

Geographic variation in compensation to damage in common milkweed (*Asclepias syriaca*)

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Abstract

Background and aims – Plants display a variety of resistance and tolerance responses to herbivory. Compensation, or changes in growth, allocation, and/or physiology, after damage is one way that plants tolerate herbivory, but geographic patterns in intraspecific plant compensatory responses are understudied. We aimed to study geographic variation in tolerance to herbivory to help explain geographic patterns in the distribution of resistance traits and the relationship between tolerance and resistance traits in common milkweed, *Asclepias syriaca*.

Material and methods – We grew milkweed from 14 different populations in the greenhouse, mechanically applied 25% leaf damage to an experimental group, and compared the control and experimental groups to measure compensatory responses in final biomass, root:shoot ratios, stem investment, and relative growth rate. We compared compensatory responses across populations grouped by latitude and by temperature.

Key results – Compared to controls, milkweed plants that were damaged lost mass and expressed reduced root:shoot ratios. However, the effect of damage on total mass, stem investment, and relative growth rate varied among genetic families. In regional contrasts, plants from colder climates grew larger and invested less in stems and roots than plants from warmer climates under control conditions, but they were less able to compensate for damage in terms of biomass. Plants from cold regions also showed a tendency to reduce growth rate and stem investment after damage; whereas, plants from warmer climates tended to increase their growth rate and stem investment in response to damage.

Conclusion – While plants from high latitudes and colder climates were less able to compensate for damage than those from lower latitudes, we are not confident that these differences are caused by geographic differences in growth rate, or that they explain differences in resistance to herbivory. Instead, we suspect that differences in the phenology of development in plants from regions with different climates affect the impact of damage and the potential for compensatory growth. Milkweed plants from colder regions with short growing seasons grew larger during our measurement period, while those from regions with longer growing seasons invested more in stems and roots, traits which may have facilitated greater long-term growth, as well as the greater compensatory ability observed in our study. Future studies should explicitly manipulate the timing of damage applied to plants from different regions to test the relationship between phenology and compensation.

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Keywords

Apocynaceae, compensation, latitude, phenology, simulated herbivory, tolerance

INTRODUCTION

Herbivores are important agents of selection on plants (Mauricio and Rausher 1997; Stowe et al. 2000; Ramos and Schiestl 2019), yet their fitness impact can be highly variable. Plants typically perform better in the absence of herbivory, and there has been selection for chemical and physical resistance traits that reduce damage due to herbivory (Mauricio and Rausher 1997). Another strategy for handling herbivore pressure is tolerance, meaning that plants maintain or increase fitness in the presence of damage (Paige and Whitham 1987; Maschinski and Whitham 1989; Rosenthal and Kotanen 1994; Garcia and Eubanks 2019). One mechanism of tolerance is compensation, or regrowth in response to damage (Rosenthal and Kotanen 1994). Because authors sometimes report tolerance using growth metrics like height or biomass that correlate with fitness (e.g. Croy et al. 2020), compensation and tolerance can be confounded. Although tolerance and resistance have been hypothesized to be redundant strategies that should exhibit trade-offs (van der Meijden et al. 1988), many researchers argue selection favours both resistance and tolerance (Mauricio et al. 1997; Leimu and Koricheva 2006; Nuñez-Farfán et al. 2007; Mesa et al. 2017), although there are some exceptions (e.g. Lehndal and Ågren 2015; Salgado-Luarte et al. 2023).

Geographic patterns in resistance to herbivory and associated plant traits are well-studied, and resistance traits can be distributed according to geographic mosaics of species interactions (Berenbaum and Zangerl 1998; Zangerl and Berenbaum 2003; Thompson 2005), resource gradients (Coley et al. 1985; Fine et al. 2004), and latitudinal gradients (Schemske et al. 2009; Moles et al. 2011a, 2011b; Anstett et al. 2016; Headrick et al. 2024). In contrast to resistance, traits that contribute to compensation or tolerance of herbivory (Tiffin 2000) and patterns of geographic variation in compensation or tolerance are less well understood (Johnson and Rasmann 2011; Hahn and Maron 2016). A variety of traits can facilitate compensatory regrowth and tolerance to herbivory, including 1) phenological differences such as the developmental stage of a plant when herbivory occurs (Lowenberg 1994; Del-Val and Crawley 2005; Lehndal and Ågren 2015) or delayed flowering to allow longer recovery (Krimmel and Pearse 2016), 2) pre-damage storage in roots and stems combined with reallocation of carbon after damage (van der Meijden et al. 1988; Strauss and Agrawal 1999; Hochwender et al. 2000; Stevens et al. 2007; Lurie et al. 2017), 3) high relative growth rate (Coley et al. 1985; Fine et al. 2004), and 4) a variety of damage-induced plant responses like increased photosynthesis, activation of dormant meristems, delayed reproduction

(Tiffin 2000), and increased relative growth rate (Strauss and Agrawal 1999). In many cases, there is no evidence for intraspecific geographic patterns in compensation or associated traits across latitude (Więski and Pennings 2014; Sakata et al. 2017), altitude (Dostálek et al. 2016), or climate (Knappová et al. 2018). Two studies, however, have reported a positive association between latitude of origin and compensation in common gardens (Lehndal and Ågren 2015; Croy et al. 2020), though one of these observed a nonlinear and u-shaped trend (Croy et al. 2020). These limited data demonstrate a need for more further investigation.

