Ecology, 93(5), 2012, pp. 1059–1070

Successional changes in plant resistance and tolerance to herbivory

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Abstract. Despite considerable research on plant defenses, we know very little about how temporal changes in the environment may influence resistance and tolerance levels, or the costs and benefits of these defense strategies for long-lived plant species. We hypothesized that, in successional habitats, predictable environmental changes should favor strong plasticity in defense phenotypes and that the costs, benefits, and levels of tolerance and resistance will change with environmental context. Using a widely distributed, old-field perennial, late goldenrod (*Solidago altissima*), we conducted a field experiment to test these predictions. We planted goldenrod genets exhibiting varying levels of resistance and tolerance into three early-successional and three late-successional fields (approximately three and 15 years in age, respectively) and experimentally measured resistance and tolerance levels and their associated costs and selection coefficients. We found a significant effect of successional stage but no effect of genotype or stage–genotype interaction on defense levels. Genets planted in early-successional fields appeared to be more resistant and less tolerant to herbivory than those same genets planted in late-successional fields. There were significant trade-offs between resistance and tolerance in early-successional fields but not in late-successional fields. Each late-successional field exhibited a significant cost or selection gradient for resistance, but there was no general pattern of resistance costs or selection gradients specific to a successional stage class. In contrast, there was evidence of stage-specific costs of tolerance; late-successional fields exhibited significant costs of tolerance whereas early-successional fields did not. There was no evidence of direct selection for or against tolerance in either stage. Our results suggest that defense phenotypes might change in qualitative ways during succession. High resistance in early stages may be attributed to associational effects of the early-successional community, reducing the probability of damage, and despite a cost of tolerance in late stages, tolerance may be beneficial in mitigating the effects of both herbivory and environmental stresses (i.e., low light availability) that limit fitness in these fields. This study provides experimental evidence that succession can strongly influence defense phenotypes and promote temporal variability in relative resistance and tolerance levels.

Key words: costs; goldenrod; phenotypic plasticity; plant defense; selection;Solidago altissima.

INTRODUCTION

Resistance and tolerance are two types of defense phenotypes that plants can express to reduce herbivore damage or the negative effects of herbivore damage, respectively. Both resistance and tolerance may yield benefits of higher fitness in the presence of herbivores relative to nondefended plants. However, both defense strategies may involve fitness costs when herbivores are rare or absent if resources are allocated toward maintaining resistance or tolerance traits at the expense of plant growth or reproduction (reviewed in Stamp 2003). The type of defense strategy expressed is assumed to be influenced by the fitness costs and benefits associated with that strategy (Mauricio et al. 1997, Stamp 2003).

The adaptive value of resistance and tolerance will fluctuate if their associated costs and benefits vary spatially and/or temporally. A fluctuating adaptive landscape may favor the evolution of plasticity in defense expression (Via and Lande 1985) and promote spatiotemporal variability in defense levels for long-lived plant species (e.g., Laine and Tellier 2008). Recent studies have shown that plant defense traits can vary spatially owing to heterogeneity in environmental variables such as light, nutrient, and water availability (Covelo and Gallardo 2004, Brenes-Arguedas and Coley 2005, Hakes and Cronin 2011*a*). Studies have also documented temporal variability in plant defenses (e.g., Pilson 1992, Cronin et al. 2001, Tiffin 2002, Takahashi and Yamauchi 2010) and have predicted that plant species along a successional gradient may vary in their pattern of defense (e.g., Rasmann et al. 2011). Mechanisms promoting temporal variability in plant defense may include induction of defenses following exposure to herbivores (e.g., Haukioja 1990, Karban and Baldwin 1997) and ontogenetic changes in the plant (e.g., Böege et al. 2007, Barton and Koricheva 2010, McCall and Fordyce 2010). To date, there has been little consideration

Manuscript received 18 August 2010; revised 7 October 2011; accepted 1 November 2011; final version received 3 December 2011. Corresponding Editor: N. J. Sanders.

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of how successional changes in the environment influence the level or adaptive value (i.e., fitness benefits relative to costs) of resistance and tolerance in long-lived plants.

During succession, environmental conditions and community composition change in predictable ways (e.g., Huston and Smith 1987, Tilman 1987) that could potentially affect the costs, benefits, and levels of plant defenses. For example in old-field habitats, the neighboring plant community transitions from an open canopy with a dense understory dominated by forbs and grasses to a closed canopy with an open understory forest dominated by trees and shrubs (Hartnett and Bazzaz 1985, Hakes and Cronin 2011*a*). A growing list of studies has demonstrated that the density and/or identity of neighboring plants can alter resistance and tolerance levels of a focal plant, directly via competition or indirectly via associational resistance or susceptibility (Agrawal et al. 2006). For example, a high density of neighboring plants may increase costs and decrease plant defense if there is a resource-allocation trade-off between defense traits and competitive ability (e.g., Bazzaz et al. 1987, Cipollini and Bergelson 2002). Alternatively, the presence of neighbors may decrease costs and increase defense expression if defense traits serve a dual purpose, mitigating herbivory and competitive stress (e.g., Strauss and Agrawal 1999, Siemens et al. 2003, Jones et al. 2006). Spatial associations with neighboring plants may also decrease the likelihood of damage and increase the apparent resistance of a focal plant if neighbors reduce its apparency to herbivores, or if herbivores prefer to feed on more palatable neighbors (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976, Rausher 1981). As succession progresses and woody plants begin to dominate the landscape, neighboring plant density in the understory decreases and canopy cover increases (Hartnett and Bazzaz 1985, Hakes and Cronin 2011*a*). The existing literature provides equivocal support for whether shading should cause plants to be more resistant (e.g., Cipollini 2005, Hakes and Cronin 2011*a*) or less resistant (e.g., Izaguirre et al. 2006). In contrast, the well-supported limiting-resource model of Wise and Abrahamson (2007, 2008) predicts that tolerance to herbivory should decrease when the acquisition of a limiting resource is further limited by herbivore damage. In this case, tolerance to leaf-chewing herbivores is expected to be lower in shaded than in open environments, where reinvestment into biomass production is limited by low light availability. Although numerous studies have reported the individual effects of neighboring plant density and shading on the expression of plant resistance and tolerance in controlled experiments (e.g., Siemens et al. 2003, Cipollini 2005, Izaguirre et al. 2006, Jones et al. 2006), it is not understood how these environmental variables interact within the context of early- and late-successional communities to influence defense expression in long-lived plants.

