

Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests

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Received 1 September 2004; accepted in revised form 18 November 2005

Key words: biological control, *Clidemia hirta*, demography, elasticity analysis, invasive species, matrix models, near-term dynamics

Abstract

Introduction of biological control agents to reduce the abundance of exotic invasive plant species is often considered necessary but risky. I used matrix projection models to investigate the current population dynamics of *Clidemia hirta* (Melastomataceae), an invasive shrub, in two rainforest stands on the island of Hawaii and to predict the efficacy of hypothetical biological control agents in reducing population growth rates. Stage-structured matrix models were parameterized with field data collected over 3 years from 2906 *C. hirta* plants in a recently invaded forest with an open overstory (Laupahoehoe) and 600 plants in a less recently invaded forest with a closed canopy (Waiakea). Asymptotic population growth rates (λ) for both populations in all years were greater than one, demonstrating that both populations were growing. Composite elasticities were high for the seedling life-history stage and fecundity, and near-term demographic elasticities suggested that changes in seedling survival would have the largest effect on population size in the short term. However, simulations showed that almost 100% of seedlings or new recruits produced per reproductive adult would have to be destroyed to cause populations to go locally extinct under current environmental conditions. Herbivores or pathogens that decrease survival across all vegetative stages by 12% at Waiakea and 64% at Laupahoehoe were projected to cause the populations to decline. Thus, biocontrol agents that reduce survival of multiple life-history stages rather than seed production should be pursued to control *C. hirta* in Hawaiian rainforests.

Introduction

Exotic invasive plant species have substantial environmental and economic costs (Parker et al. 1999; Pimentel et al. 2000), and methods most effective for control of these species are often far from obvious (McEvoy and Coombs 1999). Biological control is one method that has been used with varying success to control invasive plant populations. In classical biocontrol, non-native natural enemies (herbivores and pathogens) are introduced

to reduce seed production, stunt growth, or kill exotic invasive plants outright. Biocontrol agents have been notably successful in controlling some plant species such as *Senecio jacobaea* in the northwestern United States (McEvoy et al. 1991), *Opuntia ficus-indica* in South Africa (Zimmermann and Moran 1982), and *Hypericum perforatum* in California (Huffaker and Kennett 1959). However, biocontrol introductions have not been effective in controlling invasive plants in most other cases (Debach and Rosen 1991; McFadyen 1998). In

addition, concerns have been raised about the risks exotic biocontrol agents pose to non-target species (Howarth 1991; Simberloff and Stiling 1996a, b; Louda et al. 1997; Thomas and Willis 1998), especially when many insects or pathogens are introduced against one target species (Thomas and Willis 1998). Therefore, there is interest in determining whether or not biocontrol would likely be effective given the population dynamics of plants and estimating which among several potential agents is likely to cause the greatest decline in population growth rates of target invasive species (McEvoy and Coombs 1999).

Stage-structured matrix projection models can be used to project the effects of potential control agents. These models use probabilities of survival, growth, and retrogression (returning to a previous stage by shrinking) as well as the fecundity of each life-history stage to estimate the asymptotic population growth rate, stable stage distribution, and stage-specific reproductive values under particular environmental conditions (Caswell 2001). Effects of differences in survival, growth, or reproduction in time or space can be modeled easily with these calculated variables. Elasticity analysis is an important tool in matrix model analysis for invasive species because it projects the relative contribution of each matrix element (survival, growth, or reproduction of each stage) to the population growth rate in the current environment (de Kroon et al. 1986). Biocontrol agents that affect the stages or transitions with the largest elasticities can then be identified. These agents should, in theory, be effective at reducing population growth rates (Shea and Kelly 1998; McEvoy and Coombs 1999; de Kroon et al. 2000).

An important caveat of traditional matrix population models for invasive species is that they estimate asymptotic population growth rates assuming that the environmental conditions do not change and that density dependence does not occur (Bierzychudek 1999; Fox and Gurevitch 2000). However, most environments are dynamic, populations rarely approach stable stage distributions, and density dependence may be very important. Nevertheless, matrix models can be used as heuristic tools to project what could happen under a given environment, to evaluate the relative contributions of each life-history stage on the population growth rate, and to simulate

the effect of biocontrol agents that attack one or more stages (Shea and Kelly 1998; Parker 2000; Caswell 2001). In addition, they can be coupled with near-term demographic analysis, which examines how proportional changes in vital rates may affect population size in the short term (Fox and Gurevitch 2000). Together, these analyses can help to address questions such as: should seed predators be introduced at the front line of the attack as suggested by some biological control practitioners (De Loach 1981; Moran et al. 2004) or would leaf-chewing or sucking insects be predicted to have larger demographic effects (Crawley 1989; Hoffmann and Moran 1998; Radford et al. 2001)?

The goal of this study was to evaluate the potential effects of different types of biocontrol agents on the population dynamics of an exotic invasive tropical shrub, *Clidemia hirta* (L.) D. Don (Melastomataceae) in Hawaiian rainforests. This species is native to Central and South America and the Caribbean Islands where it is a minor weed in disturbed areas in mesic to wet environments from sea level to 1500 m elevation (Wester and Wood 1977). Though absent in forest understory in its native range, the species has become an aggressive invader of open areas and forest understory in its introduced range including tropical islands in the Indian and Pacific Oceans and continental areas of Asia and Africa (Wester and Wood 1977; Gerlach 1993; Sheil 1994; Renner et al. 2001). It is a problematic weed in Hawaiian rainforests (Smith 1992).

Since 1953, several biocontrol agents have been introduced in Hawaii to control *Clidemia hirta*. Of the Lepidoptera biocontrol agents that have become established, *Carposina bullata* (Carposinidae) feeds on flower buds and *Mompha trithalama* (Mompidae) feeds on flowers and berries (Nakahara et al. 1992). Leaf-feeding beetles and moths, terminal bud-attacking thrips, and a leaf spot fungus also have been introduced and become established (Nakahara et al. 1992). None of the biocontrol agents introduced thus far have caused declines in *C. hirta* abundance in forest understory in Hawaii (Nakahara et al. 1992). However, insect herbivores and fungal pathogens are at least partially responsible for excluding this species from forest understory in Costa Rica, part of its native range, suggesting

that certain biocontrol agents could provide effective control of this species in shaded habitats in Hawaii (DeWalt et al. 2004; DeWalt 2005).

