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Santini, B.A., Hodgson, J.G., Thompson, K. et al. (7 more authors) (2017) The triangular seed mass-leaf area relationship holds for annual plants and is determined by habitat productivity. *Functional Ecology*. ISSN 0269-8463

<https://doi.org/10.1111/1365-2435.12870>

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1 **The triangular seed mass-leaf area relationship holds for annual**
2 **plants and is determined by habitat productivity.**
3

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18 **Summary**
19

- 20 1. Plant allometries help us to understand resource allocation in plants and provide
21 insight into how communities are structured. For woody species, a triangular
22 allometric relationship between seed size and leaf size was found, in which all
23 combinations are all possible, except for species with big seeds and small leaves
24 (Cornelissen 1999). This relationship is thought to be a consequence of between
25 habitat variation in abiotic conditions.
26 2. In this study, we tested if the triangular relationship between seed mass and leaf area
27 holds for annual species, and if soil productivity and light (measured as Ellenberg
28 indicator values: EIVs) are driving this relationship.
29 3. We show that the triangular relationship also exists for annuals, which suggests that
30 the allometric combinations between leaf area and seed mass are conserved across
31 life-forms. We also found that the triangular relationship is driven by between-habitat
32 variation in productivity.

33 4. This means that as soil productivity increases, plants with bigger leaves could have
34 either big or small seeds. However, in low-productive habitats, plants are constrained
35 in their options, plants with small leaves can only have small seeds.

36

37 **Key-words** Leaf size, leaf area, annual species, phylogenetic regression, plant allometries,
38 seed size, seed mass, Ellenberg indicator values, habitat productivity.

39

40

41 **Introduction**

42

43 Leaves are the main organ where photosynthesis occurs in plants, making leaves a key
44 determinant in the functioning of ecosystems (Wright *et al.* 2004). Leaves display great
45 variation in their morphology, anatomy, and physiology within climatic areas and in response
46 to growing conditions (Givnish 1987a; Witkowski & Lamont 1991). Within species, leaf
47 area varies in relation to both water and light availability (Xu *et al.* 2009). Despite this
48 variation, comparative studies have shown that there are leaf strategies that can be recognized
49 globally. For example, using a global database Wright *et al.* (2004) found that there is a
50 positive relationship between leaf life-span and leaf dry mass (LMA per unit of light-
51 intercepting leaf area deployed) implying that longer-lived leaves are thicker and/or denser.

52 One of the most studied leaf traits is size or area, as it is easy to measure, and is
53 involved in the control of leaf energy and water balance (Givnish 1987a; Cornelissen *et al.*
54 2003). Leaf area is positively correlated with precipitation (Hamann 1979 in Dolph & Dilcher
55 1980), and soil nutrient availability (Ashton & Hall 1992; McDonald *et al.* 2003a), but
56 negatively correlated to light availability (Niinemets & Kull 1994) and altitude (Milla &
57 Reich 2011). Small leaves are therefore generally interpreted as an adaptation to drought and
58 high-radiation (Ackerly 1999; Ackerly & Reich 1999; Cornelissen *et al.* 2003)

59 In relation to the reproductive output, plants with bigger leaves also have bigger seeds
60 in woody (Cornelissen 1999; Westoby & Wright 2003). Bigger seeds are thought to be
61 advantageous in nutrient-limited habitats (Lee & Fenner 1989; Dainese & Sitzia 2013).
62 However, there is conflicting evidence on this subject with other studies suggesting bigger
63 seeds are advantageous in fertile, competitive, closed habitats due to their higher food reserve
64 ratios and high seedling survival (Salisbury 1974; Mazer 1990; Grubb & Coomes 1997).

65 Leaf area is also positively related to twig-thickness (Yang *et al.* 2010) and to plant
66 height, which is linked with competitive ability (Cornelissen *et al.* 2003). Other allometric
67 studies show that leaf area correlates negatively with specific leaf area (SLA – leaf area/leaf
68 mass; (Ackerly 1999; Ackerly & Reich 1999; Milla & Reich 2007), which is a good predictor
69 of the relative growth rate (RGR; Cornelissen *et al.* (2003)). Also, bigger leaves are wider
70 and have higher dry mass (Wilson, Thompson & Hodgson 1999; Niklas, Cobb & Spatz 2009).
71 This means that larger leaves with broader, thicker laminas have less effective heat loss and
72 lower photosynthetic rates (Givnish 1987a). The ecological significance of leaf area may
73 relate to resource capture in productive habitats where big leaves are advantageous, and
74 resistance to grazing, where small leaves are better (Diaz & Cabido 2001; Diaz, Noy-Meir &
75 Cabido 2001).

76 Midgley & Bond (1989) found that leaf size and cone size were positively correlated
77 in species from the *Leucadendron* genus. Further research was conducted by Cornelissen
78 (1999) who hypothesized that if the infructescence size and seed size are positively correlated,
79 then leaf size and seed size should be positively correlated too. However, given the existence
80 of pioneer species with large infructescences and small seeds, there should be a deviation from
81 this allometry, in which small seeded species can have either small or large leaves. In
82 agreement with his hypothesis, Cornelissen (1999) found a triangular relationship between
83 leaf area and seed mass in mature, woody species, suggesting that small-seeded species can

84 have large or small leaves, whereas large-seeded species with small leaves do not occur. The
85 triangular relationship seemed to be underpinned by variation between habitats in plant
86 ecological strategies with: A) fast growing (ruderal) species with small seeds and large
87 leaves found in early successional habitats, B) slow-growing (stress-tolerant) species with
88 small seeds and leaves, found in stress-prone habitats, and C) slow-growing, tall plants
89 (competitive) species with large leaves and seeds, found in mid-late successional habitats. So
90 in summary the triangular relationship appears to be driven by variation between rather than
91 within habitats. However, it should be noted that Cornelissen (1999) did not have any
92 measures of habitat quality.

93 Given the clear links between variation in the environment and leaf size (Hamann
94 1979; Dolph & Dilcher 1980; Givnish 1987b; Witkowski & Lamont 1991; Ashton & Hall
95 1992; Niinemets & Kull 1994; Ackerly & Reich 1999; Wright *et al.* 2004) it is therefore
96 important to control for environmental variation when conducting comparative analyses. In
97 this study, we explored the relationship between seed mass (the weight of an individual seed
98 [mg]) and leaf area (the one-sided surface area of a lamina mm²) in annual species.