We conducted a field experiment to test whether late goldenrod (*Solidago altissima*; Asteraceae) relative resistance and tolerance levels, fitness costs, and selection gradients differ with respect to field successional stage and genotype. We out-planted clones of 14 genets into replicate early- and late-successional fields. We predicted that the transition from an open-canopy environment dominated by an herbaceous understory (i.e., early fields) to a closed-canopy environment dominated by trees and shrubs (i.e., late fields) will elicit strong phenotypic changes in resistance and tolerance levels, as well as changes in their associated costs and selection gradients. In particular, based on the predictions from the limiting-resource model (Wise and Abrahamson 2005, 2007, 2008), we expected to find reduced costs and strong selection for and greater levels of tolerance in goldenrods planted into early than late fields. We also tested whether a genet × stage interaction was evident, which would suggest a fundamental change in defense expression among genets during succession. Lastly, we examined whether the adaptive landscape for resistance and tolerance was temporally dynamic by testing for differences in costs, selection gradients, and defense trade-offs between successional stages.

Methods

Solidago altissima L. subsp. *altissima* is common throughout eastern North America (Semple and Cook 2006) and is a dominant plant of successional old-field habitats. More than 100 species of generalist and specialist herbivores feed on goldenrod, including spittlebugs (*Philaenus spumarius*), gall-making flies (e.g., *Eurosta solidaginis*), and various grasshoppers and beetles (e.g., Acrididae, *Trirhabda* spp.; Maddox and Root 1987, Abrahamson and Weis 1997). These herbivores have been found to significantly decrease goldenrod biomass and sexual and asexual reproduction, increase photosynthetic rates, and delay leaf senescence and flowering (Meyer 1993, Abrahamson and Weis 1997, Meyer 1998, Cronin and Abrahamson 1999, 2001).

Goldenrods can persist in old-field habitats for 50–75 years (Hartnett and Bazzaz 1985, Maddox et al. 1989). In early-successional fields, continued colonization by seed and rapid clonal expansion occurs through approximately the fifth year after field abandonment, at which time genet density and diversity are maximal (Hartnett and Bazzaz 1985, Maddox et al. 1989). After the fifth year, recruitment of new genets generally ceases (Hartnett and Bazzaz 1985). As old-field succession progresses, the number of goldenrod genets begins to decline, and herbaceous plants become displaced by woody plants (Maddox et al. 1989).

Experimental design

The goldenrod genets used for our field experiment were selected from a common-garden study that had been conducted during the previous year (see Hakes and Cronin [2011*b*]). Our goal in propagating genets in the common garden for a year was to minimize maternal effects on fitness and resistance and tolerance levels that might derive from their habitat of origin. A total of 103 genets, excavated from one early-successional field ($n = 55$) and one late-successional field ($n = 48$) in February 2007, were propagated from 5-cm rhizome cuttings and replanted into a common garden. From March to November 2007, the resistance and tolerance levels of all 103 genets were evaluated. Resistance varied significantly among goldenrod genets, ranging from 0.8 to 1.0 (where 1 is the proportion of tissue damaged by chewing herbivores). Tolerance levels ranged from −3.1 to 10.7 (slope of the regression of inflorescence biomass against damage) but did not differ significantly among genets (see Hakes and Cronin [2011*b*]). For this experiment, we selected 14 genets (eight originating from the early-field population and six from the late-field population) representing a wide range in resistance and tolerance levels.

In early February 2008, we excavated the root bundles of the 14 selected genets from the common garden, cut the rhizome material into 5-cm sections, and propagated the cuttings in flats of vermiculite in a greenhouse at Louisiana State University. After four weeks, eight replicates of each genet were out-planted into each of three early- and three late-successional field sites in East Baton Rouge Parish, Louisiana, USA (see Plate 1). Early fields had been mown within the past three years and were dominated by forbs and grasses (e.g., *S. altissima*, *Ambrosia* spp., *Liatris* spp., *Dichanthelium* spp.). Late fields were ~15 years postmowing and were dominated by trees and shrubs (e.g., *Triadica sebiferum*, *Cornus foemina*, *Acer negundo*, *Rubus* spp.). Fields ranged in size from 1–3 ha, and our experiment was conducted within a 240-m^2 area in each field. Within each field, eight replicates of each of the 14 genets were assigned at random to a position within an 8×14 grid (vertices 1.5 m apart). We did not attempt to alter the composition of the neighboring plants surrounding each out-planted ramet. An insecticide treatment was applied to encourage a gradient of damage among replicates for the purpose of estimating tolerance levels for each genotype. One-half of the replicates per genet were randomly assigned to the insecticide treatment and sprayed biweekly with Sevin (Bayer CropScience, Research Triangle Park, North Carolina, USA). The remaining ramets were assigned as controls and exposed to natural levels of herbivory. Using a similar carbaryl insecticide, Meyer et al. (2005) concluded that the treatment had no effect on goldenrod growth.

Every eight weeks from March to November 2008, we measured ramet height and the number of new leaves produced since the previous census. The proportion of leaves damaged by leaf-chewing herbivores was determined, and leaf area removed per damaged leaf was assessed from digital photographs of three randomly chosen leaves using the program UTHSCSA ImageTool (*available online*).[4] In addition to damage from insect herbivores (mainly grasshoppers in the families Acrididae and Tettigoniidae and the genus *Romalea*), goldenrods experienced browsing damage by white-tailed deer (*Odocoileus virginianus*) and eastern cottontail rabbits (*Sylvilagus floridanus*). Damage by mammals typically resulted in the apical meristem being completely grazed. We estimated damage from mammals as the proportional change in ramet height since the previous census. We recorded other types of plant damage (i.e., by galling and sucking herbivores) but they were scarce and thus were ignored in this study (see also Hakes and Cronin [2011*a*, *b*]). During each census, all herbivores on ramets were identified to family and their numbers recorded. In late spring, the insect community within the grid was surveyed using a sweep net (four 10-m transects consisting of 20 back-and-forth sweeps per field). The relative abundance (number per sweep net) of herbivores known to feed on goldenrod was estimated per field.

