

**Title**

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

**Running title:** Traits to predict plant growth

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## Abstract

Despite long-standing theory for classifying plant ecological strategies, limited data directly links organismal traits to whole-plant growth. We compared trait-growth relationships based on three prominent theories: growth analysis, Grime's CSR triangle, and the leaf economics spectrum (LES). Under these schemes, growth is hypothesized to be predicted by traits related to biomass investments, leaf structure or gas exchange, respectively. In phylogenetic analyses of 30 diverse milkweeds (*Asclepias* spp.) and 21 morphological and ecophysiological traits, growth rate varied 50-fold and was best predicted by growth analysis and CSR traits, as well as total leaf area and plant height. Despite two LES traits correlating with growth, they contradicted predictions and leaf traits did not scale with root and stem characteristics. Thus, although combining leaf traits and whole-plant allocation best predicts growth, when destructive measures are not feasible, we suggest total leaf area and plant height, or easy-to-measure traits associated with the CSR classification.

## Introduction

Predicting variation in plant growth is a long-standing problem in ecology. Because autotrophic plants largely determine ecosystem productivity and global nutrient cycling, estimating current and future plant growth is increasingly relevant as global change drivers impact ecosystem services (Helbig *et al.* 2017; Arndt *et al.* 2019). As 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. These trait-based approaches take advantage of a large body of literature that analyzes co-variation and trade-offs among plant traits (Lambers & Poorter 1992; Wright *et al.* 2004; Enquist *et al.* 2007; Diaz *et al.* 2015). 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 to estimate growth based on defining characteristics or trait combinations: growth analysis, Grime's CSR triangle, and the leaf economics spectrum (Table 1). In growth analysis, variation in plant growth rate is predicted based on the relative allocation of biomass among roots, stems, and leaves (Evans 1972; Lambers & Poorter 1992). Faster growing plants are expected to invest more in leaf biomass relative to stems and roots. Due to the importance of leaf investment, growth rates are additionally dependent on specific leaf area (SLA), the ratio of leaf area to dry mass. Grime's CSR (competition-stress tolerant-ruderal) framework predicts that these 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: the average leaf surface area (individual leaf size, LS), SLA, and leaf dry matter content (leaf dry mass density, LD). In this context, the C-strategy is defined by large LS and intermediate LD and SLA. The S-strategy has small LS and SLA with large LD, and R-strategy has small LS, small LD and large SLA (Pierce *et al.* 2016).

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

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; Grady *et al.* 2013) and non-significant (Feng & Dietze 2013; Goud *et al.* 2019; Midgley *et al.* 2004) trait-growth rate relationships. It is possible that

inconsistent results could be influenced by environmental variation (Wright *et al.* 2005; Maire *et al.* 2015), 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 (Edwards *et al.* 2014a; Messier *et al.* 2016).

In an effort to link these theoretical frameworks to observed growth rate, we simultaneously tested trait-growth rate predictions of the three classic approaches (Table 1) using a diverse set of closely related species in a multivariate phylogenetic analysis. We measured 21 traits that spanned the defining traits: leaf, stem and root biomass fractions (LMF, SMF, RMF) and SLA for growth analysis, CSR-associated traits (LS, LD, SLA), and leaf economic spectrum traits ( $A_{\max}$ ,  $R_d$ ,  $N$ ,  $P$ , SLA). We included six traits that we expected to be predictors of plant growth but are not used in any of the three approaches: total leaf area (LA), leaf thickness ( $L_{th}$ ), leaf carbon isotope ratio ( $\delta^{13}C$ ), specific root length (SRL), root clonality, seed mass (SM), and plant height (H). LA is the total amount of area available for photosynthesis and can positively correlate with biomass accumulation (Weraduwage *et al.* 2015; Goud *et al.* 2019) and ecosystem carbon exchange (van Dijk *et al.* 2005; Stark *et al.* 2012; Goud *et al.* 2017).  $L_{th}$  is often associated with a trade-off between stress tolerance and rapid growth (Nautiyal *et al.* 1994; Coneva & Chitwood 2018).  $\delta^{13}C$  is a measure of the long-term difference between  $CO_2$  supply and demand that integrates over the lifespan of the leaf and may provide an integrated measure of carbon gain (Farquhar *et al.* 1989; Goud & Sparks 2018). SRL is the ratio of root length to dry mass and is a measure of root economics. Similar to SLA, SRL integrates the trade-off between resource acquisition and structural investment (Weemstra *et al.* 2016; Zhou *et al.* 2018). Root clonality may correspond to growth rate through increased vegetative reproduction and nutrient foraging ability (Klimešová & Martínková 2004; Keser *et al.* 2014). SM and H largely define plant size, which is a major axis of plant functional diversity world-wide (Westoby 1998; Díaz *et al.* 2015). To control for potential effects of environmental variation, species interactions, and evolutionary history, we grew species from the same genus under controlled, common resource conditions in a growth chamber. This approach allowed us to compare growth rates and traits of interest within a similar functional group (i.e., all  $C_3$ , diploid, herbaceous, and perennial) that share a recent common ancestor, and yet display large variation in growth, habitat affinities, and traits.

