2000

Avian seed dispersal of Cinnamomum burmannii in Nuuanu Valley O'ahu Hawaii and its implications for alien species invasion

Sarah E. Laughlin
The University of Montana

Recommended Citation

Laughlin, Sarah E., "Avian seed dispersal of Cinnamomum burmannii in Nuuanu Valley O'ahu Hawaii and its implications for alien species invasion" (2000). *Graduate Student Theses, Dissertations, & Professional Papers*. 6841.
https://scholarworks.umt.edu/etd/6841

Yes, I grant permission X
No, I do not grant permission ____

Author's Signature Sarah E. Laughlin

Date March 6, 2000

AVIAN SEED DISPERSAL OF *CINNAMOMUM BURMANII* IN NUUANU VALLEY, O'AHU, HAWAII AND ITS IMPLICATIONS FOR ALIEN SPECIES INVASION.

By

Sarah E. Laughlin

B. S. The University of Illinois, 1994

Presented in partial fulfillment of the requirements

for the degree of

Master of Science

The University of Montana

2000

Approved by:

Chairperson

Dean, Graduate School

3-6-2000

Date

Laughlin, Sarah E., M. S., May 2000 Forestry

Avian seed dispersal of *Cinnamomum burmannii* in Nuuanu Valley, O'ahu, Hawaii and its implications for alien species invasion. (54 pp.)

Director: Stephen F. Siebert SFS

The avian seed dispersal of *Cinnamomum burmannii*, an exotic species native to Southeast Asia, was monitored during the initial fruiting period in Nuuanu and Manoa Valleys, O'ahu, Hawaii. This study was conducted to determine which species might be responsible for the establishment of satellite populations, furthering *C. burmannii* invasion. Avian observations were made in one urban and two forest sites. Evaluation of disperser quality was based upon the time spent in the canopy, the number of fruits consumed, the number of fruits dropped, the feeding behaviors, and the exiting flight relative distance of each species. Germination trials determined whether seeds were still viable after gut passage.

The Red-vented Bulbul, Red-whiskered Bulbul, Japanese White-eye, and the Spotted Dove were the most common consumers of *C. burmannii* fruits, in both the forest and urban sites, and seed dispersal by both bulbul species appears likely. Compared to other species, the bulbuls made relatively short visits to *C. burmannii* canopies, consumed whole fruits, were more likely to fly a greater distance after leaving the canopy, and passed viable seeds. The Red-billed Leiothrix and Common Myna may also play a role as dispersers because they too consumed fruits, although not as frequently, and passed viable seeds.

I also observed increasingly complex alien and native species interactions, specifically growing numbers of exotic species from a variety of environments coexisting within a single invaded ecosystem that still contains vestiges of its original flora and fauna. Because little background information is available for many of the invading species, and because the consequences of native-exotic and exotic-exotic interactions are unknown, resource managers face increasingly complex and uncertain management decisions.

Table of Contents

List of Tables

Introduction

Invasive species literature has exploded in the last decade as more and more scientists and land managers are realizing the devastation caused by these invasions. Pyšek (1995) estimates roughly 100 papers a year are being published in the field of invasion biology. Concerns range from predicting introduction success to long term biological control of aliens. Alien plant and animal invasions are responsible for native and endemic species decline (Warshauer 1998), habitat destruction (Moulton & Pimm 1986), and ecosystem alterations (Smith 1989).

For example, *Miconia calvescens,* introduced to Tahiti in 1937 as an ornamental, has spread to all mesic and wetland habitats between 10 and 1300m in less than 50 years (Meyer & Florence 1996). Today, *M. calvescens* covers over two-thirds of the island (Meyer & Florence 1996).

The Brown tree snake, *Bioga irregularis*, was introduced on Guam in 1947. By 1985, the Guam Broadbill, *Myiagra freycineth,* and the Rufous-fronted Fantail, *Rhipidura rufifrons uraniae*, had been reduced to a few individuals while the Guam Bridled White-eye, *Zosterops conspicillatus conspicillatus*, was already extinct due to predation by the brown tree snake (Macdonald et al. 1989).

On Pinzon Island, in the Galapagos, the introduced black rat (*Rattus rattus*) killed virtually every tortoise hatchling that emerged from its nest. One study calculated that in a period of 10 years, 7000 – 19000 tortoise (*Geochelone elephantopus ephippium*) hatchlings were produced, but only a single one-year old tortoise was found on the entire island (MacFarland et al. 1974).

One of the most often cited examples, and most severely effected alien-invaded ecosystems, are the Hawaiian Islands. They have been bombarded by roughly 4600 species of exotic plants, 600 of which are now naturalized and at least 86 are thought to be a serious threat to native species (Smith 1985). More species of alien birds have become established here than any other island group on earth (Long 1981). The islands have also suffered invasions by mammals, insects, and amphibians. With this type of invasion becoming more and more common place throughout the world due to increased travel and development (Baskin 1998), understanding invasions, how they function, and how they can be controlled is critical.

Whether plant and ecosystem characteristics can be used to predict successful invasion is unknown (Baskin 1998). However, certain characteristics seem to promote invasion success. In general, plants that can reproduce early and often will be more likely to succeed in a foreign environment. Rejmánek's (1995) study on pine species showed that those species with a small mean seed mass, short juvenile period, and short interval between large seed crops were more likely to become successful invaders. Small seeds seemed to be associated with a higher number of seeds produced, better dispersal, and high initial germination success (Rejmánek 1995). Reichard and Hamilton (1997) expand that list of plant characteristics to include short-lived seeds that can germinate without pretreatment, have long flowering periods, vegetative reproduction, and self pollination (Harlow et al. 1991).

Successful invaders tend to be native to extensive non-insular habitats within continents (Brown 1989) and have a large natural range (Pimm 1989). Invasion success can also be enhanced by the similarity in physical environments between the original and invaded areas (Brown 1989). Invading exotics fair better if they are entering an environment where there are fewer native species (Pimm 1989) and where native species do not occupy similar niches (Brown 1989). In addition, each successful invasion makes a community more difficult to invade by subsequent exotics (Pimm 1989). Therefore, the earlier the invasion, the fewer competitors there are likely to be and the more successful the invasion.

Isolated environments generally have a lower diversity of native species and tend to be more susceptible to invasions (Brown 1989; Loope 1992). The species in these environments evolved in isolation and therefore lack the many powerful selective forces found on most continental systems. These species also evolved with reduced aggressiveness (Loope 1992), few predators, and a lower resistance to disease. While oceanic islands fall into this category, so do distinct isolated environments such as the temperate tip of South America, parts of the Florida peninsula, and insular habitats like lakes and desert springs (Brown 1989), and isolated montane environments.

The only certainty surrounding invasions is that they will continue to occur. Two global trends consistently and strongly encourage invasions: land-use change, and the increased movement of species between habitats (Baskin 1998). Humans are the primary vectors in species movement, whether it is intentional introduction for agricultural and ornamental purposes, or accidental introductions by tourists or businesses. Global trade connects the most remote regions of the world to markets by truck, train, ship, and airplane, all of which act as a means of transportation for alien species (Baskin 1998). As more people travel, work, and research in remote locations, the spread of alien propagules will continue.

Land use changes can have cascading ecological effects on both the area directly disturbed and the surrounding area. Land use changes usually involves disturbance, such as clearing, draining, or burning. If the land is allocated for agricultural purposes, alien species are often deliberately introduced (e.g., crops, timber species, grasses for grazing) along with any unseen parasite or pest traveling with them (Baskin 1998). If development is to follow, land clearing, increased runoff, pollution, and heavy traffic can further disturb the surrounding areas. The end result is increased fragmentation and insularization of natural areas (Wilcove et al. 1986).

For example, Purple loosestrife (*Lythrum salicaria*) has invaded both the Indiana Dunes and Sleeping Bear Dunes National Lakeshores (Edwards et al. 1995), European wild boar (*Sus scrofa*) are in the Great Smoky Mountains National Park (Power Bratton 1975) and countless alien species have invaded both Hawaii Volcanoes and Haleakala National Parks in Hawaii. These natural areas not only have the onus of protecting the world's remaining wild genetic resources (Macdonald et al. 1989), but also as isolated ecosystems, are more vulnerable to alien invasions themselves.

What is becoming more and more obvious is the lack of knowledge and means to fight invading species. Land managers are forced to deal with plants, animals, pathogens, insects, and diseases from all corners of the world and about which they know very little. For example, the European wild boar (*Sus scrofa*) found in the Great Smoky Mountains National Park has significantly disturbed the natural landscape. They destroy wildflower areas, damage grassy balds, tree roots and seedlings, and prey on native animals (Power Bratton 1975). While the boar has been present in the park since the 1940's, the lack of knowledge on hog population changes, food preferences, habitat preferences, and behavior has inhibited control efforts (Power Bratton 1975). Many invading species come from tropical and subtropical regions where extensive research is slim. Therefore, even in their native countries little is known about the basic ecology of these species (Heywood 1989).

The following *Cinnamomum burmannii* case study examines a little known invasive tree, and its potential avian dispersers. Birds disperse trees by ingesting their seeds and then later depositing them in a hospitable habitat, preferably far away from the parent tree. These newly deposited individuals may then start new satellite populations. It is important to evaluate the dispersal quality of such avian species to determine whether they play a major, minor, or no role in the spread of an invasive species. If managers know which bird species are helping to spread these trees, they can better predict where new satellite populations may appear and be better prepared to control the new tree populations early in their establishment. They can do this by tracking the movements of the disperser species, or perhaps prevent the establishment of satellite populations by controlling the movement and/or population sizes of these dispersers.

Cinnamomum burmannii on O'ahu, Hawaii

Cinnamomum burmannii is an invasive alien species on the Hawaiian islands of O'ahu, Maui, Kaua'i, and Lana'i (Meidell et al. 1997; J. Lau, The Nature Conservancy, Honolulu, HI, Pers. Comm.; Pers. Obs.). This species is native to Southeast Asia, where it is harvested for ground cinnamon, a valuable cash crop (Aumeeruddy & Sansonnens 1994). However, on O'ahu and Maui, it has become extensively naturalized, forming monotypic stands, and is considered a serious pest (Meidell et al. 1997; C. Smith, University of Hawaii, Honolulu, HI, Pers. Comm.).