99 The advantage of using annuals species for our study is that they are a homogeneous
100 group, which allocate most of their resources to reproduction rather than to vegetative growth
101 (Friedman & Rubin 2015). Contrasting to perennials, annual species have higher reproductive
102 effort (seed number per fruit; (Primack 1979) no secondary growth, and shorter life cycles.
103 Also, annual plant height is mostly determined by habitat productivity, whereas woody
104 species height also depends on the time and interval of disturbance (Westoby 1998). Given
105 this distinct differences compared to woody species, it might be expected that the allometric
106 relationships would be different between these groups of plants.

107 We used a large database (provided by JG Hodgson, the Unit of Comparative Plant
108 Ecology and Department of Archaeology, University of Sheffield), containing trait

109 information for annuals in the UK and Ellenberg indicator values for nitrogen (EIV-N) and
110 for light (EIV-L). EIVs are proxies for assessing habitat characteristics (Ertsen, Alkemade &
111 Wassen 1998), or indicators for general productivity and light (Hill, Preston & Roy 2004).
112 They were first assessed for Central Europe, however calibrations for these values in the UK
113 showed that EIV-N correlate very well for nitrogen content in leaves, and EIV-L with habitat
114 shadiness (Thompson *et al.* 1993).

115 We examined two main questions: 1) Does the triangular relationship of seed mass-
116 leaf area also occur in annual plants? 2) If so, does variation between environments drive this
117 relationship? To understand these two questions, we also explored the relationship between
118 the components of the triangular relationship (leaf area and seed mass) separately in relation
119 to EIV-N and EIV-L. Additionally, we looked at the relationship between leaf area and seed
120 mass with plant height, as this trait plays an important role in determining the competitive
121 ability of a species for light and is positively correlated to leaf area (Cornelissen *et al.* 2003).
122 In each case, we ask if the relationship depends on EIV-N and EIV-L.

123 **Materials and methods**

124
125 The dataset contained information on 401 annual species from the UK, belonging to 37
126 families (Family level summary presented in Table 1). Two types of data were incorporated
127 into the database:

- 128 1) Measurements from mature field specimens; the range of per species sample sizes in
129 brackets;
 - 130 a. Leaf area [mm^2] measured as the one-sided surface area of a lamina ($n = 1 -$
131 17).
 - 132 b. Seed weight [mg], ($n = 1-21$), with some values extracted from Kew (2016).

133 The individual measurements for leaf area and seed weight were averaged at the species level
134 and then \log_{10} transformed.

135 2) Literature-based measurements; EIVs for light and nitrogen for each of the species
136 were extracted from the literature (Ellenberg, Weber & Dull 1992), and for plant
137 height species were assigned a class following (Stace 1987; Grime, Hodgson & Hunt
138 2007). In total, there were nine plant height classes. In the database, the species EIV-
139 L ranged from 4 to 9 (shade-semi shade plants, to plants in full light) and for EIV-N
140 from 1 to 9 (low to high productive habitats).

141
142 We calculated the mid-point values between each plant height class (mm) and then \log_{10}
143 transformed these. EIV-N and EIV-L were used as categorical variables in all the analyses.

144 We did two types of analysis: 1) Generalized least squares (gls) models, which allows one to
145 test for variance reduction and the inclusion of the phylogenetic relatedness in our analysis,
146 and 2) Standardized major axis (SMA), which allows one to test for the scaling relationship
147 between two traits. However, this later method does not allow us to test for variance
148 reduction along the fitted line, nor to account for phylogenetic correction whilst including
149 environmental factors into the model (i.e. nitrogen and light EIVs). For the relationship
150 between plant traits, we find that the values for the slopes were steeper when using the SMA
151 analysis. Despite this, we did not find major differences between the two analysis. Hence, we
152 present the results from the gls method in the main text and results from SMA in the
153 supporting information (see Appendix S1 in Supporting Information). SMA analysis was
154 done using the R package SMART (Warton *et al.* 2012).

155 The inclusion of the phylogenetic relatedness in gls models is done using a variance-
156 covariance matrix, which incorporates the distance between each species and its ancestor
157 (variance) and the distance between each species (covariance) (Paradis 2012). These values
158 were extracted from Daphne phylogeny, which is an ultrametric tree for 4685 species of
159 vascular plants from the British Isles, Germany, The Netherlands, and Switzerland (Durka &
160 Michalski 2012). Phylogenetic regression analyses were performed using the R packages ape

161 (Paradis, Claude & Strimmer 2004) and nlme (R Development Core Team 2010). Variation
162 in sample size of the explanatory variable, when available, was incorporated into the model,
163 as we expect estimates based on small samples will be more variable.

164 To explore the relationship between leaf area and seed mass we constructed a range
165 of different models. To test for a triangular relationship between seed mass and leaf area we
166 allowed the variance about the fitted line to be a function of the fitted values. This assumes
167 the variance of the residuals is given by,

$$168 \quad \text{Var}(y) = \sigma^2 \exp(2 * t * \hat{y}) \quad [1]$$

169 where \hat{y} is the fitted value and t an estimated parameter. When t is negative the variance
170 decreases as the fitted values become larger creating a triangular relationship.

171 To test whether the triangular relationship was a result of variation between habitats
172 we fitted models including variation in EIV-N and EIV-L (as factors), and tested if the
173 variance function was still significant.

174

175 **Results**

176 *Triangular relationship in leaf area and seed mass*

177

178 The positive triangular relationship between leaf area and seed mass described for woody
179 species by (Cornelissen 1999) was also found in annual plants (Fig. 1, $F_{1, 373} = 106.47$ $P <$
180 0.0001 , slope = 0.43 ± 0.042 , $r^2 = 0.318$). As in (Cornelissen 1999), plants with small seeds
181 had either small or large leaves, and plants with big seeds had big leaves, but the combination
182 of big seeds with small leaves did not occur. As expected the variance about the fitted line
183 decreased as the sample size of leaf area became larger (Likelihood ratio test = 7.81, $P =$
184 0.0052), but even after taking this effect into account, there was a highly significant decrease
185 in the variance about the fitted line (Likelihood ratio test = 10.66, $P = 0.0011$) resulting in a
186 triangular relationship (Fig. 1).

