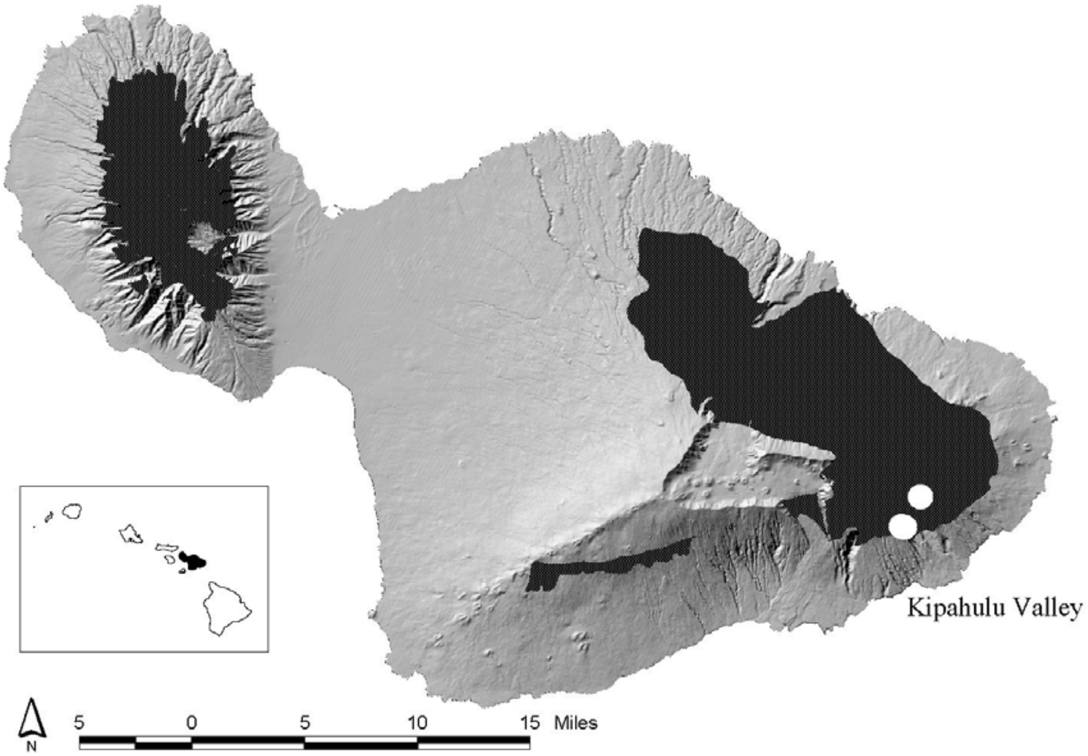
Clidemia hirta was first reported in Hawai'i on O'ahu (1941), then on Hawai'i island (1972), Moloka'i (1973), Maui (1976), Kaua'i (1982), and Lāna'i (1988) (Smith 1992). On O'ahu, where it first became established, Clidemia forms dense thickets that exclude many native plant species (Smith 1992). In 1976, Clidemia first became established on Maui in the Nāhiku district and spread rapidly from the lower disturbed wet forests into the native rain forests, apparently facilitated by copious seed dispersal by common non-native resident passerines (Chapter Three). In 1988, a single Clidemia plant was first discovered in Kīpahulu Valley at 855m elevation (Cuddihy and Santos 2240) (Higashino et al. 1988). By the early 1990s, Clidemia had become widely established in the valley at 825-1040 m elevation, having spread much faster than the other two study species (Medeiros et al. 1998).

MATERIALS AND METHODS

Three primary study sites were selected on Haleakalā Volcano (East Maui) in Kīpahulu Valley, within Haleakalā National Park (Figure 4). At each of these sites, only one of the study species was present and was a dominant component of the site's vegetation. Besides this, the primary vegetation type of the study sites in

Kīpahulu Valley is diverse native Metrosideros-Acacia rain forest dominated by koa with well-developed native shrub, fern, and bryophyte layers. The study site for Clidemia was at 820 m elevation (804,866E, 2,292,361N UTM-NAD83); for Hedychium at 825 m elevation (803,520E, 2,290,297N UTM-NAD83); and for Psidium at 880 m elevation (803,740E, 2,290,231N UTM-NAD83). All study sites were located in remote areas requiring access by helicopter.

Figure 4. Map of Maui, Hawaiian Islands, showing distribution of rain forest dominated by native species in black shading and Kīpahulu Valley study sites as white dots. The northernmost white dot marks the location of the Clidemia study site. The two southernmost study sites (Hedychium and Psidium) are sufficiently close that the white dots partially overlap.



At twelve consecutive monthly intervals (eleven in the case of Psidium), reproductive units (flower buds, open flowers, immature fruits, and mature fruits) of tagged plants/units of the three study species were counted and recorded (Kearns and Inouye 1993). A few supplemental dates were added at the peak of the ripe fruit production for each species to enrich this important data point in a subsequent year. Clidemia phenology was monitored from May 1996 through April 1997 and as a supplement, September 1997. Hedychium phenology was monitored from July 1996 through June 1997 and as a supplement, September, October, and November 1997. Psidium phenology was monitored from July 1996 to June 1997 and as a supplement, November 1997.

Clidemia hirta (Clidemia) is a shrub usually 2-4 m in height, native to Mexico, West Indies, Central America, and northern South America to Bolivia and southern Brazil (Smith 1992). It is a serious forest pest that has become widely naturalized around the world from approximately 20 degrees S to 22 degrees N latitude on Pacific and Indian Ocean islands, Indonesia, Malaysia, Southeast Asia, and Africa (Chapter One).

Hedychium gardnerianum (kahili ginger) is a large rhizomatous herb up to 2 m in height, native to the Himalayas and adjacent regions (Nagata 1990; Stainton 1997). Hedychium has become naturalized from approximately 42 degrees S to

22 degrees N latitude on islands in the Pacific Ocean (Hawai'i, New Zealand), Indian Ocean (La Reunion), and Atlantic Ocean (Azores, Madeira), as well as in Jamaica, Australia, and South Africa (Chapter One).

Psidium cattleianum (strawberry guava) is a small tree up to 8 m in height, native to South America (Hodges 1988). Introduced extensively in tropical and subtropical areas for its edible fruit, Psidium has become widely naturalized from approximately 27 degrees S to 32 degrees N latitude on islands of the Pacific, Atlantic, and Indian Oceans, as well as Australia, Central America, Asia, Africa, the Caribbean, and North America (Chapter One).

Two color forms of Psidium cattleianum are invasive in Kīpahulu Valley, a yellow-fruited type referred to as forma lucidum and a red-fruited type referred to as f. cattleianum (Medeiros et al. 1998) The two types have been hybridized under experimental conditions (Hirano 1967), but intermediates are not common in Kīpahulu. The population sampled for phenology was exclusively that of the more invasive red-fruited form, i.e., Psidium cattleianum f. cattleianum.

At the study sites, ten to twenty-five reproductively mature individuals or units of the study species were located and tagged so as to be re-locatable throughout the study period. For Clidemia, 25 entire reproductive-sized plants were used as the study units. The 25 Clidemia plants used in determining phenology had an average cover of about 0.5m^2, heights averaged 84 cm (ranged from 55 to 126 cm), and basal diameters averaged 1.5 cm (ranged from 0.9 to 3.7 cm). For Hedychium, individuals were nearly impossible to distinguish because of their interlocking rhizome systems. To delineate units for assessing phenology of Hedychium, ten discrete 2 m by 2 m squares (each $4m^2$) were marked at their corners with plastic stakes. A straight ruled object placed between corner stakes was used to help delineate the phenology units. For Psidium, due to the difficulties of doing repeated counts accurately and non-destructively on large trees with dense foliage, large branches of 25 different trees were tagged and used as the units for assessing phenology. Even relatively large thickets of Psidium cattleianum can be clonal, formed by root suckering (Huenneke and Vitousek 1990). Because of this and to maximize the likelihood that the 25 phenology plants were distinct, only clumps separated by three or more meters were selected for this study. Statistical analyses were performed with Minitab Release 13.30 software.

To assist in tracking the phenology of Hedychium, 100 culms were tagged and numbered on 29 April 1997 and the height, basal diameter, number of leaves, and the presence of any budding, flowering, or fruiting was noted. The culms were re-measured six months later on 29 October 1997.

When marked phenology plants did not appear to be producing fruit, it was decided to also assess the fruiting status of Psidium in the general vicinity of the 915 m Psidium phenology site. Presence or absence of leaf buds, flower buds, and immature and ripe fruits was noted for 50 neighboring non-tagged Psidium trees, not including study trees. This supplemental monitoring was conducted monthly for eight consecutive months, October 1996 to May 1997, and November 1997.

To estimate the reproductive potential of the study species, the number of seeds present in the reproductive unit (i.e., Clidemia berry, Hedychium inflorescence, Psidium fruit/berry) was determined for 25-50 individuals. Individuals and fruits were selected non-randomly but the first individuals with fruit and the first fully ripe fruit encountered were selected to avoid bias. Clidemia fruit were sampled from the phenology study site. Psidium fruit were sampled from a lower elevation population within Kīpahulu Valley when fruiting was more prolific. Hedychium were sampled from the Makawao Forest Reserve.

In Hedychium, fruiting culms are persistent and identified by their wilted infructescences, allowing the annual number of infructescences to be determined. In Clidemia and Psidium, ripe fruits are ephemeral and thus poor indicators of the total numbers of fruits produced. For these species, monthly counts of immature fruits were used to estimate the total number of fruits produced per year and as the basis for estimating annual reproductive potential. If immature fruits ripen slowly, and hence are counted twice by two successive monthly monitoring trips, the reproductive estimates given here are higher than actual values. If immature fruit ripen quickly, and hence more fruits are produced and shed in a month than are counted, the reproductive estimates given here would be underestimates of actual values. The rate of ripening is unknown for the two species.

RESULTS

I. PHENOLOGY

In twelve consecutive monthly surveys, all three species demonstrated distinct, seasonal cycles of flower and fruit production. *Clidemia* in Kīpahulu Valley produced flowers and fruits year round with maximum fruit production peaking from late summer through fall (Table 4, Figure 5). *Hedychium* produced ripe fruits only in a relatively short but intense period from late fall through mid-winter (Table 5, Figure 6). *Psidium* ripe-fruit production peaked in fall (Table 6, Figure 7) but appeared to be relatively limited at the study site.

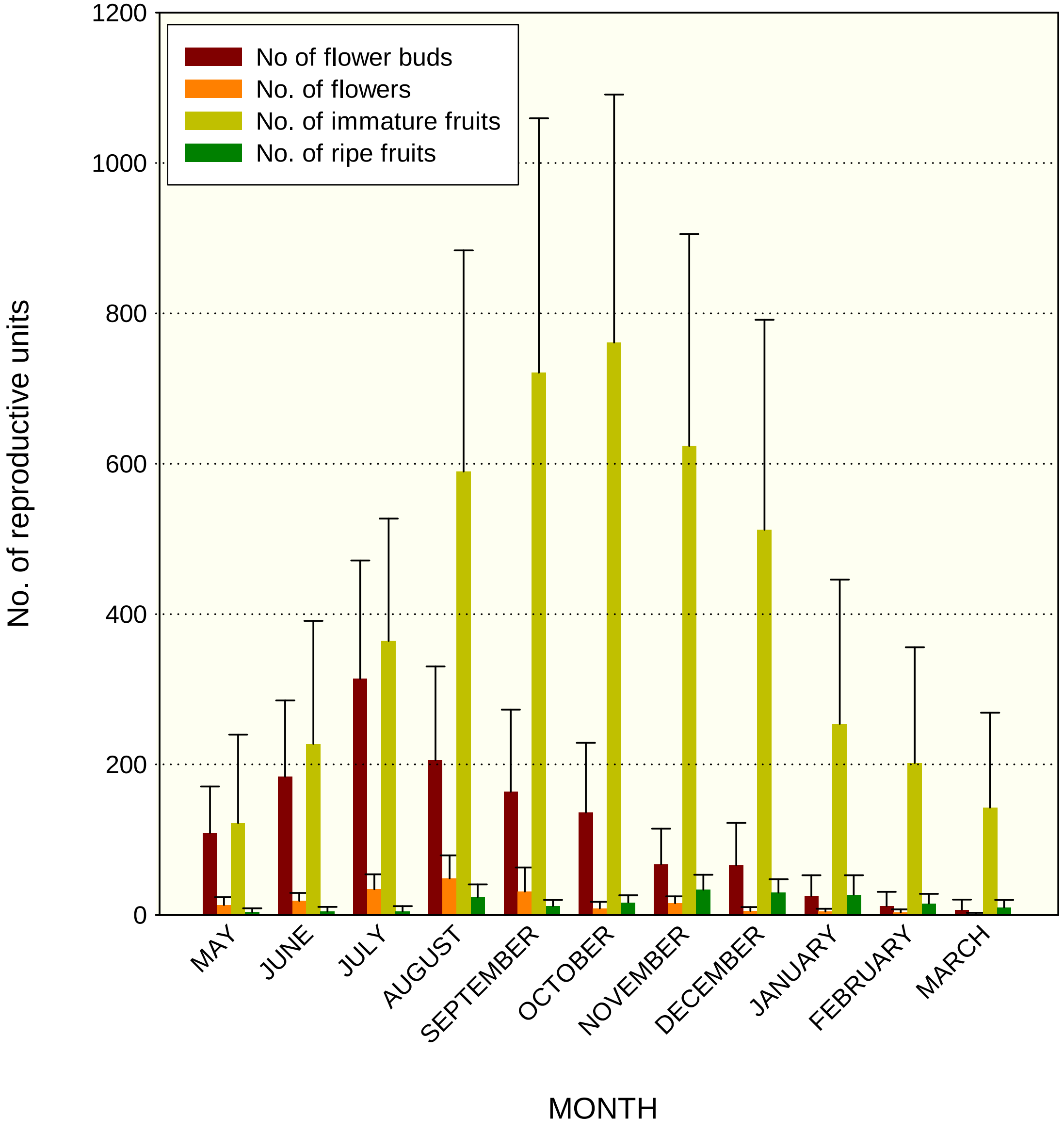
Clidemia:

Clidemia flower bud production occurred at low levels from January through April, building from late spring (May), peaking in the summer and early fall months (June through October). The highest numbers of flower buds (314 buds/plant) occurred in July and in the ANOVA model with Tukey’s comparisons July flower bud production differed significantly from the other 11 sampled months. August flower production was highest (48.8 flowers/plant) and significantly separate from the other 11 months. July (34.2 flowers/plant) and September (31.1 flowers/plant)

Table 4. Mean monthly numbers of reproductive structures (buds, flowers, immature and ripe fruits) of 25 Clidemia hirta plants at 820 m elevation, Kīpahulu Valley. Supplemental data taken from non-consecutive months and their values are included and asterisked.

Date	Mean no. of flower buds/plant	Mean no. of flowers/plant	Mean no. of immature fruits/ plant	Mean no. of ripe fruits/ plant
5/14/96	109.16	13.00	122.04	3.80
6/19/96	183.76	18.68	227.36	4.36
7/25/96	314.08	34.24	364.52	4.92
8/28/96	205.80	48.64	589.48	23.96
9/13/96	163.76	31.08	721.12	11.84
10/20/96	136.12	8.84	761.24	16.80
11/14/96	67.32	15.48	623.64	33.56
12/3/96	65.88	5.16	512.28	29.72
1/23/97	25.40	4.44	253.96	27.04
2/12/97	11.84	3.28	201.88	15.20
3/13/97	6.84	1.00	147.72	10.00
4/21/97	19.84	0.68	65.52	7.60
9/17/97*	176.64*	37.80*	300.72*	3.08*

Figure 5. Mean monthly number with error bars of reproductive units (flower buds, flowers, immature fruit, and ripe fruit) for 25 shrubs of <u>Clidemia</u> <u>hirta</u> at 820 m elevation, May 1996 through March 1997.



were also peak flowering months. Following this, the production of immature fruits began increasing from May and peaked in October when sampled plants carried a range of 273 to 1318 immature fruits and averaged 761 immature fruits/plant. The ANOVA showed that October, November, and December were the months when plants bore the largest numbers of immature fruits and clustered together and significantly higher than other months. In the six-month period from July through December, study plants averaged 595.4 immature fruits/plant. Clidemia produced the highest numbers of ripe fruits from late summer through early winter (August to January) and peaked in November through January. The mean numbers of ripe fruit recorded monthly throughout the year remained relatively low and constant with a maximum in November of 34 ripe fruits per plant. The rate of gradual turnover of fruits that ripen and are eaten or dehisce and fall to the ground is highest between December and January when the mean reduction from 512 to 254 average immature fruits suggests a rate of 8.6 ripe fruits shed per day.

Clidemia flower buds, flowers, and immature and ripe fruits occurred in every month of the year that phenology was recorded (Table 4, Figure 5). Smaller plants sometimes produced no flowers and/or buds in winter to early spring (December to March) and no ripe fruits from May through July. However, eleven of the larger plants of the 25 sampled plants produced ripe fruits at every monthly sampling period for the entire year.

Hedychium:

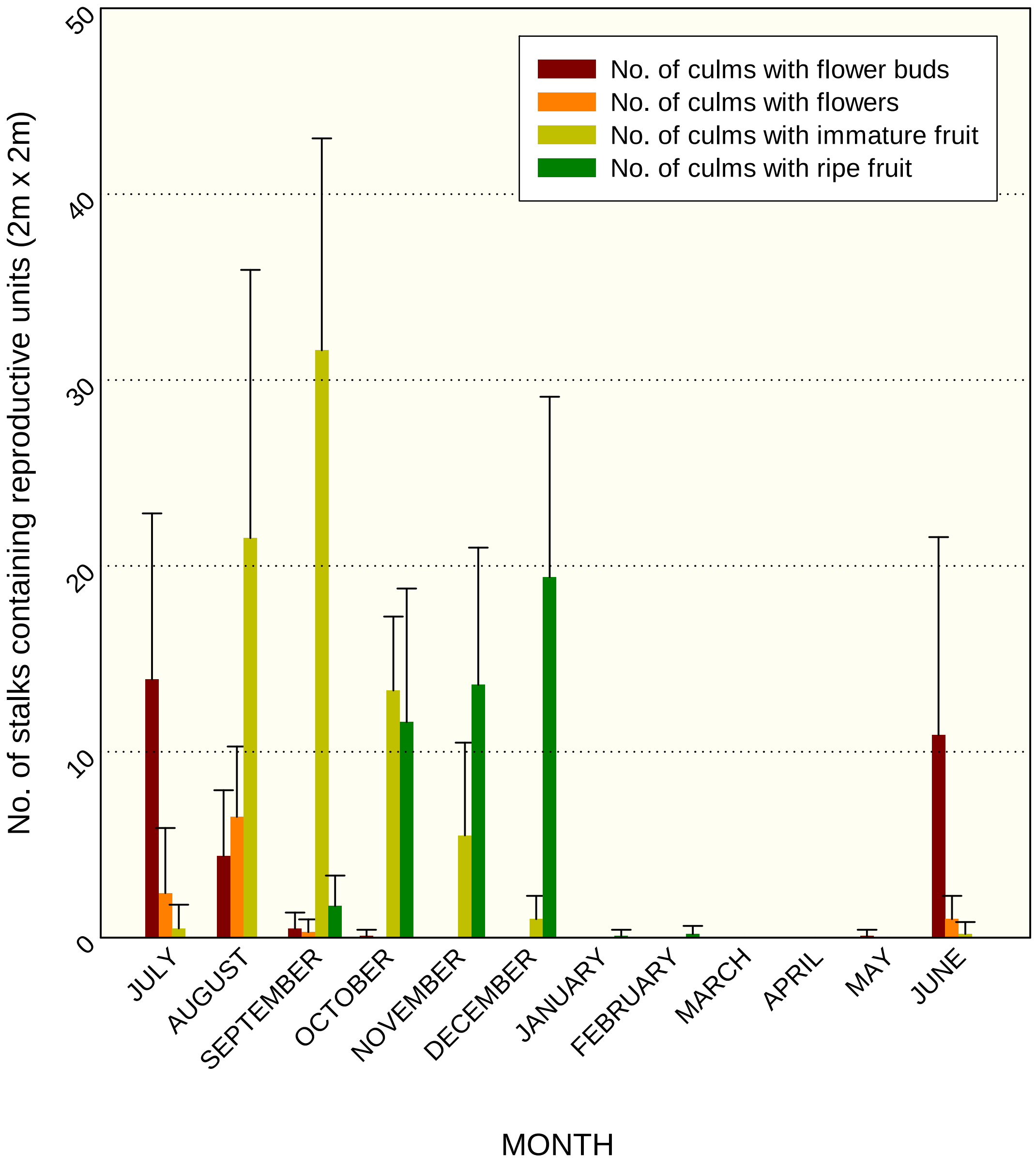
Young Hedychium shoots (<10 cm ht) were initiated throughout the 12-month sampling period with highest numbers recorded in March, April, May and August. The number of mature sterile culms increased from March through May, and decreased rapidly thereafter as these culms flowered. Based on these data and observations of tagged culms, individual culms live for approximately 8 months before wilting. Of 100 young Hedychium culms (<30 cm ht) that were tagged and measured in April, 78% flowered by late October. The remaining culms (22%) remained sterile and did not flower.

Hedychium produced flower buds from May through October and peaked strongly in June-July, these two months being significantly (P<0.05) distinct from other months in the ANOVA (Table 5, Figure 6). Hedychium flowered from June to September and peaked from late July through August, also significantly (P<0.05) distinct from other months in the ANOVA. Immature fruits were produced from July through early December and peaked in August through October, these three months being significantly (P<0.05) distinct from other months in the ANOVA. Hedychium produced ripe fruits and seeds from September through February and peaked during October-December. October, November, and December were significantly (P<0.05) distinct from other months in the ANOVA.

Table 5. Mean monthly numbers of reproductive structures (buds, flowers, immature and ripe fruits) of 10 *Hedychium gardnerianum* units (4m^2 squares) at 825 m elevation, Kīpahulu Valley. Supplemental data taken from non-consecutive months and their values are included and asterisked.

Date	Mean no. of culms with flower buds/plant	Mean no. of culms with flowers/plant	Mean no. of culms with immature fruits/plant	Mean no. of culms with ripe fruits/plant
5/31/96*	0.2*	0.0*	0.0*	0.0*
7/10/96	13.9	2.4	0.5	0.0
8/7/96	4.4	6.5	21.5	0.0
9/17/96	0.5	0.3	31.6	1.7
10/16/96	0.1	0.0	13.3	11.6
11/9/96	0.0	0.0	5.5	13.6
12/3/96	0.0	0.0	1.0	19.4
1/23/97	0.0	0.0	0.0	0.1
2/12/97	0.0	0.0	0.0	0.2
3/14/97	0.0	0.0	0.0	0.0
4/22/97	0.0	0.0	0.0	0.0
5/21/97	0.1	0.0	0.0	0.0
6/27/97	10.9	1.0	0.2	0.0
9/25/97*	1.2*	0.1*	39.2*	0.0*
10/30/97*	0.0*	0.2*	31.3*	4.0*
11/25/97*	0.0*	0.0*	16.1*	28.2*

Figure 6. Mean monthly number with error bars of reproductive units (culms with flower buds, culms with flowers, culms with immature fruit, and culms with ripe fruit) for ten 2m x 2m quadrats of Hedychium gardnerianum at 825 m elevation, July 1996 through June 1997.

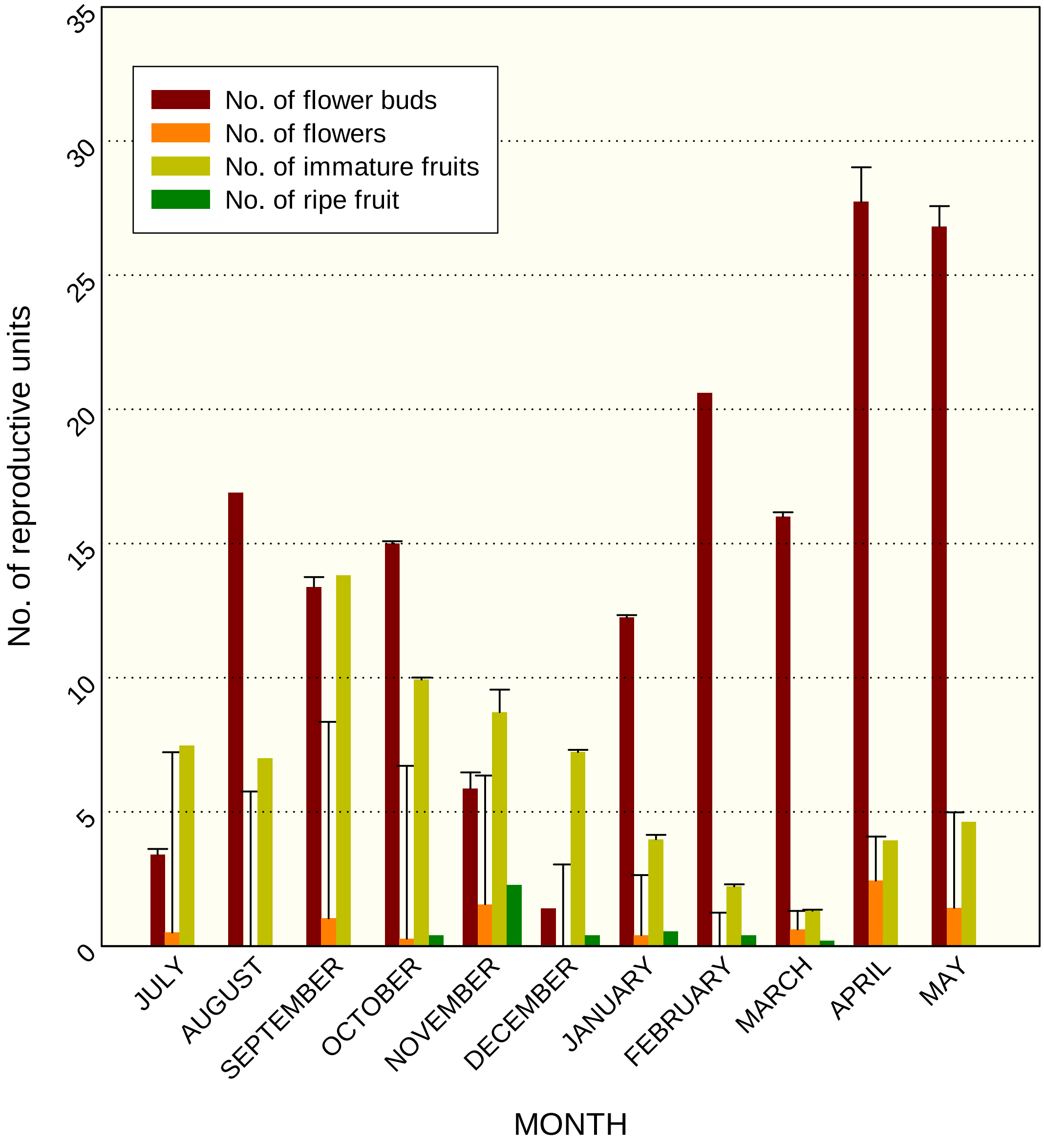


Psidium:

Psidium flower and flower bud production when averaged for all 25 individuals occurred throughout the year (or nearly throughout, in the case of flowers), but the number of flower buds peaked in April and May, which, differed significantly ($P<0.05$) from other months in the ANOVA (Table 6, Figure 7). Some immature fruits were present throughout the year, with numbers highest from May through October; however, no month was significantly ($P<0.05$) distinct from any other month in the ANOVA. Ripe fruits were found only infrequently from October through March and always at low numbers on tagged phenology study branches. The peak month for production of ripe fruits during the study period was November with only 0.84 ripe fruits/large branch, yet this was enough to differ significantly ($P<0.05$) from other months in the ANOVA. Abundant fruiting was not observed in the 25 Psidium trees selected for phenology during the study period. Eighteen of 25 (72%) tagged Psidium individuals had young vegetative buds present every month of the study period; the remaining seven trees had vegetative buds an average of 10.3 months of the year.

The results of the qualitative assessment of 50 entire Psidium trees (flower buds, immature fruits, and ripe fruits) (Table 7) agreed with those of the quantitative phenology study. Flowering peaked in spring (44-72% in March to May), but trees bore immature fruit throughout the monitoring period. Ripe fruits were only

Figure 7. Mean monthly number with error bars of reproductive units (flower buds, flowers, immature fruit, and ripe fruit) for 25 large marked branches of 25 individual trees of Psidium cattleianum at 880 m elevation, July 1996 through May 1997.



infrequently observed (3.1% of all trees in total) and then at low frequency in October through January (7% of observed trees during this season).

Table 6. Mean monthly numbers of reproductive structures (buds, flowers, immature and ripe fruits) of 25 Psidium cattleianum plants counted monthly for 12 consecutive months at 890 m elevation, Kīpahulu Valley. Supplemental data taken from non-consecutive months and their values are included and asterisked.

Date	Mean no. of flower buds/branch	Mean no. of flowers/branch	Mean no. of immature fruits/branch	Mean no. of ripe fruits/branch
5/29/96*	42.04*	1.36*	5.60*	0.16*
7/10/96	2.36	0.20	6.72	0.00
8/8/96	5.32	0.00	5.76	0.00
9/17/96	5.80	0.36	7.32	0.00
10/18/96	6.44	0.08	6.44	0.08
11/10/96	2.36	0.60	4.80	0.84
12/3/96	0.28	0.00	3.04	0.08
1/24/97	4.72	0.08	2.24	0.16
2/13/97	10.00	0.00	1.24	0.08
3/13/97	11.00	0.16	0.68	0.04
4/21/97	26.16	1.28	1.64	0.00
5/21/97	22.28	0.76	3.56	0.00
6/27/97	6.84	0.36	2.44	0.00
11/24/97*	1.84*	0.04*	3.44*	0.00*

Table 7. Percentage and frequency of the presence of leaf buds, flower buds, immature and ripe fruits for 50 Psidium cattleianum trees at 880 m elevation, Kīpahulu Valley.

Date	Vegetative buds present	Flower buds present	Flowers present	Immature fruits present	Ripe fruits present
10/18/96	98%	52%	10%	52%	8%
	49/50	26/50	5/50	26/50	4/50
11/10/96	96%	40%	32%	58%	14%
	48/50	20/50	16/50	29/50	7/50
12/3/96	100%	12%	4%	18%	2%
	50/50	6/50	2/50	9/50	1/50
1/24/97	98%	66%	22%	44%	4%
	49/50	33/50	11/50	22/50	2/50
2/13/97	96%	60%	6%	18%	0%
	48/50	30/50	3/50	9/50	0/50
3/13/97	100%	72%	44%	22%	0%
	50/50	36/50	22/50	11/50	0/50
4/21/97	100%	90%	72%	44%	0%
	50/50	45/50	36/50	22/50	0/50
5/21/97	100%	90%	48%	80%	0%
	50/50	45/50	24/50	40/50	0/50
11/24/97*	86%	10%	2%	46%	0%
	43/50	5/50	1/50	23/50	0/50

II. ESTIMATES OF REPRODUCTIVE POTENTIAL

The 25 Clidemia phenology study plants were estimated to have produced from 2191 to 8011 fruits/yr and averaged 4586 fruits/yr. Clidemia hirta has very small (ca. 0.5-0.7 mm) seeds. The number of seeds contained in 50 Clidemia fruits ranged from 618 to 932 and averaged 832. Hence, each Clidemia phenology study plant could produce from 1,354,038 to 7,466,252 seeds/yr and averaged 3,815,552 seeds/yr. Over the three-month period from October to January, each plant ripened an average of 5.6 fruits per day. With the observed average of 872 seeds/fruit, that is 4883 seeds per plant per day. Over the one-month period of peak fruiting (December to January), each plant produced ca. 8.6 fruits per day, or about 7,499 seeds/day.

Hedychium inflorescences bore 40-154 flowers each and averaged 104 flowers (based on 25 inflorescences). Each infructescence produced 7 to 50 fruits, averaging 27.4 fruits per infructescence, and from 39 to 443 seeds, averaging 206 seeds per infructescence. Each fruit produced 0-21 seeds and averaged 7.5 seeds (based on 685 fruits). Each 4m^2 phenology study quadrat produced 22 to 79 infructescences per year, averaging 39.3 infructescences per year for the ten quadrats. Hence, each 4m^2 quadrat could produce 858 to 34,997 seeds/yr and averaged 8096 seeds/yr.

Each Psidium fruit (n = 50) contained 2 to 13 seeds and averaged 6.7 seeds. The number of immature fruits counted on one branch per year was multiplied by an estimate of the proportion of the entire tree that the phenology study branch constituted, to get an estimate of the reproductive potential of the entire tree. These estimates ranged from 0 to 3915 fruits/yr with an average of 543 fruits/yr. Hence, seed production of each of 25 phenology study trees was estimated at 0 to 5090 seeds/tree/yr and averaged 3638 seeds/tree/yr. This number may be too high, as there appeared to be discrepancies between the moderate number of immature fruits and very low numbers of ripe fruits observed in immediately successive months.

The units used to determine phenology and the basis for estimating the reproductive potential of the three study species are not of equal size and hence not directly comparable. To roughly standardize and compare them, the reproductive potential of 1m^2 areas can be calculated. The cover values of 25 Clidemia plants used for assessing phenology and reproductive potential averaged 0.37m^2 each; hence multiplication of the mean reproductive potential by a factor of 2.7027 will yield an estimation of the reproductive potential of a 1m^2 area. Hedychium phenology units were 4m^2 so the mean reproductive potential is divided by 0.25. The 25 Psidium trees used for phenology and reproductive potential estimates averaged 6.4m^2 cover, hence the factor to estimate the reproductive potential of a 4m^2 unit is 0.15625. This analysis is an estimate that will only consider area and not volume considerations and hence may underestimate the potential of species of greater height such as Psidium. Based on these data, it is estimated that the mean annual reproductive potential of a square meter area of Clidemia is 10,312,292 seeds; for Hedychium is 2,024 seeds; and for Psidium is 568 seeds.

