

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

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## Article

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1 **Title**

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3 growth

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13  
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15 plant ecology, plant strategies

16  
17 **Abstract**

18  
19 Despite long-standing theory for classifying plant ecological strategies, limited data directly links  
20 organismal traits to whole-plant growth. We compared trait-growth relationships based on three  
21 prominent theories: growth analysis, Grime's CSR triangle, and the leaf economics spectrum  
22 (LES). Under these schemes, growth is hypothesized to be predicted by traits related to biomass  
23 investments, leaf structure or gas exchange, respectively. In phylogenetic analyses of 30 diverse  
24 milkweeds (*Asclepias* spp.) and 21 morphological and ecophysiological traits, growth rate varied  
25 50-fold and was best predicted by growth analysis and CSR traits, as well as total leaf area and  
26 plant height. Despite two LES traits correlating with growth, they contradicted predictions and  
27 leaf traits did not scale with root and stem characteristics. Thus, although combining leaf traits  
28 and whole-plant allocation best predicts growth, when destructive measures are not feasible, we  
29 suggest total leaf area and plant height, or easy-to-measure traits associated with the CSR  
30 classification.

31

32 Predicting variation in plant growth is a long-standing problem in ecology. Because plants  
33 largely determine ecosystem productivity, estimating current and future plant growth is  
34 increasingly relevant as global change drivers impact ecosystem services <sup>1,2</sup>. As it is typically  
35 impractical to measure the total vegetative biomass of a community or ecosystem, an emerging  
36 method is to apply plant traits to predict growth rate. These trait-based approaches take  
37 advantage of a large body of literature that analyzes co-variation and trade-offs among plant  
38 traits <sup>3-6</sup>. Given that morphological and physiological characters are central to resource  
39 acquisition and allocation, they are likely to shape plant productivity in predictable ways.

40  
41 Three classic approaches have attempted to distill plant diversity into cohesive strategies and  
42 estimate growth based on defining characteristics: growth analysis, Grime's CSR triangle, and  
43 the leaf economics spectrum (Table 1). In growth analysis, growth rate is predicted by the  
44 relative allocation of biomass among roots, stems, and leaves <sup>3,7</sup>. Faster growing plants are  
45 expected to invest more in leaves relative to stems and roots. Due to the importance of leaf  
46 investment, growth rates are additionally dependent on specific leaf area (SLA), the ratio of leaf  
47 area to dry mass. Grime's CSR (competition-stress tolerant-ruderal) framework predicts that  
48 these three plant strategies have repeatedly evolved in response to combinations of stress and  
49 disturbance <sup>8</sup>. Until recently, the CSR framework was conceptual rather than empirically trait-  
50 based. However, Pierce *et al.* 2016 showed that three leaf traits were predictive of the scheme:  
51 average leaf surface area (individual leaf size, LS), SLA, and leaf dry matter content (LD). In  
52 this context, the C-strategy is defined by large LS and intermediate LD and SLA. The S-strategy  
53 has small LS and SLA with large LD, and R-strategy has small LS, small LD and large SLA <sup>9</sup>.

54  
55 The most commonly applied trait-based framework is the leaf economics spectrum, which  
56 describes patterns of co-variation among six leaf traits: leaf lifespan, SLA, leaf nitrogen (N) and  
57 phosphorus (P) contents, rates of light-saturated photosynthesis ( $A_{max}$ ) and dark respiration ( $R_d$ ).  
58 Together, these traits represent the return on investment of fixed carbon at the leaf-level <sup>4,10</sup>. On  
59 one end of the spectrum is a 'resource-acquisitive' strategy with short leaf lifespan and larger  
60 SLA, N, P,  $A_{max}$ , and  $R_d$ . On the other end is a 'resource-conservative' strategy with the opposite  
61 combination of trait values. It is generally predicted that plants with resource-acquisitive leaf  
62 traits have relatively faster growth rates than those with resource-conservative leaves <sup>10</sup>. As such,  
63 leaf economics traits have been applied to predict growth at genotypic, community, ecosystem,  
64 and global scales, often using a subset of traits as direct proxies for plant growth <sup>11,12</sup>.

65  
66 Despite the intuitive appeal of these theories, experiments that directly use traits to predict  
67 whole-plant growth are surprisingly limited. Studies to date show mixed results, including  
68 significant <sup>13</sup> and non-significant <sup>14</sup> trait-growth rate relationships. Inconsistent results could be  
69 influenced by environmental variation <sup>15,16</sup>, species interactions <sup>13</sup>, or because studies compare  
70 plants at different scales - from broadly divergent taxonomic and functional groups at the  
71 community scale, to closely related plants within a clade, to among plant individuals within a  
72 species <sup>17,18</sup>.

73  
74 In an effort to link these theoretical frameworks to observed growth rate, we simultaneously  
75 tested these growth-trait predictions (Table 1) using a diverse set of closely related species in a  
76 multivariate phylogenetic analysis. We measured 21 traits: leaf, stem and root biomass fractions  
77 (LMF, SMF, RMF) and SLA for growth analysis, CSR-associated traits (LS, LD, SLA), and leaf

78 economic spectrum traits ( $A_{\max}$ ,  $R_d$ ,  $N$ ,  $P$ ,  $SLA$ ). We included six traits that we expected to be  
79 predictors of plant growth but are not used in any of the three approaches: total leaf area ( $LA$ ),  
80 leaf thickness ( $L_{th}$ ), leaf carbon isotope ratio ( $\delta^{13}C$ ), specific root length ( $SRL$ ), root clonality,  
81 seed mass ( $SM$ ), and plant height ( $H$ ). Growing species from the same genus under controlled,  
82 common resource conditions in a growth chamber allowed us to compare growth rates and traits  
83 of interest within a similar functional group (i.e., all  $C_3$ , diploid, herbaceous, and perennial) that  
84 share a recent common ancestor, and yet display large variation in growth, habitat affinities, and  
85 traits.

