Intraspecific variation in plant economic traits predicts trembling aspen resistance to a generalist insect herbivore

Clay J. Morrow1 · Samuel J. Jaeger2,3 · Richard L. Lindroth2

Received: 23 June 2021 / Accepted: 30 March 2022 / Published online: 21 April 2022
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Abstract
Patterns of trait expression within some plant species have recently been shown to align with the leaf economics spectrum paradigm. Resistance to herbivores is also expected to covary with leaf economics traits. We selected 36 mature *Populus tremuloides* genotypes in a common garden to assess whether aspen leaf economics patterns follow those observed among species globally. We also evaluated leaf economics strategies in the context of insect resistance by conducting bioassays to determine the effects of plant traits on preference and performance of *Lymantria dispar*. We found that: (1) intraspecific trait patterns of *P. tremuloides* parallel those exhibited by the interspecific leaf economics spectrum, (2) herbivores preferred leaves from genotypes with resource-acquisitive strategies, and (3) herbivores also performed best on genotypes with resource-acquisitive strategies. We conclude that a leaf economics spectrum that incorporates defense traits is a useful tool for explaining intraspecific patterns of variation in plant strategies, including resistance to herbivores.

Keywords Bioassays · Chemical defense · Ecological strategy · *Lymantria dispar* · *Populus tremuloides*

Introduction

Plants exhibit phenotypic variation, both within and among species, that results in variable resistance to phytophagy. Metabolic, allocational, and genetic trade-offs between growth and defense traits contribute to this variation and have been well documented (Züst et al. 2015; Züst and Agrawal 2017; Heckman et al. 2019). Growth and defense traits, however, do not exist in isolation. Rather, they are single components of larger phenotypic expression networks. Patterns of trait covariation are typically complex, with trade-offs occurring among multiple traits simultaneously (Züst and Agrawal 2017; Cole et al. 2021). Accordingly, hypotheses addressing variation in plant defense strategies, especially those that incorporate growth–defense associations, would benefit by considering co-expression of resistance and non-resistance traits alike.

Plant traits are intercorrelated in predictable ways across a broad array of species, worldwide. Mass-based rates of photosynthesis are positively associated with leaf nitrogen and phosphorous content, dark respiration, and specific leaf area (SLA). Developed by Wright et al. (2004), the leaf economics spectrum (LES) summarizes these patterns as a trade-off between resource-conservative and resource-acquisitive strategies of adaptation across biomes and has proven useful for predicting the distribution of plant traits and fitness (Donovan et al. 2011; Reich 2014). Differentiation of plant strategies arises partly because of investment costs associated with one trait or function over another. Allocation trade-offs extend to plant defense. Predictions that plants in resource-poor environments should grow slowly and invest in defense traits (Coley et al. 1985; Coley 1987) have been generally supported (Endara and Coley 2011). As a consequence, slow-growing plants are expected to sustain less herbivore damage than their fast-growing counterparts (Price 1991; Herms and Mattson 1992). Recognition of the ubiquity of growth–defense trade-offs and the importance...
of herbivore resistance to plant fitness has led to the recent incorporation of defense traits, specifically phytochemical resistance, into the LES paradigm (Agrawal 2020).

If increased growth is associated with decreased herbivore resistance, then herbivores should both prefer and perform best on growth-optimized plants (Levins and MacArthur 1969; Price 1991; Mayhew 1997). This means that insect preference and performance should be aligned and that growth-associated plant traits drive these outcomes. Little evidence exists, however, that insect preference and performance are linked to each other or to plant growth in general. Some sessile insects, which are closely associated with their host plants, do exhibit a preference–performance linkage (e.g., Fritz et al. 2000). Additionally, Gripenberg et al. (2010) demonstrated a link between ovipositional preference and offspring survival across 21 plant–insect systems. Yet, studies of preference–performance relationships have been limited in scope and evidence of a broad linkage remains largely inconsistent. For example, investigations of insect preference and performance within the same experimental system are uncommon and host selection behaviors other than oviposition preference have rarely been considered (Gripenberg et al. 2010). Moreover, although many studies have focused on the relationship between plant growth and defense, and implications thereof for herbivores, research directly comparing insect performance to plant growth was relatively scarce a decade ago (Cornelissen et al. 2008; Gripenberg et al. 2010) and has not increased appreciably since.