A better understanding of geographic variation in tolerance to herbivory and associated regrowth traits will help predict plant-herbivore dynamics over space and in response to range shifts. It could also help to explain geographic patterns in the distribution of resistance traits and the relationship between tolerance and resistance traits. For example, Woods et al. (2012) reported a latitudinal cline in growth patterns across populations of common milkweed, *Asclepias syriaca* L., a species in which the ecology and evolution of both resistance and tolerance traits have been well-studied (e.g. Malcolm 1991; Hochwender et al. 2000; Agrawal 2005; Agrawal and Fishbein 2008; Tao and Hunter 2013). In that study, *A. syriaca* plants displayed clinal trends in which high-latitude populations grew larger early in the season (an indication of earlier phenology), were smaller by the end of the growing season, allocated more biomass to roots, invested more in clonal reproduction, produced more latex, and displayed greater resistance to aphids (*Aphis nerii* Fonscolombe, 1841) and larval monarch (*Danaus plexippus* (Linnaeus, 1758)) (Woods et al. 2012). Although higher resistance in high-latitude populations did not match geographic patterns in herbivory, which was greatest in the central part of the range, Woods et al. (2012) posited that such a pattern could be explained if high-latitude populations were less tolerant of herbivory, implicitly hypothesizing a trade-off between resistance and tolerance (see also van der Meijden et al. 1988).

This study investigated intraspecific, geographic patterns in *A. syriaca* tolerance of damage by compensation using a common garden greenhouse study. We studied plants from 14 populations that spanned more than 10° latitude, and we predicted that region of origin would affect compensatory responses in at least one of three ways. First, plants from colder regions with shorter growing seasons (high latitude) exhibit relatively earlier phenology in a common garden, so their larger size when herbivores emerge could facilitate greater compensation (Lehndal and Ågren 2015). We predict different phenologies could affect compensation, even to experimentally imposed damage applied proportionally

to leaf area. Second, plants originating from high latitudes invest more in roots (Woods et al. 2012) and other storage organs that facilitate regrowth after damage (Hochwender et al. 2000; Więski and Pennings 2014; Hahn and Maron 2016). Alternatively, plants originating from colder climates (high latitude) might be slower growing and consequently less tolerant of damage than their warmer-climate counterparts (Woods et al. 2012). We report patterns based on latitudinal variation to test predictions based on previous studies, and temperature variation to provide evidence about the degree to which temperature might drive regional responses.

MATERIAL AND METHODS

Natural history

Asclepias syriaca is a weedy perennial plant native to the Great Plains and northeast regions of the United States and into Canada (Woodson 1954; Bhowmik 1994), although its range has been extending farther south, perhaps following human disturbance (Wyatt 1996). It reproduces asexually using underground rhizomes, as well as sexually and primarily through outcrossing (Kephart 1981; Bhowmik 1994). Milkweed pollination occurs via transfer of pollinia, meaning that each wind-dispersed seed pod contains seeds that are full siblings.

Milkweeds, including *A. syriaca*, are known for a suite of defensive traits, including sticky latex, toxic cardenolides, and trichomes; nevertheless, they harbour a variety of specialist insect herbivores that consume all parts of the plant (Agrawal 2005) and that could select for high tolerance. Plausible mechanisms of compensation have been reported for *A. syriaca*. These include responding to damage by reducing photosynthesis in damaged leaves, but increasing photosynthesis slightly in neighbouring undamaged leaves (Delaney et al. 2008), and by shifting allocation of nitrogen to stems after damage to leaves and roots (Tao and Hunter 2013). Previous studies have shown latitude-based patterns in phenology, growth, defence, and reproductive traits (Woods et al. 2012). However, we are not aware of any studies reporting geographic variation in compensatory growth responses to damage in this species.

Experimental design

We grew seeds from 16 genetic families collected from 14 different sites across the range of *A. syriaca* (Fig. 1; Table 1). Seedpods from naturally-occurring plants were collected in the fall of 2016 and sent to St. Olaf College for storage until planting. We planted seeds from a single seed pod per plant. This design maximizes our ability to measure compensation by comparing damaged and undamaged plants from the same genetic family. However,