Records show that two species, *Cinnamomum camphora* and *Cinnamomum zeylanicum* were introduced onto O'ahu in the 1930's for reforestation purposes (Skolmen 1980). It is possible, however, that *C. burmannii* was accidentally included in the plantings or that one of the species was misidentified (C. Corne, Department of Lands and Natural Resources, Honolulu, HI, Pers. Comm.). By 1975, *C. burmannii* had naturalized on O'ahu (Wagner et al. 1990).

Birds are presumably attracted to *Cinnamomum burmannii* because of its fleshy, shiny fruits (J. Meidell, Maui Pineapple Company, Ltd., Lahaina, HI, Pers. Comm.). Opportunistic generalist frugivores, a number of which have been introduced to Hawaii, may contribute significantly to the invasiveness of fruit bearing species (Panetta & McKee 1997) by widely disseminating their fruits and influencing where the digested seeds are dropped. Both the behavior and abundance of such dispersers may affect invasive tree colonization patterns (D'Antonio 1990).

The goal of my study was to increase the general ecology knowledge of *Cinnamomum burmannii* by evaluating the avian disperser quality of species that feed on its fruit. The quality of a disperser is measured by how often the bird feeds on the fruit, how long the bird remains in the tree canopy (Pratt & Stiles 1983), how the fruit is ingested, how far the bird removes the seed from the parent plant (Chavez-Ramirez & Slack 1994), and if the seed is still viable after passing through the gut (Janzen 1969). I hoped to identify specific bird species that may be responsible for dispersing *C. burmannii* fruits to new potential invasion sites. By identifying such species, land managers may be able to predict future sites of new *C. burmannii* satellite populations and therefore better prepared to control its invasion.

I also estimate average fruit crop production for adult *Cinnamomum burmannii* and analyze fruit nutritional content. Both the number and quality of fruits of an invasive species are important factors because they might indicate how abundant and valuable of a food source it is to local avian species.

Methods

Site description

This study was conducted in the Nuuanu and Manoa valleys of O'ahu, Hawaii, (N 21° 21', W 157° 49'). The Nuuanu valley is densely populated with people to the southwest, as it flows into downtown Honolulu, but sparsely populated to the northeast, as elevation increases. The forested area of this study was within the Honolulu Forest Watershed Reserve.

The forest in both study sites was dominated by exotic tree species, including *Cinnamomum burmannii*, *Schefflera actinophylla* (octopus tree), *Ficus microcarpa* (banyan), and *Araucaria columnaris* (Cooke pine). Understory species were also dominated by exotics, particularly *Ardisia eliptica* (Shoe button), *Citharexylum caudatum* (Fiddlewood), *Cordyline fruticosa* (Ti), young *Cinnamomum burmannii*, and a variety of native and exotic ferns. Native tree species found in the study site were ohia lehua (*Metrosideros polymorpha*) and koa (*Acacia koa*).

Two native forest bird species inhabit the study area, the Common Amakihi (*Hemignathus virens*) and the O'ahu Creeper (*Paroreomyza maculata*). While the Amakihi's population numbers appear to be increasing (Peter Luscomb, Honolulu Zoo General Curator, Pers. Comm.), the O'ahu Creeper is extremely rare.

Observations

Three observation sites were used for this study. The sites were chosen based on their visibility of multiple fruiting *C. burmannii* tree crowns from a forest gap, and their accessibility to existing trails, and therefore, were not randomly selected.

Site one was located in a mesic area in the Nuuanu valley at roughly 315m elevation. Rain showers and tradewinds of 50 – 110 m s^{-1} were common in this site. Ten *C. burmannii* crowns were visible due to a small tree fall gap just off the Nuuanu trail. Two Ohia crowns were mixed within the *C. burmannii* crowns. The Nuuanu Trail leads to this site. It is used regularly, but not intensively (i.e., usually not more than one hiker on the trail per day).

Site two, also in the Nuuanu valley, was located in a transition zone between mesic and wet forest at roughly 440m elevation. Rain showers and tradewinds of 50 – 110 m s^{-1} were also common. Seven *C. burmannii* crowns were visible due to a forest gap, and the observation point's relative high vantage point. *Acacia koa*, *Ficus microcarpa*, and *Schefflera actinophylla* were also in the area. The first and second sites were used for the majority of observation hours.

The third site was located on the University of Hawaii-Manoa campus located in the lower Manoa valley, at an elevation of 65m where rain showers were common. It consisted of one open grown *C. burmannii* crown. This tree's fruiting period was more than one month ahead of the forest trees. Only two days of observations were taken at this site due to the lack of ripe fruit.

To ascertain bird species utilization of *Cinnamomum burmannii* fruits, I recorded the following information during each feeding observation: time in canopy (in seconds), number of fruit eaten, number of fruit dropped, feeding behavior, and relative distance of exiting flight. Feeding behaviors were coded as follows: 1= swallowed fruit whole, 2= mashed pulp in bill before swallowing whole fruit, 3= ate pulp only. Relative distance of exiting flight was coded as "N" = flew to near-by perch, "O" = flew out of sight. Time spent in the canopy is an indicator of dispersal agent efficiency as those species that spend less time in a canopy are more likely to deposit the ingested seed away from the parent tree (Howe & Estabrook 1977). I made roughly 70 hours of observations over 17 days, thought to be the initial part of the fruiting season.

Observations took place at site three on June 27 and July 8. The initial observation day was to train field observers in observation techniques, and to see if urban birds were also feeding on *C. burmannii* fruit. After noting a fair amount of feeding activity, site three was observed on July 8 as well. Only two days of observations were completed because the birds had removed all ripe fruit before additional observations could be made. This tree was observed for one hour in the early morning, and 1.5 hours in the mid-afternoon.

Observations at sites one and two took place during the initial fruiting period between September 1 – 15th, spanning the fruiting period from 75% of the fruit ripe to 95% of the fruit ripe, based on size and color. Most of the observation hours occurred when 90% of the fruit was ripe on each individual tree crown. Observations were done between 7:00 –11:00 a.m. and 3:00 and 6:30 p.m. One to 10.5 hours of observations were done per day using the following schedule: Sept. 1st approximately 7.5 hours, Sept. 2nd and 4th approximately 4.25 hours, Sept. 3rd and 5th, 1 hour, Sept. 6th, 12th and 15th, 10 hours, and Sept. 13th and 14th approximately 9 hours. Variable observation time was due to asynchronous fruiting among tree crowns among the two sites, weather, and other data collection obligations. As a result, any temporal or daily fluctuations in avian visitation to *C. burmannii* crowns may have been missed, or biased the results in some way. Only complete observations, those with accurate values for all data parameters, were used when analyzing results.

Germination trials

In order for a bird to act as a disperser, a seed must survive passing through its gut so that it may germinate once deposited onto a new, hospitable site. To determine whether *C. burmannii* seeds can survive the gut passage, I conducted a germination experiment using seeds that had passed through captive birds.

C. burmannii fruits were collected randomly from a number of accessible individual fruiting trees to use in germination trials, over six nonconsecutive days. The fruits were refrigerated in a plastic bag until used, but not longer than four days. From each daily fruit collection, a random number of fruits were removed and kept separate to use as control seeds in the germination trial. The remaining fruits were taken to the zoo to be fed to caged birds.

Wild birds (all exotic) were caught using mist nets for the feeding trials to determine the viability of seeds that had passed through the gut of a bird. The birds included those species observed feeding on *C. burmannii*: three Japanese White-eye (*Zosterops japonicus*), three Red-whiskered Bulbul (*Pycnonotus jocosus*), two Red-vented Bulbul (*Pycnonotus cafer*), two Common Myna (*Acridotheres tristis*), and two Spotted Doves (*Streptopelia chinensis*) which were trapped on Honolulu Zoo grounds, and one Red-billed Leiothrix (*Leiothrix lutea*) trapped in the forest, along Nuuanu Trail.

All birds were kept at the Honolulu Zoo in 30 by 30 by 60cm cages made of RFP reinforced fiberglass panels (Peter Luscomb, Honolulu Zoo, Honolulu, HI, Pers. Comm.) for eight days. All birds were fed papaya and mealworms until eating normally. Once regular-eating habits developed, the birds were given *C. burmannii* fruits with their usual papaya and mealworms. Over time, the amount of papaya and mealworms was reduced, and the number of *C. burmannii* fruits was increased. Each morning the cages were inspected for passed seeds. These seeds were collected and placed in labeled (by species) paper bags to dry. This was done for eight days. The Spotted Dove did not consume *C. burmannii* fruit in captivity and therefore was not part of the germination experiment.

On the final day of captivity, the birds were monitored for roughly three hours to watch for gut passage time and feeding behaviors. Any previously existing passed seeds were removed from the cage floor. Twenty fruits were given to each Red-whiskered Bulbul, Red-vented Bulbul, and Red-billed Leiothrix. Forty fruits were given to the three Japanese White-eyes and an unknown quantity was given to the Common Myna. The Myna received an unknown quantity of fruit because it was not seen in the forest and therefore not considered a contributor to forest spread of *C. burmannii*. The cages were checked every five minutes. The seeds were counted to determine consumption and the floor of the cage checked for passed seeds. Times were recorded when fruits were missing and seeds were found on the cage floor. Occasional feeding observations were also made, but were limited because the birds were reluctant to feed while an observer was present.

Remaining uneaten fruits and the seeds that passed through the bird guts were collected. The pulp of the uneaten fruits was removed by hand and used as the control.

The seeds were then placed in a labeled paper bag at the zoo to dry. At the end of the feeding trials, all labeled paper bags were folded, stapled, and placed in plastic bags for travel. All seeds were dried for a minimum of 15 days, because this was the time necessary to complete the feeding trials, transport the seeds, and set up the germination experiment.

Nine-centimeter glass petri dishes with two Whatman #42 ashless 11.0-cm filter papers, cut to size, per dish were used for the germination trial. The dishes were washed with liquid soap then washed in a 1:9 bleach to water solution. The filter papers were dampened with distilled water from a spray bottle. All pulp remnants on the passed seeds were left on the seeds. The dishes were placed on the top three shelves of a plastic four-shelf unit with a 25-watt light bulb on the bottom shelf facing up. A thermometer was placed in the upper most and lower most shelves to monitor temperature. Temperatures were kept between approximately 22.8°C (73° F) (upper shelf) and 25.5°C (78° F) (lower shelf). The lower shelf was warmer due to its proximity to the light bulb. Light plastic was used to cover the entire shelving unit to maintain temperature and humidity, and to reduce dust.