187 The relationship between leaf area and seed mass varied with EIV-N ($F_{8, 329} = 12.62$, P
188 < 0.001), but there was no interaction (EIV-N \times Seed mass, $F_{8, 321} = 1.83$, $P = 0.069$; Fig.
189 1A). After including EIV-N ($r^2 = 0.43$), there was no longer a significant decrease in the
190 variance about the fitted line (Likelihood ratio test = 0.043, $P = 0.83$). This suggests that the
191 triangular relationship between seed mass and leaf area (Fig. 1A) is a consequence of the
192 variation between habitats. The parameters for this model suggest that the intercepts increase
193 with productivity, *i.e.* at a given seed mass, plants in productive habitats typically have larger
194 leaves than plants from less-productive habitats (Fig. 1A, Table 2).

195 For light values, we found a marginally significant interaction between EIV-L \times Seed
196 mass ($F_{5, 332} = 2.56$ $P < 0.027$, $r^2 = 0.31$; Fig. 1B). In the model with the EIV-L \times Seed mass
197 interaction the variance about the fitted line still declined (Likelihood ratio test = 8.41, $P =$
198 0.003). This result suggests that the triangular relationship between seed mass and leaf area is
199 not driven by between-habitat variation in EIV-L. The intercept values for the relationship
200 between seed mass and leaf area tend to decrease as EIV-L increased, *i.e.* at high illuminance
201 (Fig. 1B, Table 2),

202
203
204
205

206 *Leaf area and habitat variables*

207

208 Leaf area in our dataset varied by 4 orders of magnitude (from $\sim 4 \text{ mm}^2$ to $41,000 \text{ mm}^2$),
209 which represents a large proportion of the global variation among species (≈ 7 orders of
210 magnitude (Wright *et al.* 2007). In our dataset leaf area was related to habitat quality, as in
211 previous studies (Ashton & Hall 1992; Niinemets & Kull 1994; McDonald *et al.* 2003b)
212 (EIV-N: $F_{8, 330} = 8.79$, $P < 0.0001$, $r^2 = 0.30$; Fig. 2A, and EIV-L: $F_{5, 338} = 6.84$, $P < 0.0001$,
213 $r^2 = 0.193$; Fig. 2B). To explore how leaf area varied with habitat quality we then refitted the
214 models with EIV-N and EIV-L as ordered factors. This allows us to partition the variation in
215 leaf area between EIVs into linear and quadratic components. We found there were
216 significant linear ($t_{339} = 6.79$, $P < 0.0001$) and quadratic ($t_{339} = -2.19$, $P = 0.02$) terms for leaf
217 area and EIV-N. However, for EIV-L, only the linear term was marginally significant ($t_{344} = -$
218 1.97 , $P = 0.049$). So, leaf area increased with habitat productivity (or higher EIV-N), and
219 possibly with shadiness (low EIV-L).

220

221 *Seed mass and habitat variables*

222

223 In our dataset, seed mass varied 5 orders of magnitude, from 10^{-3} to 10^2 grams, which
224 represents half of the global variation among species: 13 orders of magnitude (Díaz *et al.*
225 2015). Seed mass varied with EIV-N ($F_{8, 330} = 4.821$, $P < 0.0001$, $r^2 = 0.108$; Fig. 3A) and
226 EIV-L ($F_{5, 338} = 7.127$, $P < 0.0001$, $r^2 = 0.093$, Fig. 3B). In the model with EIV-N as an
227 ordered factor, there were significant linear ($t_{339} = 3.16$, $P = 0.0017$) and quadratic ($t_{339} = -$
228 3.52 , $P < 0.001$) terms. However, neither of these terms was significant for EIV-L: linear
229 ($t_{344} = -1.27$, $P = 0.20$) or quadratic ($t_{344} = -1.91$, $P = 0.055$).

230

231 We also explored the relationship between seed mass and plant height ($r^2 = 0.171$),
232 and its interaction with EIV-N and EIV-L. Our results showed that there was an effect of

233 EIV-N ($F_{8, 329} = 4.82, P < 0.0001$) and plant height ($F_{1, 329} = 14.87, P = 0.0001$) on seed
234 mass, but the interaction was not significant (EIV-N \times Plant height, $F_{8, 321} = 1.47, P = 0.16,$
235 $r^2 = 0.15$, Fig. 4A). Similar results were found for EIV-L ($F_{5, 337} = 7.86, P < 0.0001$), plant
236 height ($F_{1, 337} = 22.54, P < 0.0001$), and the interaction (EIV-L \times Plant height, $F_{5, 332} = 0.64,$
237 $P = 0.66, r^2 = 0.07$, Fig. 4B). So larger seeds occurred on taller plants and the intercept of
238 this relationship tended to increase with habitat productivity and decreased with light.

239

240 *Leaf area in relation to habitat and other plant traits*

241

242 Leaf area was positively related to plant height ($F_{1, 373} = 214.62, P < 0.0001, r^2 = 0.55$; Fig.
243 5). The slope was 0.43 ± 0.028 indicating that leaf area tends to increase more slowly than
244 plant height. For this relationship, there was a marginally significant interaction with EIV-N
245 ($F_{8, 321} = 2.26, P = 0.022, r^2 = 0.73$), but not for EIV-L ($F_{5, 332} = 1.67, P = 0.13, r^2 = 0.60$). As
246 the relationship between plant height and EIV-L was similar in light levels 4 to 8 (Table 2),
247 we collapsed the light levels into two groups (4-8 and 9) and compared this model to the full
248 model (that included EIV-L from 4-9). The resulting model was not significantly different
249 from the full model (Likelihood ratio test = 3.80, $P = 0.43$). The reduced model showed that
250 there was an effect of plant height ($F_{1, 340} = 177.76, P < 0.0001$) and EIV-L ($F_{1, 340} = 40.22, P$
251 < 0.0001) on leaf area. There was also evidence of an interaction between EIV-L and plant
252 height ($F_{1, 340} = 6.34, P < 0.05, r^2 = 0.61$), suggesting that the slope of the relationship
253 between leaf area and plant height was shallower in full light (0.28 ± 0.06 vs 0.45 ± 0.03).
254 Therefore, at a given height, plants tended to have larger leaf areas in more productive
255 habitats (larger EIV-N, Fig. 5A), and shady habitats (lower EIV-L, Fig. 5B), although in the
256 latter case this was largely driven by a single habitat.

257

258 We also analyzed the relationship between plant height and habitat variables. We found that
259 it was positively related to habitat productivity, fitting EIV-N as an ordered factor there were
260 significant linear ($t_{339} = 5.45, P < 0.0001$) and quadratic ($t_{339} = -2.15, P = 0.03$, Fig.6A) terms.
261 However, for EIV-L, neither the linear ($t_{344} = -1.57, P = 0.11$) nor the quadratic ($t_{339} = -1.74,$
262 $P = 0.08$, Fig.6B) terms were significant.

