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ARTICLE

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A direct comparison of ecological theories for predicting the relationship between plant traits and growth

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Abstract

Despite long-standing theory for classifying plant ecological strategies, limited data directly link organismal traits to whole-plant growth rates (GRs). We compared trait-growth relationships based on three prominent theories: growth analysis, Grime's competitive–stress tolerant–ruderal (CSR) triangle, and the leaf economics spectrum (LES). Under these schemes, growth is hypothesized to be predicted by traits related to relative biomass investment, leaf structure, or gas exchange, respectively. We also considered traits not included in these theories but that might provide potential alternative best predictors of growth. In phylogenetic analyses of 30 diverse milkweeds (*Asclepias* spp.) and 21 morphological and physiological traits, GR (total biomass produced per day) varied 50-fold and was best predicted by biomass allocation to leaves (as predicted by growth analysis) and the CSR traits of leaf size and leaf dry matter content. Total leaf area (LA) and plant height were also excellent predictors of whole-plant GRs. Despite two LES traits correlating with growth (mass-based leaf nitrogen and area-based leaf phosphorus contents), these were in the opposite direction of that predicted by LES, such that higher N and P contents corresponded to slower growth. The remaining LES traits (e.g., leaf gas exchange) were not predictive of plant GRs. Overall, differences in GR were driven more by whole-plant characteristics such as biomass fractions and total LA than individual leaf-level traits such as photosynthetic rate or specific leaf area. Our results are most consistent with classical growth analysis—combining leaf traits with whole-plant allocation to best predict growth. However, given that destructive biomass measures are often not feasible, applying easy-to-measure leaf traits associated with the CSR classification appear more predictive of whole-plant growth than LES traits. Testing the generality of this result across additional taxa would further improve our ability to predict whole-plant growth from functional traits across scales.

KEYWORDS
biomass, competitive–stress tolerant–ruderal (CSR), ecophysiology, growth analysis, leaf area, leaf economics spectrum, plant ecology, plant strategies

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INTRODUCTION

Predicting variation in plant growth is a long-standing problem in ecology. Because plants largely determine terrestrial ecosystem productivity, estimating current and future plant growth is increasingly relevant because global change drivers impact ecosystem services (Arndt et al., 2019; Helbig et al., 2017). Because it is typically impractical to measure the total vegetative biomass of a community or ecosystem, an emerging method is to apply plant traits to predict growth rate (GR). These trait-based approaches take advantage of a large body of literature that analyzes covariation and trade-offs among plant traits (Dìaz et al., 2015; Enquist et al., 2007; Lambers & Poorter, 1992; Wright et al., 2004). Given that morphological and physiological characters are central to resource acquisition and allocation, they are likely to shape plant productivity in predictable ways.

Three classic approaches have attempted to distill plant diversity into cohesive strategies and estimate growth based on defining characteristics: growth analysis, Grime's CSR triangle (competitive–stress tolerant–ruderal), and the leaf economics spectrum (LES) (Table 1). In growth analysis, GR is predicted by the relative allocation of biomass among roots, stems, and leaves (Evans, 1972; Lambers & Poorter, 1992). Faster growing plants are expected to invest more in leaves relative to stems and roots. Due to the importance of leaf investment, GRs are additionally dependent on specific leaf area (SLA), the ratio of leaf area to dry mass.

Grime's CSR framework predicts that three plant strategies have repeatedly evolved in response to combinations of stress and disturbance (Grime, 1977). Until recently, the CSR framework was conceptual rather than empirically trait-based. However, Pierce et al. (2016) showed that three leaf traits were predictive of the scheme: average leaf surface area (individual leaf size), SLA, and leaf dry matter content (LDMC). In this context, the competitive strategy is defined by large leaves with intermediate SLA and LDMC. The stress-tolerant strategy has small leaves with large SLA and LDMC, and the ruderal strategy has small leaves with small LDMC and large SLA (Pierce et al., 2016).

The most commonly applied trait-based framework is the LES, which describes patterns of covariation among six leaf traits: leaf lifespan, SLA, leaf mass-based nitrogen (N) and phosphorus (P) contents, and leaf mass-based rates of light-saturated photosynthesis ($A_{\max}$) and dark respiration (R_d). Together, these traits represent the return on investment of fixed carbon at the leaf level (Reich, 2014; Wright et al., 2004). On one end of the spectrum is a "resource-acquisitive" strategy with short leaf lifespan and larger SLA, N and P contents, and gas exchange rates (photosynthesis, respiration). On the other end of the spectrum is a "resource-conservative" strategy with the opposite combination of trait values. It is generally predicted that plants with resource-acquisitive leaf traits have relatively faster GRs than those with resource-conservative leaves (Reich, 2014). As such, leaf economics traits have been applied to predict growth at genotypic, community, ecosystem, and global scales, often using a subset of traits as direct proxies for plant growth (Blonder et al., 2015; Grady et al., 2013).

TABLE 1 Traits and growth predictions of three classic ecological strategy schemes (growth analysis [GA], Grime's competitive–stress tolerant–ruderal [CSR] triangle, leaf economics spectrum [LES]), and additional traits considered in this study.

Strategy scheme	Trait	Acronym	Growth predictions
GA	Leaf mass fraction	LMF	+
	Stem mass fraction	SMF	+
	Root mass fraction	RMF	−
	Specific leaf area	SLA	+
CSR triangle	Average leaf size	LS	+, −
	Leaf dry matter content	LDMC	−
	Specific leaf area	SLA	+
LES	Photosynthetic rate	$A_{\max}$	+
	Respiration rate	R_d	+
	Specific leaf area	SLA	+
	Leaf nitrogen content	N	+
	Leaf phosphorus content	P	+
	Leaf lifespan	LL	−
Additional traits	Total leaf area	LA	+
	Leaf carbon isotope ratio	$\delta^{13}C$	−
	Leaf thickness	L_{th}	−
	Plant height	H	+
	Root clonality		+
	Seed mass	SM	+
	Specific root length	SRL	+

Note: "+" and "−" indicate positive and negative correlations, respectively.

