Resistance and tolerance to herbivory in *Solidago altissima* (Asteraceae): Genetic variability, costs, and selection for multiple traits[1]

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- *Premise of the study*: Quantifying the genetic variability, fitness costs, and selection gradients associated with plant defense traits is necessary to understand their evolution and continued persistence in populations. Few studies have simultaneously examined the costs, benefits, and genetic variability in multiple traits related to plant resistance and tolerance to herbivory.
- *Methods*: Using 103 *Solidago altissima* (Asteraceae) genets from two populations previously studied in situ, we conducted a common garden experiment to assess genetic variability, costs, selection gradients, and correlations among resistance, tolerance, and various resistance and tolerance traits (i.e., lateral branching, relative growth rate, leaf addition and senescence rate, specific leaf area, and leaf toughness).
- *Key results*: We report evidence for significant genetic variability in resistance and various tolerance-related traits but low broad-sense heritability ($H^2 < 0.14$) for all traits. For all traits examined, no correlation existed between trait levels of parent ramets (measured in their field of origin) and daughter ramets (measured in the common garden), suggesting plasticity in goldenrod traits. We found a strong cost of resistance and selection gradient against high resistance. Conversely, we found no evidence of costs but did find significant selection gradients favoring increased tolerance and many tolerance trait levels.
- *Conclusions*: Our study suggests that herbivores impose selection favoring increased tolerance and reduced resistance in goldenrods. In this environment, we expect that over time, resistant genets will decrease in frequency. Despite strong selection pressures, the evolution of tolerance in this environment may be constrained by the low broad-sense heritability in tolerance traits.

Key words: adaptive landscape; goldenrod; phenotypic plasticity; plant defense strategies; trait evolution.

In response to herbivore pressure, plants have evolved a variety of defense traits to reduce herbivore damage (i.e., resistance) or the negative fitness effects of herbivore damage (i.e., tolerance; Painter, 1958; Pilson, 2000; Stamp, 2003). Within a population, plants often express various levels of both resistance and tolerance traits (Mauricio et al., 1997; Stevens et al., 2007). This observation runs counter to theoretical expectations that resistance and tolerance represent mutually exclusive defense strategies owing to separate costs and similar benefits (e.g., van der Meijden et al., 1988; Herms and Mattson, 1992; Mauricio et al., 1997). An active area of research in plant-defense theory focuses on understanding the evolution of diverse defense traits and uncovering the mechanisms maintaining their variability within natural populations (e.g., Tiffin, 2000; Fornoni et al., 2004; Núñez-Farfan et al., 2007). To this end, it is necessary to determine the extent to which these traits are genetically based and to characterize their adaptive value (i.e., fitness benefits relative to fitness costs) across a gradient of herbivory.

There is much that we do not know about the adaptive value and heritability of resistance and tolerance traits, or associations among defense traits. Few studies have examined both resistance and tolerance in the same plant population, and fewer studies have quantified costs and benefits of both resistance and tolerance levels (but see Simms and Triplett, 1994; Mauricio et al., 1997; Pilson, 2000; Siemens et al., 2003; Fornoni et al., 2004; Ivey et al., 2009) or have explored how defense levels covary with each other and with other plant traits (e.g., Carr et al., 2006; Leimu and Koricheva, 2006; Travers-Martin and Muller, 2008). For example, synergistic interactions among traits may allow plants to exhibit a greater level of defense against herbivory than would otherwise be possible for independent traits (Agrawal and Fishbein, 2006). Correlative selection may be especially important for tolerance traits, which are associated with plant vigor and can serve in tolerating other types of environmental stresses (Chapin, 1991; Siemens et al., 2003; Jones et al., 2006). Studies that examine correlations among resistance and tolerance traits and characterize the costs and selection gradients associated with individual traits and suites of related traits are needed to develop a solid framework for understanding the evolution of defense traits.

We conducted a common garden experiment to quantify genetic variability, costs, and selection gradients for, and correlations among, resistance, tolerance, and various defense- and fitness-related traits (e.g., relative growth rate, leaf addition and senescence rates, specific leaf area, leaf toughness, ramet height, and inflorescence biomass) of tall goldenrod (*Solidago altissima*;

Asteracea). In this study, we used 103 goldenrod genets propagated from ramets previously surveyed in one early- and one late-successional field (Hakes and Cronin, 2011). The common garden environment controlled for variability in neighboring plants, light, and water availability that may otherwise affect the phenotypic expression of plant defensive and fitness-related traits (e.g., Horner and Abrahamson, 1992; Cipollini, 2005; Wise and Abrahamson, 2007). For the various fitness and defense-related traits that were measured from source genets in their field of origin and in daughter ramets in the common garden, we examined whether strong parent–offspring correlations existed in trait expression. If resistance and tolerance traits are mainly genetically based, then we expect to find significant variation among genets for various defense traits, high broad-sense heritability, and strong correlations between plant trait levels from source ramets measured in their field of origin and daughter ramets measured in the common garden. We expect to find that strong selection gradients favor increased levels of resistance and tolerance and that defense traits will exhibit costs when herbivores are rare or absent.

MATERIALS AND METHODS

The goldenrod system—Late goldenrod (*Solidago altissima* L. subsp. *altissima*) is common throughout eastern North America (Semple and Cook, 2006) and is a dominant plant of midsuccessional, old-field habitats. The interactions between goldenrod and its diverse herbivore assemblage have been well studied (Maddox and Root, 1987; Pilson, 1992; Root, 1996; Abrahamson and Weis, 1997; Meyer, 1998a, b; Uriarte, 2000; Cronin and Abrahamson, 2001a; Cronin et al., 2001; Wise and Abrahamson, 2008; Hakes and Cronin, 2011). Dominant herbivores include spittlebugs (*Philaenus spumarius*), gall-making flies (*Eurosta solidaginis*), and various grasshopper and beetle species (e.g., *Acrididae* spp. *Trirhabda* spp.). Herbivore damage can decrease goldenrod biomass, increase photosynthetic rates, and delay leaf senescence and flowering time (e.g., Cain et al., 1991; Meyer, 1993; Meyer and Root, 1993; Meyer, 1998b; Carson and Root, 1999; Cronin and Abrahamson, 1999; 2001b).

Goldenrod resistance and tolerance—Many studies have demonstrated significant genetic variability in goldenrod resistance to insect–herbivore attack (Maddox and Root, 1987; McCrea and Abrahamson, 1987; Maddox and Root, 1990; Cronin and Abrahamson, 2001b; Wise, 2009), but few have examined costs and/or selection for resistance (Uriarte et al., 2002; Wise et al., 2008). These few studies suggest that there is generally strong selection for increased resistance, but there is low broad-sense heritability for resistance. To date, no study has experimentally measured tolerance to herbivory in goldenrods.