The light bulb was kept on 24 hours/day to maintain temperatures. The dishes were exposed to indirect sunlight for about 8 hours/day. Sunlight was not thought to be critical because of the extreme shade tolerance exhibited by this species and the dense shade in which they germinate on the forest floor (Pers. Obs.).

The seeds were placed in petri dishes as follows: Red-whiskered Bulbul, Red-vented Bulbul, Common Myna, and Control: 100 total seeds per species; four replicates of 25 seeds, each replicate separated into three dishes (8 seeds, 8 seeds, and 9 seeds respectively); Red-billed Leiothrix: 39 total seeds; three replicates of 13 seeds, each separated into three dishes (4 seeds, 4 seeds, and 5 seeds respectively). The Japanese White-eyes produced 90 passed seeds. Because feeding observations showed that the White-eyes both swallow the seeds whole, and eat only the pulp of the fruit, these seeds were divided into three classes: "eaten", "pecked", and "unknown" as determined by marks found on the seeds. "Eaten" seeds were smooth with no bite marks and therefore assumed to have passed through the gut. "Pecked" seeds had multiple bite marks and therefore may have simply had the pulp pecked from it, and not passed through the gut. And "unknown" seeds which had very few bite marks and therefore could not be determined whether they were ingested or not. The "unknown" seeds were not used in the germination trials. Forty-five "eaten" and 45 "pecked" seeds were used in the germination trials but kept separate. "Eaten" and "pecked" seeds were divided into three replicates of 15 seeds, each separated into three dishes of 5 seeds each.

Seeds were checked daily and misted with distilled water as needed. Two days after the germination trial began, large amounts of mold were found on the majority of seeds. All seeds were wiped clean of mold and pulp remnants with a clean towel. Seeds without mold were also wiped to control for any affect wiping may have had. All petri dishes were washed in a 1:9 bleach to water solution again. Filter papers were changed and replaced with one Whatman #1 11.0 cm, cut to size, per dish. The germination trial began again using the same procedure as above.

Petri dishes were rotated by shelves and position on the shelf every other day and rotated within the 3-dish stack once every six days. This was done to reduce the effect of shelf position. As seeds germinated, defined as the point at which the primary root protrudes from the seed coat (Starr & Taggart 1989), they were recorded and removed from the dish to reduce mold growth. The germination trial began on October 7th and was terminated on December 5th due to copious amounts of mold. Remaining seeds showed no signs of germination.

Fruit crop estimation

The total fruiting potential of adult *C. burmannii* was estimated by selecting three reachable branches (Wheelwright 1991), on each of ten climbable, fruiting trees ranging from 4.9 to 12.8 dbh in size. The branches were cut from the crown using a handsaw and lowered to the ground. All fruits and flowers were counted on each branch. All stages of flower and fruit development were included. Individual branch volume was estimated by multiplying the measured length, width, and depth of each branch crown. The crown volume was estimated by visually estimating the crown's length, width, and depth and multiplying these values. Fruit/m^3 was estimated by first dividing the number of fruit counted per branch by the individual branch volume, then averaging the results of the three individual branches. Flowers were not considered as only 11 flowers were counted on all 10 trees. The number of fruit/m^3 was multiplied by the crown volume estimate to give the total number of fruit per tree. The diameter at breast height (dbh) was also measured.

Fruit pulp analysis

The nutritional content of a fruit may indicate what type of feeder it attracts, either specialist or generalist (McKey 1975; Snow 1971). Specialist feeders typically feed on fruits high in fat and protein (Snow 1971) while generalists feed on fruits high in water and carbohydrates (McKey 1975). Discovering the nutritional content of *C.*

burmannii fruits will not only provide another bit of basic life history information, but might also help to predict likely disperser species.

The pulp removed from control fruits used in the germination trial was submitted for chemical nutrient analysis to the University of Hawaii-Manoa, College of Tropical Agriculture and Human Resources, Agricultural Diagnostic Service Center. The fruit was analyzed for dry weight, crude fat, crude protein, ash content, acid detergent fiber (cellulose and lignin), and natural detergent fiber (hemicellulose, cellulose, lignin, and unsoluable minerals; Herd & Dawson 1984).

Caveats

There are several limitations in this study. First, is the lack of life history information available for *Cinnamomum burmannii* in Hawaii. The fruiting period was thought to begin in June (C. Smith, University of Hawaii-Manoa, Honolulu, HI, Pers. Comm.). However, in 1999, *C. burmannii* fruits did not begin to ripen until late August. This reduced the proposed observation time from 270 hours to 70 hours, and consequently, reduced the observation sample size. All trees did not ripen simultaneously, therefore, only two of the six originally proposed observation sites were used. And finally, because of the shortened observation period, the samples were not temporally representative of the fruiting season.

Secondly, the observation sites used in this study were not randomly chosen, nor did they necessarily represent the forest around them. Only forest areas that contained *C. burmannii* and an appropriate gap could be used as the forest canopy was too dense to see tree crowns and associated avian feeding patterns, without a gap. Also, only forest gaps that exposed tree crowns with ripe fruit could be used.

Thirdly, due to time limitations and lack of forest feeding activity, sample sizes were small. After separating observations into forest and urban sites, sample sizes varied from 2 to 58 per bird species. This reduced the possibility of having statistically robust analyses.

Results and Discussion

Species observed in C. burmannii canopy

Avian activity was observed for a total of 70 hours at the three observation sites. A total of ten bird species were seen in the *Cinnamomum burmannii* canopy in either the forest or urban sites (Table 1): Common Amakihi, Common Waxbill, House Finch, White-rumped Shama, Japanese White-eye, Common Myna, Red-billed Leiothrix, Red-vented Bulbul, Red-whiskered Bulbul, and Spotted Dove. All species, except the Common Amakihi, are alien. All of the exotic species are from south and east Asia except the Common Waxbill, which is from Africa. The Common Amakihi, Common Waxbill, House Finch and White-rumped Shama were not observed eating *C. burmannii* fruits.

Observation results show that three species of birds play a role in *C. burmannii* dispersal. They include Japanese White-eye, Bulbuls and Spotted Dove for the forest observations, and two species of birds, Japanese White-eye and Bulbuls, for the urban observations. The Red-vented Bulbul and the Red-whiskered Bulbul were lumped together (Bulbuls) for the statistical analysis of the time spent in the canopy, number of fruit eaten, and number of fruit dropped because of their similarity in life history characteristics. Both species are native to India where they inhabit gardens, shrub, second growth, and forest edges (Ali & Ripley 1996).

Table 1. Avian species observed in the canopy of *Cinnamomum burmannii* trees in Nuuanu and Manoa Valleys, O'ahu, Hawaii. (*) indicates native species.

Species in *C. burmannii* canopy	Fed on *C. burmannii* fruits?
Common Amakihi (*Hemignathus virens*)*	No
Common Waxbill (*Estrilda astrild)*	No
House Finch (*Carpodacus mexicanus*)	No
White-rumped Shama (*Copsychus malabaricus*)	No
Red-vented Bulbul (*Pycnonotus cafer*)	Yes
Red-whiskered Bulbul (*Pycnonotus jocosus)*	Yes
Red-billed Leiothrix (*Leiothrix lutea*)	Yes
Common Myna (*Acridotheres tristis*)	Yes
Spotted Dove (*Streptopelia chinensis*)	Yes
Japanese White-eye (*Zosterops japonica*)	Yes

They are also similar in their morphology, nesting habits, and feeding habits (Ali & Ripley 1996). The Red-vented Bulbul and Red-whiskered Bulbul were treated as separate species for the feeding behavior and exit flight relative distance results because these results were not statistically compared. The Japanese White-eye and Spotted Dove were not grouped with other species because of their unique characteristics. Other species seen eating *Cinnamomum burmannii* fruits were not included in the results due to small sample size.

Non-parametric statistics (Mann-Whitney U-test and Kruskal-Wallis test) were used to analyze the observation results because the sample sizes were small, of unequal size, and not normally distributed (Fowler et al. 1998). Results shown are grouped according to observation site location (forest and urban), in addition to a combined result which includes both forest and urban observations.

Time spent in canopy

The Bulbuls had the smallest median time in the canopy: 26.0 sec. for the forest site, 32.5 sec. for the urban site, and 30.0 sec. for the two sites combined (Table 2).

Table 2. *Cinnamomum burmannii* tree canopy use by bird species in Nuuanu and Manoa Valleys, O'ahu, Hawaii and the significance of difference based on Kruskal-Wallis tests and Mann-Whitney U-tests. P-value (<0.05) implies significant difference between only the longest and shortest median time spent in canopy.

Species	Japanese White-eye	Bulbul	Spotted Dove	p-value	K-test statistic	U-test statistic
Observation time in seconds:						
Forest	(N=26)	(N=47)	(N=16)	<0.001	16.800	
Median	28.5	26.0	102.0			
Urban	(N=10)	(N=10)		0.015		18.000
Median	98.0	32.5				
Combined	(N=36)	(N=57)	(N=17)	<0.001	18.913	
Median	49.5	30.0	110.0			

The Spotted Dove had the largest median time per visit for each of the categories: 102.0 sec. for the forest median and 110.0 for the combined median. While the Spotted Dove also had the longest time spent in the urban setting, the sample size was a single feeding observation. The Japanese White-eye had the next longest median with 98.0 sec. per visit. Because the Kruskal-Wallis non-parametric test is applied to the samples as a group, statistical significance cannot be determined for particular pairs of samples. However, it is safe to assume that there is a significant difference between the two samples that show the highest and lowest values (Fowler et al. 1998).

The time spent in the canopy is important not only as an indicator of general feeding habits, but also in conjunction with gut passage times. The Japanese White-eye and both species of Bulbul exhibited gut passage times of roughly 15 –20 minutes, as noted in captive observations. The gut passage time for the Spotted Dove is unknown. While the median value of the time spent in the canopy for both species was significantly shorter than 15 minutes, the median time spent in the canopy by the Spotted Dove was roughly four times longer than the Japanese White-eye or Bulbuls. Therefore, if the Spotted Dove and Japanese White-eye (or Bulbuls) were to make the same number of canopy visits within a single hour, the Spotted Dove is likely to spend four times the amount of time within the canopy as either of the other two species. Thereby making it more likely that the Spotted Dove deposits previously ingested seeds beneath the parent tree.