Despite the intuitive appeal of these theories, experiments that directly use traits to predict whole-plant growth are surprisingly limited. Studies to date show mixed results, including significant (Bongers et al., 2020) and nonsignificant (Goud et al., 2019) trait–GR relationships. Inconsistent results could be influenced by environmental context (Maire et al., 2015; Wright et al., 2005) or species interactions (Bongers et al., 2020) or because studies compare plants at different scales—from broadly divergent taxonomic and functional groups at the community scale, to closely related plants within a clade, to among plant individuals within a species (Anderegg et al., 2018; Edwards et al., 2014; Messier et al., 2016).

In an effort to link these theoretical frameworks to observed GR, we simultaneously tested these growth–trait predictions (Table 1) using a diverse set of closely related species in a multivariate phylogenetic analysis. Growing species from the same genus under controlled, common resource conditions in a growth chamber allowed us to compare GRs and traits of interest within a similar functional group (i.e., all C_3, diploid, herbaceous, and perennial angiosperms) that share a recent common ancestor and yet display large variation in growth, habitat affinities, and traits.

We measured leaf, stem, and root biomass to calculate whole-plant GRs and measured 21 traits: leaf, stem, and root biomass fractions and SLA for growth analysis, CSR-associated traits, and leaf economic spectrum traits (Table 1). The LES originally defined leaf N content, phosphorus content, and gas exchange rates on a dry mass basis, but it has become customary to consider both mass-based and area-based traits (Lloyd et al., 2013; Osnas et al., 2013). Although trait covariance is often weaker with area-based normalizations, given the functional dependence between leaf area and photosynthesis, we included both mass- and area-based LES traits together and in separate analyses.

We also considered seven additional traits that are not used in these three classic approaches but play a prominent role in the plant ecological literature. Some of these traits are expected to predict plant growth because they measure aspects of plant size, such as height, total leaf area (LA), root clonality, and seed mass (SM). For example, the total amount of LA available for photosynthesis can positively correlate with biomass accumulation (Goud et al., 2021; Weraduwage et al., 2015) and ecosystem carbon exchange (Goud et al., 2017; Stark et al., 2012; van Dijk et al., 2005). Root clonality may correspond to GR through increased vegetative reproduction and nutrient foraging ability (Keser et al., 2014; Klimešová & Martínková, 2004). The other traits are related to leaf metabolism and structural investments such as leaf thickness, leaf carbon isotope ratio ($\delta^{13}C$), and specific root length (SRL). Leaf thickness is often associated with a trade-off between stress tolerance and rapid growth (Coneva & Chitwood, 2018; Nautiyal et al., 1994). Leaf carbon isotope ratio ($\delta^{13}C$) is a measure of the long-term difference between CO_2 supply and demand that integrates over the lifespan of the leaf and can provide an integrated measure of carbon gain (Farquhar et al., 1989; Goud & Sparks, 2018). Similar to SLA, SRL is the ratio of root length to dry mass and is a measure of root economics that integrates the trade-off between resource acquisition and structural investment (Zhou et al., 2018).

METHODS

Study system and plant growth conditions

We assessed growth–trait relationships across 30 closely related yet functionally diverse milkweed species (Appendix S1: Figure S1). Milkweeds (*Asclepias* spp., Apocynaceae) are herbaceous perennials that display remarkable variation in morphology, ranging from desert subshrubs with small, narrow leaves (e.g., *A. linaria, A. subulata*) to large, highly productive plants of temperate and subtropical wetlands with large, broad leaves (e.g., *A. curassavica, A. incarnata*) (Woodson Jr., 1954). Milkweeds vary widely in GR and traits when grown under common garden conditions (Agrawal et al., 2009; Goud et al., 2019). Seeds collected by colleagues or purchased from native plant suppliers were germinated by moistening and stratifying at 4°C for at least 10 days and then at 28°C for 3 days. Seedlings were planted in 500-mL plastic pots and grown in Metro Mix soil (Scotts-Sierra, Marysville, OH, USA) in a walk-in growth chamber (Conviron CMP 6050) for 6 weeks at 26°C during a 14-h day and 24°C during a 10-h night with an average relative humidity of 50%. Seedlings were fertilized on Day 10 and Day 30 with a dilute fertilizer (N:P:K = 21:5:20) with a N concentration of 150 ppm (mg L^{-1}). Pots were spatially rearranged every week to minimize potential effects of spatial variation in light intensity within the chamber (Poorter et al., 2012).

GR definitions and calculations

Whole-plant growth can be defined and measured in various ways, including absolute GR and relative growth rate (RGR). Absolute GR is calculated as the total oven-dried biomass accrued over the number of days from seedling emergence until the end of the experiment in grams per day^{-1} and requires a single harvest. RGR is calculated either as the slope of a linear regression model fitted to the natural logarithm (ln) of whole-plant dry mass (M, in grams) over time or using the classical GR formula $\text{RGR} = (\ln M_2 - \ln M_1)/(t_2 - t_1)$, where t = time (days) and the subscripts indicate sequential sampling points (Evans, 1972). Either approach for RGR requires multiple harvests, which can constrain replication. Before proceeding with the single-harvest GR approach, we grew seedlings in a separate experiment to assess relationships between absolute and RGR calculations. We selected four milkweed species that, based on previous growth chamber experiments, represented the range of functional variation across the 30 species: *A. curassavica, A. incarnata, A. pumila*, and *A. verticillata* (Agrawal et al., 2009; Agrawal & Fishbein, 2006; Goud et al., 2019). We measured total biomass (g) in three successive harvests spaced 15 days apart (Appendix S1: Figure S2A) and calculated GR and RGR using the regression slope approach and the classical RGR formula. GR was positively associated with RGR based both on the slope of the growth curve (exponential $R^2 = 0.96$; Appendix S1: Figure S2B) and the RGR formula (exponential $R^2 = 0.99$; Appendix S1: Figure S2C). Therefore, we proceeded with GR for the purpose of our main study.