DISCUSSION

The primary limitation of this investigation was that the study period was restricted to a single year. Marked annual variation in weather patterns such as El Nino can profoundly influence the timing and intensity of plant phenology. Because of variations in the annual phenological patterns of species, quantitative single-year phenology investigations have limitations (Wheelwright 1986). Quantitative estimations of numbers of seeds produced are difficult, especially for those species with exceptionally high reproductive output. Nonetheless, intensive quantitative phenological studies of marked individuals offer important insights into plant reproductive strategies (Wheelwright 1986).

Smith (1992) stated that Clidemia flowers and fruits throughout the year except in drier areas, where it ceases flowering and fruiting in times without rainfall. This research demonstrated that, even though Clidemia can flower and fruit year round, there are marked increases in ripe fruit production from late summer through early winter. The phenological pattern expressed here differs from that documented for another invasive melastome, Miconia calvescens, in Tahiti

(French Polynesia), which flowers in short intense periods (1-2 wk duration) three times annually, perhaps in response to heavy rainfall (Meyer 1994). Compared to the results reported here, the reproductive potential of Clidemia appears to have been underestimated. Smith (1992) reported estimates for Clidemia reproductive potential as over 500 fruits per season with over a 100 seeds per fruit, hence over 50,000 seeds/year. Results reported hence suggest an underestimate of nearly two order of magnitude.

Generally, my results agree with other investigations of the reproductive phenology of Psidium with the exception that several sources report the production of ripe fruit earlier than this investigation documented (Table 8). Diong (1982) observed that Psidium flowered in Kīpahulu Valley from April to July, a more prolonged and generally later timing than suggested by the present study. This study observed flowers in 9 of the 12 monthly surveys, peaking in April and May. Flower bud production, which may be a better quantitative indicator of flowering activity (as individual flowers are ephemeral), occurred from February to June. Ripe fruits were observed by this study from October through March. Diong (1982) noted fruit fall occurred from late August to December. Diong's comments may have referred to more extensive Psidium populations occurring at lower elevations in Kīpahulu Valley. On Reunion Island, P. cattleianum flowers

Table 8. Comparison of reports of Psidium cattleianum phenology.

	Production of flower buds	Production of flowers	Production of immature fruits	Production of ripe fruits
data reported here re: Kīpahulu Valley, Hawai'i	February to June	April to May	April to November?	October to March
Diong (1982) re: Kīpahulu Valley, Hawai'i	No information given	April to June	No information given	Late August to December
Huenneke (1991) re: Hawai'i island, Hawai'i	No information given	No information given	August to December	August to September at all elevations, extending to late fall in mid-elevations (460-610 m)
Webb, Sykes, & Garnock-Jones (1988) re: New Zealand	No information given	June to March	No information given	No information given
Normand and Habib (2001) re: Reunion Island	No information given	November to January	---	"fruit from February to June"

from November to January and fruits from February through June (Normand and Habib 2001).

This study focused on the more invasive red-fruited form (f. cattleianum) of Psidium cattleianum, but the yellow-fruited form (f. lucidum) and less commonly, apparent intermediates also are invasive and were observed in the study area. In its native habitat, the yellow-fruited Psidium cattleianum is characteristic of low elevation forest such as restinga (coastal forest) and capoeiras (secondary growth after clear cutting native forests) at 5 to 100 m elevation (Hodges 1988). Little information is available on the more invasive red-fruited type in its native range, apparently because it is largely unknown there, though it may occur in forests above 700 m (Hodges 1988). The reproductive system of the two Psidium cattleianum color forms is still poorly understood. Psidium cattleianum is likely apomictic (C.W. Smith pers. comm. 2002; Buwalda and van der Wal, unpublished report, 1989, cited in Ellshoff et al. 1995). In an early investigation, Atchinson (1947) reported the chromosome count for an unspecified form of Psidium cattleianum as 2n = 88. Hirano and Nakasone (1969a) reported the red-fruited type (f. cattleianum) as heptaploid (2n = 77) and the yellow-fruited type (f. lucidum) as octaploid (2n =88). Hirano and Nakasone (1969b) reported that Psidium cattleianum pollen germinated only at relatively low levels (32% for f. cattleianum), or not at all (f. lucidum).

The relatively high levels of flower buds and flowers compared to low levels of immature and ripe fruits strongly suggest that most flowers of plants at the study site did not form fruits. The reason for the low numbers of fruits produced by Psidium in upper elevation Kīpahulu, such as the study site at 890 m elevation, is not understood, but others have observed the pattern as well. Diong (1982), who worked in this area of Kīpahulu, noted that fruiting Psidium trees were not observed at 900-1200 m elevation. He noted that the Psidium trees at higher elevation represent those at the invasive front of the species and are in smaller size classes. Insufficient plant size seems unlikely as an explanation for low fruit set as the Psidium trees used in assessing phenology were individuals that appeared as large and old as vigorously fruiting trees at lower elevations. Diong (1982) also stated that fruit maturity among individual Psidium trees was not uniform.

Another hypothesis for the lack of fruit production by Psidium at higher elevations in Kīpahulu Valley might be related to some disadvantage of the relatively sparse stands of the species at its invasive front, such as reduced cross-pollination. Where Psidium fruits abundantly at lower elevations, the species occurs in dense, genetically heterogeneous stands.

A third plausible explanation is that Psidium has reached its uppermost elevational limits at the study site and is expressing low levels of fruit production. However, at 880 m the sampling site is still considerably below the upper elevational limits of the species in Hawai'i reported as 1220 m (Wagner *et* *al*. 1990). In addition, *Psidium* has been recently observed as high as 1615 m elevation in the Manawainui planeze of Haleakalā National Park (W. Haus pers. comm.).

In an extensive survey of Hawai'i island, *Psidium* was the most common of studied weeds found up to 1308 m elevation (Jacobi and Warshauer 1985; J. Jacobi pers. comm. 2002). Tunison (unpubl. The Nature Conservancy element abstract) remarked regarding *Psidium* "single-stand formation is well underway at 1,100 m in Hawai'i Volcanoes National Park." Huenneke (1991) noted that fruit production of *Psidium* occurred in her six-month period of fieldwork at the uppermost elevational station at 915 m elevation but does not provide information regarding the levels of ripe fruit production. Diong (1982) reported this species at 1200 m elevation in Kīpahulu, while Medeiros *et* *al*. (1998) reported it up to 1355 m in Kīpahulu and up to 1585 m in the adjacent Manawainui rain forest. In field germination experiments, Diong (1982) concluded that environmental conditions were suitable for *Psidium* germination in the *Psidium*-free areas of Kīpahulu at 1450 m elevation. However, with copious vegetative root suckering (Huenneke 1991; Huenneke and Vitousek 1990), low level of local seed production, and seed rain from lower elevations by non-native birds (Chapter Three), *Psidium* seems quite capable of spreading in Kīpahulu (and other protected East Maui rain forest without feral pigs) and forming dense thickets that exclude native species as at lower elevations. The conversion of diverse native forests to that of increasingly monospecific Psidium stands is accelerated by ground disturbance and where large-scale seed dispersal by feral pigs occurs. Examples on Maui include Ko’olau Gap, the Manawainui district, and Haleakalā National Park's newly acquired Ka'apahu addition of southeast Haleakalā.

In the course of phenological work, observations of diurnal pollinators of the study weeds were also made. Clidemia flowers were conspicuous in their near total absence of diurnal and crepuscular insect visitors. Syrphid flies and Apis mellifera (honeybee) routinely closely approached Clidemia flowers only to ultimately avoid the flower and leave without visiting. Hedychium flowers were visited by Apis mellifera and at least four bird species: one non-native, Zosterops japonicus (Japanese white-eye) and three endemic species, Hemignathus virens ('amakihi), Himatione sanguinea ('apapane), and Vestiaria coccinea ('i'iwi). Only honeybees (Apis mellifera) were observed visiting Psidium flowers.

CONCLUSION

Though the three species studied are globally recognized as among the most invasive of tropical plant species, remarkably little is known about Clidemia, Hedychium, Psidium, and other ecosystem-damaging weeds. This study documented the distinct, seasonal cycle of flower and fruit production of each of the three study species as well as marked differences in reproductive potential. This and similar information may assist in developing effective control and containment strategies for these invasive plant species as well as in fine-tuning the development of trait assessments used in quarantine and importation screening to evaluate non-native species and perhaps help prevent serious weed introductions in the future. In addition to the theoretical value that detailed knowledge of weed life-history traits contributes, it is hoped that practical applications may be found, since the fate of the biodiversity of the Hawaiian Islands and other tropical areas rests on effective and timely actions.

CHAPTER THREE:

AVIAN SEED DISPERSAL IN A HAWAIIAN RAIN FOREST, WITH SPECIAL REFERENCE TO THREE IMPORTANT WEED SPECIES.

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ABSTRACT

The objective of this study was to determine whether and to what extent seeds of three invasive rain forest weeds (Clidemia hirta, Hedychium gardnerianum, Psidium cattleianum) of Hawaiian rain forests are being dispersed by birds and to provide some information about the length of gastrointestinal passage time. Wild birds were mist netted in the vicinity of fruiting weed patches in Maui rain forests (Kīpahulu and Makawao Forest Reserve) and their droppings examined for weed seeds. Bird species whose droppings contained study weed species were then kept in aviary conditions and offered the three study weed species under controlled conditions to provide estimates of seed retention after ingestion. Birds, especially two common non-native species (Zosterops japonicus and Leiothrix lutea), are dispersing all three weed species. Leiothrix and Zosterops are serving as seed dispersers for 11 other plant species including at least six native plant species (Cheirodendron, Melicope, Broussaisia, Pipturus, Coprosma, Vaccinium) and one other non-native species (Rubus rosifolius). Under experimental cage conditions, the passage time for Clidemia seeds was as long as 210 minutes, for Hedychium seeds as long as 270 minutes, and with limited results, for Psidium seeds less than 60 minutes. With the extinction of native fruit-eating bird species in Hawai'i, dispersal of seeds of weed and native species is occurring in Maui rain forests by common, generalist, non-native small passerines.

INTRODUCTION

Invasive non-native species increasingly threaten the stability of world biodiversity (Soule 1990; van Driesche and van Driesche 2000). In many cases of species invasions, opportunistic mutually beneficial interactions among non-native species occur, and these may be important in the success of these invasions (Richardson et al. 2000). Especially on Pacific islands, an important mutualistic species interaction occurs between fruit-bearing invasive plants and seed-dispersing animals (Mueller-Dombois and Fosberg 1998).

In this investigation, I report information regarding avian seed dispersal of three problematic fleshy-fruited weed species in a native rain forest on Maui island. The study species are Clidemia hirta (L.) D. Don, Melastomataceae (clidemia), Hedychium gardnerianum Ker.-Gawl., Zingiberaceae (kahili ginger), and Psidium cattleianum Sabine, Myrtaceae (strawberry guava) (hereafter Clidemia, Hedychium, and Psidium).

Effective seed dispersal is a critical stage of plant life histories and of particular importance for invasive species. An effective dispersal system can accelerate the spread of an invasive plant species at a fast enough rate that human efforts to control them are much less likely to succeed. Wind dispersal can transport seeds long distances and although often compensated for by large numbers of seeds, is of limited efficacy for delivery of seeds to optimum sites for germination and establishment. Especially in the structurally-complex surrounds of forest habitats, dispersal by animals, especially birds, is the most effective method of moving seeds to favorable establishment sites (Loiselle and Blake 1999). Fleshiness of fruits, presumably an adaptation to facilitate dispersal by birds, is a trait that occurs in 62% of highly invasive woody species (Rejmanek 1996a, 1996b). The lag phase, the initial temporal stage of invasive plant spread that sometimes begins slowly or appears stalled, may in part be due to the initial sparse utilization of the weed fruit crop by local avian seed dispersers. On remote oceanic islands, opportunistic seed-dispersal species interactions among non-native birds and non-native plants are common (Mueller-Dombois and Fosberg 1998), especially in light of widespread extinctions of native frugivorous faunas, documented especially well in Polynesia (McConkey and Drake 2002).

Throughout the Hawaiian Islands, invasive plant species are one of the greatest threats to native rain forests (Medeiros et al. 1995; Scott et al. 1986). In many cases in Hawai’i, dispersal of seeds of invasive plants by birds appears to have been an important factor in the rapid spread and resultant difficulty of control of these weeds.

Perkins (1924) noted that the rapid increase of the Neotropical weed Lantana camara (lantana) in Hawai'i occurred only after the establishment of two non-native bird species, Geopelia striata (zebra dove, native from Malaya to Australia) and Acridotheres tristis (common myna, native to India). Perkins (1924) observed, "There is no doubt that, had other conditions remained as they were at the time when it was introduced, the plant would never have increased and spread to the extent that was subsequently reached." Despite what is generally regarded as highly successful biological control, lantana still occupies thousands of acres in the Hawaiian Islands (Wagner et al. 1990).

First introduced to the island of Hawai'i in the late 1800s, Morella faya (Ait.) Wilbur(formerly Myrica faya) (Myricaceae) spread rapidly after 1950 and by 1992 occupied 29,245 ha (2.8% of the island's total area). Morella's explosive spread from forestry plantations to native Metrosideros woodlands of Hawai'i Volcanoes National Park (HAVO) has been attributed to population increases in its primary seed disperser, Zosterops japonicus (Japanese white-eye, native to eastern Asia) during 1950-1970 (Kjargaard 1994). The distribution of Zosterops in HAVO increased from 23% of the Park in the 1940s to 100% of the Park by 1970 (van Riper 2000). Bird-dispersed Morella is now extensively established within 12,345 ha of HAVO, which is 14% of the park's area (Whiteaker and Gardner 1992) and still spreading. With HAVO, the nitrogen-fixing abilities of Morella have disrupted the natural succession of native species while facilitating the proliferation of other non-native plant species (Vitousek and Walker 1989). Morella is currently considered one of the park's most ecosystem-disrupting weeds (T. Tunison pers. comm.).

On La Reunion and Mauritius (Mascarene Islands) in the Indian Ocean, native vertebrate seed dispersers have been largely extirpated. Introduced bird species, especially an introduced bulbul, Pycnonotus jocosus (red-whiskered bulbul, native to India), as opportunistic seed dispersers, have greatly accelerated the spread of several fleshy-fruited invasive weed species (Lorence and Sussman 1986; Macdonald et al. 1991; Clergeau and Mandon-Dalger 2001). On La Reunion, Pycnonotus, introduced in 1972, has quickly become a common, effective seed disperser of the invasive forest weed Rubus alceifolius (Macdonald et al. 1991). In the Seychelles, the main dispersal agent for the highly invasive weed Clidemia hirta is the endemic bulbul Hypsipetes crassirostris (Seychelles bulbul) (Gerlach 1993).

In the Juan Fernandez Islands, invasive weeds threaten the native flora. The most problematic of these are fleshy-fruited, bird-dispersed species, such as Aristotelia chilensis, Lantana camara, Lonicera japonica, Rubus ulmifolia, and Ugni molinae (Swenson et al. 1997).

Dispersal of seeds by non-native birds has also been a major factor in perhaps the worst forest weed invasion of a remote oceanic island, that of the invasive Neotropical tree Miconia calvescens (Melastomataceae) on Tahiti. Broadly dispersed by the introduced Zosterops lateralis (silvereye, native to Fiji and from western Australia to New Zealand), Miconia in Tahiti increased from a few botanical garden specimens introduced in 1937 to occupying approximately 68% of the island by 1988 (Meyer 1994, 1996). Dense, monospecific stands of Miconia threaten an estimated 40-50 endemic Tahitian plant species, currently near extinction (Meyer and Florence 1996). In the Hawaiian Islands, news of the establishment and rapid spread of Miconia calvescens on several main Hawaiian islands triggered large control campaigns (Medeiros et al. 1997; Medeiros et al. 1998). Miconia seeds are apparently dispersed in Hawai'i nearly exclusively by non-native bird species, including Zosterops japonicus, Geopelia striata, Acridotheres tristis, Garrulax canorus (melodious laughing-thrush, native to China), and Cardinalis cardinalis (northern cardinal, native to North America) (Medeiros et al. 1997).

Knowledge of the details of key plant-animal interactions such as seed dispersal increases our understanding of how invasive species and invaded systems interact and provide insights into a key species interaction, which may predispose some species to readily naturalize and reach problematic levels. By such studies, we can predict spread rates essential for effective control and containment models for plant species already established. This information can assist in identifying traits by which potential plant introductions could be screened to prevent the establishment of additional, potentially ecosystem-damaging species into Hawai’i’s delicate biota.

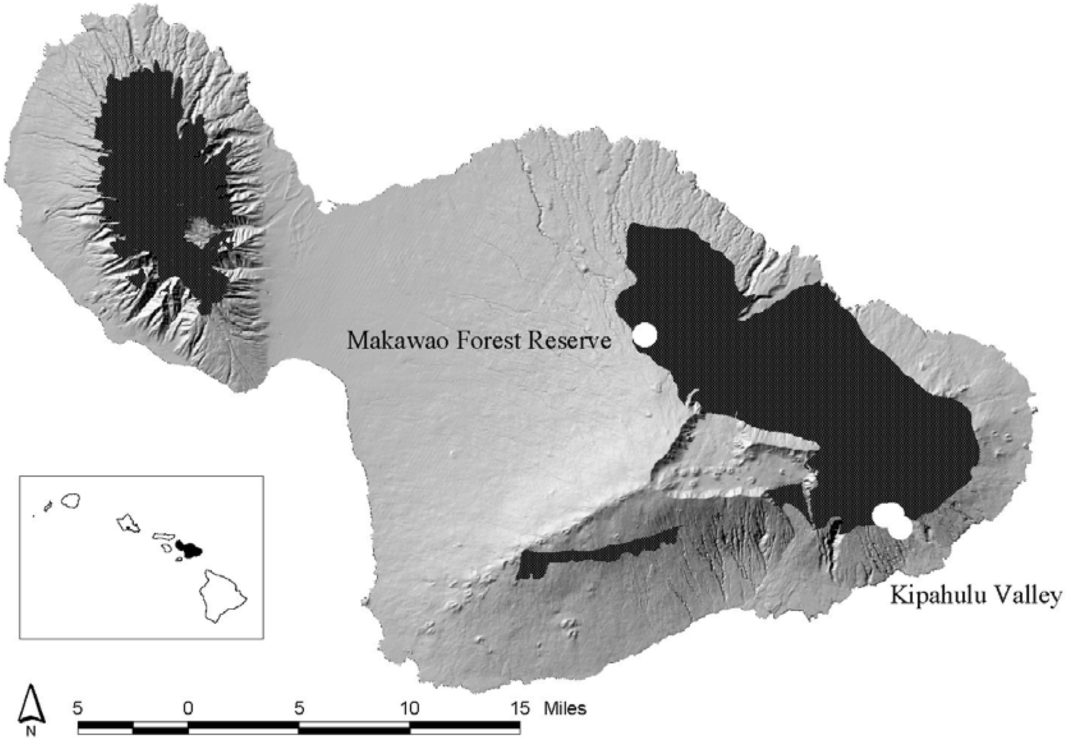
MATERIALS AND METHODS

This investigation comprises two main parts. In the first, the role of birds as the primary dispersers of seeds of the three study weed species and other plant species is investigated directly by mist-netting wild birds in fruiting weed patches, holding them and examining droppings for plant seeds. In the second part, I used the primary seed-dispersing bird species to measure gastrointestinal (GI) passage time of the three study weed seeds.

Four primary study sites were selected on Haleakalā Volcano, East Maui (Figure 8). Three study sites were located in Kīpahulu Valley, within Haleakalā National Park on eastern Haleakalā Volcano and the fourth in State-owned Makawao Forest Reserve (hereafter Makawao F.R.) on northwestern Haleakalā.

The Kīpahulu Valley study sites were all located in remote areas requiring helicopter transport. The Makawao F.R. study site was accessible by four-wheel drive vehicle. The study site for Clidemia was at 820 m elevation, Kīpahulu Valley (804,070E, 2,290,339N UTM-NAD83); for Hedychium at 825 m elevation, Kīpahulu Valley (803,520E, 2,290,297N UTM-NAD83) and 1220 m elevation, Makawao F.R. (786,084E, 2,303,393N UTM-NAD83); and for Psidium at 670 m elevation, Kīpahulu Valley (804,636E, 2,289,408N UTM-NAD83). At each study site, only one of the study weed species was dominant. With one exception (Psidium), the sites were selected in areas at the leading edge of an invasion front, yet located in a dense thicket of the study weed (>50% vegetative cover). Besides the study weed, the vegetation type of all but one study site (Psidium) was diverse native rain forest dominated by tree cover of Metrosideros polymorpha and Acacia koa with well-developed native shrub, fern, and bryophyte layers. The areas surrounding these sites are considered some of the finest quality rain forest in Hawai'i (Medeiros, Loope, and Hobdy 1995). The

Figure 8. Map of Maui, Hawaiian Islands, showing distribution of rain forest dominated by native species in black and Makawao Forest Reserve and Kīpahulu Valley study sites as white dots.



Psidium study site in Kīpahulu Valley differed from the other study sites in that it was not at the invasion front of the species, but at lower elevation and nearly completely dominated by the study weed Psidium. This site was formerly diverse Metrosideros polymorpha-Acacia koa rain forest but has been nearly completely transformed within the past 30-50 years by feral pig disturbance and Psidium invasion. Only small patches of native forest and very large solitary Acacia koa trees remain. Attempts to establish a mist-netting study site within Psidium patches at higher elevations amidst native rain forest in Kīpahulu Valley were confounded by the infrequency and irregularity of fruiting of the study species there.

Clidemia hirta (clidemia) is native to Mexico, the West Indies, Central America and northern South America south to Bolivia and southern Brazil. It is a serious forest pest that has become widely naturalized around the world from approximately 20 degrees S to 22 degrees N latitude on Pacific and Indian Ocean Islands, Indonesia, Malaysia, Southeast Asia, and Africa (Chapter One).

Hedychium gardnerianum (kahili ginger) is a large rhizomatous herb up to 2 m in height, native to the Himalayas and adjacent regions and occurring to 1900 m elevation (Graf 1992; Nagata 1990; Stainton 1997). Hedychium has become naturalized from approximately 42 degrees S to 22 degrees N latitude on Pacific, Indian, and Atlantic Ocean Islands, as well as Jamaica, Australia, and South Africa (Chapter One).

Psidium cattleianum (strawberry guava) is a small tree up to 6 m in height that is native to South America. Introduced extensively in tropical and subtropical areas for its edible fruit, Psidium has become widely naturalized from approximately 27 degrees S to 32 degrees N latitude on Pacific, Atlantic, and Indian Ocean

Islands, as well as Australia, Central America, Asia, Africa, the Caribbean, and North America (Chapter One).

The literature was reviewed and regional forest bird researchers were consulted as to putative seed dispersers of Hawaiian rain forest. Based on this, six common, forest-dwelling passerine species of the East Maui study area were selected as study species, including four non-native species (Zosterops japonicus, Leiothrix lutea, Garrulax canorus, and Cettia diphone) and two native species (Hemignathus virens and Himatione sanguinea).

The Japanese White-Eye or Mejiro (Zosterops japonicus) (hereafter Zosterops) is a small (10 cm length) olive-green passerine, native to southern and eastern China, Taiwan, Japan to northern Philippine islands (van Riper 2000). First introduced to the Hawaiian Islands in 1929, it rapidly increased in abundance and range (Caum 1933; Munro 1944) and is now the most abundant and widespread bird species in the Hawaiian Islands, found from sea level to tree line of high elevation rain forests (Scott et al. 1986; van Riper 2000). This understory species is rarely found in open habitats that lack tree or shrub cover and is most common along forest edges (Scott et al. 1986). Zosterops is omnivorous, feeding on fruit, nectar, and insects (Brazil 1991; Guest 1973; Scott et al. 1986).

The Red-billed Leiothrix (Leiothrix lutea) (hereafter Leiothrix) is a medium-sized (14 cm length), brightly colored species, native to the Himalayas regions of India, Nepal, China, and Myanmar at 350-3390 m elevation (Long 1981; Male et al. 1998; Grimmett et al. 1999). Members of the family Rhipiduridae, Leiothrix are omnivorous, consuming about equal parts fruits and invertebrates (Male et al. 1998; Ralph et al. 1998). Leiothrix were first imported to Hawai’i in 1911, intentionally released after 1918, and became established on most main Hawaiian islands (Caum 1933; Male et al. 1998). Potentially found from sea level to high mountain summits and once very common on certain islands (Kaua’i, O’ahu, Hawai’i), this species has declined dramatically in some cases in population range and size (Male et al. 1998). Currently much less abundant than Zosterops, Leiothrix on East Maui is most common in moist upland forests above 1000 m elevation (Scott et al. 1986). The babblers (subfamily Timaliinae), to which Leiothrix belongs (as well as Garrulax), are generally a sedentary, highly social group of birds that communally defend territories with noisy, scolding calls. In their native habitat, Leiothrix form small resident groups of about six birds, given to small altitudinal movements, from which pairs separate during breeding season (Grimmett et al. 1999).

The Melodious Laughing-Thrush (Garrulax canorus) (hereafter Garrulax) is a jay-like passerine, native to China, which naturalized in the Hawaiian Islands around 1900 (Hawai'i Audubon Society 1996; Pratt et al. 1987). Currently on Maui, this habitat generalist occurs from near sea level to upper elevation forests and is the largest (25 cm length) passerine of Maui rain forests (Berger 1981; Scott et al.

1986). Garrulax feeds primarily on insects and fruit (Hawai'i Audubon Society 1996).

The dull olive-gray, medium sized (14 cm length) Japanese Bush-Warbler (Cettia diphone) (hereafter Cettia), native to Japan, was first noted on East Maui in 1980, but has since increased markedly in both abundance and range (Scott et al. 1986; F. Duvall pers. comm.). Largely restricted to the understory of upland native forests, it is primarily an insectivorous species that also feeds on fruit and nectar (Berger 1981; Scott et al. 1986).

The Common Amakihi (Hemignathus virens) (hereafter Hemignathus) is a medium-sized (11 cm length), endemic, green honeycreeper that feeds on nectar, insects, other invertebrates, fruit, and the juice from fruits (Henshaw 1902; Berger 1981; Scott et al. 1986). In terms of habitat and food plant utilization and probable disease resistance, Hemignathus is the most adaptable of native forest birds, found in dry, mesic, and wet forests, mostly above 500 m (Lindsey et al. 1998; Scott et al. 1986).

The Apapane (Himatione sanguinea) (hereafter Himatione) is a medium-sized (13 cm length), endemic, predominantly-crimson honeycreeper found on all main islands above 600 m elevation, and is the most abundant native bird in the archipelago (Pratt et al. 1987). Himatione feeds primarily on Metrosideros nectar and insects, while immature birds may feed on berries when nectar is scarce

(Henshaw 1902; Scott et al. 1986). Though potentially found from near sea level to 2900 m elevation, it is largely restricted to native wet forests dominated by Metrosideros (Scott et al. 1986).

Mist netting was done in dense thickets of the study weed species and only when these species were producing abundant fruits. Sites were searched for suitable net locations and space for net lanes cleared of surrounding vegetation with machetes. Mist nets used were five-shelved and ranged from 3.1 to 12.2 meters in length. Depending upon availability of net lanes and number of personnel available to check nets and extract birds, 7 to 14 mist nets were opened at one time. When opened, mist nets were hoisted up to 3.5 m height on telescoping poles. Nets were opened one hour after daybreak (from 0700) and remained opened while passerine birds were actively foraging, as late as 1600 hours (one hour before sunset), weather permitting. This timing allowed captured birds to forage during critical dawn and dusk feeding periods. Mist nets were closed during prolonged rainy periods to prevent hypothermia of captured birds. In upland rain forest sites, this was an important factor that greatly restricted the number of net-hours. When mist nets were opened, they were checked approximately every 30 minutes for captures to minimize bird trauma and entanglement in the net fabric.

The total mist netting sampling intensity differed among the three study weed species because of difficulty of access, availability of personnel, and timing issues related to peak fruiting intensity of the target weeds. To help describe this, I use net-hours, with one net-hour defined here, according to the Monitoring Avian Productivity and Survivorship (MAPS) standard, as a 3.7 meter long mist net open for one hour. Mist netting was conducted at the Kīpahulu Clidemia site in September 1996 for five days for a total of 23.9 hours using 70.1 to 115.9 meters of net for a total of 693.9 net-hours. Mist netting was conducted at the Kīpahulu Hedychium site in October and November 1996 for six days for 30.3 hours using 82.3 to 115.9 meters of net for a total of 1056.3 net-hours. At the Makawao F.R. Hedychium site (December 1996, April and October 1998, and January 1999), mist netting occurred over eleven days for 53.3 hours using 64.0 to 109.8 meters of net for a total of 1,454.1 net-hours. Mist netting was conducted at the Kīpahulu Psidium site in October 1999 for three days for 18 hours using 109.8 meters of net for a total of 540 net-hours.

Captured birds were removed from the mist net, transferred into a drawstring bag and suspended from a branch in a quiet, shaded location for about 30 minutes to allow time for defecation (Karasov 1990). An aluminum tag attached to the holding bag recorded the bird species, mist net location, and time and date of capture. After the holding period, the captured bird was banded and the band combinations recorded on the aluminum tag. The bird was weighed, molt condition recorded, and wing, bill, and tail measurements recorded in an attempt to sex and age it. The bird was checked for brood patches and cloacal protuberances (indications of breeding condition) and released. The aluminum-tagged cloth bag with the bird's droppings was placed in a sealed plastic bag in an ice chest or cool location until analysis. This methodology was adapted from Herrera (1981), Loiselle (1990), and Loiselle and Blake (1990). Snow and Snow (1988) discussed the advantages of this methodology over observational information.

In the laboratory, droppings were removed from the cloth bag with forceps and irrigated with water. The droppings were suspended in a small amount of distilled water in a Petri dish and examined with a dissecting stereoscope. All seeds, other plant parts, and invertebrate parts extracted from droppings were preserved in 90% ethanol and categorized according to morphological type. Recovered seeds were identified by comparing them with vouchers of known seeds extracted from fresh fruits collected at the study site. Viability of target weed seeds excreted by wild birds was tested for Hedychium (placed on Petri dishes on moistened filter paper) and Psidium (placed in pots of sterile soil mix). Clidemia seeds excreted by mist-netted birds were not tested for viability because of spoilage associated with poor field preservation facilities (plastic cooler with ice packs) and the delay in processing associated with the remote field locale. Invertebrate parts were identified to the most specific taxonomic level possible. Laboratory methodology generally followed that of Ralph et al. (1985).

An important component of seed dispersal by animals is passage time, the range of time that seeds of various plant species are retained after ingestion into the gastrointestinal (GI) tract. Wild passerine birds were mist netted from 20 January 1999 to 22 January 1999 in Makawao F.R., northwest Haleakalā, and held in individual cages at the capture site for a maximum of three hours to evaluate their behavior and their potential as captive birds. Any birds that failed to eat the captive diet within the three-hour period were released at the capture site.

Birds that passed initial acclimation tests were transported to the Maui Veterinarian Services Office aviary, managed by the State of Hawai'i, at Olinda, Maui (1220 m elevation), where they were housed in a structure custom-built for this experiment and located on the aviary grounds. Each bird was placed in an individual birdcage. Individual cages were enclosed within a larger polyvinyl chloride framed structure (ca. 4 m x 3 m) with attached walls of mosquito netting and hardware cloth. This larger exclosure provided protection for the birds from predators (mice, rats, cats, mongoose) and mosquitoes (potential avian-disease vectors). The individual birdcages were constructed of predator-proof wire, approximately 60-cm length, 30-cm width, and 30-cm height with multiple perches and false ceilings constructed with shade cloth to minimize head injuries. Shade cloth also extended approximately 15 cm down the sides of individual cages to calm the birds. Additional predator protection was provided by a series of baited snap traps set around the perimeter of the larger exclosure.

Each bird was acclimated to captivity for a minimum of three days prior to initiation of the experimental period. Food consumption and fecal droppings were monitored and the birds weighed every other day in cloth bird bags. Captive diet consisted of chopped fruits, a commercial nectar product (Roudybush Nectar 15), a commercial pellet food (Kaytee Exact Canary Pellets), and fresh water.

Twenty-four hours prior to testing, the birds were placed in smaller cages with their regular non-experimental diet (pellet food, fruit, and nectar). Nectar and pellet food were available to the birds throughout the experiment, excepting the hour prior to the initiation of the food exposure period. The night before the experimental trial, a stack of clean wax paper sheets was positioned on the floor of each cage and fruits of one of the three study weed species were prepared for the next day's experiment. Large numbers of fruits of the selected weed were used to assure that the display of study weed fruits was conspicuous to the birds. All birds were presented with the fruit of a single weed species (<u>Clidemia</u>, <u>Hedychium</u>, or <u>Psidium</u>) in the food exposure period. When placed in the cage the night before the experiment, the weed fruits were covered with a partition and were unavailable for feeding. At daybreak of the experiment day, the partitions were removed over all the food containers in the individual cages. During the 90-minute food exposure period, the birds were left in quiet isolated conditions to consume fruits of the study weed species. At the end of the food exposure period, all unconsumed weed seeds were withdrawn and replaced with their non-experimental diet.