263

264 **Discussion**

265 *Triangular relationship between leaf area and seed mass*

266

267 We found that the triangular relationship described by Cornelissen (1999) for woody species,
268 also occurred in our dataset of annual plants (Fig. 1). This triangular relationship was a
269 consequence of small seeded species having large leaves. (Cornelissen 1999), predicted this
270 latter result for woody species, suggesting that pioneers with large infructescences and small
271 seeds, can have either small or large leaves. Additionally, (Cornelissen 1999) proposed
272 several possible explanations for this pattern, these included: 1) phylogeny, 2) allometry, and
273 3) ecology, specifically variation in life-history, successional stage, and between-habitat
274 variation in nutrients and shade. Our analysis was restricted to annuals, and so the variation in
275 life-history is likely to be small. Likewise, our statistical analyses included phylogenetic
276 relatedness and so this is unlikely to explain the relationship. Our results suggest that
277 allometry in combination with between-habitat variation in productivity (as measured by
278 EIV-N) could be driving the triangular relationship in annual species (Fig. 1A), since there is
279 a significant decrease in the variance of the fitted leaf area – seed mass relationship when
280 between habitat variation in productivity is ignored, but not when it is included in the model.

281 The upper left corner of the triangle is likely to be regulated by the seed size/number
282 trade-off (Jakobsson & Eriksson 2000). This would imply that the large leaf species in this
283 corner produce small seeds in a relatively large quantity. This could occur when species with

284 a large mass and large leaves distribute resources between many offspring to promote a high
285 fecundity (Aarssen & Jordan 2001). In contrast, large leaf species in the upper right corner,
286 which have relatively big seeds, should produce a fewer number of them. An evolutionary
287 advantage of producing smaller seeds can occur if the survival of the numerous smaller seeds
288 is not substantially lower than the survival of bigger seeds (Smith & Fretwell 1974) .

289

290 *Leaf area, habitat variables and plant height*

291

292 Several studies have demonstrated that leaf size is positively related to nutrient rich habitats
293 (Ashton & Hall 1992; Fonseca *et al.* 2000; McDonald *et al.* 2003b). Our results were in
294 agreement with this (linear: $t_{339} = 6.79$, $P < 0.0001$, and quadratic term: $t_{339} = -2.19$, $P = 0.02$;
295 Fig. 2A). Explanations for this pattern are usually framed in terms of high leaf construction
296 costs, which limit leaf size in nutrient poor habitats (Givnish 1987b; Xu *et al.* 2009).
297 However, several studies suggest that leaf size forms part of a trade-off with leaf number
298 (Falster & Westoby 2003; Westoby & Wright 2003; Kleiman & Aarssen 2007) and so plants
299 could in principle produce either many small leaves or a few large ones. Alternatively, plant
300 size might limit leaf area in infertile habitats, and in agreement with this hypothesis we found
301 that plant height increased with soil fertility (Fig. 6A). It has also been suggested that higher
302 transpiration in small leaves could be an adaptation for acquiring nutrients in low fertility
303 habitats (Yates *et al.* 2010).

304 In the case of light, previous studies have reported a negative relationship with leaf area
305 (Niinemets & Kull 1994; Markesteijn, Poorter & Bongers 2007). However, for annuals, the
306 relationship was only marginally significant ($P < 0.049$), with larger leaves occurring in
307 shaded habitats, *i.e.* low EIV-L (Fig. 2B). The negative relationship between leaf area and
308 light availability may be explained in terms of larger leaves allowing greater light
309 interception in less lit habitats (Markesteijn *et al.* 2007), whereas in open habitats, plants

310 construct smaller leaves, with low SLA, which would increase their photosynthetic capacity
311 (Björkman 1981; Markesteijn *et al.* 2007).

312
313 Leaf area was positively related to plant height class (Fig. 5). A similar relationship
314 was reported for woody species (Senn, Hanhimaki & Haukioja 1992; Niinemets & Kull
315 1994; Cornelissen 1999). The increase in leaf area with plant height is not surprising as the
316 size of an axis or stem is linked to the size of its appendages, in this case leaves (Cornelissen
317 1999). In our study, the intercept for the relationship between leaf area and plant height
318 increased with EIV-N (Fig. 5A). These results are expected from theory: bigger leaves and
319 taller plants are adaptive in nutrient-competitive habitats (Falster & Westoby 2003; Wright *et*
320 *al.* 2007), where competition for light is strong. However, in our study we found that only the
321 slope, and not the intercept, declines with EIV-L (EIV-L = 9), suggesting that in full light
322 environments, there is a restriction for leaf area values to increase even in taller plants (Fig.
323 5B).

324

325 *Seed mass, habitat variables and plant height*

326
327 Evidence for the relationship between seed mass and fertility is equivocal (Leishman *et al.*
328 2000; Pakeman *et al.* 2008) with positive (Grubb & Coomes 1997) negative (Lee & Fenner
329 1989; Parolin 2000; Dainese & Sitzia 2013) and no relationship (Hammond & Brown 1995;
330 Wright & Westoby 1999; Pakeman *et al.* 2008), all being found. However, these studies often
331 used relatively few species, for example: (Lee & Fenner 1989) used 12 species in the
332 *Chionochloa* genus. Repeating this analysis using the data from the paper, we found that the
333 significant negative relationship ($P < 0.04$) was no longer significant if a single species was
334 removed ($P = 0.42$).

335 Several explanations have been presented in the literature to account for the range of
336 relationships found. Positive relationships might arise if small seeds were advantageous in
337 low fertility habitats because they have higher RGR, and so potentially outcompeting their
338 neighbours (Marañón & Grubb 1993). In contrast, negative relationships would occur if large
339 seeds allowed greater seedling establishment in low fertile soils, say as a result of greater
340 seed reserves (Lee & Fenner 1989; Dainese & Sitzia 2013). In our dataset, we found a
341 positive relationship between seed mass and habitat productivity (for the linear term: $t_{339} =$
342 3.16, $P = 0.0017$; quadratic term: $t_{339} = -3.52$, $P < 0.001$, Fig. 3A). Another possible
343 explanation for this positive relationship relates to plant height, since small plants can only
344 support small seeds and taller plants can produce structures to bear bigger seeds (Aarssen
345 2005; Pierce *et al.* 2014). Also, larger plants typically occur in more productive habitats
346 (Moles *et al.* 2009). So bigger plants in higher EIV-N habitats would be able to produce
347 bigger seeds. Our results for annuals showed plants were taller as habitat productivity
348 increased (Fig. 6A). Also, seed mass was positively related to plant height and this
349 relationship tended to increase with habitat productivity (Fig. 4A). Note here that taller
350 species would in principle be able to produce either a few big or many small seeds (Aarssen
351 2005). In contrast, species from the low productivity habitats are restricted in their seed size
352 (Fig.3A); in a global analysis, seed mass decreases with latitude, and net primary
353 productivity. The data also shows that species in lower latitudes have a wider range of seed
354 mass (Moles *et al.* 2007). This would in principle give species from productive habitats the
355 possibility to tune life history strategies given the aforementioned seed size/number trade-off
356 (Jakobsson & Eriksson 2000).