Trait and biomass measurements

We sampled five replicate plants per species for trait and growth measurements. SM was calculated before germination by dividing the total SM (g) by the number of seeds used for germination ($n = 30$ seeds per species). We measured leaf gas exchange rates using a LICOR LI-6400 CO_2 gas exchange analyzer (LICOR, Lincoln, NE, USA) on one fully expanded leaf per plant at 36–41 days old. We measured rates of leaf dark respiration (R_d) and light-saturated photosynthesis (A_{max}). Leaf dark respiration (R_d) was measured at zero light intensity (photosynthetically active radiation, PAR = 0 μmol photons m^{-2} s^{-1}). We generated light response curves to obtain light-saturated photosynthesis rates (A_{max}). Briefly, we equilibrated the leaf at ambient light intensity (PAR = 1000), then worked up from dark (PAR = 0) to high light (PAR = 2000) in steps of 200 PAR, allowing the leaf to equilibrate for 1–2 min between each light level. The light-saturated photosynthesis rate was then calculated from the nonrectangular model of the photosynthetic light response curve using nonlinear least-squares regression (Marshall & Biscoe, 1980). Leaf humidity inside the cuvette was maintained between 45% and 60%, and the cuvette temperature was maintained at 25°C.

Plants were harvested at 42–45 days old, representing prereproductive vegetative growth and to prevent roots from becoming pot-bound. At the time of harvest, the height of each plant was measured (H, cm), total leaf number was recorded, leaves were removed from the stems, and roots were separated and washed to remove soil. For each individual, LA was measured using a LICOR LI-3100 leaf-area meter. Average leaf area (leaf size, LS) was calculated by dividing LA by the total number of leaves. SRL was measured as the ratio of root length (cm) to dry mass using subsamples of lateral roots ($n = 10$ per plant). Root subsamples were identified under a dissecting microscope and were predominantly first through second-order roots, approximately 0.5 mm in diameter (Kramer-Walter et al., 2016). Root clonality was measured as the number of buds on roots, rhizomes, and caudices of each plant (Pellissier et al., 2016).

Following fresh weight measurements of leaves, stems, and roots, samples were oven-dried at 60°C for 48 h and measured for dry mass (g). SLA was measured as LA divided by total oven-dried leaf mass (g). LDMC was measured as oven-dry leaf mass (mg) divided by water-saturated fresh mass (g). Leaf thickness (L_{th}) was estimated as $1/(\mathrm{SLA} \times \mathrm{LDMC})$ (Pérez-Harguindeguy et al., 2013).

Isotope ratio mass spectrometry and elemental analyses were performed at the Cornell University Stable Isotope Laboratory. Carbon isotope ratios and N percentage element of leaf material were measured using a continuous-flow isotope ratio mass spectrometer (Thermo Environmental Delta V Advantage) coupled to an elemental analyzer (Carlo Erba NC2500). Isotope ratios are expressed as δ values (per mil):

$$\delta^{13}\mathrm{C} = \left(R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1\right) \times 1000\ (‰),$$

where R_{sample} and R_{standard} are the ratios of heavy isotope to light isotope of the sample relative to Vienna-Pee-Dee Belemnite, the international standard for C. Leaf P content was measured by dry ash analysis at the Cornell Nutrient Analysis Laboratory (Jones, 2001). Leaf N and P were calculated on both a leaf dry mass and leaf area basis.

Statistical analyses

All statistical analyses were performed in R version 3.5.3 (R Core Team, 2019). We assessed the relative ability of each individual trait to predict GR using general linear models (GLMs) and tested for the potential effects of shared evolutionary history using phylogenetic generalized least-squares (PGLS) regressions using the "pgls" function of the caper package in R (Orme et al., 2012). All variables were natural log-transformed to reduce nonnormality, and individual regression models were developed using species means. For the PGLS analyses, a maximum likelihood phylogeny of 111 *Asclepias* species was pruned with the retention of branch lengths to create a phylogram for the 30 species (Appendix S1: Figure S1). Briefly, the phylogeny was estimated from three noncoding plastid genome regions: *rpl16* intron, $trnC^{GCA}$–*rpoB* intergenic spacer, and the contiguous $trnS^{GCU}$–$trnG^{UUC}$ intergenic spacer/$trnG^{UUC}$ intron (Fishbein et al., 2011). We estimated the phylogenetic signal of GR and all traits by calculating Pagel's λ using the "phylosig" function in the picante R package (Kembel et al., 2010). We included the SE of the mean for each variable. A λ value of 1 indicates that trait similarity among species is directly proportional to the extent of shared evolutionary history, while a λ value of 0 indicates no relationship between shared ancestry and trait values. We tested for significance in phylogenetic signal using likelihood ratio tests (Pagel, 1999). For the PGLS analyses, linear regression parameters were estimated from the default $\lambda = 1$ Brownian motion model.

We used Ward's agglomerative clustering and principal component analysis using the "vegan" R package (Oksanen et al., 2019) to classify the 30 species into distinct groups, hereafter referred to as strategies. We grouped species based on (1) growth analysis traits, (2) CSR traits, (3) LES traits, and (4) all 21 measured traits. We then used Kendall's coefficient of concordance (999 permutations) to identify how many strategies identified by Ward's clustering were significantly distinct and which species were significantly contributing to each strategy (Legendre & Legendre, 2012). We also classified species using the CSR method outlined in Pierce et al. (2016), where ratios of C:S:R values were calculated based on leaf traits (size, SLA, LDMC) for each species.

We used linear regression to assess relationships between GR and the first two principal component axes for each strategy scheme. Linear regression models were directly compared using the Akaike information criterion (AIC).