In late October 2008, newly opened inflorescences, stems, and root bundles were collected and dried in an oven at 65°C for four days. Only 24% of ramets planted in early fields and none planted in late fields flowered. Results from a logistic regression indicated that vegetative biomass was a significant predictor of whether ramets flowered or not (odds ratio = 1.49, $\chi^2 = 80.95$, df = 2, $P < 0.001$). Other studies have also shown that goldenrod biomass is positively correlated with survival and reproduction (e.g., Goldberg 1988, Cronin and Abrahamson 1999) and that perennials with high end-of-season biomass have higher survival and lifetime fitness in terms of sexual and clonal reproduction (Gardner and Mangel 1999, Ehrlen and Van Groenendael 2001). Thus we used total biomass (inflorescence, stem, and rhizome) as our estimate of fitness. Considering that goldenrod's persistence and spread in old-field habitats depends almost exclusively on clonal reproduction after the first two years of succession (Hartnett and Bazzaz 1985) and that flowering rates are naturally lower in late-successional fields (Hakes and Cronin 2011*a*), biomass is an appropriate proxy for fitness.

Resistance and tolerance measures

We estimated resistance and tolerance levels for each genet in each field. Resistance was measured as 1 minus the proportion of tissue lost to chewing herbivores (e.g., Rausher and Simms 1989, Fineblum and Rausher 1995, Fornoni et al. 2004). Genet resistance was computed in each field as the average resistance of control ramets (i.e., those not treated with an insecticide). Because we did not attempt to standardize the environment within and between field sites, we cannot determine whether measured resistance levels were primarily influenced by characteristics of the plant or characteristics of the successional environment. Tolerance (i.e., compensatory growth) per genet was measured as the slope of a linear regression of ln(biomass) against the level of damage per ramet (e.g., Mauricio et al. 1997, Tiffin and Rausher

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[4] http://ddsdx.uthscsa.edu/dig/itdesc.html

1999, Fornoni et al. 2004). These are operational measures of resistance and tolerance that are contingent upon environmental context. Most studies of tolerance control for herbivory (Strauss and Agrawal 1999), whereas in our study it varied naturally. The main advantage of estimating tolerance from natural herbivory is that plants experience the natural timing, distribution, and pattern of damage. However, tolerance measures based on natural levels can be less accurate if the range of herbivore damage is small or if genotypes vary in resistance (Tiffin and Inouye 2000).

Statistical analyses

We first tested whether plant resistance (or herbivore damage) and biomass was significantly affected by successional stage (early or late), field ($n = 3$), genotype ($n = 14$), and insecticide treatment (control or sprayed) using separate nested ANOVAs for each herbivore category (insects, mammals, both combined). Successional stage, genotype, and insecticide treatment were considered fixed effects, and field within successional stage was a nested, random effect. Resistance (1 minus proportion damaged) was logit-transformed and biomass was log-transformed prior to analysis to normalize the distribution. Nested ANOVAs were conducted using the PROC MIXED procedure (SAS Institute 2007). A simpler, two-way ANOVA was used to assess treatment effects on tolerance. Because tolerance was measured at the level of the genet rather than the individual, field became our unit of replication ($n = 3$). Trade-offs between resistance and tolerance in early- and late-successional stages were examined using a nested ANCOVA (PROC MIXED procedure; SAS Institute 2007). Tolerance was the dependent variable, field successional stage (early vs. late) was the fixed factor, and resistance was the covariate. A negative relationship between resistance and tolerance levels would indicate a trade-off between the two phenotypes, and a significant interaction between stage and the covariate would indicate that the relationship between resistance and tolerance varied with successional stage.

Costs of defense are best measured when herbivores are rare or absent (Simms and Rausher 1989, Mauricio et al. 1997). For each of the 14 genets, we determined the y-intercept of the regression of relative fitness (average biomass subtracted from biomass values) against the level of herbivore damage among ramets (Mauricio et al. 1997, Tiffin and Rausher 1999, Fornoni et al. 2004). This quantity (W_A) provides an estimate of fitness in the absence of herbivores for a particular genet. To determine linear fitness costs of tolerance and resistance in response to different successional stages, separate nested ANCOVAs were performed. W_A was the dependent variable, field successional stage (early vs. late) was the fixed factor, field within successional stage was a nested term, and resistance or tolerance was the covariate. A significant negative relationship between W_A and resistance/tolerance would indicate a cost for that particular defense strategy (Mauricio et al. 1997, Tiffin and Rausher 1999, Fornoni et al. 2004). A significant interaction between resistance/tolerance and stage would indicate succession-dependent differences in the cost of the defense strategy between successional stages (i.e., slopes differ between stages). Nested ANCOVA models that included a quadratic term of the covariate were also run to examine nonlinear costs of resistance or tolerance.

Using W_A as an estimate of genet fitness produces a bias in the estimation of the cost of tolerance owing to nonindependence between the y-intercept (fitness in the absence of herbivory) and slope (tolerance; see Mauricio et al. 1997, Tiffin and Rausher 1999, Fornoni et al. 2004). Thus we used a second method to test for a cost of tolerance by estimating the true covariance (corrected for the bias on sample covariance; see Mauricio et al. 1997: Appendix B). Confidence intervals of the corrected covariance between tolerance and fitness were obtained using a jackknife procedure (Tiffin and Rausher 1999). An estimated covariance with a negative value and 95% confidence intervals that do not overlap zero indicates a significant tolerance cost (Mauricio et al. 1997, Tiffin and Rausher 1999, Fornoni et al. 2004).

In contrast to the calculation of costs, the fitness benefits of resistance and tolerance are estimated in the presence of herbivores (i.e., the control plants). To determine selection gradients for tolerance and resistance in early and late fields, we used the same nested ANCOVA model as for costs, with the exception of the dependent variable, which was the mean relative fitness of control ramets (i.e., W_P, those in which herbivory was present). Selection gradients favoring increased or decreased levels of resistance or tolerance would be indicated by a significant positive or negative linear relationship, respectively, between W_P in and defense level (Lande and Arnold 1983, Mauricio et al. 1997, Tiffin and Rausher 1999). Stabilizing or disruptive selection would be evident if the quadratic term of the covariate was significantly positive or negative, respectively (Lande and Arnold 1983, Mauricio et al. 1997, Tiffin and Rausher 1999). A significant interaction between stage and defense level would indicate succession-dependent differences in selection gradients between stages.