C. burmannii fruit consumption

C. burmannii fruits were consumed only by alien species. Obviously, the more fruit an individual bird consumes, the more likely that bird will disperse the seeds assuming the seed survives gut passage. The Spotted Dove consumed the greatest number of fruit per visit for the forest location (median = 0.25), significantly more than the Japanese White-eye (median = 0.0) (Table 3). The Spotted Dove also consumed more fruits per visit for the combined category, but not significantly so. The Spotted Dove's results for the urban location were not included because it was taken from just one observation. Fruit consumption by the Japanese White-eye and Bulbuls at the urban site was not significantly different.

The reliability of these feeding observations is somewhat questionable due to differences in the size and feeding behavior of the observed birds, and thus likelihood that they will be observed. For example, the Japanese White-eye is a small, green, very quick bird that generally fed on the underside of the canopy, making it difficult to see. The Spotted Dove, on the other hand, is large, slow, clumsy, and spent most of its time in the outer canopy, where it is much more obvious to the observer.

Table 3. ***Cinnamomum burmannii*** **fruit consumption by bird species in Nuuanu and Manoa Valleys, O'ahu, Hawaii, and the significance of difference based on Mann-Whitney U-tests and Kruskal-Wallis tests.** P-value (< 0.05) implies significant difference between only the greatest and smallest median number of fruit eaten per visit.

Species	Japanese White-eye	Bulbuls	Spotted Dove	p-value	K-test statistic	U-test statistic
Forest	(N=26)	(N=47)	(N=16)			
Median	0.00	0.00	0.00	0.031	6.957	
Urban	(N=10)	(N=10)				
Median	1.0	1.0		0.737		54.000
Combined	(N=36)	(N=57)	(N=17)			
Median	0.00	0.00	0.00	0.696	0.725	

The Bulbuls also fed on the outer canopy where they were easier to observe. There were six observations of Red-vented Bulbuls, and three observations of Red-whiskered Bulbuls, flying long distances with a single fruit in their bill, again, an obvious behavior.

Dropped C. burmannii fruits

The number of fruit dropped per visit indicates how many seeds the bird indirectly deposits beneath the parent tree. Seeds can be dropped intentionally, after being inspected and rejected for consumption, or accidentally, as the individual moves through the canopy. The Spotted Dove dropped fractionally more fruits in the forest location (median = 0.06) than did the Japanese White-eye and the Bulbuls (median = 0.0) (Table 4). At the urban site and the combined category, the Japanese White-eye dropped slightly more than did the Bulbuls and Spotted Dove. However, none of the differences in dropped fruits are statistically significant.

Table 4. *Cinnamomum burmannii* fruits dropped by bird species in Nuuanu and Manoa Valleys, O'ahu, Hawaii, and the significance of difference based on Mann Whitney U-tests and Kruskal-Wallis tests. P-value (<0.05) implies significant difference between only the greatest and smallest median and mean number of fruit dropped per visit.

Species	Japanese White-eye	Bulbuls	Spotted Dove	p-value	K-test statistic	U-test statistic
Forest	(N=26)	(N=47)	(N=16)			
Median	0.00	0.00	0.00	0.102	4.562	
Urban	(N=10)	(N=10)				
Median	0.00	0.00		0.121		34.500
Combined	(N=36)	(N=57)	(N=17)			
Median	0.00	0.00	0.00	0.152	3.768	

Feeding behaviors of three bird species

The Bulbuls and Spotted Dove show feeding habits of either swallowing the fruit whole, or some amount of mashing of the pulp before swallowing the fruit (Table 5). These feeding behaviors ensure consumption of the seed, making dispersal more likely.

Table 5. Behavioral observations of bird species feeding on *Cinnamomum burmannii* fruits in Nuuanu and Manoa Valleys, O'ahu, Hawaii. 1= swallowed fruit whole, 2= mashed pulp in bill before swallowing whole fruit, 3= ate pulp only. “0” represent no observations recorded.

Species	Japanese White-eye			Bulbuls			Spotted Dove		
Feeding Behavior	1	2	3	1	2	3	1	2	3
Forest Observations	0	0	1	4	0	0	6	0	0
Urban Observations	3	3	0	7	1	0	1	0	0
Combined Observations	3	3	1	11	1	0	7	0	0

The Japanese White-eye showed examples of all three feeding behaviors: swallowing fruit whole, fruit mashing before swallowing whole, and plucking pulp only from the fruit. The White-eye was seen swallowing the fruit whole in the urban setting, and plucking the pulp from the fruit in the forest and captive setting. The fruit was often struck against a hard surface (e.g., wooden perch in the captive setting) before plucking the pulp. If only the pulp is eaten, the seed is presumably left to fall under the parent tree.

It is possible that the Japanese White-eye would remove the fruit from the parent tree and fly to a different location to consume the fruit, but this was not observed.

Feeding behavior observations cannot be statistically compared because so few observations were noted; thus these results can be used only as an indication of possible feeding behaviors. The dense canopy and quick movements of the birds prevented a clear view of most individuals while feeding.

Exit flight relative distance

Species more likely to fly a farther distance after feeding in the canopy are also more likely to take the ingested seed and deposit it in a new location, away from the parent tree. In conjunction with fruit consumption, this behavior is most likely to result in the formation of new satellite populations, given successful germination. Table 6 shows the results of the exit flight relative distance. "N" represents an exit flight to a perch within sight. "O" represents an exit flight out of sight.

In this study, Red-whiskered Bulbuls showed a greater tendency to fly further after exiting the tree than did the other species. The Japanese White-eye was most likely to fly to a near-by perch. Again, thick canopy and quick movements of the birds made this information difficult to collect. Target birds often "disappeared" into the canopy, never to be seen again. Therefore, sample sizes are small, and no actual distance was estimated or statistically analyzed.

If seeds are carried to a new, hospitable site, satellite populations can begin and eventually offer more food sources to species spreading the seed (Warshauer 1998).

Table 6. Exit flight relative distance observations from *Cinnamomum burmannii* canopies by bird species, in Nuuanu and Manoa Valleys, O'ahu, Hawaii. N = exit flight was to a near-by perch, O= exit flight was out of sight.

Species	Japanese White-eye		Red-vented Bulbul		Red-whiskered Bulbul		Spotted Dove	
Relative Distance	N	O	N	O	N	O	N	O
Combined Observations	27	14	14	8	15	27	6	10
Forest Observations	22	14	14	6	15	23	6	10
Urban Observations	5	0	0	2	0	4		

For example, Fiddlewood (*Citharexylum caudatum*) was an innocuous ornamental tree in Hawaii until the Red-whiskered Bulbul became established. It is now spreading rapidly and becoming a problem (Cronk & Fuller 1995). This shows that the interactions between exotic species are complex, unpredictable, and often unknown until problems arise.

Germination trial

Seeds must survive digestion for avian species to serve as alien plant dispersers. In this trial, all of the birds that ingested the seeds produced viable seeds, as did the control (Table 7). Seeds ingested by Red-billed Leiothrix and Common Myna were included in the germination trial because these species were seen consuming fruit, although not frequently enough to warrant including them in the other results sections.

Seed collection from caged birds produced a total of 429 seeds that had passed through the gut of a bird.

Table 7. Germination success of *Cinnamomum burmannii* fruit ingested by captive bird species held in the Honolulu Zoo, O'ahu, Hawaii. Four repetitions combined. * indicates three repetitions combined.

Species	N	Mean Percent Germination
Control	100	50
Japanese White-eye* (pecked)	45	42
Red-vented Bulbul	100	39
Japanese White-eye* (eaten)	45	36
Red-whiskered Bulbul	100	27
Red-billed Leiothrix*	39	21
Common Myna	100	17

Between groups p-value = 0.101; means are not significantly different at $p<0.05$. No significant differences ($p>0.05$) for pair-wise tests as determined by Bonferroni post hoc test. Data was arcsin transformed for analysis.

Seed germination commenced after 20 days in the control, Red-vented Bulbul, Red-whiskered Bulbul, Japanese White-eye, and Myna trials. Seed germination was highest in the control and Japanese White-eye (pecked) trials (50% and 42%, respectively) although not significantly so. Relatively high germination success of seeds not ingested by birds, like the control and pecked seeds, mimic the widespread germination seen immediately under the parent tree. In an accompanying study, multiple 1m^2-plots were used to count *C. burmannii* seedlings in sites similar to those mentioned here. While results varied, one particular 1m^2-plot contained over 1400 *C. burmannii* seedlings (A. Horcher, unpubl.). This prolific germination implies that gut passage is not a requirement for seedling success. Based on the germination trials and observed feeding behavior, it would appear that germination success is not adversely affected by gut passage and therefore, that *Cinnamomum burmannii* dispersal may be enhanced, particularly by bulbuls.

Fruit pulp analysis

It is thought that producing fruits high in fat and protein is expensive for trees and is therefore linked evolutionarily with specialized seed dispersers (Snow 1971). On the other hand, trees that produce fruits high in water and carbohydrates are thought to appeal to opportunistic feeders (McKey 1975). The pulp of *C. burmannii* fruits was submitted for nutritional analysis to determine where it fell within this dichotomy. If the fruits are highly nutritious or more likely to appeal to specialized feeders then it is likely that fewer species of birds would be dispersers. If however, the fruits resemble those high in water and carbohydrates, and therefore appeal to more opportunistic feeders, then the number of bird species likely to feed on the *C. burmannii* fruits would likely be higher as Hawaii has more opportunistic feeders than specialist feeders. Fruit pulp analysis showed *C. burmannii* to be relatively nutritious (Table 8) and therefore fall somewhere in the middle. Values of 9-15% protein and 24-45% fat are considered relatively high for fruits (McKey 1975), therefore *C. burmannii* with almost 6% protein and over 28% fat, can be considered a nutritious fruit. However, the relative attraction of *C. burmannii* to opportunistic feeders, in Hawaii and in its native Sumatra environment, is unknown because both forests contain many fruit bearing tree species of unknown nutritional content.

Table 8. Nutritional content of *Cinnamomum burmannii* fruit collected in Nuuanu Valley, O'ahu, Hawaii. One composite sample of 500 fruits, results given in percents.

				Detergent Fiber		
Dry Matter	Ash	Crude Protein	Crude Fat	Natural	Acid	Carbohydrate
50.3	1.0	5.9	28.4	36.4	27.2	14.9

Fruit crop estimation

The number of fruit produced within a fruiting season is an indicator of the tree's potential spread. Those that fruit copiously are more likely to successfully spread their seeds than those species that produce significantly fewer fruits.