## 86 **Materials and methods**

### 87 *Study system and plant growth conditions*

88  
89 We assessed growth-trait relationships across 30 closely related yet functionally diverse  
90 milkweed species. Milkweeds (*Asclepias* spp., Apocynaceae) are herbaceous perennials that  
91 display remarkable variation in morphology, ranging from desert subshrubs with small, narrow  
92 leaves (e.g., *A. linaria*, *A. subulata*) to large, highly productive plants of temperate and  
93 subtropical wetlands with large, broad leaves (e.g., *A. curassavica*, *A. incarnata*)<sup>19</sup>. Milkweeds  
94 vary widely in growth rate and traits when grown under common garden conditions<sup>14,20</sup>. Seeds  
95 collected by colleagues or purchased from native plant suppliers were germinated by moistening  
96 and stratifying at 4°C for at least 10 days and then at 28°C for 3 days. Seedlings were planted in  
97 500 ml plastic pots and grown in Metro Mix soil (Scotts-Sierra, Marysville, OH, USA) in a  
98 walk-in growth chamber (Convion CMP 6050) for 6 weeks at 26°C during a 14-hour day and  
99 24°C during a 10-hour night with an average relative humidity of 50%.

### 100 *Trait and biomass measurements*

101  
102 We sampled five replicate plants per species for trait and growth measurements. Seed mass ( $SM$ )  
103 was calculated before germination by dividing the total seed mass (g) by the number of seeds  
104 used for germination ( $n=30$  per species). We measured leaf gas exchange rates using a LI-COR  
105 LI-6400 CO<sub>2</sub> gas exchange analyzer (LI-COR, Lincoln, NE) on one fully expanded leaf per plant  
106 at 36 - 41 days old. We generated light response curves to obtain the light intensity  
107 (photosynthetically active radiation, PAR, spanning 0 - 2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) at which  
108 photosynthesis saturated ( $A_{\max}$ ). Leaf dark respiration ( $R_d$ ) was measured at a PAR of zero. Leaf  
109 humidity inside the cuvette was maintained between 45-60%, and the block temperature was  
110 maintained at 25°C.

111  
112  
113 At the time of harvest, the height of each plant was measured ( $H$ , cm), total leaf number was  
114 recorded, leaves were removed from the stems, and roots were separated and washed to remove  
115 soil. For each individual, total leaf area ( $LA$ ) was measured using a LI-COR LI-3100 leaf-area  
116 meter (LI-COR, Lincoln, NE). Specific root length ( $SRL$ ) was measured as the ratio of root  
117 length (cm) to dry mass using subsamples of lateral roots ( $n= 10$  per plant). Root clonality was  
118 measured as the number of buds on roots, rhizomes and caudices of each plant<sup>21</sup>. After fresh  
119 weight measurements of leaves, stems, and roots, samples were oven-dried at 60°C for 48 hours  
120 and measured for dry mass (g). Average leaf area (leaf size,  $LS$ ) was calculated by dividing  $LA$   
121 by the total number of leaves. Specific leaf area ( $SLA$ ) was measured as  $LA$  divided by total  
122 oven-dried leaf mass (g). Leaf density ( $LD$ ) was measured as oven-dry leaf mass (mg), divided  
123 by water-saturated fresh mass (g). Leaf thickness ( $L_{th}$ ) was estimated as  $SLA * LD$ <sup>22</sup>.

124  
125 Carbon isotope ratios and N percent element of leaf material was measured using a continuous  
126 flow isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an  
127 elemental analyzer (Carlo Erba NC2500). Isotope ratios are expressed as  $\delta$  values (per mil):

$$128 \delta^{13}\text{C} = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1) \times 1000 (\text{‰})$$

129  
130 where  $\text{R}_{\text{sample}}$  and  $\text{R}_{\text{standard}}$  are the ratios of heavy isotope to light isotope of the sample relative to  
131 Vienna-Pee-Dee Belemnite, the international standard for C. Mass spectrometry and elemental  
132 analyses were performed at the Cornell University Stable Isotope Laboratory. Leaf P content was  
133 measured by dry ash analysis at the Cornell Nutrient Analysis Laboratory. Leaf N and P were  
134 calculated on both a leaf dry mass and leaf area basis.

135  
136 Plant growth can be defined and measured in various ways, including relative growth (RGR) and  
137 absolute growth rate (GR, the total oven-dried biomass accrued over the number of days from  
138 seedling emergence until the end of the experiment in  $\text{g d}^{-1}$ ). RGR requires multiple harvests and  
139 can often constrain replication<sup>7</sup>. We found a robust correlation between RGR and GR ( $R^2 =$   
140  $0.97$ ,  $p < 0.001$ ) for four milkweed species that represented the range of functional variation  
141 across the 30 species: *A. curassavica*, *A. incarnata*, *A. pumila*, *A. verticillata*. Therefore, we used  
142 GR for the purpose of this broader study.

#### 143 144 *Statistical analyses*

145 We assessed the relative ability of each trait to predict growth using generalized linear models  
146 (GLM), and tested for potential effects of shared evolutionary history using phylogenetic  
147 generalized least squares (PGLS) regressions using the ‘ppls’ function of the caper package in R  
148<sup>23</sup>. A maximum likelihood phylogeny of 111 *Asclepias* species was pruned with the retention of  
149 branch lengths to create a phylogram for the 30 species (Figure S1). Briefly, the phylogeny was  
150 estimated from three non-coding plastid genome regions: *rpl16* intron, *trnC<sup>GCA</sup>–rpoB* intergenic  
151 spacer, and the contiguous *trnS<sup>GCU</sup>–trnG<sup>UUC</sup>* intergenic spacer/*trnG<sup>UUC</sup>* intron<sup>24</sup>. We estimated  
152 the phylogenetic signal of growth rate and all traits by calculating Pagel’s  $\lambda$  using the ‘phylosig’  
153 function in the picante R-package<sup>25</sup>. We included the standard error of the mean for each  
154 variable. A  $\lambda$ -value of 1 indicates that trait similarity among species is directly proportional to  
155 the extent of shared evolutionary history, while a  $\lambda$ -value = 0 indicates no relationship between  
156 shared ancestry and trait values. For the PGLS analyses, linear regression parameters were  
157 estimated from a  $\lambda=1$  model.