Using Lefkovich stage-structured projection matrices, I addressed three questions: (1) How does the asymptotic population growth rate of *C. hirta* vary among years and locations in Hawaii? (2) What is the relative importance of different vital rates to the asymptotic population growth rate at each site in each year? (3) How are proportional changes in vital rates likely to affect population sizes in the short term? and (4) What are the potential effects of hypothetical biocontrol agents that affect different parts of the life cycle? To address these questions, I tagged and measured plants during four censuses in a *C. hirta* population representing recently invaded forest with a relatively open canopy (Laupahoehoe) and another population representing less-recently invaded forest with a dense canopy (Waiakea).

Methods

Study species and sites

Clidemia hirta is a densely branching, slightly woody shrub that grows to a maximum of 2–3 m in height in its introduced range. Although it does not grow clonally, it is a vigorous resprouter and may root along fallen stems. The fruits are pulpy, dark-blue berries that contain hundreds of ca. 0.5 mm-diameter seeds (Wester and Wood 1977). Flowering and fruiting may occur throughout the year. Seeds are primarily dispersed by birds.

In 1998, I established permanent plots at two forest reserves, Waiakea and Laupahoehoe, on the windward side of the island of Hawaii. At both sites, forests were dominated by the native canopy tree *Metrosideros polymorpha* (Myrtaceae) but were heavily invaded by exotic shrubs and trees, such as *Psidium cattleianum* (Myrtaceae) and *Melastoma candidum* (Melastomataceae) at Waiakea and *P. cattleianum* and *Buddleja asiatica* (Scrophulariaceae) at Laupahoehoe. *Clidemia hirta* has likely been present at Waiakea for at least 15 years, but it was rare at the Laupahoehoe site in 1988 (DOFAW Natural

Areas Reserve survey, B. Stormont, Pers. Comm.). Mean annual rainfall is ca. 3500 mm at Waiakea (400 m a.s.l.) and Laupahoehoe (790 m a.s.l.) (Giambelluca et al. 1986). Relatively nutrient-poor soils at Waiakea are derived from a recent (750–1500 y BP) Mauna Loa Volcano lava flow, whereas the relatively nutrient-rich soils at Laupahoehoe are derived from a more highly-weathered Mauna Kea flow (5000–10,000 y BP) (Crews et al. 1995; Wolfe and Morris 1996).

At each site, I established a plot in an area heavily invaded by *C. hirta*. Approximately 300 plants were tagged initially at each site; therefore, plots were 20 m×100 m at Laupahoehoe and 10×20 m at Waiakea. Plants were censused in June or July of 1998, 1999, 2000, and 2001. Because of differences in population growth rates, I ended up marking and following 2906 plants at Laupahoehoe and 600 plants at Waiakea over the 4 years of the study.

Stage classification

Stages were assigned using life-history characteristics and estimated plant biomass (Figure 1). Only plants greater than or equal to 4.5 cm were tagged and followed. Independently rooted ramets for which connections to larger individuals were obvious were measured separately but were treated as part of the larger individual. Aboveground biomass (g) for each individual was estimated from plant height (cm) and basal stem diameter (cm) with a regression equation developed from samples of plants harvested outside of the two plots ($n=22$ for Waiakea and 35 for Laupahoehoe). The plants were cut at the soil surface, dried, and weighed. The resulting equation was $\ln(\text{biomass}) = 1.08 + 2.27 \ln(\text{diameter}) + 0.706 \ln(\text{height})$, which fit the data well ($r^2=0.98$). The five stages with their biomass range were seedling (<10 g), small adult (10–50 g), medium adult (50–100 g), large adult (100–200 g), and extra-large adult (≥ 200 g). No seedlings larger than 10 g were found as new recruits in any year. I assumed that no adults could retrogress to be a seedling because elements in that row of the matrix were reserved for fecundity estimates. There were only three instances when adults shrank this substantially. All adults were potentially reproductive (see below).

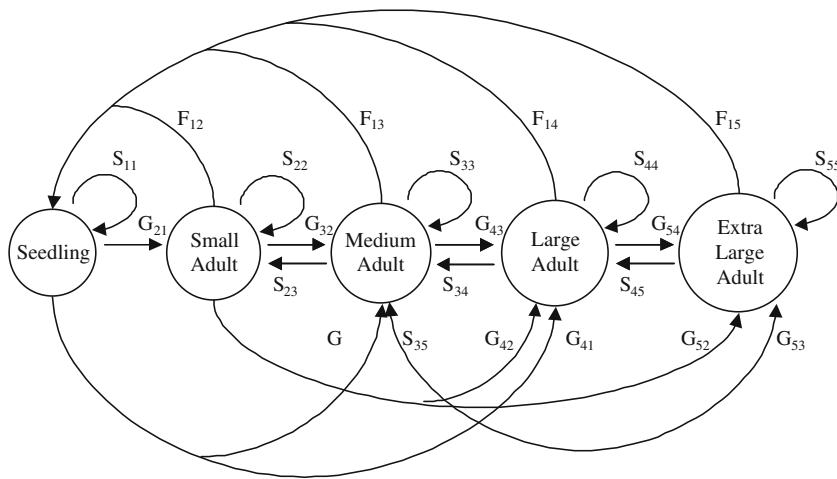


Figure 1. Life-cycle graph of *Clidemia hirta*, showing all transitions observed in at least one of the two Hawaiian populations studied between 1998 and 2001. Circles represent plant stages, arrows represent transitions between stages, and letters correspond to non-zero matrix entries.

Fecundity was calculated as the mean number of seedlings per adult that recruited into the population during the growth year. Calculations follow those of Valverde and Silvertown (1998). First, I estimated the number of fruits a plant of biomass b in year t would produce before year $t+1$ using equations specific to the site:

$$\begin{aligned} &\text{fruits/year(Laupahoehoe)} \\ &= -77.09 + 5.79b (r^2 = 0.79, n = 95, P < 0.001), \end{aligned}$$

$$\begin{aligned} &\text{fruits/year(Waiakea)} \\ &= -8.868 + 0.977b (r^2 = 0.71, n = 163, P < 0.001). \end{aligned}$$

These equations were developed from a subset of plants monitored monthly for ripe fruit in each population between June 1998 and June 1999. *Clidemia hirta* fruit in Hawaii generally contain between 300 and 500 seeds, but may occasionally contain up to 900 seeds (mean \pm SD: 412 ± 65 ; $n=10$). Thus, I estimated the total number of seeds produced per plant by multiplying the number of fruit per year by 412. Second, I summed the estimated number of seeds produced by all plants in each stage class. This number was then divided by the estimated total number of seeds produced each year across all stage classes. The resulting number was the proportional contribution of each adult stage class to seed production in that year. Third, I multiplied this proportion by the total number of seedlings

counted the following year to determine the number of recruits produced by each stage class. Finally, the mean fecundity per adult in each adult stage class was calculated by dividing the number of recruits produced by each stage class by the number of adults in each adult category at time t .