The capacity to explain plant variation and herbivore resistance with a small number of LES traits is appealing, but may be scale dependent. The applicability of the LES across taxonomic and ecological scales has been assessed in several recent studies. Anderegg et al. (2018) found that some leaf economics traits exhibited different correlations when compared within versus among species (962 genera). They concluded that, due to phenotypic plasticity, the LES may not be indicative of plant strategies at smaller taxonomic scales. Agrawal (2020) found similar inconsistencies in Asclepias across populations, species, and environmental gradients; at some scales, no LES correlations were found. It remains unclear under what conditions patterns of intraspecific trait co-expression differ from patterns among species. Phenotypic variation within plant species, and effects on their communities and ecosystems, can be substantial in certain systems (Des Roches et al. 2018; Koricheva and Hayes 2018; Westerband et al. 2021). Co-expression of plant phenotype and its impact on herbivores is key to understanding intraspecific strategies of resistance.

This research used an ecologically and economically important tree–insect system to investigate the impacts of trait co-expression on resistance to herbivores. Trembling aspen (Populus tremuloides) is a foundation tree species with an expansive range across northern and western North America (Mitton and Grant 1996). The species has exceptional levels of phenotypic variation in growth and defense traits (Mitton and Grant 1996; Cole et al. 2021), and trade–offs thereof, making it an ideal candidate for linking plant growth, leaf economics patterns, and resistance to defoliators. A key defoliator, Lymantria dispar (formerly known as “gypsy moth” and now as “spongy moth”), is an invasive forest insect (McManus and Csóka 2007), for which aspen is a preferred host (Liebhold et al. 1997). Trembling aspen expresses a wide range of heritable variation in phytochemical defense that reduces performance of L. dispar (Hemming and Lindroth 2000; Osier et al. 2000; Donaldson and Lindroth 2007). This experimental system, therefore, provided an ideal opportunity to assess the utility of the LES at the intraspecific level. The trade–offs, across multiple traits, exhibited by aspen are complex and age dependent (Cole et al. 2016, 2021; Cope et al. 2019), but whether overall trait expression is consistent with LES patterns is unknown. The system also provided a unique opportunity to test the preference–performance linkage with an herbivore underrepresented in prior research. Lymantria dispar are mobile, leaf-chewing, generalist lepidopterans and exhibit host selection as larvae (Doane and McManus 1981). These types of insects are largely absent from the preference–performance literature (Gripenberg et al. 2010).

This study evaluated the LES paradigm, including chemical defense traits, at the intraspecific level and assessed its ability to explain preference and performance patterns of L. dispar on trembling aspen. We addressed the following questions: (1) Are patterns of intraspecific trait expression consistent with predictions of the LES? (2) Do herbivores preferentially feed on aspen with resource-acquisitive strategies? (3) Are herbivores advantaged by feeding on resource-acquisitive plants over resource-conservative plants?

**Materials and methods**

To investigate the effects of leaf economics strategies on resistance to herbivory, we conducted two concurrent bioassays comparing larval preference and performance among aspen clones with varying intrinsic growth rates. We assessed host selection and growth of larvae as indicators of aspen resistance, as both metrics influence L. dispar fitness. We selected aspen clones to represent a wide range of variation in growth over a 6-year period, thereby enhancing the probability of detecting intraspecific patterns of leaf economics traits and their effects on larval preference and performance.
Aspen genotype selection

This study used 36 aspen genotypes from a common garden population of 492 genotypes. We established the garden by collecting rootstock from throughout Wisconsin (358 km latitude range, 186 km longitude range) and planting root sprouts with 2.5×2.5 m spacing at the University of Wisconsin-Madison Arlington Agricultural Research Station (43.32° N latitude, 89.33° W longitude) in 2010. One year prior to the study reported here, we selected experimental genotypes to maximize variation in growth over the garden’s 7-year life. To achieve the desired variation, we randomly selected 12 genotypes, with three replicate trees, from each of the bottom, middle and top deciles of the experimental population’s growth distribution and classified them as low-, moderate- and high-growth genotypes, respectively.

Insect bioassays

We performed two bioassays to evaluate *L. dispar* preference for, and performance on, aspen genotypes from different growth classes. We obtained multiple *L. dispers* egg masses from the USDA APHIS insect production facility (Buzzards Bay, MA), incubated (25–18 °C, 50–70% humidity, 16:8 L:D cycle), hatched, and reared them to third and fourth instars for use in bioassays. Larvae were fed a standardized diet of non-experimental *P. tremuloides* leaves and *L. dispers* wheat germ diet (MP Biomedicals) prior to experimental deployment.