A variety of traits have been linked to goldenrod resistance or tolerance. Morphological resistance traits may include leaf toughness, though evidence for this is equivocal (e.g., Choong, 1996; Siska et al., 2002; Hakes and Cronin, 2011). Goldenrods with a "nodding" apex morphology experience increased resistance to galling herbivores (Wise, 2009). Goldenrods also may employ secondary defense chemicals such as diterpenes and phenolics for defensive purposes (Gershenzon, 1994; Abrahamson and Weis, 1997; Hull-Sanders et al., 2007). Putative tolerance traits, which aid in compensatory growth and photosynthesis, have been explored in some detail in goldenrods. Specifically, lateral stem branching, increased leaf addition rate, relative growth rate, specific leaf area, and delayed leaf senescence have been experimentally shown to be associated with compensatory growth after damage in *S. altissima* (Meyer, 1998a) and other species (e.g., Oesterheld, 1992; Moriondo et al., 2003). In addition to tolerating herbivory, these traits may be associated with plant vigor and may serve in tolerating other types of environmental stresses (e.g., Siemens et al., 2003; Jones et al., 2006; Hakes and Cronin, unpublished manuscript). None of these studies has explored the fitness costs and benefits of any resistance or tolerance trait.

Source of goldenrod genets—Goldenrod genets originated from an early- and late-successional field in Baton Rouge, Louisiana, USA. As part of another study conducted in 2006 (Hakes and Cronin, 2011), we surveyed levels of various defense- and fitness-related traits from goldenrod ramets in three early- and three late-successional fields. The early fields had been mown within the past 3 y

and were dominated by goldenrods and other forbs and grasses (e.g., *S. altissima*, *Ambrosia* spp., *Liatris* spp., *Dichanthelium* spp.). The late fields had remained fallow for approximately 15 y and were dominated by trees and shrubs (e.g., *Triadica sebiferum*, *Cornus foemina*, *Acer negundo*, *Rubus* spp.). All fields were approximately 1–2 ha in size. Ramets selected for study were spaced 10 m apart in a rectangular grid within each field (Hakes and Cronin, 2011). The objective of this spacing was to obtain broad representation of the unique genets present in each field (Meyer and Schmid, 1999). A thorough description of these field surveys is provided in Hakes and Cronin (2011). In February 2007, we excavated the root bundles of ramets from alternating grid points (20 m apart) from one early-successional field (n = 55) and one late-successional field (n = 48). Rhizome material was cut into 5-cm sections, and clones were propagated in flats of vermiculite for 4 wk in a greenhouse at Louisiana State University.

Common garden—We created the common garden plot inside a 1-ha, midsuccessional field previously dominated by goldenrods. Two months before the start of our experiment (January 2007), the field was mowed and cleared, and remaining plants were sprayed with a glyphosate herbicide (Roundup, Monsanto Company, St. Louis, Missouri, USA). We planted 6 replicates of each genet into a 30 × 46 m grid with 1.5-m spacing among ramets. Assignment of goldenrods to locations in the garden was determined by a random draw. To minimize microsite differences, ramets were fertilized at the start of the experiment and were watered in times of drought. Also, all plants within a 0.25-m radius of each ramet were routinely clipped at ground level to discourage neighbor competition. We administered an insecticide treatment to encourage a gradient of herbivore damage among clonal replicates for the purpose of estimating tolerance (see *Resistance and tolerance measures* section). Half the replicates per genet were randomly assigned to an herbivory-reduced treatment and were sprayed biweekly with Sevin carbaryl insecticide (Bayer CropScience, Research Triangle Park, North Carolina, USA). The remaining ramets were assigned as controls and were spayed with an equivalent amount of water. Because the common garden was created within a field dominated by goldenrods, the herbivore community in our garden was similar to those of other nearby goldenrod fields (Hakes and Cronin, 2011).

Every 8 wk from March to November 2007, we measured ramet height and the number of new leaves produced since the previous census. Proportion of leaves damaged by leaf-chewing insects and leaf area removed were calculated for new leaves at each census. Leaf area lost to herbivores was assessed through digital photographs of three haphazardly chosen damaged leaves (representing approximately 9.3 ± 6.6% of the total number of new leaves per census) by using the program UTHSCSA *ImageTool* (University of Texas Health Science Center at San Antonio, Texas, USA). The proportion of total plant tissue damaged by leaf-chewing herbivores was estimated from this procedure. Herbivores on ramets were surveyed by visual counts and were identified to family. Other types of herbivores (i.e., galling and sucking herbivores) were scarce in our fields and were ignored in this study.

We measured plant traits known to be associated with tolerance to herbivory in *S. altissima* (lateral branching, leaf addition rate [LAR], leaf senescence rate [LSR], relative growth rate [RGR], and specific leaf area [SLA]; see Meyer, 1998b). Leaf addition rate and LSR were measured as the number of leaves added or senesced per day, respectively, and RGR was calculated as the change in height between successive census dates divided by the number of days between censuses (Meyer, 1998a). In the summer census, we collected leaf tissue samples for assessment of leaf toughness and SLA. Three leaves were collected haphazardly from the upper two thirds of the stem (representing 9.3 ± 6.6% of the leaves). Leaf toughness was measured as the average force (in grams) needed to push a metal rod through leaf tissue using a penetrometer (Itin Scale Co., Brooklyn, New York, USA; Siska et al., 2002). Leaves were transported to the laboratory on dry ice, lyophilized (72 h), and weighed. Leaf area was calculated from digital photographs with ImageTool and was used to compute SLA (leaf area per unit dry leaf mass). Specific leaf area is positively correlated with mass-based photosynthetic rate, and higher SLA in regrowth leaves allows damaged plants to gain more leaf area for a given biomass investment (e.g., Meyer, 1998a; Gunn et al., 1999). The number of clonal propagates was recorded as an estimate of asexual reproduction. Finally, newly opened inflorescences were collected and dried in an oven at 65°C for 4 d, and the biomass was determined as an estimate of short-term sexual reproduction (our proxy for fitness). Ramets that did not flower were scored as having zero biomass and were included in our analyses (see also Heschel and Riginos, 2005).

Resistance and tolerance measures—Resistance per ramet was measured as 1 – the proportion of tissue damaged by chewing herbivores (e.g., Rausher and Simms, 1989; Simms and Triplett, 1994; Stinchcombe and Rausher, 2001;

Fornoni et al., 2004). Resistance at the genet level was determined as the average resistance among the control ramets (i.e., the three ramets per genet that were exposed to herbivory). Tolerance per genet was measured as the slope of a linear regression of inflorescence biomass (our proxy for short-term fitness) against the level of damage sustained by each of six individual ramets (Simms and Triplett, 1994; Strauss and Agrawal, 1999; Tiffin and Rausher, 1999). Tolerance levels increase as the slope decreases or becomes flatter. A positive slope indicates overcompensation to damage (e.g., Belsky et al., 1993).