Stage-class transitions

The life-history transitions of *C. hirta* plants are represented in its life-cycle graph (Figure 1). The seed stage is not included in this life cycle because the transition probabilities of such small seeds are poorly known and were not examined in this study. Enforced dormancy in *C. hirta* does not occur, but seeds may live in the soil for more than 1 year (S. J. DeWalt, unpublished data). Thus, the transition from adult to seedling comprises multiple vital rates including germination, establishment, and growth to 4.5 cm in height. Incorporation of a seed bank into the life cycle would likely decrease the asymptotic population growth rate because it would slow down moving juveniles into larger size classes.

Asymptotic demographic analysis

I used stage-based matrices (Lefkovich 1965) to describe the demography of *C. hirta* populations. The projection matrix model has the form:

$n_{(t+1)} = \mathbf{A} n_{(t)}$ where $n_{(t)}$ and $n_{(t+1)}$ are vectors of the number of individuals in each stage at time t and $t+1$, and \mathbf{A} is a matrix of elements, a_{ij} , which represent transitions or contributions of individuals in stage j to stage i after one time step. Matrix entries are subdivided into fecundity (F, production of new seedlings), growth (G, transition to larger stages), and survival (S, persistence in the same stage or retrogression to smaller stages). Non-fecundity matrix elements above the main diagonal of the matrix represent retrogression to smaller stage classes. In the studied populations, plants occasionally shrank (retrogressed) if they decreased in height or lost a ramet.

Each population was censused four times, yielding a total of six transition matrices. MATLAB 6.0 (Mathworks 2001) was used to calculate eigenvalues, eigenvectors, and elasticities. For each matrix, I calculated the elasticity of every matrix element to λ , the dominant eigenvalue. Elasticity analysis estimates the effect of a proportional change in vital rates on λ and is used to assess the importance of different life stages and vital rates on population dynamics (Caswell 2001). I summarized the elasticity analyses using the property that elasticities sum to unity. As in Horvitz and Schemske (1995) and Parker (2000), I calculated composite elasticities for the fate of each vegetative stage by summing elasticities for each column, excluding fecundity values. A composite elasticity for fecundity was also calculated.

I estimated the standard error of λ using series expansion (Caswell 2001). First-order approximation to the variance $V(\lambda)$ was calculated by summing the variances among the matrix elements. This method assumes small variances and no covariance among the elements (Caswell 2001), and thus serves only to approximate values of variance. The variance for each adult stage for fecundity was estimated from the variance each year in the number of new recruits attributed to each adult in each stage. The standard error (σ) was calculated as the square root of the variance and was used to approximate 95% confidence intervals ($\lambda \pm 2\sigma$). Because this method assumes no covariance among the elements, the calculated confidence intervals likely are conservative and may be much wider.

Log-linear analyses were used to determine whether transition probabilities differed among

populations or years. Initial state (stage_{*t*}), time period (1998–1999, 1999–2000, and 2000–2001), location (Waiakea and Laupahoehoe), and fate (stage_{*t+1*}; including ‘dead’ as a stage) were the categorical variables in these analyses and are referred to as *S*, *T*, *L*, and *F*, respectively. The response variable was the observed frequency of tagged individuals per category. A constant of 0.5 was added to each cell to avoid estimation problems (Fingleton 1984).

I examined several models to test whether time (*T*) or location (*L*) affected the fate of *C. hirta* plants, given the initial state. The null model where fate is dependent on the initial state but not on time or location is denoted as *FS*, *STL*. As in Caswell (2001), interaction terms, such as *STL*, imply that all the single-factor terms (*S*, *T*, *L*) and the lower-order interactions (*ST*, *SL*, *TL*) are also present in the model. G^2 statistics were calculated for each model using the GENMOD procedure with a Poisson distribution and log link in SAS Version 8 (SAS Institute 2000).

Near-term demographic analysis

Following the work of Fox and Gurevitch (2000), I examined transient dynamics of the Waiakea and Laupahoehoe populations using initial population structures from the year 2000 and the 2000–2001 matrices. Time-normalized elasticities of population size to changes in transition rates were examined for populations projected 5 years in the future. These analyses produce vectors estimating the proportional change in the population size of each stage in response to proportional changes in transition rates. The amount of information produced by these analyses is substantial, and therefore I report only (1) the transition changes that would have the largest effect on seedling numbers, (2) the transition changes that would have the largest effect on any stage, and (3) the projected effect on each stage of perturbations in the transition rate of seedlings growing to small adults.

Biocontrol simulations

Biocontrol simulations were used in addition to the elasticity analyses to project the level of damage

needed for hypothetical herbivores or pathogens to cause a decline in *C. hirta* population growth rates at Laupahoehoe and Waiakea. The elasticity analyses described above only examine proportional contributions of one transition at a time to the population growth rate, whereas the simulations can examine the effect of changes on multiple transitions. Leaf-chewing and sucking insects often affect multiple stages, which can be modeled by the simulations but not the elasticity analysis. The two analyses are complementary because the elasticity analyses can identify which transitions to target while the simulations project the magnitude to which they would need to be altered.

I conducted three simulations using values in the 2000–2001 matrices for each population. First, I investigated the potential impact of biocontrol agents that affect seed production or seedling establishment by reducing fecundity values for all adult stages by fixed proportions. Second, I evaluated the effect of a control agent that causes mortality only in seedlings by decreasing the survival rate of seedlings by a fixed proportion. Third, I examined the impact of biocontrol agents that decrease survival rates of all vegetative plants by reducing all non-fecundity elements of the matrix by a fixed proportion. The latter two analyses assumed that growth is unaffected by the control agents and therefore growth transitions were decreased only by the fixed proportion of plants killed.

Results

Population growth rates

Both populations of *C. hirta* studied in Hawaii were growing quickly. This result is demonstrated by the increase in total biomass (Figure 2a) and density (Figure 2b) over time in both populations, as well as the asymptotic population growth rates (λ) greater than one (Figure 3). Survivorship was high for all stage classes, particularly post-seedling stages, which approached or equaled 1 in all years for both locations (Table 1). Even seedlings had high survivorship, ranging from 95% to 97% at Waiakea and 81% to 91% at Laupahoehoe.