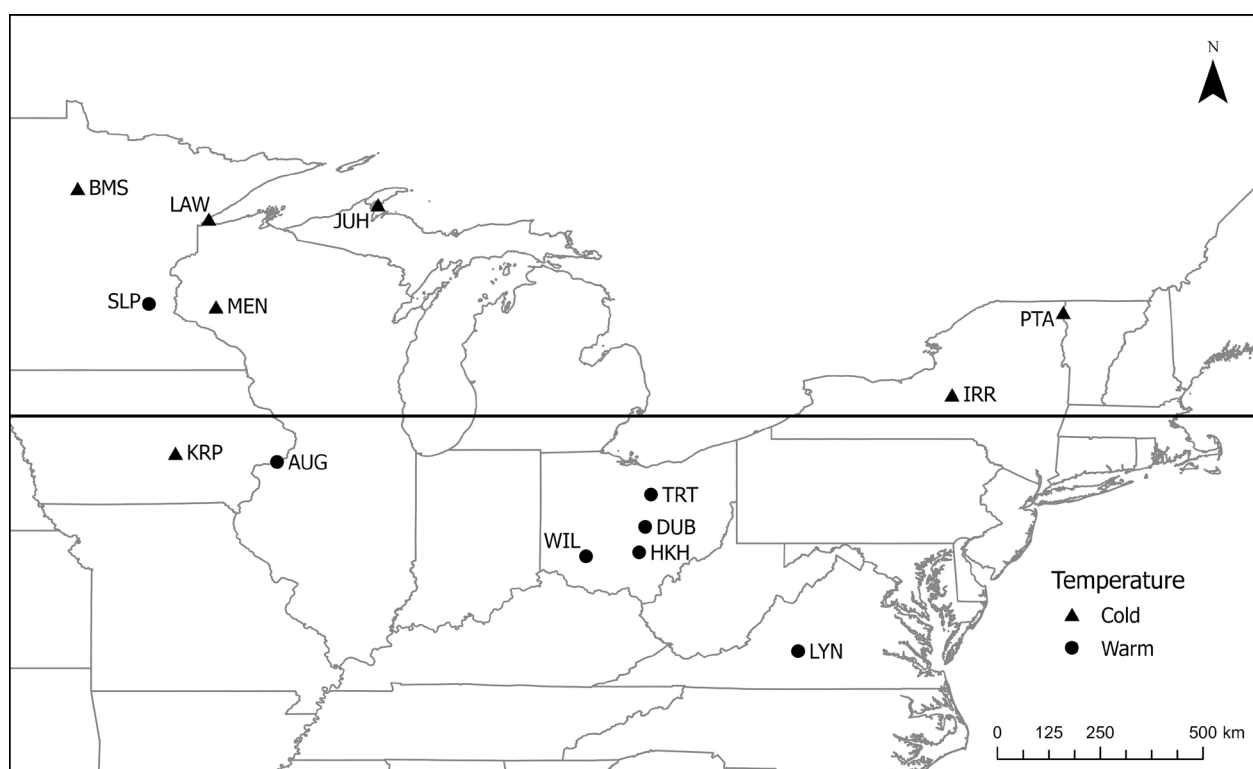


Figure 1. The distribution of milkweed source populations (*Asclepias syriaca*), bisected at 42.5°N. There are seven populations in the high-latitude regional group, above the line, and seven populations in the low-latitude regional group, below the line. There are also seven populations in the high-temperature group, with a mean annual temperature above 8°C, and seven populations in the low-temperature group, with a mean annual temperature below 8°C. To control for genetic variation, a single genetic family was studied from most source populations; however, two genetic families were studied from the highest and lowest latitude sites: BMS and LYN.

Table 1. Replicate number of plants from each *Asclepias syriaca* source population in each experimental treatment.

Site ID	Latitude	Longitude	30 year average temperature (°C)	No. of replicates, control plants (Total: 245)	No. of replicates, damage treatment (Total: 125)	No. of replicates, total
LYN ^a	37°22'7.284"N	79°10'47.388"W	12.67	31	16	47
WIL	39°26'22.02"N	83°48'43.812"W	10.94	16	8	24
HKH	39°31'32.556"N	82°39'5.436"W	11.78	15	8	23
DUB	40°5'2.688"N	82°31'10.596"W	10.56	16	8	24
TRT	40°47'10.752"N	82°23'28.392"W	9.72	16	8	24
AUG	41°29'47.724"N	90°33'37.62"W	11.11	16	8	24
KRP	41°42'26.892"N	92°46'42.312"W	6.72	12	6	18
IRR	42°58'56.676"N	75°49'0.66"W	6.72	15	8	23
PTA	44°46'59.736"N	73°23'19.068"W	7.11	15	8	23
MEN	44°54'4.608"N	91°53'33.216"W	6.67	16	8	24
SLP	44°56'35.988"N	93°21'33.012"W	8.56	15	8	23
LAW	46°49'9.804"N	92°2'57.192"W	4.28	16	8	24
JUH	47°7'54.012"N	88°21'14.076"W	4.72	16	8	24
BMS ^a	47°29'11.004"N	94°54'47.016"W	3.72	30	15	45

^a Two genetic families were sampled from these sites.

12 sites were represented by just a single genetic family, and two additional sites were represented by two genetic families (Fig. 1; Table 1). This decision limits our ability to detect fine-scale (site-by-site) patterns in geographic variation. For analyses, we divided the range of common milkweed (60–105°W and 35–50°N; Bhowmik 1994) into two regions which allows us to run ANCOVAs with higher levels of replication than were available at the site level (see Data analysis section below). First, we split the sites into regions of high and low latitude, split at 42.5°N, and we also split the sites into groups of high and low temperature, based on the 30-year mean annual temperature from the nearest weather station to each site (1981–2010 US Normals Data, Arguez et al. 2010; Fig. 1; Table 1). Average temperatures at sites ranged from 3.72–12.67°C, and we divided sites into temperature groups above and below 8°C. We acknowledge geographic variation correlates with variation in a variety of other environmental factors; we also investigated grouping sites by 30-year mean annual precipitation (1981–2010 US Normals Data, Arguez et al. 2010), but we did not find significant patterns, so we do not report these analyses.