158  
159 We used Ward’s agglomerative clustering and principal components analysis using the ‘vegan’  
160 R-package<sup>26</sup> to classify the 30 species into distinct groups, hereafter referred to as ‘strategies’.  
161 We grouped species based on (1) growth analysis traits, (2) CSR traits, (3) LES traits, and (4) all  
162 21 measured traits. We then used Kendall’s coefficient of concordance (999 permutations) to  
163 identify how many strategies identified by Ward’s clustering were significantly distinct and  
164 which species were significantly contributing to each strategy<sup>27</sup>. We also classified species using  
165 the CSR method outlined in Pierce *et al.* 2016, where ratios of C:S:R values were calculated  
166 based on LS, LD, and SLA for each species. We used linear regression to assess relationships  
167 between GR and the first two principal components axes for each strategy scheme. Linear  
168

169 regression models were directly compared by Akaike information criterion (AIC). All analyses  
170 were performed in R3.5.3 <sup>28</sup>.

## 171 172 **Results**

### 173 174 *Growth-trait relationships across species*

175 Across 30 milkweed species, individual plant growth ranged over 50-fold, from 0.005 g d<sup>-1</sup> to  
176 0.258 g d<sup>-1</sup> (Table S1). Overall, in phylogenetically controlled analyses (PGLS), three traits each  
177 explained over 50% of the variation in growth among the 30 *Asclepias* species (total leaf area,  
178 nitrogen content on a mass basis, and phosphorus content on an area basis). In total, growth rate  
179 positively correlated with  $\delta^{13}\text{C}$ , H, LA, LD, LMF, LS, area-based photosynthetic rate ( $A_{\text{area}}$ ) and  
180 SMF and negatively correlated with leaf N and P (analyses and abbreviations in Table 2).

181 Growth did not correlate with  $R_d$  (per mass or per area),  $L_{\text{th}}$ , mass-based photosynthetic rate  
182 ( $A_{\text{mass}}$ ), root clonality, RMF, SM, SLA, or SRL. Accounting for shared evolutionary history did  
183 not change the relationships, with the exception of LMF (not significant in PGLS) and  $A_{\text{mass}}$   
184 (became significant in PGLS). Nine of the 21 traits showed phylogenetic signal ( $\lambda$ -value > 0.70,  
185  $P < 0.05$ ):  $\delta^{13}\text{C}$ , H,  $R_{\text{mass}}$ , LD, LMF,  $N_{\text{mass}}$ ,  $L_{\text{th}}$ , SM, and SMF (Table 2).

### 186 187 *Plant strategies*

188 In order to assess growth-trait relationships at the level of plant strategies, we classified species  
189 into groups using diagnostic traits of the three theories (Table 1, 3). Using growth analysis traits,  
190 we identified three strategies primarily defined by the relative allocation between above and  
191 belowground biomass (PC1 = 70%; Fig. 1A). When grouped by CSR traits, species distributed  
192 among four strategies corresponding to CR, CSR, SR and S. Consistent with previous studies <sup>9,29</sup>,  
193 variation in LS was orthogonal to variation in SLA and LD, with differences among groups  
194 driven primarily by variation in average leaf size (LS) (PC1 = 93%; Fig. 1D). For LES traits,  
195 species distributed among three strategies primarily defined by variation in  $A_{\text{mass}}$ ,  $A_{\text{area}}$ ,  $P_{\text{area}}$ , and  
196  $N_{\text{area}}$  (PC1 = 51%), and secondarily by leaf  $N_{\text{mass}}$  and  $P_{\text{mass}}$  (PC2 = 30%; Fig. 1G).

197  
198 In addition to these well-established schemes, we classified species using all 21 traits measured  
199 in this study. Using this approach, the 30 species distributed among four groups (Fig. 1J).  
200 Consistent with global trait analyses <sup>5</sup>, the first PC axis (52%) corresponded to plant size-related  
201 traits LA, H, LS, biomass fractions (LMF, SMF, RMF) and LD. The second PC axis (19%)  
202 corresponded to leaf economic and metabolic traits ( $\delta^{13}\text{C}$ , N, P,  $A_{\text{max}}$ ,  $L_{\text{th}}$ ). We describe the four  
203 strategies identified from all measured traits by their overall plant size (small, medium, large)  
204 and primary biomass allocation (roots, leaves, stems).

### 205 206 *Growth-trait relationships across plant classification schemes*

207 Across strategies, growth correlated most strongly with the first principal component axis (PC1)  
208 of growth analysis ( $R^2 = 0.91$ ,  $P < 0.0001$ , AIC = -90; Fig. 1B), and for all 21 traits combined ( $R^2$   
209 = 0.84,  $P < 0.0001$ , AIC = -72; Fig. 1K), driven primarily by variation in LA and H (Table S2).  
210 Growth also positively correlated with PC1 of CSR ( $R^2 = 0.49$ ,  $P < 0.0001$ , AIC = -39; Fig. 1E).  
211 Growth negatively correlated with PC1 of LES ( $R^2 = 0.29$ ,  $P = 0.001$ , AIC = -29), PC2 of LES  
212 ( $R^2 = 0.31$ ,  $P = 0.001$ , AIC = -30), and PC2 of all measured traits ( $R^2 = 0.16$ ,  $P = 0.006$ , AIC = -  
213 26). Growth was not predicted by PC2 of GA or CSR (both  $R^2 < 1.0$ ,  $P > 0.05$ ,  $-20 < \text{AIC} < -19$ ;  
214 Fig. 1C,F).