## Materials and methods

### *Study system and plant growth conditions*

We assessed growth-trait relationships across 30 closely related yet functionally diverse milkweed species. 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 1954). Milkweeds vary widely in growth rate 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-hour day and 24°C during a 10-hour night with an average relative humidity of 50%.

#### *Trait and biomass measurements*

We sampled five replicate plants per species for trait and growth measurements. Seed mass (SM) was calculated before germination by dividing the total seed mass (g) by the number of seeds used for germination (n=30 per species). We measured leaf gas exchange rates using a LI-COR LI-6400 CO<sub>2</sub> gas exchange analyzer (LI-COR, Lincoln, NE) on one fully expanded leaf per plant at 36 - 41 days old. We generated light response curves to obtain the light intensity (photosynthetically active radiation, PAR, spanning 0 - 2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) at which photosynthesis saturated ( $A_{\text{max}}$ ). Leaf dark respiration ( $R_d$ ) was measured at a PAR of zero. Leaf humidity inside the cuvette was maintained between 45-60%, and the block temperature was maintained at 25°C.

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, total leaf area (LA) was measured using a LI-COR LI-3100 leaf-area meter (LI-COR, Lincoln, NE). Specific root length (SRL) was measured as the ratio of root length (cm) to dry mass using subsamples of lateral roots (n= 10 per plant). Root clonality was measured as the number of buds on roots, rhizomes and caudices of each plant (Pellissier *et al.* 2016). After fresh weight measurements of leaves, stems, and roots, samples were oven-dried at 60°C for 48 hours and measured for dry mass (g). Average leaf area (leaf size, LS) was calculated by dividing LA by the total number of leaves. Specific leaf area (SLA) was measured as LA divided by total oven-dried leaf mass (g). Leaf density (LD) was measured as oven-dry leaf mass (mg), divided by water-saturated fresh mass (g). Leaf thickness ( $L_{\text{th}}$ ) was estimated as  $\text{SLA} * \text{LD}$  (Pérez-Harguindeguy *et al.* 2013).

Carbon isotope ratios and N percent element of leaf material was measured using a continuous flow isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyzer (Carlo Erba NC2500). Isotope ratios are expressed as  $\delta$  values (per mil):

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

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the ratios of heavy isotope to light isotope of the sample relative to Vienna-Pee-Dee Belemnite, the international standard for C. Mass spectrometry and elemental analyses were performed at the Cornell University Stable Isotope Laboratory. Leaf P content was measured by dry ash analysis at the Cornell Nutrient Analysis Laboratory. Leaf N and P were calculated on both a leaf dry mass and leaf area basis.

Plant growth can be defined and measured in various ways, including relative growth (RGR) and absolute growth rate (GR, the total oven-dried biomass accrued over the number of days from seedling emergence until the end of the experiment in  $\text{g d}^{-1}$ ). RGR requires multiple harvests and can often constrain replication (Evans 1972). We found a robust correlation between RGR and GR ( $R^2 = 0.97$ ,  $p < 0.001$ ) for four milkweed species that represented the range of functional variation across the 30 species: *A. curassavica*, *A. incarnata*, *A. pumila*, *A. verticillata*. Therefore, we used GR for the purpose of this broader study.