After the food exposure period had concluded and at periodic (1 hour, 2 hours, 3 hours, 4 hours, 8.5 hours) intervals afterwards, the uppermost wax paper sheet with droppings corresponding to that time period was removed and labeled with the date, time, bird species, and an identification letter. The droppings on the chronologically-segregated wax paper sheets were examined for seeds of Clidemia, Hedychium, or Psidium.

The Hedychium trial was conducted on 26 January 1999 and the Clidemia trial on 28 January 1999 (both trials with one Garrulax, five Leiothrix, and five Zosterops). The Psidium trial was conducted on 3 February 1999 (with five Zosterops). Because of their failing health as determined by weight loss, listless behavior and decreased food consumption, the Garrulax and all five Leiothrix were released earlier than planned. Low quantities of Psidium fruits were offered to Garrulax, Leiothrix, and Zosterops individuals during non-experiment days. The five Zosterops adapted relatively well to captivity and were released on 6 February 1999 after three non-testing quarantine days, to make sure they had excreted all weed seeds. Birds were released at the sites where they had originally been mist-netted within Makawao F.R.

Weed seeds extracted from captive bird droppings were labeled as to the time interval they represented, and then washed with distilled water. Viability and the timing of germination were tested as with Part One of this investigation, Clidemia and Hedychium seeds on moistened paper discs in Petri dishes and Psidium seeds in pots with potting soil. Seeds of the study weed species were also extracted from fresh fruits and treated in a like manner as controls (i.e., Clidemia and Hedychium on filter paper in Petri dishes and Psidium in potting soil). The Petri dishes were placed indoors in an area of ample but indirect natural light. The potted samples were placed in a greenhouse with ample diffused natural light. The Petri dishes (containing Clidemia and Hedychium seeds) and the pots with soil (containing Psidium seeds) were periodically monitored weekly for a calendar year for emergence, testing viability and the timing of germination. As needed, usually every four to six days, the filter paper in the Petri dishes and the soil in the potted samples were remoistened with distilled water. As a seed germinated (determined as the point at which the root radicle emerged from the seed coat in Petri dish samples or at which the cotyledon stem became visible in potted soil samples), the seedling was removed and recorded. Petri dish and potted soil samples were weekly reordered in position to avoid bias in terms of amount of light received. Natural sunlight was the light source.

All wild-caught birds were treated humanely in accordance with the Vertebrate Animal Use Protocol approved by the University of Hawai'i's Institutional Animal Care and Use Committee.

RESULTS

I. STUDY SPECIES

During the course of fieldwork at the four study sites in Kīpahulu Valley and Makawao F.R., Maui, all six common forest passerine species were captured (Cettia, Garrulax, Hemignathus, Himatione, Leiothrix, and Zosterops) (Table 9). The preponderance of bird captures were two species of non-native birds: Zosterops and Leiothrix. In order of decreasing number of seeds per capture, Leiothrix, Zosterops, and Hemignathus were dispersing Clidemia seeds, Leiothrix and Zosterops were dispersing Hedychium seeds, and Leiothrix and Garrulax were dispersing Psidium seeds. Five of the six bird species (excluding Cettia) were found to be dispersing at least some quantity of native or non-native plant seed(s). Other species observed but not captured at sampling sites were ‘i’iwi (Vestiaria coccinea) and Northern Cardinal (Cardinalis cardinalis) at Kīpahulu and Makawao F.R., and Nutmeg Mannikin (Lonchura punctulata) at Kīpahulu.

Clidemia:

In 840 net-hours at the Kīpahulu Clidemia study site, 29 captures (averaging 29.0 net-hours/capture) were made of 20 individual birds and nine recaptures (Table 9).

Table 9. List of bird species mist-netted and frequency of captures which excreted seeds of the three invasive study plant species. The frequency value refers to the percentage of the sample size that excreted seeds of the weed species that infested the particular study site where the bird was captured. Sample size (n) refers to the number of captures of a given bird species at a particular study site.

bird species	Frequency of captures excreting Clidemia hirta seeds	Frequency of captures excreting Hedychium gardnerianum seeds	Frequency of captures excreting Psidium cattleianum seeds
Cettia diphone (non-native)	no captures made of Cettia at the Clidemia study site	0 (n = 13)	no captures made of Cettia at the Psidium study site
Garrulax canorus (non-native)	no captures made of Garrulax at the Clidemia study site	0 (n = 4)	1.000 (n = 1)
Hemignathus virens (native)	0.125 (n = 9)	0 (n = 11)	no captures made at the Psidium study site
Himatione sanguinea (native)	0 (n = 4)	0 (n = 1)	no captures made of Himatione at Psidium study site
Leiothrix lutea (non-native)	1.000 (n = 6)	.231 (n = 78)	.500 (n = 10)
Zosterops japonicus (non-native)	.778 (n = 9)	.146 (n = 41)	no captures made of Zosterops at the Psidium study site

Table 10. Average number of study weed seeds excreted per capture of wild caught forest passerines in Hawaiian rain forests at Kīpahulu and Makawao F.R., Maui.

	Garrulax	Hemignathus	Leiothrix	Zosterops
Clidemia	no captures made of Garrulax at Clidemia study site	5.8 (+/- 17.3) seeds/capture (n = 9)	101.5 (+/- 116.2) seeds/capture (n = 6)	314 (+/- 569) seeds/capture (n = 9)
Hedychium	no seeds excreted by any of 10 Garrulax captures made at Hedychium study site	no seeds excreted by any of 10 Hemignathus captures made at Hedychium study site	0.72 (+/- 1.70) seeds/capture (n = 78)	0.29 (+/- .84) seeds/capture (n = 41)
Psidium	13 seeds/capture (n = 1)	no captures made of Hemignathus at the Psidium study site	1.8 (+/- 2.7) seeds/capture (n = 10)	no captures made of Zosterops at the Psidium study site

Ten Zosterops captures were made of five individual birds and five recaptures but one recapture was released immediately without collecting a fecal sample because the bird was in poor condition due to having become soaked in the mist net. Zosterops captures yielding fecal samples (n = 9) within fruiting Clidemia patches overall averaged 314 seeds/capture; the seven (77.8%) captures that excreted Clidemia seeds had from 67 to over 1800 seeds/capture. Leiothrix captures (n = 6, six individual birds with no recaptures) within fruiting Clidemia patches averaged 102 seeds/capture; all six (100%) captures excreted Clidemia seeds and had from three to 289 seeds per sample. Hemignathus captures (n = 9, five individual birds and four recaptures) within fruiting Clidemia patches averaged 5.8 seeds/capture; the single (11.1% of total captured) capture that excreted Clidemia seeds had 52 seeds. At the Clidemia study site, none of the four Himatione captures (four individuals with no recaptures) excreted any Clidemia seeds. Cettia and Garrulax were not captured at the Clidemia study site.

Hedychium:

In 2510.4 net-hours at the Kīpahulu and Makawao F.R. Hedychium study sites, 143 captures (averaging 17.5 net-hours/capture) were made of 124 individuals and 19 recaptures (Table 9). Zosterops captures (n = 41, 39 individuals and two recaptures) within fruiting Hedychium patches averaged 0.29 seeds/capture; the six (14.6%) captures that excreted Hedychium seeds had one to four seeds/capture. Leiothrix captures (n = 78, 66 individuals and 12 recaptures) within fruiting Hedychium patches averaged 0.72 seeds/capture; the 18 (23.1%) captures that excreted Hedychium seeds had from one to ten seeds/capture. Within fruiting Hedychium patches, no other capture of thirteen Cettia (including four recaptures), ten Garrulax, ten Hemignathus, and one Himatione excreted any Hedychium seed or aril material.

Psidium:

In 540 net-hours at the Kīpahulu Psidium study site, 11 captures (averaging 49.1 net-hours/capture) were made with no recaptures (Table 9). Leiothrix captures (n = 10) within fruiting Psidium patches averaged 1.8 seeds/capture; the five captures (50%) that excreted Psidium seeds had from one to eight seeds/capture. The single Garrulax capture mist-netted in a fruiting Psidium patch excreted 13 Psidium seeds. Cettia, Hemignathus, Himatione, and, most surprisingly, the common Zosterops were not captured at the Psidium study site.

Bird-excreted Clidemia seeds were not tested in Part One of this investigation (due to sample spoilage); hence, the results presented in Table 11 represent only those obtained from captive birds in Part Two of the investigation. As the viability of bird-excreted Hedychium and Psidium seeds was similar in Part One (wild caught) and Part Two (captive diet) of this investigation, the results were pooled and are presented in Tables 12 and 13.

Table 11. Comparison of germination percentage and time required for germination of Clidemia hirta seeds extracted from fresh fruits versus those excreted by rain forest passerines.

	germination percentage (sample size)	mean no. of days for germination (*x* +/- SE)
control from fresh fruit	67.3% (n = 300, i.e., 100 seeds each from three individual plants)	72.4 (+/- 18.4)
Leiothrix-excreted seeds	71.4% (n = 10)	94.9 (+/- 35.0)
Zosterops-excreted seeds	64.7% (n = 17)	116.4 (+/- 37.1)

Table 12. Comparison of germination percentage and time required for germination of Hedychium gardnerianum seeds extracted from fresh fruits versus those excreted by rain forest passerines.

	germination percentage (sample size)	mean no. of days for germination (*x* +/- SE)
control from fresh fruit	87.5% (n = 120, i.e., 40 seeds each from three individual plants)	16.1 (+/- 5.8)
Leiothrix-excreted seeds	76.7% (n = 60)	21.9 (+/- 13.0)
Zosterops-excreted seeds	85.0% (n = 20)	27.4 (+/- 6.0)

Table 13. Comparison of germination percentage and time required for germination of Psidium cattleianum seeds extracted from fresh fruits versus those excreted by rain forest passerines.

	germination percentage (sample size)	mean no. of days for germination (*x* +/- SE)
control from fresh fruit	51.5% (n = 600, i.e., 100 seeds each from six individual plants)	42.3 (+/- 11.5)
Leiothrix-excreted seeds	72.2% (n = 18)	50.1 (+/- 26.7)
Garrulax-excreted seeds	84.6% (n = 13)	51.4 (+/- 48.4)

II. OTHER DISPERSED PLANT SPECIES

Though this investigation was focused on the dispersal of the three important weed species, it was also discovered that Leiothrix and Zosterops are serving an important role as seed dispersers for native plant species. Besides the three study weed species, the most common seeds dispersed by Zosterops were Cheirodendron trigynum, Melicope cf. clusiifolia, Rubus rosifolius, Broussaisia arguta, Pipturus spp., Coprosma spp., and Vaccinium calycinum (Table 14). Besides the three study weed species, the most common seeds dispersed by Leiothrix were Cheirodendron, Pipturus, Rubus rosifolius, an unidentified seed, Vaccinium calycinum, Broussaisia arguta, Melicope cf. clusiifolia, and Coprosma spp (Table 15). Besides Psidium, Garrulax was discovered to be dispersing seeds of Cheirodendron trigynum, Myrsine lessertiana, Rubus rosifolius, and an unidentified species (Table 16). The only other non-native weed seeds encountered in wild-caught bird droppings in this investigation were those of the invasive but relatively innocuous Rubus rosifolius.

The endemic Cheirodendron trigynum (Araliaceae) is one of the most common tree species of native rain forests in Hawai'i. It was also the most common seed of native plant species encountered in bird droppings of the three most common genera of non-native birds: Leiothrix (60.6% frequency), Zosterops (28.0% frequency), and Garrulax (83.3% frequency). Interestingly, no Cheirodendron seeds were excreted in captures of the two native bird species, Himatione (n= 5) and Hemignathus (n= 18). Cheirodendron seeds recovered from droppings during this investigation proved viable by germination on moist paper towels in Petri dishes, 5 of 13 seeds (38.5%) germinated from Zosterops and 57 of 193 seeds (29.5%) from Leiothrix. Cheirodendron fruits are available year round with individual trees producing several hundred to several thousand fruits annually (Medeiros, Loope, and Chimera 1998a). Based on the importance of Cheirodendron in the diet of several species of Hawaiian thrush (Berger 1981; van Riper and Scott 1979), and its abundance in the droppings of non-native frugivorous species, it appears clear that Cheirodendron is strongly adapted for avian seed dispersal.

Table 14. Frequency of presence and mean number of seeds of native and non-native plant species besides the study weed species excreted per capture of Zosterops japonicus in rain forests at Kīpahulu and Makawao F.R., Maui island.

Plant species	Frequency of wild caught Zosterops birds carrying apparently viable seeds of respective plant species	Mean no. of seeds per capture (range of no. of seeds per capture)
Cheirodendron trigynum (Araliaceae)	14/50 birds 28%	0.80 (0-8) seeds
Melicope cf. clusiifolia (Rutaceae)	7/50 birds 14%	0.22 (0-3) seeds
Rubus rosifolius (Rosaceae)	3/50 birds 6%	0.03 (0-1) seeds
Broussaisia arguta (Saxifragaceae)	3/50 birds 6%	4.98 (0-211) seeds
Pipturus spp. (Urticaceae)	2/50 birds 4%	0.12 (0-3) seeds
Coprosma spp. (Rubiaceae)	1/50 birds 2%	0.03 (0-1) seed
Vaccinium calycinum (Ericaceae)	1/50 birds 2%	0.03 (0-1) seed
4 spp. unidentified seed(s)	6/50 birds 12%	0.12 (0-1) seed

Table 15. Frequency of presence and mean number of seeds of native and non-native plant species besides the study weed species excreted per capture of Leiothrix lutea in rain forests at Kīpahulu and Makawao F.R., Maui island.

Plant species	Frequency of wild caught Leiothrix birds carrying apparently viable seeds of respective plant species	Mean no. of seeds per capture (range of no. of seeds per capture)
Cheirodendron trigynum (Araliaceae)	57/94 birds 60.6%	4.8 (0-46) seeds
Pipturus spp. (Urticaceae)	11/94 birds 11.7%	1.5 (0-55) seeds
Rubus rosifolius (Rosaceae)	10/94 birds 10.6%	0.64 (0-24) seeds
unidentified seed	9/94 birds 9.6%	2.7 (0-63) seeds
Vaccinium calycinum (Ericaceae)	7/94 birds 7.5%	1.7 (0-61) seeds
Broussaisia arguta (Saxifragaceae)	6/94 birds 6.4%	2.4 (0-117) seeds
Melicope cf. clusiifolia (Rutaceae)	6/94 birds 6.4%	0.11 (0-3) seeds
Coprosma spp. (Rubiaceae)	4/94 birds 4.3%	0.12 (0-5) seeds
Clermontia arborescens (Lobeliaceae)	1/94 birds 1.1%	0.01 (0-1) seed
Rubus hawaiensis (Rosaceae)	1/94 birds 1.1%	.01 (0-1) seed
5 spp. unidentified seed(s)	11/94 birds 11.7%	0.25 (0-6) seeds

Table 16. Frequency of presence and mean number of seeds of native and non-native plant species besides the study weed species excreted per capture of Garrulax canorus in rain forests at Kīpahulu and Makawao F.R., Maui island.

Plant species	Frequency of wild caught Garrulax birds carrying apparently viable seeds of respective plant species	Mean no. of seeds per capture (range of no. of seeds per capture)
Cheirodendron trigynum (Araliaceae)	5/6 birds 83.3%	1.5 (0-3) seeds
Rubus rosifolius (Rosaceae)	1/6 birds 16.7%	0.2 (0-1) seeds
Myrsine lessertiana (Myrsinaceae)	1/6 birds 16.7%	0.2 (0-1) seeds
Unidentified seed(s)	1/6 birds 16.7%	1.8 (0-11) seeds

The discovery of Melicope seeds in Zosterops and Leiothrix droppings was somewhat surprising in that the fruit is a capsule with no pulp and shiny non-fleshy seeds. Despite the absence of any apparent reward, Melicope was the second most common seed type encountered in Zosterops (14% frequency) and occasionally in Leiothrix droppings (6.4% frequency). Bird dispersal in Melicope has been cited as a factor in the broad distribution of the genus across the Pacific (Hartley 2001).

Two Pipturus species occur in the study areas (Medeiros, Loope, and Chimera 1998a) and both commonly appear in the droppings of Leiothrix (11.7% frequency) and, less often, in Zosterops (4.0% frequency). Despite its restricted occurrence on steep slopes and along stream drainages, the relative frequency of its seeds in droppings indicates that Pipturus is a preferred food species.

The relatively large (4 mm) seeds of the small tree, Coprosma, were rarely encountered in droppings of captured birds: Zosterops (2.0% frequency) and Leiothrix (4.3% frequency). Seeds of the two endemic species, Coprosma pubens Gray and C. ochracea Oliver (Medeiros, Loope, and Chimera 1998a), are morphologically variable and hence, identification of Coprosma seeds was made only to the generic level.

The largest and most common baccate fruits of Hawaiian rain forests are those of Clermontia whose numerous very small seeds are reported as being bird dispersed (Rock 1919). Despite this, evidence of frugivory on them is rarely seen (pers. obs.). In 168 captures of four fruit-eating genera (Leiothrix, Zosterops, Hemignathus, Garrulax), only one Leiothrix capture excreted a single seed of Clermontia arborescens (Mann) Hbd.

Rubus rosifolius, native to Asia, was the only non-native species other than the target species whose seeds were found in local frugivores, occurring at low but consistent levels in Zosterops (6% frequency), Leiothrix (10.6% frequency), and Garrulax (16.7% frequency). Only one Leiothrix capture excreted a single seed of the endemic R. hawaiensis. Rubus rosifolius seeds (1 of 2 seeds germinated from Zosterops and 3 of 5 seeds from Leiothrix) and the single R. hawaiensis seed recovered from droppings during this investigation proved viable.

A graminoid-like dry seed, viable at low levels (9/100) excreted only by Leiothrix (9.6% frequency, up to 63 seeds/capture) in Makawao F.R. was designated as an unidentified dry seed in Table 15. Though rarely documented, avian dispersal of non-baccate dry seeds such as found in graminoids does occur and may be an important factor in their spread (Ridley 1930).

Besides those described above, captured birds excreted seeds of ten other as yet unidentified species (0.25-4.4 mm diameter) (five in Leiothrix, four in Zosterops, two in Hemignathus, and one in Himatione), bryophyte fragments, fern and moss sporangia, crushed young leaves, and flower anthers. Seven

Leiothrix individuals excreted rocks (2-4 mm) and/or small clay particles. The consumption of soil particles (geophagy) was restricted to Leiothrix, unique among birds in the study area in frequently foraging on the ground.

Part One of this inquiry (Table 10) identified Zosterops, Leiothrix, and Garrulax as the primary seed-dispersing birds for the study species and the appropriate subjects of the GI passage time experiment. The experiment was initiated with 11 wild-caught captive birds (five Leiothrix, five Zosterops, and one Garrulax).

Captive birds ingested low numbers of weed seeds. Only one of five Leiothrix passed four Hedychium seeds and three Leiothrix passed a single Clidemia seed each during the trial. Two of four Zosterops birds passed eight Clidemia seeds during the trial, while a single Zosterops individual passed two Hedychium seeds.

During non-experimental days, Psidium fruits were repeatedly offered to four Leiothrix individuals and five Zosterops individuals. In 60 bird/hours of exposure of Leiothrix to large quantities of ripe Psidium fruit, the birds ingested no seeds. In 85 bird/hours of exposure of Psidium to Zosterops, a single Zosterops individual ingested and excreted five Psidium seeds in four separate feeding episodes.

Under experimental cage conditions, the passage time for Clidemia seeds can be up to 90 minutes with Leiothrix and 210 minutes with Zosterops (Table 17).

Under experimental cage conditions, the passage time for Hedychium seeds can be up to 270 minutes with Leiothrix and 150 minutes with Zosterops (Table 17). In the experimental trials for Psidium, Zosterops consumed five seeds but all were quickly defecated before the weed fruits were withdrawn. Hence, the GI passage time for Psidium with Zosterops, in this limited experiment, was less than an hour. The single captured Garrulax individual did not consume any study weed fruit throughout all the trial periods. Seeds of all three study weed species proved viable after being excreted by their avian seed dispersers (Tables 11-13).

In the GI passage time experiment, the primary limitation was low number of study weed seeds ingested by birds. There appear to be two apparent reasons for this. The first is that the majority of wild caught study birds did not adapt readily to captivity. It is known that restraining wild caught passerines, especially Leiothrix and Garrulax, induces considerable stress (J. G. Massey pers. comm.). The second reason was that, of birds that did adapt, they either did not consume the fruits of the study weed species, or did so only at low levels. It appeared that study weed fruits proved unpalatable compared to other provided foods in their captive diet, which showed greater levels of feeding activity. Nevertheless, passage times recorded here are consistent with values obtained for other small fruit eating and nectarivorous birds (Karasov 1990; Stiles and White 1986).

Table 17. Mean and maximum GI passage times and sample size (n = number of weed seeds excreted).

	Leiothrix mean GI passage time	Leiothrix maximum GI passage time	Zosterops mean GI passage time	Zosterops maximum GI passage time
Clidemia	50 minutes (n = 3)	90 minutes (n = 3)	112.5 minutes (n = 8)	210 minutes (n = 8)
Hedychium	90 minutes (n = 4)	270 minutes (n = 4)	90 minutes (n = 2)	150 minutes (n = 2)

DISCUSSION

In this investigation, four bird species (Hemignathus, Garrulax, Zosterops, and Leiothrix) were found to be dispersing seeds of at least one of the three target weed species. The two most prominent seed dispersers were the two most common, non-native bird species of the study area, Leiothrix and Zosterops. Leiothrix had the greatest frequency and variety of seeds in defecations. Besides Clidemia, Hedychium, and Psidium, seeds of at least 15 other plant species were discovered in Leiothrix defecations. Zosterops defecations contained intact seeds of Clidemia, Hedychium, and at least 11 other plant species. Despite the abundance of Zosterops in Hawaiian forests, a week long mist netting trip in a dense, fruiting Psidium cattleianum forest at 730 m elevation in Kīpahulu produced no Zosterops captures. Despite the high densities of Zosterops in native forests, thick Psidium stands appear to have noticeably fewer Zosterops and other bird species, based on bird vocalizations. Lower Zosterops densities in Psidium-dominated forests may be a result of reduced abundance and diversity of plant and invertebrate foods than in native rain forests.

The two native birds Himatione and Hemignathus did not appear to be important seed-dispersing species. Himatione (n = 5) yielded only a single small unidentified seed. The locally common Hemignathus was found to be dispersing the small-seeded Clidemia in comparatively small quantities, but not the other two larger-seeded weed species.

Captures of Cettia yielded no fruit or seed material of the three weed species or any other plant species and the birds appeared to be entirely insectivorous (100% frequency, average of 5.1 prey items/capture) (Table 10, Appendix II), much more than any of the other five study species (ranging from 0.8 to 1.5 arthropod prey items/capture). Most identifiable fragments appeared to be from native invertebrate species. One Cettia individual captured in Makawao F.R. contained the remains of 21 small beetles, a spider, a cricket, and an unidentified arthropod. Cettia predation on small Coleoptera (beetles) accounted for 62.3% of all prey items, an average of 3.2 beetles/Cettia capture. Given its highly insectivorous diet and the population increases of Cettia in Hawai'i, there is substantial predation on the native invertebrate fauna reducing food availability for native passerines.

As a seed-disperser, Zosterops may be particularly important because of its high population levels and wide elevational and ecological range. Colonizing Maui by interisland dispersal without human assistance (van Riper 2000), Zosterops is now the most abundant bird species of the study area (East Maui rain forests) with densities up to 1600 birds per km^2 (Scott et al. 1986). The estimated upland East Maui Zosterops population of 114,000 birds is 20% larger than the most common native bird (Himatione) and six times larger than that of the next most common, non-native forest bird (Leiothrix) (Table 18). On East Maui, Zosterops

Table 18. Characteristics of four species of Hawaiian rain forest passerines that disperse seeds (densities, population estimates, and population trends from Scott _et_ _al_.,1986).

bird species	ecological range	East Maui elevation range	East Maui rain forest densities	East Maui population estimate	population trend
Garrulax	forests	300-2500 m	1-100 birds/km2	2100 birds (+/- 300)	increasing?
Leiothrix	upland forests and shrublands	500-2900 m	1-400 birds/km2	19,000 birds (+/- 1200)	stable or decreasing
Hemignathus	upland forests	400-2700 m	1-800 birds/km2	44,000 birds (+/- 3500)	stable?
Zosterops	sea level to tree line	0-2700 m	1-1600 birds/km2	114,000 birds (+/- 7000)	increasing?

Table 19. Comparison of excretion of seeds and invertebrates by six species of rain forest passerines, Kīpahulu and Makawao F.R., Maui island.

bird species	plant seeds only in droppings	plant seeds and invertebrate remnants in droppings	invertebrate remnants only in droppings	neither plant seeds nor invertebrate remnants in droppings
<u>Cettia</u>	0	0	100% (12/12)	0
<u>Garrulax</u>	17% (1/6)	83% (5/6)	0	0
<u>Himatione</u>	0% (0/0)	40% (2/5)	40% (2/5)	20% (1/5)
<u>Leiothrix</u>	12% (11/94)	76% (71/94)	10% (9/94)	3% (3/94)
<u>Hemignathus</u>	0% (0/0)	11% (2/18)	44% (8/18)	44% (8/18)
<u>Zosterops</u>	14% (7/50)	42% (21/50)	36% (18/50)	8% (4/50)

populations seem to be increasing and expanding into dense upper-elevation rain forests (Scott et al. 1986; van Riper 2000).

Within their breeding seasons (approximately March through August for Leiothrix and January to August for Zosterops), Leiothrix and Zosterops are centered around the nest, not frequently making long-distance flights, and hence are not good candidates for long-distance seed dispersal (Boles 1998; Male et al. 1998; van Riper 2000). Outside the breeding season, however, both species become gregarious and from approximately September through February, they form large nomadic flocks sometimes exceeding 100 birds with individual birds ranging up to 8 km (Male et al. 1998; van Riper 2000). These flocks have been observed feeding vigorously as a group on Coprosma fruits (A. Medeiros pers. obs.). These semi-nomadic groups of Leiothrix and Zosterops are probably one of the most likely mechanisms of dispersal of weed seeds (as well as native species) over long distances across forested landscapes (Munro 1944; Lindsey 1998).

In their native habitat, Zosterops japonicus are described as wanderers outside the breeding season, often traveling in mixed-species flocks (Brazil 1991). Once introduced to the Hawaiian Islands, Zosterops japonicus increased rapidly and spread to Lāna'i (minimum distance of 14.5-16.1 km) and other islands probably without assistance from humans (Munro 1944). Individuals of this species have been encountered far out at sea (Pratt et al. 1987). A related species, Zosterops lateralis, native to Australia and western and central Pacific islands, colonized

New Zealand (<1850) and Norfolk Island (ca. 1904) without human assistance, with minimum over water flight distances of 1600 km and 600 km, respectively (Long 1981).

The study population of *Psidium* *cattleianum* in Kīpahulu has been in place for many decades (Diong 1982). However, the populations of *Clidemia* *hirta* and *Hedychium* *gardnerianum* in Kīpahulu Valley were both first discovered in 1987 (Higashino *et* *al*. 1988; Medeiros *et* *al*. 1998a). These weed discoveries have always been somewhat of a mystery to park managers because the nearest known populations of both species were in the Nāhiku district, approximately 10 km distant. The saltatory spread of these weeds coincides with population increases of *Zosterops* on windward Haleakalā during 1960-1980 reported by Scott *et* *al*. (1986) and may represent long-range seed dispersal events by *Zosterops*.

In many respects, the seed dispersal and spread patterns of *Clidemia* may be considered as analogous to those of another small-seeded melastome, the highly invasive *Miconia* *calvescens* (Medeiros *et* *al*. 1997). The size (0.7 mm x 0.5 mm) and appearance of *Clidemia* seeds are very similar to those of *Miconia*. Within the same region as the study area of this investigation, *Miconia* achieves effective seed dispersal of at least 1 km (M. Walker pers. comm.). Certain conditions would seem to increase the likelihood of a long-distance dispersal event. High-wind conditions and storm systems have the capacity to transport birds, potentially facilitating long-range seed dispersal.

In this study, the maximum seed size dispersed by the two most common forest frugivores, Zosterops and Leiothrix, was that of large Hedychium gardnerianum seeds, i.e., 4-5 mm. Because of the elastic nature of the esophagus, even small birds are known to be able to ingest relatively large seeds (Wheelwright 1985). The largest seed recovered in this investigation (and possibly regurgitated rather than defecated) by a Garrulax was an entire drupe of the endemic tree, Myrsine lessertiana, 5.5 mm in diameter. Garrulax has also been observed at the Makawao F.R. study site swallowing fruit, and subsequently regurgitating sizeable seeds during feeding (J.T. Foster pers. comm. 2003). Garrulax are uncommon in Maui rain forest and characteristically sedentary, reducing their potential role in dispersing large-seeded invasive plant species in Hawaiian rain forests.

Seed size appears to have been an important factor in the number of seeds dispersed by birds. Clidemia has numerous small seeds, 0.5-0.7 mm in diameter, while Hedychium and Psidium seeds are much larger, both approximately 4 mm in diameter. In general, the much smaller size of Clidemia seeds facilitates the carriage of larger seed loads by resident frugivores: 229 Clidemia seeds/capture (for Leiothrix and Zosterops combined) versus 0.47 Hedychium seeds/capture (for Leiothrix and Zosterops combined), and 1.8 Psidium seeds/capture (for

Leiothrix only). The greater seed size of Psidium and Hedychium may have limited the number of seeds ingested and excreted by small passerines such as Leiothrix and Zosterops, the primary seed-dispersers in this study. Hedychium seeds are firmly attached to a bushy, bright scarlet aril, 5-6 mm long and fleshy in texture. Birds may attempt to separate the seed from the aril and ingest only the aril; 14.6% of Zosterops (6/41 birds) and 14.1% of Leiothrix (11/78 birds) that were captured in an area of fruiting Hedychium had the aril or aril fragments but no seeds in their droppings.

On Kaua'i island, the native Hawaiian thrush, the puaiohi (Myadestes palmeri), is known to disperse seeds of the lapalapa tree (Cheirodendron platyphyllum) (Berger 1981). It has also been observed consuming and then regurgitating Hedychium gardnerianum seeds, apparently after detaching the aril (J.T. Foster pers. comm. 2003). Seed regurgitations likely result in shorter dispersal distances than those achieved if the seed is passed through the bird's GI tract. Within the fruit, a viscous pulp layer surrounds each seed of Psidium cattleianum. Both the aril of Hedychium and the slippery pulp layer of Psidium are likely adaptations that facilitate ingestion by feeding birds. Bright red color, such as that of the Hedychium aril and seed coat, is known to be attractive to birds (Willson and Whelan 1990; Puckey et al. 1996). Despite this, Hedychium seed dispersal by birds has not been documented in some areas of its native range (Larsen et al. 1999). Snow (1981) described the production of numerous, small seeds, as in Clidemia, as typical of plants utilizing unspecialized, generalist frugivores. The production of fewer, larger, often drupaceous or arillate seeds, such as found in Psidium and Hedychium, is often associated with plant species that utilize more specialized seed-dispersers (Snow 1981). In an area where native frugivores have been largely replaced with small-sized, opportunistic, generalist bird species, such as in Hawai'i, it may not be surprising that the weed with the smallest seeds (Clidemia) has much higher numbers of seeds per bird feeding episode than Hedychium or Psidium. Small seeds tend to be ingested by birds in larger numbers, carried farther from their source, and scattered more widely than larger seeds (Levey 1986).

Regarding the role of the newly established Leiothrix lutea in seed dispersal of invasive plant species on Reunion Island, Tassin and Riviere (2001) characterized the species as a “potential noxious species” and “efficient candidate for dispersion of Hedychium gardnerianum and Ligustrum robustum.” They compared germination of weeds after passage through captive Leiothrix against fresh seed and found passage increased germination percentage of H. gardnerianum (highly significant, $p<0.01$) and L. robustum (significant, $p < 0.05$), but not Psidium cattleianum (no significant difference). One limitation of the study was that fecal samples of wild populations were not analyzed and no field observations of wild weed populations were made (J. -Y. Meyer pers. comm.).

The length of time it takes for a seed to pass through a bird's GI tract is dependent on a number of factors, including the species of bird (Levey 1986), size of bird (Herrera 1984; Levey 1986), size of seed (Stiles and White 1986), fruit ripeness (Stiles and White 1986), fruit pulp texture (Levey 1986), the degree of mixing of seeds with other foods (Stiles and White 1986), length of bird intestine (Karasov 1990), and laxative or constipative effects of fruit pulps (Murray et al. 1994; Wahaj 1998). Retention time is known to be relatively short and digestive efficiency relatively low in frugivorous birds (Karasov 1990).

In this investigation, non-native passerines were found to be the primary avian dispersers of native plant species as well as invasive weeds. These results are not surprising. In pre-contact Hawai'i, seed dispersal mutualisms were apparently developed with corvids and passerines (especially thrushes, some finches, and meliphagids), and perhaps with large geese that were either flightless or had limited flying ability (James and Olson 1991; Olson and James 1982a, 1982b, 1991). Many native Hawaiian forest plants have fleshy fruits, apparent adaptations favoring seed dispersal by birds. In the study area of this inquiry, 62% of native flowering plant species (69% of endemic species) produce seeds in fleshy fruits apparently adapted for bird dispersal (Table 20). However, widespread extinctions of Hawaiian birds have decimated nearly all the native seed-dispersing species, except a few generalist finches, the now rare Myadestes thrushes, and the Endangered Hawaiian crow (Banko et al. 2001; Fancy et al. 2001; van Riper and Scott 2001). As a result, frugivory of both native and invasive plant species in Hawaiian forests has fallen largely to opportunistic interactions involving small, generalist passerine species.