Preference bioassays were designed to test host selection of *L. dispers* larvae in response to aspen phenotype. We maintained third instars (69–90 mg) without food for 24 h preceding the experiment, after which time they were placed individually into Petri dishes (15 cm diameter) with two leaves. Dishes contained pairs of leaves such that larvae had a choice between genotypes from different growth classes (i.e., low vs. moderate, low vs. high, moderate vs. high). We replicated each growth class pairing with 12 distinct genotype pairs, for a total of 36 dishes in the bioassay. We replicated each genotype twice and assigned genotype pairs randomly. Larvae fed freely within dishes for 60 h.

Leaves used in the preference bioassays were obtained from a single representative tree for each genotype. On the morning that trials were begun, we collected a single proleptic short shoot from each tree and kept them refrigerated until use. Two bioassay leaves were randomly selected from each shoot, weighed, and measured for specific leaf area (SLA). We inserted petioles of the bioassay leaves through a hole punched into lids of 2.0 mL microcentrifuge tubes containing water and placed them into their experimental dishes prior to larval introduction. We then developed genotype-specific water content calibrations with remaining short shoot leaves by comparing leaf weights before and after vacuum drying. We estimated initial dry mass of bioassay leaves by subtracting genotype-specific water content from initial leaf weights. We measured final dry mass of bioassay leaves upon conclusion of the trials.

At the end of the preference bioassays, we removed larvae and leaves from dishes and determined genotype preference by comparing the mass consumed from each leaf (i.e., final mass – initial mass). We used the proportional consumption of a leaf by a larva as our metric of preference (i.e., leaf mass consumed ÷ total mass consumed). We then created a genotype-specific preference index by averaging preference for each genotype across dishes in which they occurred.

Performance bioassays were designed to assess the growth of *L. dispers* larvae in response to aspen growth strategy. The experiment followed a nested factorial design where three replicate trees of 12 genotypes were nested within each of the three growth classes for a total of 108 trees. We selected and weighed sets of ten newly molted third instars and deployed them to trees in the common garden. Fine mesh bags, secured with zip ties, contained larvae on northeast-facing branches at approximately 1.4 m above ground. After 10 days, we collected, counted, sexed (Lavenseau 1982), vacuum dried, and weighed surviving larvae. As a performance metric, we estimated average relative growth rate (RGR) for larvae on each tree with the formula: (final mass – initial mass) ÷ (initial mass × 10 days). We estimated the initial dry mass of larvae from fresh weights with the formula: initial aggregate weight ÷ 10 larvae × 0.13 mg + 0.27 mg, as determined via calibration from additional third instars from our colony. Immediately before deployment of larvae, we collected four to six mature leaves from each experimental branch for quantification of morphological and phytochemical traits.

Phenotypic trait measurements

We quantified aspen growth rates to evaluate their relationship with expression of other traits and resistance to herbivores. We calculated growth metrics for each of two time periods. First, a long-term growth metric was calculated to assess the relationship of phenotypic traits measured in 2018 to the average annual growth of trees over the preceding eight years. Long-term growth was measured as basal area increment (BAI) averaged over the 8-year life of the trees [BAI = (πr² 2018 – πr² 2010) ÷ 8; measured at stem base in 2010 and 1.4 m above ground in 2018].

Second, a short-term growth metric was calculated to evaluate the relationship of phenotypic traits measured in 2018 to the growth rates of trees in that same year. We used relative growth rate [RGRr = ln(πr² 2018 ÷ πr² 2017); Hunt 1982] as our short-term metric, as it accommodates for variation in tree size at the beginning of the 1-year period
(2017–2018). The long-term growth metric (BAI) was not relativized because initial sizes did not vary significantly in 2010. RGR_{st} is a log-transformed ratio of diameters and accounts for the exponential growth exhibited by aspen (Supp. Figure 1).

We also quantified leaf morphological and chemical traits to evaluate their effects on herbivore resistance and their relationships with growth. We used leaves collected during the performance bioassays for quantification of leaf traits for all experimental trees. We first measured leaf area with a LI-COR 3100 area meter. Next, we vacuum dried, weighed, and ground leaves (ball mill) for phytochemical analyses. We measured salicinoid phenolic glycosides as chemical resistance traits in this study because of their documented deleterious effects on *L. dispar* and other Lepidoptera (Donaldson and Lindroth 2007; Lindroth and St. Clair 2013). Condensed tannins, which do not negatively impact lepidopterans, were not measured. We extracted salicinoids from leaf tissue into methanol and quantified them by UPLC mass spectrometry (Rubert-Nason et al. 2018). Our chemical standards for salicinoid analyses consisted of commercially available salicin and lab-purified salicortin, tremulacin, and tremulolidin. We measured nitrogen concentrations with a ThermoFlash carbon/nitrogen elemental analyzer. All chemical concentrations are expressed as a percentage of leaf dry weight. Finally, we calculated specific leaf area by dividing total leaf area by total mass of all leaves collected from a tree.