## Statistical analyses

We assessed the relative ability of each trait to predict growth using generalized linear models (GLM), and tested for 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). A maximum likelihood phylogeny of 111 *Asclepias* species was pruned with the retention of branch lengths to create a phylogram for the 30 species (Figure S1). Briefly, the phylogeny was estimated from three non-coding plastid genome regions: *rpl16* intron, *trnC<sup>GCA</sup>* – *rpoB* intergenic spacer, and the contiguous *trnS<sup>GCU</sup>*–*trnG<sup>UUC</sup>* intergenic spacer/*trnG<sup>UUC</sup>* intron (Fishbein *et al.* 2011). We estimated the phylogenetic signal of growth rate and all traits by calculating Pagel’s  $\lambda$  using the ‘phylosig’ function in the picante R-package (Kembel *et al.* 2010). We included the standard error of the mean for each variable. A  $\lambda$ -value of 1 indicates that trait similarity among species is directly proportional to the extent of shared evolutionary history, while a  $\lambda$ -value = 0 indicates no relationship between shared ancestry and trait values. For the PGLS analyses, linear regression parameters were estimated from a  $\lambda=1$  model.

We used Ward’s agglomerative clustering and principal components 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 LS, LD, and SLA for each species. We used linear regression to assess relationships between GR and the first two principal components axes for each strategy scheme. Linear regression models were directly compared by Akaike information criterion (AIC). All analyses were performed in R3.5.3 (R Core Team 2019).

## Results

### Growth-trait relationships across species

Across 30 milkweed species, individual plant growth ranged over 50-fold, from 0.005 g d<sup>-1</sup> to 0.258 g d<sup>-1</sup> (Table S1). Overall, in phylogenetically controlled analyses (PGLS), three traits each explained over 50% of the variation in growth among the 30 *Asclepias* species (total leaf area, nitrogen content on a mass basis, and phosphorus content on an area basis). In total, growth rate positively correlated with  $\delta^{13}\text{C}$ , H, LA, LD, LMF, LS, area-based photosynthetic rate ( $A_{\text{area}}$ ) and SMF and negatively correlated with leaf N and P (analyses and abbreviations in Table 2). Growth did not correlate with  $R_d$  (per mass or per area),  $L_{\text{th}}$ , mass-based photosynthetic rate ( $A_{\text{mass}}$ ), root clonality, RMF, SM, SLA, or SRL. Accounting for shared evolutionary history did not change the relationships, with the exception of LMF (not significant in PGLS) and  $A_{\text{mass}}$  (became significant in PGLS). Nine of the 21 traits showed phylogenetic signal ( $\lambda$ -value > 0.70,  $P < 0.05$ ):  $\delta^{13}\text{C}$ , H,  $R_{\text{mass}}$ , LD, LMF,  $N_{\text{mass}}$ ,  $L_{\text{th}}$ , SM, and SMF (Table 2).

### Plant strategies

In order to assess growth-trait relationships at the level of plant strategies, we classified species into groups using diagnostic traits of the three theories (Table 1, 3). Using growth analysis traits,

we identified three strategies primarily defined by the relative allocation between above and belowground biomass (PC1 = 70%; Fig. 1A). When grouped by CSR traits, species distributed among four strategies corresponding to CR, CSR, SR and S. Consistent with previous studies (Pierce *et al.* 2016; Li & Shipley 2017), variation in LS was orthogonal to variation in SLA and LD, with differences among groups driven primarily by variation in average leaf size (LS) (PC1 = 93%; Fig. 1D). For LES traits, species distributed among three strategies primarily defined by variation in  $A_{\text{mass}}$ ,  $A_{\text{area}}$ ,  $P_{\text{area}}$ , and  $N_{\text{area}}$  (PC1 = 51%), and secondarily by leaf  $N_{\text{mass}}$  and  $P_{\text{mass}}$  (PC2 = 30%; Fig. 1G).

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 (Fig. 1J). Consistent with global trait analyses (Diaz *et al.* 2015), the first PC axis (52%) corresponded to plant size-related traits LA, H, LS, biomass fractions (LMF, SMF, RMF) and LD. The second PC axis (19%) corresponded to leaf economic and metabolic traits ( $\delta^{13}\text{C}$ , N, P,  $A_{\text{max}}$ ,  $L_{\text{th}}$ ). 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).

