Selection on Herbivory Resistance and Growth Rate in an Invasive Plant

Steven J. Franks,[1,*] Paul D. Pratt,[2,†] F. Allen Dray,[2,‡] and Ellen L. Simms[3,§]

1. Department of Biological Sciences, Fordham University, Bronx, New York 10458;
2. Invasive Plant Research Laboratory, United States Department of Agriculture, Agricultural Research Service, Fort Lauderdale, Florida 33314;
3. Department of Integrative Biology, University of California, Berkeley, California 94720

ABSTRACT: The evolution of increased competitive ability (EICA) hypothesis proposes that invasive species evolve decreased defense and increased competitive ability following natural enemy release. Previous tests of EICA examined the result of evolution by comparing individuals from home and introduced ranges, but no previous study of this hypothesis has examined the process of evolution by analyzing patterns of selection. On the basis of EICA, there should be selection for competitive ability without herbivores and selection for defense with herbivores. Selection on competitive ability should be stronger for genotypes accustomed to herbivores (home range genotypes), and selection on defense should be stronger for genotypes unaccustomed to herbivores (introduced range genotypes). Using a field experiment, we tested these hypotheses for the invasive plant *Melaleuca quinquenervia*. There was a negative genetic correlation between resistance and growth, indicating a trade-off. However, selection for stem elongation (an indicator of competitive ability) was always positive, and selection on resistance was always negative and did not depend on genotype source or the presence of herbivores. The patterns of selection found in this study contrast with predictions from EICA and accurately predict the lack of evolutionary change in growth and resistance following the introduction of this species from Australia to Florida.

Keywords: biological control, EICA hypothesis, Florida Everglades, natural enemies, phenotypic plasticity, phenotypic evolution.

* E-mail: franks@fordham.edu.

† E-mail: paul.pratt@ars.usda.gov.

‡ E-mail: allen.dray@ars.usda.gov.

§ E-mail: esimms@berkeley.edu.

When a species colonizes a new habitat, the biotic and abiotic conditions of the new habitat may differ from the source location, which could alter selection pressures on the new population and ultimately lead to evolutionary change (Ehler et al. 2004). This idea forms the basis for one of the central tenets of invasion biology theory, the evolution of increased competitive ability (EICA) hypothesis, which states that invasive species that are released from natural enemies in their new range will evolve decreased defense and increased allocation to traits enhancing competitive ability, such as growth rate (Blossey and Nötzold 1995). This prediction rests on the assumptions that the fitness benefits of competitive ability trade off with the fitness benefits of defense and that the relative benefits of competitive ability and defensive traits differ depending on the presence of natural enemies.

Alternatively, invasiveness could be facilitated by phenotypic plasticity for resistance or competitive ability (Bazzaz 1996; Alpert et al. 2000; Bossdorf et al. 2005). By adjusting its phenotype to the local environment, a plastic genotype might maintain high fitness across a wide range of environmental conditions (Alpert and Simms 2002). Despite the importance of these alternative hypotheses for our understanding of species invasions, direct experimental measurements of selection on resistance or competitive ability of an invasive species and of plasticity in these traits are lacking (Franks et al. 2004). In fact, while EICA is fundamentally an evolutionary hypothesis, no previous study has used the methods of quantitative genetics and selection analysis to elucidate current patterns of natural selection on invasive species, compare these patterns with expectations based on EICA, or predict evolutionary changes in natural enemy resistance or competitive ability in an invasive species.

Previous studies have either compared growth rates or resistance traits of species in their home versus in their introduced ranges (Thébaud and Simberloff 2001; Wolfe 2002) or compared traits of recently introduced genotypes with those of descendants from earlier introductions when both were raised under common conditions (Willis et al.

2000; Siemann and Rogers 2001; Vilá et al. 2003; Stastny et al. 2005). These comparisons are useful for determining whether increased competitive ability or decreased allocation to defense has evolved since the introduction of the invasive species. However, these methods show only whether evolutionary changes have occurred in the past, do not identify the agents of selection and change in selection pressures responsible for the changes in traits, and also do not help distinguish selection from drift as the evolutionary mechanism. To establish whether the absence of natural enemies is currently selecting for decreased defense or increased growth and determine whether evolutionary changes are expected to occur in the future, it is necessary to measure how natural enemies influence the strength and direction of selection on these traits (Simms and Rauscher 1992).

The response to selection on resistance to herbivory, competitive ability, or any other quantitative trait can be examined using the breeders' equation (Falconer and Mackay 1996) as follows:

$$R = h^2 s, \qquad (1)$$

where R is the response to selection (difference in mean phenotypic value for the trait of interest), h^2 is the heritability, or proportion of total phenotypic variance in a trait due to additive genetic factors, and s is the univariate selection differential, or covariance between the trait and fitness. Selection acts on traits not only directly but also indirectly through correlated responses (Lande and Arnold 1983). To examine both direct and correlated responses to selection, the following equation (Falconer and Mackay 1996) can be used:

$$R_1 = h_1^2 \beta_1 + h_1 h_2 r_A \beta_2 \delta_{P2} + h_1^2 \gamma_1, \qquad (2)$$

where β_1 is the selection gradient on trait 1, $h_1 h_2$ is the coheritability between traits 1 and 2, r_A is the genotypic correlation between traits 1 and 2, δ_{P2} is the phenotypic variance of trait 2, and γ is the quadratic selection gradient, which measures the degree of stabilizing or disruptive selection. Differences in the pattern of selection in different environments can be determined by comparing linear and quadratic selection gradients in the different environments. Statistical tests of differences in the pattern of selection are accomplished by evaluating the environment × selection gradient interaction terms in an ANCOVA, while visualizations of the selection surfaces and selection difference surfaces between environments can also aid in interpretation of fitness functions (Mauricio and Rauscher 1997).