Table 20. Dispersal methods of flowering plants of Kīpahulu rain forest and environs (n = 239 species total) (based on full species listing in Appendix III).

	wind-dispersed	bird dispersed	no obvious mechanism	external animal transport	misc.	totals
Endemic plant species only	14 spp. (5.9%)	96 spp. (40.2%)	29 spp. (12.1%)	none	1 sp. (0.4%)	140 spp. (58.6%)
Indigenous plant species only	2 spp. (0.8%)	7 spp. (2.9%)	14 spp. (5.9%)	1 sp. (0.4%)	none	24 spp. (10.0%)
All non-native plant species	28 spp. (11.7%)	10 spp. (4.2%)	32 sp. (13.4%)	3 spp. (1.3%)	2 spp. (0.8%)	75 spp. (31.4%)
totals	44 spp. (18.4%)	113 spp. (47.3%)	75 spp. (31.4%)	5 spp. (1.7%)	3 spp. (1.3%)	239 spp. (100%)

CHAPTER FOUR:

PRE-DISPERSAL SEED PREDATION AND DISPERSAL OF INVASIVE WEED SPECIES BY NON-NATIVE SMALL MAMMALS IN A HAWAIIAN RAIN FOREST

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ABSTRACT

Invasive species are hypothesized to thrive in newly occupied areas partially because of freedom from coevolved parasites and predators. The objective of this study was to determine whether, and to what level seed predation is occurring among three non-native plant species (Clidemia hirta, Hedychium gardnerianum, Psidium cattleianum) that are important weeds of Hawaiian rain forests. In this study, flowers and fruits of the study species were tagged and monitored for evidence of seed predation. In addition, small mammal droppings were collected at the time and place where study weeds were fruiting, and any recovered seeds assessed for the viability and timing of germination versus controls. This study provides information regarding the role of a non-native rodent (Rattus spp.) in seed dispersal of Clidemia and high levels of seed predation of Hedychium. Observation and analysis of Psidium populations suggested rodents feed only on rind and fruit pulp with no impact on the seeds themselves. In a Two-Sample T-Test, germinability ($p = 0.066$) and rate of germination ($p = 0.700$) did not differ significantly between control and Rattus-passed Clidemia seeds. In light of high levels of seed dispersal of Clidemia by common rain forest passerine bird species, the dispersal of these seeds by rodents is not likely to be important ecologically. Though high levels of seed predation of Hedychium were documented here, the phenomenon does not apparently occur at all sites during all fruiting seasons. Nonetheless, Rattus-induced seed predation appears to be an exception to the generally accepted theory that non-native species that thrive in new areas lack predators.

INTRODUCTION

Herbivory is one factor thought to moderate the abundance of plant species in their native habitats. Despite potentially high seed production levels, many plant species within their native ranges produce only limited numbers of seedlings partially due to the effects of seed predation by vertebrate and invertebrate animals (Crawley 2000; Janzen 1971). Freedom from herbivores, such as seed predators, may act powerfully to facilitate the rapid proliferation of non-native plants in invaded habitats by permitting much greater quantities of seeds to be produced (Blossey and Notzold 1995; DeBach 1974; Crawley 1987). Many animal groups have radiated apparently because of the central role of seeds as a food source, and conversely, angiosperm seed diversity has proliferated in part because of selection pressures exerted by seed predators (Willson and Traveset 2000).

Rodents are among the most important vertebrate predators of seeds (Jensen 1985; Jensen and Nielsen 1986; Ridley 1930). In studies of areas with a matrix of interspersed plant communities, those communities capable of sustaining higher rodent populations had significantly higher levels of seed predation (Wada 1993; Wada and Uemura 1994). Of rodents, the genus Rattus is among the most destructive (Howe et al. 1985; McConkey and Drake 2002; Sanchez-Cordero and Martinez-Gallardo 1998).

Seed predation by rodents often has striking ecological consequences on islands, especially where floras have evolved without native rodents and hence adaptations to prevent devastating levels of seed predation are not well developed. Also on islands, plant species often have relatively small populations, so that seed predation can be disastrous. The ecological consequences of seed predation may be exacerbated in areas such as in the Hawaiian and other Pacific islands where native seed dispersing agents such as birds and fruit bats have been eliminated or dramatically reduced. In these cases, the foreshortening of seed dispersal shadows acts to concentrate poorly-dispersed seeds around parent trees, making them especially vulnerable to seed predators (McConkey and Drake 2002).

Rodents can act as seed dispersers, through external transport of larger seeds (> 2 cm diameter) to food caches (Pizo 2002) or through ingestion and passage of very small seeds imbedded in fleshy fruits that escape mastication (Ridley 1930). One of the best-documented examples is that of the highly invasive, small seeded Miconia calvescens in French Polynesia dispersed by rats (Rattus) (Meyer 1994).

This study investigated three of the most invasive and ecosystem-modifying plant species of Hawaiian rain forests: Clidemia hirta (L.) D. Don (clidemia), Hedychium gardnerianum Ker.-Gawl. (kahili ginger), and Psidium cattleianum Sabine (strawberry guava) (hereafter Clidemia, Hedychium, and Psidium).

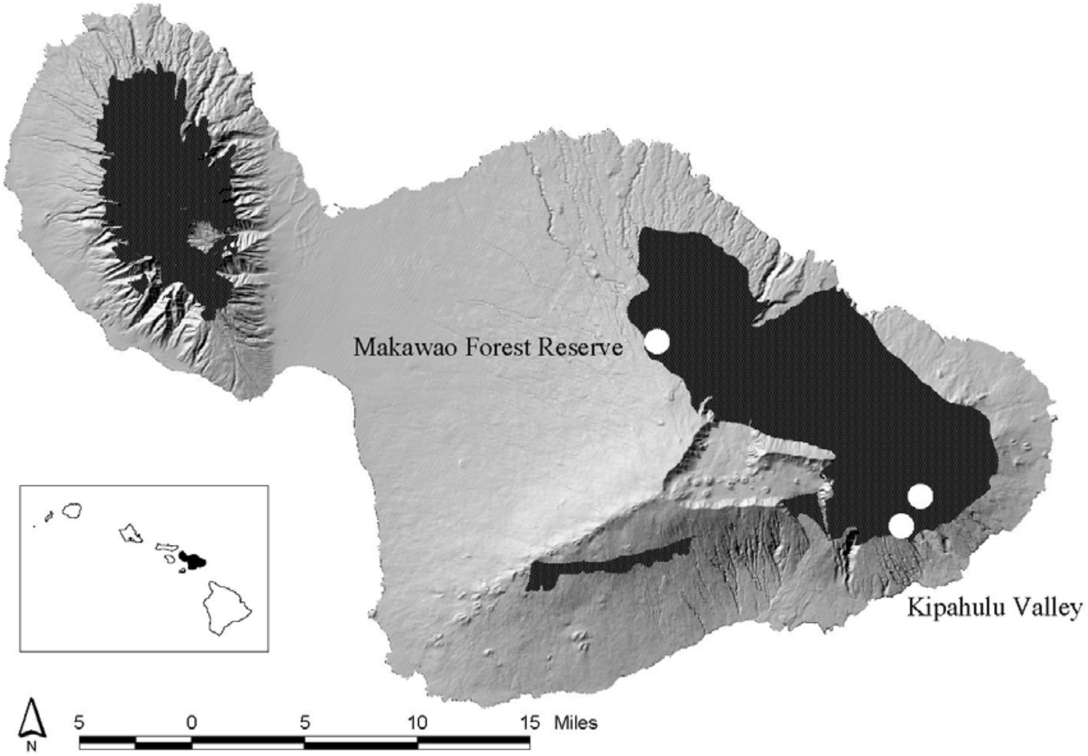
Evidence is provided regarding the role of non-native rodents as both seed predators and seed dispersers.

MATERIALS AND METHODS

Four primary study sites were selected on Haleakalā Volcano (East Maui) (Figure 9). Three study sites were located in Kīpahulu Valley, within Haleakalā National Park on eastern Haleakalā Volcano, whereas the fourth was in State-owned Makawao Forest Reserve (hereafter Makawao F.R.) on northwestern Haleakalā. At each of these four study sites, only one of the study weed species was present, but that species occurred in substantial local density. The study site for Clidemia was at 820 m elevation, Kīpahulu Valley (804,866E, 2,292,361N UTM-NAD83); for Hedychium at 825 m, Kīpahulu Valley (803,520E, 2,290,297N UTM-NAD83) and 1220 m Makawao F.R. (786,084E, 2,303,393N UTM-NAD83); and for Psidium at 670 m, Kīpahulu Valley (804,636E, 2,289,408N UTM-NAD83).

The Kīpahulu Valley study sites were all located in remote areas requiring helicopter transport, whereas the Makawao F.R. site was accessible by four-wheel drive vehicle. Besides the presence of the large population of the study weed, the primary vegetation type of the Clidemia and Hedychium study sites in Kīpahulu Valley and the Hedychium study site in Makawao F.R. is diverse native rain forest dominated by the trees Metrosideros polymorpha and Acacia koa with well-developed native shrub, fern, and bryophyte layers. The Psidium study site in Kīpahulu Valley differs in that it is at somewhat lower elevation and the

Figure 9. Map of Maui, Hawaiian Islands, showing distribution of rain forest dominated by native species in black and Makawao Forest Reserve and Kīpahulu Valley study sites as white dots.



vegetation is nearly completely dominated by the study weed, Psidium cattleianum. This site was selected because of the inconsistent ripe fruit production of higher elevation populations.

Clidemia hirta is native to Mexico, the West Indies, Central America and northern South America (Smith 1992). Clidemia is a suffrutescent shrub up to 3 m tall that thrives in disturbed regions of moist forest and forest clearings. It bears numerous purple berries (ca. 1 cm diam.) year round with numerous (x = 832 seeds), small (0.5-0.7 mm length) seeds (Chapter Two). It is a serious forest pest that has become widely naturalized around the world from approximately 20 degrees S to 22 degrees N latitude on Pacific and Indian Ocean islands, Indonesia, Malaysia, Southeast Asia, and Africa (Chapter One).

Hedychium gardnerianum is a large rhizomatous herb up to 2 m in height, native to the Himalayas and adjacent regions and occurring to 1900 m elevation (Graf 1992; Nagata 1990; Stainton 1997). Hedychium fruits once a year with bright yellow, fragrant inflorescences; thyrses with 40-160 flowers are organized in two-flowered cymes, termed cincinni within the family Zingiberaceae (Nagata 1990). Hedychium infrutescences are brightly colored with inner seed pods bright orange, seeds bright red (ca. 4 mm long) and fleshy arils. An average of 206 seeds are produced per infrutescence (Chapter One). Hedychium has become naturalized from approximately 42 degrees S to 22 degrees N latitude on islands in the Pacific Ocean (Hawai'i, New Zealand), Indian Ocean (La Reunion), and Atlantic Ocean (Azores, Madeira), as well as in Jamaica, Australia, and South Africa (Chapter One).

Psidium cattleianum is a small tree up to 6 m in height that is native to South America (Hodges 1988). Psidium produces berry-like fruits that contain on average 6.7 seeds/fruit; each Psidium seed is ca. 4 mm in length (Chapter Two). Introduced extensively in tropical and subtropical areas for its edible fruit, Psidium has become widely naturalized from approximately 27 degrees S to 32 degrees N latitude on islands of the Pacific, Atlantic, and Indian Oceans, as well as Australia, Central America, Asia, Africa, the Caribbean, and North America (Chapter One).

To evaluate the potential impact of invertebrate seed predators, two methods were used. First, ripe fruits from field sites were examined directly under a dissecting microscope (Clidemia, 100 fruits, Hedychium, 100 capsules, Psidium, 100 fruits) to directly evaluate impacts to seeds. Secondly, ripe fruits (Clidemia, 300 fruits, Hedychium, 100 capsules, Psidium, 50 fruits) from field sites were kept in rearing jars to monitor the emergence of insects associated with seed predation. The rearing jars were initially refrigerated to slow fruit spoilage and monitored for approximately six months.

Hawaiian rain forests have four common small mammals including three common rodent species and the lesser Indian mongoose, all of which are non-native (Tomich 1986). Rattus exulans (Polynesian rat) arrived with voyaging Polynesians from South Pacific islands at least 1600 years ago (Kirch 1982). Mus domesticus (house mouse) arrived in the Hawaiian Islands by the 1780s and Rattus rattus (black rat) by 1870 (Tomich 1986). Herpestes auropunctatus (small Indian mongoose), native from central to southeast Asia, is a small mammal and opportunistic fruit eater of Hawaiian rain forests (Tomich 1986).

All fresh rodent droppings were collected at rain forest study sites from within three 100m^2 quadrats amidst dense fruiting stands of the three target weed species. Droppings were measured, examined under a dissecting microscope, and their contents identified and quantified to the extent possible. Havahart live traps and snap traps were placed near fruiting plants for three trap-nights in an attempt to determine the species of local rodents. The plan was to determine the species of a captured animal, collect droppings at the time of capture associated with its natural diet, leave fruit of the study weed species in the cage with the animal overnight, and release the animal the following morning. The fruits left with the animal were examined for feeding damage and any droppings left by the animal overnight were collected. Captured animals were treated in accordance with the Vertebrate Animal Use Protocol approved by the University of Hawai'i's Institutional Animal Care and Use Committee.

To test the germination percentage (germinability) and rate (speed) of germination of Clidemia seeds excreted by rats versus germination of fresh seeds (control), seeds were placed on paper discs moistened with distilled water in Petri dishes (sterilized initially with near boiling water). Three replicates of 100 seeds from three fresh droppings were extracted, washed, and placed on moistened paper towels in separate Petri dishes. Three replicates of 100 seeds were also extracted from fresh fruits, washed, and placed in separate Petri dishes to serve as controls. The seeds of each control replicate originated from a separate fruit, which was collected at the same time and place, as were the droppings. Only very ripe fruits were collected in an attempt to match the fruit maturity selected by rodents for consumption. The Petri dishes were placed indoors in an area of ample but indirect natural light. The Petri dishes were periodically monitored weekly for a calendar year for germination, testing viability and timing. As needed, usually every four to six days, the filter paper in the Petri dishes was remoistened with distilled water. As a seed germinated (determined as the point at which the root radicle emerged from the seed coat in Petri dish samples), the seedling was removed and recorded. Petri dish samples were weekly rearranged in position to avoid bias in terms of amount of light received. Natural sunlight was the only light source. Statistical analyses were performed with Minitab Release 13.30 software.

For Hedychium, where seed predation by rodents was evident, 100 culms of the weed species were numbered, tagged, and quantitatively assessed periodically throughout the flowering and fruiting period to estimate the impact of rodent seed predation on seed production. Additional one-time surveys were also made opportunistically when high levels of seed predation were ongoing. In these surveys, the following information was recorded: plant number (for 100 tagged stems only), phenological condition, the number of flower/fruit sites (cyme bases) previously damaged by rodents, the number of flower/fruit sites recently damaged by rodents, and the number of flower/fruit sites with undamaged flowers or fruits. Determination that flower and fruit damage was due to rodents (versus birds or insects) was based on the presence of gnaw grooves. Rodent damage was classified as older if the gnawed areas were brown or severely wilted; areas of damage were classified as recent if gnawed areas still had green, non-desiccated margins. In all surveys, every inflorescence in a given area was sampled rather than selecting inflorescences with or without apparent rat damage. By doing this, inflorescence selection was minimized as a source of bias in the data.

To assess *Rattus* damage throughout an entire reproductive cycle, four separate populations of *Hedychium* were monitored during the 1997 fruiting season (Table 21). Unmarked stems at two populations were sampled once (one on 24 September 1997 and the other on 29 October 1997). As these one-time surveys only quantify damage for part of the fruiting cycle (either flower buds/flowers or immature fruits), they are underestimates of the total reduction of seed production. In the other two populations, *Hedychium* stems were numbered and tagged just after elongation of stem, which precedes flowering. These stems were monitored throughout the fruiting season until remaining fruits had dehisced naturally. The two tagged populations occurred at Makawao F.R., where 100 stems were monitored from 26 August 1997 to 5 November 1997, and Kīpahulu Valley, where 48 stems were monitored from 26 September 1997 to 25 November 1997.

RESULTS

No insects associated with seed predation were reared from or observed in fruits of the three target weed species. Numerous individuals of non-native Fruit Flies (Tephritidae), whose larvae consume fruit pulp, were reared from Psidium cattleianum fruits. These larvae likely serve as an important protein source for feral pigs, which feed voraciously on Psidium fruits when in season (Diong 1982).

Attempts to live-trap and snap-trap rodents at the study sites to positively identify the rodent species met with limited success. In nine trap-nights, there was only a single capture, a Rattus rattus at the Makawao F.R. Hedychium site. Droppings from this animal were examined and contained no evidence of Hedychium seed, aril, or fruit parts. When 25 Hedychium seeds and arils were left with the captured animal overnight, the embryos and arils of all seeds were consumed completely. Droppings from this animal collected after experimental exposure to Hedychium seed were comprised entirely of finely-masticated Hedychium seed and aril fragments.

In total, 45 rodent droppings (1 Mus and 43 Rattus) and one Herpestes dropping were collected in fruiting patches of the target weeds (Appendix IV). As plots used for collecting droppings of the study species were all 300m^2, the number of droppings found in the plots might be taken as a rough index of comparative utilization by small mammals. Hedychium plots contained the greatest number of droppings (n = 31, i.e., one dropping/9.7m^2), followed by Psidium (n = 11, i.e., one dropping/27.3m^2), and Clidemia (n = 3, i.e., one dropping/100m^2).

The length of dropping has been used to distinguish the two local species, with droppings longer than 15 mm identified as R. rattus and shorter than this as R. exulans (Meyer 1994). Rattus droppings collected during this inquiry ranged over 6-24 mm in length. If classified by length, 20 droppings would be attributed to Rattus exulans and 23 to Rattus rattus. Though two species appear to be involved, dropping length appeared unreliable in differentiating species in this study.

Three Rattus droppings were recovered in the three 10m^2 plots of fruiting Clidemia in Kīpahulu Valley. The three droppings were largely composed of Clidemia fruit skin, pulp, and large numbers of apparently intact Clidemia seeds. The three droppings contained 885, 1091, and 1295 Clidemia seeds (x = 1090 seeds).

Despite the direct evidence obtained that Clidemia fruit formed at least a part of the local rat diet, little information was obtained that this phenomenon was widespread. When fruiting Clidemia plants were examined, no evidence of rodent feeding on either immature or ripe fruits was observed. Ripe Clidemia fruits detach easily so that any rodent feeding would be likely to cause fruit separation. Ripe Clidemia fruits are very common beneath fruiting plants. At the Kīpahulu study site, it was estimated that 90% of ripe fruits lying on the ground were intact, less than 10% with any type of feeding damage present. The relative paucity of Rattus droppings with Clidemia seeds in the plots and the lack of apparent rodent damage to fruits provided some evidence that Clidemia fruits are consumed only at low levels.

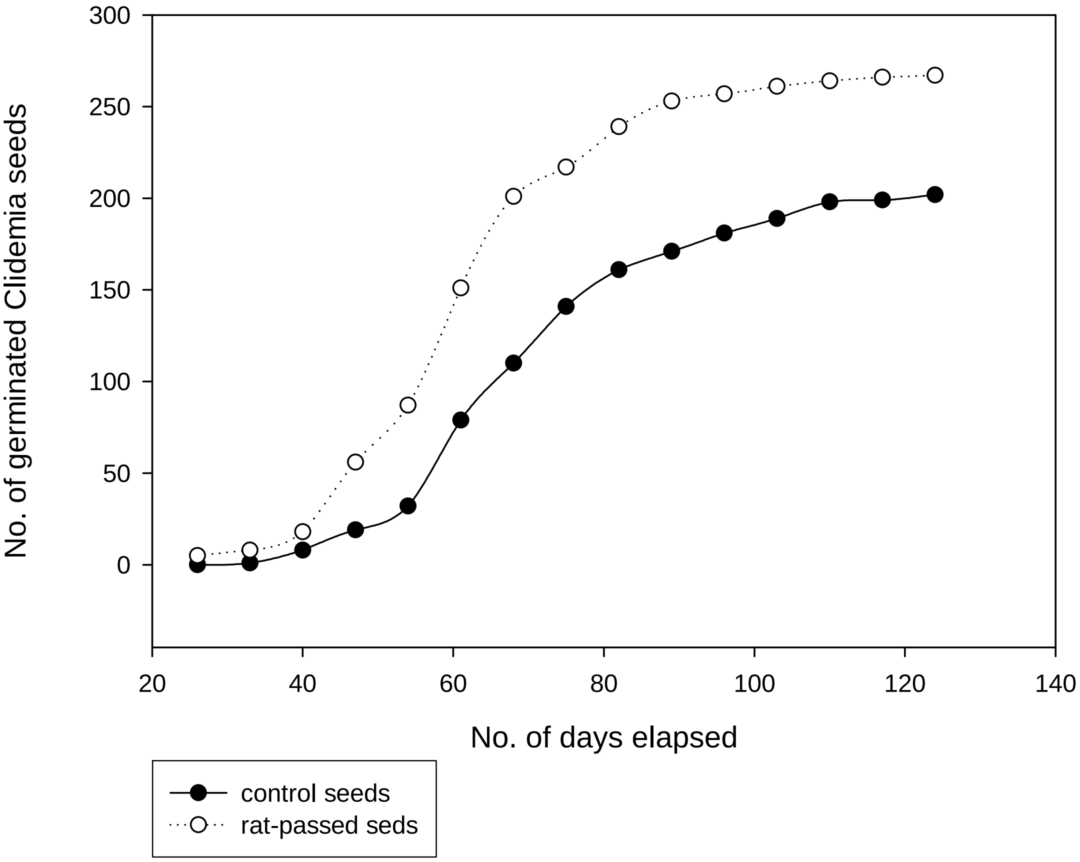
In terms of overall germinability, 89% (+/- 10.5) of Rattus-passed Clidemia seeds and 67.3% (+/- 8.1) of control Clidemia seeds extracted from fresh fruits germinated (Figure 10). After 124 days, three replicates of 100 Rattus-passed seeds yielded 79, 88, and 100 germinants, and three replicates of 100 seeds extracted from fresh fruits had 60, 66, and 76 germinants. In a Two-Sample T-Test, germinability did not differ significantly (p = 0.066) between control and Rattus-passed seeds.

In terms of germination rate (speed), Rattus-passed Clidemia seeds (n = 267/300) germinated in an average of 65.7 (+/- 4.0) days while seeds (n = 202/300) extracted from fresh fruit germinated in an average of 84.3 (+/- 8.1) days (Figure 10). Just as with germinability, in a Two-Sample T-Test, these results do not differ significantly (p = 0.070).

In addition to Clidemia seeds, two other species of intact plant seeds were identified in rat droppings. Seventeen seeds of a single morphotype (ca. 1 mm length) were discovered in three droppings collected in Kīpahulu Valley at 825 m.

Three of five seeds (60%) placed on moist tissue paper in a Petri dish germinated and were grown until of sufficient size to identify them as the non-native Rubus rosifolius Sm. (thimbleberry), Rosaceae. Eleven intact seeds of a second morphotype (ca. <1 mm) were recovered from a dropping from Kīpahulu and stored in alcohol as a voucher for identification and comparison. Later, they were compared with fresh seeds from known plant species of the area and identified, based on their morphology, as seeds of the endemic lobelioid shrub,

Figure 10. Rate of germination of Clidemia seeds extracted from fresh fruit (control) (n = 300) versus seeds extracted from Rattus droppings(n = 300), Kīpahulu Valley, Haleakalā National Park, Maui.



Clermontia arborescens (Mann) Hillebr., ('ōhā wai nui), Campanulaceae. Because the seed sample was stored in alcohol and no other seeds of that type were encountered, the viability was untested and is unknown. However, the voucher seeds appeared completely intact and when dissected had cotyledons and embryo that appeared normally developed.

Examination of ten R. rattus droppings collected in three 10m^2 plots of fruiting Psidium forest revealed only Psidium rind and pulp, with no intact seeds or seed fragments. Regular examination of Psidium plants including buds, flowers and immature and ripe fruit as well as ripe fruit lying on the ground, showed no sign of rodent predation. A single Herpestes dropping collected in Kīpahulu Valley in fruiting Psidium forest but from outside the plots was composed of ca. 20% Psidium fruit and seeds, including 12 Psidium seeds.

Rodent droppings were very common in the three 10m^2 Hedychium plots located in Makawao F.R. where 31 droppings were collected (one Mus, 19 R. exulans and 11 R. rattus). The single Mus dropping contained only invertebrate remains with no trace of Hedychium. Rattus droppings were very common in and near fruiting Hedychium patches, especially on leaves adjacent to the flowering axis. Of the 19 R. exulans droppings, Hedychium fruit and seed fragments averaged 91.8% of total contents. Of the 11 R. rattus droppings, all were composed of 100% Hedychium fruit and seed fragments. The predominant components of these droppings were masticated pieces of the fleshy orange seed capsule, the fleshy scarlet arils, and the seed coats and embryos of Hedychium. The relatively large Hedychium seeds (4 mm length) consumed by rats were invariably destroyed by fragmentation. Twenty-six out of 30 Rattus droppings at this site (87%) were composed entirely of Hedychium reproductive parts, the scarlet arils and seed coats, which turned the entire dropping a distinctive bright red-orange color.

In both Kīpahulu Valley and Makawao F.R., it became apparent that at least during the study period, Rattus was severely limiting the potential seed production of Hedychium. Over large areas where flowering Hedychium stems were very conspicuous, extensive damage by Rattus to Hedychium flowers and flower buds was often observed. Rattus removed the flowers or flower buds by chewing at the base of the cincinnus, apparently seeking nectar and consuming the base of the styles. As the surviving flowers progressed through the early stages of fruit development, damage by Rattus declined dramatically. However, as the seedpods began to become enlarged, Rattus began to gnaw open the closed pods to eat the ripening but immature seeds. Just as with flower predation, the destruction of immature fruits was observed in Hedychium populations extending over hundreds of square meters. When the remaining pods matured and dehisced naturally, rats consumed ripe seeds directly from pods as well as from the ground. When Hedychium fruits were ripe from October to December, Rattus were active feeding on and destroying Hedychium seeds, non-native birds, especially Leiothrix and Zosterops, fed on Hedychium arils and ingested and dispersed viable seeds (Chapter Three).

At Makawao F.R., from 26 August 1997 to 5 November 1997, 11.6% of Hedychium flowers and/or flower bud cymes were destroyed. From 2 October 1997 to 5 November 1997, 35.7% of cymes at immature fruit stage were destroyed. Hence, predation by Rattus reduced total seed production at the Makawao F.R. site by almost half (47.3%).

At Kīpahulu, Rattus destroyed 55.3% of the potential seed production. Most damage (53.9% of all cymes produced) occurred early in the season (26 September 1997) when the plants were in the flower bud and flower stage. Rodent impacts declined markedly at this site in the later part of the season as an additional 1.4% of cymes were destroyed at the immature fruit stage.

Patterns of flower and fruit destruction were quite varied. Rattus destroyed an average of 25.3% (11.6% to 54.0%) of all cymes with flower buds and/or flowers (n = 187 stems). Rattus also destroyed an average of 23.0% (1.4% to 37.0%) of cymes with immature fruits (n = 198 stems). In total for all samples (n = 237 stems), seed production for Hedychium during the 1997 fruiting season was reduced by Rattus predation on average 48.3% (37.0% to 56.1%) (Table 21).

I did not attempt to quantify the pre-dispersal predation of Rattus on ripe seeds gathered from naturally split pods and post-dispersal seed predation from fallen seeds on the ground below infructescences. Based on sequential observations during the study period, these types of Hedychium seed predation by rodents were very high. Hedychium seeds were rarely, if ever, found intact on the ground. The ground beneath infructescences was often littered with fragments of seedpods and numerous emptied and split bright red Hedychium seed coats, signs characteristic of Rattus predation. When the post-dispersal predation of ripe Hedychium seeds by Rattus is considered, the net seed production of Hedychium was reduced as much as 80-90% by Rattus.

Table 21. Effect of Rattus predation on flower and immature fruit production of Hedychium at Makawao Forest Reserve and Kīpahulu Valley, Maui.

study site location	date	total no. of stems investigated	total no. of potential cymes	total no. of flower cymes destroyed by Rattus	total no. of immature fruit cymes destroyed by Rattus	percentage of reproductive potential reduced by Rattus
Kīpahulu	**9/24/97**	**39**	**2,668**	**1,496**	**NA**	**56.1**
Kīpahulu	**9/26-11/25/97**	**48**	**2,767**	**1,493**	**38**	**55.3%**
Makawao F.R.	**8/26-11/5/97**	**100**	**6,122**	**710**	**2,186**	**47.3%**
Kīpahulu	**10/29/97**	**50**	**3,060**	**NA**	**1,132**	**37.0%**
Total		**237**	**14,617**	**3,699**	**3,356**	**48.3%**

DISCUSSION

This study demonstrated that Rattus, probably both R. exulans and R. rattus, dispersed Clidemia seeds and consumed Hedychium flower buds, flowers, fruits, and seeds, thereby substantially reducing Hedychium seed production. No evidence was obtained that rodents either preyed on or dispersed Psidium seeds.

Diong (1982) noted the dispersal of Psidium seeds by mongoose (Herpestes auropunctatus). Such dispersal has apparently minimal ecological consequences; however, because the mongoose is so uncommon in the study area. Despite copious evidence of the consumption of fruit pulp by rodents (Appendix IV), no evidence of Psidium seed predation by rodents was discovered in this study presumably because of the tough, bony testa that protects the embryo and accounts for over 50% of the seed diameter. Seed dispersal of Psidium cattleianum occurs seasonally in Hawai'i in large quantities via the droppings of feral pig (Sus scrofa) (Diong 1982) and in lesser quantities via the droppings of several passerine bird species (Leiothrix lutea, Garrulax canorus and presumably Zosterops japonicus, Streptopelia chinensis, Pycnonotus cafer, and P. jocosus) (Chapter Three). Despite the formidable testa, a recent investigation (Medeiros unpubl.) has confirmed that Aratinga mitrada (Mitred Conure) is a formidable seed predator of the common guava (Psidium guajava), cracking the extremely tough seed coats into multiple fragments. Aratinga mitrada also likely acts as a seed predator of the strawberry guava (Psidium cattleianum), which has seeds nearly indistinguishable from those of common guava.

Are these findings important ecologically? Clidemia has excellent seed dispersal from two non-native birds, Leiothrix and Zosterops (Chapter Three), the latter being the most common bird in the Hawaiian Islands (van Riper 2000). Given this, any additional dispersal benefits that rodents provide for Clidemia appear minimal. On the other hand, high levels of seed predation of Hedychium like those observed here would appear to be much more important ecologically, especially for small or founder populations.

Rodents are generally known as important seed predators (Gonzalez-Espinosa and Quintana-Ascencio 1986; Heithaus 1981; Janzen 1986; van der Pijl 1972), and sometimes as seed dispersers because they cache seeds (Price and Jenkins 1986). Less commonly, rodents disperse very small seeds embedded in fleshy fruits after ingestion and gastrointestinal passage (Ridley 1930). In this investigation, all three species whose seeds were recovered intact from rodent dropping were less than 1mm length. In its native South American range, the forest rat Bolomys lasiurus is known to disperse the small seeds (<1 mm) of Miconia albicans (Magnusson and Sanaiotti 1987). Rattus exulans has been documented as a disperser of the seeds of ten plant species in Tahitian rain forests, including the invasive melastome, Miconia calvescens (Meyer, 1994), which has seeds of nearly the same size as Clidemia hirta. In a broad review of the family Melastomataceae (to which Clidemia belongs), seeds which germinated more quickly following passage through birds compared to control seeds extracted from fresh fruit belonged to species which require habitats with high light intensity (Ellison et al. 1993).

In many instances, rodents inadvertently disperse larger seeds by transporting seeds and fruits to sites to feed on them later. The sites may be relatively protected from rain (Campbell et al. 1984), predators (Begg and Dunlop 1980), and food competition (Campbell et al. 1984). These sites have been variously interpreted as “food stores”, “food caches” and “husking stations” (Campbell et al. 1984). It is possible that in accumulating caches of seed found near fruiting Hedychium patches, rats transport viable seeds, which remain uneaten. However, perhaps because of the large seed size and conspicuous scarlet coloration, the Hedychium seeds in all cache sites examined had been destroyed.

Only one R. rattus was trapped at one site (Hedychium) in this study. Rattus rattus is known to adapt more quickly to new food sources and to show trap site dominance over R. exulans. Hence, R. rattus is often the only species trapped until its numbers are reduced, after which R. exulans is trapped more often (P. Banko pers. comm.). Data provided here are too limited to add substantial insight into the species identification of the seed predator(s). The identification of droppings here was based on length, and so is tentative.

Though droppings apparently of both species of Rattus contained Hedychium fruit and seed fragments, R. rattus consume more fleshy fruits, seeds, and plant materials than R. exulans, and adults more fruit and seeds than do juveniles (Sugihara 1995). In New Zealand, R. exulans is known to consume a wide variety of plant and animal foods and is a seed predator of at least six native species (Campbell et al. 1984).

In Kīpahulu Valley and Makawao F.R., there was marked site-to-site variability in the type and intensity of Rattus predation, even in continuous stands. Isolated Hedychium clusters were often less affected by rodents than were plants growing in larger patches. For example, the Hedychium clumps used in the phenology study were largely unaffected by rodent flower and seed predation (Chapter Two). An analysis of the Hedychium population at Makawao F.R. revealed low numbers of Hedychium seeds stored in the soil even under dense stands of the species (Medeiros unpubl.); high rates of seed predation by Rattus are likely a contributing factor.