RESULTS

Growth–trait relationships across species

Across 30 milkweed species, individual plant GRs ranged over 50-fold, from 0.005 to 0.258 g day^{-1} (Appendix S1: Table S1). Overall, in phylogenetically controlled analyses (PGLS), three traits each individually explained over 50% of the variation in whole-plant growth among the 30 *Asclepias* species: LA, N content on a mass basis (N_{mass}), and phosphorus content on an area basis (P_{area}). In total, GR was positively associated with leaf carbon isotope composition ($\delta^{13}C$), plant height (*H*), LA, LDMC, leaf mass fraction (LMF), LS, area-based photosynthetic rate (A_{area}), and stem mass fraction (SMF). GR was negatively associated with leaf N and P contents (N, P, area and mass based). Growth was not associated with leaf dark respiration (R_d, per mass or per area), leaf thickness (L_{th}), mass-based photosynthetic rate (A_{mass}), root clonality, root mass fraction (RMF), SM, SLA, or SRL. Accounting for shared evolutionary history did not change these relationships, with the exception of LMF (not significant in PGLS) and mass-based photosynthesis (A_{mass}; became significant in PGLS). Nine of the 21 traits showed phylogenetic signal (λ value >0.70, $p < 0.05$): plant height (*H*), leaf carbon isotope ratio ($\delta^{13}C$), mass-based respiration and leaf N (R_{mass}, N_{mass}), LDMC, leaf thickness (L_{th}), SM, and LMF and SMF (Table 2).

Plant strategies

To assess growth–trait relationships at the level of plant strategies, we classified species into groups using diagnostic traits of the three theories (Tables 1 and 3). Using growth analysis traits, we identified three strategies primarily defined by the relative allocation between above- and belowground biomass (PC1 = 70%; Figure 1A).

When grouped by CSR traits, species distributed among four strategies corresponding to competitive–ruderal (CR), competitive–stress tolerant–ruderal (CSR), stress tolerant–ruderal (SR), and stress-tolerant (S). Consistent with previous studies (Li & Shipley, 2017; Pierce et al., 2016), variation in LS was orthogonal to variation in SLA and LDMC, with differences among groups driven primarily by variation in average LS (PC1 = 93%; Figure 1D).

For LES traits, we analyzed the area-based and mass-based traits together and separately, as these are not wholly independent, being statistically linked by SLA (Osnas et al., 2013). In all three analyses, species were distributed among three strategies with variation in photosynthesis rate (A_{mass}, A_{area}) and SLA being orthogonal to leaf N and phosphorus (Appendix S1: Figure S3). In keeping with the original LES definition, we present results from the mass-based multivariate analysis (other analyses presented in Appendix S1: Figure S3), where differences among groups were driven primarily by variation in photosynthesis rate (A_{mass}) and SLA (PC1 = 75.7%) and secondarily by leaf N_{mass} and P_{mass} (PC2 = 12%; Figure 1G). Variation in leaf respiration rate (R_{mass}) contributed equally to PC1 and PC2 (Appendix S1: Table S2).

In addition to these well-established schemes, we classified species using all 21 traits measured in this study. Using this approach, the 30 species distributed among four groups (Figure 1J). Consistent with global trait analyses (Dìaz et al., 2015), the first PC axis (52%) corresponded to plant size-related traits: LA, average LS, plant height (*H*), and biomass fractions (LMF, SMF, RMF). The second PC axis (19%) corresponded to leaf economic and metabolic traits, such as leaf carbon isotope ratio ($\delta^{13}C$), gas exchange rates, leaf thickness (L_{th}), and nutrient contents (N, P). We describe the four strategies identified from all measured traits by their overall plant size (small, medium, large) and primary biomass allocation (roots, leaves, stems). The direction and strength of all trait loadings on the PC axes are described in Appendix S1: Table S2.

Growth–trait relationships across plant classification schemes

Across strategies, growth correlated most strongly with the first principal component axis (PC1) of growth

TABLE 2 Linear associations between 21 plant traits and growth rate (GR) using both general linear models (GLMs) and phylogenetic least-squares regression (PGLS) for 30 *Asclepias* species grown under common conditions.

		Associations with GR								
		GLM			PGLS			Phylogenetic signal		
Trait	**Sign**	**R^2**	**t**	**p**	**R^2**	**F**	**p**	**λ**	**LR**	**p**
LA	+	**0.56**	**5.97**	**<0.0001**	**0.61**	**44.22**	**<0.0001**	0.18	0.79	0.37
δ^{13}C	+	**0.35**	**3.88**	**0.001**	**0.36**	**15.68**	**0.0005**	**0.7**	**4.61**	**0.03**
R_{area}	n.s	0.02	0.84	0.41	0.01	0.18	0.67	<0.001	0.001	0.98
R_{mass}	n.s	0.01	0.64	0.53	0.004	0.13	0.73	**0.93**	**8.56**	**0.003**
LDMC	+	**0.1**	**2.11**	**0.05**	**0.17**	**5.85**	**0.02**	**0.64**	**3.81**	**0.05**
LMF	+	**0.14**	**2.09**	**0.04**	0.01	0.22	0.64	**0.92**	**6.21**	**0.01**
$\mathrm{N}_{\mathrm{area}}$	−	**0.27**	**3.18**	**0.004**	**0.2**	**6.98**	**0.01**	0.45	1.10	0.29
$\mathrm{N}_{\mathrm{mass}}$	−	**0.38**	**4.13**	**0.0003**	**0.5**	**28.45**	**<0.0001**	**0.97**	**11.10**	**0.001**
$\mathrm{P}_{\mathrm{area}}$	−	**0.51**	**6.24**	**<0.0001**	**0.55**	**51.79**	**<0.0001**	0.06	0.13	0.72
$\mathrm{P}_{\mathrm{mass}}$	−	**0.26**	**3.17**	**0.004**	**0.19**	**6.49**	**0.02**	0.03	0.02	0.88
LS	+	**0.24**	**2.25**	**0.04**	**0.31**	**12.76**	**0.001**	<0.001	0.0002	0.98
L_{th}	n.s.	0.06	1.33	0.2	0.05	1.44	0.24	**0.74**	**5.51**	**0.02**
A_{area}	+	**0.23**	**2.86**	**0.008**	**0.32**	**13.06**	**0.001**	0.49	0.05	0.97
A_{mass}	+	0.03	0.96	0.34	**0.19**	**6.75**	**0.01**	0.7	1.61	0.2
H	+	**0.47**	**5.02**	**<0.0001**	**0.36**	**15.43**	**0.0005**	**0.99**	**16.98**	**<0.001**
Clonality	n.s	0.01	0.34	0.73	0.03	0.93	0.34	<0.001	0.001	0.98
RMF	n.s	0.08	1.57	0.13	0.01	0.18	0.67	0.5	1.85	0.17
SM	n.s	0.01	0.49	0.63	0.04	1.11	0.3	**0.99**	**10.90**	**0.001**
SLA	n.s	0.001	0.15	0.88	0.01	0.002	0.96	<0.001	0.001	0.98
SRL	n.s	0.05	1.17	0.25	0.06	1.83	0.19	<0.001	0.001	0.98
SMF	+	**0.36**	**4.01**	**0.0004**	**0.17**	**5.77**	**0.02**	**0.95**	**17.66**	**<0.001**

Note: Data are from species means (all df = 29). "Sign" indicates the direction of the significant correlation (positive, +, or negative, −). Phylogenetic signal using Pagel's λ is shown for each trait, with $p < 0.05$ indicating significant phylogenetic signal. Bold font indicates significance at $p < 0.05$. Trait acronyms are defined in Table 1.