357

358 In the case of light, several studies have reported that bigger seeds are associated with
359 closed habitats (Salisbury 1974; Metcalfe & Grubb 1995; Hodkinson *et al.* 1998; Thompson

360 & Hodkinson 1998), although, in some cases the relationship seems to depend on the
361 taxonomic level at which comparisons are made. For example, (Grubb & Metcalfe 1996)
362 found larger-seeded species in shaded habitats when the comparison was made between
363 genera within families, but no difference when comparisons are made within genera (see also
364 (Mazer 1990)).

365 In contrast to these studies, within annuals we found no evidence for a positive
366 relationship between seed mass and shade, as neither the linear ($t_{344} = -1.27$, $P = 0.20$), nor
367 the quadratic terms ($t_{344} = -1.91$, $P = 0.055$, Fig. 3B) were significant. We believe this is
368 largely a consequence of annuals being restricted to open habitats (there were no species with
369 EIV-L less than 4, *i.e.* very shady habitats). Nevertheless, when relating seed mass to plant
370 height at different EIV-L, we found that taller plants produce bigger seeds, and this
371 relationship tended to increase with shadiness (Fig. 4B). This could be mainly a result of
372 plant height, as taller plants are dominant when competing for light (Weiner & Thomas 1986;
373 Aarssen, Schamp & Pither 2006), and so in less lit habitats taller plants get selected (Fig.4B).
374 The associated increase in seed mass in the shadier habitats may also be driven by selection
375 pressures related to competition for light, in which higher resource investment per individual
376 offspring is advantageous (Venable 1992). This altered resource allocation strategy could
377 improve seedlings' probability of establishment and their competitive ability (Venable 1992).

378

379 As shown above, habitat variables (as indicated by EIVs) are affecting the relationships
380 between plant traits, such as the one between leaf area and seed mass. We think that the use
381 of EIVs is a necessary alternative when lacking actual habitat measurements. Especially
382 when studying comparative large datasets and hence getting actual habitat measurements
383 would be a hard and costly task. EIVs have previously been related to plant ecophysiological
384 characteristics such as RGR, seed mass and SLA, among others (see review by Bartelheimer

385 & Poschlod (2016) for more examples of this). These findings are in correspondence to those
386 reported for relationships between the same plant traits made with actual measurements for
387 soil fertility and light (Metcalfe & Grubb 1995; Grubb & Coomes 1997; Hodkinson *et al.*
388 1998; Thompson & Hodkinson 1998; Quero *et al.* 2006; Sevillano *et al.* 2016). This evidence
389 supports the use of EIVs as a proxy for actual habitat measures when actual measurements
390 are lacking.

391

392 By explicitly including measures of habitat quality in our analyses, we have shown that
393 between-habitat variation in productivity (as indicated by EIV-N) is driving the triangular
394 relationship between leaf area – seed mass. We show that the allometries between leaf area
395 and seed mass can be extended to annual plants. This is an important finding as it suggests
396 that similar constraints operate across a wide array of plant species.

397

398 **Acknowledgments**

399 BAS was funded by Consejo Nacional de Ciencia y Tecnología (CONACyT) and Secretaria
400 de Educación Pública (SEP). We would like to thank to Jason I Griffiths for comments on the
401 early and later versions of this manuscript, to Edgar J Liceaga for help with the analysis, to
402 Capeta Santini for overall support and finally to the reviewers, whose valuable comments
403 made improvements on the manuscript. The authors report no conflict of interest.

404

405 **Data accessibility**

406 The data are part of a larger database that Professor Glynis Jones will shortly publish in
407 Dryad.

408

409

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605 SUPPORTING INFORMATION

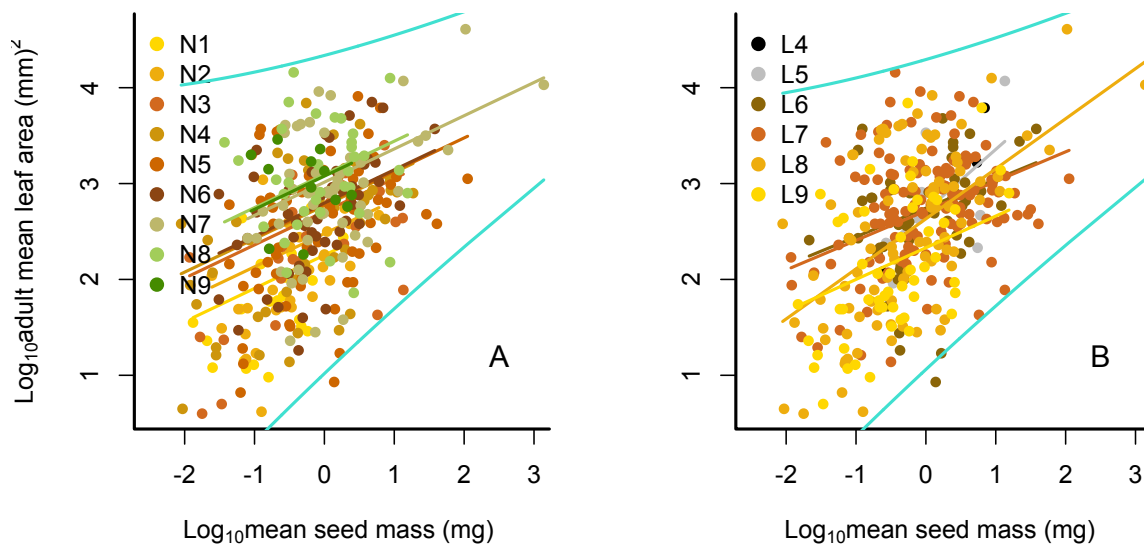
606 Additional Supporting Information may be found online version of this article.