Cinnamomum burmannii produces far fewer fruits than some other serious alien pests; for example, a single *Miconia calvescens* can produce 5 million seeds per year (Meyer 1996). However, *C. burmannii* does produce enough fruit to warrant concern. The mean number of fruits/m^3 was 818.3 and the mean fruits/tree was 33760 (Table 9). Given the formation of monotypic *C. burmannii* stands, and their ability to produce fruit at roughly four years of age (Aumeeruddy & Sansonnens 1994), the landscape level seed crop will increase exponentially.

Table 9. Estimated number of *Cinnamomum burmannii* fruits per m^3 and estimated number of *Cinnamomum burmannii* fruits per adult tree in Nuuanu Valley, O'ahu, Hawaii.

Tree No.	Diameter at breast height (Dbh)	Fruits/m^3	Fruits/tree
1	4.9	788.7	4690
2	6.6	653.3	8160
3	6.9	398.8	5420
4	8.0	1404.5	40090
5	9.2	602.3	15520
6	10.8	851.4	133080
7	11.3	2077.3	43240
8	12.5	549.0	31720
9	12.3	319.6	27690
10	12.8	538.4	27990
Mean	9.5	818.3	33760

Implications

The Red-vented Bulbul, Red-whiskered Bulbul and Common Myna, all native to India; the Japanese White-eye from east Asia; the Spotted Dove from southeast Asia; and the Red-billed Leiothrix from south Asia all play a role in the seed dispersal of the invasive *Cinnamomum burmannii* on O'ahu, Hawaii. Each species fed on *C. burmannii* fruits in the forest and/or urban setting and, with the exception of the Spotted Dove (due to lack of seed consumption in captivity), experimentally showed that *C. burmannii* seeds survived gut passage. These results reveal modes of possible dispersal, and perhaps more significantly, the trend towards increasing complexity in invaded ecosystems. They do not, however, prove dispersal methods of *Cinnamomum burmannii.*

Increasing complexities

One complicating factor in managing lands with alien species is the growing complexities of these systems. This *Cinnamomum burmannii* study on O'ahu revealed that birds native to Malaysia, India, West Pakistan, and China feed on a tree native to Indonesia. As more and more alien species enter an ecosystem, interactions between native and alien species, and multiple alien-alien species interactions become more complex and involve life histories from diverse environments and countries, all of which have few, if any precedents. Multiple alien species interactions introduce the possibility of species facilitation, or the enhancement of a population of one species by the activities of another (Ricklefs 1990). While relatively little information on possible facilitation exists (Usher 1989) it is suspected in many systems. In Ireland, for example, the European rhododendron (*Rhododendron ponticum*) and the Japanese sika deer (*Cervus nippon*) coexist and it is believed that land disturbance by the sika deer facilitates the establishment of rhododendron (Usher 1989). This type of interaction is difficult to predict or control since information about facilitation is generally unavailable and control methods may be both complex and multi-faceted (Usher 1989).

Another complicating issue with alien-alien interactions is the unpredictability of species response. The eastern North American gray squirrel, *Sciurus carolinensis*, has been introduced into Britain, California, and South Africa. In England, the squirrel is found throughout the countryside (Williamson 1999). However, in South Africa it is found only among introduced trees even though there are no native squirrels, and food and habitat types (i.e., niches) appear to be appropriate among native trees (Williamson 1999). This example shows that although multiple species success predictors are present (e.g., open niche, available similar habitat, and available similar food), the alien squirrel is not invading native areas.

Several factors may explain the lack of invasion into native tree species habitats. First, perhaps what appears to be suitable habitat to scientists may not be suitable for squirrels. Second, perhaps there are unknown interactions between the native trees and other agents (e.g., insects, pathogens), either native or alien, which make the native trees undesirable for squirrels. And finally, there may be interactions between alien tree species that the squirrel does inhabit that make it more suitable than the native trees. If this were the case, efforts to remove alien trees might not eliminate the alien squirrels, but cause them to shift habitats to less desirable native tree species.

Cinnamomum burmannii has been on both O'ahu and Kaua'i for decades and yet exhibits dramatically different levels of spread. *C. burmannii* covers much of Nuuanu valley and the Pauoa flats on O'ahu, but has not spread much beyond a few groups of individuals on Kaua'i. Seed dispersers may be the answer. The Red-vented and Red-whiskered Bulbul are common on O'ahu but absent from Kaua'i. It seems unlikely that another opportunistic fruit eating bird has not taken the place of Bulbuls on Kaua'i, but no research has been done. These scenarios illustrate the many interactions that must be understood if alien species invasions are to be understood.

A final area of concern in dealing with native-alien-alien interactions is the growing complexity of competition. Invasive species often affect a multitude of factors in the habitats of native wildlife (e.g., nesting sites, mating behaviors, and refuge sites). Competition can be down the food chain, horizontal by direct behavioral interaction between species, or upwards, from shared predators (Williamson 1999). For example, *Miconia calvenscens* has caused a reduction in available brooding sites and sources of food for many Tahitian endemic birds, such as the Tahitian Reed-warbler (*Acrocephalus caffer*) and the Tahitian Green heron (*Butorides striatus patruelis* L.) (Vitousek 1990). As *C. burmannii* continues to spread, out-competing the native ohia and koa, it too may reduce valuable breeding sites and replace nectar-producing trees, which are important to native bird species. On the island of Madeira, the European speckled wood butterfly (*Parage aegeria*) is displacing the native endemic butterfly (*P. xiphia*) by territorial fights between males (Jones et al. 1998). Finally, in Sweden, the American crayfish (*Pacifastacus leniusculus*) is displacing the native *Astacus astacus* through its superior ability to seek out refuges from predation by the European perch (*Perca fluviatilis*) (Soderback 1994).

Predation and competition for resources are known areas of conflict between native and alien species, however, indirect effects of invasives can be as great or greater than direct effects (Brown 1989). *Cinnamomum burmannii* competes directly with other tree species for soil nutrients, water, and seed dispersers. Indirectly, *C. burmannii* may reduce site quality by intercepting less precipitation, which could increase overland flow (Pers. Obs.). Unfortunately, indirect effects of native-alien species interactions are not understood until researchers have the time and budget to investigate them on a case by case basis. Until then, managers are forced to simply observe the decline in native species or attempt control measures that may or may not have anything to do with the real problem.

Ecosystem alterations

Invading species may exert confounding effects at many different levels of ecosystem function including altering vegetation composition or nutrient and energy availability. For example, Fire tree (*Myrica faya*), a shrub native to the Azores, Madeira, and the Canary Islands in the Atlantic Ocean (Whiteaker & Gardner 1992), was first discovered in Hawaii Volcanoes National Park in 1961 and has since become a dominant pest in that system (Macdonald et al. 1989). Because of Hawaii's recent volcanic eruptions, many areas in the park are in early successional stages. Early successional systems are often nitrogen deficient, but have native nitrogen fixing plants that are symbiotic with vascular plants. In Hawaii, however, there are no native nitrogen fixers in early stages of the rain forest zone (Vitousek et al. 1983). Fire tree, which is an introduced actinorrhizal nitrogen fixer, has a distinct advantage in these areas of primary succession (Vitousek 1990). Not only does the fire tree have the advantage of rapid initial growth, but it is also capable of altering the entire ecosystem by quadrupling the amount of nitrogen present in the system (Vitousek 1990). Increased nitrogen may adversely affect native species and facilitate establishment of other non-native species, thereby altering species composition and nutrient dynamics.

Unfortunately, the fire tree is not the only example of such a species. In Channel Islands National Park, California the introduced annual iceplant, *Mesembryanthemum crystallinum*, accumulates salt which then enters the soil profile during its annual decomposition. Over time the increase in salt excludes all other species from sites inhabited by iceplants (Halvorson 1992; Macdonald et al. 1989).

Another example is the introduced feral pig in Hawaii. The pig not only disturbs the soil and ground vegetation, encouraging alien species establishment through constant rooting, but also creates a habitat suitable for mosquitoes to breed which in turn carry avian pox and avian malaria (Warshauer 1998). These diseases have caused declines in several native avian species populations (Conant 1998).

Alien species are also known to affect ecosystem fire regimes (D'Antonio & Vitousek 1992). For example, Cheatgrass, *Bromus tectorum*, invasions have radically altered fire regimes in several reserves (e.g., Capital Reef, Zion, Canyonlands, and Arches National Parks in Utah; Macdonald et al. 1989) as have other grass species in Volcanoes National Park (C. D'Antonio, University of California, Berkeley, CA, Pers. Comm.).

Finally, saltcedar (*Tamarix ramosissima*), has been known to cause multiple system disturbances in areas it has invaded. Saltcedar was introduced into Spring Lake, New Mexico in the early 1800's (Duncan 1997). Invading moist pastures, rangelands, and riparian habitats, saltcedar not only provides little browse and no seed source for wildlife, but also causes a reduction in streamflow, an increase in area inundated by floods, and an increase in sediment production (Blackburn et al. 1982). The increase in sediment production causes other cascading effects to the native fish living in effected streams.

Cinnamomum burmannii creates a number of potential ecosystem level affects. They include: increase in shade, increase in small tree fall gaps, changes in decomposition or soil structure as a result of shallow roots systems, and possible allelopathic affects. First, the dense canopy creates a much darker forest floor, thereby allowing only shade tolerant species to exist. As more monotypic *C. burmannii* stands form, this dense shade will potentially cover vast areas of the forest floor. Second, *C. burmannii's* shallow root system and dense canopy, in conjunction with the constant tradewinds of O'ahu, results in a relatively large number of windblown trees. These small tree fall gaps create areas of intense sunlight where established *C. burmannii* seedlings grow to close the gap. Third, the shallow root systems may change soil organic matter contents by reducing the amount of roots deep in the soil, as well as change the soil structure due to the lack of root penetration in the deeper soil horizons. And finally, *C. burmannii* may have allelopathic capabilities. Cinnamon oil is a relatively common essential oil, implying it has a potent fragrance and used for medicinal purposes. These oils may be capable of inhibiting the growth of other vegetation via canopy through-fall or stem flow.

Continental "islands" on the rise

> "Given the fragmentation of the world's major biomes into relatively small 'quasi-insular' reserves with all the attendant changes in faunal composition, altered microclimates, altered fire regimes, and increased proximity to transformed areas, we can actually predict that the circumstances conducive to the invasion of introduced species will become more widespread in the future..." (Macdonald et al. 1989).

If this is the case, the vulnerability to invasion and adverse effects currently seen on oceanic islands will increasingly affect continental, anthropogenicaly-created islands as well. For example, exotic plants are now believed to pose the greatest threat to the South Florida environment (Loope 1992).