Seeds from each pod were massed, and we cold-stratified 50 seeds per family in moist sand in the refrigerator for three weeks before sowing seeds for germination in M1 potting mix (Grower Select; BFG Supply, Burton, OH). Greenhouse conditions were set to 25/18°C on a 16:8 day/night cycle and flats were watered as necessary. Three weeks after germination, we transplanted seedlings into their experimental 3"-square pots and added ~2.5 g 14-14-14 NPK slow-release fertilizer (Osmocote).

The experiment was conducted in eight spatial blocks of approximately 48 plants each, spread across two bays

of the St. Olaf College greenhouse. The placement of each plant was randomized within the block. Each family was represented by 24 plants divided such that there were twice as many plants in the control group as in the damage treatment group for each family. Not all plants survived, so replication was slightly uneven across family groups (Table 1). Damage was applied manually seven weeks after sowing by tearing leaves along the midrib (following Kula et al. 2020) to remove half of each of the top 50% of the leaves on the plant, with the goal of removing approximately 25% of the total leaf area (Fig. 2A).

Measurements

The end of the experiment occurred 10 weeks post-germination. We assessed plant compensation to damage by measuring total plant biomass (roots, shoots, leaves) after the final harvest. Groups exhibit overcompensation if they grow more in the damage treatment than in the control treatment, and undercompensation if they grow less in the damage treatment than in the control treatments (Fig. 2B). We also evaluated possible mechanisms for variation in compensation responses, including phenology (early stem height, following Woods et al. 2012), resource allocation (stem investment, root:shoot ratio), and relative growth rate (RGR).

Early stem height, our metric of phenology, was measured at 5 weeks from the soil to the top of the stem. Prior to damage at week 7, we measured stem height and the basal diameter of the stem 1 cm above the soil, a metric which was used as a covariate in many analyses to account for initial plant size. While the plants were early in their development, seven weeks represents a period in the plant lifespan when exposure to insect herbivores in

a natural field setting is high. We harvested plants at 10 weeks to prevent loss of leaf tissue due to senescence. Our experiment was slightly shorter than similar experiments with milkweed (Hochwender et al. 2000 applied damage at 70 days and harvested at 100 days; Woods et al. 2012 destructively harvested at 85 days).

At the end of the experiment, resource allocation was measured both as root:shoot ratio, a predictor of tolerance under some conditions (Hochwender et al. 2000), and as “stem investment,” because milkweeds shift some resources to stems after damage (Tao and Hunter 2013). We also measured the basal diameter and height of each plant. Then, plants were harvested by cutting the roots from the shoots (stems and leaves), washing soil from the roots over a sieve, and freeze-drying (Labconco FreeZone 4.5). Once freeze-dried, the roots and shoots were separately massed (Mettler MS1602TS) to calculate root:shoot ratios. We estimated the final volume of the stem, using the basal diameter and final stem height measurements, and assuming the stem is roughly cylinder shaped. Stem investment was calculated as the ratio of estimated final stem volume to final shoot biomass. We calculated the relative growth rate (RGR) over the treatment period as the log of the ratio of the final stem

height to the pre-damage stem height, divided by the days between measurements.

Data analysis

We log-transformed root:shoot ratios to improve normality of the residuals for analyses, and we log-transformed total biomass to facilitate proper interpretation because damage was applied proportionally (Wise and Carr 2008).

Pre-damage tests

We used mixed models to test for regional differences in early stem height (week 5) as a way to test for differences in phenology. We also tested for differences in pre-damage basal diameter, our covariate in post-damage models. Planting block and genetic family were modelled as random effects. We were able to rule out differences in initial resource availability provided by seeds by using a standard linear model to test for differences in the average seed mass of each pod collected from each geographic region ($F_{1,14} = 0.2702$, $p = 0.611$) and temperature group ($F_{1,14} = 0.3247$, $p = 0.5778$).

Response to damage tests

We were interested in both family-level and regional differences in the response to damage, so we identified the

A Treatments

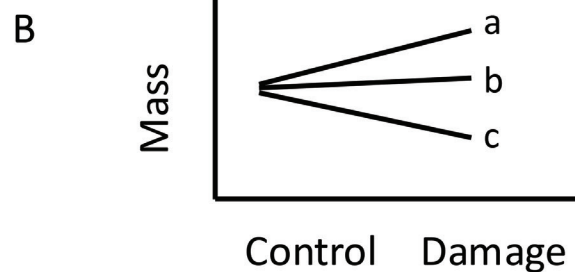
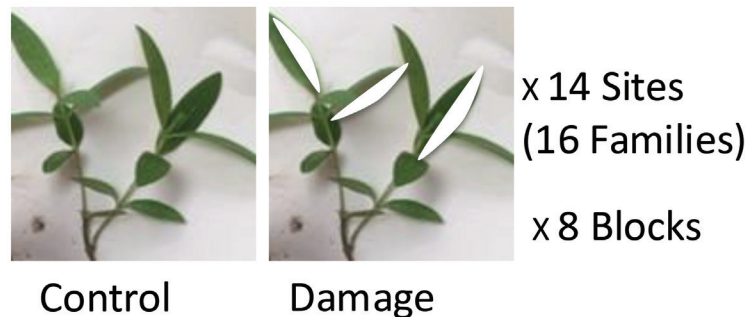