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608 **Appendix S1.** Standardized major axis analysis

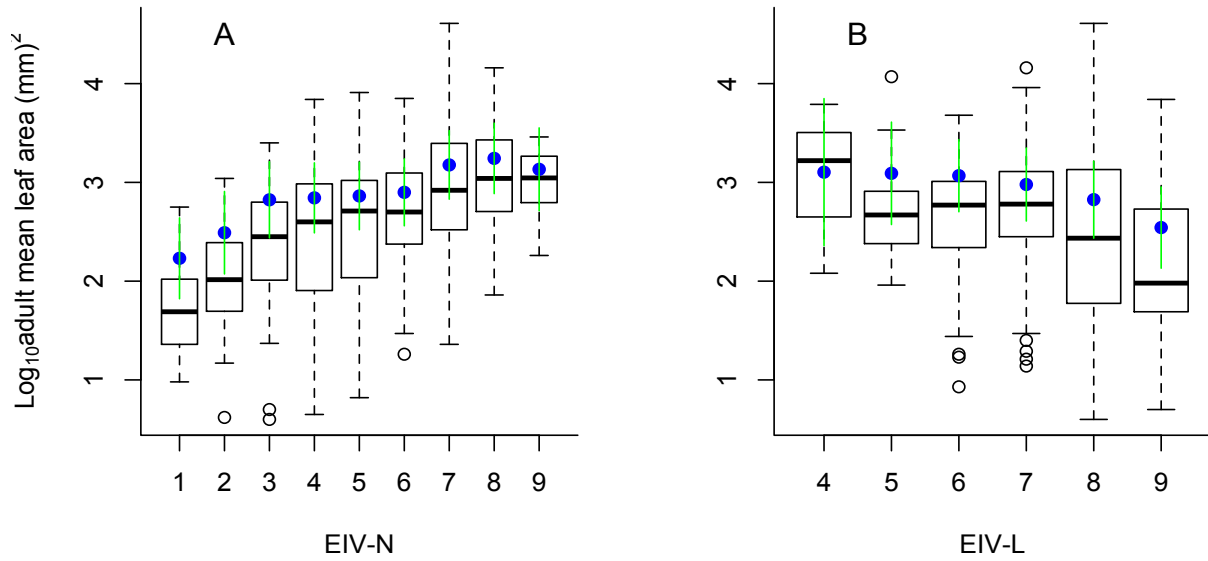
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Figures



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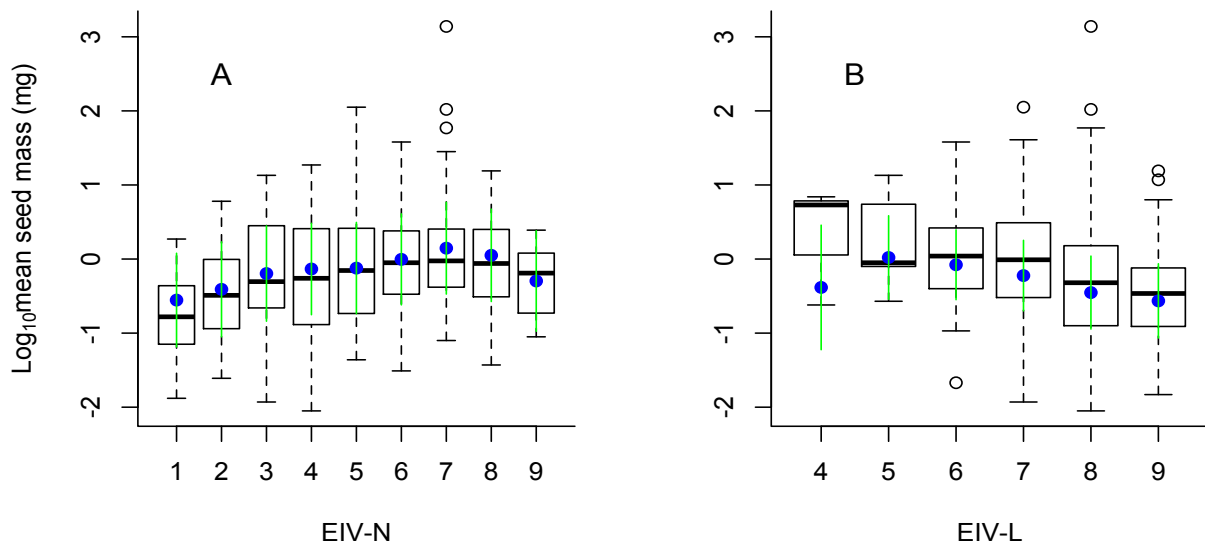
Figure 1. Log_{10} adult leaf area in relationship to log_{10} seed mass at different: A) EIV-N and B) EIV-L levels. The blue lines are the fitted variance function for each model, calculated as the fitted mean $\pm 1.96 \times \sqrt{\text{Var}(y)}$, where $\text{Var}(y)$ is given by equation [1]. Values for EIV-N (N1-N9) and EIV-L (L4-L9) are indicated by different colors, and represent a different line.



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633 Figure 2. Relationship between \log_{10} adult leaf area and: A) EIV-N and B) EIV-L levels. Blue
 634 points are the fitted values and 95% confidence intervals are shown in green.

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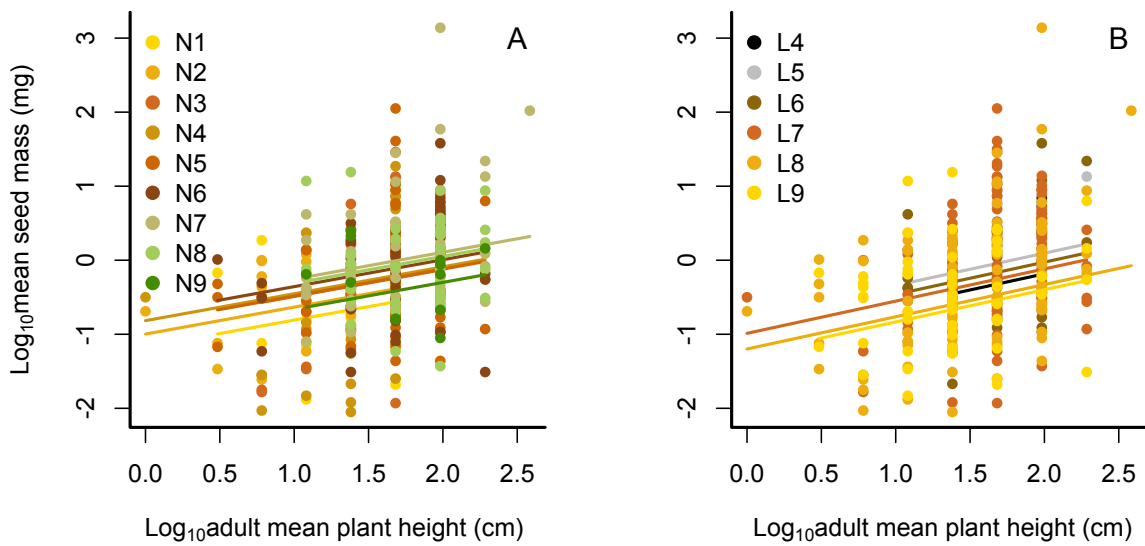


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637 Figure 3. Relationship between \log_{10} seed mass and: A) EIV-N and B) EIV-L levels. Blue
 638 points are the fitted values and 95% confidence intervals are shown in green.