The 48.3% reduction in seed production for Hedychium by Rattus spp. documented here is comparable to high levels of seed predation by rodents reported elsewhere. However, the impact of seed predation by rodents is best documented on grasses. In North American deserts, heteromyid rodents and harvestor ants together reduce seed densities of grasses by 30-80% (Louda

1989). In California annual grasslands, rodents depleted the seed bank of grasses causing relative abundance changes of the four primary species (Borchert and Jain 1978). In North American prairie grasslands, extensive seed predation by rodents has reduced seed reproduction and accentuated vegetative reproduction as a survival mechanism of dominant grass species. Seed predation by rodents has been documented not only with grasses but also with forbs such as *Ranunculus acris*, *R. bulbosa*, and *R. repens*, with reductions of 35-50% (Sarukhan 1974). In southern Africa, the native rodent *Mastomys natalensis* can destroy 80-100% of crops (Keesing 2000).

The impact of *Rattus* predation on *Hedychium* seed production on Maui varied from 1996-1997 (pers. obs.), but has not been quantitatively assessed. More extensive populations of *Hedychium gardnerianum* at Hawai'i Volcanoes National Park on Hawai'i island and the Kōke'e region of Kaua'i have relatively low levels of destruction of flowers and fruits (pers. obs.; P. Banko pers. comm. 2003; Sugihara 1995). The reasons for the absence of rodent impacts elsewhere are not understood. Though little is known about the dynamics of rodents in Hawaiian forests, it is known that *Rattus* spp. occur at extremely high population levels in Kīpahulu Valley (P. Banko pers. comm. 2002).

Freedom from predators and parasites is one trait often associated with non-native, invasive species (Blossey and Notzold 1995; Mitchell and Power 2003; Torchin *et al*. 2003). One advantage of this freedom is the generally greater quantities of seeds produced by plants in non-native habitats (Blossey and Notzold 1995). Despite the fact that Hedychium remains a serious rain forest invader, the Hedychium-Rattus interaction discussed here is an exception to that rule.

CHAPTER FIVE:

DIFFERENTIAL ESTABLISHMENT OF THREE INVASIVE WEED SPECIES IN ECOSITES OF A HAWAIIAN RAIN FOREST, MAUI, HAWAI'I.

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ABSTRACT

The removal of feral pigs from Hawaiian rain forests triggers succession from uprooted bare ground and non-native grassy areas to shaded native fernland sites. After pigs were removed from diverse rain forest within Kīpahulu Valley, Haleakalā National Park, Maui island, most non-native plant species declined, but three weeds (Clidemia hirta, Hedychium gardnerianum, Psidium cattleianum) continued to spread and concern Park resource managers. The objective of this investigation was to determine which sites are suitable for germination and initial establishment of the weeds. Weed seed was added to four site types (mechanically-scalped areas, non-native grassy areas, native fernlands, and epiphytic substrates). Control areas of the same site types where no seed was added were used to determine the effects of soil seed banks and seed rain. The number and height of weed seedlings present after one year in the four site types where seed was added and not added were compared. Results from Clidemia sites (but not Hedychium and Psidium) indicated a large, viable Clidemia seed bank or seed rain. Clidemia produced the greatest number of seedlings in scalped sites and the tallest seedlings in grassy and scalped sites. Hedychium seedlings occurred in all four treatment sites with the greatest number in epiphytic sites. The tallest Hedychium seedlings were found in fernland sites and the shortest in epiphytic sites where seedlings appeared stunted. Psidium seedlings were found sparsely in fernland, grassy, and scalped sites without preference. Fernland sites had, by far, the tallest Psidium seedlings. The data tentatively suggest that Clidemia is disturbance-adapted and less adapted to

protected, shaded sites, whereas Hedychium and Psidium are greater threats to recovering and intact rain forests.

INTRODUCTION

At the current rate of degradation, it is clear that Hawaiian rain forests that are unprotected from feral ungulates have little chance of long term survival and will likely disappear within the next 50 years or so, except in highly degraded and modified forms. Beginning in the 1980s, efforts were made to protect selected Hawaiian rain forests from the impacts of feral pigs `with fences and control efforts. The increasing and related threat of domination by non-native plant species was addressed by manual and chemical control. The beginning of recovery of native vegetation after removal of pigs has been apparent in many areas (Medeiros et al. 1995). Will these areas recover largely with native plant species or will the cover of certain highly invasive and habitat-modifying weed species continue to increase and overcome the native vegetation of these areas? Will the conservation management efforts made to date to save Hawaiian rain forests be effective in the decades to comer or will they amount to naught? Considering the often substantial presence of nearby seed sources of these weeds in lowland and adjacent unprotected rain forest tracts and the abundance of local avian dispersal vectors such as Zosterops, the information needed to answer this question seems to rest largely in the ability of these weeds to germinate and become established in dense thickets of recovering native ferny vegetation instead of the ground disturbance and open grassy areas promoted by feral pig activity. This investigation attempts to determine whether three highly invasive plant species can continue to spread in a protected rain forest within Haleakalā National Park at Kīpahulu Valley, Maui island, Hawai'i.

Degradation of native vegetation by non-native ungulates, common in Hawai'i and other oceanic islands, greatly facilitates invasion by weeds that become progressively more dominant and difficult to remove. The first step in restoration of native ecosystems in Hawai'i is the removal of ungulate species by exclusionary fencing and control of these animals within the fenced units. Following ungulate removal, the responses of non-native plant species range from the decline of the weeds ("colonizing" species sensu Bazzaz 1986) to continued expansion ("invader" species sensu Bazzaz 1986).

Even in Hawaiian rain forests from which ungulates have been removed, invasive plant species pose a formidable threat to the long-term survival of native biodiversity. The mechanisms of the threat posed by invasive plants include the direct displacement of native vegetation, the extirpation or reduction of key animal pollinators and dispersers, and marked alterations in nutrient cycling. Invasive plant species limit the effectiveness of restoration efforts, affect the recovery trajectories of individual native species, and influence the long-term composition of restored ecosystems (Hobbs and Mooney 1993). Once non-native species have become broadly established across extensive, often rugged landscapes, long-term mitigation has proven so costly in terms of human, technical and financial resources that managers have virtually abandoned large areas, relegating them to the gradual but likely permanent and irreversible transformation into regions dominated by or even solely comprised of non-native species.

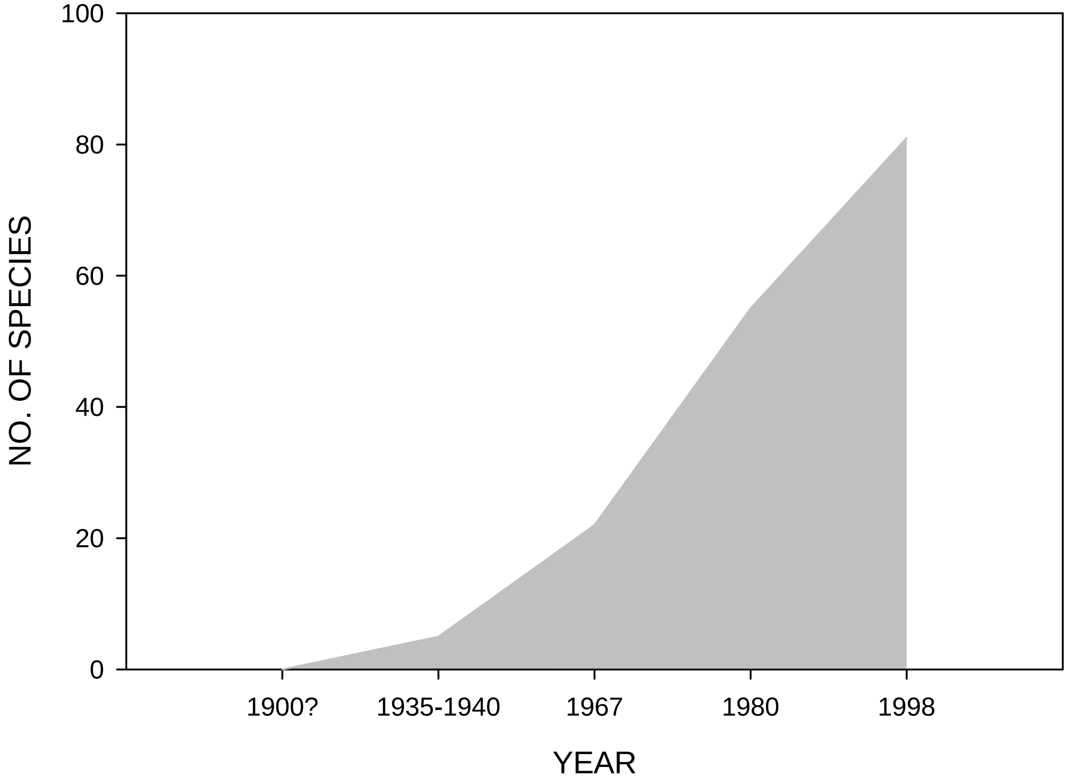
The rain forest of windward Haleakalā (East Maui) is one of the most diverse contiguous examples of this forest type in Hawai'i. One of the most outstanding tracts is Haleakalā National Park's Kīpahulu Valley, partly because of the exceptional biological diversity included in large tracts of koa (Acacia koa Gray) that extend from ca. 250 to 1430 meters elevation and partly because of effective feral pig management. Koa forest with diverse shrub, vine, herb and matted fern layers, grades upslope into ōhi`a lehua (Metrosideros polymorpha Gaud.) forest, interspersed with montane bogs, and bounded above ca. 2300 m elevation by extensive native Deschampsia nubigena Hillebr. grasslands. The region clearly is a unique biological resource and one of the most diverse rain forests in Oceania.

Pigs, though originally brought by Polynesians beginning in the 4th or 5th century A.D., were virtually unknown in Maui rain forests prior to modern times (Diong 1982). Beginning in the early 1900s, escaped domestic pigs, derived from European breeds, began to become feral in East Maui rain forests (Diong 1982). These pigs invaded Kīpahulu Valley rain forest via two pathways, with the first individuals entering the valley from 1935-1945 from above via Haleakalā Crater and adjacent grasslands from stock believed to have originated from farms in the coastal Ke’anae-Pi’ina’au area (Diong 1982). The chasing of pigs with hunting dogs, a practice discontinued in the Crater in 1961, aggravated the spread of pigs from the sub alpine Crater into the rain forests of Kīpahulu Valley (Diong 1982). During the 1950s and 1960s, a second invasion of the valley occurred from below, as pigs escaped from pig farms in coastal Kīpahulu. The upslope spread of pig populations, accelerated by hunting pressure, was perhaps also facilitated by the seasonal availability of ripe fruit fall of strawberry guava (<u>Psidium</u> <u>cattleianum</u> Sabine) (hereafter <u>Psidium</u>) as a food resource (Diong 1982). From the two converging sources, Kīpahulu Valley was fully invaded by 1967 (Diong 1982; Warner 1968).

Over the past 50 years, the widespread establishment of feral pigs has facilitated the invasion of East Maui rain forests by non-native plant species (Figure 11). Primary plant diet items for feral pigs are native ground herbs and sedges, <u>Psidium</u> fruits, and ferns, especially the native tree ferns <u>Cibotium</u> spp. (<u>hapu'u</u>) (Diong 1982). The removal of native, shade-providing ferns, shrubs, and herbs and repeated ground disturbance caused by feral pigs facilitated the invasion of the valley by weed species. When pigs first invaded the upper reaches of Kīpahulu Valley around 1935-1945 (Diong 1982), only five non-native plant species were known from the valley (Fagerlund 1945). By the time pigs had reached all parts of the valley in or before 1967 (Diong 1982), 22 non-native plants were recorded in the valley (Lamoureux 1968). By 1980, the number of non-native plants in the valley had increased to 55 species (Yoshinaga 1980) and to 81 species by 1998 (Medeiros et al. 1998).

By the 1980s, pig populations had increased so dramatically that the resultant ground disturbance, herbivory, and displacement of native species by invasive plant species threatened irreversible degradation of the forest (Diong 1982; Medeiros et al. 1995). In the mid-1980s, nearly all pigs were removed from

Figure 11. Number of non-native plant species recorded in upland regions of Kīpahulu Valley, Maui, Hawai'i (1900-1998) based on Fagerlund 1945; Lamoureux 1968; Yoshinaga 1980; and Medeiros et al. 1998.



Kīpahulu Valley with a control program and a series of exclosure fences (Anderson and Stone 1993). After elimination of pigs, the cover of most native plants increased and the cover of most non-native plants declined. However, the spread of three invasive plants began to alarm park biologists and resource managers: clidemia (Clidemia hirta (L.) D. Don, Melastomataceae) (hereafter Clidemia), kahili ginger (Hedychium gardnerianum Ker.-Gawl., Zingiberaceae) (hereafter Hedychium), and strawberry guava (Psidium cattleianum, Myrtaceae). All three species are considered serious threats to wet forest in Hawai'i, on other oceanic islands, and elsewhere.

Until the mid-1980s, prior to their control in Kīpahulu Valley, the rooting and movements of feral pigs had reduced many areas of rain forest understory to bare ground with cover values in plots ranging up to 30-60% bare ground (pers. obs.). Since feral pigs have been controlled, however, bare ground in the valley has substantially decreased, and is now restricted to trails, fence routes, landslides, and watercourse sides.

Many non-native plant species that had proliferated in pig-disturbed clearings declined sharply after pigs were eliminated. The non-native grass Paspalum conjugatum Bergius increased initially as it colonized areas of bare ground (Medeiros, Loope, and Chimera 1998). Based on field observations and permanent plots, the general trend appears to indicate that the sites dominated by P. conjugatum and other alien grasses and sedges are slowly being replaced by a native matted fern community, composed primarily of Diplazium sandwichianum (C. Presl) Diels (pers. obs.). Now that upland Kīpahulu Valley is again free of feral pigs, information is needed about the vulnerability of plant communities to the establishment of invasive species. The spread of a non-native plant species is determined by characteristics of the environment being invaded as well as the plant's dispersal system, its ability to germinate and establish into various microhabitats, and the time it takes for newly established germinants to reach reproductive size.

Establishment of each species is dependent upon "safe sites" where dispersed seeds find the proper microhabitats for successful germination and growth (Harper 1977). Understanding the species-specific profile of suitable safe sites is especially important in evaluating the trajectories of invasive plant species in a given environment. The most problematic invasive plants are those species that spread even in areas of limited disturbance regimes, such as in protected natural areas where non-native ungulates have been excluded.

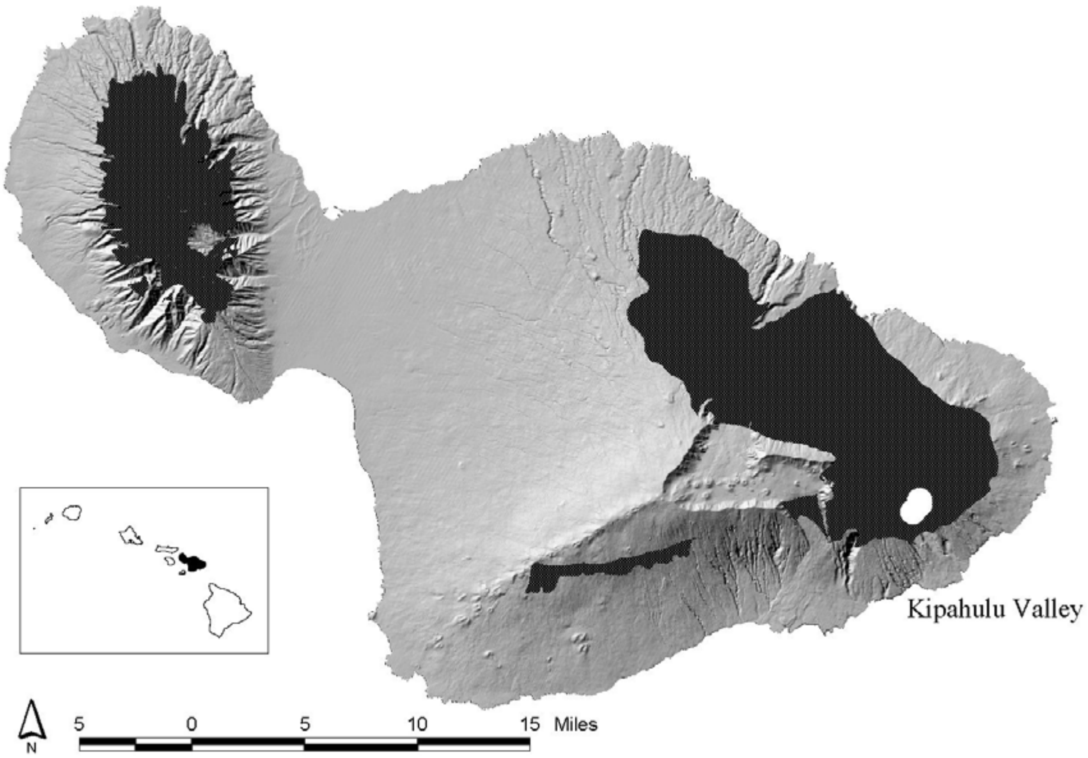
This study is intended to identify potential "safe sites" or microhabitats suitable for successful germination and establishment for each of the three study species. Using information about this critical life history phase, meaningful predictions can be made regarding the potential of spread of invasive species, such as the three study species, across varying landscapes. The four sites characteristic of

Kīpahulu rain forests that were investigated in this study are 1) grassy areas dominated by non-native grasses and sedges, especially the Neotropical Paspalum conjugatum, 2) grassy areas where all vegetation was removed and mechanically-scalped to mineral soil to simulate the effect of pig rooting, 3) the dense, shaded understory of matted thickets of the endemic fern Diplazium sandwichianum, and 4) epiphytic substrates, along horizontal sections of moss-covered tree limbs.

MATERIALS AND METHODS

Three primary study sites were selected in Kīpahulu Valley, within Haleakalā National Park on eastern Haleakalā Volcano (Figure 12). At each of these three study sites, only one of the study weed species was present but that species occurred in substantial local density. The study sites occurred for Clidemia at 820 m elevation (804,819E, 2,292,241N UTM-NAD83); for Hedychium at 700 m elevation (804,835E, 2,291,934N UTM-NAD83); and for Psidium at 855 m elevation (804,316E, 2,291,388N UTM-NAD83). All study sites were located in remote areas requiring helicopter transport. Besides the presence of the large population of the study weed, the primary vegetation type of the study sites in

Figure 12. Map of Maui, Hawaiian Islands, showing distribution of native rain forest dominated by native species (black shading) and three study sites in Kīpahulu Valley (white dots).



Kīpahulu Valley is diverse native rain forest dominated by the trees Metrosideros polymorpha and Acacia koa with well-developed native shrub, fern and bryophyte layers.

Clidemia hirta (clidemia) is native to Mexico, the West Indies, Central America and northern South America to Bolivia and southern Brazil. It is a serious forest pest that has become widely naturalized around the world from approximately 20 degrees S to 22 degrees N latitude on Pacific and Indian Ocean islands, Indonesia, Malaysia, Southeast Asia, and Africa (Chapter One).

Hedychium gardnerianum (kahili ginger) is a large rhizomatous herb up to 2 m in height, native to the Himalayas and adjacent regions and occurring to 1900 m elevation (Graf 1992; Nagata 1990, Stainton 1997). Hedychium has become naturalized from approximately 42 degrees S to 22 degrees N latitude on islands in the Pacific Ocean (Hawai'i, New Zealand), Indian Ocean (La Reunion), and Atlantic Ocean (Azores, Madeira), as well as in Jamaica, Australia, and South Africa (Chapter One).

Psidium cattleianum (strawberry guava) is a small tree up to 6 m in height that is native to South America (Hodges 1988). Introduced extensively in tropical and subtropical areas for its edible fruit, Psidium has become widely naturalized from approximately 27 degrees S to 32 degrees N latitude on islands of the Pacific, Atlantic, and Indian Oceans, as well as Australia, Central America, Asia, Africa, the Caribbean, and North America (Chapter One).

Within invasive populations of the study species in Kīpahulu rain forest, a number of transects were established in two dominant groundcover vegetation types. In areas dominated by alien grasses, transects totaling 60 meters were laid out. In adjacent areas dominated by native matted ferns, transects totaling 30 meters were laid out. Transect locations were determined non-randomly, primarily to facilitate maximum site utilization without crossing existing trail networks. Along these transects, 0.25 m^2 plots (0.5 m x 0.5 m) were located and marked with one-meter buffers between plots to assure independence. This arrangement yielded 40 quarter-meter^2 plots in alien grass areas and 20 quarter-meter^2 plots in native fern areas.

To evaluate the response of the study species to disturbed sites (simulating pig diggings), half of the 0.25 m^2 plots (i.e., 20 plots) in areas dominated by alien grasses were mechanically scalped of all living vegetation and leaf litter and scraped down to mineral soil. Selection of sites in alien grass areas to be scalped was random. As a result, sixty quarter-meter plots were randomly selected, 20 to be scalped to mineral soil, 20 in sites dominated by alien grasses, and 20 in sites dominated by native ferns. To consider epiphytic sites for suitability of establishment, 20 sections of elevated moss-covered living tree branches were randomly identified and marked.

Because of ethics associated with distributing seeds of invasive plant species in a nature reserve such as Kīpahulu and as stipulated by National Park Service personnel, these experiments were conducted within known populations of the study species being considered. As a result, three separate experimental areas (one for each study species in a preexisting population) were used. To account for seedlings arising as a result of stored seed bank and seed rain of the study species, control plots were established to which study species seed was not added.

Using a random number table to assign treatment, 10 of 20 treatment plots of each of four potential establishment sites (grass-dominated areas, fern-dominated areas, bare ground, and epiphytic sites) were selected to add seeds of the study species. In the treatment plots, seeds were added at the center of the plot, incorporated into a small amount of mud to reduce their attractiveness to rodents and birds. Copious seed was added to ensure that the effects of stochastic events such as seed predation, loss by flooding rains, etc. would be minimized. Because of large differences in the seed sizes of the three species, the numbers of seeds added per plot differed among the three study species. For the large seeded species (<u>Hedychium</u> and <u>Psidium</u>), 25 seeds were added per plot; for the very small-seeded <u>Clidemia</u>, three crushed fruits were added per plot (approximately 1800 seeds).

One year after the start of the experiment, all plots were examined and the number and size (height and basal diameter) of all emergent seedlings of the study species recorded. By comparing numbers of seedlings present in control versus treatment plots, the number of seedlings contributed by the stored seed bank was estimated. By comparing the number and size of seedlings found in the four establishment sites, suitable establishment sites were identified for each study species. Statistical analyses were performed with Minitab Release 13.30 software. Where necessary, transformations were used to help meet assumptions of normality and variance.

Maui field biologists (S. Anderson, P. Bily, M. Chimera, W. Haus, R. Hobdy, A. Medeiros, H. Oppenheimer, P. Welton) were consulted to produce distribution maps for the three study species on Haleakalā with ArcView mapping software and the technical expertise of Dan McNulty-Huffman of Haleakalā National Park (Figs. 3-5). As defined here, the designation of invaded means that the study weed is known to occur in these areas. It does not mean the vegetation of the area is totally dominated by the study weed. Invaded areas were designated based on bird transect data, helicopter surveys with attached GPS system, and field knowledge of consulting biologists.

RESULTS

After one year, Clidemia seedlings were present in at least some treatment plots in all four establishment sites and in three of the control plots (all except in epiphyte sites without added seeds) (Table 22). After one year, Hedychium seedlings were found in at least some treatment plots in all four establishment sites but not in any of the control plots (Table 22). With Psidium, seedlings were found in treatment plots of three of the four establishment sites (the exception being epiphytic sites) and in none of the control plots (Table 22).

With Clidemia, the number of seedlings differed among the treatment areas (two-way ANOVA, F = 3.73, df = 6, P = 0.003). The largest number of seedlings was found in scalped sites; seedlings were found in 8/10 treatment plots (x = 11.3 seedlings/plot) and 10/10 control plots (x = 10.5 seedlings/plot). The establishment site with the next highest number of seedlings was grassy areas; seedlings were found in 7/10 treatment plots (x = 5.9 seedlings/plot) and 3/10 control plots (x = 0.8 seedlings/plot). In fernland sites, seedlings were found in 2/10 treatment plots (x = 0.3 seedlings/plot) and 2/10 control plots (x = 0.2 seedlings/plot). In epiphytic treatment sites, seedlings were found in 5/10 plots (x = 2.8 seedlings/plot). When the data is square root transformed, and the ANOVA model with Tukey's comparisons is applied, significant differences (P = <0.05) are found in the number of seedlings found among scalped treatment and control sites and fernland treatment and control sites and grassy control areas.

<u>Clidemia</u> sites were unique among the three study species tested in that control plots also produced <u>Clidemia</u> seedlings, indicating the presence of a large viable soil seed bank and/or seed rain. In all plots combined, <u>Clidemia</u> seedlings were found in 22/40 treatment plots (x = 5.1 seedlings/plot) and 15/40 control plots (2.9 seedlings/plot). Overall, there was no significant difference in the number of seedlings found between treatment and control plots (two-sample T-test, P = 0.237).

Table 22. Contingency tables for presence of seedlings after one year for the three study species in four establishment sites. An X indicates the presence of observed seedlings and dashes (---) indicate the absence of seedlings.

	Grassy sites	Scalped sites	Fernland sites	Epiphytic sites
Clidemia seeds added	X	X	X	X
Clidemia seeds not added	X	X	X	---
Hedychium seeds added	X	X	X	X
Hedychium seeds not added	---	---	---	---
Psidium seeds added	---	X	X	X
Psidium seeds not added	---	---	---	---

With Hedychium, the number of seedlings differed among the treatment areas (two-way ANOVA, F = 3.81, df = 3, P = 0.000). The largest number of seedlings was found in epiphytic treatment sites. Seedlings were found in 8/10 treatment plots (x = 3.4 seedlings/plot). Scalped treatment sites and fernland treatment sites were next with seedlings found in 4/10 sites (x = 1.2 seedlings/plot) and 3/10 plots (x = 1.1 seedlings/plot) respectively. Grassy treatment sites produced the lowest number of Hedychium seedlings (x = 0.3 seedlings/plot), found in 3/10 plots. The per plot frequency and mean number of seedlings found in epiphytic treatment sites were at least double that of other sites. When the data is square-root transformed, and the ANOVA model with Tukey's comparisons is applied, significant (P = <0.05) differences in the number of seedlings were found among epiphytic and grassy treatment sites and epiphytic and fernland treatment sites.

With Psidium, the number of seedlings did not differ among the treatment areas (two-way ANOVA, F = 0.49, df = 2, P = 0.617). The largest number of seedlings was found in epiphytic treatment and fernland treatment sites where seedlings were found in 5/10 plots (x = 1.9 seedlings/plot) and 2/10 plots (x = 1.4 seedlings/plot) respectively. In scalped treatment sites, Psidium seedlings were found in 4/10 plots (x = 0.7 seedlings/plot).

The height of Clidemia seedlings differed among the treatment areas (two-way ANOVA, F = 3.16, df = 6, P = 0.006). After one year, the tallest Clidemia seedlings were found in grassy control sites (x = 61.6 mm +/- 74.1), followed by grassy treatment sites (x = 49.2 mm +/- 79.1), scalped treatment areas (x = 33.2 mm +/- 29.8), and scalped control areas (x = 33.2 mm +/- 53.1). Smaller Clidemia seedlings were found in epiphytic treatment plots (x = 1.1 mm +/- 0.3), fernland treatment plots (x = 1.3 mm +/- 0.6), and fernland control plots (x = 1.0 mm +/- 0.0). When the data are square-root transformed, and the ANOVA model with Tukey's comparisons is applied, significant differences (P = <0.05) in the height of Clidemia seedlings are found between epiphytic treatment sites and four other sites: grassy treatment and control sites and scalped treatment and control sites.

The height of Hedychium seedlings differed among the treatment areas (two-way ANOVA, F = 15.93, df = 3, P = 0.000). The tallest Hedychium seedlings were found in fernland treatment plots (x = 27.0 mm +/-12.8), followed by scalped treatment plots (x = 19.7 mm +/- 6.2), grassy treatment plots (x = 18.0 mm +/- 3.6), and epiphytic treatment plots (x = 10.9 mm +/- 3.0). Square root transformed data using the ANOVA model with Tukey's comparisons yielded significant differences (P = <0.05) between the heights of Hedychium seedlings found in epiphytic treatment plots and grassy treatment plots, as well as between epiphytic treatment plots and fernland treatment plots.

The height of Psidium seedlings differed among the treatment areas (two-way ANOVA, F = 20.81, df = 2, P = 0.000). The tallest Psidium seedlings by far were those found in fernland treatment plots (x = 130.6 mm +/- 76.2) where mean seedling height was several times greater than that of seedlings found in epiphytic treatment plots (x = 35.1 mm +/- 12.7) and in scalped treatment plots (x = 24.6 mm +/- 8.5). Square-root transformed data using the ANOVA model with Tukey's comparisons reflected this and yielded significant differences (P = <0.05) between the heights of Psidium seedlings found in fernland treatment plots and epiphytic treatment plots, as well as between those found in fernland treatment plots and scalped treatment plots.

The East Maui rain forest distributional maps produced for the three study species distribution maps provide the basis for the following estimates. Currently, Clidemia occupies 21,848 ha on Haleakalā including 6,037 ha of native rain forest (24% of total rain forest on Haleakalā), and 1,405 ha within Haleakalā National Park including 46% of the Park's native rain forest (Tables 22 and 23, Figure 13). Hedychium occupies 4,221 ha on Haleakalā including 3,176 ha of native rain forest (12% of total rain forest on Haleakalā), and 797 ha within the Park including 27% of the Park's native rain forest (Tables 22 and 23, Figure 14). Psidium occupies 35,687 ha on Haleakalā including 8,890 ha of native rain forest (35% of total rain forest on Haleakalā), and 1,603 ha within the Park including 50% of the Park's native rain forest (Tables 22 and 23, Figure 15).

DISCUSSION

Of the three weed species assessed in this study, the primary results suggested by the experimental addition of Clidemia seeds to various microhabitats are that this species establishes the greatest number of seedlings in disturbed areas.

Ground disturbance, and not the experimental seed addition, was the single greatest factor contributing to the establishment of Clidemia. The mean number of Clidemia seedlings that became established in scalped treatment sites was double that of grassy treatment sites, four times that of epiphytic treatment sites, and more than 37 times higher than that of fernland treatment sites. Grassy sites with Paspalum, which colonizes following ground disturbance (Medeiros, Loope, and Chimera 1998), produced the second highest number of Clidemia seedlings.

After one year, Clidemia seedling height was greater in grassy treatment (x = 49 mm) and control sites (x = 62 mm) and scalped treatment (x = 37 mm) and control sites (x = 33 mm), by more than an order of magnitude over Clidemia seedling heights in epiphytic or fernland sites (all x = 1 mm). All seedlings of epiphytic and fernland sites were at or barely beyond the cotyledon stage of development. This may be a result of tardy germination in these sites compared to early germination in scalped and grassy sites. However, subsequent visits to epiphytic and fernland sites failed to reveal larger seedlings or saplings, suggesting that although germination can occur here, survival of Clidemia in epiphytic and fernland sites is poor and establishment is at best infrequent.

One of the strongest conclusions that can be drawn from this experiment is that there was a substantial Clidemia soil seed bank and or seed rain in the study area that germinated following the disturbance of the mechanical scalping. In fact, this seed bank was so substantial that using a two-sample t-test, there was no significant difference (P = 0.237) between the numbers of Clidemia seedlings produced in all treatment sites when compared to the pooled results of control sites. This was surprising in two ways. The first was the scale of the experimental seed addition, which totaled approximately 1800 added Clidemia seeds per plot ($0.25m^2$) off approximately 70% viability (Medeiros unpubl.). The second is that at the time of the initiation of this study, Clidemia was not a dominant part of the surrounding vegetation, comprising approximately only 5-10% of local vegetation cover. These results are perhaps more understandable if we consider the very high reproductive potential of even single Clidemia plants (Chapter Two) as well as the tendency for seeds to be dispersed in large quantities by common resident passerines (Chapter Three). The microhabitats that showed the greatest differences between treatment and control site were grassy sites and epiphytic sites. Assuming seed rain was universal across these microhabitat types, it seems likely that non-native Paspalum grassy areas, native Diplazium fernlands, and epiphytic sites may retard the establishment of Clidemia.

The establishment of Clidemia seedlings was notable in experimental plots for the other two study species, once again suggesting the presence of a prodigious Clidemia seed bank and/or seed rain. This is remarkable considering that at the onset of the experiment; Clidemia was present as scattered, uncommon plants in locations where Hedychium and Psidium dominated the local vegetation respectively. Despite this, in Hedychium plots after one year, one Clidemia seedling appeared in the scalped treatment plots and one in the fernland treatment plot. In Psidium plots, 12 Clidemia seedlings appeared in the scalped treatment and control plots and one in the grassy control plots. The Clidemia seedling that emerged in the Hedychium fernland plot was at the cotyledon stage and approximately 1 mm tall, as were the five seedlings that appeared in the Clidemia fernland plots, providing some verification that Clidemia can germinate but tends not to thrive in densely-shaded Diplazium fernlands. Surprisingly, the number of Clidemia seedlings (n = 12) that opportunistically appeared in scalped Psidium plots exceeded the number of Psidium seedlings (n = 7) that appeared in those same treatment plots, despite the addition of 250 Psidium seeds.