Following the reasoning of the EICA hypothesis, selection on plant growth (a potential measure of competitive ability) and resistance traits, and thus the selection parameters in equations (1) and (2), should differ depending on the presence or absence of herbivores and for native and introduced genotypes (fig. 1). In the presence of herbivores (fig. 1A), fitness should increase with increasing resistance until reaching an optimum point, beyond which added investment in resistance is exceedingly costly. In the absence of herbivores (fig. 1B), fitness should decrease with increasing resistance because plants with low allocation to defense can devote resources to functions such as growth and competitive ability. This function is likely not strictly linear but slightly curved since there would be a relative large increase in fitness for a small decrease in resistance for genotypes high in resistance, but genotypes that are already low in resistance would see a relatively smaller increase in fitness with further decreased resistance. In the presence of herbivores (fig. 1C), fitness should increase
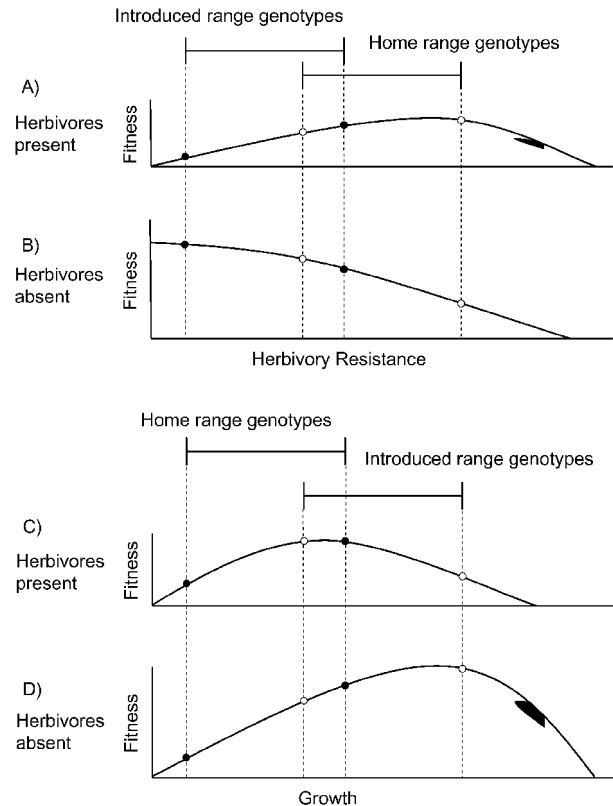

Figure 1: Hypothesized fitness functions. Shown are the predicted relationships between herbivory resistance and fitness in the presence (*A*) and absence (*B*) of herbivores and between growth and fitness in the presence (*C*) and absence (*D*) of herbivores. Curves show the underlying fitness function for the entire range of possible resistance and growth values. Bars show the range of predicted trait values for the home and introduced range genotypes. The expected selection parameters can be obtained by projecting the trait ranges onto the fitness functions.

Table 1: Predictions for patterns of selection based on the evolution of increased competitive ability model

Range	Herbivores	Resistance	Growth	s	β	γ	$\beta_{R \times G}$	$\beta_{G \times R}$
Resistance:								
Home	Present	High		>0	>0	<<0	0	
Home	Absent	High		<0	<<<0	0	<<<0	
Intro	Absent	Low		<0	<<0	<0	<<0	
Intro	Present	Low		>>>0	>>>0	0	0	
Growth rate:[a]								
Home	Present		Low	>0	>0	<<<0		0
Home	Absent		Low	>>>0	>>>0	0		<<0
Intro	Absent		High	>0	>0	<0		<0
Intro	Present		High	<0	<0	<0		<0

Note: Shown are predictions for genotypes from the home and introduced ranges, given experimental treatments of herbivory present or absent for resistance and growth. Predictions are shown for the average initial trait values, selection differentials (s), linear selection gradients (β), quadratic selection gradients (γ), and correlational selection. Selection differentials correspond to the s in equation (1). Linear and quadratic selection gradients correspond to, respectively, the β's and γ's in equation (2). Multiple symbols (>>) indicate the relative strength and direction of the parameter coefficients. See text and figure 1 for the reasoning behind the predictions.

  [a] Growth rate is an indicator of competitive ability.

with increasing growth up to an optimal level and then decrease, since resources being used for growth would not be available for defense or for other functions. The overall patterns should be similar in the absence of herbivores (fig. 1D), but the fitness peak should be shifted higher and farther toward greater growth. There would still be a peak, since beyond some optimal point, greater growth is costly and resources would be better devoted to other functions such as reproduction. The bars at the top of figure 1 show the range of resistance values expected for the introduced range and home range genotypes, which should be different because of different past selection pressures in the home and introduced ranges. Because the introduced range genotypes have been released from herbivores, they should have lower resistance values and higher growth values than the home range genotypes. By projecting the expected range of resistance values for the home and introduced range genotypes onto the fitness functions, the expected selection parameter values can be obtained. For example, in the presence of herbivores (fig. 1A), there should be strong positive selection on increasing resistance for the introduced range genotypes (which have been released from herbivores and previously selected for decreased resistance) but weak positive and/or stabilizing selection on resistance for the home range genotypes since these genotypes should already be near the optimum.

The expected multivariate selection parameters for resistance and growth are based not only on the shapes of the individual fitness functions and trait ranges but also on correlations among traits. The predicted univariate and multivariate linear, quadratic, and correlational selection parameters are given in table 1. When there are differences between the selection differentials (s) and selection gradients (β), and when there are significant correlational selection gradients ($\beta_{R \times G}$), then selection on one trait is acting in part due to the action on another correlated trait. For example, for the home range genotypes, selection for decreased resistance in the absence of herbivores is in part due to selection for increased growth and to the trade-off between growth and resistance. In general, selection should be strongest in the cases in which there is a mismatch between the current conditions and the conditions to which the genotypes have been previously adapted. For example, selection for increased resistance in the presence of herbivores should be stronger for the genotypes from the introduced range, which should have been released from natural enemies and adapted to the absence of herbivores, than for the home range genotypes, which have had a history of consistent exposure to herbivores.

To test these predictions about patterns of selection, we conducted a natural selection experiment with home range (Australia) and introduced range (Florida) genotypes of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake (hereafter referred to by genus) grown with and without insect herbivores. We asked whether populations of this invasive plant would be expected to evolve decreased resistance and increased competitive ability or, alternatively, increased plasticity for these traits by testing whether (1) there is a negative genetic correlation between growth and resistance, (2) resistance traits or growth rates are under selection, (3) patterns of selection differ in the presence or absence of insect herbivores, and (4) resistance and competitive ability are plastic in response to herbivory. If the EICA hypothesis correctly explains patterns of selection on this species, we would predict that selection for decreased resistance and increased growth would be greater

in the absence of natural enemies than when enemies are present and that directional selection on these traits would be stronger for genotypes from Australia, which have not been previously released from herbivory, than for genotypes from Florida.

Previously, Franks et al. (2007) compared resistance traits and growth rates of native and introduced genotypes of *Melaleuca* grown under common conditions both with and without insect herbivores. Although insect herbivores initially preferred introduced (Florida) host genotypes, those genotypes exhibited neither less resistance nor faster growth than native (Australia) genotypes. These results do not support the EICA hypothesis. This failure of the EICA hypothesis could arise because the benefits of resistance and competitive ability do not actually differ depending on the presence or absence of herbivores. Alternatively, resistance and/or competitive ability could be highly plastic in response to herbivory in *Melaleuca*, allowing the plants to adjust to the absence of herbivores via plasticity rather than evolution. It is also possible that a lack of time since introduction or lack of genetic variation has prevented *Melaleuca* from evolving in response to changes in selection pressure in the introduced range.