Abbreviations: LDMC, leaf dry matter content; LMF, leaf mass fraction; LR, likelihood ratio; n.s, not significant; RMF, root mass fraction; SM, seed mass; SLA, specific leaf area; SRL, specific root length; SMF, stem mass fraction.

analysis ($R^2 = 0.91$, $p < 0.0001$, AIC = −90; Figure 1B), corresponding to variations in LMF and SMF. The second strongest predictor was PC1 for all 21 traits combined ($R^2 = 0.83$, $p < 0.0001$, AIC = −72; Figure 1K), driven primarily by variation in LA and plant height (H). Growth also positively correlated with PC1 of CSR ($R^2 = 0.49$, $p < 0.0001$, AIC = −39; Figure 1E), corresponding to variation in average LS. Growth did not correlate with PC1 of LES ($p = 0.72$, AIC = −17; Figure 1H), corresponding to variation in photosynthesis and SLA. Growth negatively correlated with PC2 of LES ($R^2 = 0.43$, $p \leq 0.0001$, AIC = −36; Figure 1I), driven by mass-based leaf N and P contents. Growth also negatively correlated with PC2 of all measured traits ($R^2 = 0.22$, $p = 0.006$, AIC = −26; Figure 1L), driven primarily by variation in leaf carbon isotope ratios and LES traits (Appendix S1: Table S2). Growth was not predicted by PC2 of growth analysis (RMFs, SLA) or CSR (SLA, LDMC) (both $p > 0.05$, $-20 < \mathrm{AIC} < -19$; Figure 1C,F). All trait loadings can be found in Appendix S1: Table S2, and all statistical reporting for growth correlations are in Appendix S1: Table S3.

DISCUSSION

In this work, we bridge classic ecological theory with current trait-based approaches to better predict whole-plant growth from functional traits. We tested predictions that faster growing plant species will (1) allocate more biomass to aboveground tissues (based on growth analysis), (2) have larger leaves with larger SLA and lower dry matter contents (based on Grime's CSR triangle), or (3) have "acquisitive" leaf traits defined by larger leaf gas exchange rates, SLA, and N and P contents (based on the LES) relative to

TABLE 3 Whole-plant growth rate (GR, g day^{-1}) ± SE and strategic classifications for 30 *Asclepias* species grown under common conditions, in order of increasing GR.

			Strategy			
Species		**GR**	**GA**	**CSR**	**LES**	**All traits**
17	*A. longifolia*	0.013 ± 0.003	Root	SR	Acq/cons	Small, root
11	*A. hirtella*	0.014 ± 0.003	Root	SR	Acq/cons	Small, root
6	*A. cryptoceras*	0.017 ± 0.001	Root	SR	Acq/cons	Small, root
1	*A. amplexicaulis*	0.018 ± 0.001	Root	CSR	Acq/cons	Small, root
22	*A. solanoana*	0.021 ± 0.002	Root	CSR	Acq/cons	Small, root
30	*A. viridis*	0.024 ± 0.002	Leaf	CR	Acq/cons	Medium, leaf
26	*A. sullivantii*	0.029 ± 0.008	Leaf	CR	Acq/cons	Medium, leaf
3	*A. asperula*	0.032 ± 0.004	Root	CSR	Acq/cons	Small, root
29	*A. verticillata*	0.040 ± 0.003	Stem	S	Acq/cons	Medium, stem
4	*A. brachystephana*	0.045 ± 0.006	Leaf	SR	Acq/cons	Medium, leaf
18	*A. mexicana*	0.045 ± 0.005	Stem	S	Acq/cons	Medium, stem
14	*A. latifolia*	0.047 ± 0.010	Leaf	CR	Conservative	Medium, leaf
21	*A. pumila*	0.048 ± 0.005	Leaf	S	Acquisitive	Medium, stem
15	*A. linaria*	0.048 ± 0.004	Leaf	S	Acq/cons	Medium, stem
2	*A. arenaria*	0.051 ± 0.008	Root	SR	Acq/cons	Small, root
23	*A. speciosa*	0.053 ± 0.014	Leaf	CR	Conservative	Medium, leaf
28	*A. tuberosa*	0.060 ± 0.010	Leaf	S	Acq/cons	Medium, leaf
8	*A. engelmanniana*	0.060 ± 0.007	Root	SR	Conservative	Medium, stem
16	*A. linearis*	0.064 ± 0.005	Stem	SR	Acquisitive	Medium, stem
19	*A. perennis*	0.072 ± 0.005	Stem	CR	Conservative	Large, leaf and stem
5	*A. californica*	0.075 ± 0.005	Leaf	CR	Conservative	Medium, leaf
13	*A. labriformis*	0.076 ± 0.004	Leaf	CSR	Acq/cons	Medium, leaf
10	*A. fascicularis*	0.082 ± 0.008	Stem	SR	Conservative	Large, leaf and stem
9	*A. eriocarpa*	0.094 ± 0.005	Leaf	CR	Conservative	Large, leaf and stem
24	*A. subulata*	0.098 ± 0.010	Stem	S	Acquisitive	Medium, stem
25	*A. subverticillata*	0.101 ± 0.009	Stem	SR	Conservative	Large, leaf and stem
27	*A. syriaca*	0.111 ± 0.012	Leaf	CR	Conservative	Large, leaf and stem
12	*A. incarnata* ssp. *incarnata*	0.134 ± 0.015	Stem	CR	Conservative	Large, leaf and stem
7	*A. curassavica*	0.136 ± 0.007	Stem	CR	Conservative	Large, leaf and stem
20	*A. incarnata* ssp. *pulchra*	0.205 ± 0.016	Stem	CR	Conservative	Large, leaf and stem