With Hedychium, epiphytic treatment sites produced the highest numbers of seedlings, more than twice those of scalped treatment sites, thrice that of fernland treatment sites, and ten times that of grassy treatment sites. This result was somewhat unexpected. The genus Hedychium does have some primarily epiphytic species (Larsen et al. 1999). Though this species occasionally grows epiphytically throughout the study area, H. gardnerianum, in Hawai’i at least, is overwhelmingly a terrestrial species. Relatively low numbers of emerged seedlings and high variation between plots restricted significance to between epiphytic treatment and grassy treatment sites, though values near statistical significance were also obtained between epiphytic treatment sites and scalped treatment and fernland treatment sites.

The height of Hedychium seedlings was greatest in fernland treatment sites, followed by scalped treatment and grassy treatment sites. Though more frequently found than in other sites, epiphytic Hedychium seedlings were also consistently smaller than in other tested microhabitats, significantly so in the case of scalped treatment and fernland treatment sites.

The absence of Psidium germinants in the grassy treatment plots (25 seeds x 10 plots) in an area where Psidium was common is notable. Even in the epiphytic treatment, fernland treatment, and scalped treatment sites, germination of Psidium occurred only sparingly and with high variation among plots marked by a standard deviation that twice exceeded the mean (x = 1.3 seedlings/ plot +/- 2.7).

Hedychium and Psidium control plots failed to produce any seedlings, presumably due to low soil seed bank levels of these species. In contrast, Clidemia, which did produce seedlings in control plots, has prolific seed production throughout the year. In the study area, Clidemia has been estimated to produce many more seeds than the other two study species: at least three orders of magnitude more than Hedychium and at least four orders of magnitude more than Psidium per square unit of cover area (Chapter Two). Nonetheless, in East Maui rain forests, both Hedychium and Psidium are also known to be commonly and effectively dispersed by resident passerines (Chapter Three). The absence of evidence of a Psidium soil seed bank as indicated by lack of germinants in control plots may in part be due to low levels of seed production locally (Chapter Two). Potentially high levels of reduction of Hedychium seed crops by rodent predation on flower bud, flower, and pre- and post-dispersal seed predation (Chapter Four) makes the absence of a substantial Hedychium soil seed bank more understandable.

Differing heights of seedlings among plots and treatment types suggests two possible causes: either earlier germination and/or faster growth rates. The fact that only cotyledon-sized Clidemia seedlings (ca. 1 mm height) were found in fernland and epiphytic sites suggests recent germination. The stunted, achlorotic Hedychium seedlings found in epiphytic sites suggest slow growth rates in suboptimum conditions, perhaps because of the seasonal desiccation characteristic of these sites. The tallest Clidemia seedlings occurred in the microsite (i.e., grassy area) most likely to have had small seedlings that escaped detection at the onset of the experiment.

The ability of a species to colonize new areas is highly dependent on its ability to reach and exploit favorable establishment sites, some of which can be ephemeral, such as light gaps, watercourse associated landslides, and in the cases of pig-occupied areas, diggings. This ability is greatly enhanced by an effective dispersal system. In Hawai’i, many native frugivores, which presumably co-evolved with native baccate plants, have become extinct, through the effects of habitat destruction, introduced avian diseases, and mammalian predators (James and Olson 1991; Olson and James 1991). Consequently, the majority of seeds from both native and non-native species are dispersed in rain forests of East Maui by small, generalist non-native passerine species, especially Zosterops and Leiothrix (Chapter Three). Non-native plant species are at least as likely to be dispersed by these birds, as are native plant species. Non-native plant species that produce abundant, small-sized seeds in fleshy fruits year-round may be better adapted for widespread dispersal by resident frugivore species.

Of the species studied in this investigation, Clidemia clearly has effectively exploited the resident non-native frugivores in generating prolific dispersal and seed rain. In the study area, Clidemia seeds maintain high levels of seed viability after three years of burial (Medeiros unpubl.). Based on these results and greenhouse trials (Medeiros unpubl.), Clidemia produces a prolific soil seed bank, that responds rapidly to disturbance by producing numerous rapidly-growing seedlings that are shade intolerant. These attributes are characteristics of pioneer species of other tropical forests (Garwood 1989). They also favor prolific spread of Clidemia in its naturalized range, especially where disturbance is frequent, such as after canopy disturbance, periodic flooding, or in areas where ungulates perturb native vegetation.

The other two study species, Hedychium and Psidium, have characteristics more typical of late successional stage tropical forest species with larger seeds that produce slow-growing, shade-tolerant seedlings and longer-lived individuals

(Garwood 1989). Larger seed size is strongly correlated with greater survival in shaded conditions, especially in the early stages of growth (Grime and Jeffrey 1965; Leishman et al. 2000; Seiwa and Kikuzawa 1996).

One disadvantage of larger seed size is vulnerability to seed predators, especially vertebrates. This vulnerability is counteracted by traits like tough seed integument, the presence of secondary compounds that deter predators, prolific and/or episodic seed production, and a highly effective seed dispersal mechanism.

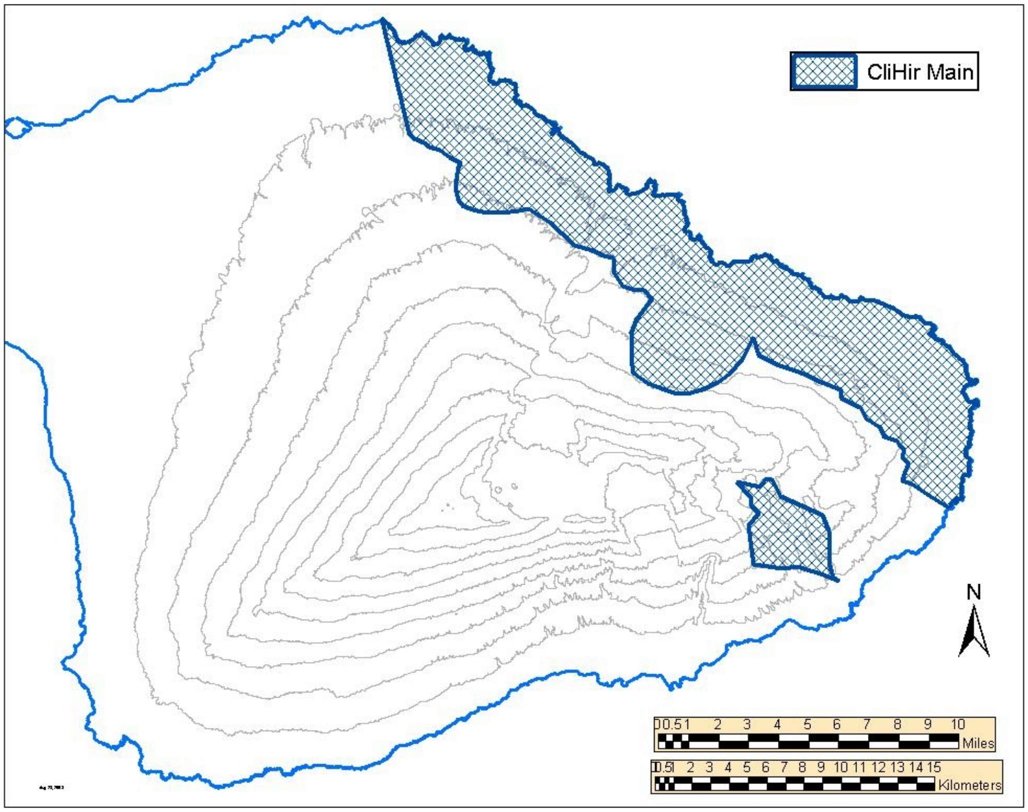
In November of 2003, a massive defoliation of the primary native canopy species koa (Acacia koa) occurred in the study area. Defoliation was precipitated, at least in part by the wilt fungus Fusarium oxysporum (Anderson et al. 2002) and grazing by the larva of the endemic moth Scotorythra paludicola (Bultler) (Geometridae: Lepidoptera) (M. Heddle pers. comm. 2003). The extensive defoliation of an estimated 40% of the canopy dramatically increased sunlight levels onto normally shaded middle and understory vegetation layers. Early naturalist R.C.L. Perkins recorded similar accounts of defoliation events in the 1890s on Maui (Perkins 1913). He attributed the defoliation events to outbreak level population increases of S. paludicola. The impact of the defoliation on weed establishment and spread in the study area is unknown, but based on results presented here, suggest that at least is likely to precipitate the proliferation of shade-intolerant species such as Clidemia. On the island of Kaua'i, after the native tree canopy of Limahuli Valley was largely destroyed by Hurricane ‘Iniki in September 1992, *Clidemia* spread catastrophically, with an estimated fifty-fold increase within just a few years (S. Perlman pers. comm.; K. Wood pers. comm.). The phenomenal spread of the non-native *Miconia* *calvescens* (Melastomataceae) on Tahiti from two plants in 1937 to domination of two-thirds of the island (over 650 square kilometers), by the 1980s may be partially due to defoliation and damage to canopy trees by successive tropical typhoons (Medeiros *et* *al*. 1997).

The East Maui Watershed Partnership (EMWP), formed in 1991, consists of seven primary partners (State of Hawai`i Department of Forestry and Wildlife, Haleakalā National Park, East Maui Irrigation Company, Haleakalā Ranch, Hāna Ranch, The Nature Conservancy, and Maui County Department of Water Supply) and coordinates the resource management activities of 100,000 acres (40,000 ha) of watershed of windward Haleakalā. The partnership’s most ambitious project thus far has been the partial construction (nearly 70% complete in 2004) of 16 km (10 miles) of exclosure fencing along the 1100 m (3600 ft) elevational contour to protect the upper 10,000 acre (4000 ha) core of near pristine upper elevation rain forest. Once completed, this core management unit will abut fenced units of Haleakalā National Park’s Kīpahulu Valley. Once ungulates have been eliminated, these areas will face similar problems of management of invasive weed problems. This research aims at providing important insights into management of all East Maui rain forests.

One criteria by which the seriousness of an invasive species may be judged is the rate of spread in a native ecosystem, or the area of native ecosystem colonized per year of occupation. The maps presented in the results section document the current distribution of the three study species. Statewide, Clidemia is found from near sea level to 1,500 m (Smith 1992), Hedychium from 610-1,525 m (pers. obs.; P. Bily pers. comm.), and Psidium from near sea level to 1,615 m elevation (pers. obs.; B. Haus pers. comm.). By comparing the area currently occupied by the species versus the area potentially occupied (the area of East Maui rain forest within the species potential elevational limits), the percentage of potentially occupied rain forest can be calculated. Based on this, Clidemia, Hedychium, and Psidium have reached 24%, 12% and 35% of their respective maximum invasion potentials in East Maui rain forest (Table 24).

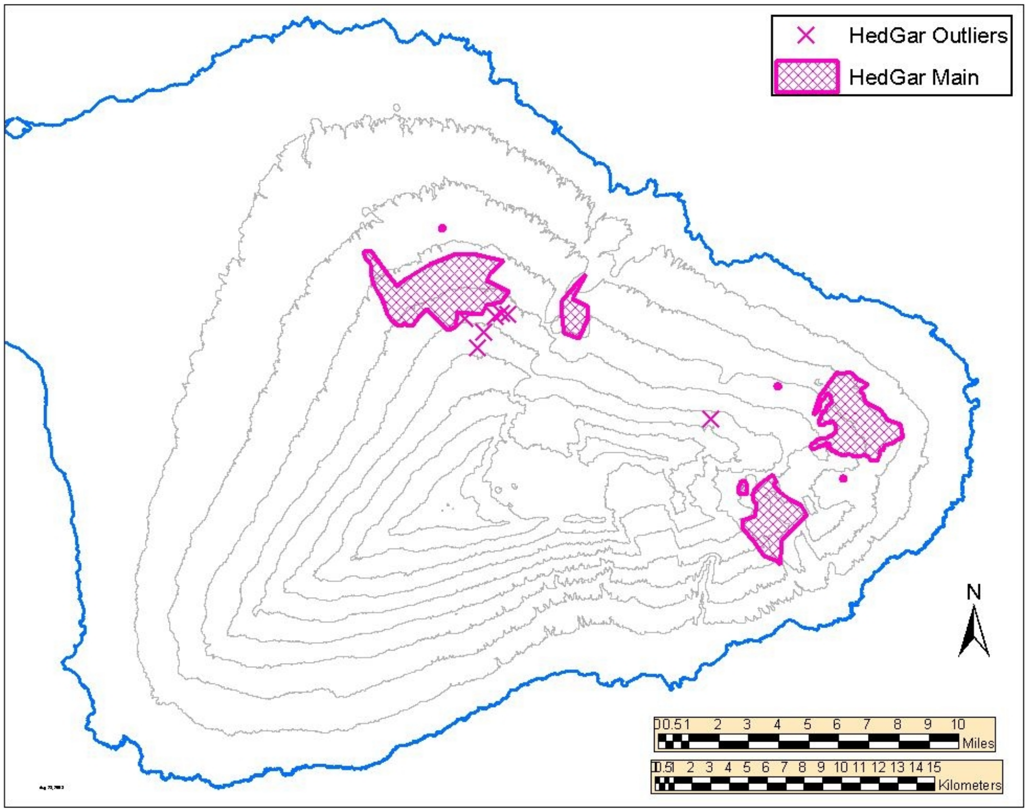
By dividing the current area of East Maui rain forest occupied by the study species by the number of years the species has been present on East Maui, historical spread rates of the three study species on Maui can be calculated (Table 23 and 24). Clidemia has spread at nearly twice the rate of the other species, at 94ha/year in Haleakalā National Park (HALE) and 796 ha/year on East Maui. Psidium has spread at 25 ha/year in HALE and 400 ha/year on East Maui, and Hedychium at 53 ha/year in HALE to 80 ha/year on East Maui. Using the two historical rate of spread for both East Maui and HALE, predictions can be

Figure 13 . Current distribution of Clidemia hirta on Haleakalā, Maui.



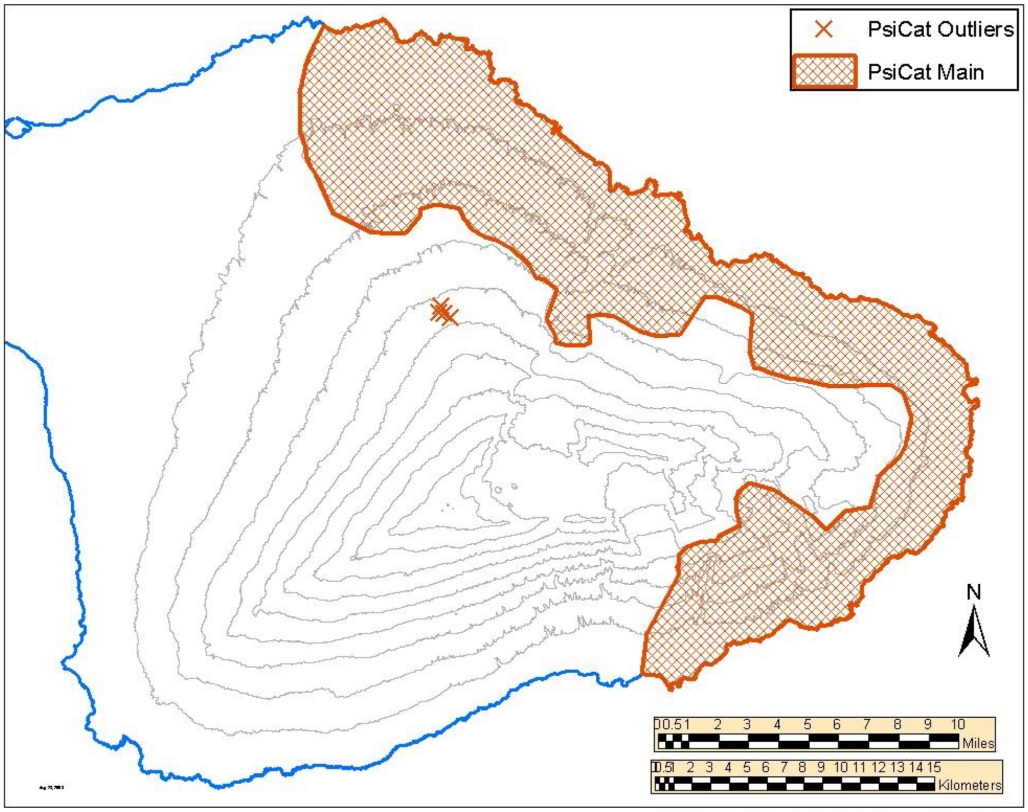
made on how many years it will take for each of the three study species to fully invade the portion of East Maui rain forests (25,688 ha in total) within their respective elevation limits. The most rapidly expanding species, Clidemia, would fully invade vulnerable East Maui native rain forest (21,165 ha, i.e., that portion of East Maui rain forest below 1500 m elevation) in 19 to 160 years. Psidium would invade vulnerable East Maui native rain forest (i.e., 22,289 ha below 1615 m elevation) in 34 to 536 years. Hedychium, the slowest expanding species, would invade vulnerable East Maui rain forest (i.e., 20,675 ha below 1,525 m) in 219 to 330 years.

Figure 14. Current distribution of Hedychium gardnerianum on Haleakalā, Maui.



This model is simplistic but intended as a guide. One factor, which may tend to slow the spread rate, is the cooler temperatures of upper elevations. Another factor which will definitely slow the spread rate of Psidium is the widespread control of feral pigs in sites like HALE. Pigs are formidable seed dispersers with an average of 2875 Psidium seeds per dropping (Diong 1982). Factors that would tend to quicken the spread rate would be the greater fecundity of large population sizes, and greater utilization by seed dispersers. These historical spread rates do not, of course, reflect changes which would occur with greater success with mechanical, chemical, or biological control.

Figure 15. Current distribution of <u>Psidium</u> <u>cattleianum</u> on Haleakalā, Maui.



CONCLUSIONS

Some of the most profound ecosystem changes in Kīpahulu Valley following removal of feral pigs occurred immediately. The primary effect was the cessation of trampling and rooting that resulted in the chronic, widespread exposure of mineral soil and the direct consumption of selected palatable native herb and shrub species. Successional changes in vegetation and presumably nutrient cycling have taken longer and are still ongoing, even though pigs have been largely excluded from many parts of the valley for more than a decade. Vegetation has become denser and more structurally complex, lowering light levels at soil level. This trend would seem to provide progressively fewer establishment sites for light-loving species like Clidemia, while concurrently increasing establishment sites for Hedychium and Psidium, especially the latter.

The taller Psidium seedlings associated with the shaded understory of Diplazium fernland were in some way expected at least compared to the much smaller seeded Clidemia, which thrived in open, disturbed sites. With increasingly dark shaded understory conditions becoming more common in the recovering rain forests of Kīpahulu, one would hope, from a conservation management standpoint, that dense shade would provide conditions that would deter vigorous establishment of highly modifying invasive species such as Psidium cattleianum. This field experiment while limited in scope supports observations of field biologists and managers that P. cattleianum can establish in dense shade.

One limitation of this experiment is that the duration of the experiment period did not allow the monitoring of the study species long enough to document that full reproductive size could be achieved. Another limitation was the relatively small sample size and single sample design without spatial and/or temporal replicates. Larger and longer-term experiments could contribute to our understanding of establishment site preferences and requirements for highly invasive plant species and provide critical information, that can shape managers decisions and actions. On the other hand, the long term maintenance and scale of such experiments

Table 23. Calculations of extents of three study weed species in comparison with land categories on East Maui. The total area of native rain forest on East Maui (Haleakalā) is approximately 25,688 ha.

STUDY SPECIES	Total area of East Maui infestation (Ha)	Average annual spread rate on East Maui	Total area of East Maui infestation within native rain forest	Percentage of native rain forest on East Maui within infestation	Area of native rain forest on East Maui within known elevational range of weed	Percentage of native rain forest on Maui within known elevational range of weed
<u>Clidemia</u>	21,848	796 Ha/year over 27 years	6,037	24	21,165	82
<u>Hedychium</u>	4,221	79.6 Ha/year over 53 years	3,176	12	20,675	80
<u>Psidium</u>	35,687	400 Ha/year over 89 years	8,890	35	22,289	87

Table 24. Calculations of extents of three study weed species in comparison with land categories for Haleakalā National Park. The total area of native rain forest within HNP is approximately 2923 ha.

STUDY SPECIES	Year of first record on East Maui	Total area of East Maui infestation (Ha)	Estimated spread rate on East Maui (current infestation area/years present on East Maui)	Year first recorded in Haleakalā National Park	Total infestation area in Haleakalā National Park	Estimated spread rate in Haleakalā National Park (current infestation area/years present on East Maui)
<u>Clidemia</u>	1976	21,848 Ha	796 Ha/year over 27 years	1988	1405 Ha	93.6 Ha/year over 15 years
<u>Hedychium</u>	1950s	4,221 Ha	79.6 Ha/year over 53 years	1988	797 Ha	53.1 Ha/year over 15 years
<u>Psidium</u>	?1920	35,687 Ha	400 Ha/year over 89 years	1940s?	1603 Ha	25.4 Ha/year over 63 years

that can insure information fidelity can ironically complicate the mission of land managers, especially in sites where the presence of these weeds is as of yet incipient and where there is still the opportunity for effective control. In these cases, the preference of land managers, who are perennially challenged by restricted financial budgets, for immediate control versus greater depth of data useful for nuanced decision-making is critical. It is hoped that data such as those presented here can help increase awareness of the importance of this type of information for land managers and even for government agencies responsible for dealing with quarantine and importation issues, since the priorities we establish today will inevitably effect the efficacy of our ability to manage plant invasions.

CHAPTER SIX:

CONCLUSIONS

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The following is a discussion of selected ecological traits (reproductive phenology, avian seed dispersal, mammalian seed predation and dispersal, and seedling establishment sites) and implications for management for three problematic fleshy-fruited weed species based on fieldwork on Maui island. The study species are Clidemia hirta (L.) D. Don (clidemia), Melastomataceae, Hedychium gardnerianum Ker.-Gawl., Zingiberaceae (kahili ginger), and Psidium cattleianum Sabine, Myrtaceae (strawberry guava) (hereafter Clidemia, Hedychium, and Psidium). I had four null hypotheses. They were: 1. H_O: there is no annual pattern of ripe fruit production in the study species; 2. H_O: seeds of the study species are not dispersed by resident vertebrate species; 3. H_O: the reproductive potential of the study species is not substantially reduced by seed predators; and 4. H_O: establishment of the study species is not affected by microhabitat type.

The first hypothesis was H_O: there is no annual pattern of ripe fruit production in the study species. The classic weed model suggests that a characteristic of invasive plant species is the ability to produce large numbers of small seeds annually with minimum duration between episodes of fruit production is cited as a (Rejmanek and Richardson 1996). Of the three study species Clidemia clearly is the one that fits this description. Regarding seed size, Clidemia has very small seeds (0.7 mm x 0.5 mm) compared to Psidium and Hedychium that produce seeds approximately 3 mm x 4mm. Regarding numbers of seeds, Clidemia was estimated to produce more than four orders of magnitude more seeds than Hedychium and Psidium of equal cover. Based on data from this study, it is estimated that the mean annual reproductive potential of a square meter area of Clidemia is 10,312,292 seeds; for Hedychium is 2,024 seeds; and for Psidium is 568 seeds. Regarding the production of fruit annually with minimum duration Clidemia once again is the species that most clearly fits the existing weed model. Clidemia ripe fruit production was highest from October through January when each plant ripened an average of 5.6 fruits per day, that is, 4883 seeds per plant per day. However, Clidemia flowered and fruited year round while Hedychium fruited only in a relatively short but intense period from late fall through mid-winter. Though Psidium produced flower buds and flowers year-round, many of these apparently aborted without maturation as ripe fruit production (which peaked in fall) occurred only at very low levels. As a result of these data, I reject the first null hypothesis for all three study species.

The second hypothesis was H_O: seeds of the study species are not dispersed by resident vertebrate species. Typically, invasive plant species have effective seed dispersal systems that allow the non-native species to reach new habitats and expand throughout their limits (Baker 1986; Rejmanek and Richardson 1996). Important invasive plant species with extensive distributional ranges characteristically also have high spread rates (Forcella 1985). Vertebrate seed dispersal is an important trait associated with invasive woody plant species because of the efficacy of seed delivery to optimum sites for germination and establishment (Rejmanek 1996).

This study determined that seeds of all three study species were dispersed by non-native opportunistic passerines. Birds, especially two common non-native species (Zosterops japonicus and Leiothrix lutea), were discovered to be dispersing seeds of all three weed species as well as 11 other plant species including at least six important native plant genera (Cheirodendron, Melicope, Broussaisia, Pipturus, Coprosma, Vaccinium) and one other non-native species (Rubus rosifolius). With the extinction of native fruit-eating bird species in Hawai'i, dispersal of seeds of weed and native species is occurring in Maui rain forests by common, generalist, non-native small passerines. All three species meet the model weed characteristic cited in the literature regarding an effective dispersal system. Among the three study species, the degree of utilization of local bird species for seed dispersal was clearly highest though with Clidemia. Small seed size, important in Clidemia's prodigious reproductive potential, plays a role in its highly effective dispersal system. The fruits of the three study species all have adaptations that would appear to facilitate dispersal by vertebrate animals (fleshiness, sugar content, and color of fruit). However, the size of Clidemia seeds clearly facilitates the common transport of large numbers of seeds.

Zosterops and Leiothrix captures within fruiting Clidemia patches averaged 314 seeds/capture averaged 102 seeds/capture respectively. One captured Zosterops excreted over 1800 Clidemia seeds, or approximately 2.2 fruits. In comparison, the other two study species had much lower seed dispersal rates. For Hedychium, Zosterops and Leiothrix captures averaged 0.29 seeds/capture and 0.72 seeds/capture respectively with the maximum number of seeds excreted by a single bird (Leiothrix) being ten. For Psidium, Leiothrix captures averaged 1.8 seeds/capture and the single mist-netted non-native Garrulax excreted 13 Psidium seeds; Zosterops was not captured at the Psidium site.

The seeds excreted from these captures at best likely only represent a fraction of the feeding activities of these very common passerines. The most effective seed disperser Zosterops is the most abundant bird species of the study area (East Maui rain forests) with densities up to 1600 birds per km^2 (Scott et al. 1986). As weed densities increase, the birds will likely increase their role in seed dispersal as a response to greater fruit availability.

In this study’s investigation of dispersal, passage time of seeds through the gastrointestinal (GI) tract of birds was also tested experimentally for the study weed species. GI passage time is another aspect of a highly developed dispersal system. Seeds retained for longer periods of time greatly increase the potential for long-range seed dispersal and potential for establishing remote populations.

In this case, the passage time for Hedychium, Clidemia, and Psidium seeds was as long as 270 minutes, 210 minutes, and less than 60 minutes respectively.

In regards to its seed dispersal system, Clidemia is the species that most clearly meets the characteristics cited in the literature as typifying a highly invasive species. In many respects, the seed dispersal and spread patterns of Clidemia may be considered as analogous to those of another highly invasive, small-seeded melastome, Miconia calvescens (Medeiros et al. 1997). As a result of these data, I reject the second null hypothesis for all three study species.

The third hypothesis was H_O: the reproductive potential of the study species is not substantially reduced by seed predators. One central tenant of the invasive species model is that these newly arrived species thrive in newly occupied areas partially because of freedom from coevolved parasites and predators, such as seed predators (Harper 1977; Louda 1989). The predicted absence of, in this case, seed predators was verified for two of the study species (Clidemia and Psidium) as this study failed to provide evidence of seed predation for both. In fact, for Clidemia, evidence was obtained to the contrary that non-native rodents (Rattus) with well-developed reputations as seed predators were dispersing Clidemia seeds, though not increasing the seeds germinability and germination rate. Considering the more common status and motility of birds, seed dispersal of Clidemia by rodents is not likely to be important ecologically. However, it does reiterate the variability in outcome when non-native species interact opportunistically. In distinct contrast to the other two species and the predictions of the weed model, seed predation by non-native rodents (Rattus) was estimated to have caused a 48.3% reduction in seed production for Hedychium. This level of seed destruction is comparable to high levels of seed predation by rodents reported elsewhere, such as can be the case with grass seeds. Clearly with Hedychium, Rattus-induced seed predation appears to be an exception to the generally accepted theory that non-native species that thrive in new areas lack predators. As a result of these data, I cannot reject the third null hypothesis for Clidemia and Psidium, but I can reject it for Hedychium.

The fourth null hypothesis was H_O: establishment of the study species is not affected by microhabitat type. The objective of this investigation was to determine which sites are suitable for germination and initial establishment of the study weeds. Though many invasive species are known to thrive in the aftermath of disturbance, the most serious invaders are those that can become established in thickly vegetated, structurally intact native ecosystems. For example, the presence of feral pigs in native Hawaiian rain forests progressively transforms shaded thickets into uprooted bare ground and non-native grassy areas. Pig removal from these forests prompts the re-establishment of shaded native fernland and shrubland sites. Clidemia produced the greatest number and heights of seedlings in scalped and grassy sites. Hedychium produced the greatest number of seedlings in epiphytic sites and the least in grassy sites. Psidium were found in three site types, with the tallest seedlings being found in fernland sites. The data tentatively suggest that Clidemia is disturbance-adapted and less adapted to protected, shaded sites, whereas Hedychium and Psidium are greater threats to feral pig-free forests. Results from Clidemia sites (but not Hedychium and Psidium) also indicated a large, viable Clidemia seed bank or prolific seed rain. The methods I used had two metrics for determining establishment success: number of seedlings per plot and seedling height within plots. Based on the seedling numbers data, I can reject the fourth null hypothesis for Clidemia and Hedychium, but I cannot reject it for Psidium. Based on the seedling height data, I can reject the fourth null hypothesis for all three study species.

Overall in these investigations, Clidemia was notable for its high and prolonged fecundity and substantial dispersal powers which are perhaps somewhat counterbalanced by its apparent inability to become established in thickly vegetated sites, even despite high levels of seed rain. Clidemia seed are viable for at least three years of storage in soil in Kīpahulu Valley (Medeiros unpublished data).

Adapted to its native range in the Himalayas, Hedychium is a middle to high elevation species that in Hawai'i is not recorded as being found below 610 m elevation. As such it is primarily a threat to higher elevation wet montane areas of islands of oceanic islands. Its vulnerability to seed predation to an opportunistic species interaction with a non-native rodent is somewhat unexpected in that it violates the premise that invasive species are free from predators and parasites. Various factors make Hedychium seemingly less of a threat than Clidemia or Psidium. These factors are: 1) conspicuous appearance suitable when flowering for detection by helicopter surveys 2) relatively low fecundity 3) relatively high seed predation 4) higher elevation habitats preferred by this species are often distant from introduction sites. When flowering, the species is one of great beauty and aromatic fragrance and being easily grown is of great and perennial interest with horticulturalists and flower growers. As such has been frequently imported and deliberately cultivated into tropical and subtropical locations. Regional control of this species can be greatly enhanced with targeted information to horticulturists and seed sources of the threat this species poses and perhaps promotion of cultivars such as the Hedychium cultivar ‘Betty Ho’ which is nearly identical to H. gardnerianum but produces no seed (R. Hirano pers. comm.).

Of the three study species, Psidium appears to pose the greatest threat to the long-term status of rain forests of the Hawaiian Islands. Psidium also represents a clear threat to the biodiversity of islands of the Pacific and Indian Oceans. Poor fruiting, temporally restricted fruiting period, moderate fecundity and dispersal mark Psidium in the study area. The attribute investigated here, which makes this species such a serious threat, is its apparent ability to become established in thickets of native vegetation. The implication for management appears to be that the recovery of native vegetation may not deter establishment of this species. Though the mechanism of this effect is unexplored in Hawai’i, the second attribute, which makes Psidium such a formidable species, is what is apparently powerful allelopathic effects. The understory of dense Psidium stands in Hawai'i typically is species-depauperate and largely non-vegetated.

Once established in an area, control or eradication of these species is so difficult that successful case examples are lacking in the literature. As a result, the most hopeful solution is the development of classic biological control (biocontrol). Clidemia is historically the species which has the received the greatest biocontrol research. Six insects including four moths (Lepidoptera) (Antiblemma acclinalis Hubner, Ategumia matutinalis (Guenee), Carposina bullata Meyrick, Mompha trithalama Meyrick,), a thrip (Liothrips urichi Karny), a beetle (Lius poseidon Napp), and a fungus pathogen (Colletotrichum gloeosporioides have all been reasonably effective in their attacks on Clidemia (Conant 2002).

The most promising biocontrol agent for Hedychium is the bacterial wilt pathogen Ralstonia (Pseudomonus) solanacearum 'ginger strain' (R. Anderson pers. comm.). In August 2003, the first large-scale field experiment was initiated and though results are not final, they are somewhat optimistic (R. Anderson pers. comm.).

The prospects of biocontrol of Psidium are less developed and perhaps less hopeful. The related P. guajava L. is a species whose fruits are valued by local people and form the basis for a small jam industry. As a result, the mission of appropriate control of P. cattleianum was complicated because many herbivorous insects feed on both Psidium spp. In their native range of Brazil (Wikler and Smith 2002).

Over the past 226 years (as of 2004) of European contact, approximately 13,000-15,000 non-native plant species have been introduced to Hawai'i (George Staples pers. comm.). About 100 of these are considered as highly invasive, habitat-modifying species (Smith 1985b; C.W. Smith pers. comm., 1998). On average, this means a new plant species has become established in the Hawaiian Islands every 5.5 to 6.4 days and a new highly invasive, habitat-modifying plant species every 2.3 years. Once established, the cost of control and/or eradication of even reasonably dispersive and/or widespread species can be prohibitively high. At the historical introduction rate and considering the cadre of highly invasive species already established, it is clear that limited financial resources will fall short of complete protection of our natural, agricultural resources and may compromise our life style expectations. Clearly, the cost-effective way to manage invasive species is to prevent indiscriminate species introductions.