We used data from this same experiment (Franks et al. 2007) to examine patterns of selection on growth and defense. If invasive species evolve decreased defense and increased growth when released from natural enemies, as predicted by the EICA hypothesis, then we would also expect that invasive species in their introduced range would evolve increased defense and decreased growth when natural enemies are reintroduced, as occurs in biological control programs. If this is true, then we might expect that biological control programs that are initially very effective could become somewhat less effective over time as the invasive species evolve stronger defenses. However, there could be limits and constraints to the degree of evolutionary changes in defense, and the natural enemies could also evolve the increased ability to circumvent the defenses.

Methods

Study Species

Melaleuca quinquenervia (Myrtaceae), is native to Australia and is among the most troublesome invaders in the Florida Everglades (Turner et al. 1998; Serbesoff-King 2003). *Melaleuca* was introduced into Florida in the late 1800s and thus was free from herbivores in its new habitat for more than a century (Dray et al. 2006). At the time of this study, which began in 2003, two herbivorous insects from Australia had been recently released as biological control agents for *Melaleuca*: *Oxyops vitiosa* (Pascoe) (Coleoptera:

Curculionidae), a leaf-chewing weevil released in 1997 (Center et al. 2000), and *Boreioglycaspis melaleucae* (Moore) (Hemiptera: Psyllidae), a sap-feeding psyllid released in 2002 (Pratt et al. 2004; Center et al. 2006).

Experimental Design

In 1999, *Melaleuca* seeds were obtained throughout the native and introduced ranges from 60 maternal trees in Florida and 60 in Australia and New Caledonia, germinated in a greenhouse, and transplanted to the field, which was cleared of all other plants (Franks et al. 2007). Plants were spaced 5–10 cm apart within a plot, which is within the range of densities found in natural populations in Florida (Franks et al. 2006) and was expected to be close enough for intraspecific competition to occur. Plants were arranged in 1.5 × 0.5-m split plots, each containing one individual from each maternal family. One split plot of each whole plot was randomly assigned a herbivore exclusion treatment, which involved regularly spraying with the insecticide acephate (Franks et al. 2007). There were 24 split plots containing 120 seedlings each (1 seedling from each family) for a total of 2,880 plants.

We assessed plant attractiveness, resistance, competitive ability, and fitness as follows. We recorded presence/absence and species identity of all insects on all plants every 2–3 months during the experiment. We defined attractiveness to an insect species as the occurrence of that insect on a plant at a particular census. Attractiveness is thus a binomial variable (1 = insect present, 0 = insect absent). We also recorded the presence/absence of herbivory damage by each insect species on all plants every 2–3 months. Resistance was defined as the lack of damage by a given insect species (1 = damage absent, 0 = damage present). Leaf pubescence, a trait previously found to be correlated with resistance in *Melaleuca* (Franks et al. 2007), was assessed as a categorical variable with three levels, which we visually estimated for all plants and compared with standards within the experimental population. Specific leaf area (SLA; ratio of leaf area to mass) was previously found to be associated with resistance to herbivory in *Melaleuca* (Franks et al. 2007) and is likely linked to other ecologically important traits such as water use efficiency and shade tolerance (Reich et al. 1994; Ackerly 2004; Hoffman et al. 2005). To assess SLA, we collected the first fully expanded leaf of all plants, scanned each leaf, obtained its area using ImageJ software (National Institutes of Health, Bethesda, MD), and recorded its dried mass. Ratio of the mass of leaves to the mass of stems, which represents allocation to leaf area and is potentially related to resistance to herbivory, was also recorded. Rate of stem elongation, which is likely associated with the ability to compete for light, was assessed as the difference in plant height between the beginning and the end of the

Table 2: Selection values

Range	Herbivores	Resistance	Growth (cm)	s	β	γ	$\beta_{R \times G}$	$\beta_{G \times R}$
Resistance:								
Home	Present	.303 (.017)		−**.10 (.04)***	−.06 (.03)	−.03 (.03)	.04 (.04)	
Home	Absent	.892 (.012)		−**.12 (.05)***	−.06 (.04)	.01 (.03)	.06 (.05)	
Intro	Absent	.883 (.012)		−**.08 (.04)***	−.03 (.03)	−.02 (.03)	.04 (.07)	
Intro	Present	.310 (.017)		−.03 (.04)	.03 (.03)	.02 (.02)	.05 (.04)	
Growth:								
Home	Present		122.0 (1.54)	**.19 (.03)****	**.17 (.03)****	−.01 (.03)		.04 (.04)
Home	Absent		130.1 (1.63)	**.21 (.04)****	**.19 (.04)****	.01 (.04)		.06 (.05)
Intro	Absent		129.0 (1.59)	**.25 (.03)****	**.24 (.03)****	.03 (.03)		.04 (.07)
Intro	Present		122.0 (1.62)	**.23 (.23)****	**.23 (.03)****	.03 (.02)		.05 (.04)

Note: Shown are mean character values (resistance and growth), selection differentials (s), and linear (β), quadratic (γ), and correlational genotypic selection gradients (SE) for resistance and growth for genotypes from Australia (home range) and Florida (introduced range) exposed to (herbivores present) and protected from (herbivores absent) herbivory. Resistance is proportion of resistant plants (showing no herbivory), and growth is final height minus initial height. For trait values, N ranged from 661 to 691 per treatment group. For genotypic selection values, $N = 60$ families per source location. Values in bold indicate $P < .05$ for test of hypothesis of selection parameter values different from 0.

* $P < .05$.

** $P < .001$.

experiment. Fitness was estimated from total aboveground biomass of each plant harvested at the end of the experiment and dried at 70°C to constant weight (at least 2 weeks). Biomass is highly correlated with reproductive effort in *Melaleuca* (Rayachhetry et al. 2001). We could not measure reproduction because it was necessary to prevent pollen dispersal from the Australia genotypes by harvesting as soon as flowering began in June and July 2004, 12 months after transplanting.

Analysis

All statistical analyses were performed with SAS 9.1 (SAS Institute). Genetic correlations were determined by using Pearson product-moment correlations on the best linear unbiased predictors (BLUPs) of traits that were first standardized to a mean of 0 and a variance of 1, with the mean and variance pooled across populations and treatments. This type of variance standardization is especially appropriate for proportional traits such as resistance to herbivore damage (Stinchcombe 2005), and pooling across populations and treatments reduces the chances of spurious differences being detected among groups. BLUPs are superior to family means because they use all available information to obtain the parameter estimates (Shaw et al. 1995).