## 215 Discussion

216

217 Here we bridge classic ecological theory with current trait-based approaches in order to better  
218 predict whole-plant growth from functional traits. We tested predictions that faster growing plant  
219 species will (1) allocate more biomass to aboveground tissues (based on growth analysis); (2)  
220 have larger LS, SLA and lower LD (based on CSR); or (3) have ‘acquisitive’ leaf traits defined  
221 by larger  $A_{\max}$ ,  $R_d$ , N, P, and SLA (based on LES) relative to slower growing plants. The results  
222 supported predictions of growth analysis and CSR, but not LES. Remarkably, although two LES  
223 traits did have strong predictive power (N per leaf mass and P per leaf area, contributing to  
224 multivariate correlations, Fig. 1), these traits were predictive in the opposite direction to that  
225 derived from LES theory such that more N and P predicted less growth. Overall, differences in  
226 growth rate were driven more by whole-plant (e.g., LA, SMF) than individual leaf-level traits  
227 (e.g., SLA), in part because of the contribution of root and stem characteristics that did not scale  
228 with individual leaf traits. Combining organ-specific and whole-plant traits provided a more  
229 integrated view of plant strategies that was better able to predict growth.

230

231 For decades, plant mass fractions have been successfully applied to estimate variation in growth  
232 rate, and our study is no exception. Indeed, growth analysis traits together were the strongest  
233 predictors of whole-plant growth across a diverse set of 30 milkweed species (Fig. 1B). Although  
234 theoretically and empirically appealing, the major shortcoming with growth analysis is feasibility  
235 - it is typically not practical to obtain the necessary root mass fraction that is critical for growth  
236 analysis. Alternatively, the CSR triangle has been a classic predictor of plant strategic variation  
237 for decades, but quantitative metrics were not developed until recently<sup>9</sup>. Recent studies show  
238 promising applications of CSR defined by leaf traits to better describe functional diversity<sup>30</sup> and  
239 species interactions<sup>31</sup> within<sup>32,33</sup> and across<sup>9,30,31</sup> species. In this novel application of CSR to  
240 predict plant growth, we found strong growth-trait relationships across species, driven primarily  
241 by variation in average leaf size with minimal contributions from LD and SLA (Fig. 1 F, J).

242

243 Variation in total leaf area (LA) was by far the strongest and most consistent predictor of plant  
244 growth across all species individually ( $R^2 = 0.6$ ; Table 2) and in multivariate plant strategies  
245 (associated with PC1; Fig. 1F, H; Table S2). When all 21 traits were considered together, plant  
246 height was the second-best predictor of growth (associated with PC1; Fig. 1F, H; Table S2).  
247 Specifically, two strategies with similar growth and LA differed in height, suggesting that LA  
248 may be most predictive for plants that invest primarily in photosynthesizing leaf biomass, while  
249 plant height may be most effective for plants investing in more structural stem biomass. These  
250 results are consistent with positive correlations with ecosystem productivity and LA<sup>34,35</sup> and  
251 height<sup>35,36</sup>. Although total leaf area and height are not considered in growth analysis, LES or  
252 CSR theories, height is a key component of plant size and has been used to differentiate among  
253 plant functional diversity and ecological strategies at local<sup>36</sup> and global scales<sup>5</sup>. Importantly, LA  
254 and height can be remotely sensed, which is particularly useful where it is not feasible to directly  
255 measure traits for all individuals (e.g., forest canopies) or for repeated measurements that require  
256 non-destructive sampling<sup>35,37</sup>.

257

258 *Leaf economics spectrum*

259

260 The leaf economics spectrum (LES) has gained considerable attention and is often turned to as  
261 the primary approach to understand plant functional diversity<sup>5</sup>. However, the work presented  
262 here suggests that LES traits do not predict within-clade differences in plant growth as expected;  
263 resource-acquisitive leaf traits negatively correlated with growth and SLA was not predictive of  
264 growth at the scales that we investigated. We note that although our multivariate analysis of five  
265 out of six LES traits yielded strong predictive power for growth rate (PC1 and PC2 combining to  
266 60% of the variation, Fig. 1), the fact that these were not in the expected direction and that these  
267 traits can be challenging to measure, suggest caution in using the LES framework to predict  
268 growth within clades. The best application of LES traits to predict growth may be in comparing  
269 broadly divergent plant groups (e.g., angiosperms vs gymnosperms), rather than being  
270 generalizable across all scales of biological organization.

271  
272 Species groups identified by LES traits did not adhere to a linear spectrum of increasing leaf  
273 economics or nutrient concentrations with increasing growth. Rather, each multivariate grouping  
274 expressed a mixture of ‘acquisitive’ and ‘conservative’ trait values. For example, some plants  
275 with resource ‘conservative’ leaves (e.g., small, thick leaves with low N and P) grew  
276 considerably faster than species with the opposite set of resource ‘acquisitive’ traits because  
277 these plants were taller and had larger overall LA. Similarly, species with the largest growth had  
278 lower foliar N and P and similar rates of leaf gas exchange than other, less productive species.

279  
280 In contrast to predictions, leaf gas exchange ( $A_{\max}$ ,  $R_d$ ) were not strong predictors of growth (Fig.  
281 1, Table 2). When all 21 traits were considered, the four plant strategies identified had similar  
282 average  $A_{\max}$  and  $R_d$ , suggesting that the area available for photosynthesis (i.e., LA, LS) is more  
283 important for growth than instantaneous gas exchange rates in this plant group. As an alternative  
284 to instantaneous gas exchange rates, we measured leaf carbon isotope composition ( $\delta^{13}\text{C}$ ).  
285 Contrary to expectations, the fastest growing plants were the most enriched in  $\delta^{13}\text{C}$ , which is  
286 typically associated with slower rates of leaf metabolism<sup>14,38</sup>. For milkweeds, species achieved  
287 faster growth by producing numerous large leaves and tall stems. Together, results for  
288 instantaneous leaf-level gas exchange rates and  $\delta^{13}\text{C}$  suggest that the influence of leaf  
289 metabolism is often overwhelmed by differences in total plant LA and, therefore, does not  
290 consistently scale to whole-plant growth<sup>14,20</sup>.