RESULTS

Herbivore damage and abundance

Goldenrods ranged in damage by chewing insects and mammals from 0% to 100% of the total plant tissue removed. In early fields, 87% ± 3% (mean ± SE) of plants received insect damage, and 10% ± 4% of plants received mammal damage compared to 92% ± 3% and 54% ± 18% of plants, respectively, in late fields. Damage by chewing insects and mammals was significantly lower in early- than in late-successional fields (63% and 89% lower, respectively; Appendix A: Fig. A1), resulting in a combined total of 85% lower damage by herbivores in early than in late fields (proportion of plant damaged: early, 0.05 ± 0.01, mean ± SE; late, 0.31 ± 0.10; $F_{1,4} = 16.01$, $P = 0.012$; Appendix A: Fig. A1). Contrary to the distribution of goldenrod damage between successional stages, we found that the relative abundance of chewing insect herbivores of goldenrod was 57% higher in early than in late stages, but this difference was not significant (insects per sweep sample: early, 5.67 ± 2.38, mean ± SE; late, 2.42 ± 1.12; $F_{1,4} = 1.52$, $P = 0.285$; Appendix A: Fig A2).

Ramets treated with an insecticide experienced statistically less herbivore damage (insects and mammals combined) than control ramets, but the difference was small (percentage damage: control, 20% ± 1%, mean ± SE; sprayed, 15% ± 1%; $F_{1,4} = 16.93$, $P = 0.014$; Appendix B: Table B1). Although the insecticide treatment reduced insect damage by 25% ($F_{1,4} = 27.57$, $P = 0.006$), mammals were undeterred by the insecticide ($F_{1,4} = 0.09$, $P = 0.776$; Appendix B: Table B1). We noted that even though the insecticide treatment did not eliminate herbivores, it served its intended purpose: to increase the range of damage to ramets within a genet to allow for meaningful estimates of tolerance, costs, and selection (see *Methods: Experimental design*).

Resistance, tolerance, and fitness

Successional stage had a significant effect on relative resistance and tolerance levels. Specifically, plants in early-successional fields appeared 41% more resistant to insect and mammalian herbivores combined than those in late-successional fields ($F_{1,4} = 12.45$, $P = 0.024$; Fig. 1a; Appendix B: Table B1), and plants in late-successional fields were significantly more tolerant of damage than those in early-successional fields ($F_{1,54} = 7.76$, $P = 0.007$; Fig. 1b; Appendix B: Table B2). Interestingly, there was no effect of genotype or its interaction with stage on resistance or tolerance levels (Appendix B).

Although total biomass (our proxy for fitness) averaged six times greater in early than in late stages (early, 5.31 ± 3.6 g, mean ± SE; late, 0.87 ± 0.23 g), stage was not a significant factor in the model ($F_{1,4} = 2.03$, $P = 0.227$; Appendix B: Table B1), owing to the variability among fields within a stage class (nested term). Biomass did not differ among genets, nor was there a significant stage × genotype interaction (Appendix B: Table B1).

The relationship between goldenrod resistance and tolerance levels differed between successional stages. In the ANCOVA model, the covariate (resistance) had a marginally significant effect on tolerance, and there was a significant interaction between resistance and stage ($F_{1,4} = 5.43$, $P = 0.08$, and $F_{1,4} = 13.33$, $P = 0.02$, respectively; Appendix C: Table C1). Interestingly, resistance and tolerance exhibited a trade-off in each early field ($r = -0.50 \pm 0.01$, mean ± SE; Fig. 2a) and were positively correlated in all late fields ($r = 0.29 \pm 0.1$; Fig. 2b). Although the relationship was not significant in any one late field, when all late fields were combined, there was an overall significant positive relationship between resistance and tolerance ($r = 0.34$, $P = 0.026$, $n = 42$).

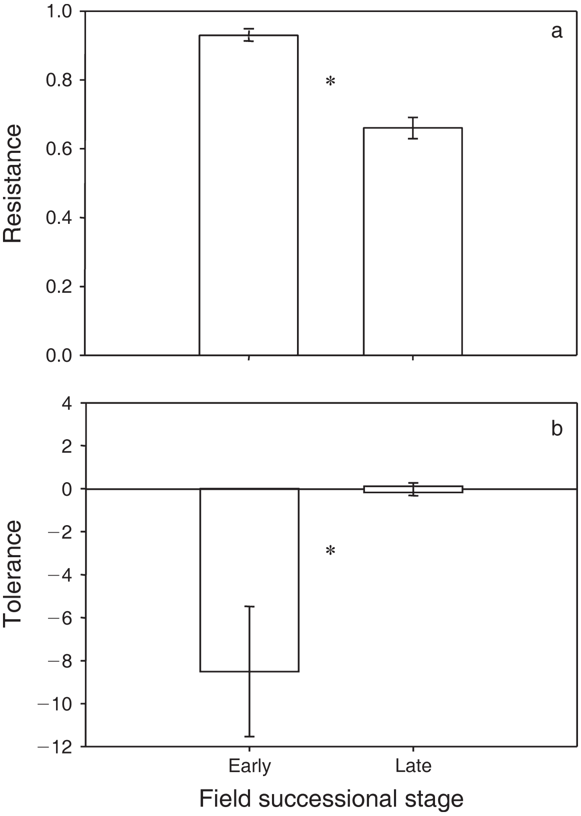

FIG. 1. (a) Resistance and (b) tolerance of late goldenrods (*Solidago altissima*) planted into three early- and three late-successional fields in East Baton Rouge Parish, Louisiana, USA. For each field, the genet-level value of tolerance and resistance was determined and then averaged across genotypes. Bars represent mean ± SE of the field means ($n = 3$ fields). Resistance was measured as 1 minus the proportion of the plant damaged. Tolerance was measured as the slope of the regression of ln(biomass) over herbivore damage. Asterisks note significance at $P < 0.05$; see Appendix B.