We conducted genotypic selection analysis, which minimizes biases due to environmental factors that directly affect both traits and fitness (Rausher 1992). Discrepancies between phenotypic and genotypic selection analyses and significant block effects in the phenotypic selection model suggested that this bias may have been present in our data, so only genotypic selection analyses are shown. For the genotypic selection analysis, we used BLUPs to estimate

breeding values for each maternal family. For resistance and attractiveness to insects, we obtained BLUPs from generalized linear mixed models using the GLIMMIX macro in SAS with a binomial error distribution and a logit link function. Leaf pubescence was modeled with a normal error distribution and a log link function. Genotypic selection analysis was then conducted by regressing the residuals of relative fitness (biomass) after accounting for initial size and block against trait breeding values. For both types of selection analysis, quadratic selection gradients were estimated from a model including both linear and quadratic terms, and linear selection gradients were estimated from a model containing only linear terms (Lande and Arnold 1983; Agrawal et al. 2004). To test whether the pattern of selection differed between source locations (Australia and Florida) and between treatments (herbivore exclusion and no herbivore exclusion), interactions between source location and treatments and the traits were examined in a mixed-model analysis.

To examine heritability and plasticity of *Melaleuca* traits, we conducted a mixed-model ANOVA using the MIXED procedure with traits as dependent variables; insecticide treatment (E), source country (S), and their interaction as fixed effects; and maternal family nested within country (G), block (B), and the block by treatment, genotype by environment, and source country by treatment by block interactions as random effects. Significance of the fixed effects was determined using F-tests, and significance of random effects was determined by χ^2 values from likelihood ratio tests (Littell et al. 1996), each with 1 degree of freedom. Patterns of herbivore attraction and resistance were assessed for the unsprayed plots only, since sprayed plants experienced minimal damage. For each trait in this analysis, a significant effect of herbivory treatment poten-
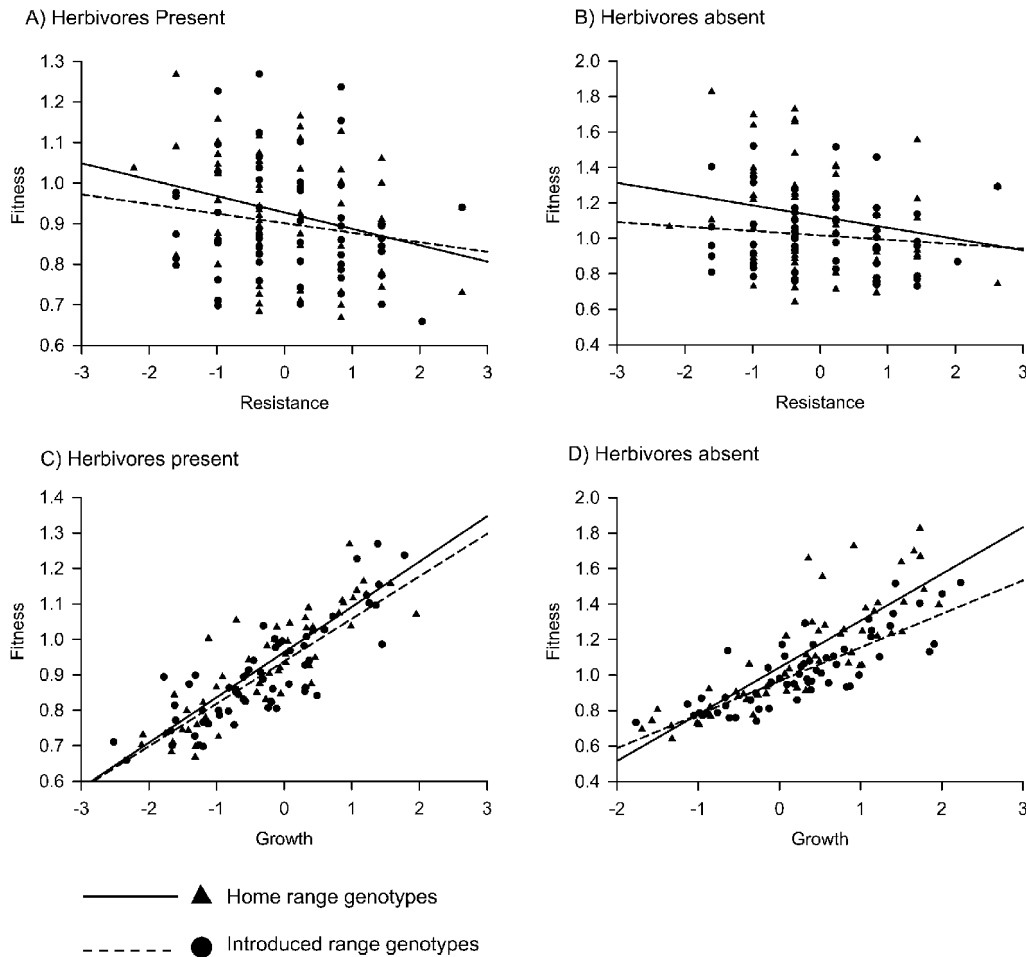
Figure 2: Realized fitness functions. Shown are the observed relationships between herbivory resistance and fitness in the presence (*A*) and absence (*B*) of herbivores and between growth and fitness in the presence (*C*) and absence (*D*) of herbivores. Fitness values are relative fitness (biomass), and resistance and growth values are standardized across populations (see "Analysis"). Lines show the fitness functions. Triangles and solid lines represent the home range (Australia) genotypes, while circles and dashed lines show the introduced range (Florida) genotypes. The regression coefficients (slopes of the fitness functions) are the selection differentials (*s*) given in table 2.

tially indicates plasticity for the trait, although an effect of herbivory on traits such as biomass or growth could also simply be due to herbivores removing biomass. A significant family effect indicates genetically based variation (heritability) of the trait, with the caveat that this term could include maternal and environmental effects. Although the possibility of maternal effects reduces our confidence that variance among families represents additive genetic variance, the likelihood that maternal effects create a significant bias is small for several reasons, including extremely small seed size and the elimination from the experiment of plants too small to be viable (Kaufman and Smouse 2001). A significant genotype by environment interaction indicates genetic variation in plasticity, which is necessary for plasticity to evolve. A significant source

by treatment interaction indicates that source populations show different responses to the treatment and thus show different plastic responses.