291  
292 Both leaf N and P are predicted to positively correlate with growth due to the functional need for  
293 N and P in photosynthesis<sup>4,39</sup>. However, non-linear or insignificant relationships are frequently  
294 reported<sup>40,41</sup>. Here, growth negatively correlated with leaf N and P (Fig. 1G-I; Table 2), driven  
295 by higher N and P content yet lower growth in species from arid environments (e.g., *A.*  
296 *brachystephana*, *A. mexicana*). Higher leaf N without an accompanying increase in  
297 photosynthesis and growth is common for many plants from dry or high irradiance environments  
298 that retain leaf N and P<sup>16,42,43</sup> and can operate at a higher leaf N, with the high leaf N serving to  
299 economize water use during photosynthesis<sup>44,45</sup>. Further, not all N is used for photosynthesis,  
300 and recent estimates indicate that herbaceous plants may invest less than 50% of their leaf N to  
301 photosynthesis, with the remaining N invested in compounds that support structural and  
302 defensive functions<sup>46</sup>. Thus, positive linear relationships between leaf N, P and growth are  
303 clearly not universal.

304  
305 ***Synthesis and speculation***

306  
307 Although SLA is a component of all three theories, and one of the most commonly reported plant  
308 functional traits, growth did not correlate with SLA across species or strategies. SLA represents  
309 the investment in leaf area per unit leaf mass, reflecting a potential tradeoff between productivity  
310 (i.e., area available for carbon capture), and structural investment (i.e., mass of proteins,  
311 carbohydrates, and cell walls). Inconsistent or insignificant correlations between SLA and  
312 growth or growth proxies (e.g., leaf gas exchange) are commonly reported<sup>40,47,48</sup>. Thus, although  
313 SLA may correlate with growth across broadly divergent species, inconsistencies at smaller  
314 scales are likely driven by co-variation with other morphological traits (e.g., LD, L<sub>th</sub>) and  
315 environmental conditions that are largely independent of growth rate variation<sup>17</sup>.

316  
317 There is increasing interest in whether functional trait correlations generally apply across scales.  
318 Particularly for LES traits, an emerging literature has considered cross-scale relationships. At  
319 large taxonomic (e.g., from *Arabidopsis* to *Sequoia*) and spatial (e.g., cross-continental  
320 ecosystems) scales, patterns of LES trait covariation appear strong and relatively consistent<sup>5,6,15</sup>.  
321 However, at finer scales (e.g., within-genus, within-habitat, etc.) patterns are far less consistent  
322 and sometimes contrary to theory<sup>11,12,49-51</sup>, as we also found here for milkweeds. This is not  
323 necessarily surprising, as trait relationships are often only predictive at the largest scales, where  
324 both the range of expression and fundamental biological attributes are revealed<sup>6,50-52</sup>.

325  
326 In this study, size-related anatomical traits consistently predicted whole-plant growth, while leaf  
327 economic and metabolic traits did not. Although we found specific traits to be predictive of  
328 growth, we caution against using single traits as their relevance as a consistent predictor of  
329 growth is likely to be highly clade-specific. Still, the generality of plant size and CSR-related  
330 traits (average leaf size, leaf dry matter content, and SLA) appears the most promising across  
331 scales. Practically speaking, these traits can be measured inexpensively and non-destructively,  
332 facilitating both use from databases and large-scale field sampling.

333  
334 The species we studied were distributed along multivariate axes defined by traits, including LES,  
335 irrespective of variation in growth rate. In other words, plant size may define growth differences,  
336 while economics and metabolism may better differentiate between variation in plant ecology and  
337 life-history (Goud *et al.* 2019). This is consistent with global analyses that found diversity in  
338 plant form and function to fall along two major axes of variation related to plant size and leaf  
339 economics<sup>5</sup>. Indeed, not all ecological strategies are directly related to growth rate. For example,  
340 strategies largely defined by secondary metabolism, such as pollination and defense syndromes,  
341 focus on traits that often show little direct connection with grow rate (e.g., flower color, toxic  
342 secondary compounds). Therefore, although some traits, and LES traits in particular, may not  
343 predict variation in growth as expected, they do capture other important axes of plant functional  
344 diversity. Evolutionarily conserved traits within clades are an important driver of differences that  
345 promote biodiversity. Ultimately the extent of clade-specificity in which traits or suites of traits  
346 predict growth will be highly revealing, not only in terms of scaling generalities, but also in  
347 terms of clade-specific traits or strategies that modify expectations.