Cost of resistance and tolerance

In examining the factors that affect fitness in the absence of herbivory (W_A) we did not find evidence of a significant fitness cost of resistance ($F_{1,4} = 0.15$, $P = 0.721$), nor did we find a significant interaction between stage and resistance ($F_{1,4} = 1.45$, $P = 0.295$; Appendix C: Table C2). Although the general relationship between resistance and fitness in the absence of herbivores appears to be negative in late-successional stages and positive in early-successional stages (Fig. 3a), only one late-successional field exhibited a significant fitness cost of resistance ($r = 0.52$, $P = 0.05$, $n = 14$), and none of the relationships within early-successional fields were significant (Fig. 3a). We found no evidence that W_A was nonlinearly related to resistance level (i.e., the quadratic

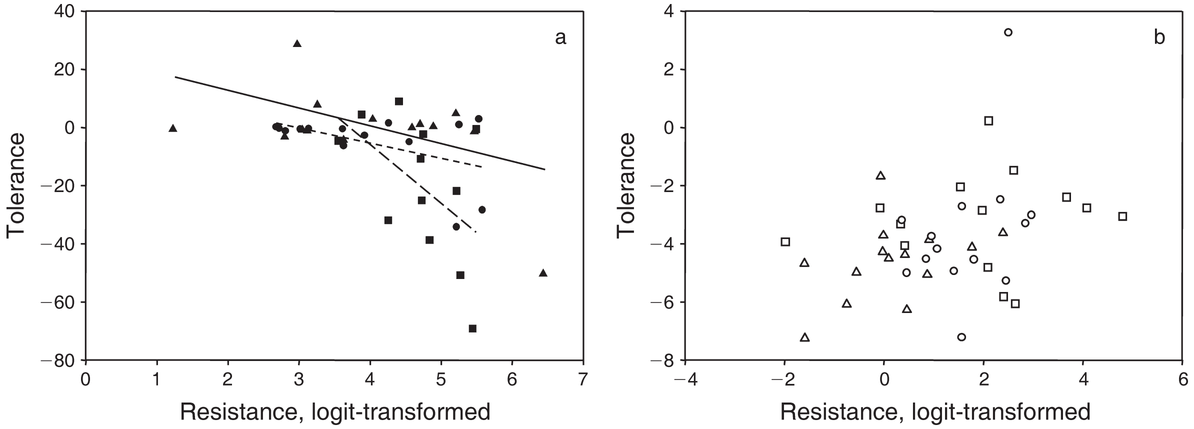

FIG. 2. The relationship between tolerance and resistance in each (a) early-successional and (b) late-successional field. A significant relationship is depicted by a line fit × least-squares regression (where $P \leq 0.05$). A negative relationship, as found for all early-successional fields, indicates a trade-off between defenses. Each data point represents the genet average within a field, and each field within a successional stage ($n = 3$) is distinguished by a different symbol (solid symbols for genets in early fields and open symbols for genets in late fields).

covariate term was nonsignificant; $F_{1,4} = 1.81$, $P = 0.250$; Appendix C: Table C2).

In comparison to resistance, tolerance exhibited a linear cost irrespective of successional stage (i.e., a significant negative relationship between W_A and tolerance; $F_{1,4} = 7.45$, $P = 0.041$; Fig. 3b; Appendix C: Table C3). However, these negative relationships differed in strength between successional stages (i.e., significant interaction term, $F_{1,4} = 32.22$, $P = 0.002$; Appendix C: Table C3). In early-successional fields, costs were nonsignificant ($r = -0.27 \pm 0.12$, mean ± SE; Fig. 3b), whereas there were strong, significant costs to tolerance in all three late-successional fields ($r = -0.79 \pm 0.05$, mean ± SE; Fig. 3). There was no evidence for a nonlinear cost of tolerance (i.e., nonsignificant quadratic term, Appendix C: Table C3). Application of a correction for possible bias in the relationship between tolerance and W_A yielded a true covariance estimate ± 95% CI of -5.11 ± 5.52 in early fields, and -1.77 ± 0.88 in late fields. Because the confidence intervals overlap zero for the early-field estimate and fail to overlap zero for the late-field estimate, a significant cost of tolerance is confirmed in late-successional stages only.

Selection gradients

Goldenrod fitness in the presence of herbivores (W_P) was not dependent on resistance level ($F_{1,4} = 0.39$, $P = 0.56$; Appendix C: Table C4). Although there was no difference in selection gradients between early and late stages (nonsignificant interaction term, $F_{1,4} = 0.78$, $P = 0.427$; Fig. 4a; Appendix C: Table C4), two late-successional fields exhibited significant directional selection gradients, one favoring increased resistance ($r = 0.56$, $P = 0.04$) and another favoring decreased resistance ($r = -0.64$, $P = 0.02$; Fig. 4c). There was no evidence for disruptive or stabilizing selection on resistance (nonsignificant quadratic covariate term (Appendix C: Table C4).

In comparison, a regression involving the quadratic covariate indicated significant disruptive selection acting on tolerance ($F_{1,4} = 12.61$, $P = 0.016$; Appendix C: Table C5). However, when examining selection gradients within individual fields, there was no evidence for significant linear or nonlinear selection gradients for or against tolerance (Fig. 4b, d), and there were no selection trends specific to a successional stage (as indicated by the nonsignificant interaction term; Table C5).

DISCUSSION

Our main finding was an apparent nongenetic, succession-induced shift in goldenrod defense phenotype from high resistance and low tolerance in early stages to low resistance and high tolerance in late stages. Moreover, the relationship between resistance and tolerance also appears to change dramatically between successional stages. These results suggest that the predictable changes associated with successional communities may favor strong plasticity in defense phenotypes. Because all communities undergo succession, and succession is concomitant with anthropogenic activity, the general linkages we describe between the level of damage, impact of damage, and succession may be common to many long-lived plants.

Goldenrods planted into early-successional fields appeared to be 41% more resistant to herbivory compared to goldenrods planted into late-successional fields. Similar results were found in our previous survey of goldenrod defense traits within a different set of early- and late-successional fields (Hakes and Cronin 2011*a*). In that survey, resistance was 31% greater in early vs. late fields. Resistance is typically measured as 1 minus the proportion of tissue damaged (Fineblum and Rausher 1995, Tiffin and Rausher 1999, Fornoni et al. 2004). Therefore, higher resistance in early fields could have been a consequence of there being fewer herbivores available to damage plants.

However, our sweep-sample data suggested that this was not necessarily the case for insects. The abundance of chewing insects was 57% greater in early vs. late fields, although the difference was not significant. Therefore, early-field goldenrods suffered less insect herbivore damage in spite of equivalent, if not higher, insect herbivore abundances (see Appendix A: Fig. A2). In contrast, we cannot rule out the possibility that differences in resistance to mammalian herbivores in early and late fields (resistance was 89% higher in early fields) was an artifact of changing mammal abundances during succession. We did not attempt to directly quantify rabbit and deer abundance between stages, but we observed more fecal pellets from these herbivores in late fields (A.S. Hakes, *personal observation*).