Data analysis—Differences among genets for resistance and each of the defense- and fitness-related trait levels (i.e., RGR, LAR, LSR, SLA, leaf toughness, lateral branching, ramet height, clonal reproduction, and inflorescence biomass) were assessed with separate nested ANOVAs. Insecticide treatment (control or sprayed) was a fixed factor, and source population (early field or late field) and genotype nested within source population (48 early genets, 55 late genets) were random effects in the model. Without replicate fields for each successional stage, a source-population effect is open to interpretation. We included this source of variation in the model only to partition the effects of population of origin from our estimates of a genotype effect on trait variation. A significant genotype effect indicates genetic variability for a particular trait, a significant insecticide treatment effect indicates that fitness and/or defense levels vary with the level of herbivory, and a significant interaction indicates that the effect of herbivory on trait levels varies among genets.

To determine whether there was variability among genets in tolerance levels, we conducted a nested analysis of covariance (ANCOVA) using inflorescence biomass (fitness estimate) as the dependent variable, herbivore damage as the covariate, and source population and genotype nested within source population as random effects. The degree of tolerance is indicated by the slope of the relationship between damage and fitness. A significant damage by genotype interaction would indicate that tolerance differs among genets from each population (i.e., the slopes differ among genets).

With the exception of height, leaf toughness, and SLA, plant defense and fitness variables required transformations to normalize distributions. Resistance was logit-transformed, number of lateral branches and clonal propagates were square-root transformed, and the remaining variables were *ln*-transformed. Tests were conducted using R (R Development Core Team, 2008), and sequential Bonferroni corrections to α were made to account for multiple tests.

Broad-sense heritabilities for resistance and defense traits were computed with the methods of Falconer (1989) and Mitchell and Shaw (1993). Broad-sense heritability (i.e., clonal repeatability) was estimated as V_g/V_p, where V_p = total variance, and $V_g = (MS_{genotype} - MS_{error})/(number of ramets per genet) from the ANOVA models described previously (Falconer, 1989; Mitchell and Shaw, 1993). Because tolerance is measured at the level of the genet rather than in individual ramets, we were unable to obtain a broad-sense heritability estimate for tolerance.

We also assessed whether defense traits were heritable by examining correlations between trait levels of source genets measured in their field of origin and trait levels of their daughter ramets (mean of unsprayed clonal replicates, n = 3) measured in the common garden. ANCOVA tests were performed separately for each trait to test the strength of the relationship between parent and offspring trait values with source population included as a covariate (random effect). If goldenrod fitness- and defense-related traits are heritable, then we would expect a strong positive correlation between the trait values for parents and offspring, regardless of whether they grew naturally in the field or in a common garden. Alternatively, the absence of a correlation would suggest that the traits have low heritability or strong phenotypic plasticity.

To examine relationships between putative defense traits and fitness, resistance, and tolerance levels, we first performed separate ANCOVA tests that included source population as a random effect, pairs of mean trait levels (i.e., resistance and leaf toughness) as the dependent and independent variables, and their interaction with population. However, none of the effects of population or interaction terms was significant after Bonferroni corrections were applied to account for multiple tests. Therefore, we report pairwise correlations between genet-level measures of resistance, tolerance, lateral branching, RGR, LAR, LSR, SLA, leaf toughness, height, number of clones, and inflorescence biomass using separate, simple regressions. Pairwise correlations among traits were calculated by using transformed trait values.

The fitness benefits of defense traits are estimated in the presence of herbivores (i.e., the control plants). For selection analyses, the untransformed mean trait levels per genet were standardized to a mean of 0 and a variance of 1, and relative fitness for each genet in the presence of damage (control ramets) was determined by dividing inflorescence biomass by the total mean (Lande and Arnold, 1983; Tiffin and Rausher, 1999; Heschel and Riginos, 2005; Donovan

et al., 2007). Selection gradients for tolerance and resistance, RGR, LAR, LSR, SLA, and leaf toughness were estimated as the slope of the regression of relative fitness (i.e., inflorescence biomass in the presence of herbivores; W_P) against the standardized mean value of a particular trait (Lande and Arnold, 1983). Selection gradients favoring increased or decreased levels of defense traits would be indicated by a significant positive or negative linear relationship, respectively, between W_P and trait levels (Mauricio et al., 1997; Tiffin and Rausher, 1999). Because these selection estimates include both the effects of direct selection on a trait and indirect selection resulting from direct selection on other, correlated traits, we also conducted a multiple regression analysis to determine the strength and direction of direct natural selection on each trait while holding constant the value of other traits (Lande and Arnold, 1983; Heschel and Riginos, 2005). Trait-by-trait interactions were included in the model to test for correlative selection, and a step function in both directions was applied to determine the best-fit model. A separate model that included quadratic terms was created to examine nonlinear relationships between W_A and trait levels. Stabilizing or disruptive selection would be evident if there were significant negative or positive quadratic terms in the relationship, respectively (Mauricio et al., 1997; Tiffin and Rausher, 1999).

Costs of defense traits are best determined from the relationship between defense level and fitness in the absence of herbivores (Simms and Rausher, 1989; Mauricio et al., 1997). In situations where herbivores are not completely excluded, fitness in the absence of herbivory can be estimated by using the following procedure. For each genet, we determined the *y*-intercept of the regression of fitness (inflorescence biomass) over the gradient of damage among ramets and divided each *y*-intercept by the total mean to determine the estimate of relative fitness in the absence of herbivory (W_A) for a particular genet (Tiffin and Rausher, 1999). Fitness costs of resistance and tolerance and of other defense traits (RGR, LAR, LSR, SLA, leaf toughness) were estimated as the slope of the regression of genet W_A against its standardized mean defense trait value for insecticide-sprayed ramets. A significant negative relationship between W_A and defense trait level would suggest a cost for that particular trait (Mauricio et al., 1997; Tiffin and Rausher, 1999; Fornoni et al., 2004). A separate model that included a quadratic term was created to examine nonlinear relationships between W_A and trait levels. Because 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 absence of herbivory) and slope (tolerance), we used a second method to test for a cost of tolerance by estimating the true covariance between tolerance and fitness (corrected for the bias on sample covariance; see appendix B in Mauricio et al., 1997). We obtained 95% confidence intervals of the estimated corrected covariance between tolerance and fitness using a jackknife procedure (Tiffin and Rausher, 1999). An estimate of the true covariance with a negative value and an interval that does not overlap zero indicates a significant cost of tolerance (Mauricio et al., 1997; Tiffin and Rausher, 1999; Fornoni et al., 2004).