Figure 2. Experimental design and analysis plan. **A.** We tested for variation in the effect of 25% mechanical leaf area removal on total mass. Genetic families were divided between high- and low-latitude regional groups and high- and low-temperature groups, and separate models tested for a genetic family \times treatment interaction and a group \times treatment interaction. **B.** We interpret results as follows: groups exhibit overcompensation if they grow more in the damage treatment than in the control treatment (a), exact compensation if they grow similarly in the damage and control treatments (b), or undercompensation if they grow less in the damage than in the control treatments (c).

pre-damage measurement that best accounted for variation in the final response to use as a covariate. Pre-damage basal diameter was used as a covariate in our analysis of total mass, root:shoot ratio, and stem investment. RGR involved measurements prior to damage, so we did not use covariates to test this response. For the family-level analysis, we used analysis of covariance (ANCOVA) to compare mean final trait measures among genetic families and treatments, and to test for an interaction between them. A statistical interaction between genetic family and damage treatment for a growth measurement was interpreted as evidence for genetic variation in the growth response to damage. For the grouped analyses, a mixed-model ANCOVA was used to compare mean final trait measures between groups (region or temperature group) and damage treatment, and to test for a group \times damage interaction. A statistical interaction between group and damage treatment for a growth measurement was interpreted as evidence for variation in the growth response to damage among groups. Experimental block and genetic family were modelled as random effects. Mixed-model ANCOVAs were run using the lmer function of the lme4 package (Bates et al. 2015) in R

v.4.4.0 (R Core Team 2024), and we report p values from the Anova function in the car package using Type II sums of squares (Fox and Weisberg 2019).

RESULTS

Geographical differences pre-damage

For our measure of phenology, high-latitude plants were not significantly taller on average than low-latitude plants during the early season at week 5 ($X^2 = 2.3779$, d.f. = 1, $p = 0.1231$), nor were there differences among temperature groups ($X^2 = 0.5439$, d.f. = 1, $p = 0.4608$). There were also no significant differences between groups in pre-damage basal diameter, the covariate used in models evaluating response to damage (Region: $X^2 = 0.4019$, d.f. = 1, $p = 0.5261$; Temperature Group: $X^2 = 0.3715$, d.f. = 1, $p = 0.5422$).

Responses to damage among families

Damage (25% leaf area removal) reduced final plant biomass by 18% on average, but its effects (assessed three

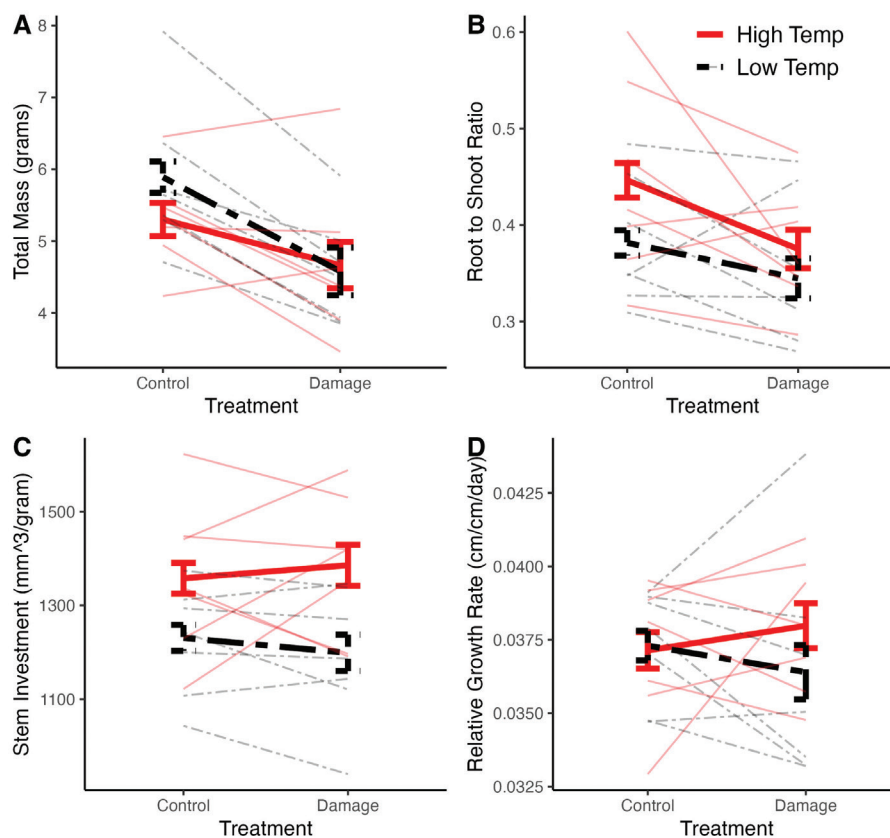


Figure 3. Variation among temperature groups and genetic families (background) in the effects of damage on milkweed traits. Compared to plants from warmer regions (average temperature > 8°C; red solid lines), plants from colder regions (dashed black lines, average temperature < 8°C) (A) had constitutively higher mass but experienced greater reductions in total mass in response to damage. (B) Plants from both regions responded similarly to damage by reducing root:shoot ratios. Damaged plants from warmer regions tended to (C) increase stem investment (interaction $p = 0.088$), and (D) increase relative growth rate (based on height) compared to plants from colder regions (interaction $p = 0.095$). Variation among genetic families in the slope of damage responses (background lines) was significant for all traits shown except for root:shoot ratios.