Statistical analyses

To test the hypothesis that *L. dispar* larvae should prefer resource-acquisitive aspen, we performed multifactor analysis of variance (ANOVA) and pairwise *t* tests comparing the mass consumed between leaves within dishes in the preference bioassays. All treatment specifications (dish treatment, genotype identity, and growth class) were included as factors in both analyses. We then performed multiple linear regression analysis relating a leaf’s preference index with aspen phenotype to determine which traits best explain larval preference.

To test the hypothesis that *L. dispar* larvae should grow faster on resource-acquisitive aspen genotypes, we performed further multifactor ANOVAs and pairwise *t* tests of performance assay data, comparing larval relative growth rates among aspen growth classes and genotypes. We also performed multiple linear regression analysis of larval relative growth rates to determine which traits best explain larval performance.

Finally, we conducted a redundancy analysis (RDA) to investigate the effects of aspen phenotype on herbivore resistance. RDA is a constrained ordination that partitions variation of a multivariate regression. We used larval growth on, and preference for, genotypes as our multivariate response indicative of resistance. We included genotype averages of all traits as predictors. We assessed variation in larval metrics attributable to variation in trait expression using the RDA loadings. We also graphically assessed alignment of intraspecific trait variation with the LES.

All statistical analyses were performed using the R statistical software package (R Core Team 2020). We used a significance threshold of 0.05 for all hypothesis tests and considered results marginally significant for *P* values between 0.05 and 0.10. We performed stepwise selection to obtain linear models that best explain (i.e., lowest AIC) insect metrics with tree traits and growth class. We also calculated adjusted *R*^2* (R*^2*_{adj}) to assess overall fit of the selected models. RDA was performed using the rda function from the vegan R package and statistical significance was determined via permutation test (Oksanen et al. 2020).

Results

Here, we first present variation observed among growth classes for each aspen trait. Next, we explore resistance to *L. dispar* by comparing insect metrics among aspen growth classes and genotypes, and by assessing associations between insect metrics and plant traits. Finally, we describe correlated patterns of leaf economics traits among genotypes and their associations with herbivore resistance.

Aspen trait variation

Trait expression differed among aspen genotypes from the three different growth classes. Of all traits measured, only BAI differed among all three growth classes (Fig. 1A). Genotypes in the high-growth class had slightly lower RGR_{st} than those in the low-growth class, indicating that average long-term aspen growth was not a strong indicator of short-term growth (Fig. 1B). Of the four salicinoids, salicortin and tremulacin were most abundant and concentrations of both were lowest for high-growth genotypes (Fig. 1D–E). In contrast, tremulolidin concentrations were very low, but were higher among high-growth genotypes than among low-growth genotypes (Fig. 1F). Salicin concentrations were similarly low, but did not differ among growth classes (Fig. 1C). Notably, one low-growth genotype had extraordinarily high concentrations of all four salicinoids when compared with other low-growth genotypes (Fig. 1C–F). Nitrogen did not differ among growth classes (Fig. 1G) and had the lowest variation of any trait. SLA was lower for low-growth genotypes than for high-growth genotypes (Fig. 1H).
Herbivore resistance bioassays

Larvae preferred to feed on leaves from fast-growing aspen (Fig. 2). Aspen growth class and genotype affected preference independent of treatment combination (Supp. Table 1). Larvae consumed twice as much tissue from high-growth than from low-growth genotypes, and 53% more from high-growth than from moderate-growth genotypes. Larvae did not discriminate between low-growth and moderate-growth genotypes. BAI and total salicinoids were positively and negatively associated with leaf consumption, respectively (Table 1, Supp. Figure 2). Together, these traits best explained larval preference for a genotype (R$^2_{adj} = 0.23$), with salicinoids explaining more than BAI (Table 1).

Larvae also performed well on fast-growing aspen (Fig. 3). Larvae grew faster on high-growth genotypes than on moderate-growth genotypes. Interestingly, larval growth rates were intermediate, and most variable, on low-growth genotypes. SLA and tremulacin were positively and negatively associated with larval growth, respectively (Table 2, Supp. Figure 3). These traits, along with growth class, best explained variation in larval performance (R$^2_{adj} = 0.38$) and SLA explained the most (Table 2). Increased nitrogen was also associated with increased larval growth (Supp. Figure 3G) but the strong correlation between nitrogen and SLA (Table 3) made their effects largely redundant.