The greater resistance levels of goldenrods in early-successional fields, despite high abundances of insects, could be attributed to characteristics of the plant (i.e., resistance traits) or to characteristics of the neighboring plant community (i.e., associational resistance). In our previous survey, we measured goldenrod traits putatively associated with resistance in early- and late-successional fields and found that leaf toughness and total phenolics were 65% and 42% higher, respectively, in early fields than in late fields (Hakes and Cronin 2011*a*). Higher levels of leaf toughness and phenolics in early fields suggests that plant traits may contribute to higher levels of goldenrod resistance observed during early succession; however, within early fields, herbivore damage was not strongly correlated with leaf toughness and phenolics. Instead, the distribution of herbivore damage in early-successional fields was associated with ground vegetative cover (i.e., characteristics of the neighboring plant community; Hakes and Cronin 2011*a*). Neighboring plants may affect insect foraging. For example, the higher diversity and density of neighboring forbs and grasses found in early relative to late stages (Hakes and Cronin 2011*a*) may attract and retain herbivores away from focal plants or reduce the apparency of focal plants, thereby reducing damage on focal plants (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976, Rausher 1981). Further experimentation is needed to determine whether specific plant traits or associational effects contribute to the strong differences in goldenrod resistance between successional stages. Regardless of the particular mechanism, goldenrod damage from insect herbivores seems to be heavily influenced by the context of its environment.

The change in goldenrod defense levels from being highly resistant in early fields to highly tolerant in late fields suggests a successional shift in defense phenotype that has not previously been reported. Studies have found ontogenetic changes in plant defense expression (reviewed in Barton and Koricheva [2010], McCall and Fordyce 2010), including a recent study with *Raphanus sativus* in which high levels of resistance during the juvenile stage were followed by high levels of tolerance in the mature stage (Böege et al. 2007). Although our

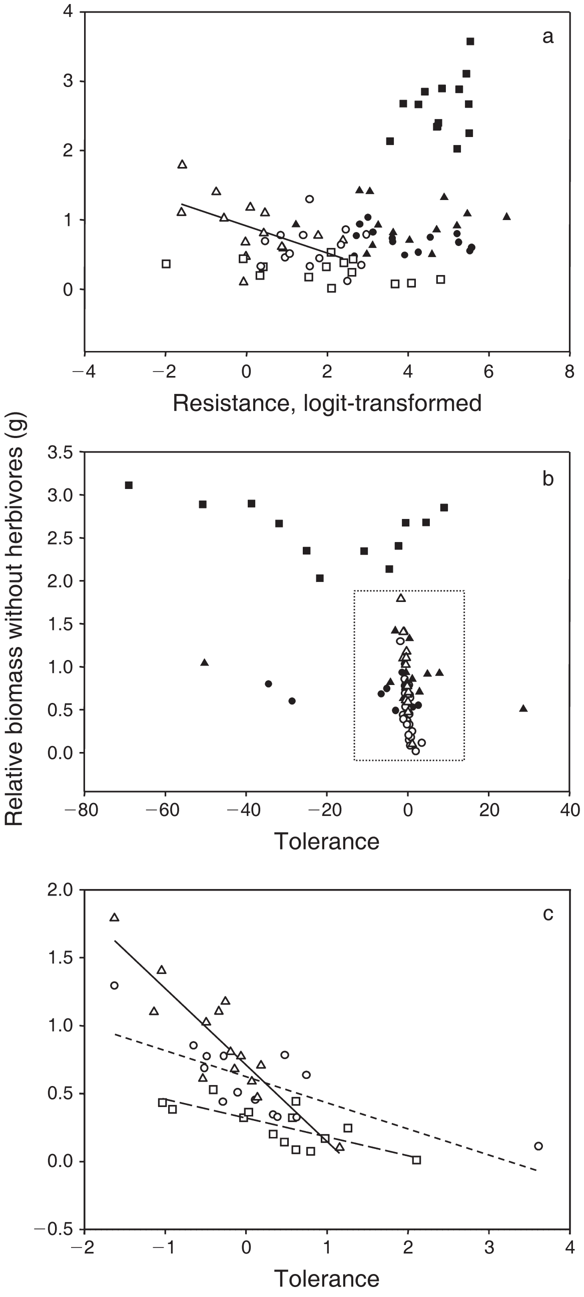

FIG. 3. The relationship between (a) goldenrod resistance and (b) tolerance and relative biomass in the absence of herbivory (where relative biomass is a proxy for relative fitness in the absence of herbivory, W_A) in early- and late-successional fields. (c) The relationship between tolerance and relative biomass in the absence of herbivory in late fields shown in the dotted rectangle in panel (b) is redrawn at a smaller scale to reveal the relationship more clearly. Each data point represents the genet average within a field, and each field within a successional stage ($n = 3$) is distinguished by a different symbol (solid symbols for genets in early fields and open symbols for genets in late fields). A significant negative relationship is indicative of a cost associated with resistance or tolerance and is depicted by a line fit × least-squares regression (where $P \leq 0.05$).