Table 2. Tests of variation in compensatory responses to herbivory among *Asclepias syriaca* full-sibling families. F statistics are reported for each factor in the ANCOVA, and significant p values are shown in bold. Results are from models including block and pre-damage basal stem diameter as covariates (when significant) and individuals from 16 genetic families were included in the test.; na = not available.

Response variable	Range (units)	Residual degrees of freedom	Family F (p)	Treatment F (p)	Interaction F (p)
Total mass ^a	0.15–13.7 (g)	330	3.64 (< 0.0001)	22.79 (< 0.0001)	1.71 (0.047)
Root:shoot ratio ^b	0.12–1.14	330	8.20 (< 0.0001)	14.77 (0.0001)	1.39 (0.150)
Relative growth rate ^c	-0.02057–0.05519 (cm cm ⁻¹ day ⁻¹)	330	4.79 (< 0.0001)	0.11 (0.74)	1.62 (0.019)
Stem investment ^d	655.1–2525.3 (mm ³ g ⁻¹)	329	7.85 (< 0.0001)	0.13 (0.73)	1.76 (0.040)
Early stem height ^e	2.9–17.2 (cm)	347	12.45 (< 0.0001)	na	na

^a Total mass was log transformed to meet assumptions implicit in tests of compensatory responses to proportional damage (Wise and Carr 2008) and pre-damage basal stem diameter was a covariate.

^b Root:shoot ratio was log transformed to improve normality and constant variance assumptions, and pre-damage basal stem diameter was a covariate.

^c Relative growth rate (RGR) of height = log (post-damage height/pre-damage leaf height) / time. No covariates were used in this model.

^d Stem investment = (basal diameter/2)2 π *stem height / shoot mass; stem investment was log transformed to improve normality. Pre-damage basal area was included as a covariate.

^e Early stem height measured after 5 weeks of growth, prior to the application of any treatments, is an estimate of phenology (following Woods et al. 2012).

weeks after damage treatment) varied with genetic family, ranging from 30% average decrease to 10% average increase in mass following damage (Fig. 3A; Table 2). Damaged plants also shifted their biomass allocation toward shoots, reducing root:shoot ratios by an average of 12%, a response that did not vary significantly among families (Fig. 3B; Table 2). There were no overall effects of damage on stem investment (Fig. 3C) or relative growth rate (Fig. 3D), but the effects of damage on these traits varied significantly among families (Table 2).

Variable group responses to damage

At week 10, we found that plants from high latitudes and colder sites were larger in the control treatment but less able to compensate for damage. Damage reduced the total mass of plants from low-temperature populations by 24% (21% in high-latitude sites), compared to a 12% reduction in the total mass of plants from high-temperature populations (14% in low-latitude sites; Table 3; Fig. 3A). High-latitude and low-temperature plants tended to invest less in stems and roots, though the main effect is only significant for the effect of temperature group on stem investment (Fig. 3; Table 3). We found no significant regional differences in plant responses to damage via root investment, stem investment, or relative growth rate. However, there was a marginally significant trend for plants from the cold-temperature group to reduce stem investment and relative growth rate in the damage treatment while those from the high-temperature group tended to increase stem investment and relative growth rate (Fig. 3C, D; Table 3).

DISCUSSION

Contrary to our first two predictions, our data provide evidence consistent with reduced compensatory ability in high-latitude/colder populations compared to low-latitude/warmer common milkweed populations. However, the data were not entirely consistent with the rationale for our third prediction that reduced compensation results from a slow growth rate (Woods et al. 2012) because high-latitude plants in our study were actually larger than their low-latitude counterparts in the control treatment, suggesting a faster initial growth rate for these populations. Furthermore, there were no differences in relative growth rate in the control treatments; however, plants from warmer environments tended to respond to damage by increasing their relative growth rate while those from colder environments tended to decrease their relative growth rate. Though our evidence is weak, such regional differences in response to damage could contribute to geographic differences in compensation.

Two other studies have documented geographic variation in compensation or tolerance, and both demonstrated relationships contrary to our findings: Lehdal and Ågren (2015) report a positive linear relationship between tolerance and latitude of origin, and Croy et al. (2020) report a u-shaped relationship with a strong positive trend. Interestingly, our findings are more consistent with interspecific studies that report less tolerance to damage (Reese et al. 2016) or less over-compensation to herbivory (Garcia and Eubanks 2019) in species with higher-latitude ranges. However, a latitudinal gradient in herbivory is unlikely to explain this intraspecific pattern since Woods et al. (2012) reported

Table 3. Group differences in *Asclepias syriaca* compensatory responses to damage treatment. We report analyses of plant responses to damage based on two grouping factors: Latitude (Lat) and Average Long Term Temperature (Temp) at the site of origin (see Fig. 1; Table 1). We show the number of replicate plants, genetic families, and experimental blocks used in the mixed model ANCOVAs. We report estimates (North/Low-Temp group is the reference) and statistics (t) from mixed models; p values are from Wald Type II Chi square tests. Significant effects are bolded; marginally significant effects are italicized. High- and low-latitude sites are divided at 42.5°N, the latitude that bisects the reported range of common milkweed. High- and Low- Temperature groups are split at a long-term average temperature of 8°C. Results shown are from models including block and significant covariates.