Note: Growth analysis (GA) strategies defined by species' predominant biomass fraction (root, stem, leaf); CSR by competitive (C), stress tolerant (S), ruderal (R), or their combination. Leaf economic spectrum (LES) strategies defined as resource acquisitive (acq) or conservative (cons). Strategies identified from 21 measured traits are defined by relative plant size (small, medium, large) and predominant biomass fraction (root, stem, leaf).

slower growing plants. The results supported predictions of growth analysis and CSR, but not LES. Remarkably, although two LES traits did have strong predictive power (N per leaf mass and phosphorus per leaf area, contributing to multivariate correlations, Figure 1), these traits were predictive in the opposite direction to that derived from LES theory such that more N and P predicted less growth. Overall, differences in GR were driven more by whole-plant (e.g., leaf area, SMF) than individual leaf-level traits (e.g., leaf thickness, SLA). Combining organ-specific and whole-plant traits provided a more integrated view of plant strategies that was better able to predict growth.

For decades, plant mass fractions have been successfully applied to estimate variation in GR, and our study is no exception. Indeed, growth analysis traits together were the strongest predictors of whole-plant growth across this diverse set of 30 milkweed species (Figure 1B). Although theoretically and empirically appealing, the

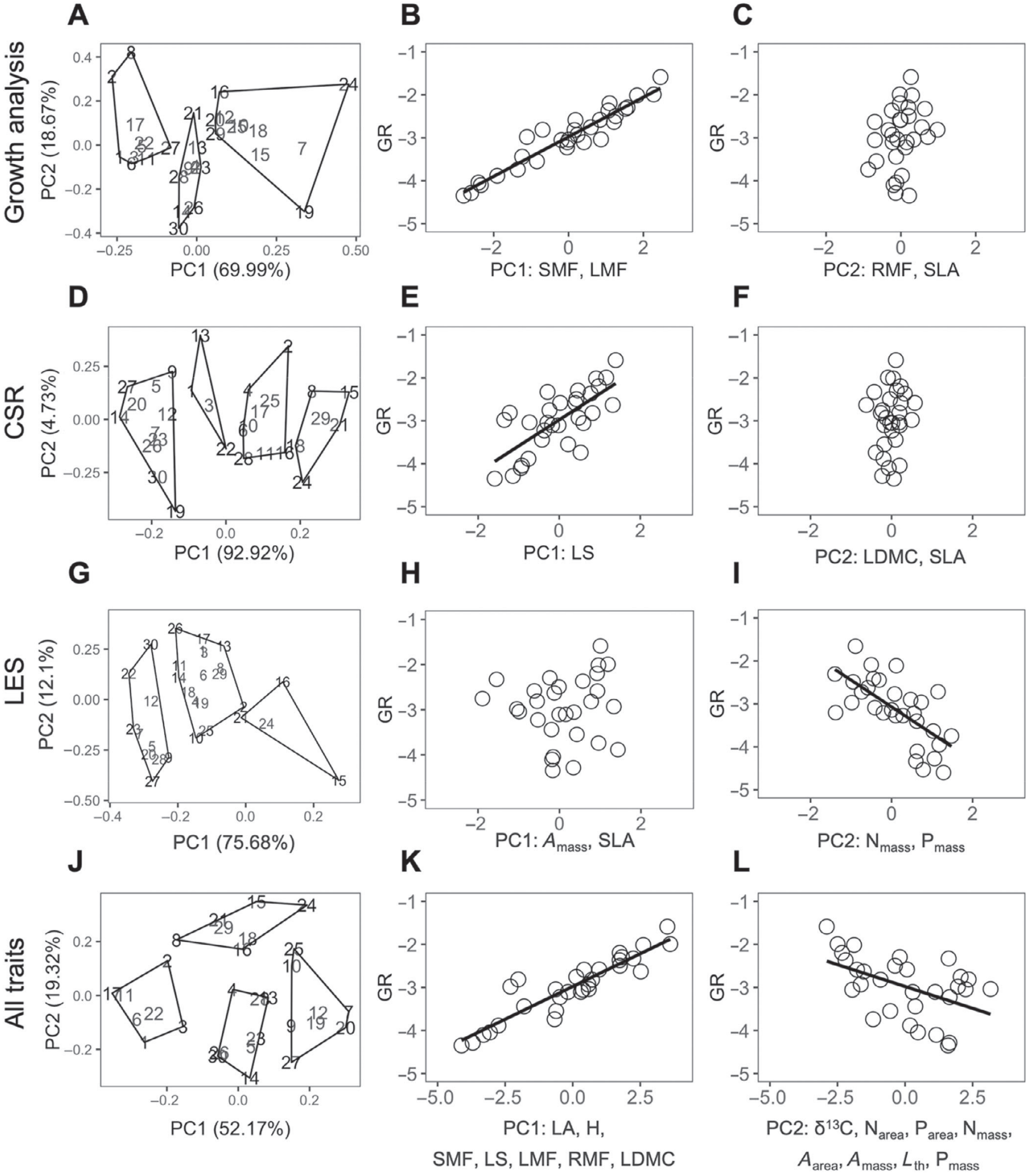

FIGURE 1 (Left) Biplots of principal component analysis (PCA) of 30 *Asclepias* species grouped by the defining traits of three classic ecological theories: (A) growth analysis, (D) Grime's competitive–stress tolerant–ruderal (CSR) triangle, (G) leaf economics spectrum (LES), and (J) a combined suite of all 21 measured traits. Species groups are represented as convex based on Ward's agglomerative clustering defined by trait similarity. (Center) Associations between growth rate (GR, natural log-transformed) and PC1 (B, E, H, K) and (right) between GR and PC2 (C, F, I, L). Lines of best fit are included when the slopes were significantly different from zero (Appendix S1: Table S3). The trait variables with the highest eigenvector scores on PC1 and PC2 are presented from left to right for each axis. Data are species means. Trait abbreviations are in Table 1. Species names are in Table 3.

major shortcoming of growth analysis is feasibility—it is typically not practical to obtain the necessary RMF that is critical for growth analysis.