348  
349

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351  
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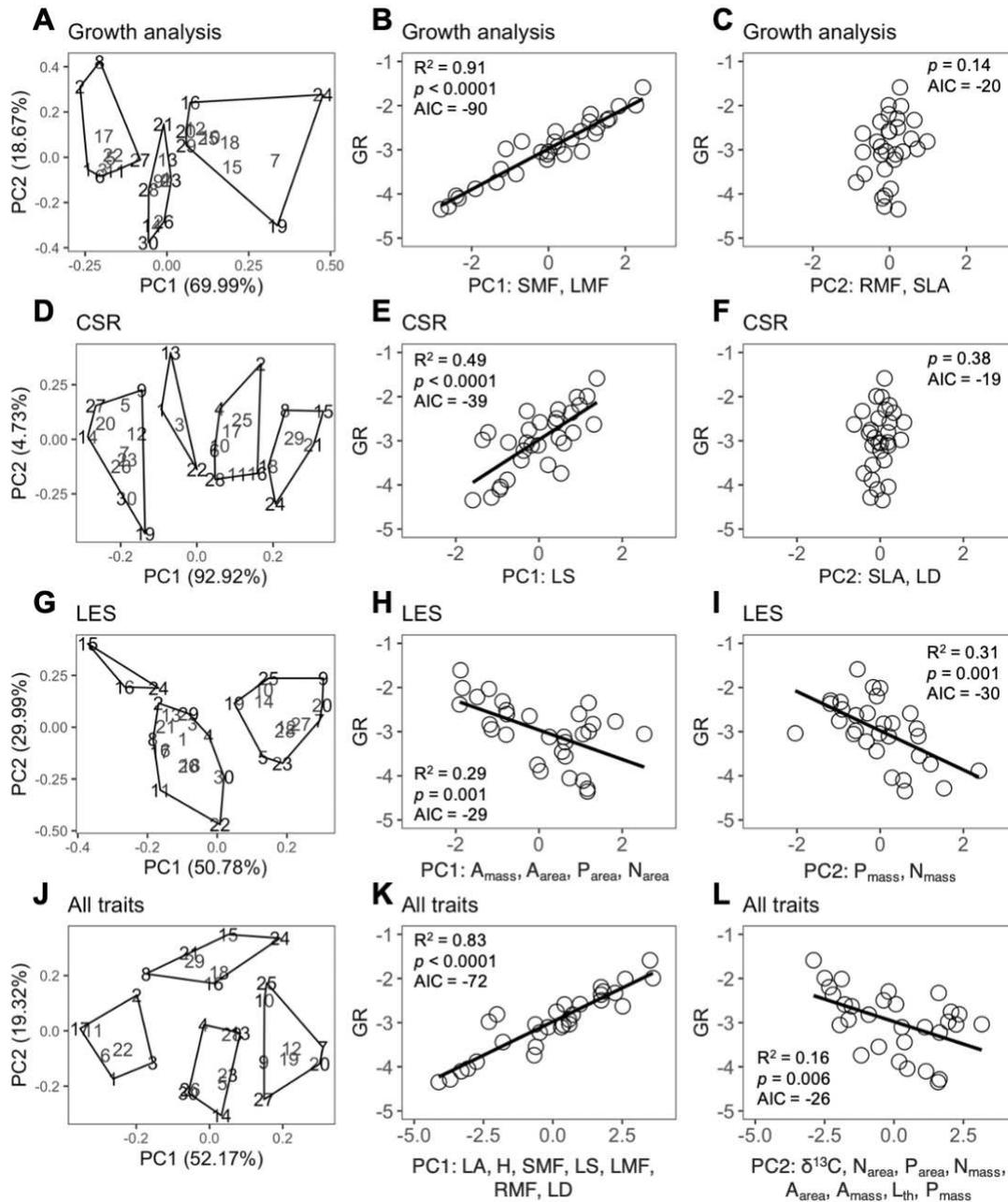
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359 *Statement of authorship:* EMG, AAA, and JPS conceived of the research idea and wrote the  
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362 **References**

- 363  
364 1. Helbig, M. *et al.* Direct and indirect climate change effects on carbon dioxide fluxes in a  
365 thawing boreal forest-wetland landscape. *Global Change Biology* **23**, 3231–3248 (2017).  
366 2. Arndt, K. A. *et al.* Arctic greening associated with lengthening growing seasons in  
367 Northern Alaska. *Environ. Res. Lett.* **14**, 125018 (2019).  
368 3. Lambers, H. & Poorter, H. in *Advances in Ecological Research Volume 23* **23**, 187–261  
369 (Elsevier, 1992).  
370 4. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004).  
371 5. Diaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167–171  
372 (2015).  
373 6. Enquist, B. J. *et al.* A general integrative model for scaling plant growth, carbon flux, and  
374 functional trait spectra. *Nature* **449**, 218–222 (2007).  
375 7. Evans, G. C. *The quantitative analysis of plant growth*. **1**, (Univ of California Press,  
376 1972).  
377 8. Grime, J. P. Evidence for the Existence of Three Primary Strategies in Plants and Its  
378 Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**, 1169–  
379 1194 (1977).  
380 9. Pierce, S. *et al.* A global method for calculating plant CSR ecological strategies applied  
381 across biomes world-wide. *Funct Ecol* **31**, 444–457 (2016).  
382 10. Reich, P. B. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J*  
383 *Ecol* **102**, 275–301 (2014).  
384 11. Grady, K. C. *et al.* Conservative leaf economic traits correlate with fast growth of  
385 genotypes of a foundation riparian species near the thermal maximum extent of its  
386 geographic range. *Funct Ecol* **27**, 428–438 (2013).  
387 12. Blonder, B. *et al.* Testing models for the leaf economics spectrum with leaf and whole-  
388 plant traits in *Arabidopsis thaliana*. *AoB Plants* **7**, 1–12 (2015).  
389 13. Bongers, F. J. *et al.* Growth–trait relationships in subtropical forest are stronger at higher  
390 diversity. *J Ecol* **108**, 256–266 (2020).  
391 14. Goud, E. M., Sparks, J. P., Fishbein, M. & Agrawal, A. A. Integrated metabolic strategy:  
392 A framework for predicting the evolution of carbon-water tradeoffs within plant clades. *J*  
393 *Ecol* **107**, 1633–1644 (2019).  
394 15. Wright, I. J. *et al.* Assessing the generality of global leaf trait relationships. *New Phytol*  
395 **166**, 485–496 (2005).