This study may serve to indicate that this task of creating a predictive weed model is far from a simple one. The three study species are recognized worldwide as among the most destructive and formidable of invasive species. Yet even among this suite of three species, commonalities between them appear no more frequent than their differences. Even when traits are clearly recognized as those of invasive species, there may be incomplete knowledge regarding the species being evaluated. Near the time of its first introduction into Hawai'i (ca. 1941), Clidemia was grown at Wahiawa Botanical Garden and thought "very promising because it won't be spread by birds" (Binggelli 1997).

The three study species are amongst the most formidable of invasive plant species known. Yet perhaps surprisingly, each seems to have its own individualistic set of traits which predisposes it to become invasive. The greatest commonality among the species in this study was that of an effective seed dispersal system, utilizing small opportunistic passerines. Perhaps some other research avenue that was not explored here will identify a trait or set of traits that could be used to effectively distinguish and predict latent invasiveness in newly arrived species or those being considered for importation.

APPENDIX A. Comparison of area and species diversity of Hawai'i and the United States as a whole.

	Hawai'i total	U.S. total (including Hawai'i)	%
Area	16,642 sq. km.[1]	9,363,130 sq. km.[2]	0.18%
Vascular plants	1200 spp.[3]	18,200 spp.[4]	6.6%
Birds	62 spp.[5]	862 spp.[6]	7.2%
Insects	5287 spp.[7]	96255 spp.[8]	5.5%
Land snails	750 spp.[9]	1469 spp.[9]	51.1%

1. Department of Geography, University of Hawai'i 1983; 2. Reader's Digest Bartholomew 1992; 3. Wagner, Herbst, and Sohmer 1990 and W.H. Wagner pers. comm.; 4. Morin 1995; 5. ; 6. 7. Howarth and Mull 1992; 8. Hodges 1995; 9. Cowie 1996, Cowie, Evenhuis, and Christensen 1995, Solem 1990, and R.H. Cowie, pers. comm.

APPENDIX B. Composition of invertebrate prey identified from droppings of six species of wild-caught rain forest birds, Kīpahulu Valley, Haleakalā National Park and Makawao F.R., East Maui, Hawaiian Islands.

LEIOTHRIX:

Orthoptera	18 prey/12.4%
Arachnida	15 prey/10.3%
Coleoptera; Carabidae	5 prey/3.5%
Coleoptera, other	17 prey/11.7%
Lepidoptera	9 prey/6.2%
Homoptera	13 prey/9.0%
Mollusca – snail	5 prey/3.5%
Diptera	13 prey/9.5%
unidentified	45 prey/31.0%

total:
145 prey/94 captures = 1.5 prey/capture

ZOSTEROPS:

Orthoptera	1 prey/2.0%
Arachnida	9 prey/18.0%
Coleoptera; Carabidae	2 prey/4.0%
Coleoptera, other	2 prey/4.0%
Lepidoptera	6 prey/12.0%
Homoptera	2 prey/4.0%
Diptera	2 prey/4.0%
unidentified	26 prey/52.0%

total:
50 prey/50 captures = 1.0 prey/capture

CETTIA:

Orthoptera	3 prey/4.9%
Arachnida	1 prey/1.6%
Coleoptera; Carabidae	6 prey/9.8%
Coleoptera, other	32 prey/52.5%
Lepidoptera	1 prey/1.6%
Homoptera	3 prey/4.9%
Mollusca - snail	2 prey/3.3%
Diptera	1 prey/1.6%
unidentified	12 prey/19.7%

total:
61 prey /12 captures = 5.1 prey/capture

GARRULAX:

Orthoptera	1 prey/14.3%
Arachnida	1 prey/14.3%
Coleoptera; Carabidae	2 prey/28.6%%
Homoptera	1 prey/14.3%
unidentified	2 prey/28.6%

total:
7 prey/6 captures = 1.2 prey/capture

HEMIGNATHUS:

Arachnida	3 prey/20.0%
Coleoptera, other	1 prey/6.7%
Lepidoptera	1 prey/6.7%
Homoptera	1 prey/6.7%
unidentified	9 prey/60.0%

total:
15 prey /18 captures = 0.8 prey /capture

HIMATIONE:

Arachnida	1 prey/25.0%
Homoptera	1 prey/25.0%
Mollusca - snail	1 prey/25.0%
unidentified	3 prey/50.0%

total:
6 prey/5 captures = 1.2 prey/capture

APPENDIX C. List of flowering plants of Kīpahulu Valley, Haleakalā National Park and their putative seed dispersal methods (based on fruit morphology, i.e., whether fleshy fruited or not).

PLANT SPECIES:	STATUS:	DISPERSAL METHOD:
Acacia koa	Endemic	no obvious mechanism
Adenostemma viscosum	Indigenous	wind
Ageratina adenophora	Non-native	wind
Ageratina riparia	Non-native	wind
Ageratum conyzoides	Non-native	wind
Agrostis avenacea	Non-native	wind
Alyxia oliviformis	Endemic	bird
Andropogon virginicus	Non-native	wind
Anthoxanthum odoratum	Non-native	wind
Anoectochilus sandvicensis	Endemic	wind
Antidesma platyphyllum	Endemic	bird
Ardisia elliptica	Non-native	bird
Arundina graminifolia	Non-native	wind
Astelia menziesiana	Endemic	bird
Axonopus compressus	Non-native	wind
Bidens campylotheca	Endemic	no obvious mechanism
Bobea elatior	Endemic	bird
Boehmeria grandis	Endemic	bird?
Broussaisia arguta	Endemic	bird
Canavalia hawaiiensis	Endemic	no obvious mechanism
Canna indica	Non-native	no obvious mechanism
Carex alligata	Endemic	no obvious mechanism
Carex ovalis	Non-native	no obvious mechanism
Castilleja arvensis	Non-native	wind?
Centella asiatica	Non-native	no obvious mechanism
Charpentiera ovata	Endemic	wind
Cheirodendron trigynum	Endemic	bird
Chloris divarcata	Non-native	no obvious mechanism
Cladium jamaicense	Indigenous	no obvious mechanism
Claoxylon sandwicense	Endemic	mechanical - explosive capsules
Clermontia arborescens	Endemic	bird
Clermontia grandiflora	Endemic	bird
Clermontia kakeana	Endemic	bird
Clermontia samuelii	Endemic	bird
Clermontia tuberculata	Endemic	bird?
Clidemia hirta	Non-native	bird
Coix lachryma-jobi	Non-native	no obvious mechanism

PLANT SPECIES:	STATUS:	DISPERSAL METHOD:
Commelina diffusa	Non-native	no obvious mechanism
Conyza canadensis	Non-native	wind
Coprosma ernodeoides	Endemic	bird
Coprosma foliosa	Endemic	bird
Coprosma granadensis	Indigenous	bird
Coprosma montana	Endemic	bird
Coprosma ochracea	Endemic	bird
Coprosma pubens	Endemic	bird
Cortaderia jubata	Non-native	wind
Crassocephalum crepidioides	Non-native	wind
Cuphea carthagenensis	Non-native	no obvious mechanism
Cyanea aculeatiflora	Endemic	bird
Cyanea aff. glabra	Endemic	bird
Cyanea asplenifolia	Endemic	bird
Cyanea copelandii	Endemic	bird
Cyanea elliptica	Endemic	bird
Cyanea grimesiana	Endemic	bird
Cyanea hamatiflora	Endemic	bird
Cyanea horrida	Endemic	bird
Cyanea kunthiana	Endemic	bird
Cyanea longissima	Endemic	bird
Cyanea macrostegia	Endemic	bird
Cyperus halpan	Non-native	wind
Cyperus sandwicensis	Endemic	no obvious mechanism
Cyrtandra grayi	Endemic	bird
Cyrtandra hashimotoi	Endemic	bird
Cyrtandra hawaiensis	Endemic	bird
Cyrtandra paludosa	Endemic	bird
Cyrtandra platyphylla	Endemic	bird
Cyrtandra spathulata	Endemic	bird
Deschampsia nubigena	Endemic	wind
Digitaria ciliaris	Non-native	wind
Dodonaea viscosa	Indigenous	wind
Drymaria cordata	Non-native	external animal transport
Dubautia plantaginea	Endemic	wind
Dubautia scabra	Endemic	wind
Dubautia waianapanapaensis	Endemic	wind
Ehrharta stipoides	Non-native	external animal transport
Eleocharis obtusa	Indigenous	no obvious mechanism
Embelia pacifica	Endemic	bird
Epidendrum x obrienianum	Non-native	wind
Epilobium billardierianum	Non-native	wind
Eragrostis grandis	Endemic	no obvious mechanism

PLANT SPECIES:	STATUS:	DISPERSAL METHOD:
Erechtites valerianifolia	Non-native	wind
Fimbristylis dichotoma	Indigenous	no obvious mechanism
Fragaria chiloensis	Indigenous	bird
Freycinetia arborea	Endemic	bird
Gardenia remyi	Endemic	bird
Garnotia acutigluma	Indigenous?	no obvious mechanism
Gunnera petaloidea	Endemic	bird
Hedychium coronarium	Non-native	bird
Hedychium flavescens	Non-native	no seeds?
Hedychium gardnerianum	Non-native	bird
Hedyotis acuminata	Endemic	no obvious mechanism
Hedyotis centranthoides	Endemic	no obvious mechanism
Hedyotis hillebrandii	Endemic	bird
Hedyotis terminalis	Endemic	bird
Hillebrandia sandwicensis	Endemic	no obvious mechanism
Holcus lanatus	Non-native	no obvious mechanism
Hypochoeris radicata	Non-native	wind
Hydrocotyle verticillata	Non-native	no obvious mechanism
Ilex anomala	Indigenous	bird
Isachne distichophylla	Endemic	no obvious mechanism
Joinvillea ascendens	Endemic	bird
Juncus bufonius	Non-native	no obvious mechanism
Juncus effusus	Non-native	no obvious mechanism
Juncus planifolius	Non-native	no obvious mechanism
Juncus polyanthemos	Non-native	no obvious mechanism
Korthalsella complanata	Endemic	bird
Korthalsella cylindrica	Endemic	bird
Korthalsella latissima	Endemic	bird
Korthalsella platycaula	Endemic	bird
Kyllinga brevifolia	Non-native	no obvious mechanism
Kyllinga nemoralis	Non-native	no obvious mechanism
Labordia hedyosmifolia	Endemic	bird
Labordia hirtella	Endemic	bird
Labordia tinifolia	Endemic	bird
Labordia venosa	Endemic	bird
Lapsana communis	Non-native	wind
Leptecophylla tameiameiae	Indigenous	bird
Liparis hawaiensis	Endemic	wind
Lobelia grayana	Endemic	wind
Lobelia hillebrandii	Endemic	wind
Lobelia hypoleuca	Endemic	wind
Ludwigia octovalvis	Non-native	no obvious mechanism
Ludwigia palustris	Non-native	no obvious mechanism

PLANT SPECIES:	STATUS:	DISPERSAL METHOD:
Luzula hawaiiensis	Endemic	no obvious mechanism
Lysimachia hillebrandii	Endemic	no obvious mechanism
Lysimachia remyi	Endemic	no obvious mechanism
Machaerina angustifolia	Indigenous	no obvious mechanism
Machaerina mariscoides	Indigenous	no obvious mechanism
Melaleuca quinquenervia	Non-native	no obvious mechanism
Melicope balloui	Endemic	bird
Melicope clusiifolia	Endemic	bird
Melicope haleakalae	Endemic	bird
Melicope molokaiensis	Endemic	bird
Melicope orbicularis	Endemic	bird
Melicope ovalis	Endemic	bird
Melicope peduncularis	Endemic	bird
Melicope volcanica	Endemic	bird
Melinis minutiflora	Non-native	wind
Metrosideros polymorpha	Endemic	wind
Miconia calvescens	Non-native	bird
Mucuna urens	Indigenous?	no obvious mechanism
Myrsine emarginata	Endemic	bird
Myrsine lessertiana	Endemic	bird
Myrsine sandwicensis	Endemic	bird
Nothocestrum longifolium	Endemic	bird
Oplismenus hirtellus	Non-native	no obvious mechanism
Oxalis corymbosa	Non-native	no obvious mechanism
Paspalum conjugatum	Non-native	no obvious mechanism
Paspalum dilatatum	Non-native	no obvious mechanism
Paspalum scrobiculatum	Non-native	no obvious mechanism
Paspalum urvillei	Non-native	no obvious mechanism
Peperomia cookiana	Endemic	no obvious mechanism
Peperomia eekana	Endemic	no obvious mechanism
Peperomia expallescens	Endemic	no obvious mechanism
Peperomia globulanthera	Endemic	no obvious mechanism
Peperomia hirtipetiola	Endemic	no obvious mechanism
Peperomia kipahuluensis	Endemic	no obvious mechanism
Peperomia latifolia	Endemic	no obvious mechanism
Peperomia leptostachya	Indigenous	no obvious mechanism
Peperomia ligustrina	Endemic	no obvious mechanism
Peperomia macraeana	Endemic	no obvious mechanism
Peperomia membranacea	Endemic	no obvious mechanism
Peperomia obovatilimba	Endemic	no obvious mechanism
Peperomia remyi	Endemic	no obvious mechanism
Peperomia tetraphylla	Indigenous	no obvious mechanism
Perrottetia sandwicensis	Endemic	bird

PLANT SPECIES:	STATUS:	DISPERSAL METHOD:
Phaius tankarvilleae	Non-native	wind
Phyllostegia ambigua	Endemic	bird
Phyllostegia bracteata	Endemic	bird
Phyllostegia glabra	Endemic	bird
Phyllostegia macrophylla	Endemic	bird
Phytolacca sandwicensis	Endemic	bird
Pilea peploides	Indigenous	no obvious mechanism
Pipturus albidus	Endemic	bird
Pipturus forbesii	Endemic	bird
Pittosporum confertiflorum	Endemic	bird
Pittosporum glabrum	Endemic	bird
Pittosporum terminalioides	Endemic	bird
Plantago princeps	Endemic	wind
Platydesma spathulata	Endemic	no obvious mechanism
Pluchea carolinensis	Non-native	wind
Polygonum glabrum	Non-native	no obvious mechanism
Polygonum punctatum	Non-native	no obvious mechanism
Pouteria sandwicensis	Endemic	bird
Pritchardia arecina	Endemic	bird?
Prunella vulgaris	Non-native	no obvious mechanism
Psidium cattleianum	Non-native	bird
Psidium guajava	Non-native	bird
Psydrax odorata	Indigenous	bird
Psychotria hawaiiensis	Endemic	bird
Psychotria kaduana	Endemic	bird
Psychotria mariniana	Endemic	bird
Psychotria mauiensis	Endemic	bird
Rhynchospora caduca	Non-native	no obvious mechanism
Rhynchospora rugosa	Indigenous	no obvious mechanism
Rhynchospora sclerioides	Indigenous	no obvious mechanism
Rubus argutus	Non-native	bird
Rubus hawaiensis	Endemic	bird
Rubus macraei	Endemic	bird
Rubus penetrans	Non-native	bird
Rubus rosifolius	Non-native	bird
Rumex giganteus	Endemic	wind
Sacciolepis indica	Non-native	no obvious mechanism
Scaevola chamissoniana	Endemic	bird
Schiedea diffusa	Endemic	no obvious mechanism
Schiedea pubescens	Endemic	no obvious mechanism
Schoenoplectus lacustris	Indigenous	no obvious mechanism
Setaria gracilis	Non-native	no obvious mechanism
Sicyos cucumerinus	Endemic	bird

PLANT SPECIES:	STATUS:	DISPERSAL METHOD:
Smilax melastomifolia	Endemic	bird
Solanum americanum	Indigenous?	bird
Solanum incompletum	Endemic	bird
Sonchus oleraceus	Non-native	wind
Spathodea campanulata	Non-native	wind
Spathoglottis plicata	Non-native	wind
Stachytarpheta jamaicensis	Non-native	no obvious mechanism
Stenogyne kamehamehae	Endemic	bird
Stenogyne rotundifolia	Endemic	bird
Streblus pendulinus	Indigenous	bird
Strongylodon ruber	Endemic	no obvious mechanism
Syzygium jambos	Non-native	dispersal by large vertebrate?
Syzygium sandwicensis	Endemic	bird
Tetraplasandra kavaiensis	Endemic	bird
Tetraplasandra oahuensis	Endemic	bird
Tibouchina herbacea	Non-native	wind?
Torulinium odoratum	Indigenous	no obvious mechanism
Touchardia latifolia	Endemic	bird
Trematolobelia macrostachys	Endemic	wind
Triumfetta semitriloba	Non-native	external animal transport
Uncinia uncinata	Indigenous	external animal transport
Urera glabra	Endemic	bird
Vaccinium calycinum	Endemic	bird
Vaccinium dentatum	Endemic	bird
Verbena litoralis	Non-native	no obvious mechanism
Vernonia cinerea	Non-native	wind
Wikstroemia oahuensis	Endemic	bird
Wikstroemia villosa	Endemic	bird
Xylosma hawaiiense	Endemic	bird
Youngia japonica	Non-native	wind

APPENDIX D. Analysis of rodent droppings collected within fruiting weed patches at study sites in Kīpahulu Valley and Makawao F.R., Maui.

Sample no.	Tentative species identification	Sample collection site	Species of fruiting weed stand where sample was collected	size (l x w) (mm) of dropping	Analysis
1	Mus domesticus ?	Makawao F.R.	Hedychium	5x1.5	100% arthropod remains
2	Rattus exulans?	Makawao F.R.	Hedychium	10x2	75% arthropod and 25% Hedychium aril and seed fragments
3	Rattus exulans?	Makawao F.R.	Hedychium	12x3	70% Hedychium aril and seed fragments and 30% unidentified
4	Rattus exulans?	Makawao F.R.	Hedychium	12x3	100% Hedychium aril, bract, and seed fragments
5	Rattus exulans?	Makawao F.R.	Hedychium	13x5	100% Hedychium aril, bract, and seed fragments
6	Rattus exulans?	Makawao F.R.	Hedychium	10x5	50% Hedychium aril, bract, and seed fragments

					and 50% unidentified
7	Rattus exulans?	Makawao F.R.	Hedychium	10x4	50% Hedychium aril, bract, and seed fragments and 50% unidentified
8	Rattus exulans?	Makawao F.R.	Hedychium	12x4	100% Hedychium aril, bract, and seed fragments
9	Rattus exulans?	Makawao F.R.	Hedychium	10x3.5	100% Hedychium aril, bract, and seed fragments
10	Rattus exulans?	Makawao F.R.	Hedychium	11x4.5	100% Hedychium aril, bract, and seed fragments
11	Rattus exulans?	Makawao F.R.	Hedychium	14x4	100% Hedychium aril, bract, and seed fragments
12	Rattus exulans?	Makawao F.R.	Hedychium	13x3	100% Hedychium aril, bract, and seed fragments
13	Rattus exulans?	Makawao F.R.	Hedychium	12x4	100% Hedychium aril, bract, and seed fragments
14	Rattus exulans?	Makawao F.R.	Hedychium	10x3	100% Hedychium aril, bract, and seed fragments

15	Rattus exulans?	Makawao F.R.	Hedychium	10x5	100% Hedychium aril, bract, and seed fragments
16	Rattus exulans?	Makawao F.R.	Hedychium	11x4	100% Hedychium aril, bract, and seed fragments
17	Rattus exulans?	Makawao F.R.	Hedychium	6x4	100% Hedychium aril, bract, and seed fragments
18	Rattus exulans?	Makawao F.R.	Hedychium	7x4	100% Hedychium aril, bract, and seed fragments
19	Rattus exulans?	Makawao F.R.	Hedychium	14x6	100% Hedychium aril, bract, and seed fragments
20	Rattus exulans?	Makawao F.R.	Hedychium	14x6	100% Hedychium aril, bract, and seed fragments
21	Rattus exulans?	Kīpahulu Valley	Clidemia	13x4	885 Clidemia seeds + Clidemia pulp (65%) + 9 Rubus rosifolius seeds + parts of microlepidotera + planthopper (35%)
22	Rattus rattus?	Kīpahulu Valley	Clidemia	16.5x5.5	1295 Clidemia seeds + Clidemia pulp (65%) + 11 Clermontia seeds

					+ 5 Rubus rosifolius seeds + Laupala (35%)cricket parts
23	Rattus rattus?	Kīpahulu Valley	Clidemia	15.5x5	1091 Clidemia seeds + Clidemia pulp (99%) + 3 Rubus rosifolius seeds
24	Rattus rattus?	Makawao F.R.	Hedychium	16x4	100% Hedychium aril and seed fragments
25	Rattus rattus?	Makawao F.R.	Hedychium	22x4	100% Hedychium aril and bract fragments
26	Rattus rattus?	Makawao F.R.	Hedychium	22x4	100% Hedychium aril and seed fragments
27	Rattus rattus?	Makawao F.R.	Hedychium	18x5	100% Hedychium aril and seed fragments
28	Rattus rattus?	Makawao F.R.	Hedychium	18x6	100% Hedychium aril and seed fragments
29	Rattus rattus?	Makawao F.R.	Hedychium	24x5	100% Hedychium aril and seed fragments
30	Rattus rattus?	Makawao F.R.	Hedychium	16x5	100% Hedychium aril and seed

					fragments
31	Rattus rattus?	Makawao F.R.	Hedychium	15x6	100% Hedychium aril and seed fragments
32	Rattus rattus?	Makawao F.R.	Hedychium	16x6	100% Hedychium aril and seed fragments
33	Rattus rattus?	Makawao F.R.	Hedychium	16x7	100% Hedychium aril and seed fragments
34	Rattus rattus?	Makawao F.R.	Hedychium	16x7	100% Hedychium aril and seed fragments
35	Rattus rattus?	Kīpahulu Valley	Psidium	16.5x5.5	50% Psidium fruit pulp and skin + 50% unidentified
36	Rattus rattus?	Kīpahulu Valley	Psidium	15x6	100% Psidium fruit pulp and skin
37	Rattus rattus?	Kīpahulu Valley	Psidium	15x5.5	20% Psidium fruit pulp and skin + 70% arthropod
38	Rattus rattus?	Kīpahulu Valley	Psidium	15.5x5.5	60% Psidium fruit pulp and skin + 40% unidentified
39	Rattus rattus?	Kīpahulu Valley	Psidium	16.5x7	90% Psidium fruit pulp and skin + 10% orthroptera

40	Rattus rattus?	Kīpahulu Valley	Psidium	15x6	100% Psidium fruit pulp and skin
41	Rattus rattus?	Kīpahulu Valley	Psidium	16.5x5.5	100% Psidium fruit pulp and skin
42	Rattus rattus?	Kīpahulu Valley	Psidium	15x5	80% Psidium fruit pulp and skin + 20% arthropod
43	Rattus rattus?	Kīpahulu Valley	Psidium	16x5	100% Psidium fruit pulp and skin
44	Rattus rattus?	Kīpahulu Valley	Psidium	16.5x5.5	70% Psidium fruit pulp and skin + 30% arthropod
45	Herpestes auropunctatus	Kīpahulu Valley	Psidium	74x11	50% unidentified; 30% invertebrate; 20% Psidium seeds and pulp

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Table 20. Dispersal methods of flowering plants of Kīpahulu rain forest and environs (n = 239 species total) (based on full species listing in Appendix II).

	wind-dispersed	bird dispersed	no obvious mechanism	external animal transport	misc.	totals
Endemic plant species only	14 spp. (5.9%)	96 spp. (40.2%)	29 spp. (12.1%)	none	1 sp. (0.4%)	140 spp. (58.6%)
Indigenous plant species only	2 spp. (0.8%)	7 spp. (2.9%)	14 spp. (5.9%)	1 sp. (0.4%)	none	24 spp. (10.0%)
All non-native plant species	28 spp. (11.7%)	10 spp. (4.2%)	32 sp. (13.4%)	3 spp. (1.3%)	2 spp. (0.8%)	75 spp. (31.4%)
totals	44 spp. (18.4%)	113 spp. (47.3%)	75 spp. (31.4%)	5 spp. (1.7%)	3 spp. (1.3%)	239 spp. (100%)

Table 21. Effect of Rattus predation on flower and immature fruit production of Hedychium at Makawao Forest Reserve and Kīpahulu Valley, Maui.

study site location	date	total no. of stems investigated	total no. of potential cymes	total no. of flower cymes destroyed by Rattus	total no. of immature fruit cymes destroyed by Rattus	percentage of reproductive potential reduced by Rattus
Kīpahulu	9/24/97	39	2,668	1,496	NA	56.1
Kīpahulu	9/26-11/25/97	48	2,767	1,493	38	55.3%
Makawao F.R.	8/26-11/5/97	100	6,122	710	2,186	47.3%
Kīpahulu	10/29/97	50	3,060	NA	1,132	37.0%
Total		237	14,617	3,699	3,356	48.3%

Table 22. Contingency tables for presence of seedlings after one year for the three study species in four establishment sites. An X indicates the presence of observed seedlings and dashes (---) indicate the absence of seedlings.

	Grassy sites	Scalped sites	Fernland sites	Epiphytic sites
<u>Clidemia</u> seeds added	X	X	X	X
<u>Clidemia</u> seeds not added	X	X	X	---
<u>Hedychium</u> seeds added	X	X	X	X
<u>Hedychium</u> seeds not added	---	---	---	---
<u>Psidium</u> seeds added	---	X	X	X
<u>Psidium</u> seeds not added	---	---	---	---

Table 23. Calculations of extents of three study weed species in comparison with land categories on East Maui. The total area of native rain forest on East Maui (Haleakalā) is approximately 25,688 ha.

	Total area of East Maui infestation (Ha)	Average annual spread rate on East Maui	Total area of East Maui infestation within native rain forest	Percentage of native rain forest on East Maui within infestation	Area of native rain forest on East Maui within known elevational range of weed	Percentage of native rain forest on Maui within known elevational range of weed
Clidemia	21,848	796 Ha/year over 27 years	6,037	24	21,165	82
Hedychium	4,221	79.6 Ha/year over 53 years	3,176	12	20,675	80
Psidium	35,687	400 Ha/year over 89 years	8,890	35	22,289	87

Table 24. Calculations of extents of three study weed species in comparison with land categories for Haleakalā National Park. The total area of native rain forest within HNP is approximately 2923 ha.

	Year of first record on East Maui	Total area of East Maui infestation (Ha)	Estimated spread rate on East Maui (current infestation area/years present on East Maui)	Year first recorded in Haleakalā National Park	Total infestation area in Haleakalā National Park	Estimated spread rate in Haleakalā National Park (current infestation area/years present on East Maui)
<u>Clidemia</u>	1976	21,848 Ha	796 Ha/year over 27 years	1988	1405 Ha	93.6 Ha/year over 15 years
<u>Hedychium</u>	1950s	4,221 Ha	79.6 Ha/year over 53 years	1988	797 Ha	53.1 Ha/year over 15 years
<u>Psidium</u>	?1920	35,687 Ha	400 Ha/year over 89 years	1940s?	1603 Ha	25.4 Ha/year over 63 years

Figure 1. Native and naturalized range of Clidemia hirta (green dots are native range; red dots are invasive range).

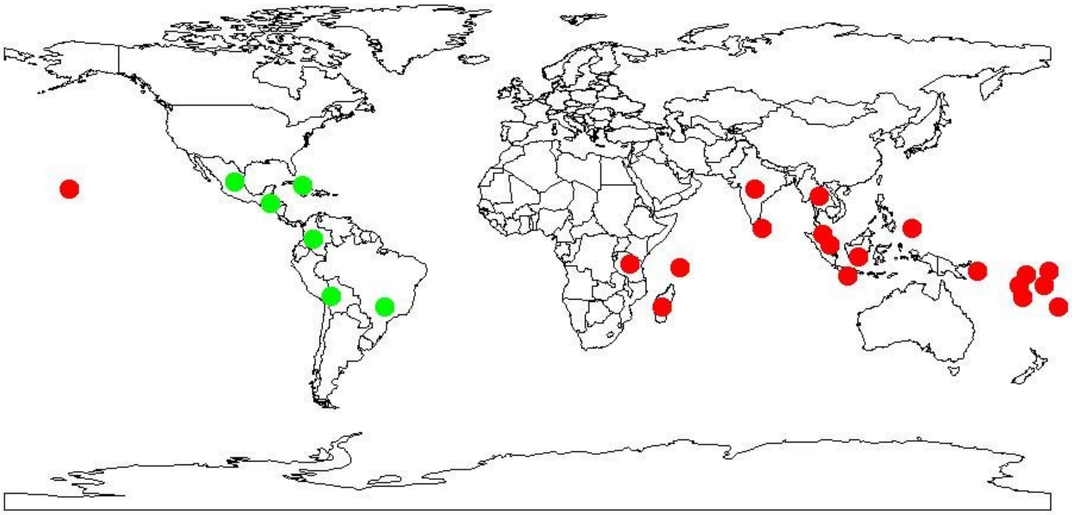

Figure 2. Native and naturalized range of <u>Psidium</u> <u>cattleianum</u> (green dot is native range; red dots are invasive range).

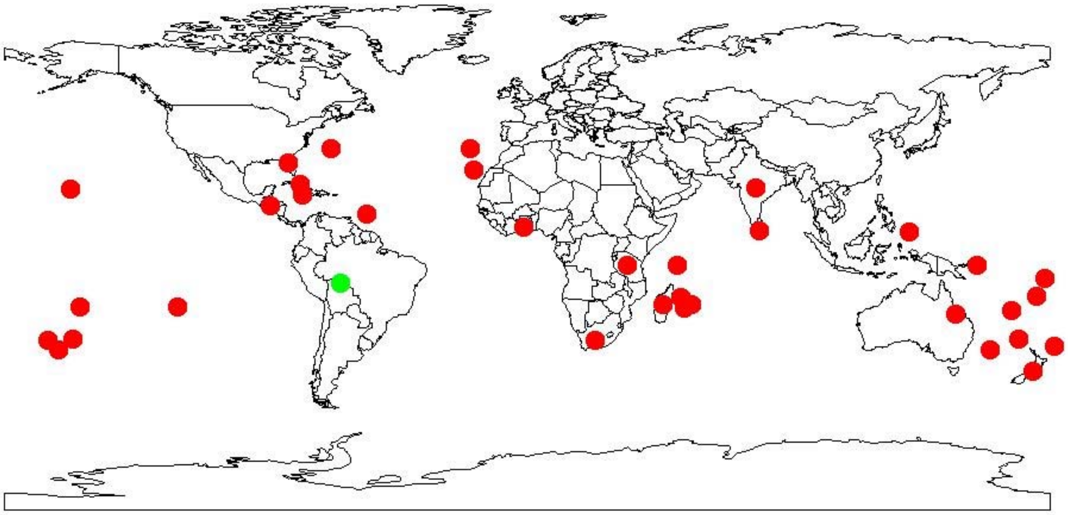

Figure 3. Native and naturalized range of Hedychium gardnerianum (green dot is native range; red dots are invasive range).

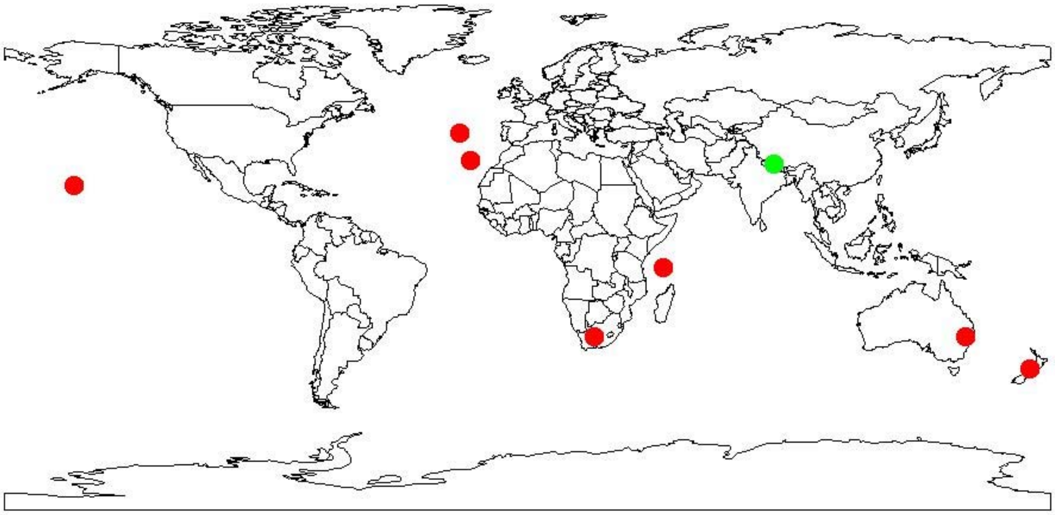

Figure 4. Map of Maui, Hawaiian Islands, showing distribution of rain forest dominated by native species in black shading and Kīpahulu Valley study sites as white dots. The northernmost white dot marks the location of the Clidemia study site. The two southernmost study sites (Hedychium and Psidium) are sufficiently close that the white dots partially overlap.