Response variable	N Plants Families Blocks	Group effect	Damage treatment effect	Interaction effect
		Lat/Temp t (p)	Lat/Temp t (p)	Lat/Temp t (p)
Total mass ^a	370	-0.22/-0.19	-0.26/-0.26	0.17/0.16
	16	-3.39/-2.80	4.98/-4.81	2.29/2.11
	8	(0.0068/0.03)	(< 0.0001/< 0.0001)	(0.022/0.035)
Root:shoot ratio ^b	370	0.11/0.15	-0.12/-0.098	-0.005/-0.046
	16	1.24/1.73	-2.58/-2.09	-0.070/-0.70
	8	(0.21/0.11)	(0.00021/0.00021)	(0.94/0.48)
Relative growth rate ^c	370	0.00034/0.000023	-0.00054/-0.00074	0.0014/0.0018
	16	0.30/0.02	0.71/-0.96	1.34/1.67
	8	(0.44/0.56)	(0.74/0.74)	(0.18/0.095)
Stem investment ^d	370	0.068/0.096	-0.016/-0.028	0.052/0.073
	16	1.22/1.88	-0.54/-0.91	1.21/1.71
	8	(0.11/ 0.014)	(0.66/0.66)	(0.23/0.088)

^a Total mass (g) was log transformed to meet assumptions implicit in tests of compensatory responses to proportional damage (Wise and Carr 2008), and pre-damage basal stem diameter was a covariate.

^b Root:shoot ratio was log transformed to improve normality of residuals and pre-damage basal stem diameter was included as a covariate.

^c Relative growth rate = $\log(\text{post-damage height/pre-damage height}) / \text{time}$.

^d Stem investment ($\text{mm}^3 \text{g}^{-1}$) = $(\text{basal diameter}/2)^2 \pi * \text{stem height} / \text{shoot mass}$; stem investment was log transformed to improve normality. Pre-damage basal stem diameter was included as a covariate.

greater herbivory in central rather than low-latitude sites. Of the latitudinal gradients that could drive the regional differences in compensation we observed, we hypothesize that differences in the phenology of resource allocation, both root and stem investment, could explain regional variation in compensation, but other explanations are worthy of further investigation. We note that family-level variation in the damage responses of mass (compensation), relative growth rate, and stem-investment suggest that there is potential for these traits to continue to evolve.

Growing season length and phenology of resource allocation

Growing season length varies dramatically with latitude and could explain the regional variation in compensation we observed by one of three different pathways. First, genetic differences in germination timing and phenology could cause plants to be at different developmental stages when damaged, potentially affecting both the resources and time available for plants to recover from damage (e.g. Lehndal and Ågren 2015).

Second, traits associated with adaptation to short growing seasons or stress, such as root investment and fast growth rates, often facilitate compensation (Więski and Pennings 2014; Hahn and Maron 2016; Croy et al. 2020). However, we observed a trend for faster relative growth rates in the damage treatment in plants from warmer sites, where fast growth is unlikely to be an adaptation to a short growing season, but may be associated with phenological differences in resource allocation (see below). Compensatory ability following damage is associated with storage of resources in roots and stems (Strauss and Agrawal 1999; Boege et al. 2007; Stevens et al. 2008; Croy et al. 2020), and specifically root storage in *A. syriaca* (Hochwender et al. 2000). Plants from warmer sites exhibited greater stem investment, and a trend toward greater root investment, in our study. As a result, they may have been better able to compensate for damage. While a previous study led us to predict higher storage in roots (Woods et al. 2012) and stems in plants from colder high-latitude sites, stem investment can also be favoured in productive sites where height is advantageous (Poorter et al. 2015). Milkweeds grow taller in low-latitude sites (Woods et al. 2012), so increased stem investment could

be necessary in warmer regions with longer growing seasons.

Third, divergent geographic patterns in the phenology of resource allocation could also contribute to differences in compensatory responses to damage, due to the relative timing of plant damage compared to plant development (Fig. 4). For example, early flowering tarweed phenotypes (*Madia elegans* D. Don) are less able to recover from damage than late flowering phenotypes, presumably because they do not store as many resources below ground (Krimmel and Pearse 2016). The same mechanism may have occurred in our study, where high-latitude plants from colder regions with short growing seasons stored fewer resources in stems and roots and were less able to compensate for damage in terms of overall biomass.