Initial and final densities and plot biomass were lower for the Laupahoehoe than the Waiakea population, but the former population was growing more quickly (Figure 3). The declining rate of accumulation of plants over time (Figure 2b) and the smaller proportion of seedlings in the last census at Waiakea (Table 1) suggests that fewer plants were recruiting into the population. Individual plants at Laupahoehoe also were growing in size more quickly than at Waiakea. This is apparent in the non-zero probabilities of multi-stage growth transitions (e.g., from seedling to large adult in 1 year), which were zero at Waiakea (Table 1).

Location, time, and initial state significantly affected the fate of plants (Table 2). In addition, fate and time were not independent for some initial states (Table 3). For example, among years, the fate of small adults varied at Waiakea and the fates of seedlings and medium adults varied at Laupahoehoe (Table 3). There was also a significant

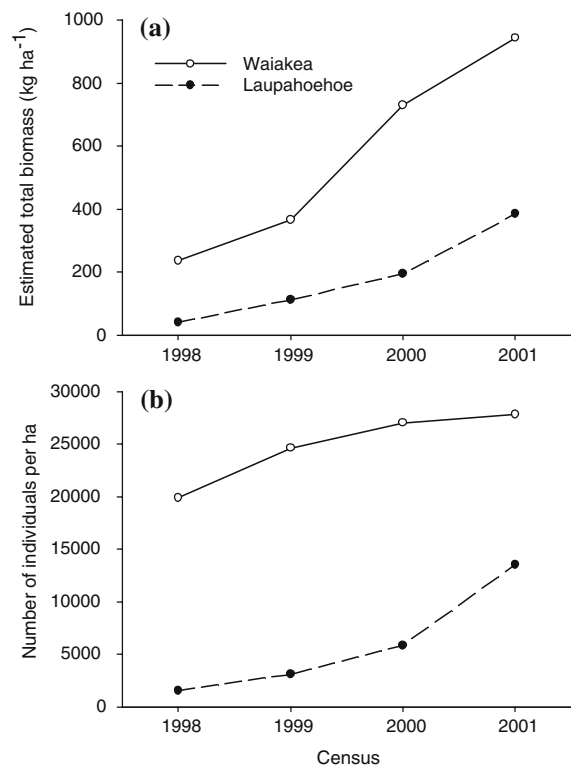


Figure 2. Increases in (a) estimated total biomass and (b) density in two *Clidemia hirta* populations censused studied between 1998 and 2001 in Hawaii.

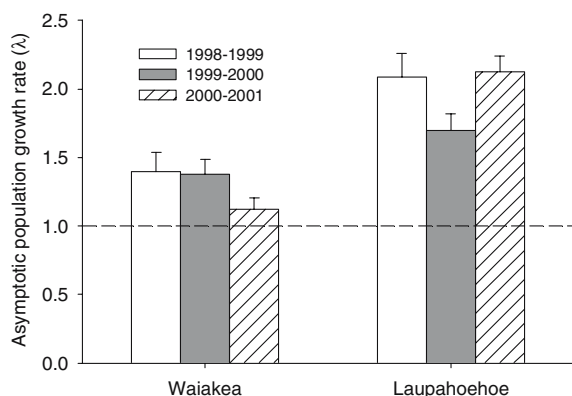


Figure 3. Asymptotic population growth rates (+2SE) for the Waiakea and Laupahoe populations for each time interval. Each population growth rate represents the dominant eigenvalue of a five-stage matrix model. The standard errors were estimated analytically by first-order approximation. The dashed horizontal line indicates a λ of one, the value of a population that is neither growing nor declining.

time \times location interaction ($T \times L$; Table 2) because the fate of plants differed significantly among years at Laupahoe ($G^2 = 101.1$, $df = 50$, $P < 0.001$), but not at Waiakea ($G^2 = 67.0$, $df = 50$, $P > 0.05$). Location had a significant effect on fate for all time intervals (1998–1999: $G^2 = 114.1$; 1999–2000: $G^2 = 84.5$; 2000–2001: $G^2 = 228.5$; $df = 25$, $P < 0.001$). This analysis confirms that the Laupahoe population was growing more quickly than the Waiakea population each year and that fate of *C. hirta* in Hawaiian populations cannot be predicted from the initial state alone. Spatial and temporal effects are important, particularly for the smaller plants (seedlings through medium adults). The time \times location interaction also indicates that the sites differed in which years were more conducive or detrimental to population growth.

Asymptotic elasticity analysis

The relative importance of each of the observed life-history transitions on the asymptotic population growth rate was relatively similar, and none were individually overwhelmingly important in the life cycle of *C. hirta*. The three transitions with the greatest proportional contribution to λ for the three time intervals made up only 39–41% of the total elasticity at Laupahoe and 42–47% at Waiakea (Table 4). The three parameters with the greatest elasticity at Laupahoe

(range = 0.104 to 0.160) were extra-large adult survival (S_{55}), extra-large adult fecundity (F_{15}), and growth of seedlings to small adults (G_{21}). At Waiakea, the three parameters with the greatest elasticity values (range = 0.120 to 0.206) varied more among years than they did at Laupahoe. The set of three always contained seedling stasis (S_{11}), but the identity of the other two parameters varied among growth of seedlings to small adults (G_{21}), small adult stasis (S_{22}), large adult survival (S_{55}), and extra-large adult survival (S_{66}).

The composite elasticity structure was fairly consistent across the three time intervals at Laupahoe but differed among years at Waiakea (Figure 4). The seedling stage class had the largest total composite elasticity in both populations in all years except the final year studied at Waiakea when the large adult class was proportionally more important to λ . For all but that year at Waiakea, the second most important stage was small adults at Waiakea and fecundity at Laupahoe. Medium, large, and extra-large adults had greater composite elasticity values at Waiakea than Laupahoe.

Near-term time-normalized elasticities

Near-term demographic analysis projected that the number of seedlings 5 years in the future at Laupahoe would be most strongly affected by changes in the fecundity of extra-large adults. The largest effect on population size to proportional changes in transition values was predicted to be on the small adult stage when the growth of seedlings to small adults was perturbed. When this transition is perturbed, a change of 11%, 27%, 14%, 17%, and 13% in the population sizes of seedlings, small adults, medium adults, large adults, and extra-large adults, respectively, would be expected compared to the size that they would have been if the transition rate had remained constant.