Leaf economics trait patterns

Aspen genotypes exhibited trait correlations consistent with growth–resistance trade–offs and LES patterns (Table 3). BAI was negatively correlated with salicortin and positively correlated with SLA. Short-term aspen RGR$_{ai}$ was not significantly correlated with long-term BAI or any other traits. Salicortin and tremulacin were strongly positively correlated, as were salicin and tremulolid. SLA was positively correlated with both tremulolid and nitrogen.

Redundancy analysis revealed that trait patterns consistent with leaf economics strategies were associated with resistance to herbivory, and that genotypes exhibited substantial variation in these strategies both within and among aspen growth classes (Fig. 4). The primary RDA axis, which accounts for twice the variation explained by the secondary RDA axis, aligns with the LES for the traits measured (RDA loadings found in Supp. Table 2). Larval preference and performance were not strongly correlated (Table 3) and were affected differently by aspen traits. Larval preference for aspen genotypes was most closely associated with high BAI and low levels of the salicinoids salicortin and tremulacin. In contrast, larval performance (growth rate) was determined by levels of tremulacin and nitrogen, as well as SLA. These multivariate results align with those from univariate analyses of the two bioassays. Aspen traits explained 35% of the variation in L. dispar resistance, of which salicortin and BAI explained the most (Supp. Table 3).

Growth class alone was not a reliable predictor of LES patterns. Although high-growth genotypes were more likely to align with resource-acquisitive patterns than those in other classes, this tendency was too weak to be differentiable (Fig. 4). High levels of genotypic variation within growth classes contributed to substantial phenotypic overlap among classes.

Discussion

This research aimed to evaluate the LES paradigm at the level of intraspecific trait variation, and its potential to explain insect herbivore resistance. Our results demonstrate that the paradigm can indeed be useful for explaining intraspecific variation in plant strategies. Fast-growing genotypes had higher SLA, higher foliar nitrogen concentrations, and lower foliar salicinoid concentrations, matching a resource-acquisitive strategy in the LES paradigm. As a result, these genotypes experienced low herbivore resistance, when compared with genotypes matching more resource-conservative strategies. No strong insect preference–performance linkage was found, and aspen traits affected the two indicators of herbivore resistance somewhat differently. Larvae preferred to feed on aspen with low salicinoid concentrations and fast growth. Larvae also performed well on aspen with low salicinoid concentrations, but performance was primarily associated with nitrogen and SLA. Generally, the primary RDA axis of aspen traits aligned well with patterns expected for a defense-integrated LES, making it a useful proxy for the paradigm. In summary, leaf economics traits were useful indicators of plant resistance strategies.

The observed trait patterns within P. tremuloides align with those found among species worldwide. Intraspecific LES patterns have been demonstrated in a variety of species (e.g., common reed: Hu et al. 2015; coffee: Martin et al. 2017). Yet, recent comparisons of the LES across diverse ecological and taxonomic scales reveal that trait correlations can be scale dependent. For example, in their meta-analysis of 2031 species, Anderegg et al. (2018) found that, although directions remain consistent, magnitudes of trait correlations with LMA (i.e., $\frac{1}{\text{SLA}}$) and nitrogen vary among taxonomic scales. In another study, Grady et al. (2013) showed that conservative leaf economics traits were associated with fast growth of Populus fremontii in hot environments. Other research also shows that conformation with LES patterns can depend upon spatial scales (Messier et al. 2017). We could not evaluate spatial dependence but trait patterns driven by genetics are unlikely spatially structured in Wisconsin aspen due to lack of population structure (Cole 2005; Barker et al. 2019b).
This work also reveals that incorporation of defense traits can benefit assessments of the LES at the intraspecific level. Recent research shows that plant defense is correlated with traditional LES traits within and among species. For example, *Helianthus* defense is correlated with interspecific LES strategy (Mason and Donovan 2015). Similarly, across species of spiny plants, physical defenses are associated with leaf productivity, whereas chemical defenses are not (Armani et al. 2020). Both chemical and physical defense traits are correlated with LES traits within *Asclepias syriaca*, but not among different *Asclepias* species (Agrawal 2020). In short, a growing body of literature suggests that the utility of incorporating herbivore defense into the LES paradigm is species or context specific. A major limitation of a defense-integrated LES paradigm is the sheer diversity of defense types, which makes comparisons across species challenging. Even so, because herbivores are ubiquitous and formative components of plant communities, incorporation of herbivore defense traits will likely enhance the value and function of LES models.