In contrast to our findings, two previous studies report greater compensation in high-latitude populations (Lehndal and Ågren 2015; Croy et al. 2020). We speculate that there may have been different geographic patterns in resource allocation for plants observed by these three studies, especially because the relative timing of damage varied dramatically. We applied damage once, seven weeks past germination, and harvested plants two weeks later. Furthermore, our study took place in a greenhouse

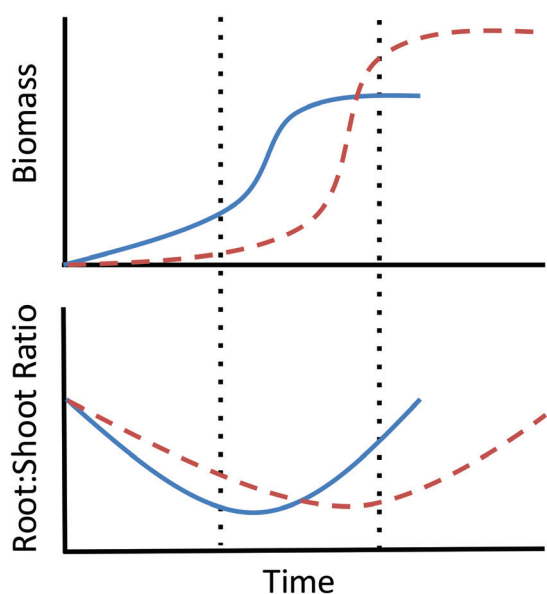


Figure 4. Hypothesized relationship between phenology, timing of measurement, and latitudinal patterns. If high-latitude plants (solid lines) have shorter growing seasons, they may grow more quickly early in the season, accruing more biomass and smaller root:shoot ratios. However, if they start to senesce earlier, there will be a window when they have higher root:shoot ratios and lower biomass than low-latitude plants, thus different geographic patterns will be observed depending upon the relative timing of measurements, as indicated by the vertical dotted lines. We suspect the timing of our final measurements corresponded with the left vertical line, and the right vertical line corresponds more with the measurements in Woods et al. (2012).

with controlled temperature and photoperiod, which may have eliminated environmental cues that would signal shifts in growth/allocation patterns. In contrast, Croy et al. (2020) applied 40% leaf area removal at monthly intervals four times before allowing regrowth for two months prior to harvest, and the study took place in an outdoor experimental garden. Lehndal and Ågren (2015) allowed natural insect damage on three-year old plants in an outdoor common garden. We agree with Lehndal and Ågren (2015) that explicit manipulation of the timing of damage applied to plants from different regions would inform interpretations about the relationship between phenology and compensation.

We observed patterns relevant to early-life stages of plants; however, it is possible we would have observed greater compensation in high-latitude/low-temperature plants if we had harvested later in the growing season. Plants from high-latitude populations (Woods et al. 2012; Więski and Pennings 2014; Lehndal and Ågren 2015) or higher altitudes (Dostálek et al. 2016) are almost universally smaller (shorter, less massive, fewer leaves) and have more root investment than plants from lower elevations or latitudes. In contrast, by week 10, we observed a regional pattern of constitutively larger plants from high latitudes and colder temperatures, and we saw more stem and root investment in plants from low latitudes and warmer temperatures. Previous research demonstrated that common milkweed plants from high-latitude sites are larger earlier in the season, indicating earlier phenologies, but by the end of season high-latitude plants are smaller than low-latitude plants (Woods et al. 2012). We suspect that high-latitude/low-temperature plants in our study initially grew rapidly, but given more time and the appropriate seasonal cues, we expect that they would have shifted to greater resource storage in roots and stems. In contrast, low-latitude/high-temperature plants may be adapted to longer growing seasons, allocating more resources to stems and roots early in the season to facilitate greater growth over time. This potential pattern of seasonal resource allocation suggests that the regional patterns of compensatory growth observed could depend on the timing, and even the location, of measurements. We posit that the timing of measurement could reverse the regional patterns of compensation observed if high-latitude plants initially grow faster and store fewer resources than low-latitude plants but also if high-latitude plants shift to senescence earlier (Fig. 4). Earlier measurement would generate patterns we observed (larger plants with less storage and less compensation from cold temperatures/high latitudes); whereas later measurement would generate patterns similar to Woods et al. (2012) (smaller plants with more storage from cold temperatures/high latitudes).

Of course, our data are limited, and these hypotheses require more rigorous tests. For example, our evidence demonstrates that grouping by temperature and latitude show similar patterns of compensation, while grouping by precipitation does not. However, other environmental

factors, such as nutrient availability, growing season length, and climate variability cannot be ruled out as potential drivers of the patterns we observed.

CONCLUSION

In contrast to other findings, we observed that compensation was greater in plants originating from warm-temperature/low-latitude milkweed populations, and we hypothesize that differences in phenology between regions of origin meant that these plants had greater resources stored in roots and stems at the time of damage, facilitating their ability to regrow. In contrast, cold temperature/high-latitude plants experienced a period of faster growth, had fewer resources stored, and were less able to compensate for damage. Although our results are potentially consistent with the hypothesis that high-latitude plants could have adaptations that make them more resistant to herbivory because they are less able to tolerate damage, we do not find support for the hypothesis that compensation is related to intrinsic plant growth rate. Instead, compensation appears to be related to plastic responses of relative growth rate to damage, and we hypothesize that compensation varies with growing season length. We posit that latitudinal trends in growth and compensation are context-dependent, specifically that they depend on the timing of both damage and harvest. Alternative hypotheses to explain variation in resistance and compensation, namely geographic variation in resource availability or in the types of herbivores, also warrant further investigation.

DATA AVAILABILITY STATEMENT

The data underlying these analyses are deposited at Figshare: <https://doi.org/10.6084/m9.figshare.30590669.v1>

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SUPPLEMENTARY MATERIAL

Supplementary material 1

Names and affiliations of people who contributed seeds to this study.

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