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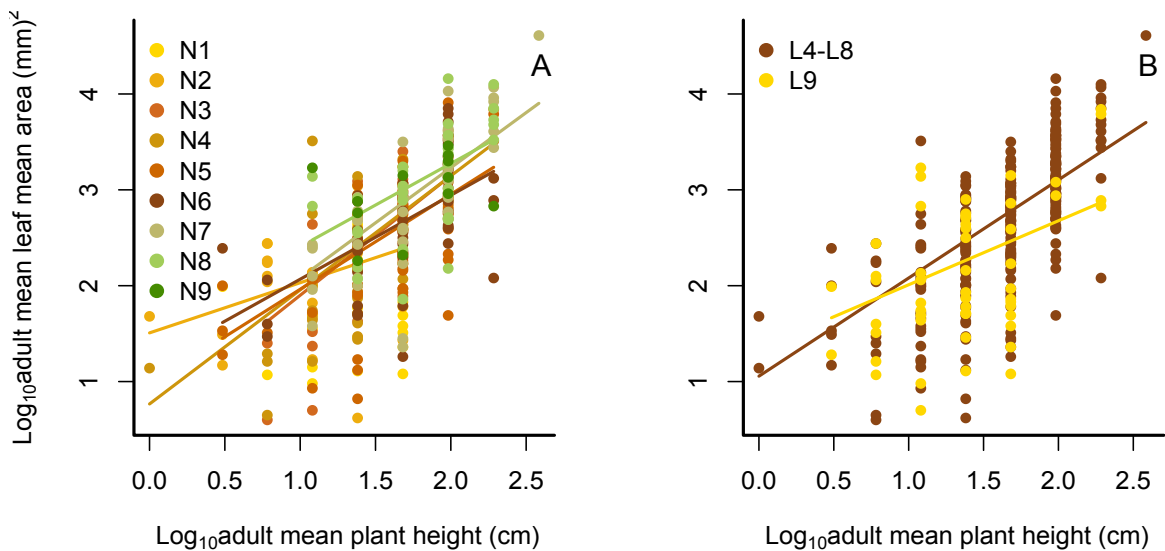
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642 Figure 4. Relationship between \log_{10} seed mass and \log_{10} adult plant height at different values
 643 for A) EIV-N and B) EIV-L levels. Only lines with significant slopes are shown. The
 644 predicted relationships for EIV-N (N1-N9) and EIV-L (L4-L9) are indicated by different
 645 colors, and represent a different line.

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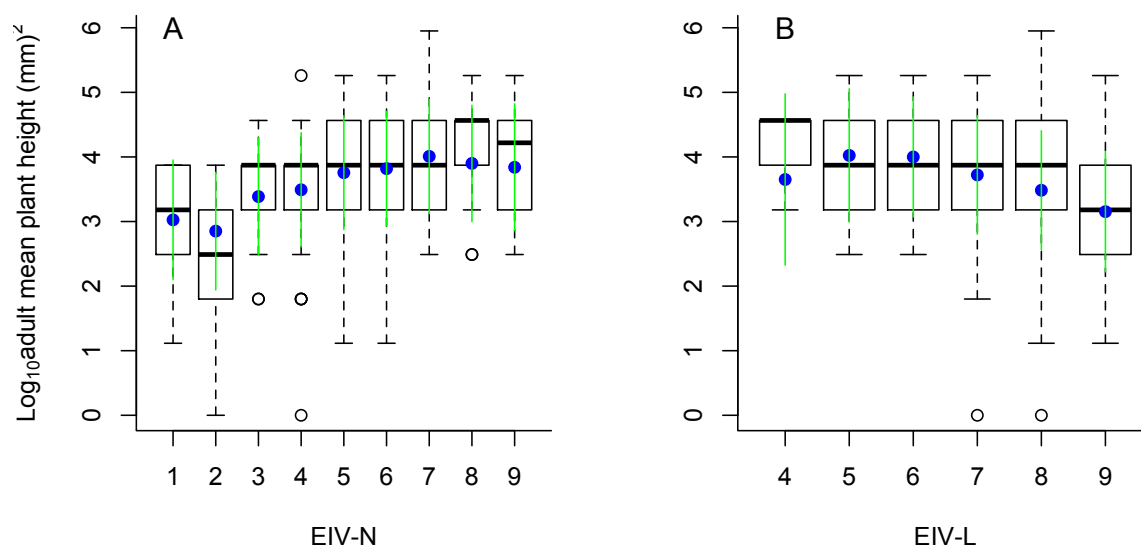
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650 Figure 5. \log_{10} leaf area in relationship \log_{10} plant height depending on: A) EIV-N and B)
 651 EIV-L levels (from the reduced model). Only lines with significant slopes are shown. Values
 652 for EIV-N (N1-N9) and EIV-L (L4-L9) are indicated by different colors, and represent a
 653 different line.

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658 Figure 6. Relationship between \log_{10} adult plant height and: A) EIV-N and B) EIV-L levels.
 659 Blue points are the fitted values and 95% confidence intervals are shown in green.

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666 Tables

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668 Table 1. Families and number of species per family used in the analysis. Mean seed mass (mg) and
 669 mean leaf area (mm^2) per family are shown; mean values were calculated as the back transformed
 670 expectation of a \log_{10} -normal distribution.