#### *Growth-trait relationships across plant classification schemes*

Across strategies, growth correlated most strongly with the first principal component axis (PC1) of growth analysis ( $R^2 = 0.91$ ,  $P < 0.0001$ , AIC = -90; Fig. 1B), and for all 21 traits combined ( $R^2 = 0.84$ ,  $P < 0.0001$ , AIC = -72; Fig. 1K), driven primarily by variation in LA and H (Table S2). Growth also positively correlated with PC1 of CSR ( $R^2 = 0.49$ ,  $P < 0.0001$ , AIC = -39; Fig. 1E). Growth negatively correlated with PC1 of LES ( $R^2 = 0.29$ ,  $P = 0.001$ , AIC = -29), PC2 of LES ( $R^2 = 0.31$ ,  $P = 0.001$ , AIC = -30), and PC2 of all measured traits ( $R^2 = 0.16$ ,  $P = 0.006$ , AIC = -26). Growth was not predicted by PC2 of GA or CSR (both  $R^2 < 1.0$ ,  $P > 0.05$ ,  $-20 < \text{AIC} < -19$ ; Fig. 1C,F).

## Discussion

Here we bridge classic ecological theory with current trait-based approaches in order 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 LS, SLA and lower LD (based on CSR); or (3) have ‘acquisitive’ leaf traits defined by larger  $A_{\max}$ ,  $R_d$ , N, P, and SLA (based on LES) relative to 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 P per leaf area, contributing to multivariate correlations, Fig. 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 growth rate were driven more by whole-plant (e.g., LA, SMF) than individual leaf-level traits (e.g., SLA), in part because of the contribution of root and stem characteristics that did not scale with individual leaf traits. 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 growth rate, and our study is no exception. Indeed, growth analysis traits together were the strongest predictors of whole-plant growth across a diverse set of 30 milkweed species (Fig. 1B). Although theoretically and empirically appealing, the major shortcoming with growth analysis is feasibility - it is typically not practical to obtain the necessary root mass fraction 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 show 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 (Pierce *et al.* 2016; Dayrell *et al.* 2018; Zanzottera *et al.* 2020) species. In this novel application of CSR to predict plant growth, we found strong growth-trait relationships across species, driven primarily by variation in average leaf size with minimal contributions from LD and SLA (Fig. 1 F, J).

Variation in total leaf area (LA) was by far the strongest and most consistent predictor of plant growth across all species individually ( $R^2 = 0.6$ ; Table 2) and in multivariate plant strategies (associated with PC1; Fig. 1F, H; Table S2). When all 21 traits were considered together, plant height was the second-best predictor of growth (associated with PC1; Fig. 1F, H; Table S2). Specifically, two strategies with similar growth and LA differed in height, suggesting that LA 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 positive correlations with ecosystem productivity and LA (Litton *et al.* 2008; Goud *et al.* 2017) and height (Westoby 1998; Goud *et al.* 2017). Although total leaf area and height are not considered in growth analysis, LES or CSR theories, 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 (Diaz *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 non-destructive sampling (Goud *et al.* 2017; Davidson *et al.* 2021).

## Leaf economics spectrum

The leaf economics spectrum (LES) has gained considerable attention and is often turned to as the primary approach to understand plant functional diversity (Diaz *et al.* 2015). However, the work presented here suggests that LES traits do not predict within-clade differences in plant growth as expected; resource-acquisitive leaf traits negatively correlated 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 growth rate (PC1 and PC2 combining to 60% of the variation, Fig. 1), the fact that these were not in the expected direction and that these traits can be challenging to measure, suggest caution 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.

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 N and P) grew considerably faster than species with the opposite set of resource ‘acquisitive’ traits because these plants were taller and had larger overall LA. Similarly, species with the largest growth had lower foliar N and P and similar rates of leaf gas exchange than other, less productive species.