TABLE 1. Results from separate nested ANOVAs for the effects of source population (P), genotype nested within population (G(P)), insecticide treatment (control vs. sprayed, I), and their interactions on *Solidago altissima* resistance and various traits associated with fitness, resistance, and tolerance. Genotype is considered a random effect, and insecticide treatment is considered a fixed effect.

Variables	Population $F_{1,101}$	Genotype(P) $F_{101\,101}$	Insecticide $F_{1,412}$	I × P $F_{101\,412}$	I × G(P)
Resistance	0.16	1.62*	136.71*	0.09	0.78
Ramet height	15.74*	1.28	69.93*	0.02	0.87
Inflorescence biomass	40.62*	1.23	2.47	2.07	0.94
Clones	3.86	1.83*	1.52	2.62	1.02
Branching	16.89*	1.84*	0.31	0.02	0.76
RGR	0.48	1.67*	15.59*	1.62	1.08
LAR	6.05	1.22	10.41*	0.30	1.03
LSR	5.62	1.63*	14.00*	0.05	1.22
Toughness	4.03	1.30	7.12*	0.19	0.82
SLA	2.41	1.14	7.97*	1.15	1.26

Note: LAR = leaf addition rate; LSR = leaf senescence rate; RGR = relative growth rate; SLA = specific leaf area.

*P values < the critical level of 0.05 following sequential Bonferroni corrections to α.

TABLE 2. Results from a nested analysis of covariance for the effects of source population, genotype nested within source population, proportion of tissue damaged by herbivores (covariate), and their interaction on *Solidago altissima* inflorescence biomass (proxy for short-term fitness). Genotype and source population are random effects, and insecticide treatment is a fixed effect.

Source of variation	df	Mean sq	F	P value
Population	1	8926.70	43.08	<0.001*
Genotype	101	207.18	1.00	0.501
Damage	1	242.76	1.13	0.288
Damage × population	1	21.48	0.10	0.752
Damage × genotype (pop.)	101	207.33	0.97	0.567
Residuals	412	214.02		

*P values < the critical level of 0.05 following sequential Bonferroni corrections to α.

RESULTS

Damage by leaf-chewing herbivores ranged from 0–50% of the total leaf tissue removed. On average, ramets in the insecticide treatment experienced 67% lower damage than ramets in the control treatment (mean ± SE: control = 7.60 ± 0.47% damage, sprayed = 2.55 ± 0.32% damage). Even though the insecticide treatment did not eliminate all herbivores, it did serve its intended purpose to increase the range of variability in damage to ramets of the same genet and to allow for meaningful estimates of tolerance, costs, and selection coefficients (see Materials and Methods).

A significant effect of source population was found on ramet height (P < 0.001), inflorescence biomass (P < 0.001), and lateral branching (P = 0.001; Table 1). Ramet height, inflorescence biomass, and lateral stem branching were each greater in genets originating from the late-successional population (mean ± SE = 118.6 ± 3.1, 14.4 ± 1.0, and 5.2 ± 0.5, respectively) than in genets from the early field population (mean ± SE = 103.2 ± 2.5, 6.8 ± 0.6, and 2.6 ± 0.2, respectively).

We found significant genetic variability for five of 10 goldenrod traits examined (Table 1). Resistance varied significantly among goldenrod genets, ranging from 0.80 to 1.00 (mean ± SE = 0.92 ± 0.05; P = 0.008; Table 1). There were also significant genotype effects on LSR (P = 0.007), RGR (P = 0.004), lateral stem branching (P = 0.001), and number of new clonal propagates (P = 0.001; Table 1). Approximately 70% of ramets flowered, and of those ramets that flowered, inflorescence biomass ranged from 0.45 to 112.0 g (mean ± SE = 14.7 ± 0.8 g). We found no evidence for significant differences among genets in ramet height, inflorescence biomass, LAR, SLA, and leaf toughness (Table 1). The interaction between genet and damage on inflorescence biomass was not significant (Table 2), suggesting that tolerance levels (i.e., slopes of the regression of inflorescence biomass against damage) did not differ strongly among genets. Tolerance levels ranged from −3.1 to 10.7 among genets (mean ± SE = 0.05 ± 1.5), with 45% of genets exhibiting positive slopes (indicating overcompensation in reproduction following damage) and 55% of ramets exhibiting negative slopes. Overall, goldenrods were very tolerant to damage; no significant relationship was found between damage and inflorescence biomass, but inflorescence biomass tended to be greater for damaged plants (n = 618, r = 0.07, P = 0.079).

A significant effect of herbivore treatment was seen on the levels of all defense and fitness traits with the exception of inflorescence biomass and the number of clonal propagates and lateral branches (Table 1). Specific leaf area was 5.5% greater for ramets exposed to natural levels of herbivory, whereas all other traits were greater in ramets in the herbivory-reduced treatment (resistance = 5.4%, height = 32.6%, RGR = 10.4%, LAR = 15.3%, LSR = 16.3%, and toughness = 7.2% greater levels in sprayed vs unsprayed ramets).

No evidence for tradeoffs was found between resistance and tolerance, but significant negative correlations existed between SLA and lateral branching and between SLA and LSR; Table 3). Many significant positive correlations existed among traits

TABLE 3. Correlations among all possible pairs of defense- and fitness-related traits of *Solidago altissima* measured in the common garden environment. Pearson's product moment correlation coefficients are reported in bold, and corresponding P values are reported below those values.

	Tolerance	Branch	RGR	LAR	LSR	SLA	Leaf toughness	Height	Inflor. biomass	Clones
Resistance	**0.13**	**0.02**	**−0.15**	**−0.13**	**−0.18**	**0.06**	**0.20**	**0.01**	**−0.06**	**0.01**
	0.17	0.81	0.15	0.78	0.07	0.57	0.04	0.92	0.55	0.99
Tolerance	—	**0.23**	**0.09**	**0.24**	**0.19**	**0.09**	**0.11**	**0.21**	**0.27***	**0.29***
		0.02	0.36	0.01	0.05	0.39	0.26	0.04	<0.01	<0.01
Branching	—	—	**0.29***	**0.68***	**0.33***	**−0.28***	**0.02**	**0.50***	**0.54***	**0.30***
			<0.01	<0.01	<0.01	<0.01	0.84	<0.01	<0.01	<0.01
RGR	—	—	—	**0.50***	**0.08**	**0.12**	**0.03**	**0.57***	**0.65***	**0.15**
				<0.01	0.41	0.25	0.75	<0.01	<0.01	0.13
LAR	—	—	—	—	**0.57***	**−0.13**	**0.02**	**0.65***	**0.56***	**0.18**
					<0.01	0.22	0.87	<0.01	<0.01	0.07
LSR	—	—	—	—	—	**-0.15**	**0.16**	**0.03**	**−0.10**	**0.09**
						0.15	0.12	0.10	0.36	0.36
SLA	—	—	—	—	—	—	**−0.01**	**−0.16**	**−0.10**	**−0.08**
							0.95	0.13	0.33	0.45
Leaf toughness	—	—	—	—	—	—	—	**0.09**	**0.13**	**0.02**
								0.36	0.20	0.85
Height	—	—	—	—	—	—	—	—	**0.65***	**0.19**
									<0.01	0.05
Inflorescence biomass	—	—	—	—	—	—	—	—	—	**0.39***
										<0.01

Note: LAR = leaf addition rate; LSR = leaf senescence rate; RGR = relative growth rate; SLA = specific leaf area.
*P values < the critical level of 0.05 following sequential Bonferroni corrections to α.