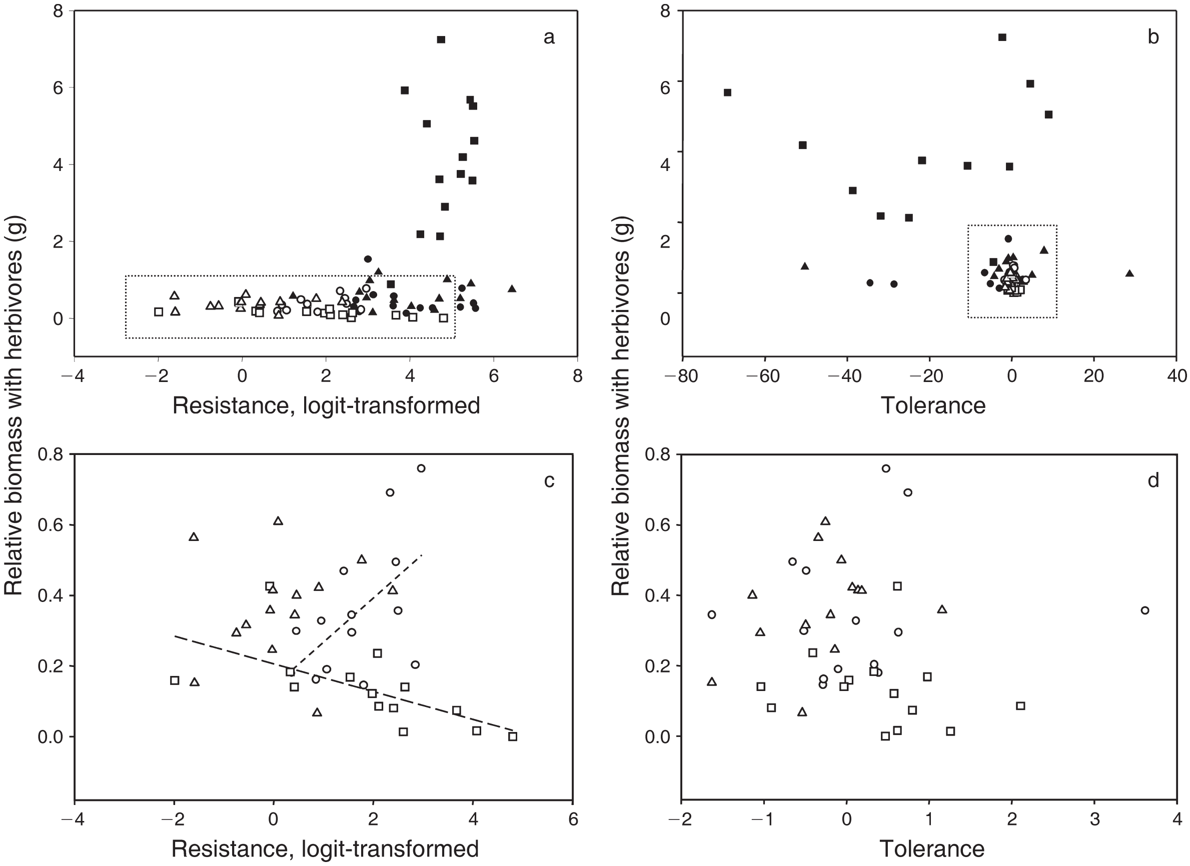

FIG. 4. (a, b) The relationship between goldenrod (a) resistance and (b) tolerance and relative biomass in the presence of herbivory (where relative biomass is a proxy for relative fitness in the presence of herbivory, W_P) in early- and late-successional fields. (c, d) In late fields, the relationships shown in the dotted rectangles in panels (a) and (b) are more clearly revealed at a smaller scale. Each data point represents the genet average within a field, and each field within a successional stage ($n = 3$) is distinguished by a different symbol (solid symbols for genets in early fields and open symbols for genets in late fields). A significant negative/positive relationship indicates selection favoring low/high levels of defense, respectively, and is depicted by a line fit × least-squares regression (where $P \leq 0.05$).

goldenrods exhibited a similar transition from high resistance to high tolerance, our experimental design controlled for ontogenetic effects by using similar-sized clonal fragments (i.e., a 5-cm rhizome cutting). Thus the differences in goldenrod resistance and tolerance levels between early- and late-successional fields were driven by stage-specific environmental factors, such as changes in the neighboring plant community and/or pressure from herbivores. Moreover, these results may suggest that there is tremendous plasticity in goldenrod resistance and tolerance. Phenotypic plasticity allows traits of plants located in spatially and temporally variable environments to respond to a changing adaptive landscape (Lloyd 1984). Plasticity in defense expression is common (e.g., Callaway et al. 2003) and has been reported previously for goldenrods (e.g., Horner and Abrahamson 1992, Pilson 1992, Cronin and Abrahamson 1999, 2001); however, it has never been reported in the context of succession. We expect plasticity to be beneficial to long-lived plants that are subjected to predictable temporal community changes that alter the adaptive value of phenotypes (Scheiner 1993). Lastly, the absence of a genotype × stage interaction effect on resistance or tolerance (i.e., plastic responses of resistance and tolerance across stages were consistent among genotypes) could be a consequence of strong selection pressures for plasticity in the past reducing the current variation in trait plasticity among genotypes (e.g., Pigliucci 2001, Richards et al. 2010).

In addition to there being a general successional trade-off between resistance and tolerance, we found that the relationship between resistance and tolerance differed between successional stages. In the early stage, there was evidence of a classic defense trade-off: resistance and tolerance were negatively correlated (see also Fineblum and Rausher [1995], Tiffin and Rausher [1999]). However, in the late stage, correlations between these two defense strategies were positive (see Fig. 3b). One possibility for the change in the resistance–tolerance relationship between successional stages is that in early stages where herbivores tended to be more abundant (and impose greater pressure on the plants; Appendix B:

PLATE 1. (a) Early-successional field approximately 3 years since disturbance and (b) late-successional field approximately 15 years since disturbance. Fields were located in Baton Rouge, Louisiana, USA. Photo creidts: A. S. Hakes.

Fig. B2), plants allocated resources to one or the other defense, as early theoretical models have suggested (i.e., Fineblum and Rausher 1995, Mauricio et al. 1997, Tiffin and Rausher 1999). In late stages, goldenrods were under greater stress from competition for light, as evidenced by their reduction in height, biomass, and flower production relative to early fields (see also Hakes and Cronin [2011*a*]). Because physiological traits conferring tolerance to herbivory may also allow plants to tolerate competition among neighbors (Siemens et al. 2003, Jones et al. 2006) and low light availability (e.g., Janse-ten Klooster et al. 2007), tolerance may be expected to increase in late succession, particularly in areas with heavy canopy cover. In our previous survey of goldenrod defense traits within early- and late-successional fields, we found strong positive correlations between a goldenrod tolerance trait, specific leaf area, and increased canopy cover within late-successional fields (Hakes and Cronin 2011*a*). In sum, we suggest that herbivore pressure in early stages and the added stress from competition in late-successional stages may explain the pattern of greater resistance in early-field goldenrods and greater tolerance in late-field goldenrods observed in our study.