In contrast to predictions, leaf gas exchange ( $A_{\max}$ ,  $R_d$ ) were not strong predictors of growth (Fig. 1, Table 2). When all 21 traits were considered, the four plant strategies identified had similar average  $A_{\max}$  and  $R_d$ , suggesting that the area available for photosynthesis (i.e., LA, LS) is more important for growth than instantaneous gas exchange rates in this plant group. As an alternative to instantaneous gas exchange rates, we measured leaf carbon isotope composition ( $\delta^{13}\text{C}$ ). Contrary to expectations, the fastest growing plants were the most enriched in  $\delta^{13}\text{C}$ , which is typically associated with slower rates of leaf metabolism (Ellsworth *et al.* 2017; Goud *et al.* 2019). For milkweeds, species achieved faster growth by producing numerous large leaves and tall stems. Together, results for instantaneous leaf-level gas exchange rates and  $\delta^{13}\text{C}$  suggest that the influence of leaf metabolism is often overwhelmed by differences in total plant LA and, therefore, does not consistently scale to whole-plant growth (Agrawal *et al.* 2009; Goud *et al.* 2019).

Both leaf N and P are predicted to positively correlate with growth due to the functional need for N and P in photosynthesis (Wright *et al.* 2004; Walker *et al.* 2014). However, non-linear or insignificant relationships are frequently reported (Midgley *et al.* 2004; Feng & Dietze 2013). Here, growth negatively correlated with leaf N and P (Fig. 1G-I; Table 2), driven by higher N and P content yet lower growth in species from arid environments (e.g., *A. brachystephana*, *A. mexicana*). 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; Wright *et al.* 2001; Maire *et al.* 2015) and can operate at a higher leaf N, with the high leaf N serving to economize water use during photosynthesis (Wright *et al.* 2003; Schrodte *et al.* 2015). 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 tradeoff 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 (Reich *et al.* 1994; Poorter & Evans 1998; Midgley *et al.* 2004). Thus, although SLA may correlate with growth across broadly divergent species, inconsistencies at smaller scales are likely driven by co-variation with other morphological traits (e.g., LD,  $L_{th}$ ) and environmental conditions that are largely independent of growth rate variation (Edwards *et al.* 2014b).

There is increasing interest in whether functional trait correlations generally apply across scales. 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 (Wright *et al.* 2005; Enquist *et al.* 2007; Díaz *et al.* 2015). However, at finer scales (e.g., within-genus, within-habitat, etc.) patterns are far less consistent and sometimes contrary to theory (Grady *et al.* 2013; Blonder *et al.* 2015; Mason & Donovan 2015; Anderegg *et al.* 2018; Agrawal 2020), as we also found here for milkweeds. This is not necessarily surprising, as trait relationships are often only predictive at the largest scales, where both the range of expression and fundamental biological attributes are revealed (Enquist *et al.* 1999; 2007; Anderegg *et al.* 2018; Agrawal 2020).

In this study, size-related anatomical 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 as their relevance as a consistent predictor of growth is likely to be highly clade-specific. Still, the generality of plant size and CSR-related traits (average leaf size, leaf dry matter content, and SLA) appears the most promising across scales. Practically speaking, these traits can be measured inexpensively and non-destructively, facilitating both use from databases and large-scale field sampling.

The species we studied were distributed along multivariate axes defined by traits, including LES, irrespective of variation in growth rate. In other words, plant size may define growth differences, while economics and metabolism may better differentiate between variation in plant ecology and life-history (Goud *et al.* 2019). This 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 (Díaz *et al.* 2015). Indeed, not all ecological strategies are directly related to growth rate. For example, strategies largely defined by secondary metabolism, such as pollination and defense syndromes, focus on traits that often show little direct connection with growth rate (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

400 of plant functional diversity. Evolutionarily conserved traits within clades are an important driver  
401 of differences that promote biodiversity. Ultimately the extent of clade-specificity in which traits  
402 or suites of traits predict growth will be highly revealing, not only in terms of scaling  
403 generalities, but also in terms of clade-specific traits or strategies that modify expectations.  
404