TABLE 4. Broad-sense heritabilities ($H^2 \pm$ SE) for resistance and various *Solidago altissima* fitness- and defense-related traits.

Variables	$H^2 \pm$ SE.
Resistance	0.04 ± 0.06
Ramet height	0.02 ± 0.06
Inflorescence biomass	0.03 ± 0.06
Clonal reproduction	0.13 ± 0.07
Branching	0.06 ± 0.06
RGR	0.12 ± 0.07
LAR	0.04 ± 0.06
LSR	0.14 ± 0.07
Toughness	0.01 ± 0.05
SLA	0.07 ± 0.06

Note: LAR = leaf addition rate; LSR = leaf senescence rate; RGR = relative growth rate; SLA = specific leaf area.

(30 of 36). Resistance was strongly positively correlated with leaf toughness ($r = 0.20$, $P = 0.04$), but this relationship was not significant after Bonferroni corrections to α. Tolerance was significantly positively correlated with inflorescence biomass ($r = 0.27$) and clonal reproduction ($r = 0.29$). In addition to being positively correlated with tolerance, inflorescence biomass was positively correlated with lateral branching, RGR, LAR, and height and was negatively correlated with LSR. There were also significant positive correlations between branching and traits RGR, LAR, LSR, height, and the number of clones; between RGR and traits LAR and height; and between LAR and traits LSR and height (Table 3).

Broad-sense heritability estimates for defense- and fitness-related traits were low ($H^2 < 0.14$; Table 4). Only traits RGR, clonal reproduction, LSR, and SLA had heritability estimates that were significantly greater than zero ($H^2 = 0.14 \pm 0.07$, 0.13 ± 0.07, $0.12 \pm 0.0.7$, and 0.7 ± 0.06, respectively, Table 4). Our power to detect significant heritability from our analyses was high for LSR (0.80) and SLA (0.86) but was lower and varied from 0.25 to 0.74 for the other traits (mean 0.47 ± 0.07). Moreover, no significant parent–offspring relationships were found for any of the fitness- or defense-related trait levels (i.e., no correlation between trait measurements of daughter ramets in the common garden and parent ramets in their source population; Table 5). There were no significant effects of source population or its interaction with parent trait levels on trait levels of daughters (Table 5).

A significant positive relationship existed between W_P (i.e., fitness in the presence of herbivory) and tolerance, indicating strong selection for increased tolerance to herbivory ($r = 0.35$, $P < 0.001$; Fig. 1A). In contrast, there was a marginally significant negative relationship between W_P and resistance ($r = -0.18$, $P = 0.052$; Fig. 1B), suggesting a selection gradient against increased resistance. When these two defense strategies were considered together in a multiple regression, there was significant selection favoring high tolerance and low resistance and no evidence for correlative selection ($r^2 = 0.18$, $P < 0.001$; Table 6).

We first examined selection gradients for resistance- and tolerance-related traits (this measure represents both direct selection on the trait and indirect selection on correlated traits), and then we partitioned direct selection on each trait and correlative selection for each pair of traits using a multivariate model regression. First, we found significant positive selection gradients for lateral branching ($r = 0.54$, $P < 0.001$), RGR ($r = 0.32$, $P < 0.001$), and LAR ($r = 0.65$, $P < 0.001$) but no evidence of selection gradients for LSR, SLA, or leaf toughness (Fig. 1C–H). A best-fit multivariate model examining direct and correlative selection for all resistance- and tolerance-related traits showed significant direct selection for branching and LAR, direct selection against LSR, and correlative selection for branching and LSR, branching and leaf toughness, and SLA and leaf toughness ($r^2 = 0.71$, $P < 0.001$; Table 7). There was no evidence for stabilizing or disruptive selection for resistance or tolerance or for any of the traits.

Significant negative relationships were found between W_A (i.e., fitness in the absence of herbivory) and tolerance ($r = -0.31$, $P < 0.001$) and resistance ($r = -40$, $P < 0.001$), respectively, suggesting significant fitness costs to employing either defense strategy when herbivores are absent (Fig. 2A, B). However, we also examined the cost of tolerance by testing whether the corrected covariance was less than zero (see Materials and Methods). Application of the correction for the bias in the relationship yielded an estimate of the true covariance of 0.88 and 95% confidence intervals between 0.86 and 0.88. Because this range is greater than zero, we conclude that there is no evidence for a significant cost of tolerance. We did not find fitness costs for any other goldenrod trait (Fig. 2C–H). On the contrary, significant positive correlations existed between W_A and the putative tolerance traits lateral branching ($r = 0.32$, $P < 0.001$) and LAR ($r = 0.46$, $P < 0.001$). Finally, we found no evidence for nonlinear relationships between W_A and the various goldenrod traits.

TABLE 5. Separate analysis of covariance tests to assess the relationship between trait levels of individual source genets measured in their field of origin (parent traits) and average trait levels of daughter ramets (mean of three control ramets) measured in the common garden environment (offspring traits). Effects of source population (random effect, n = 2) and its interaction with parent trait levels are included in the model. *F* and *P* values are reported.