At Waiakea, the number of seedlings in 5 years would be most strongly affected by survival of seedlings (stasis). Survival of seedlings was also the most likely to cause the largest effect on any stage size, in this case the number of seedlings. The second-largest effect was that of changes to extra-large adult survival on the number of extra-large

Table 1. Population projection matrices and main demographic results of the matrix analysis for *C. hirta* populations in (a) Waiakea and (b) Laupahoehoe studied during 1998–1999, 1999–2000, and 2000–2001 time intervals. The first column shows λ for each population during each time interval.

| | Seedling | Small adult | Medium adult | Large adult | Extra-Large adult | n_{t+1} distribution | Stable stage distribution | Reproductive value |
|-----------------------------|--------------------------|-----------------------------|------------------------------|-----------------------------|------------------------------------|------------------------|---------------------------|--------------------|
| (a) Waiakea | | | | | | | | |
| 1998–1999 $\lambda = 1.396$ | Seedling 0.804 | Small adult <u>0.560</u> | Medium adult 1.982 | Large adult 4.295 | Extra-Large adult 6.101 | 0.751 | 0.735 | 0.025 |
| | 0.140 | <u>0.653</u> | 0.176 | 0.000 | 0.000 | 0.162 | 0.155 | 0.101 |
| | 0.003 | 0.347 | <u>0.588</u> | 0.000 | 0.000 | 0.057 | 0.069 | 0.175 |
| | 0.000 | 0.000 | 0.235 | <u>0.667</u> | 0.000 | 0.020 | 0.022 | 0.319 |
| | 0.000 | 0.000 | 0.000 | 0.333 | <u>1.000</u> | 0.010 | 0.019 | 0.380 |
| | <i>n</i> 327 | 49 | 17 | 9 | 2 | | | |
| 1999–2000 $\lambda = 1.378$ | Seedling 0.749 | Small adult 0.178 | Medium adult 0.633 | Large adult 1.364 | Extra-Large adult 2.473 | 0.619 | 0.628 | 0.051 |
| | 0.219 | 0.450 | 0.000 | 0.000 | 0.000 | 0.216 | 0.148 | 0.142 |
| | 0.005 | 0.400 | <u>0.286</u> | 0.000 | 0.000 | 0.078 | 0.057 | 0.205 |
| | 0.000 | 0.150 | 0.714 | <u>0.500</u> | 0.000 | 0.068 | 0.072 | 0.269 |
| | 0.000 | 0.000 | 0.000 | 0.500 | <u>1.000</u> | 0.018 | 0.095 | 0.333 |
| | <i>n</i> 370 | 80 | 28 | 10 | 5 | | | |
| 2000–2001 $\lambda = 1.119$ | Seedling <u>0.779</u> | Small adult 0.045 | Medium adult 0.166 | Large adult 0.318 | Extra-Large adult 0.800 | 0.526 | 0.412 | 0.073 |
| | 0.176 | 0.718 | 0.048 | 0.000 | 0.000 | 0.260 | 0.199 | 0.138 |
| | 0.003 | 0.256 | <u>0.643</u> | 0.081 | 0.100 | 0.111 | 0.152 | 0.195 |
| | 0.000 | 0.009 | 0.310 | <u>0.838</u> | 0.000 | 0.081 | 0.173 | 0.240 |
| | 0.000 | 0.000 | 0.000 | 0.081 | <u>0.900</u> | 0.022 | 0.064 | 0.354 |
| | <i>n</i> 335 | 117 | 42 | 37 | 10 | | | |
| (b) Laupahoehoe | | | | | | | | |
| 1998–1999 $\lambda = 2.084$ | Seedling <u>0.552</u> | Small adult 0.502 | Medium adult 3.362 | Large adult 6.271 | Extra-Large adult 13.631 | 0.746 | 0.768 | 0.031 |
| | 0.238 | <u>0.162</u> | 0.043 | 0.000 | 0.000 | 0.096 | 0.096 | 0.116 |
| | 0.049 | 0.405 | <u>0.087</u> | 0.000 | 0.000 | 0.045 | 0.038 | 0.207 |
| | 0.040 | 0.351 | 0.261 | <u>0.308</u> | 0.083 | 0.053 | 0.044 | 0.261 |
| | 0.000 | 0.081 | 0.609 | 0.692 | <u>0.917</u> | 0.059 | 0.053 | 0.385 |
| | <i>n</i> 223 | 37 | 23 | 13 | 12 | | | |
| 1999–2000 $\lambda = 1.700$ | Seedling <u>0.588</u> | Small adult 0.341 | Medium adult 1.906 | Large adult 4.317 | Extra-Large adult 11.480 | 0.780 | 0.764 | 0.025 |
| | 0.185 | 0.300 | 0.000 | 0.000 | 0.000 | 0.089 | 0.101 | 0.114 |
| | 0.022 | 0.400 | <u>0.250</u> | 0.030 | 0.000 | 0.036 | 0.040 | 0.179 |
| | 0.011 | 0.267 | 0.679 | <u>0.394</u> | 0.000 | 0.045 | 0.048 | 0.269 |
| | 0.000 | 0.017 | 0.071 | 0.576 | <u>1.000</u> | 0.050 | 0.046 | 0.413 |
| | <i>n</i> 464 | 60 | 28 | 33 | 37 | | | |
| 2000–2001 $\lambda = 2.126$ | Seedling <u>0.535</u> | Small adult 0.559 | Medium adult 2.847 | Large adult 5.843 | Extra-Large adult 19.129 | 0.778 | 0.750 | 0.028 |
| | 0.293 | <u>0.183</u> | 0.024 | 0.000 | 0.000 | 0.106 | 0.114 | 0.102 |
| | 0.068 | 0.327 | <u>0.214</u> | 0.038 | 0.017 | 0.040 | 0.047 | 0.159 |
| | 0.016 | 0.433 | 0.619 | <u>0.377</u> | 0.034 | 0.040 | 0.052 | 0.251 |
| | 0.000 | 0.048 | 0.143 | 0.585 | <u>0.932</u> | 0.036 | 0.036 | 0.460 |
| | <i>n</i> 914 | 104 | 42 | 53 | 59 | | | |

n_{t+1} distribution denotes the observed proportions of plants in each stage in 1999, 2000, and 2001 for each population, n denotes the number of plants from which transition values were calculated. Diagonal matrix elements representing stasis are underlined, and fecundity entries are in bold.