- 396 16. Maire, V. *et al.* Global effects of soil and climate on leaf photosynthetic traits and rates.  
397 *Global Ecology and Biogeography* **24**, 706–717 (2015).
- 398 17. Edwards, E. J., Chatelet, D. S., Sack, L. & Donoghue, M. J. Leaf life span and the leaf  
399 economic spectrum in the context of whole plant architecture. *J Ecol* **102**, 328–336  
400 (2014).
- 401 18. Messier, J., McGill, B. J., Enquist, B. J. & Lechowicz, M. J. Trait variation and integration  
402 across scales: is the leaf economic spectrum present at local scales? *Ecography* **40**, 685–  
403 697 (2016).
- 404 19. Woodson, R. E., Jr. The North American Species of *Asclepias* L. *Annals of the Missouri*  
405 *Botanical Garden* **41**, 1–211 (1954).
- 406 20. Agrawal, A. A. *et al.* Phylogenetic ecology of leaf surface traits in the milkweeds  
407 (*Asclepias* spp.): chemistry, ecophysiology, and insect behavior. *New Phytol* **183**, 848–  
408 867 (2009).
- 409 21. Pellissier, L. *et al.* Different rates of defense evolution and niche preferences in clonal and  
410 nonclonal milkweeds (*Asclepias* spp.). *New Phytol* **209**, 1230–1239 (2016).
- 411 22. Pérez-Harguindeguy, N. *et al.* New handbook for standardised measurement of plant  
412 functional traits worldwide. *Aust. J. Bot.* **61**, 167–68 (2013).
- 413 23. Orme, D. *et al.* Caper: comparative analyses of phylogenetics and evolution in R. *R*  
414 *package version 0.5* **2**, 458 (2012).
- 415 24. Fishbein, M. *et al.* Phylogenetic Relationships of *Asclepias*(Apocynaceae) Inferred from  
416 Non-coding Chloroplast DNA Sequences. *Systematic Botany* **36**, 1008–1023 (2011).
- 417 25. Kembel, S. W. *et al.* Picante: R tools for integrating phylogenies and ecology.  
418 *Bioinformatics* **26**, 1463–1464 (2010).
- 419 26. Oksanen, J. *et al.* *vegan: Community Ecology Package, Version 2.5.-6. R Foundation for*  
420 *Statistical Computing* (2019).
- 421 27. Legendre, P. & Legendre, L. *Numerical ecology.* **24**, 1–990 (Elsevier, 2012).
- 422 28. R Core Team. *R: A language and environment for statistical computing. R Foundation for*  
423 *Statistical Computing* (2019).
- 424 29. Li, Y. & Shipley, B. An experimental test of CSR theory using a globally calibrated  
425 ordination method. *PLoS ONE* **12**, e0175404– (2017).
- 426 30. Dayrell, R. L. C. *et al.* Ontogenetic shifts in plant ecological strategies. *Funct Ecol* **32**,  
427 2730–2741 (2018).
- 428 31. Zanzottera, M., Fratte, M. D., Caccianiga, M., Pierce, S. & Cerabolini, B. E. L.  
429 Community-level variation in plant functional traits and ecological strategies shapes  
430 habitat structure along succession gradients in alpine environment. *Community Ecology*  
431 **562**, 1–11 (2020).
- 432 32. Vasseur, F. *et al.* Climate as a driver of adaptive variations in ecological strategies in  
433 *Arabidopsis thaliana*. *Annals of Botany* **122**, 935–945 (2018).
- 434 33. Astuti, G., Ciccarelli, D., Roma-Marzio, F., Trinco, A. & Peruzzi, L. Narrow endemic  
435 species *Bellevalia webbiana* shows significant intraspecific variation in tertiary CSR  
436 strategy. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant*  
437 *Biology* **153**, 12–18 (2018).
- 438 34. Litton, C. M., Sandquist, D. R. & Cordell, S. A non-native invasive grass increases soil  
439 carbon flux in a Hawaiian tropical dry forest. *Global Change Biology* **14**, 726–739 (2008).
- 440 35. Goud, E. M., Moore, T. R. & Roulet, N. T. Predicting peatland carbon fluxes from non-  
441 destructive plant traits. *Funct Ecol* **31**, 1824–1833 (2017).