Alternatively, the CSR triangle has been a classic predictor of plant strategic variation for decades, but quantitative metrics were not developed until recently (Pierce et al., 2016). Recent studies showed promising applications of CSR defined by leaf traits to better describe functional diversity (Dayrell et al., 2018) and species interactions (Zanzottera et al., 2020) within (Astuti et al., 2018; Vasseur et al., 2018) and across (Dayrell et al., 2018; Pierce et al., 2016; Zanzottera et al., 2020) species. In this novel application of CSR to predict whole-plant growth, we found strong growth–trait relationships across milkweed species driven primarily by variation in average LS with minimal contributions from LDMC and SLA (Figure 1F,J). An advantage of LS is that it can be measured on attached leaves and does not require destructive sampling of leaf material, which is essential in studies requiring repeated measures over time or in vulnerable/at-risk plant populations where leaf material should not be removed from focal plants (Davidson et al., 2021).

LA and plant height are also traits that can be sampled nondestructively. Here, variation in LA was by far the strongest and most consistent individual predictor of plant growth across all species individually ($R^2 = 0.60$; Table 2) and in multivariate plant strategies (associated with PC1; Figure 1F,H; Appendix S1: Table S2). When all 21 traits were considered together, plant height was the second-best predictor of growth (associated with PC1; Figure 1F,H; Appendix S1: Table S2). Although aspects of plant size such as leaf area and height may be expected to correlate with GRs, this should not be assumed for all species because there are cases where plant size does not correlate with GR (e.g., succulence; Ogburn & Edwards, 2010). Indeed, in our multivariate analysis using all 21 traits, we identified plant strategies with variable relationships between leaf area, height, and GR. Specifically, two strategies with similar growth and leaf area differed in height, suggesting that leaf area may be most predictive for plants that invest primarily in photosynthesizing leaf biomass, while plant height may be most effective for plants investing in more structural stem biomass. These results are consistent with previously observed positive associations between ecosystem productivity and leaf area (Goud et al., 2017; Litton et al., 2008) and height (Goud, Touchette, et al., 2022; Westoby, 1998).

LA and height are not considered in growth analysis, LES, or CSR theories; however, height is a key component of plant size and has been used to differentiate among plant functional diversity and ecological strategies at local (Westoby, 1998) and global scales (Dìaz et al., 2015). Importantly, LA and height can be remotely sensed, which is particularly useful where it is not feasible to directly measure traits for all individuals (e.g., forest canopies) or for repeated measurements that require nondestructive sampling (Davidson et al., 2021; Goud et al., 2017).

Leaf economics spectrum (LES)

The LES has attracted considerable attention and is often turned to as the primary approach to understand plant functional diversity (Dìaz et al., 2015). However, the work presented here suggests that LES traits do not predict within-clade differences in plant growth; resource-acquisitive leaf traits were negatively associated with growth, and SLA was not predictive of growth at the scales that we investigated. We note that, although our multivariate analysis of five out of six LES traits yielded strong predictive power for GR (PC1 and PC2 combining to 60% of the variation, Figure 1), the fact that these associations were not in the expected direction and that these traits can be challenging to measure suggest caution should be exercised in using the LES framework to predict growth within clades. The best application of LES traits to predict growth may be in comparing broadly divergent plant groups (e.g., angiosperms vs. gymnosperms), rather than being generalizable across all scales of biological organization (Anderegg et al., 2018).

Species groups identified by LES traits did not adhere to a linear spectrum of increasing leaf economics or nutrient concentrations with increasing growth. Rather, each multivariate grouping expressed a mixture of “acquisitive” and “conservative” trait values. For example, some plants with resource conservative leaves (e.g., small, thick leaves with low nutrient content) grew considerably faster than species with the opposite set of resource acquisitive traits because these plants were taller and had larger overall leaf area. Similarly, species with the largest GRs had lower foliar N and P and similar rates of leaf gas exchange than other, less productive species. Lower leaf N concentrations in fast-growing species may be reflective of nutrient limitations imposed by the experimental pot size. Although we took precautions to avoid nutrient limitations that could affect growth, pot studies will always carry the possibility that the growing environment itself influenced plant growth. Current thinking, however, suggests that, although pot size limitations can influence growth and photosynthetic rates, other anatomical and physiological traits are less affected (e.g., N content, biomass allocation) and that potentially fast-growing species still grow faster than inherently slow-growing ones (Lambers & Poorter, 1992). Moreover, the values we observed for leaf gas exchange and nutrient contents were in the range reported for these species in other controlled studies (Agrawal et al., 2009; Agrawal & Fishbein, 2006) and under field conditions (Agrawal et al., 2008; Mitchell et al., 2020).

In contrast to predictions, leaf gas exchange rates (photosynthesis, respiration) were not strong predictors of growth (Figure 1, Appendix S1: Table 2). When all 21 traits were considered, the four plant strategies identified had similar average photosynthetic and respiration rates, suggesting that the area available for photosynthesis (i.e., LA, LS) is more important for growth than instantaneous gas exchange rates in milkweeds. As a complement to instantaneous gas exchange rates, we measured leaf carbon isotope ratios ($\delta^{13}C$). Contrary to expectations, the fastest growing plants were the most enriched in $\delta^{13}C$, which is typically associated with slower rates of leaf metabolism (Ellsworth et al., 2017; Farquhar et al., 1989; Goud et al., 2019). However, fast growth in combination with leaves relatively enriched in $\delta^{13}C$ have been observed for other herbaceous plants (e.g., Asteraceae) when growth is achieved through adjusting biomass allocation rather than variation in individual leaf productivity (Goud et al., 2021). In support of this idea, milkweed species achieved faster growth by producing numerous large leaves and tall stems rather than adjusting leaf physiological performance. Together, results for instantaneous leaf-level gas exchange rates and $\delta^{13}C$ suggest that the influence of leaf metabolism is often overwhelmed by differences in total plant leaf area and, therefore, does not consistently scale to whole-plant growth (Agrawal et al., 2009; Goud et al., 2021).