Table 2. Results of the log-linear analysis for the models built with the entire transition matrices from two *C. hirta* populations for the three time intervals. Frequency matrices that include dead as a fate and excluded fecundities were used for this analysis. The explanatory variables are *S*=initial stage (seedling, small adult, medium adult, etc.), *L*=location (Waiakea and Laupahoehoe), and *T*=time interval (1998–1999, 1999–2000, and 2000–2001). The response variable is *F*=fate (dead, seedling, small adult, etc.). The significance of each factor is analyzed by examining the reduction in the goodness-of-fit statistic G^2 when each factor is added to a model that excludes it (ΔG^2).

| Model | Effect | df | G^2 | ΔG^2 | <i>P</i> |
|----------------------|---------------------|-----|-------|--------------|----------|
| <i>SLT, FS</i> | | 125 | 538.5 | – | <0.001 |
| <i>SLT, FST</i> | | 75 | 427.1 | – | <0.001 |
| | <i>T</i> | 50 | – | 111.4 | <0.001 |
| <i>SLT, FSL</i> | | 100 | 168.1 | – | <0.001 |
| | <i>L</i> | 25 | – | 370.4 | <0.001 |
| <i>SLT, FST, FSL</i> | <i>T</i> × <i>L</i> | 50 | 68.8 | – | <0.05 |

adults. A proportional change in seedling survival would lead to a change of 51%, 28%, 11%, 3%, and 0.3% in the population sizes of seedlings, small adults, medium adults, large adults, and extra-large adults, respectively.

Potential effects of biocontrol

The biocontrol simulations showed that smaller changes in plant survival across all vegetative stages than in fecundity or seedling survival alone would be needed to reduce the asymptotic population growth rate below one (i.e. cause a decline in the growth rate; Figure 5). For both populations, λ remained above one until almost

Table 3. Results of log-linear analyses of effects of time period on the fate of *C. hirta* plants per initial stage in the two studied Hawaiian populations. *P*-values <0.05 represent significant deviations from the null hypothesis that the fate of plants was not affected by the census interval (model *FT*).

| Initial stage | Waiakea | | Laupahoehoe | |
|-------------------|---------|----------|-------------|----------|
| | G^2 | <i>P</i> | G^2 | <i>P</i> |
| Seedling | 9.76 | 0.46 | 64.00 | <0.001 |
| Small adult | 28.32 | <0.05 | 9.00 | 0.53 |
| Medium adult | 16.97 | 0.08 | 22.75 | <0.05 |
| Large adult | 10.54 | 0.39 | 1.54 | 1.00 |
| Extra-Large adult | 1.36 | 1.00 | 3.84 | 0.95 |

df for each test = 10.

100% of the new recruits per adult (Figure 5a) or seedlings (Figure 5b) were destroyed. However, λ dropped below one when plant survival was reduced across all vegetative stages by 12% at Waiakea and 64% at Laupahoehoe (Figure 5c).

Discussion

Clidemia hirta population dynamics exhibited temporal and spatial variation, but differences were mainly in the magnitude of the high rates of population increase. The Waiakea population, with a higher initial density and plot biomass, was growing more slowly than the Laupahoehoe population, but demonstrated less temporal variation in the fate of vegetative stages. Declines in both the number of new recruits and λ in the final year at Waiakea suggest a slowing invasion, perhaps because of saturating density. Nevertheless, seedling survivorship was very high at Waiakea each year (95–97%). At Laupahoehoe, the proportion of plants in the seedling stage was relatively constant across all years (75–78%), but seedling survivorship was lower than at Waiakea (81–91%). The more open tree canopy and lower population densities of *C. hirta* at Laupahoehoe likely contributed to the higher population growth rate there despite the lower seedling survival. Overall, the 81–97% seedling survival of *C. hirta* is high compared to most other tropical plants (Pinard 1993; Horvitz and Schemske 1995; Bruna 2003) and even other invasive plants (Shea and Kelly 1998; Parker 2000) that have been studied. This suggests that the seedling stage may have been ‘released’ from natural enemies or other limiting factors when they were introduced to Hawaii.

Low elasticity of λ to changes in most transitions in *C. hirta* (all were <0.20) suggests that there is no single ‘Achilles’ heel’ that might be exploited to reduce population growth below a sustaining rate and that control might be difficult to implement for this species. In addition, the asymptotic elasticity matrices of *C. hirta* populations were not dominated by any one stage. Even the three transitions with the greatest elasticity values made up at most 47% of the contribution to the population growth rate. In contrast, the

Table 4. Elasticity matrices for each location and time interval for *Clidemia hirta* populations in Hawaii.

| | | Seedling | Small adult | Medium adult | Large adult | Extra-large adult |
|-----------------|-------------------|----------|-------------|--------------|-------------|-------------------|
| (a) Waiakea | | | | | | |
| 1998–1999 | Seedling | 0.174 | 0.026 | 0.040 | 0.028 | 0.034 |
| | Small adult | 0.123 | 0.121 | 0.015 | 0.000 | 0.000 |
| | Medium adult | 0.005 | 0.112 | 0.085 | 0.000 | 0.000 |
| | Large adult | 0.000 | 0.000 | 0.062 | 0.057 | 0.000 |
| | Extra-Large adult | 0.000 | 0.000 | 0.000 | 0.034 | 0.085 |
| 1999–2000 | Seedling | 0.150 | 0.008 | 0.012 | 0.031 | 0.075 |
| | Small adult | 0.122 | 0.059 | 0.000 | 0.000 | 0.000 |
| | Medium adult | 0.004 | 0.076 | 0.021 | 0.000 | 0.000 |
| | Large adult | 0.000 | 0.038 | 0.069 | 0.061 | 0.000 |
| | Extra-Large adult | 0.000 | 0.000 | 0.000 | 0.075 | 0.198 |
| 2000–2001 | Seedling | 0.138 | 0.004 | 0.011 | 0.024 | 0.022 |
| | Small adult | 0.059 | 0.116 | 0.006 | 0.000 | 0.000 |
| | Medium adult | 0.001 | 0.059 | 0.113 | 0.016 | 0.007 |
| | Large adult | 0.000 | 0.003 | 0.067 | 0.206 | 0.000 |
| | Extra-Large adult | 0.000 | 0.000 | 0.000 | 0.029 | 0.120 |
| (b) Laupahoehoe | | | | | | |
| 1998–1999 | Seedling | 0.085 | 0.010 | 0.026 | 0.056 | 0.145 |
| | Small adult | 0.135 | 0.012 | 0.001 | 0.000 | 0.000 |
| | Medium adult | 0.050 | 0.051 | 0.004 | 0.000 | 0.000 |
| | Large adult | 0.051 | 0.056 | 0.017 | 0.023 | 0.007 |
| | Extra-Large adult | 0.000 | 0.019 | 0.057 | 0.076 | 0.120 |
| 1999–2000 | Seedling | 0.095 | 0.007 | 0.016 | 0.044 | 0.112 |
| | Small adult | 0.135 | 0.029 | 0.000 | 0.000 | 0.000 |
| | Medium adult | 0.025 | 0.061 | 0.015 | 0.002 | 0.000 |
| | Large adult | 0.019 | 0.061 | 0.062 | 0.043 | 0.000 |
| | Extra-Large adult | 0.000 | 0.006 | 0.010 | 0.096 | 0.160 |
| 2000–2001 | Seedling | 0.076 | 0.012 | 0.026 | 0.058 | 0.130 |
| | Small adult | 0.151 | 0.014 | 0.001 | 0.000 | 0.000 |
| | Medium adult | 0.055 | 0.040 | 0.011 | 0.002 | 0.001 |
| | Large adult | 0.020 | 0.083 | 0.050 | 0.033 | 0.002 |
| | Extra-Large adult | 0.000 | 0.017 | 0.021 | 0.095 | 0.104 |