Offspring trait	Population $F_{1,1}$	Population *P* value	Parent trait $F_{1,99}$	Parent trait *P* value	Population X trait $F_{1,99}$	Population X trait *P* value
Resistance	11.34	0.18	0.53	0.47	0.01	0.97
Ramet height	139.30	0.05	0.11	0.74	0.07	0.79
Inflorescence	94.60	0.06	0.57	0.45	0.37	0.54
Branching	13.72	0.17	0.40	0.53	1.13	0.30
RGR	16.55	0.15	0.61	0.43	0.09	0.76
LAR	6.16	0.24	0.26	0.61	0.68	0.41
LSR	6.47	0.24	2.16	0.14	0.40	0.53
SLA	0.40	0.64	0.01	0.94	1.82	0.10
Toughness	15.21	0.16	3.01	0.09	0.10	0.75

Note: LAR = leaf addition rate; LSR = leaf senescence rate; RGR = relative growth rate; SLA = specific leaf area.
*P values < the critical level of 0.05 following sequential Bonferroni corrections to α.
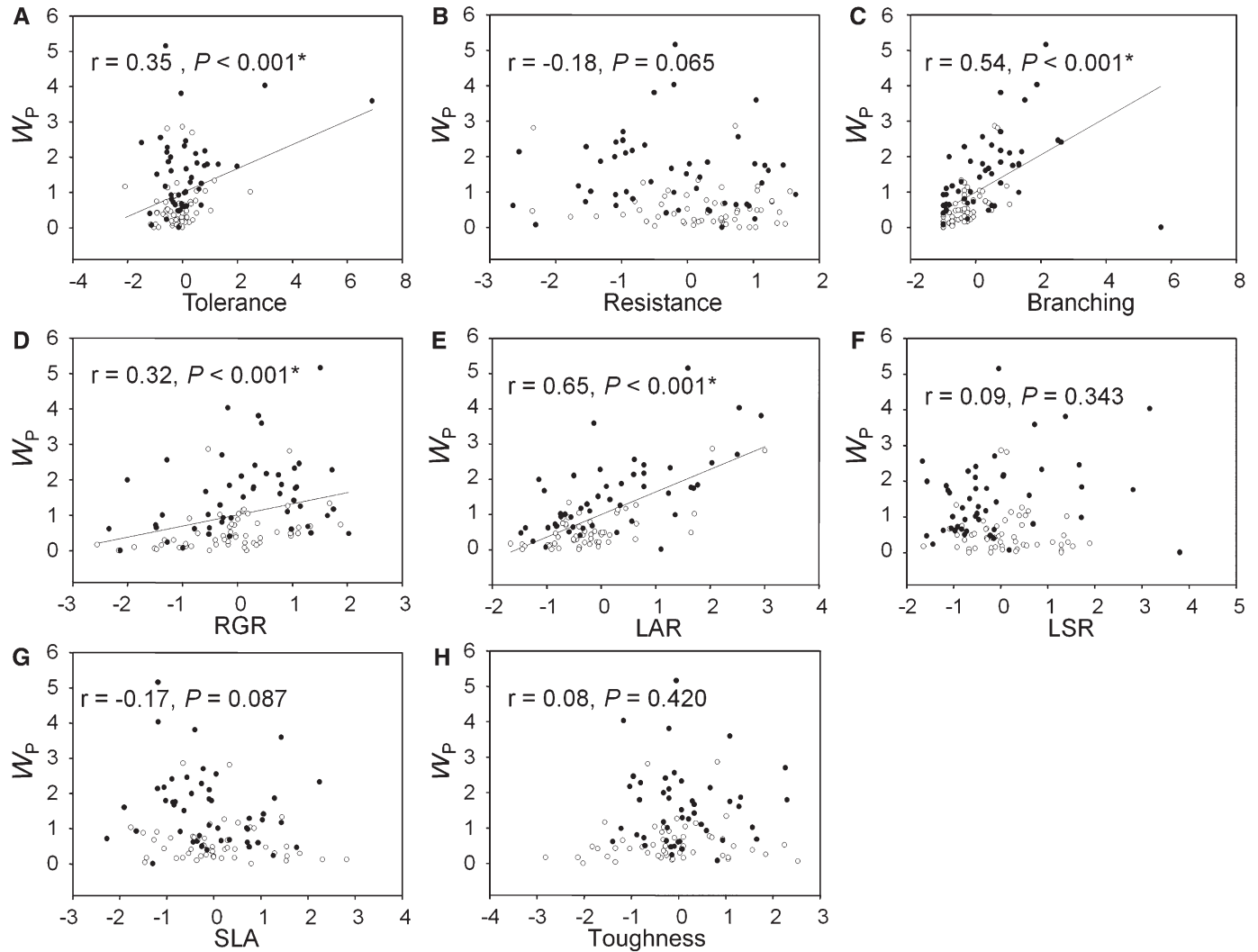
Fig. 1.   Relationships between relative inflorescence biomass in the presence of herbivory (W_P) and various goldenrod defense-trait levels: tolerance (A), resistance (B), branching (C), relative growth rate (RGR; D), leaf addition rate (LAR; E), leaf senescence rate (LSR; F), specific leaf area (SLA; G), and leaf toughness (H). A significant positive or negative relationship is indicative of selection for high or low trait levels, respectively. Each data point represents the average value for a genet (n = 103). Relationships that are significant following sequential Bonferroni corrections to α are noted with an asterisk. Open circles represent genets originating from the early successional field, and filled circles represent genets originating from the late successional field.

DISCUSSION

We found no costs and strong selection for increased levels of tolerance to herbivory and many tolerance-related traits in goldenrod (i.e., lateral branching, RGR, and LAR), but we found strong costs and direct selection against resistance. We also report evidence for genetic variability in goldenrod resistance and many tolerance- and fitness-related traits of goldenrod (i.e., clonal reproduction, lateral branching, RGR, LSR). Goldenrods had previously only been examined for genetic variation in resistance to herbivores (Maddox and Root, 1987; McCrea and Abrahamson, 1987; Maddox and Root, 1990; Cronin and Abrahamson, 2001b; Wise, 2009), although significant genetic variability in both resistance and tolerance to herbivory has been documented for other plant species (e.g., Simms and Triplett, 1994; Mauricio et al., 1997; Fornoni et al., 2004; Carr et al., 2006; Ivey et al., 2009).

Despite significant genetic variability in many goldenrod traits, we found very low broad-sense heritability estimates for resistance ($H^2 = 0.04 \pm 0.06$) and all the other traits examined (range: 0.02 to 0.14). Broad-sense heritability, which estimates the proportion of phenotypic variance that is attributed to all genetic factors, is assumed to be an upper limit to narrow-sense heritability, which includes only additive genetic variance (Falconer, 1989). Our finding of high genetic variability but low heritability of resistance is contrary to the findings of many studies that have found high heritability of resistance in other plant species (e.g., Carr et al., 2006; Agrawal and Konno, 2009; Johnson et al., 2009), but it is not unique. Similar to our findings, Wise (2007) found significant genetic variation in *Solanum carolinense* resistance but relatively low broad-sense heritability estimates in resistance toward herbivores (ranging from 0.04 to 0.30). In an earlier study of goldenrods, Maddox and Root (1987) also found low broad-sense heritability of resistance in

TABLE 6. Results from a multiple regression analysis for the effects of standardized resistance, tolerance, and their interaction on relative fitness (inflorescence biomass) (model $r^2 = 0.18$, $P < 0.001$). Significant linear terms indicate direct and interaction terms indicate correlative selection gradients, respectively. A separate model including quadratic terms also was conducted to test for disruptive or stabilizing selection, but no significant quadratic terms were found (not shown).