Results

Selection

For the plants in this experiment, there was selection for decreased resistance to herbivory, as shown by the negative selection differentials and gradients on resistance (table 2). This was true regardless of whether herbivores were present or absent (fig. 2*A*, 2*B*). The selection gradients for resistance were negative but not significantly different from 0 (table 2). The selection differentials for resistance were

all significantly <0 except for the introduced range ge- notypes with herbivores present (table 2). There was no significant quadratic selection on resistance and no cor- relational selection on resistance through growth.

Linear selection on growth (stem elongation) was strongly positive and significantly different from 0 for all groups (table 2). Selection on growth was higher for the Florida (introduced range) than for the Australia (home range) genotypes (fig. 2C, 2D), but this difference was not significant (growth × source term not significant; table 3). There was no significant quadratic selection on growth and no correlational selection on growth through resis- tance (table 2).

Patterns of linear and quadratic selection on growth and resistance did not differ between the herbivory treatments or the source location (table 3). There was, however, a significant three-way interaction between growth, defense, and source location (table 3), indicating that correlational selection between growth and defense differed by source location. This interaction can be seen in the fitness surfaces in figure 3. For the introduced genotypes, there was pos- itive selection on stem elongation at all levels of resistance and no or weak selection on resistance (fig. 3A). For the home range genotypes, there was also positive selection on stem elongation, but the strength of selection depended on the level of resistance (fig. 3B). When resistance was high, small changes in stem elongation led to relatively large increases in fitness, as shown by the steepness of the surface on the right side of the graph. At low levels of resistance, selection on stem elongation was still positive but not as strong. Figure 3C shows the difference surface created by subtracting the fitness surfaces of the Australia and Florida genotypes. This figure shows that the greatest differences in the fitness functions between the Australia and Florida genotypes occurs at areas of high resistance and low competitive ability (fig. 3C, *lower right*) and areas of low resistance and high competitive ability (fig. 3C, *upper left*).

Genetic Correlations

Stem elongation and resistance were negatively correlated in both source locations (table 4). For the genotypes from Australia, leaf : stem mass ratio and attractiveness to *Ox- yops* were negatively correlated, and there were negative genetic correlations between resistance and attractiveness to each insect species (table 4). The Australia genotypes also exhibited positive genetic correlations between resis- tance and leaf : stem mass ratio, and attractiveness between the two insect species was positively correlated (table 4). For the genotypes from Florida, attractiveness to *Oxyops* was negatively correlated to both SLA and resistance and positively correlated to stem elongation (table 4). In the herbivore exclusion treatment, the genotypes from Aus- tralia exhibited a positive genetic correlation between stem elongation and leaf pubescence (table 4). Finally, there was a significant negative genetic correlation between stem elongation and SLA for the Florida genotypes (table 4).

Plasticity and Genetic Variation

There was a significant effect of herbivory treatment on fitness (total biomass) and for the ratio of leaf mass : stem mass (table 5). This treatment effect could indicate plas- ticity if the plants are altering their resource allocation patterns in response to the presence of herbivores or could simply be the result of herbivores removing biomass. As expected, aboveground biomass was higher when plants were protected from herbivores. Plants protected from her- bivores weighed an average of 32.7 ± 2.25 g, and plants not protected from herbivores weighed an average of 24.5 ± 2.26 g. The ratio of leaf mass : stem mass was 0.42 ± 0.02 when plants were protected from herbivores and 0.39 ± 0.02 when plants were exposed to herbivores. There were significant genotypic family effects for biomass (fitness), stem elongation, SLA, leaf pubescence, attrac- tiveness to *Boreioglycaspis* and *Oxyops*, and resistance (table 5), suggesting that these traits are heritable. No trait ex- hibited a significant genotype by environment interaction (G × E; table 5). Home and introduced range population means did not differ for any measured traits (source lo- cation effects all $P > .05$; table 5), nor did the populations differ in plasticity (source location × herbivory treatment interaction effects all $P > .05$; table 5).

Discussion

Selection and Evolutionary Change in Growth and Resistance

The patterns of selection on growth and defense we found in this study accurately predict the lack of evolutionary changes in *Melaleuca* following its introduction into its new range. Previous work (Franks et al. 2007) found that the introduced range genotypes had not evolved faster growth or decreased resistance to herbivory compared with native range genotypes, in contrast to predictions from the EICA hypothesis. In this study, we found that there was strong selection on increased growth and weak selection on decreased resistance and that the patterns of selection generally did not differ for the native or introduced ge- notypes nor depending on the presence or absence of her- bivores. Thus, it would not be expected that evolutionary changes in growth or resistance would occur following release from natural enemies.

The reason for these patterns of selection and subse-

Table 3: The effects of source location (S) and herbivory treatment (E) on patterns of genotypic selection

Variable	df	F
E	1, 223	**13.78****
S	1, 223	**6.24***
E × S	1, 223	.24
Growth	1, 223	**142.58****
Growth × E	1, 223	.16
Growth × S	1, 223	2.93
Growth × E × S	1, 223	.02
Resistance	1, 223	1.68
Resistance × E	1, 223	1.15
Resistance × S	1, 223	1.26
Resistance × E × S	1, 223	.01
Growth × resistance	1, 223	.01
Growth × resistance × E	1, 223	2.22
Growth × resistance × S	1, 223	**4.39***
Growth^2	1, 217	.01
Resistance^2	1, 217	2.03
Growth^2 × E	1, 217	.53
Resistance^2 × E	1, 217	.01
Growth^2 × S	1, 217	.19
Resistance^2 × S	1, 217	.13

Note: Shown are the results of an ANCOVA with relative fitness (biomass) as the dependent variable; source location and herbivory treatment as covariates; and stem elongation, defense, squared values of the traits, and interactions as independent variables ($N = 240$ families). Interactions between the covariates and traits indicate that the covariate influenced selection. Interactions among the traits indicate correlational selection, and squared values indicate quadratic selection. Higher-order interactions not shown were not significant. Values in bold indicate $P < .05$.

* $P < .05$.
** $P < .001$.

quent evolutionary changes is likely due to the relative costs and benefits of resistance and growth in the home and introduced ranges. The insects released for biological control and included in this study did substantial damage and caused reductions in plant biomass and performance. However, there seems to be little benefit to increased resistance, as evidenced by the negative selection on resistance in the presence of herbivores. There is also evidently a cost of resistance, since there is negative selection on resistance in the absence of insects as well as a negative genetic correlation between resistance and growth. Rapid growth, in contrast to resistance, appears to be highly beneficial, since selection on stem elongation was always strongly positive. There does not appear to be a cost to growth, since there was selection for increased growth even in the presence of herbivores.