elasticity matrices of other tropical plants studied to date generally have been dominated by one vital rate with an elasticity value >0.30 (Pinar 1993; Alvarez-Buylla 1994; Horvitz and Schemske 1995; Bernal 1998). The elasticity of large adult stasis in these populations generally is large. The elasticity matrix also was dominated by few transitions for *Carduus nutans* (Asteraceae), an exotic thistle in New Zealand (Shea and Kelly 1998); for example, seed production and germination each had elasticity values >0.30 in one of the populations studied. Similar to the current study, Parker (2000) found that elasticity was evenly distributed throughout the life cycle of another exotic invasive shrub, *Cytisus scoparius* (Fabaceae), in expanding populations in northwestern United States.

Although there may be no magic bullet to control *C. hirta* in Hawaii, biological control agents

might be most effective at decreasing the long-term population growth rate and the near-term population size if they decrease survival and growth of seedlings. This recommendation is supported by the results of the asymptotic demographic analysis that showed that the composite elasticity of the seedling stage was higher than for other stages in both Hawaiian populations in most years and the results of the near-term demographic analysis that showed that changes in seedling survival or growth would cause the greatest change in size of any stage. Thus, perturbations to seedling survival or growth of seedlings to small adults would be more effective than those that target adult fecundity or adult growth transitions. However, biocontrol agents that decrease survival alone do not show much promise for control of Waiakea or Laupahoehoe populations. The simulation projected that almost 100%

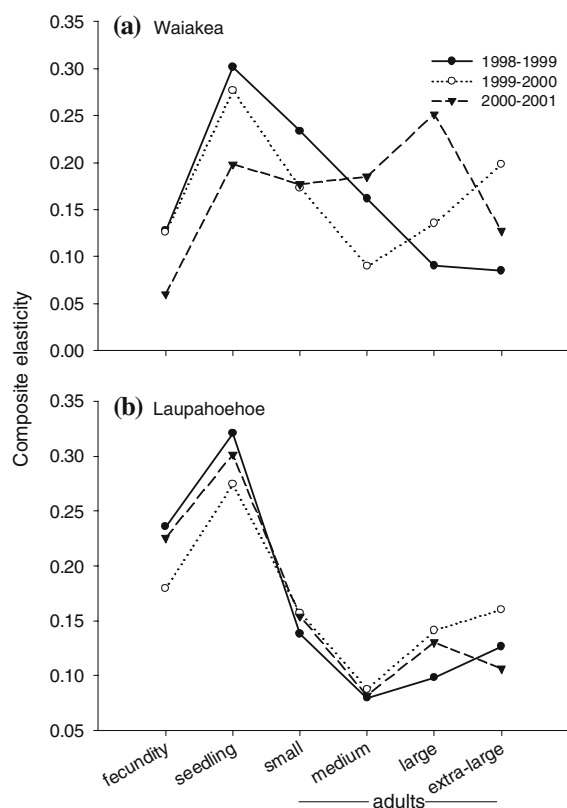


Figure 4. Composite elasticities for fecundity and the fate of each stage in the two Hawaiian populations. Different symbols represent the three time intervals.

of seedlings would have to be killed to cause the population to decline towards extinction. Nonetheless, if only one stage can be targeted, it should be the seedling stage.

Simulated reductions in recruitment (fecundity), as might occur with the introduction of seed-eating insects, seed pathogens, or damping-off fungi, showed that almost 100% of all recruits would have to be killed to cause either of the two Hawaiian populations to be exterminated. Such high levels of impact are unlikely. Other analyses have reached similar conclusions. For example, it would be necessary to destroy an estimated 97–99.9% of seeds in some *Cytisus scoparius* populations to reduce λ below one in northwestern United States and Australia (Parker 2000; Sheppard et al. 2002). Empirically, Hoffmann and Moran (1991) found that a 98% reduction in seed-set in the invasive tree *Sesbania punicea* by a bud-feeding weevil biocontrol

agent was insufficient to cause long-term reductions in plant density. In contrast, an estimated 69% seed loss was predicted to cause λ of *Carduus nutans* in New Zealand to drop below one (Shea and Kelly 1998). For *Clidemia hirta*, biocontrol agents that only reduce fecundity likely will not be the most cost-effective means of control. This is an important finding because, previously, flower- and fruit-eating moths had been pursued as biological control agents in Hawaii (Nakahara et al. 1992). The current study demonstrates that resources should not be spent primarily on seed-reducing agents. The only exception to this recommendation is if seed-reducing insects and pathogens are to be used in conjunction with complete clearing of *C. hirta* from areas using mechanical or chemical means, at which time even small reductions in the number of seeds and seedlings may reduce the intensity of follow-up operations (Moran et al. 2004).

The simulations suggest that biocontrol agents that reduce survival of *C. hirta* across all vegetative stages are more likely to cause declines in the population growth rate than those that attack seeds or seedlings only. Likewise, McEvoy and Coombs (1999) found that a flea beetle would provide the most effective control of ragwort, *Senecio jacobaea* because it affected several transitions, with the largest effect on transitions for which λ had the greatest elasticity. Reduction in populations of *Sesbania punicea* in South Africa has apparently been achieved by three weevil species that feed on different parts of the plant (Hoffmann and Moran 1998). My simulations suggest that continuous (yearly) reductions of *C. hirta* survival by 12% at Waiakea and 64% at Laupahoehoe would cause the *C. hirta* populations to go locally extinct (Figure 5c).