Two primary explanations are given for the likely increase in numbers of isolated native ecosystems: increased land development and global changes. "Global change" can be defined as predicted human-driven changes. This includes, for example, changes in land use that degrade or fragment an ecosystem, alter temperature and rainfall, and decrease biodiversity (Baskin 1998). Without question, land is being altered at increasing rates in both temperate and tropical areas. Commercial and residential development dominate in temperate regions, while agricultural development dominates in tropical regions (Whitmore 1997). Increased global trading has not only resulted in more species traveling from country to country, but has resulted in a number of changes within product producing countries. In the tropics, for example, many native crops have been replaced with exotic cash crops as a result of international aid and development activities (di Castri 1989). Arid lands have been planted with exotic species to reclaim the land (di Castri 1989) while cleared forests are replaced with more valuable exotic timber species or cattle. These activities result in greater isolation of remnant native areas.

Large-scale land disturbances and pollution are suspected to cause global climatic changes. Changes in temperature affect invasive range potential (Kowarik 1995), often by increasing the suitable range. Water temperature changes can create shifts in primary productivity, length or timing of reproductive or growing season, and also cause shifts in suitable range (Baskin 1998). Again, any ecosystem change in one area creates a greater division between disturbed and undisturbed regions.

Management options for invasive species control

The evidence is overwhelming; invasive species are a problem in desperate need of control. So how do land managers deal with altered ecosystems? There are a number of possibilities: 1) Business as usual, 2) Preventative invasive species management, 3) Systematic approaches to alien species control, 4) Biological control, and 5) Improve education and research.

Business as usual

There are conflicts of interest in some areas affected by invasive species. Purple loosestrife has altered many North American wetland ecosystems, yet it is prized by some for its role in honey production (Thompson et al. 1987). Others claim that exotic species are sometimes among the few organisms capable of inhabiting disturbed landscapes (Brown 1989). While still others believe the process of invasion has simply gone too far to expect a return to a "natural" state (Macdonald 1989; C. D'Antonio, University of California, Berkeley, CA, Pers. Comm.). *Cinnamomum burmannii* is so prevalent in the Nuuanu Valley of O'ahu that eliminating the population or controlling the spread would seem impossible. Also, the native tree species are so uncommon in the Nuuanu valley, any clearing of *C. burmannii* would most likely result in the spread of other alien species rather than the reestablishment of native species.

In the Cape of Good Hope Nature Reserve, a study monitored alien species in fixed plots. After twenty years of control operations, only 2 of the 19 introduced tree and shrub species present in the reserve were eliminated (Macdonald et al. 1989). In Hawaii's Volcanoes National Park, researchers and park managers are working to introduce plants that are native to Hawaii, but not originally found in the park, into heavily disturbed areas under the assumption that some natives are better than no natives (C. D'Antonio, University of California, Berkley, CA, Pers. Comm.). If Brown (1989) is correct in that "homogenization of the earth's biota is inevitable" perhaps managers should begin to look at global biodiversity instead of localized biodiversity. If a species becomes extinct in one locale, does it matter if it is widespread in another? At this stage, the answer is yes. A huge contributing factor to the lack of success of controlling invading species is lack of knowledge and understanding of ecosystem relationships. So while scientists and land managers may not have specific reasons to keep native, local, ecosystems intact, perhaps we should assume that those reasons will become evident in the future and in the meantime seek to maintain local biodiversity.

Preventative invasive species management

A second option is to change the focus from crisis management of threatened species to preventative management of the invading species. Frazer (1992) refers to this as "halfway technology", that is the management for species loss, not the issues behind it. Many managers focus their attention on decreasing endemic populations, but at some point the focus must turn to the cause of decreasing populations. Tahiti has developed a list of goals to help assess their current situation (Meyer & Florence 1996), and to address ways to prevent future introductions and improve control measures. Their objectives are as follows: 1) list endangered endemics, localization and degree of threat, 2) list main invasive alien plants, their distribution and impact on native plants, 3) inventory all "Natural Zones of Ecological and Biological Interests" from which most or all alien invasive species are excluded, 4) strictly and rigorously enforce the quarantine system to control the traffic of alien plants, animals, and micro-organisms to prevent introductions, 5) implement research programs to accompany control programs, and 6) improve conservation action and appropriate education (Meyer & Florence 1996). By focusing efforts on identification of problem species, control, research, and education, Tahiti is dealing with the entire problem of invasive species, not just diminishing populations. Comprehensive approaches to alien species management are more likely to address the problems of introduction and spread, as opposed to simply native species decline.

While it is probably too late to stop *C. burmannii* in the Nuuanu valley, preventative measures could be taken to control future satellite populations that might occur. For example, a volunteer group could be trained in the identification of *C. burmannii* seedlings and adults, and take monthly or biannual hikes through sensitive areas looking for early establishment. If these satellite populations are caught in time, control measures are much more likely to be successful.

Systematic approaches to alien species control

Some areas of the world, like Hawaii, are dominated by alien species. In these areas, a critical part of alien species management is prioritizing control efforts. An increasingly common way to prioritize methods is the development of systematic approaches to identifying problem species, evaluating their threat to native species, and evaluating their current and potential spread. Hawaii's Volcanoes National Park developed such an approach in 1985, called the Special Ecological Areas (SEA) approach (Tunison & Stone 1992). The idea behind SEA management is that the most intact, diverse, unique, and valuable research and interpretive sites can and should be protected. Special Ecological Areas are selected on the basis of eight criteria: 1) representativeness and/or rarity of vegetation present, 2) vegetation intactness, 3) plant species diversity and richness, 4) manageability of the area in terms of size, accessibility, intactness, and kinds of alien plant problems, 5) presence of rare flora and fauna, 6) preserve design considerations, (i.e., is the site close to other SEA, amount of edge effect in the site, and size of the site), 7) degree of immediacy of threats from alien biota, and finally, 8) research and interpretive values (Tunison & Stone 1992).

The benefits of the Special Ecological Areas approach are simple, yet important. Controlling alien species in a defined area is easier and success is more likely. Mechanical and chemical control can be used in the SEA until biological methods are developed (Tunison & Stone 1992). The SEA approach also allows for a systematic, incremental approach to management that can then be used as models for treatment and methods, in other areas. And finally, SEAs can be used as sites for integrating feral animal and alien plant management as well as serve as a focus for research and interpretation (Tunison & Stone 1992). Special Ecological Areas management, however, is not without drawbacks. The most significant weakness of SEA is the creation of highly managed "islands" in a sea of increasingly dense alien species. One means of addressing this contrast would be to create buffer zones between SEA and outside areas where alien species recruitment and dispersal are controlled (Tunison & Stone 1992). A final concern is the preservation of small populations, generally due to the relatively small size of many SEAs, and the vulnerability inherent with small populations (Tunison & Stone 1992).

Other systematic approaches concentrate on categorizing alien plant species by feasibility of control (Holt 1992; Taylor 1992). The Nature Conservancy of Hawaii first prioritizes alien plant species found in preserves according to their invasiveness, then by likelihood of progress in their control, and finally, geographically, according to an area's value in terms of rare species and levels of pristine-ness (Holt 1992). Other managers in Hawaii first categorize target species according to their distribution, either widely distributed or locally distributed. Once placed into one of these two groups, species are grouped according to feasibility of control. Widely distributed plants are controlled in areas where native vegetation is relatively intact and localized alien species are confined to small enough areas so as to enable workers to control them (Taylor 1992).

By developing systematic approaches to alien species management, managers can measure success of their efforts, identify needs for future work and funds, and demonstrate procedures and objectives to other organizations and the public (Taylor 1992).

Biological control

Biological control is the intentional introduction and establishment of a natural enemy of a target species with the hope that the newly introduced species will keep the original pest species' population low (Markin 1989). This controversial method brought the now problematic mongoose to Hawaii (Warshauer 1998). The list of negatives associated with biological control of alien species is long, but the potential payoffs are enormous. Ideally, biological control behaves as a non-hazardous, inexpensive, natural way to maintain low populations of pest species, often permanently (Cronk & Fuller 1995). Biological control is now a long-term goal of most management programs for agricultural weeds and natural areas in Hawaii (Markin et al. 1992).

Problems associated with biocontrol are serious. First, biocontrol usually involves introducing other alien species. Whether the population reduction attempt is successful or not, the approach introduces one more exotic species in the area. An even greater concern is the potential introduction of pathogens associated with the biocontrol agent (Samways 1997).

Host specificity is another serious concern of biological control. Many believe that host specificity is low among biological control agents (Cronk & Fuller 1995;

Markin et al. 1992; Samways 1997). Lack of host specificity can lead to range expansion of the introduced agent and further damage to native species. Hybridization between non-native species and natives may cause even host specific control agents to broaden their range (Huxel 1999). *Cinnamomum burmannii* is a member of the Lauraceae family, as is the avocado tree (*Persea americana*). It is possible that a biocontrol agent introduced to reduce the *C. burmannii* population could expand its range to include the economically important avocado tree.

Beginning a biological control program is often prohibitively expensive and is a long-term undertaking. An insect escape proof facility of the most basic design, necessary to carry out experiments with potential control agents, costs approximately $150,000 (Markin et al. 1992), which may be an unrealistic expense for financially burdened natural resource organizations. Time must be allowed for construction of approved quarantine facilities, testing and evaluation of potential insects, and finally, population establishment. Under normal circumstances, it can take seven to ten years to establish five insects within a problem area (Markin et al. 1992).

Finally, the success rate of biological control averages about 50% (Cronk & Fuller 1995; Markin et al. 1992). A population of insect agents may fail to establish outside of the quarantine facility, the population that does establish may be too small to be an effective control agent (Cronk & Fuller 1995), or the control agent may switch hosts, creating a new problem.

A biocontrol program for *C. burmannii* would need to start from the beginning. There is no mention of any potential control agents for *C. burmannii* in the current literature. Therefore, agencies would need to research potential agents, test for host specificity, establish a captive population of agents, and then release and monitor those agents. Because of *C. burmannii's* widespread population on O'ahu, and lack of established biocontrol program, successfully controlling the population with the use of biological agents within the next decade is not likely.

When deciding whether to implement a biological control program it is important to weigh the high economic and time costs with the potential benefits. When evaluating potential success, it is important to define success. Is the goal to eliminate the pest population completely or simply keep it from spreading? Are there significant conflicts of interest, such as an alien plant may be considered a weed in one area but a valued crop the next field over (Markin et al. 1992)? And finally, is introducing the control agent subjecting other valuable species to another potential threat? All of these questions must be answered before beginning such a program.