Coefficients	Estimate	SE	t	P value
(Intercept)	1.01	0.09	11.15	<0.001*
Resistance	−0.25	0.10	−2.64	0.010*
Tolerance	0.41	0.13	3.26	0.002*
Resistance × Tolerance	−0.05	0.12	−0.40	0.69

*P values < the critical level of 0.05 following sequential Bonferroni corrections to α.

18 *S. altissima* genets (ranging from 0.05 to 0.2) despite a high genetic variability in resistance to many different insects. Interestingly, in the same study, Maddox and Root (1987) found that the narrow-sense heritabilities (0.05–0.92) were generally much higher than broad-sense heritabilities, which suggests that when using an operational measure of resistance (i.e., the occurrence of damage rather than individual traits), estimates based on the variation among clones should not necessarily be interpreted as an upper limit of heritability (Wise, 2007). However, unlike Maddox and Root (1987), we did not find a significant parent–offspring regression for any of our traits, which suggests that narrow-sense heritability is also likely to be very low. Thus, we conclude that the low heritability estimates reported here have the potential to constrain trait evolution in the garden environment.

In our common garden environment, goldenrod genets originating from the late-field population grew significantly taller and produced greater inflorescence biomass and more lateral branches than genets from the early-field population, suggesting that a carryover effect might exist for these traits. Interest-

TABLE 7. Multiple regression model for the effects of standardized resistance- and tolerance-related trait values on relative fitness (inflorescence biomass). The full model for direct and correlative selection included linear traits (branching, RGR, LAR, LSR, SLA, toughness) and their pairwise interactions. A step function in both directions was applied to determine the best-fit model (model $r^2 = 0.71$, $P < 0.001$). A separate model including quadratic terms also was conducted to test for disruptive or stabilizing selection, but no significant quadratic terms were found (not shown).

Coefficients	Estimate	SE	t	P value
(Intercept)	0.97	0.06	15.38	<0.001*
Branching	0.51	0.10	5.16	<0.001*
LAR	0.59	0.10	6.15	<0.001*
LSR	−0.45	0.09	−5.00	<0.001*
SLA	−0.08	0.06	−1.28	0.205
Toughness	0.04	0.06	0.60	0.550
Branch × LSR	0.28	0.07	3.81	<0.001*
Branch × toughness	0.34	0.11	2.95	0.004*
LAR × toughness	−0.20	0.09	−2.18	0.032
LSR × toughness	0.19	0.07	2.58	0.012
SLA × toughness	0.20	0.07	2.68	0.009*

Note: LAR = leaf addition rate; LSR = leaf senescence rate; RGR = relative growth rate; SLA = specific leaf area.

*P values < the critical level of 0.05 following sequential Bonferroni corrections to α.

ingly, this finding contradicts the pattern observed when we surveyed goldenrod trait levels within early- and late-successional fields (two of the six fields surveyed included the genets used in this study). We found that goldenrods naturally occurring in late-successional fields were 34% shorter and were 56% less likely to flower than those occurring in early-successional fields, presumably owing to lower light availability (Hakes and Cronin, 2011). This pattern may suggest that goldenrods that exhibit low fitness in stressful environments have the ability to fully (or over-) compensate for diminished growth and/or reproduction if environmental conditions become more favorable.

As expected, goldenrods that were sprayed with an insecticide to reduce herbivory levels received less damage (i.e., higher resistance) than those exposed to natural levels of herbivory. Leaf toughness, which was positively correlated with resistance ($r = 0.20$, $P = 0.04$), was also greater in the herbivory-reduced than in the control treatment, as were ramet height, RGR, LAR, and LSR. One explanation for why height and many tolerance traits were higher in the herbivory-reduced treatment could be that the insecticide directly influenced plant growth. Although this is a possibility, Meyer et al. (2005) found no direct effects of a similar Carbaryl insecticide on the height or biomass of goldenrods. We suggest that it is more likely that goldenrod growth was lower in the control treatment owing to their exposure to more herbivores. Lastly, SLA was the only trait to exhibit higher levels in control ramets. This may reflect increased levels of SLA in new leaves after herbivore damage (Meyer, 1998a).

Goldenrod resistance and tolerance traits may exhibit strong phenotypic plasticity rather than strong heritability. Plastic defense expression is common in many plants (reviewed in Callaway et al., 2003; see also Barton, 2008; Holeski et al., 2010), and studies that have examined goldenrod resistance in multiple environments and over several years report that resistance rankings among genets can differ between environments and can change over time (Maddox and Cappuccino, 1986; e.g., Horner and Abrahamson, 1992; Meyer and Root, 1993; Cronin et al., 2001; but see Wise, 2009). By maintaining an environment with reduced vegetative ground cover and canopy cover (see Materials and Methods), the common-garden environment differed from the early- and late-successional fields from which our genets originated. These characteristics of the neighboring plant community can potentially influence plant defenses through competitive or associational interactions (e.g., Horner and Abrahamson, 1992; Cipollini and Bergelson, 2001, 2002; Siemens et al., 2003; Jones et al., 2006). In a separate experiment using a subset of these same genets, we found evidence for substantial phenotypic plasticity in resistance and tolerance (Hakes and Cronin, unpublished manuscript). In that study, goldenrod genets were grown in early- and late-successional fields, and differences in resistance and tolerance were attributed to effects of successional fields rather than to genets.