These findings have important implications for the EICA hypothesis, which assumes that decreased resistance and increased growth rate will evolve in the new range

following release from natural enemies. Whether these evolutionary changes occur depends not only on a trade-off between resistance and growth, as was found in this study, but also on the relative costs and benefits of resistance and growth in the conditions of the new range. If the benefits of resistance do not increase in the presence of herbivores, as appears to be the case in this study, then it is likely that there would be little evolutionary change in resistance following release from natural enemies even if there is, as we found, genetic variation for this trait. Similarly, if the benefits of increased growth rate do not increase in the absence of herbivores, as in this study, then it is likely that this trait also will not evolve, since, in the new range, there would not be greater selective pressure to increase growth than there already was in the native range.

The EICA Hypothesis and Patterns of Selection

While there was evidence for selection on herbivory resistance and competitive ability traits, the patterns of selection generally did not differ depending on the source population or the presence of herbivores and did not match predictions based on the EICA hypothesis. Selection on stem elongation, which may be correlated with competitive ability, was always positive and did not differ between the herbivory treatments. This finding does not support expectations based on the EICA hypothesis, which proposes that when invasive species are released from natural enemies, they evolve increased allocation to competitive ability. In addition, the EICA hypothesis would predict that in the absence of herbivores, selection on competitive ability should be stronger for genotypes from the home range than from the introduced range, since genotypes in the introduced range should have already experienced selection for increased competitive ability after escape from natural enemies. In contrast to this prediction, we did not find that selection on competitive ability was stronger on Australia than on Florida genotypes. Thus, the patterns of selection on competitive ability in *Melaleuca* do not fit predictions based on the EICA hypothesis.

Patterns of selection on resistance traits also did not fit predictions based on EICA. We found that selection on resistance was always negative (selection for decreased resistance) regardless of whether insects were present or absent. When insects were present, selection for decreased resistance was weaker for the introduced range (Florida) than the native range (Australia) genotypes. This difference in magnitude between the source populations is in the direction that would be predicted on the basis of the EICA hypothesis, since the home range genotypes should be better adapted to natural enemies. However, the fact that there was selection for decreased resistance for both the intro-
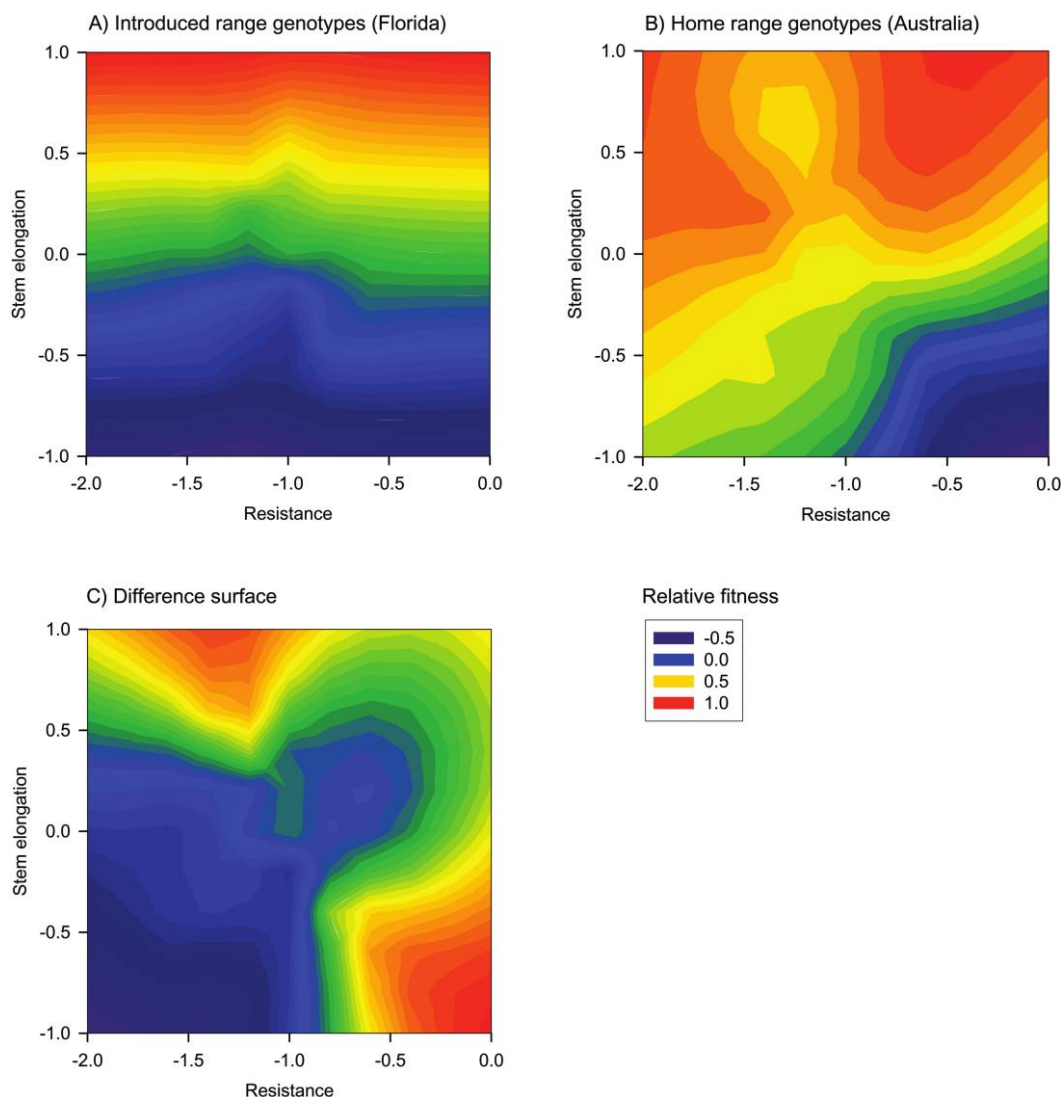
Figure 3: Fitness surface (contour plot) of resistance and competitive ability (stem elongation) plotted against fitness for plants from Florida (*A*) and Australia (*B*) and the difference in the surfaces (*C*). Only plants in the herbivores present (not sprayed with insecticide) treatment are included. Resistance and competitive ability were standardized best linear unbiased predictors for each maternal family from the genotypic selection analyses, and fitness is shown as the residual of relative biomass (see "Analysis"). The color level indicates fitness, with blue (dark color) indicating low values and red (light color) indicating high values.

duced and native range populations contrasts with expectations based on EICA. Furthermore, the EICA hypothesis would predict that in the absence of herbivores, there should be selection on decreased defense through selection on increased growth (negative correlational selection gradient), and this selection should be stronger for home range than for introduced range genotypes. In contrast, we found no correlational selection on growth through defense regardless of origin or treatment.