Family	Number of species	Mean of seed mass (mg)	Mean of leaf area (mm^2)
Amaranthaceae	26	0.61	545.66
Apiaceae	15	2.32	1571.91
Asteraceae	45	0.28	654.10
Balsaminaceae	3	7.94	4935.52
Boraginaceae	10	1.10	521.19
Brassicaceae	40	0.42	648.71
Campanulaceae	2	0.23	130.32
Caryophyllaceae	31	0.16	53.27
Cistaceae	1	0.07	436.52
Cyperaceae	1	0.05	398.11
Euphorbiaceae	6	0.50	120.23
Fabaceae	34	3.31	344.94
Gentianaceae	2	0.01	144.54
Geraniaceae	11	1.33	606.36
Juncaceae	1	0.03	117.49
Lamiaceae	13	1.36	571.38
Linaceae	1	1.41	48.98
Lythraceae	2	0.06	35.48

671	Malvaceae	7	3.98	1942.38
672	Montiaceae	3	0.55	202.61
673	Orobanchaceae	8	0.91	158.03
674	Papaveraceae	14	0.86	1057.51
675	Plantaginaceae	13	0.27	128.09
676	Poaceae	64	1.54	399.15
677	Polygonaceae	12	2.01	896.40
678	Portulacaceae	1	0.08	269.15
679	Primulaceae	2	0.46	118.85
680	Ranunculaceae	9	1.38	569.58
681	Resedaceae	1	1.15	275.42
682	Rosaceae	2	0.20	48.98
683	Rubiaceae	6	2.59	38.61
684	Saxifragaceae	2	0.02	61.66
685	Scrophulariaceae	1	0.02	25.12
686	Solanaceae	4	1.58	1688.50
687	Urticaceae	1	0.51	512.86
688	Valerianaceae	5	0.79	348.74
689	Violaceae	2	0.56	213.80

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Table 2. Intercept and slope values for each relationship at different EIV-N and EIV-L values. The non-significant values are indicated in bold. Plant traits were log₁₀ transformed for the analysis.

Plant trait	EIVs	<i>Intercept</i> (C.I.)	<i>P</i>	<i>Slope</i> (C.I.)	<i>P</i>
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<i>Leaf area vs seed mass</i>	Nitrogen					
	1	2.25 (1.83,2.66)	<0.0001	0.34 (0.26,0.41)	<0.01	
	2	2.47 (2.05,2.88)	<0.0001	0.34 (0.26,0.41)	<0.01	
	3	2.70 (2.28,3.11)	<0.0001	0.34 (0.26,0.41)	<0.0001	
	4	2.76 (2.36,3.15)	<0.0001	0.34 (0.26,0.41)	<0.0001	
	5	2.78 (2.4,3.15)	<0.0001	0.34 (0.26,0.41)	<0.001	
	6	2.79 (2.75,2.82)	<0.0001	0.34 (0.26,0.41)	<0.001	
	7	3.01 (2.61,3.4)	<0.0001	0.34 (0.26,0.41)	<0.0001	
	8	3.09 (2.69,3.4)	<0.0001	0.34 (0.26,0.41)	0.27	
	9	3.07 (2.59,3.54)	<0.0001	0.34 (0.26,0.41)	0.08	
<i>Seed mass vs plant height</i>	Light					
	4	2.7 (1.97,3.54)	<0.0001	0.13(-0.79,1.05)	0.71	
	5	2.71(2.2,3.21)	<0.0001	0.64(0.11,1.16)	<0.05	
	6	2.74 (2.3,3.17)	<0.0001	0.29(0.11, 0.46)	<0.001	
	7	2.71(2.27,3.14)	<0.0001	0.30 (0.18,0.41)	<0.001	
	8	2.63 (2.15,3.1)	<0.0001	0.52(0.4,0.63)	<0.001	
	9	2.33(1.8,2.85)	<0.0001	0.33(0.13,0.52)	<0.01	
	<i>Leaf area vs plant height</i>	Nitrogen				
		1	-1.17(-1.75,-0.58)	0.0002	0.36±0.09	<0.0001
		2	-0.99(-1.57,-0.4)	0.0013	0.36±0.09	<0.0001
3		-0.85 (-1.45,-0.24)	0.0079	0.36±0.09	<0.0001	
4		-0.81(-1.4,-0.22)	0.0085	0.36±0.09	<0.0001	
5		-0.84(-1.44,-0.23)	0.0076	0.36±0.09	<0.0001	
6		-0.72(-1.32,-0.11)	0.02	0.36±0.09	<0.0001	
7		-0.62(-1.24,0.007)	0.054	0.36±0.09	<0.0001	
8		-0.67(-1.3,-0.04)	0.036	0.36±0.09	<0.0001	
9		-1.02(-1.68,-0.35)	0.0035	0.36±0.09	<0.0001	
<i>Leaf area vs plant height</i>	Light					
	4	-1.04(-1.86,-0.21)	0.013	0.41±0.08	<0.0001	
	5	-0.74(-1.30,-0.17)	0.01	0.41±0.08	<0.0001	
	6	-0.88(-1.35,-0.40)	0.0005	0.41±0.08	<0.0001	
	7	-0.98(-1.45,-0.50)	0.0001	0.41±0.08	<0.0001	
	8	-1.18(-1.65,-0.70)	<0.0001	0.41±0.08	<0.0001	
	9	-1.25(-1.72,-0.77)	<0.0001	0.41±0.08	<0.0001	
	<i>Leaf area vs plant height</i>	Nitrogen				
		1	1.59(0.74,2.43)	0.0003	0.24±0.28	0.38
		2	1.50(0.85,2.14)	<0.0001	0.52±0.21	<0.05
3		0.65(-0.21,1.51)	0.14	1.24±0.25	<0.001	
4		0.76(0.19,1.32)	0.01	1.18±0.14	<0.001	
5		0.97(0.38,1.55)	0.0018	0.99±0.14	<0.001	
6		1.19(0.56,1.81)	0.0002	0.87±0.14	<0.001	
7		0.93(0.26,1.59)	0.007	1.14±0.16	<0.001	
8		1.54(0.73,2.34)	0.0002	0.86±0.20	<0.001	
9		2.39(1.31,3.46)	<0.0001	0.34±0.29	0.24	

Light

4	1.35(0.66,2.03)	<0.001	0.40±0.03	<0.0001
5	1.13(0.60,1.65)	<0.0001	0.40±0.03	<0.0001
6	1.14(0.70,1.57)	<0.0001	0.40±0.03	<0.0001
7	1.16(0.72,1.59)	<0.0001	0.40±0.03	<0.0001
8	1.07(0.63,1.50)	<0.0001	0.40±0.03	<0.0001
9	0.89(0.83,0.94)	0.225	0.40±0.03	<0.0001

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