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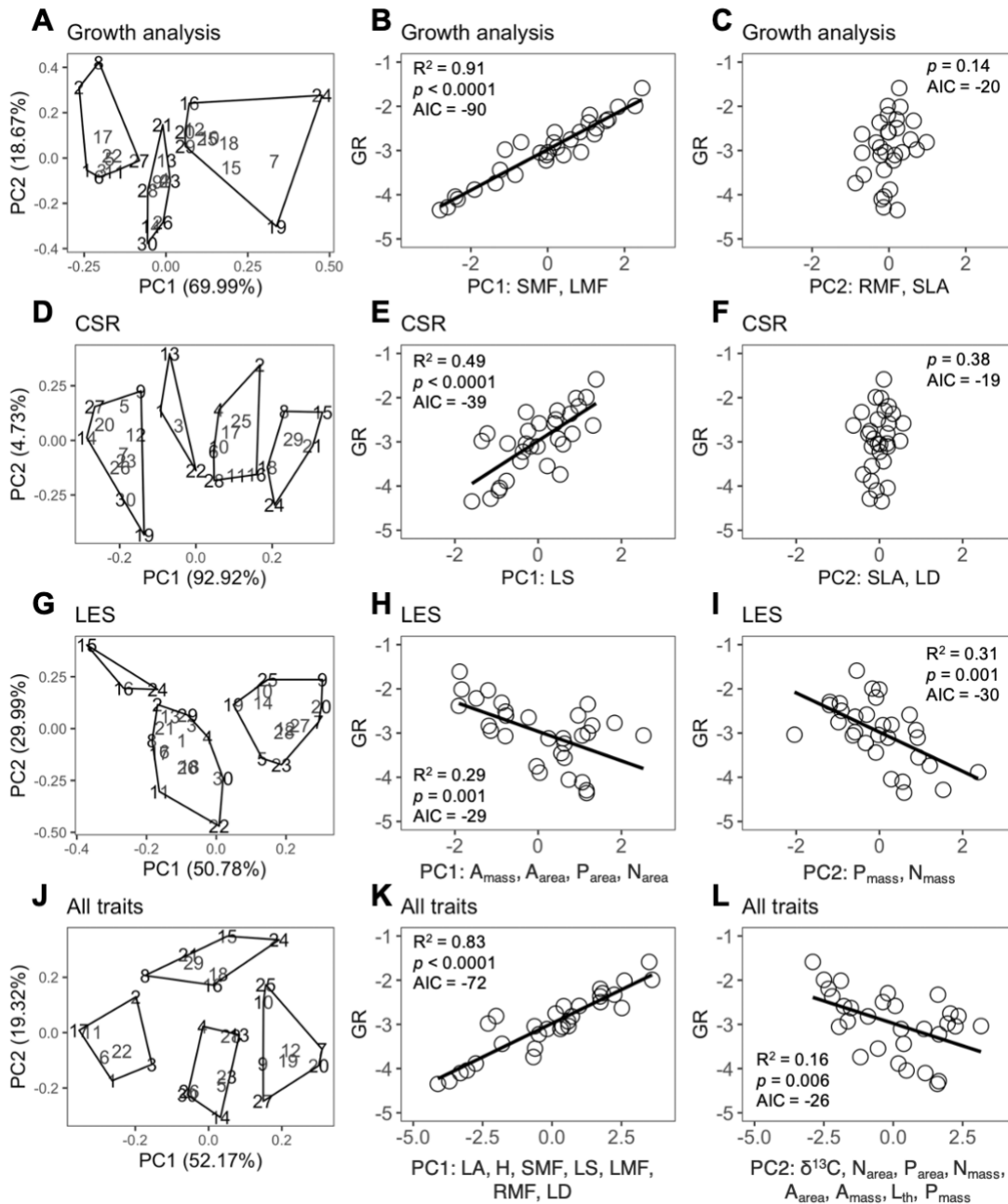
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**Figure 1.** Biplots of principal components analyses (PCA) of 30 *Asclepias* species based on the defining traits of three classic ecological theories: (A) growth analysis, (B) CSR, (C) LES, and (D) 21 measured traits. Species groups are represented as convexes based on Ward's agglomerative clustering defined by trait similarity. (E-H) Correlations between growth rate and PC1, and (I-L) between growth rate and PC2. Variables with the highest eigenvector scores on PC1 and PC2 are presented from left to right for each axis. Data are species means, species names are in Table 3.

**Table 1.** Traits and growth predictions of growth analysis, CSR triangle, and leaf economics spectrum. ‘+’ and ‘-’ indicate positive and negative correlations, respectively.