Our results show that not only are defense traits associated with leaf economics strategies, but so too are defense outcomes. While it is clear that intraspecific plant strategies result in trade-offs between growth and defense traits in many systems (Endara and Coley 2011; Züst and Agrawal 2017), to our knowledge, none of the recent evaluations of plant defense and the LES include measures of resistance outcomes. Covarying effects of plant traits on herbivore fitness are well known (e.g., Simpson and Raubenheimer 2001) and defense traits are particularly well-studied (e.g., Gong and Zhang 2014). Of the four aspen salicinoids evaluated in this study, the compounds that occur in the lowest concentrations—salicin and tremuloidin—have low biological activity (but see Cook et al. 2003). The more abundant salicortin and tremulacin are much more biologically active, due to the presence of cyclohexenone and benzoyl functional groups (Lindroth et al. 1988; Boeckler et al. 2011). Consistent with that information, our results show that salicortin and tremulacin were the salicinoids most strongly linked to herbivore performance and LES traits. This work further establishes how defense traits can be integrated across a spectrum of intraspecific functional strategies, and the consequences thereof for trophic interactions.

Intraspecific covariation in defense and conventional LES traits has important ecological and evolutionary
consequences in aspen and other *Populus* species. Foliar nitrogen and salicinoids govern the preference, performance, distribution, and abundance of herbivorous insects, as well as their rates of defoliation (Donaldson and Lindroth 2007; Falk et al. 2018). They also influence the structure of herbivorous insect communities (Bangert et al. 2006; Barker et al. 2018, 2019a) and dynamics of multitrophic interactions (Bailey et al. 2006). More recently, work with experimental aspen stands documented that intraspecific competition alters the consequences of genotypic growth–defense trade-offs, leading to divergent genetic architecture of aspen populations (Cope et al. 2021).

The relationship between host plant selection and performance of insect herbivores remains equivocal. The most comprehensive meta-analysis of preference–performance relationships to date found that survival, but not weight or development time, is associated with host preference (21 comparable plant–insect systems; Gripenberg et al. 2010). For *L. dispar* and numerous other insects, however, preference and performance appear unrelated (e.g., Valladares and Lawton 1991; Underwood 1994; Fritz et al. 2000).

*Lymantria dispar* larvae engage in host plant selection by dispersing from unsuitable hosts (Capinera and Barbosa 1976; Lance and Barbosa 1981). These decisions appear to be made primarily in response to chemical defenses; Solari et al. (2002) found that *L. dispar* larvae respond strongly to deterrent stimuli (i.e., nicotine), but not to classical nutritional stimuli. Our work reaffirms these findings. *Lymantria dispar* selected hosts according to salicinoid concentrations and largely ignored performance-associated nutrients (i.e., nitrogen).

In conclusion, our work reveals that the leaf economics spectrum can be useful for describing patterns of association among plant functional traits,—including herbivore resistance traits—at the intraspecific level. In trembling aspen, genotypes of resource-acquisitive plants tended to have high specific leaf area, high nitrogen concentrations, and low salicinoid concentrations compared with resource-conservative genotypes. This trait combination elicited higher herbivore preference, and performance, relative to insects on resource-conservative plants. Patterns of phenotypic relationships identified in this research suggest that growth-associated...
plant traits are associated with susceptibility to herbivore attack.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00442-022-05158-z.

**Acknowledgements** We thank Chris Cole and Mark Zierden for assistance with chemical analyses and Chris Cole and Jenn Riehl for genotype verification. S. Jaeger’s work was supported by a UW Holstrom Environmental Research Fellowship. Comments from Colin Orians, Carlos Ballaré, and two anonymous reviewers improved the manuscript.

**Author contribution statement** CJM, SJJ, and RLL conceived and designed the experiments. RLL secured funding. CJM and SJJ conducted fieldwork, laboratory work, and analyzed the data. CJM and RLL wrote the manuscript.

**Funding** This research was funded by USDA National Institute of Food and Agriculture grants 2016-67013-25088 and WIS01651.

**Data availability** The datasets generated in this research are available from the corresponding author upon reasonable request and at the dryad link included in the supplemental information section.

**Code availability** The code used to analyze these data is available from the corresponding author upon reasonable request.

**Declarations**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

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