The only variable to exhibit a significant fitness cost in the absence of herbivory was resistance (i.e., a negative relationship between resistance and fitness in the absence of herbivory; see Fig. 2). Moreover, we found evidence of a direct selection gradient against increased resistance when controlling for the effect of tolerance. However, there was significant correlative selection associated with the resistance trait leaf toughness; selection favored plants that had both high levels of leaf toughness and lateral branching, or high levels of leaf toughness and SLA. In general, tolerance traits were associated with high relative fitness and no fitness costs in the absence of herbivores.
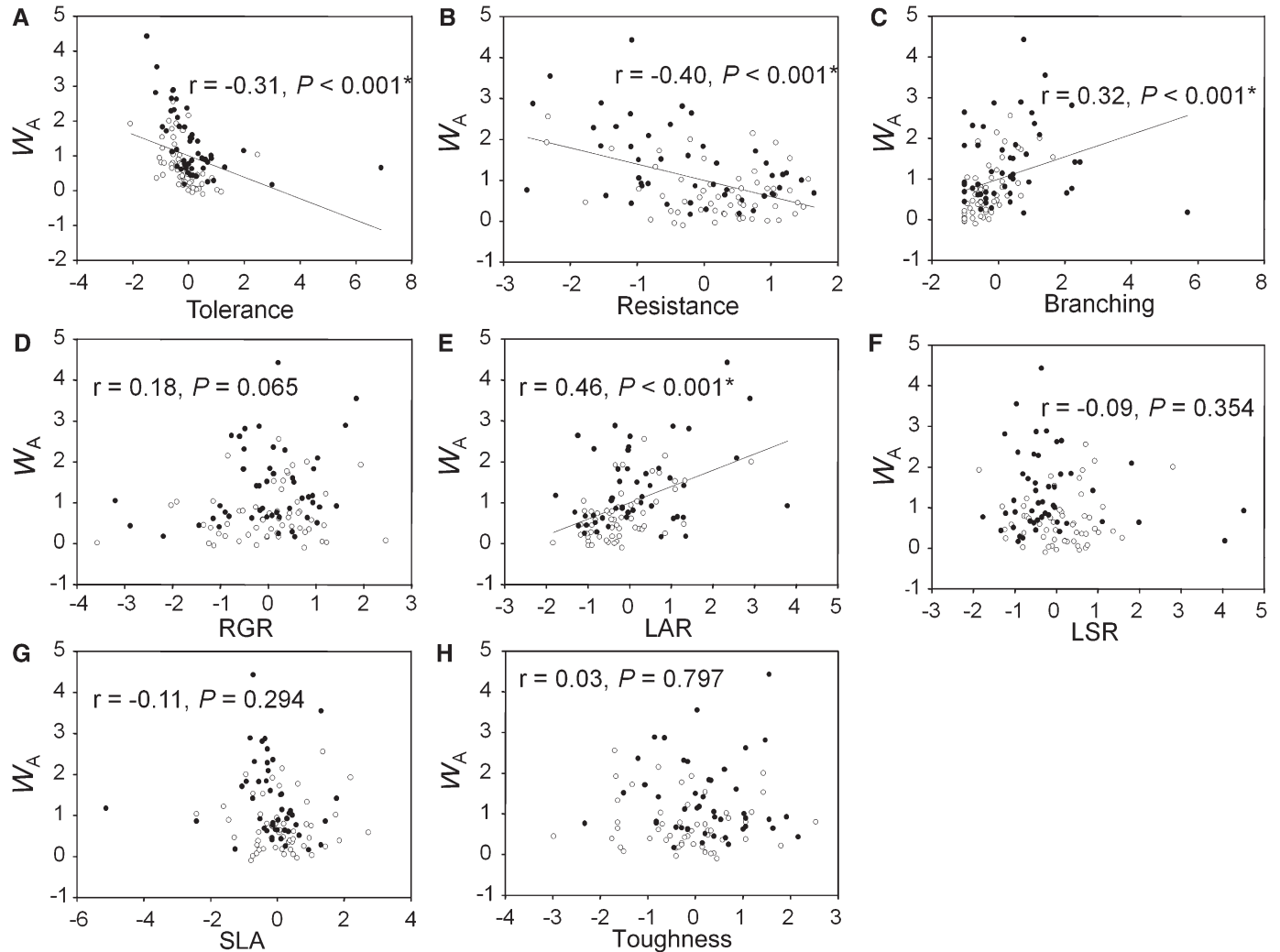
Fig. 2.   The relationships between relative inflorescence biomass in the absence of herbivory (W_A) and standardized goldenrod defense-trait levels: tolerance (A), resistance (B), branching (C), relative growth rate (RGR; D), leaf addition rate (LAR; E), leaf senescence rate (LSR; F), specific leaf area (SLA; G), and leaf toughness (H). A significant negative relationship is indicative of a cost associated with the trait. Each data point represents the average value for a genet (n = 103). Relationships that are significant following sequential Bonferroni corrections to α are noted with an asterisk. Open circles represent genets originating from the early successional field, and filled circles represent genets originating from the late successional field.

Lateral branching and LAR not only experienced fitness benefits in the presence of herbivory (i.e., positive selection), but these benefits were also evident in the absence of herbivory. The presence of fitness benefits, irrespective of herbivore damage, may be expected when plant traits also serve nondefense functions (e.g., Siemens et al., 2003; Jones et al., 2006). Significant negative selection gradients were associated with LSR and the interaction between LSR and lateral branching. Lastly, there was significant selection favoring increased tolerance to herbivory in the common garden environment. Overcompensation to damage (i.e., positive tolerance values) was highly adaptive (i.e., fitness benefits outweigh fitness costs) in the common garden, and no evidence was found for a significant cost of tolerance, despite an apparent negative relationship.

Because the competitive interactions among neighboring plants in our garden were low relative to those of unmanipulated goldenrod fields, our results may follow the expectation of the compensatory-continuum hypothesis, which predicts that high tolerance should be favored in plants located in environments with minimal competition stress from neighboring plants (e.g., Maschinski and Whitham, 1989; Pilson, 2000). For this hypothesis to be supported, an experiment is required to test whether the adaptive value of tolerance decreases (i.e., costs outweigh benefits) under conditions of greater competition (e.g., Tiffin, 2002; but see Wise and Abrahamson, 2005). Lastly, the role of specific traits in conferring resistance or tolerance to herbivory may be context dependent. For example, the tolerance trait SLA (which was uncorrelated with tolerance levels in our common garden environment) may be more important in environments with neighbor shading, where it can mitigate stress from both low light availability (e.g., Janse-ten Klooster et al., 2007; Hakes and Cronin, 2011) and herbivory (e.g., Oesterheld, 1992; Meyer, 1998a).

We conclude that herbivores are imposing selection for high tolerance to herbivory (and tolerance-related traits) in a common garden environment, but the evolutionary response to this pressure may be limited by the low heritability of tolerance traits. No evidence of selection for increased goldenrod resistance

was seen in our study; however, our finding of genetic variability for resistance and a strong fitness cost of resistance suggests that highly resistant genets may decrease in frequency over time in the common garden environment. Other studies examining costs and benefits of resistance and tolerance within plant populations have found mixed evidence for defense costs and selection gradients (e.g., Simms and Triplett, 1994; Mauricio et al., 1997; Fornoni et al., 2004). There is a growing consensus that the adaptive landscape for plant defenses may be highly dependent on a plant's environmental context (e.g., Pilson, 2000; Siemens et al., 2003; Fornoni et al., 2004). In a subsequent field experiment in which we out-planted goldenrods into early- and late-successional fields, we found strong selection for and against resistance within each of two early-successional fields and no selection gradients associated with tolerance in any field (Hakes and Cronin, unpublished manuscript). Together, these findings contribute to our understanding of how defense strategies evolve or are maintained within environments, and they lend support to the existence of environmentally variable adaptive landscapes for resistance and tolerance (see also Laine and Tellier, 2008). Given the potential for the environment to influence plant traits, the adaptive nature of resistance and tolerance may covary with spatial and temporal environmental variability.

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