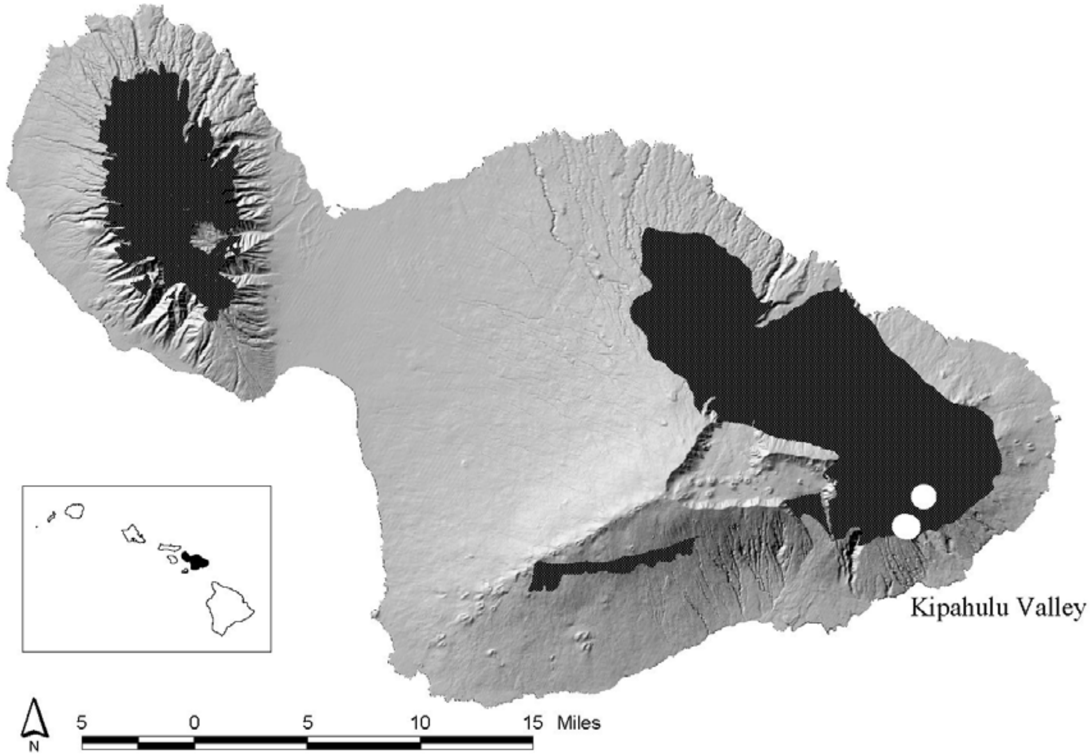

Figure 5. Mean monthly number with error bars of reproductive units (flower buds, flowers, immature fruit, and ripe fruit) for 25 shrubs of Clidemia hirta at 820 m elevation, May 1996 through March 1997.

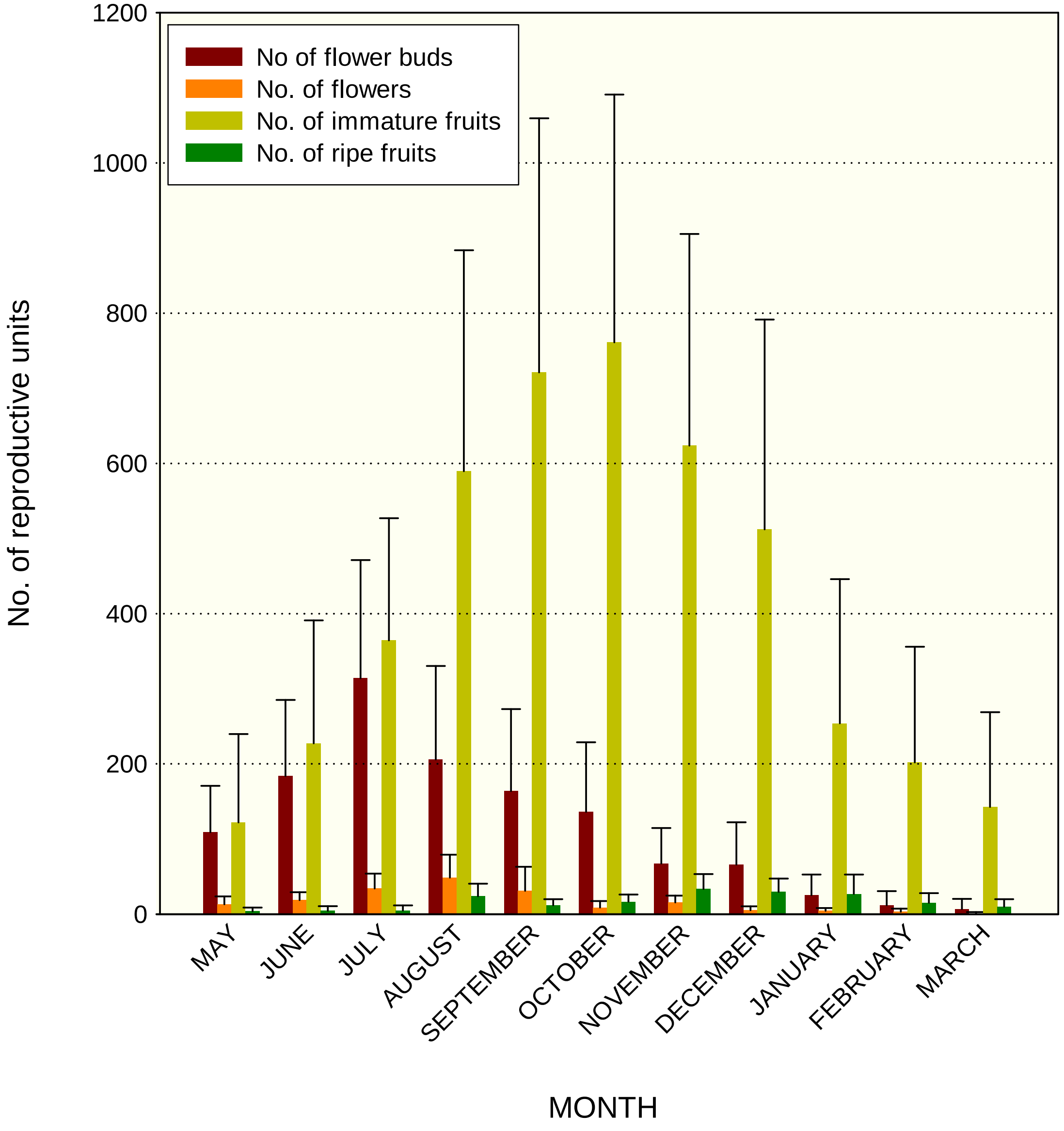

Figure 6. Mean monthly number with error bars of reproductive units (culms with flower buds, culms with flowers, culms with immature fruit, and culms with ripe fruit) for ten 2m x 2m quadrats of <u>Hedychium</u> <u>gardnerianum</u> at 825 m elevation, July 1996 through June 1997.

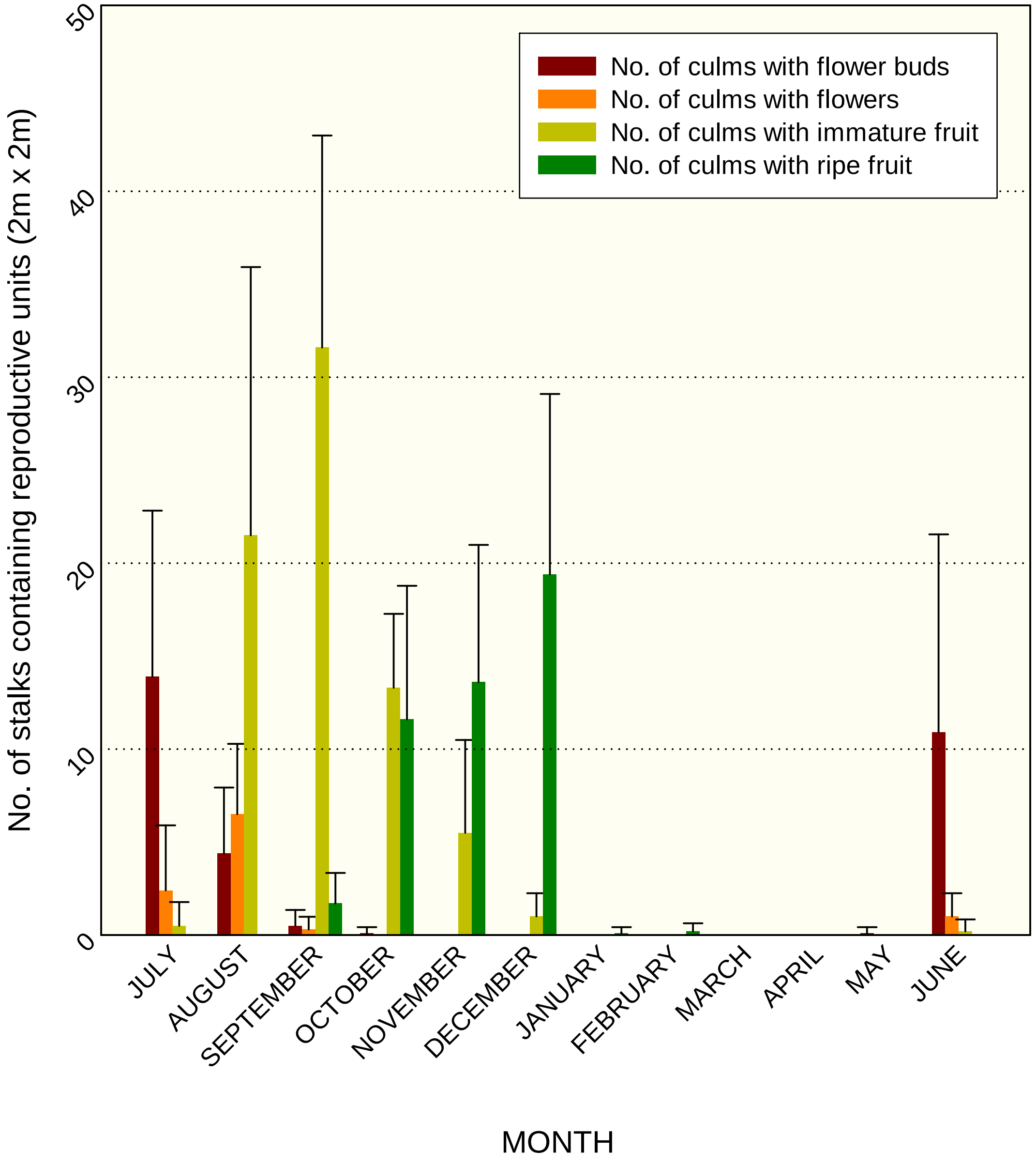

Figure 7. Mean monthly number with error bars of reproductive units (flower buds, flowers, immature fruit, and ripe fruit) for 25 large marked branches of 25 individual trees of Psidium cattleianum at 880 m elevation, July 1996 through May 1997.

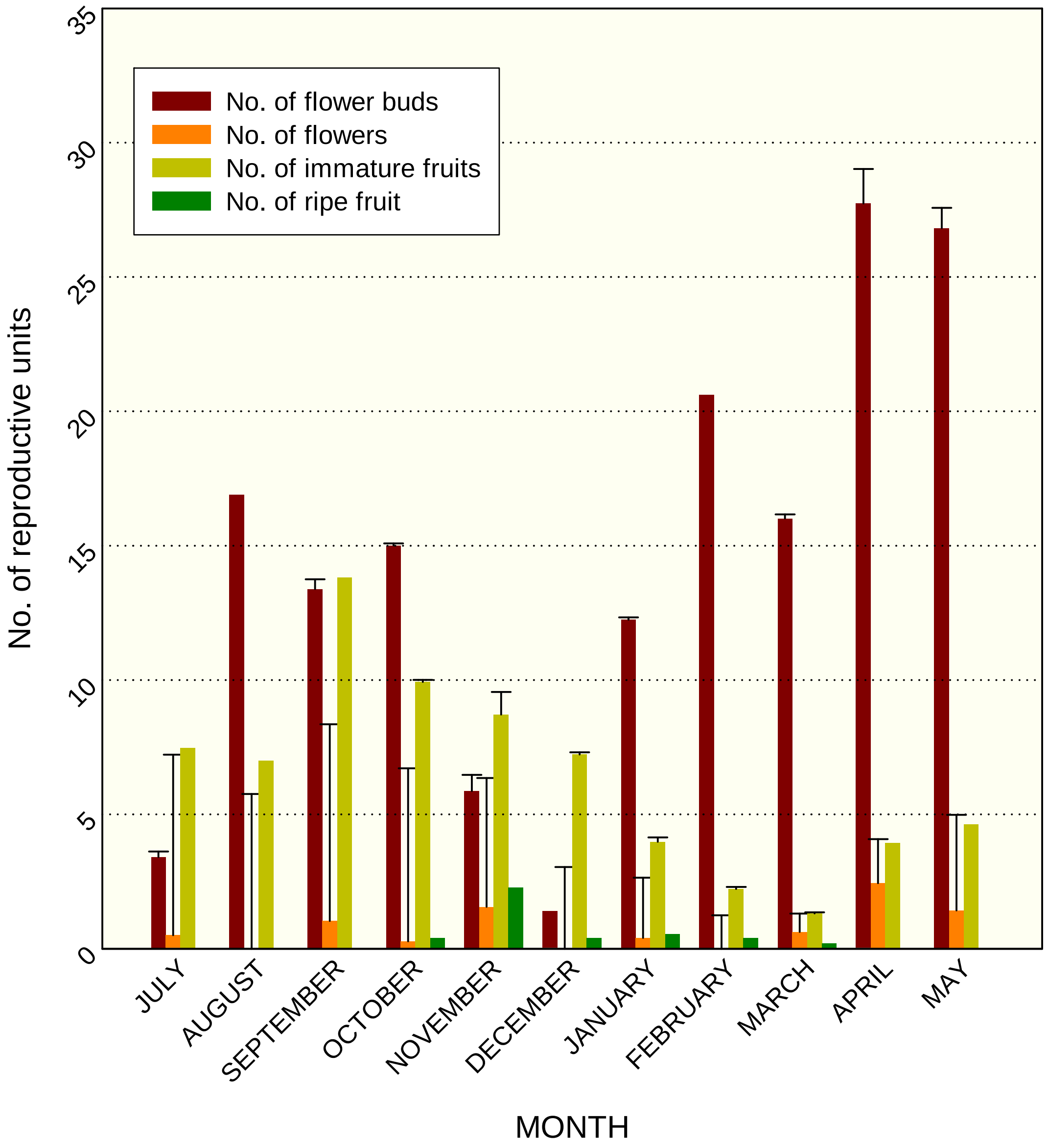

Figure 8. Map of Maui, Hawaiian Islands, showing distribution of rain forest dominated by native species in black and Makawao Forest Reserve and Kīpahulu Valley study sites as white dots.

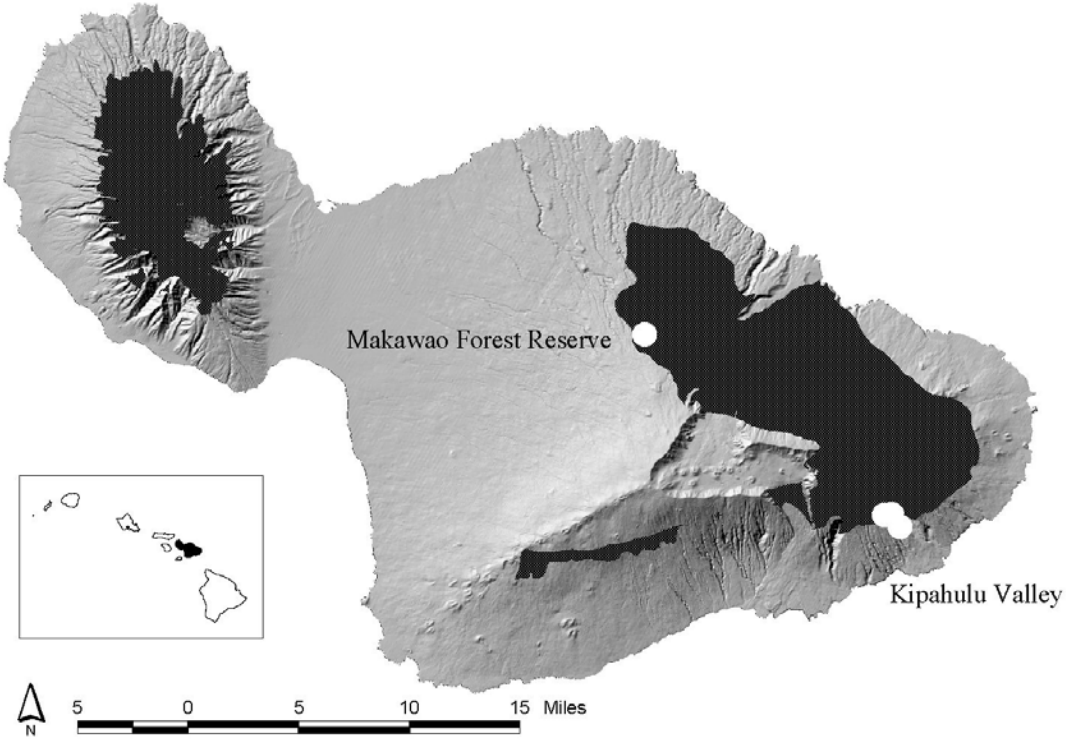

Figure 9. Map of Maui, Hawaiian Islands, showing distribution of rain forest dominated by native species in black and Makawao Forest Reserve and Kīpahulu Valley study sites as white dots.

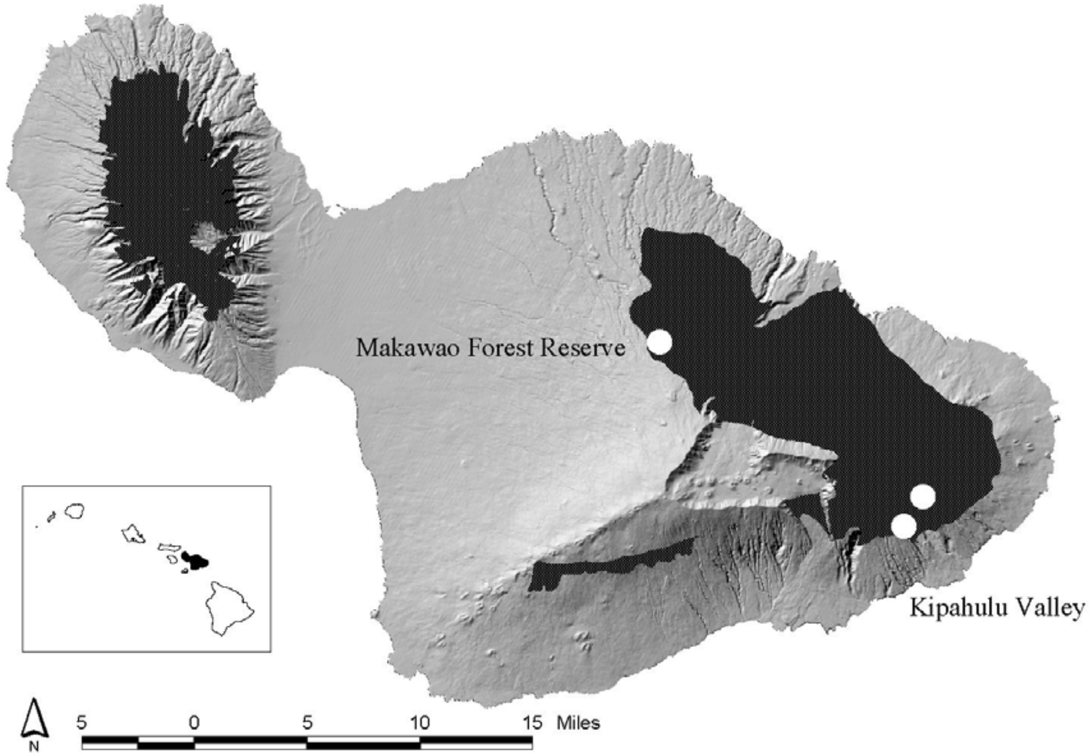

Figure 10. Rate of germination of Clidemia seeds extracted from fresh fruit (control) (n = 300) versus seeds extracted from Rattus droppings(n = 300), Kīpahulu Valley, Haleakalā National Park, Maui.

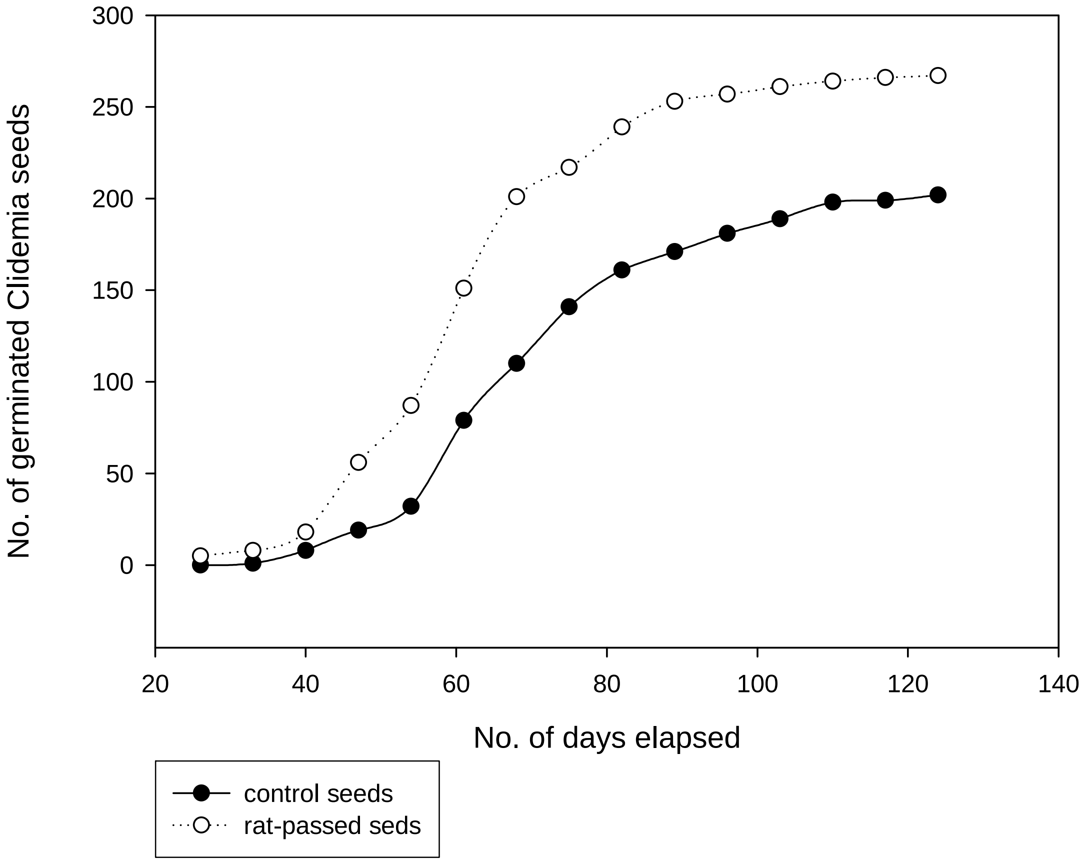

Figure 11. Number of non-native plant species recorded in upland regions of Kīpahulu Valley, Maui, Hawai'i (1900-1998) based on Fagerlund 1945; Lamoureux 1968; Yoshinaga 1980; and Medeiros et al. 1998.

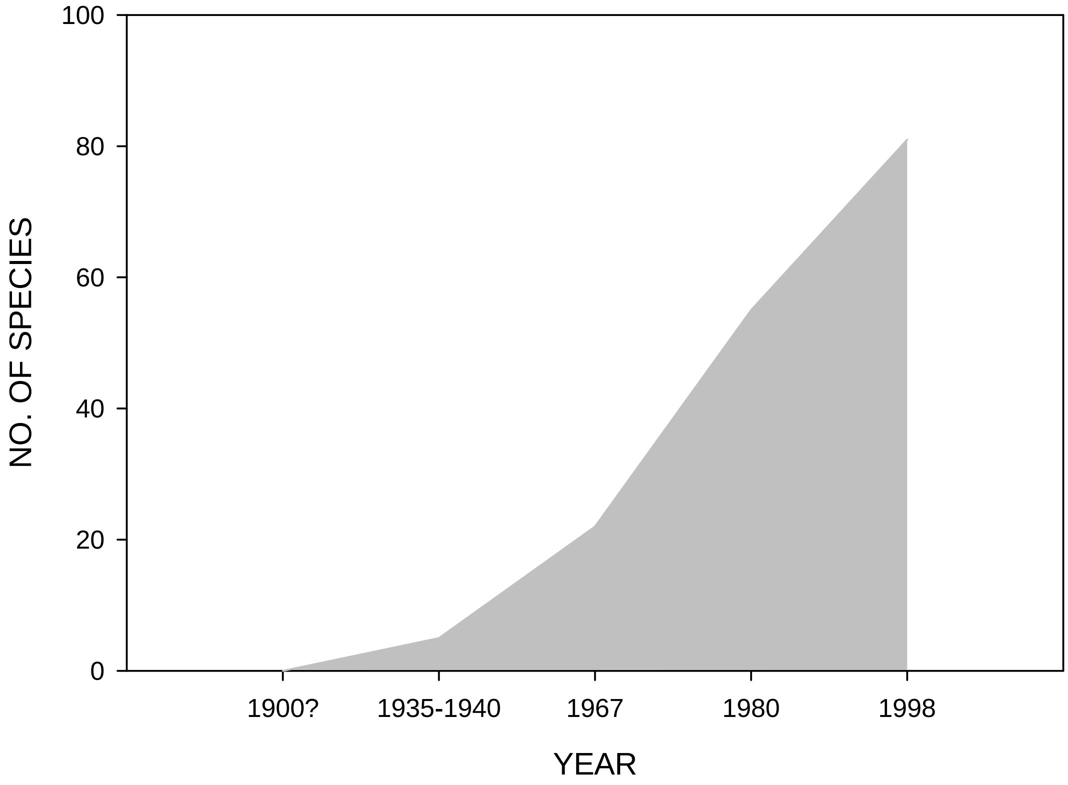

Figure 12. Map of Maui, Hawaiian Islands, showing distribution of native rain forest dominated by native species (black shading) and three study sites in Kīpahulu Valley (white dots).

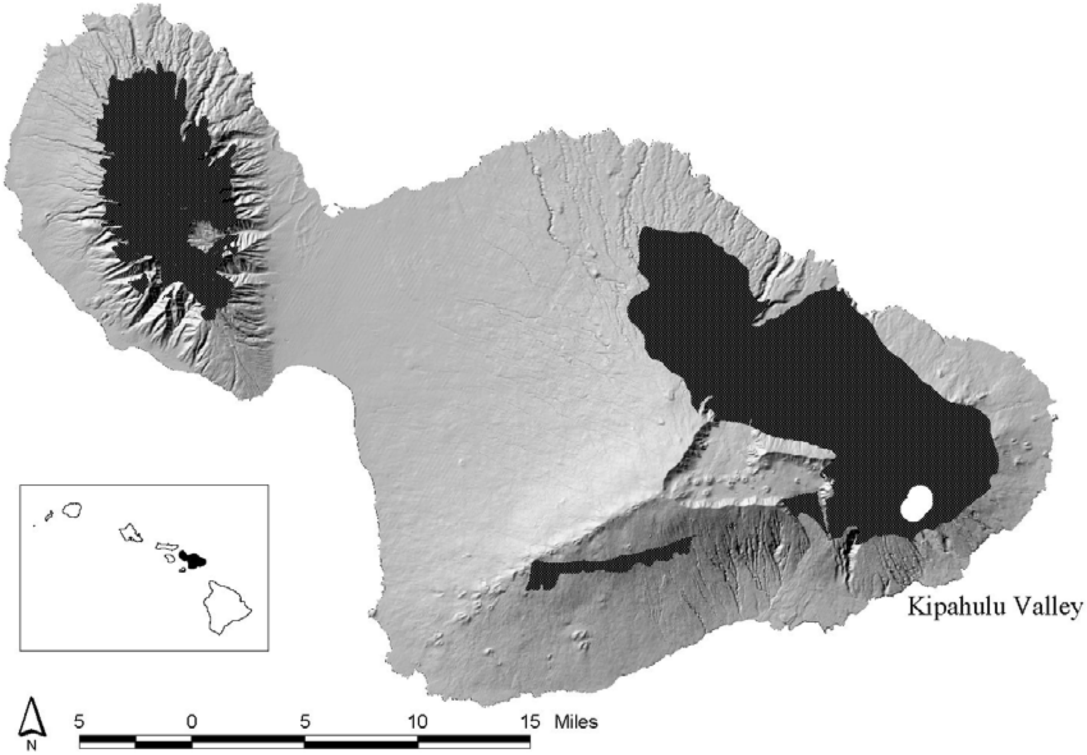

Figure 13 . Current distribution of Clidemia hirta on Haleakalā, Maui.

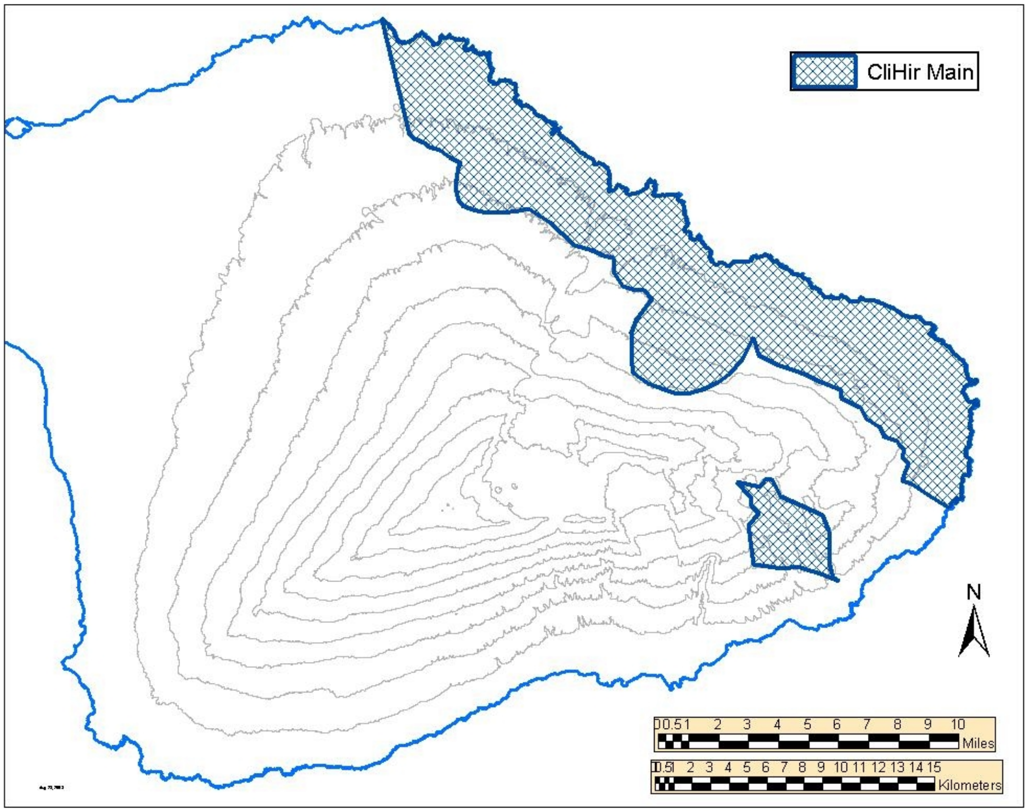

Figure 14. Current distribution of <u>Hedychium</u> <u>gardnerianum</u> on Haleakalā, Maui.

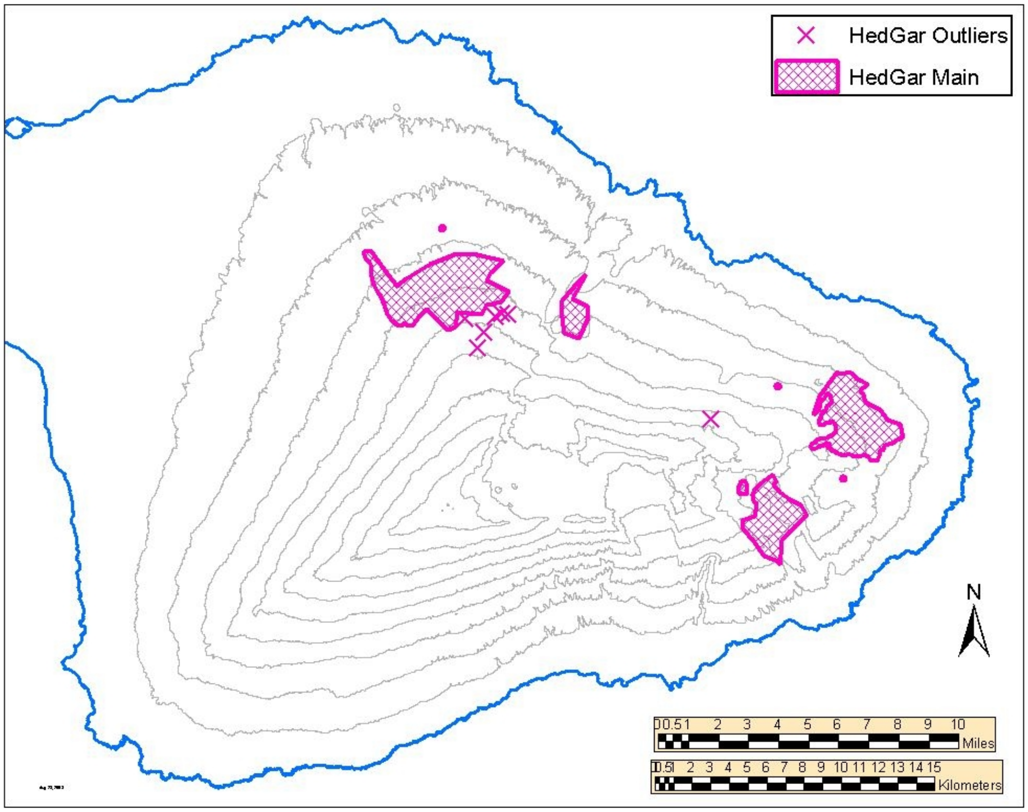

Figure 15. Current distribution of <u>Psidium</u> <u>cattleianum</u> on Haleakalā, Maui.