Improve education and research

While education seems like a simplistic option for managers in terms of alien species control, its value can not be over emphasized. If foresters, horticulturists, and tourists were educated about the destruction caused by the plant and animal species they intentionally or unintentionally introduced, perhaps there would be fewer alien introductions. If all land managers and operations staff were well trained in the identification of all native and potentially threatening alien species, perhaps alien species could be recognized earlier when there is a greater likelihood of successful eradication. The public could also benefit from alien species education. By increasing general awareness, i.e., knowing the difference between native and alien flora, the importance of native plants over alien, that alien plants can threaten native communities, and apparently harmless activities such as gardening or forestry, can result in the naturalization of plants (Cronk & Fuller 1995), people can begin to take proactive actions to prevent further introductions.

Historically, *Cinnamomum spp.* was introduced onto O'ahu for reforestation purposes. Had the foresters known about the potential problems with alien species naturalization, perhaps another species would have been chosen. Even today, *Cinnamomum burmannii* is used as an ornamental and bay leaf substitute (T. Flynn, National Tropical Botanical Garden, Kaua'i, Hawaii, Pers. Comm.; Pers. Comm.). Education directed toward horticulturists and the public might aid people in making better ornamental planting decisions. With professionals, land managers and the general public all working toward a common goal, the likelihood of avoiding the alien species problem is much higher.

There is also a need for more scientific research in tropical developing countries where so many invading species originate. Identification guides for these countries are few and often incomplete (Heywood 1989). Even in Hawaii, there is no comprehensive tree identification guide (Pers. Obs.). Identification guides are limited to native species, which are far outnumbered by alien species. While Wagner et al. (1990) and Neal (1965) have published books describing most plants found in Hawaii, these books are not identification guides. Land managers must then struggle to discover the name, originating country, and life history characteristics of alien plants finding their way into their reserves. By encouraging alien species research in other countries everyone benefits. The home country learns about the biological players in their native systems, and foreign countries that are fighting these invaders learn more about how to control them.

Indonesian farmers plant and harvest *Cinnamomum burmannii* for its bark that is then dried and sold for ground cinnamon production (Aumeeruddy & Sansonnens 1994). Researching *C. burmannii*, in its native country, could potentially benefit the local farmers as well as land managers fighting the invasion in Hawaii. By investigating site preferences, growth rates, moisture and nutrient requirements, diseases, and native dispersers, farmers may be able to increase their crop production with less effort, and Hawaii land managers would be better prepared to predict the spread of *C. burmannii* and to control it.

Future Research

In the last 25 years, roughly 27% of the invasive species studies have been about control and conservation (Pyšek 1995). In recent years, research trends have switched to more basic scientific research (e.g., mechanisms underlying invasion, impact on native flora and a search for general characteristics of invaders and invaded areas; Pyšek 1995). Long term goals now seem to focus on the ability to predict not only what species might invade and where, but why it occurs. It is important to remember to define what is meant by prediction. Are scientists interested in predicting a species potential establishment, or its ultimate impact?

Currently, research intensity depends primarily on the overall wealth of a country and its scientific traditions (Pyšek 1995). Of the roughly 900 studies done on invasive species research over the last 25 years, 27.3% were published from Australia, 25.1% from North America, 18.5% from Europe, and 11.3% from Africa, 78.4% of which were from the Republic of South Africa (Pyšek 1995). To understand more about invasive species in tropical developing countries it is likely that more wealthy developed countries will have to encourage and support scientific research in developing countries, either through supporting the countries internal scientific efforts, or by encouraging students to study abroad.

There are a number of helpful topics alien research could emphasize. Germination behavior is important in understanding invasion success and spread, as well as being relatively quick and inexpensive to study. For example, are the ground germination rates the same for *C. burmannii* in Indonesia as they are in Hawaii? What conditions do seeds germinate best under in Indonesia? Are germination rates higher or lower after passing through the gut of its native dispersers? Answers to such questions might help land mangers in invaded ecosystems predict future invasion areas and invasion behavior of *C. burmannii*. Experimental studies of competition provide direct evidence of the potential for interference (Huenneke & Thomson 1995), and reexamining those species that failed to establish may prove helpful (Wade 1997). If *C. burmannii* had been introduced into another ecosystem, but failed to establish, perhaps research might reveal the mechanisms of why it failed, providing useful information to land managers in Hawaii. By teasing apart the mechanisms of establishment and dispersal, scientists and managers can begin to understand the crux of invasions and potentially alter land management practices to slow their establishment.

Natural Area Reserve managers express the need for interaction related research; interactions between alien and native species, alien behavior in native habitat, and ecological tolerances (Tanimoto & Char 1992). Perhaps most importantly, natural reserves and parks need long term financial and political commitment and support to ensure long-term studies and monitoring.

A final area of future research is the investigation of potential alien species triggers that can occur on a global scale. For example, what changes might global warming bring in terms of suitable habitat for alien species and range expansion? How will continuing large-scale land disturbances, (e.g., loss of tropical rainforest, desertification of arid climates, and draining of wetlands) alter alien invasion success or failure?

After completing this study of *C. burmannii* on O'ahu, a number of future research possibilities come to mind. First, an additional study on both avian and mammalian disperses over the entire fruiting period would be helpful in clarifying the potential dispersers. Second, a comprehensive study of avian feeding behavior on other alien fruit bearing trees and nutritional analysis of their fruit would provide information about the relative attractiveness of *C. burmannii* compared to other fruiting alien species. Third, carrying out additional germination studies including more captive avian species under more ideal conditions (i.e., beginning germination process immediately after seed is passed) would solidify the germination results seen in this study. Including other alien fruit in the feeding trials would also test for food preference, providing information in regards to avian feeding preferences. And finally, developing a moisture, slope, and elevation gradient where *C. burmannii* is found would help land managers predict where *C. burmannii* might invade in the future.

Conclusion

Several avian species appear to play a role in the seed dispersal of *Cinnamomum burmannii* on O'ahu, in particular, the Red-vented Bulbul, Red-whiskered Bulbul, Japanese White-eye, and Spotted Dove. The bulbuls spent the least amount of time in the canopy, increasing the likelihood that any seeds they ingest are not deposited beneath the parent tree. They also consumed fruits, dropped the fewest number of fruits beneath the parent tree, swallowed the fruit whole to ensure seed ingestion, and were more likely to fly a greater distance after leaving the canopy. All of these factors indicate that the bulbuls are likely dispersers. Germination results showed a mean germination success of 39% and 27% for the Red-vented Bulbul and Red-whiskered Bulbul passed seeds, respectively. This suggests that at least some seeds carried away from the parent tree are capable of survival. If seeds survive, the potential for the formation of new *Cinnamomum burmannii* satellite populations exists.

The Japanese White-eye and Spotted Dove both ate fruit, swallowed fruit whole, and flew out of sight after leaving the canopy at least part of the time. While the Japanese White-eye's ingested seeds germinated with a mean rate of 42% and 36%, pecked and eaten respectively, the Spotted Dove did not consume *C. burmannii* fruits in captivity and therefore germination success was not determined. Other species worth mentioning are the Red-billed Leiothrix and Common Myna. Both of these species were observed feeding on *C. burmannii* fruits and had positive germination success. However, neither species produced enough observations to warrant including them in the full analyses. A future study with more observations may suggest that the Leiothrix and Myna play a larger role in the dispersal of *C. burmannii* than evidenced here.

While this information may aid land managers in their understanding of current alien species spread, it also points to a need for a broader understanding of alien species interactions. There are examples of multiple alien species interacting with native species, such as the rat, cat, and mongoose lowering the populations of native bird species in Hawaii (Warshauer 1998), and examples of multiple alien species interacting with other alien species within a habitat, like this *C. burmannii* study. Here, multiple birds from south and east Asia are dispersing seeds from an Indonesian tree. These types of multiple alien species interactions will become more common place as more exotic species are introduced into sensitive areas.

A complicating factor in working with multiple alien species interactions is not only the quantity and diversity of life histories involved, but also the lack of information about these species both in their native habitats and in their introduced environments. Land managers are then forced to conduct basic ecology studies before understanding potential interactions or devising control methods is possible.

Managers must address three primary objectives to better understand the problems associated with alien species management. First, future research must focus on invasive species ecology, species interactions in native habitats, species interactions in non-native habitats, and predicting factors of successful invasions. Second, efficient control measures must be developed and perfected. Mechanical, chemical, and biological control methods must be tested and implemented in areas containing sensitive or valuable habitats, and long-term control methods must be derived to avoid crisis management of alien species and ensure the survival of native habitats. And third, methods for the prevention of introductions should be developed. Educating foresters, horticulturists, and the general public about the dangers of alien species introductions and the value of native habitats can decrease accidental and intentional introductions and provide land managers with more lay persons to warn them of new alien invasions.

By increasing the number of basic ecology studies, such as the *Cinnamomum burmannii* work discussed here, land managers and other organizations can begin to understand the complexities of invasion biology. And by emphasizing multi-disciplinary cooperation and action against invasive species introduction and spread, perhaps alien species abatement will be more successful.

Acknowledgments

I would like to thank Pat Costales and Carol Terry of the Department of Lands and Natural Resources for their help and support in getting this project started; Peter Luscomb of the Honolulu Zoo for being a tremendous help with the care of the captive birds; and my husband Andy for countless hours of bird watching. I would also like to thank my committee members, Steve Siebert, Dan Pletscher, and Dick Sheridan for their valuable comments. This project would not have been possible without the emotional and financial help of K. and H. Horcher, and the rest of my family, to whom I am deeply grateful.

References

Literature Cited

Ali, S., and S. D. Ripley. 1996. Handbook of the birds of India and Pakistan: together with those of Bangladesh, Nepal, Bhutan, and Sri Lanka. Oxford University Press, Delhi.

Aumeeruddy, Y., and B. Sansonnens. 1994. Shifting from simple to complex agroforestry systems: an example for buffer zone management from Kerinci (Sumatra Indonesia). Agroforestry Systems 28:113-141.

Baskin, Y. 1998. Winners and losers in a changing world. BioScience 48(10):788-792.

Blackburn, W., R. W. Knight, and J. L. Schuster. 1982. Salt cedar influence on sedimentation in the Brazos River. Journal of Soil and Water Conservation 37(5):298-301.