Despite our attempt to select genets that differed markedly in tolerance and resistance phenotypes, we were surprised to find no significant effect of genotype on resistance and tolerance levels. Various greenhouse and common-garden studies have revealed considerable genotypic variability in goldenrod resistance to insect herbivore attack (e.g., Maddox and Root 1987, McCrea and Abrahamson 1987, Cronin and Abrahamson 2001). Moreover, our common-garden study revealed significant genotypic variability in resistance (but not tolerance) among goldenrod genets originating from two separate populations, one early- and one late-successional population (Hakes and Cronin 2011*b*). Of the 103 goldenrod genotypes used in the common-garden study, the 14 most different were used in this study. In the common-garden experiment, we did not find a significant effect of population of origin on genet resistance levels (Hakes and Cronin 2011*b*); however, we cannot reject the possibility that carryover effects within source populations inflated the variability seen among genets in resistance levels, and were subsequently lost in the present experiment. Alternatively, the discrepancy between this study and the previous studies on genetic variation in goldenrod resistance could be the result of our work being conducted in situ, where small-scale environmental heterogeneity within field sites (unaccounted for in our analyses) could have increased the variability among goldenrod replicates. We know that early and late stages can exhibit strong within-field environmental heterogeneity, and that the distribution of goldenrod damage and tolerance trait levels can be strongly associated with the distribution of neighboring plant variables (Hakes and Cronin 2011*a*). Because the surrounding plant neighborhood was cut back and standardized in the common garden (Hakes and Cronin 2011*b*), there may have been less variability among replicates, thereby increasing our ability to detect differences in resistance among genets. Our conclusions are similar to the work by Richards et al. (2010), who found strong plasticity in 17 traits of the salt marsh perennial *Borrichia frutescens* but no significant genetic variation in any of those traits measured across environments, despite clear allozymic differences among genets.

Costs and selection gradients for resistance were specific to individual fields rather than specific to a successional stage. We detected strong directional selection against resistance in one late field and selection favoring resistance in another late field. The remaining late field was the only site to exhibit a significant cost of resistance. Contrary to our expectation that the high levels of resistance expressed in early fields would coincide with a high adaptive value for resistance (i.e., higher fitness benefits relative to costs), we did not find significant selection gradients for resistance in any of our early-successional fields. One possibility for this result is that early-field goldenrods with low resistance were better able to compensate for herbivore damage than highly resistant goldenrods, causing fitness levels to remain similar among genets. Although the overall pattern was that goldenrods were significantly less tolerant in early- than in late-successional stages, the fact that we found significant trade-offs between resistance and tolerance evident in each early-field site indicates that poorly resistant goldenrods were relatively tolerant to herbivory within these fields. We note that without genetic variation in resistance and tolerance levels and higher rates of sexual reproduction, there cannot be an evolutionary response to the adaptive landscapes that we have described within our early- and late-successional fields.

Interestingly, in late-successional fields, goldenrods expressed high tolerance levels (in terms of compensatory biomass production) despite high costs and no selection gradients. Although this seems paradoxical, tolerance traits can serve a dual purpose in mitigating the effects of herbivory and competition (Siemens et al. 2003, Jones et al. 2006, Janse-ten Klooster et al. 2007). As we suggested earlier, goldenrods in late-successional stages are under considerable stress from competition for light, and tolerance traits may be responding primarily to environmental stress rather than herbivory. To evaluate this hypothesis, we would need to determine whether tolerance to herbivory and tolerance to competitive stress are correlated and determine if tolerance to competitive stress is costly and beneficial in the absence and presence of competitors, respectively. We do not have these data at present.

Although numerous models aim to explain how variation in resource availability affects plant tolerance, the limiting-resource model (LRM) by Wise and Abrahamson (2007, 2008) has proven the most reliable. In this model, tolerance of herbivory depends on the type of resource that is limited and the type of damage suffered, and 95% of the studies examined by Wise and Abrahamson (2008) supported the predictions of this model. However, our study system is an exception. The LRM predicts that compensatory growth in response to leaf-chewing herbivores should be lower in light-limited environments (i.e., late fields) because leaf removal hinders the plant's ability to acquire limiting light resources. Yet, we found that goldenrod genets expressed greater compensatory biomass production in more closed-canopy fields than in open-canopy fields. We suggest that the reason the LRM predictions did not match our data is because the model does not take into account the possibility that tolerance traits may serve dual purposes in tolerating herbivory and environmental stress. Because sexual reproduction was presumably too costly in light-stressed, late-successional fields, we suggest that investing in biomass production (i.e., rhizome production, stem elongation, and so forth) may be an adaptive strategy for goldenrod in late-successional fields, because plants still manage to reproduce clonally. Biomass investment toward vegetative and rhizome production may allow goldenrod genets to survive and persist until conditions are favorable for sexual reproduction. Our previous studies suggested that this is a likely possibility. In our common garden, we found that genets collected from a late-successional field grew significantly taller and had significantly greater inflorescence biomass than genets collected from the early-successional field (Hakes and Cronin 2011*b*), despite late-field genets being 34% smaller and 56% less likely to flower than early-field genets measured in their natural fields (Hakes and Cronin 2011*a*).

Our study with goldenrods, a cosmopolitan group of successional species, argues that defense phenotypes may be highly context dependent and that successional changes in the environment may be an important driver of temporal variability in plant resistance and tolerance. Our results highlight the importance of incorporating spatiotemporal environmental complexity into future studies of plant defense. In light of increasing anthropogenic activity and land-use changes, an understanding of how plants respond to environmental change and the consequences of those changes for plant–plant and plant–insect interactions is becoming increasingly important.

ACKNOWLEDGMENTS

We thank the Baton Rouge Recreation and Park Commission, Entergy Gulf Coast States Utilities, Louisiana State University South Campus, and Mostafa Khosravanipour for allowing us to conduct field experiments on their properties. Field and laboratory assistance was provided by Farrar Brown, Jon Hakes, and Erick Rietschier. This manuscript was improved thanks to comments and suggestions from anonymous reviewers. Funding was provided by NSF (grants DEB-0211359 and DEB-0515764), the American Museum of Natural History, the Association of Women in Science, SDE Graduate Women in Science, LSU Biograds, and Sigma Xi.

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SUPPLEMENTAL MATERIAL

Appendix A

Herbivore damage and insect herbivore abundances in early- and late-successional fields (*Ecological Archives* E093-092-A1).

Appendix B

Goldenrod resistance, biomass, and tolerance in response to the experimental treatments successional stage, goldenrod genotype, and insecticide application (*Ecological Archives* E093-092-A2).

Appendix C

Results from separate nested ANCOVA tests to determine whether there was evidence of trade-offs, costs, and selection gradients associated with resistance and tolerance in goldenrod (*Ecological Archives* E093-092-A3).