Both leaf N and P are predicted to positively correlate with growth due to the functional need for N and P in photosynthesis (Walker et al., 2014; Wright et al., 2004). However, nonlinear or insignificant relationships are frequently reported (Feng & Dietze, 2013; Goud, Touchette, et al., 2022; Midgley et al., 2004). Here, growth was negatively associated with leaf N and P (Figure 1G–I; Table 2), which has been observed for other herbaceous species grown under common conditions (Poorter et al., 1990). Interestingly, this negative relationship in milkweeds was driven by species from arid environments (e.g., *Asclepias brachystephana*, *Asclepias mexicana*) with higher N and P content yet lower GRs. Higher leaf N without an accompanying increase in photosynthesis and growth is common for many plants from dry or high irradiance environments that retain leaf N and P (Field et al., 1983; Maire et al., 2015; Wright et al., 2001) and can operate at a higher leaf N, with the high leaf N serving to economize on water use during photosynthesis (Schrodt et al., 2015; Wright et al., 2003). Further, not all N is used for photosynthesis, and recent estimates indicate that herbaceous plants may invest less than 50% of their leaf N to photosynthesis, with the remaining N invested in compounds that support structural and defensive functions (Ghimire et al., 2017). Thus, positive linear relationships between leaf N, P, and growth are clearly not universal.

Synthesis and speculation

Although SLA is a component of all three theories and one of the most commonly reported plant functional traits, growth did not correlate with SLA across species or strategies. SLA represents the investment in leaf area per unit leaf mass, reflecting a potential trade-off between productivity (i.e., area available for carbon capture) and structural investment (i.e., mass of proteins, carbohydrates, and cell walls). Inconsistent or insignificant correlations between SLA and growth or growth proxies (e.g., leaf gas exchange) are commonly reported (Midgley et al., 2004; Poorter & Evans, 1998; Reich et al., 1994). Thus, although SLA may correlate with growth across broadly divergent species, inconsistencies at finer taxonomic scales are likely driven by covariation with other morphological traits (e.g., LDMC, leaf thickness) and environmental conditions that are largely independent of GR variation (Edwards et al., 2014).

There is increasing interest in whether associations between growth and functional traits generally apply across scales (Walker et al., 2017). Particularly for LES traits, an emerging literature has considered cross-scale relationships. At large taxonomic (e.g., from *Arabidopsis* to *Sequoia*) and spatial (e.g., cross-continental ecosystems) scales, patterns of LES trait covariation appear strong and relatively consistent (Dìaz et al., 2015; Enquist et al., 2007; Wright et al., 2005). However, at finer scales (e.g., within-genus, within-habitat), patterns are far less consistent and sometimes contrary to theory (Agrawal, 2020; Anderegg et al., 2018; Blonder et al., 2015; Grady et al., 2013; Mason & Donovan, 2015), as we also found here for milkweeds. This is not necessarily surprising since trait relationships are often only predictive at the largest scales, where both the range of expression and fundamental biological attributes are revealed (Agrawal, 2020; Anderegg et al., 2018; Enquist et al., 1999, 2007).

In this study, size-related morphological traits consistently predicted whole-plant growth, while leaf economic and metabolic traits did not. Although we found specific traits to be predictive of growth, we caution against using single traits because their relevance as a consistent predictor of growth is likely to be highly clade-specific. For instance, *Asclepias* are herbaceous perennials; would we expect similar growth–trait relationships for annual plants, trees, or ferns? If plants adhere to a globally consistent spectrum of form and function defined by organ size and leaf economics, as put forth by Dìaz et al. (2015), then perhaps we would expect consistency across clades.

However, there is ample evidence to suggest that trait coordination is taxon-dependent (Anderegg et al., 2018; Garnier, 1991; Ji et al., 2020; Lambers & Poorter, 1992). Additionally, *Asclepias* as a clade is mostly adapted to living in open habitats (Woodson Jr., 1954), and we expect that resource allocation will differ depending on general niche adaptations (e.g., sun vs. shade) and plant life history, notably annual versus perennial or woody versus herbaceous growth form. Still, the generality of plant size and CSR-related traits (average LS, LDMC, and SLA) appear promising across scales. On the one hand, the exclusion of root and wood traits represents a shortcoming; however, these leaf traits are applicable across vascular and nonvascular plants alike. Practically speaking, these traits can be measured relatively quickly and inexpensively, facilitating use from both databases and large-scale field sampling.

The species we studied were distributed along multivariate axes defined by traits, including LES, irrespective of variation in GR. In other words, plant size may define growth differences, while economics and metabolism may better differentiate between variation in plant ecology (i.e., niche preferences) and life history such as phenology (Goud et al., 2021). This finding is consistent with global analyses that found diversity in plant form and function to fall along two major axes of variation related to plant size and leaf economics (Dìaz et al., 2015). Indeed, not all ecological strategies are directly related to GR. For example, strategies largely defined by secondary metabolism, such as pollination and defense syndromes, focus on traits that often show little direct connection with GR (e.g., flower color, toxic secondary compounds). Therefore, although some traits, and LES traits in particular, may not predict variation in growth as expected, they do capture other important axes of plant functional diversity (Agrawal & Fishbein, 2006). Evolutionarily conserved traits within clades are an important driver of differences that promote biodiversity. Ultimately the extent of clade specificity in which traits or suites of traits predict growth will be highly revealing, not only in terms of scaling generalities but also in terms of clade-specific traits or strategies that modify expectations.

AUTHOR CONTRIBUTIONS

Ellie M. Goud collected and analyzed the data; Ellie M. Goud, Jed P. Sparks, and Anurag A. Agrawal designed the experiment and wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All data (Goud, Agrawal, & Sparks, 2022) are available in Dryad at https://doi.org/10.5061/dryad.fttdz08xf.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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