There are several potential reasons that the patterns of selection on defense and growth we found did not match

predictions based on the EICA hypothesis. First, there could have been just as much herbivory pressure in the introduced range either because of herbivory by generalists or because the introduced biological control herbivores reached extremely high densities in the new range and caused selection for resistance. Both of these explanations are unlikely for *Melaleuca*. In the home range of Australia, more than 450 species of insects feed on *Melaleuca*, causing substantial damage (Turner et al. 1998). In contrast, there is almost no feeding by any generalist herbivores on *Melaleuca* in the introduced range in Florida (Turner et al.

Table 4: Genetic correlations

	Stem elongation	SLA	Leaf : stem	Hairs	Bor	Oxy	Resistance
Herbivores present:							
Stem elongation		−.121	.073	.194	.039	.166	**−.292***
SLA	−.239		−.067	.138	−.160	−.086	−.101
Leaf : stem	.042	−.021		.166	−.228	**−.304***	**.270***
Hairs	−.049	.063	.215		.004	.001	−.111
Bor	.162	−.128	−.223	−.203		**.303***	**−.272***
Oxy	**.359***	**−.286***	−.062	−.206	.144		**−.347****
Resistance	**−.251***	.146	−.056	.145	−.174	**−.300***	
Herbivores excluded:							
Stem elongation		−.056	.085	**.249***	.201	.077	**−.330****
SLA	**−.375****		.082	.057	−.174	.074	.168
Leaf : stem	.114	−.055		−.042	−.176	**−.438****	.206
Hairs	.092	.184	.166		−.027	.006	−.086
Bor	**.302***	−.084	−.019	−.084		**.303***	**−.272***
Oxy	**.265***	−.120	.029	−.065	.144		**−.347****
Resistance	**−.259***	.186	−.229	.079	−.174	**−.300***	

Note: Correlation coefficients are given for families from Australia in the upper right and families from Florida in the lower left, with herbivores present and herbivores excluded. All traits were standardized to a mean of 0 and a variance of 1, and Pearson product moment correlations were then conducted on best linear unbiased predictors of the traits for each maternal family. Traits are stem elongation (final height − initial height), SLA (specific leaf area), leaf : stem (ratio of leaf mass to stem mass), hairs (amount of leaf pubescence), bor (attractiveness to *Boreioglycaspis*), oxy (attractiveness to *Oxyops*), and resistance (resistance to insect damage). See text for further descriptions. $N = 60$ families per source location. Values in bold indicate $P < .05$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

1998). Although the biological control insects have now reached high densities in Florida, they were only introduced in 1997, and the seeds used in this study were collected from adult trees in 1999. The genotypes from Florida in this experiment therefore had arisen from trees that were free of both generalist and specialist herbivores for more than 100 years. Thus, herbivory pressure should have been substantially higher in Australia than in Florida, and it is unlikely that a lack of evolutionary response in the new range is due to equivalent selection pressure from herbivores in the home and introduced ranges.

A possible reason for failing to find differences in selection on competitive ability between the home and introduced ranges could have been in part due to the fact that we used stem elongation as an estimate of competitive ability and biomass as an indicator of fitness. Stem elongation may potentially be related to mass and not reproduction or other fitness components. We were unfortunately unable to measure total lifetime reproduction because these plants are perennials that can live for more than 100 years and produce millions of seeds (Rayachhetry et al. 1998); in addition, it was necessary to harvest the plants before flowering to prevent the introduction of foreign pollen into Florida. Biomass was thus the best indicator of fitness available. Previous work has shown that biomass is closely related to reproductive potential in *Melaleuca* (Rayachhetry et al. 2001). The relationship between stem elongation and biomass could still potentially influence the results and thus should be interpreted with caution. It would be highly useful to conduct a similar study on a species in which total lifetime reproduction or other estimates of fitness could be measured. Our results also could have been influenced by the fact that we used genotypic rather than phenotypic selection analyses. According to phenotypic selection analyses (not shown), selection on stem elongation was stronger in the absence of herbivores than when herbivores were present, and selection on stem elongation was stronger for introduced range than for home range genotypes, as predicted by EICA. However, the phenotypic selection analyses did appear to be biased as a result of environmental covariances, so the genotypic selection analyses were clearly more appropriate despite the loss of statistical power. Finally, it is possible that the EICA hypothesis may account for patterns of selection in some species but that in other species the predicted selection against defense and for growth in the absence of natural enemies simply may not occur. In these cases, differences between the native and introduced populations may be due to founder effects and drift rather than to differences in selection pressures in the different habitats. This scenario is particularly likely for invasive plants introduced through the nursery trade, since the most vigorous individuals may have been deliberately chosen for importation.

Table 5: Heritability and plasticity in *Melaleuca* traits

Trait and fixed effect	df	F	Random effect	χ^2
Fitness:				
E	1, 11	**9.93****	G	**50.6*****
S	1, 22	.73	G × E	.8
E × S	1, 22	1.93		
Stem elongation:				
E	1, 11	3.41	G	**150*****
S	1, 22	.12	G × E	.2
E × S	1, 22	1.08		
SLA:				
E	1, 11	2.15	G	**10.2****
S	1, 22	.01	G × E	.8
E × S	1, 22	.80		
Leaf : stem:				
E	1, 11	**5.64***	G	1.1
S	1, 22	2.23	G × E	.1
E × S	1, 22	.15		
Hairs:				
E	1, 11	1.94	G	**1,125*****
S	1, 22	3.17	G × E	.1
E × S	1, 22	.20		
Bor			G	**9.6****
Oxy			G	**85.8*****
Resistance			G	**19.0*****

Note: Shown are results of mixed-model ANOVAs with the trait as the dependent variable; herbivory treatment (E), source country (S), and their interaction (E × S) as fixed effects; and maternal family nested within country (G) and genotype by environment interactions (G × E) as random effects. The maternal family term, G, corresponds to the heritability term h^2 in equations (1) and (2), although in this case the term may include maternal and other nonadditive effects and thus represents broadsense heritability. The traits are biomass (fitness, $N = 2,683$), stem elongation (stem elongation, $N = 2,709$), specific leaf area (SLA, $N = 2,708$), leaf mass : stem mass ratio (leaf : stem, $N = 2,679$), leaf pubescence (hairs, $N = 2,806$), attractiveness to *Boreioglycaspis* (bor, $N = 2,812$), attractiveness to *Oxyops* (oxy, $N = 2,813$), and resistance to insect damage (resistance, $N = 2,812$). Values in bold indicate $P < .05$.

  * $P < .05$.
  ** $P < .01$.
  *** $P < .001$.