Strategy Scheme	Traits	Growth predictions
Growth analysis	Leaf mass fraction (LMF)	+
	Stem mass fraction (SMF)	+
	Root mass fraction (RMF)	-
	Specific leaf area (SLA)	+
Competition-Stress tolerant-Ruderal (CSR) triangle	Average leaf size (LS)	+, -
	Leaf dry matter content (LD)	-
	Specific leaf area (SLA)	+
Leaf economics spectrum	Photosynthetic rate ( $A_{\max}$ )	+
	Respiration rate ( $R_d$ )	+
	Specific leaf area (SLA)	+
	Leaf nitrogen content (N)	+
	Leaf phosphorus content (P)	+
	Leaf lifespan	-

**Table 2.** Linear correlations between 21 plant traits and growth rate (GR) using generalized linear models (GLM) and phylogenetic least squares regression (PGLS) for 30 *Asclepias* species grown under common conditions. Sign indicates the direction of the significant correlation (positive, + or negative, -). Phylogenetic signal using Pagel's  $\lambda$  is shown for each trait, with  $P < 0.05$  indicating significant phylogenetic signal.

Trait	Correlations with GR					$\lambda$	$P$
	Sign	GLM		PGLS			
		$R^2$	$P$	$R^2$	$P$		
$\delta^{13}\text{C}$ (carbon isotope ratio, ‰)	+	<b>0.35</b>	<b>0.001</b>	<b>0.36</b>	<b>0.0005</b>	<b>0.70</b>	<b>0.03</b>
H (height, cm)	+	<b>0.47</b>	<b>&lt; 0.0001</b>	<b>0.36</b>	<b>0.0005</b>	<b>0.99</b>	<b>&lt; 0.001</b>
LA (leaf area total, cm <sup>2</sup> )	+	<b>0.56</b>	<b>&lt; 0.0001</b>	<b>0.61</b>	<b>&lt; 0.0001</b>	0.18	0.37
R <sub>d</sub> (leaf dark respiration rate)							
per area (R <sub>area</sub> , μmol m <sup>-2</sup> s <sup>-1</sup> )	n.s	0.02	0.41	0.01	0.67	< 0.001	0.98
per mass (R <sub>mass</sub> , μmol g <sup>-1</sup> s <sup>-1</sup> )	n.s	0.01	0.53	0.004	0.73	<b>0.93</b>	<b>0.003</b>
LD (leaf density, mg g <sup>-1</sup> )	+	<b>0.10</b>	<b>0.05</b>	<b>0.17</b>	<b>0.02</b>	<b>0.64</b>	<b>0.05</b>
LMF (leaf mass fraction, %)	+	<b>0.14</b>	<b>0.04</b>	0.01	0.64	<b>0.92</b>	<b>0.01</b>
N (leaf nitrogen)							
per area (N <sub>area</sub> , gN m <sup>-2</sup> )	-	<b>0.27</b>	<b>0.004</b>	<b>0.20</b>	<b>0.01</b>	0.45	0.29
per mass (N <sub>mass</sub> , gN g <sup>-1</sup> )	-	<b>0.38</b>	<b>0.0003</b>	<b>0.50</b>	<b>&lt; 0.0001</b>	<b>0.97</b>	<b>0.001</b>
P (leaf phosphorus)							
per area (P <sub>area</sub> , gP m <sup>-2</sup> )	-	<b>0.51</b>	<b>&lt; 0.0001</b>	<b>0.55</b>	<b>&lt; 0.0001</b>	0.06	0.72
per mass (P <sub>mass</sub> , gP g <sup>-1</sup> )	-	<b>0.26</b>	<b>0.004</b>	<b>0.19</b>	<b>0.02</b>	0.03	0.88
LS (leaf size average, cm <sup>2</sup> )	+	<b>0.24</b>	<b>0.04</b>	<b>0.31</b>	<b>0.001</b>	< 0.001	0.98
L <sub>th</sub> (leaf thickness, mm)	n.s	0.06	0.20	0.05	0.24	<b>0.74</b>	<b>0.02</b>
A (photosynthetic rate)							
per area (A <sub>area</sub> , μmol m <sup>-2</sup> s <sup>-1</sup> )	+	<b>0.23</b>	<b>0.008</b>	<b>0.32</b>	<b>0.001</b>	0.49	0.97
per mass (A <sub>mass</sub> , μmol g <sup>-1</sup> s <sup>-1</sup> )	+	0.03	0.34	<b>0.19</b>	<b>0.01</b>	0.70	0.20
Root clonality (# of buds)	n.s	0.01	0.73	0.03	0.34	< 0.001	0.98
RMF (root mass fraction, %)	n.s	0.08	0.13	0.01	0.67	0.50	0.17
SM (seed mass, g)	n.s	0.01	0.63	0.04	0.30	<b>0.99</b>	<b>0.001</b>
SLA (specific leaf area, cm <sup>2</sup> g <sup>-1</sup> )	n.s	0.001	0.88	0.01	0.96	< 0.001	0.98
SRL (specific root length, cm <sup>2</sup> mg <sup>-1</sup> )	n.s	0.05	0.25	0.06	0.19	< 0.001	0.98
SMF (stem mass fraction, %)	+	<b>0.36</b>	<b>0.0004</b>	<b>0.17</b>	<b>0.02</b>	<b>0.95</b>	<b>&lt; 0.001</b>