- 442 36. Westoby, M. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* **199**,  
443 213–227 (1998).
- 444 37. Davidson, S. J. *et al.* Linear disturbances shift boreal peatland plant communities toward  
445 earlier peak greenness. *Earth and Space Science Open Archive* 1–20 (2021).  
446 doi:10.1002/essoar.10506838.1
- 447 38. Ellsworth, P. Z., Ellsworth, P. V. & Cousins, A. B. Relationship of leaf oxygen and  
448 carbon isotopic composition with transpiration efficiency in the C4 grasses *Setaria viridis*  
449 and *Setaria italica*. *Journal of Experimental Botany* **68**, 3513–3528 (2017).
- 450 39. Walker, A. P. *et al.* The relationship of leaf photosynthetic traits -  $V_{cmax}$  and  $J_{max}$  - to  
451 leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study.  
452 *Ecol Evol* **4**, 3218–3235 (2014).
- 453 40. Midgley, G. F., Aranibar, J. N., Mantlana, K. B. & Macko, S. Photosynthetic and gas  
454 exchange characteristics of dominant woody plants on a moisture gradient in an African  
455 savanna. *Global Change Biology* **10**, 309–317 (2004).
- 456 41. Feng, X. & Dietze, M. Scale dependence in the effects of leaf ecophysiological traits on  
457 photosynthesis: Bayesian parameterization of photosynthesis models. *New Phytol* **200**,  
458 1132–1144 (2013).
- 459 42. Field, C., Merino, J. & Mooney, H. A. Compromises between water-use efficiency and  
460 nitrogen-use efficiency in five species of California evergreens. *Oecologia* **60**, 384–389  
461 (1983).
- 462 43. Wright, I. J., Reich, P. B. & Westoby, M. Strategy shifts in leaf physiology, structure and  
463 nutrient content between species of high- and low-rainfall and high- and low-nutrient  
464 habitats. *Funct Ecol* **15**, 423–434 (2001).
- 465 44. Wright, I. J., Reich, P. B. & Westoby, M. Least-Cost Input Mixtures of Water and  
466 Nitrogen for Photosynthesis. *The American Naturalist* **161**, 98–111 (2003).
- 467 45. Schrodte, F. *et al.* Foliar trait contrasts between African forest and savanna trees: genetic  
468 versus environmental effects. *Functional Plant Biol.* **42**, 63–83 (2015).
- 469 46. Ghimire, B. *et al.* A global trait-based approach to estimate leaf nitrogen functional  
470 allocation from observations. *Ecol Appl* **27**, 1421–1434 (2017).
- 471 47. Reich, P. B., Walters, M. B., Ellsworth, D. S. & Uhl, C. Photosynthesis-nitrogen relations  
472 in Amazonian tree species. *Oecologia* **97**, 73–81 (1994).
- 473 48. Poorter, H. & Evans, J. R. Photosynthetic nitrogen-use efficiency of species that differ  
474 inherently in specific leaf area. *Oecologia* **116**, 26–37 (1998).
- 475 49. Mason, C. M. & Donovan, L. A. Evolution of the leaf economics spectrum in herbs:  
476 Evidence from environmental divergences in leaf physiology across  
477 *Helianthus* (Asteraceae). *Evolution* **69**, 2705–2720 (2015).
- 478 50. Agrawal, A. A. A scale-dependent framework for trade-offs, syndromes, and  
479 specialization in organismal biology. *Ecology* **101**, 243 (2020).
- 480 51. Anderegg, L. D. L. *et al.* Within-species patterns challenge our understanding of the leaf  
481 economics spectrum. *Ecology Letters* **21**, 734–744 (2018).
- 482 52. Enquist, B. J., West, G. B., Charnov, E. L. & Brown, J. H. Allometric scaling of  
483 production and life-history variation in vascular plants. *Nature* **401**, 907–911 (1999).
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 490 **Figure 1.** Biplots of principal components analyses (PCA) of 30 *Asclepias* species based on the  
 491 defining traits of three classic ecological theories: (A) growth analysis, (B) CSR, (C) LES, and  
 492 (D) 21 measured traits. Species groups are represented as convexes based on Ward's  
 493 agglomerative clustering defined by trait similarity. (E-H) Correlations between growth rate and  
 494 PC1, and (I-L) between growth rate and PC2. Variables with the highest eigenvector scores on  
 495 PC1 and PC2 are presented from left to right for each axis. Data are species means, species  
 496 names are in Table 3.

498 **Table 1.** Traits and growth predictions of growth analysis, CSR triangle, and leaf economics  
 499 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	-

500

501 **Table 2.** Linear correlations between 21 plant traits and growth rate (GR) using generalized  
502 linear models (GLM) and phylogenetic least squares regression (PGLS) for 30 *Asclepias* species  
503 grown under common conditions. Sign indicates the direction of the significant correlation  
504 (positive, + or negative, -). Phylogenetic signal using Pagel's  $\lambda$  is shown for each trait, with  $P <$   
505 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, $\text{cm}^2$ )	+	<b>0.56</b>	<b>&lt; 0.0001</b>	<b>0.61</b>	<b>&lt; 0.0001</b>	0.18	0.37
$R_d$ (leaf dark respiration rate)							
per area ( $R_{\text{area}}$ , $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	n.s	0.02	0.41	0.01	0.67	< 0.001	0.98
per mass ( $R_{\text{mass}}$ , $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	n.s	0.01	0.53	0.004	0.73	<b>0.93</b>	<b>0.003</b>
LD (leaf density, $\text{mg g}^{-1}$ )	+	<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 ( $N_{\text{area}}$ , $\text{gN m}^{-2}$ )	-	<b>0.27</b>	<b>0.004</b>	<b>0.20</b>	<b>0.01</b>	0.45	0.29
per mass ( $N_{\text{mass}}$ , $\text{gN g}^{-1}$ )	-	<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 ( $P_{\text{area}}$ , $\text{gP m}^{-2}$ )	-	<b>0.51</b>	<b>&lt; 0.0001</b>	<b>0.55</b>	<b>&lt; 0.0001</b>	0.06	0.72
per mass ( $P_{\text{mass}}$ , $\text{gP g}^{-1}$ )	-	<b>0.26</b>	<b>0.004</b>	<b>0.19</b>	<b>0.02</b>	0.03	0.88
LS (leaf size average, $\text{cm}^2$ )	+	<b>0.24</b>	<b>0.04</b>	<b>0.31</b>	<b>0.001</b>	< 0.001	0.98
$L_{\text{th}}$ (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 ( $A_{\text{area}}$ , $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	+	<b>0.23</b>	<b>0.008</b>	<b>0.32</b>	<b>0.001</b>	0.49	0.97
per mass ( $A_{\text{mass}}$ , $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	+	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, $\text{cm}^2 \text{g}^{-1}$ )	n.s	0.001	0.88	0.01	0.96	< 0.001	0.98
SRL (specific root length, $\text{cm}^2 \text{mg}^{-1}$ )	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>

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508 **Table 3.** Average growth rate (GR, g d<sup>-1</sup>) and strategic classifications for 30 *Asclepias* species  
509 grown under common conditions. Species are in order by increasing GR. Growth analysis (GA)  
510 strategies are defined by species' predominant biomass fraction (root, stem, leaf); CSR by  
511 competitive (C), stress tolerant (S), ruderal (R), or their combination. Leaf economic spectrum  
512 (LES) strategies are defined as resource acquisitive or conservative. Strategies identified by  
513 comparing all 21 measured traits are defined by relative plant size (small, medium, large) and  
514 predominant biomass fraction (root, stem, leaf).

Species		GR	Strategy			
			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

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