Previous studies have found mixed support for the EICA hypothesis. Bossdorf et al. (2005) reviewed 45 studies testing the EICA hypothesis by comparing traits of native versus introduced genotypes in common environments. Of these studies reviewed, 20 of 36 found increased growth, and 12 of 22 found decreased resistance, but <50% of studies looking at both competitive ability and resistance (19 studies) supported EICA. They conclude that there is at least some support for the hypothesis that native and introduced populations of invasive species have genetically diverged in ecologically important traits and that this divergence may be due to either selection or neutral processes, such as drift and founder effects.

Future Evolutionary Potential

Our results show evidence that selection could cause changes in herbivory resistance and competitive ability traits in *Melaleuca*. We found that plants grown in the herbivore exclusion treatment had greater fitness than plants subjected to herbivory, which supports the hypothesis that herbivory reduced performance in *Melaleuca* plants and that the insects could exert selection on plant resistance traits. There was also strong selection (genotypic selection differentials between $\beta = 0.19$ and 0.25) on stem elongation. In addition, we found significant effects of genotype (maternal family) on several traits, including stem elongation, SLA, leaf pubescence, and attractiveness to *Boreoglycaspis*, which suggests that these traits are genetically variable. These findings support previous work with other species that has shown, in some cases, that herbivory can impose selection on plant resistance traits and that these traits could evolve in natural populations (Mauricio and Rausher 1997; Stinchcombe and Rausher 2001).

Constraints to Selection

Negative genetic correlations can potentially constrain selection (Falconer and Mackay 1996); thus, examining these correlations is important for predicting evolutionary change. Additionally, an underlying assumption of the EICA hypothesis is that there should be a trade-off between competitive ability and resistance, which should be manifest as a negative correlation between these characters. We found a negative genetic correlation between stem elongation and resistance in *Melaleuca*, which supports this assumption. In contrast, we found limited evidence for negative genetic correlations among other traits. We did find a negative genetic correlation between SLA and stem elongation for genotypes from Florida. There were also some positive genetic correlations, which could potentially facilitate selection if selection on both traits is in the same direction.

Evolutionary Changes in Plasticity

Few of the traits we measured in *Melaleuca* showed significant plasticity when comparing traits in herbivore-present versus herbivore-free (insecticide-sprayed) environments. We found significant plasticity (herbivory treatment effect) only for fitness (biomass) and for leaf mass : stem mass ratio and not for stem elongation, SLA, or leaf pubescence. The herbivore treatment effect on biomass and on leaf mass : stem mass ratio may simply be due to herbivores removing leaf tissue and not to a response of the plants changing

resource allocation patterns, and thus it may not be true plasticity.

There was also little evidence from our study that plasticity in resistance or competitive ability traits has evolved or has the potential to evolve in *Melaleuca*. The home and introduced range genotypes did not differ in plasticity for any trait, indicating that plasticity in the traits we measured has probably not undergone substantial evolutionary change since the species was introduced into its invaded range. We found evidence for genetically based variation in several traits, including stem elongation, SLA, and leaf pubescence. This would indicate that these traits have the requisite genetic variation for evolution to occur if selection is acting on these traits. However, there was no significant genetic variation for plasticity (G × E) for any trait, which indicates that changes in levels of plasticity for these traits are not likely to evolve in the near future under conditions similar to those of the experiment. In addition, the lack of G × E indicates that *Melaleuca* genotypes may not be optimally adapted to local herbivory conditions. However, if there is a cost to plasticity and little cost of resistance, the same genotypes may be optimal in both the presence and absence of herbivores.

Bossdorf et al. (2005) reviewed 10 studies that compared plasticity in native versus introduced populations of invasive species and found that five of these studies demonstrated greater plasticity in the introduced range compared with the home range genotypes. One of these studies (Kaufman and Smouse 2001) was conducted on *Melaleuca quinquenervia*, the same species in this study. In contrast to our results showing lack of plasticity to herbivory, Kaufman and Smouse (2001) found that the plants did show significant plasticity to variation in water levels and soil pH. This and the other studies reviewed by Bossdorf et al. (2005) all involved plasticity to environmental factors such as water, nutrients, and shade, and no previous study examined plasticity in response to herbivory in native versus introduced genotypes. The fact that we did not find that the introduced genotypes were more plastic than the native genotypes contradicts the idea that plasticity to herbivory may enable this species to become invasive or may evolve postinvasion following natural enemy release.

Implications for Biological Control

The practice of classical biological control, in which specialist natural enemies from the home range of an invasive species are introduced into the new range in order to reduce spread and population growth of the invasive species, is one of the principal tools used in exotic species management (Debach and Rosen 1991). The evolution of defense against natural enemies, however, poses the potential for an eventual reduction in biological control ef-

fectiveness. If invasive species have, as postulated by the EICA hypothesis, evolved decreased allocation to defense in their new range, then biological control agents should be maximally effective against individuals at the beginning of a biological control program. As natural enemies become more abundant, the invasive species may then begin to evolve shifts in resource allocation back to defense, and the biological control agents could become less effective over time. This could, however, result in the introduced species becoming less invasive if it is forced to divert resources from growth to defense. Furthermore, the evolution of defense may show costs and constraints, as evidenced by trade-offs between defense and competitive ability. Despite this potential for the evolution of resistance to biological control agents in invasive species, there are few documented cases of such an evolutionary process actually taking place (Holt and Hochberg 1997).

Our results show that despite strong effects of herbivory by biological control insects on individual plant performance and fitness, there was selection for decreased resistance for both native and introduced populations both with and without herbivores. This contradicts expectations based on the fact that the genotypes from Florida should have experienced relaxed selection for resistance in the absence of natural enemies, and when the biological control insects are present, there should be strong selection for increased resistance in these genotypes. This finding also suggests that the evolution of increased resistance in the introduced genotypes is not likely to hinder biological control efforts in *Melaleuca*. Lack of selection for increased resistance could be due to a number of factors, including the possibility that resistance traits did not pose enough of a cost to be selected against in the absence of natural enemies. Alternatively, tolerance could be a major mode of defense in *Melaleuca* as well as in other invasive species, and selection on tolerance could influence the evolution of resistance. We are currently conducting an analysis of tolerance in *Melaleuca*.

Our study found evidence for selection on increased growth rates, but patterns of selection on growth and resistance ran contrary to expectations based on the EICA hypothesis. Thus, evolutionary processes can be complex in invasive species (Lee 2002) and should be further investigated in order to maximize the effectiveness of biological control efforts (Hänfling and Kollmann 2002; Müller-Schärer et al. 2004). This type of approach to invasive species research can also greatly enhance our understanding of evolutionary processes in natural populations.

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