It should be noted that small individuals are more likely to be killed by natural enemies than older individuals that can better compensate for herbivory or pathogen attack. Thus, even the low 12% reduction in survival across all stages needed at Waiakea, not to mention the relatively high 64% reduction at Laupahoehoe, may be difficult to achieve if most individuals are adult-sized. In 2001 at the end of the study, slightly more than half (53%) of plants at Waiakea were seedlings, but the percentage had dropped steadily over the course of the study (75%, 62%, 53% in 1998–

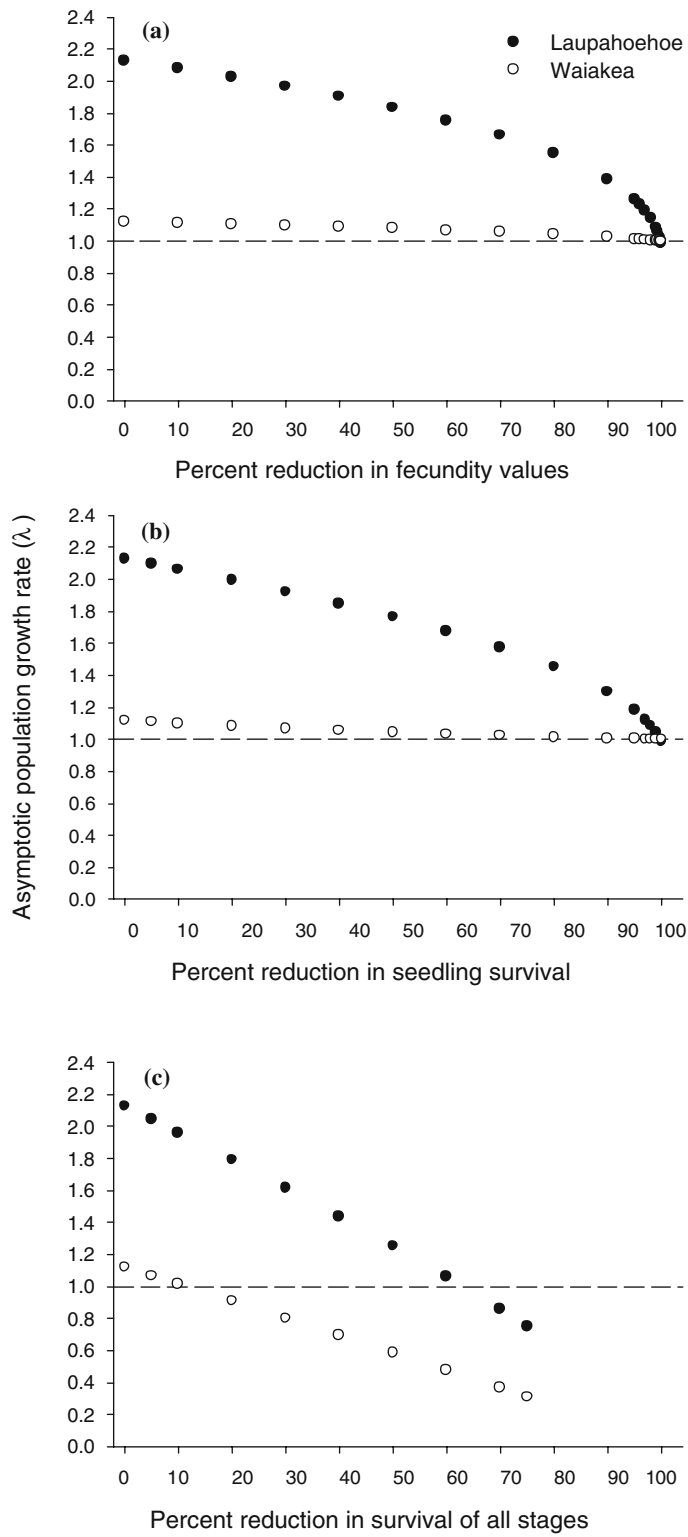


Figure 5. Asymptotic population growth rates as a function of (a) the percentage of new recruits destroyed, (b) the percentage of seedlings killed, and (c) the percentage reduction in survival of all plants by hypothetical biological control agents. The matrix model for the interval 2000–2001 for each Hawaiian population was used for these scenarios. The dashed horizontal line indicates a λ of one, representing a population that is neither growing nor declining.

1999, 1999–2000, and 2000–2001, respectively). Control may be easier to achieve at Laupahoehoe because seedlings represented a high percentage of the plants each year (75%, 78%, and 78%).

Is biological control likely to be effective against *C. hirta* in Hawaiian forests? The best evidence that it may be effective is the apparent exclusion of *C. hirta* from closed-canopy forest understory in its native range by fungal pathogens and insect herbivores (DeWalt et al. 2004). Natural enemies caused high levels of mortality for *C. hirta* seedlings planted into forest understory in its native range in Costa Rica (DeWalt et al. 2004). Survival of plants unprotected from natural enemies during a 14-month experiment was 62% lower than plants protected from natural enemies by insecticide and fungicide. Thus, the leaf-feeding Lepidoptera and weevils, gall-forming cecidomyiid flies, fungal pathogens, and stem borers that damaged *C. hirta* planted in Costa Rican forests should be explored as potential biocontrol agents. However, it remains to be seen whether one or two of the natural enemy species found in Costa Rica are responsible for the majority of the mortality in the understory or whether a suite of species would need to be introduced. Reduction in survival of plants across several stage classes may be possible only with introduction of multiple biocontrol agents, each targeting different stages. In this case, the risks of host-switching, even in Hawaii where no native Melastomataceae occur, may outweigh the benefits of controlling this plant.

Acknowledgements

I am grateful to Roddy Nagata, Gareth DeWalt, Kalan Ickes, and Bob Cabin for field assistance. Julie Denslow, Jack Ewel, Jim Hamrick, and two anonymous reviewers provided helpful comments on the manuscript. This research was supported

by a USDA Forest Service Pacific Southwest Research Station Internal Competitive grant, Sigma Xi Grants-in-Aid-of-Research, and a Board of Regents' fellowship from Louisiana State University.

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