**Table 3.** Average growth rate (GR, g d<sup>-1</sup>) and strategic classifications for 30 *Asclepias* species grown under common conditions. Species are in order by increasing GR. Growth analysis (GA) strategies are 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 are defined as resource acquisitive or conservative. Strategies identified by comparing all 21 measured traits are defined by relative plant size (small, medium, large) and predominant biomass fraction (root, stem, leaf).

			Strategy			
	Species	GR	GA	CSR	LES	All traits
17	<i>A. longifolia</i>	0.013	root	SR	acq/cons	small, root
11	<i>A. hirtella</i>	0.014	root	SR	acq/cons	small, root
6	<i>A. cryptoceras</i>	0.017	root	SR	acq/cons	small, root
1	<i>A. amplexicaulis</i>	0.018	root	CSR	acq/cons	small, root
22	<i>A. solanoana</i>	0.021	root	CSR	acq/cons	small, root
30	<i>A. viridis</i>	0.024	leaf	CR	acq/cons	medium, leaf
26	<i>A. sullivantii</i>	0.029	leaf	CR	acq/cons	medium, leaf
3	<i>A. asperula</i>	0.032	root	CSR	acq/cons	small, root
29	<i>A. verticillata</i>	0.040	stem	S	acq/cons	medium, stem
4	<i>A. brachystephana</i>	0.045	leaf	SR	acq/cons	medium, leaf
18	<i>A. mexicana</i>	0.045	stem	S	acq/cons	medium, stem
14	<i>A. latifolia</i>	0.047	leaf	CR	conservative	medium, leaf
21	<i>A. pumila</i>	0.048	leaf	S	acquisitive	medium, stem
15	<i>A. linaria</i>	0.048	leaf	S	acq/cons	medium, stem
2	<i>A. arenaria</i>	0.051	root	SR	acq/cons	small, root
23	<i>A. speciosa</i>	0.053	leaf	CR	conservative	medium, leaf
28	<i>A. tuberosa</i>	0.060	leaf	S	acq/cons	medium, leaf
8	<i>A. engelmanniana</i>	0.060	root	SR	conservative	medium, stem
16	<i>A. linearis</i>	0.064	stem	SR	acquisitive	medium, stem
19	<i>A. perennis</i>	0.072	stem	CR	conservative	large, leaf & stem
5	<i>A. californica</i>	0.075	leaf	CR	conservative	medium, leaf
13	<i>A. labriformis</i>	0.076	leaf	CSR	acq/cons	medium, leaf
10	<i>A. fascicularia</i>	0.082	stem	SR	conservative	large, leaf & stem
9	<i>A. eriocarpa</i>	0.094	leaf	CR	conservative	large, leaf & stem
24	<i>A. subulata</i>	0.098	stem	S	acquisitive	medium, stem
25	<i>A. subverticillata</i>	0.101	stem	SR	conservative	large, leaf & stem
27	<i>A. syriaca</i>	0.111	leaf	CR	conservative	large, leaf & stem
12	<i>A. incarnata</i> ssp. <i>incarnata</i>	0.134	stem	CR	conservative	large, leaf & stem
7	<i>A. curassavica</i>	0.136	stem	CR	conservative	large, leaf & stem
20	<i>A. incarnata</i> ssp. <i>pulchra</i>	0.205	stem	CR	conservative	large, leaf & stem