Brown, J. H. 1989. Patterns, modes and extents of invasions by vertebrates, pp. 85-109. *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [ed.], Biological invasions -- a global perspective Scope 37. John Wiley & Sons, New York.

Chavez-Ramirez, F., and R. D. Slack. 1994. Effects of avian foraging and post foraging behavior on seed dispersal patterns of Ashe juniper. OIKOS 71:40-46.

Conant, S. 1998. Birds, pp. 130-134. *In* S. P. Juvik and J. O. Juvik [ed.], Atlas of Hawai'i. University of Hawaii Press, Honolulu, HI.

Cronk, Q. C. B., and J. L. Fuller. 1995. Plant invaders - threat to natural ecosystems. Chapman & Hall, New York.

D'Antonio, C. M. 1990. Seed production and dispersal in the non-native, invasive succulent *Carpobrotus edulis* (Aizoaceae) in coastal strand communities of central California. Journal of Applied Ecology 27:693-702.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

di Castri, F. 1989. History of biological invasions with special emphasis on the old world, pp. 1-30. *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [ed.], Biological invasions – a global perspective Scope 37. John Wiley & Sons, New York.

Duncan, K. W. 1997. A case study in *Tamarix ramosissima* control: Spring Lake, New Mexico, pp. 115-121. *In* J. H. Brock, M. Wade, P. Pyšek, and D. Green [ed.], Plant invasions: studies from North America and Europe. Backhuys Publishers, Leiden.

Edwards, K. R., M. S. Adams, and J. Kvet. 1995. Invasion history and ecology of *Lythrum salicaria* in North America, pp.161-180. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [ed.], Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Fowler, J., L. Cohen, and P. Jarvis. 1998. Practical statistics for field biology. John Wiley & Sons, New York.

Frazer, N. B. 1992. Sea turtle conservation and halfway technology. Conservation Biology 6(2):179-184.

Halvorson, W. L. 1992. Alien plants at Channel Islands National Park, pp. 64-96. *In* C. P. Stone, C. W. Smith, and J. T. Tunison [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Harlow, W. M., E. S. Harrar, J. W. Hardin, and F. W. White. 1991. Textbook of dendrology. McGraw-Hill, Inc., New York.

Herd, R. M., and T. J. Dawson. 1984. Fiber digestion in the Emu, *Dromaius novaehollandiae*, a large bird with a simple gut and high rates of passage. Physiological Zoology 57(1):70-84.

Heywood, V. H. 1989. Patterns, extents and modes of invasion by terrestrial plants, pp. 31-60. *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [ed.], Biological invasions – a global perspective Scope 37. John Wiley & Sons, New York.

Holt, R. A. 1992. Control of alien plants on Nature Conservancy preserves, pp. 525-534. *In* C. P. Stone, C. W. Smith, and J. T. Stone [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Howe, H. F., and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. The American Naturalist 111:817-832.

Huenneke, L. F., and J. K. Thomson. 1995. Potential interference between a threatened endemic thistle and an invasive nonnative plant. Conservation Biology 9(2):416-425.

Huxel, G. R. 1999. Rapid displacement of native species by invasive species: effects of hybridization. Biological Conservation 89:143-152.

Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. Evolution 23(1):1-27.

Jones, M. J., L. A. Lace, E. C. Harrison, and B. Stevens-Wood. 1998. Territorial behaviour in the speckled wood butterflies *Pararge xiphia* and *P. aegeria* of Madeira: a mechanism for interspecific competition. Ecography 21:297-305.

Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species, pp. 15-38. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [ed.], Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Long, J. L. 1981. Introduced birds of the world. A. H. and A. W. Reed, Sydney, Australia.

Loope, L. L. 1992. An overview of problems with introduced plant species in national parks and biosphere reserves of the United States, pp. 3-28. *In* C. P. Stone, C. W. Smith, and J. T. Tunison [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Macdonald, I. A. W., L. L. Loope, M. B. Usher, and O. Hamann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective, pp. 215-255. *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H.

Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [ed.], Biological invasions – a global perspective Scope 37. John Wiley & Sons, New York.

MacFarland, C. G., J. Villa, and B. Toro. 1974. The Galapagos Giant Tortoises (*Geochelone elephantopus*) part 1: status of the surviving populations. Biological Conservation 6:118-33.

Markin, G. P., P.-Y. Lai, and G. Y. Funasaki. 1992. Status of biological control of weeds in Hawaii and implications for managing native ecosystems, pp. 466-482. *In* C. P. Stone, C. W. Smith, and J. T. Stone [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Markin, G. P. 1989. Alien plant management by biological control, pp. 70-73. *In* C. P. Stone and D. B. Stone [ed.], Conservation biology in Hawaii. University of Hawaii Press, Honolulu, HI.

McKey, D. 1975. The ecology of coevolved seed dispersal systems, pp. 159-191. *In* L. E. Gilbert, and P. H. Raven [ed.], Coevolution of animals and plants. University of Texas Press, Austin.

Meidell, J. S., H. L. Oppenheimer, and R. T. Bartlett. 1997. Records of the Hawaii biological survey for 1996-Part 2: notes. Bishop Museum Occasional Papers: No. 49:17-18.

Meyer, J.-Y., and J. Florence. 1996. Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). Journal of Biogeography 23:775-781.

Meyer, J.-Y., 1996. Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pacific Science 50(1):66-76.

Moulton, M. P., and S. L. Pimm. 1986. Species introductions to Hawaii, pp. 231-249. *In* H. A. Mooney and J. A. Drake [ed.], Ecology of biological invasion in North America and Hawaii. Springer-Verlag, New York.

Neal, M. C. 1965. In gardens of Hawaii. Bishop Museum Press, Honolulu, HI.

Panetta, F. D., and J. McKee. 1997. Recruitment of the invasive ornamental, *Schinus terebinthifolius*, is dependent upon frugivores. Australian Journal of Ecology 22:432-438.

Pimm, S. L. 1989. Theories of predicting success and impact of introduced species, pp. 351-367. *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [ed.], Biological invasions – a global perspective Scope 37. John Wiley & Sons, New York.

Power Bratton, S. 1975. The effect of the European wild boar, *Sus scrofa*, on gray beech forest in the Great Smokey Mountains. Ecology 56:1356-1366.

Pratt, T. K., and E. W. Stiles. 1983. How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. The American Naturalist 122(6):797-805.

Pyšek, P. 1995. Recent trends in studies on plant invasions, pp. 223-236. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [ed.], Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology 11(1):193-203.

Rejmánek, M. 1995. What makes a species invasive?, pp. 3-13. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [ed.], Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Ricklefs, R. E. 1990. Ecology. W. H. Freeman and Company, New York.

Samways, M. J. 1997. Classical biological control and biodiversity conservation: what risks are we prepared to accept? Biodiversity and Conservation 6:1309-1316.

Skolmen, R. G. 1980. Plantings on the forest reserves of Hawaii 1910-1960: reference distribution. Honolulu, HI: U.S. Dep. Agric. For. Serv. Pac. Southwest For. Range Exp. Stn. 441p.

Smith, C. W. 1989. Non-native plants, pp. 60-69. *In* C. P. Stone and D. B. Stone [ed.], Conservation biology in Hawaii. University of Hawaii Press, Honolulu, HI.

Smith, C. W. 1985. Impact of alien plants on Hawaii native biota, pp. 180-243. *In* C. P. Stone and J. M. Scott [ed.], Hawaii terrestrial ecosystems preservation and management. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu, HI.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113:194-202.

Soderback, B. 1994. Interactions among juveniles of two freshwater crayfish species and a predatory fish. Oecologia 100:229-235.

Starr, C., and R. Taggart. 1989. Biology: the unity and diversity of life. Wadsworth Publishing Company, Belmont, CA.

Tanimoto, V. M., and W. P. Char. 1992. Alien plant control on state lands including natural areas, pp. 536-550. *In* C. P. Stone, C. W. Smith, and J. T. Stone [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Taylor, D. 1992. Controlling weeds in natural areas in Hawaii: a manager's perspective, pp. 752-756. *In* C. P. Stone, C. W. Smith, and J. T. Stone [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Thompson, D. Q., R. L. Stuckey, and E. B. Thompson. 1987. Spread, impact and control of Purple Loosestrife (*Lythrum salicaria*) in North American wetlands, 55pp. Fish & Wildlife Research Report 2. U.S. Department of Interior, Fish & Wildlife Service, Washington, D. C.

Tunison, J. T., and C. P. Stone. 1992. Special ecological areas: an approach to alien plant control in Hawaii Volcanoes National Park, pp. 781-798. *In* C. P. Stone, C. W. Smith, and J. T. Stone [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Usher, M. B. 1989. Ecological effects of controlling invasive terrestrial vertebrates, pp. 463-490. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [ed.], Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. OIKOS 57:7-13.

Vitousek, P. M., K. Van Cleve, N. Balakrishnan, and D. Mueller-Dombois. 1983. Soil development and nitrogen turnover in montane rainforest soils on Hawaii. Biotropica 15(4):268-274.

Wade, M. 1997. Predicting plant invasions: making a start, pp. 1-18. *In* J. H. Brock, M. Wade, P. Pyšek, and D. Green [ed.], Plant invasions: studies from North America and Europe, Backhuys Publishers, Leiden.

Wagner, W., D. R. Herbst, and S. H. Sohmer. 1990. Manual of the flowering plants of Hawaii Volume 1 and 2. University of Hawaii Press, Bishop Museum Press, Honolulu, HI.

Warshauer, F. R. 1998. Alien species and threats to native ecology, pp. 146-149. *In* S. P. Juvik and J. O. Juvik [ed.], Atlas of Hawai'i. University of Hawaii Press, Honolulu, HI.

Wheelwright, N. T. 1991. How long do fruit-eating birds stay in the plants where they feed? Biotropica 23(1):29-40.

Whitmore, T. C. 1997. Tropical forest disturbance, disappearance, and species loss, pp. 3-12. *In* W. F. Laurance, and R. O. Bierregaard, Jr. [ed.], Tropical forest remnants. The University of Chicago Press, Chicago.

Wilcove, D. S., C. H. Mclellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone, pp. 237-256. *In* M. E. Soulé [ed.], Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, MA.

Williamson, M. 1999. Invasions. Ecography 22:5-12.

Whiteaker, L. D., and D. E. Gardner. 1992. Firetree (*Myrica faya*) distribution in Hawaii, pp. 225-240. *In* C. P. Stone, C. W. Smith, and J. T. Tunison [ed.], Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.