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

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Summary

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

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

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

Introduction

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

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

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

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

Midgley & Bond (1989) found that leaf size and cone size were positively correlated in species from the *Leucadendron* genus. Further research was conducted by Cornelissen (1999) who hypothesized that if the infrutescence size and seed size are positively correlated, then leaf size and seed size should be positively correlated too. However, given the existence of pioneer species with large infrutescences and small seeds, there should be a deviation from this allometry, in which small seeded species can have either small or large leaves. In agreement with his hypothesis, Cornelissen (1999) found a triangular relationship between leaf area and seed mass in mature, woody species, suggesting that small-seeded species can have large or small leaves, whereas large-seeded species with small leaves do not occur. The triangular relationship seemed to be underpinned by variation between habitats in plant ecological strategies with: A) fast growing (ruderal) species with small seeds and large leaves found in early successional habitats, B) slow-growing (stress-tolerant) species with small seeds and leaves, found in stress-prone habitats, and C) slow-growing, tall plants (competitive) species with large leaves and seeds, found in mid-late successional habitats. So in summary the triangular relationship appears to be driven by variation between rather than within habitats. However, it should be noted that Cornelissen (1999) did not have any measures of habitat quality.

Given the clear links between variation in the environment and leaf size (Hamann 1979; Dolph & Dilcher 1980; Givnish 1987b; Witkowski & Lamont 1991; Ashton & Hall 1992; Niinemets & Kull 1994; Ackerly & Reich 1999; Wright *et al.* 2004) it is therefore important to control for environmental variation when conducting comparative analyses. In this study, we explored the relationship between seed mass (the weight of an individual seed [mg]) and leaf area (the one-sided surface area of a lamina mm^2) in annual species.

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

We used a large database (provided by JG Hodgson, the Unit of Comparative Plant Ecology and Department of Archaeology, University of Sheffield), containing trait information for annuals in the UK and Ellenberg indicator values for nitrogen (EIV-N) and for light (EIV-L). EIVs are proxies for assessing habitat characteristics (Ertsen, Alkemade & Wassen 1998), or indicators for general productivity and light (Hill, Preston & Roy 2004). They were first assessed for Central Europe, however calibrations for these values in the UK showed that EIV-N correlate very well for nitrogen content in leaves, and EIV-L with habitat shadiness (Thompson *et al.* 1993).

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

Materials and methods

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

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

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

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

We calculated the mid-point values between each plant height class (mm) and then $\log_{10}$ transformed these. EIV-N and EIV-L were used as categorical variables in all the analyses. We did two types of analysis: 1) Generalized least squares (gls) models, which allows one to test for variance reduction and the inclusion of the phylogenetic relatedness in our analysis, and 2) Standardized major axis (SMA), which allows one to test for the scaling relationship between two traits. However, this later method does not allow us to test for variance reduction along the fitted line, nor to account for phylogenetic correction whilst including environmental factors into the model (i.e. nitrogen and light EIVs). For the relationship between plant traits, we find that the values for the slopes were stepper when using the SMA analysis. Despite this, we did not find major differences between the two analysis. Hence, we present the results from the gls method in the main text and results from SMA in the supporting information (see Appendix S1 in Supporting Information). SMA analysis was done using the R package SMART (Warton *et al.* 2012).

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

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

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

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

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

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

Results

Triangular relationship in leaf area and seed mass

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

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

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

Leaf area and habitat variables

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

Seed mass and habitat variables

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

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

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

Leaf area in relation to habitat and other plant traits

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

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

Discussion

Triangular relationship between leaf area and seed mass

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

The upper left corner of the triangle is likely to be regulated by the seed size/number trade-off (Jakobsson & Eriksson 2000). This would imply that the large leaf species in this corner produce small seeds in a relatively large quantity. This could occur when species with a large mass and large leaves distribute resources between many offspring to promote a high fecundity (Aarssen & Jordan 2001). In contrast, large leaf species in the upper right corner, which have relatively big seeds, should produce a fewer number of them. An evolutionary advantage of producing smaller seeds can occur if the survival of the numerous smaller seeds is not substantially lower than the survival of bigger seeds (Smith & Fretwell 1974) .

Leaf area, habitat variables and plant height

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

In the case of light, previous studies have reported a negative relationship with leaf area (Niinemets & Kull 1994; Markesteijn, Poorter & Bongers 2007). However, for annuals, the relationship was only marginally significant ($P < 0.049$), with larger leaves occurring in shaded habitats, *i.e.* low EIV-L (Fig. 2B). The negative relationship between leaf area and light availability may be explained in terms of larger leaves allowing greater light interception in less lit habitats (Markesteijn *et al.* 2007), whereas in open habitats, plants construct smaller leaves, with low SLA, which would increase their photosynthetic capacity (Björkman 1981; Markesteijn *et al.* 2007).

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

Seed mass, habitat variables and plant height

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

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

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

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

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

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

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

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

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Data accessibility

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

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SUPPORTING INFORMATION

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

Appendix S1. Standardized major axis analysis

Figures

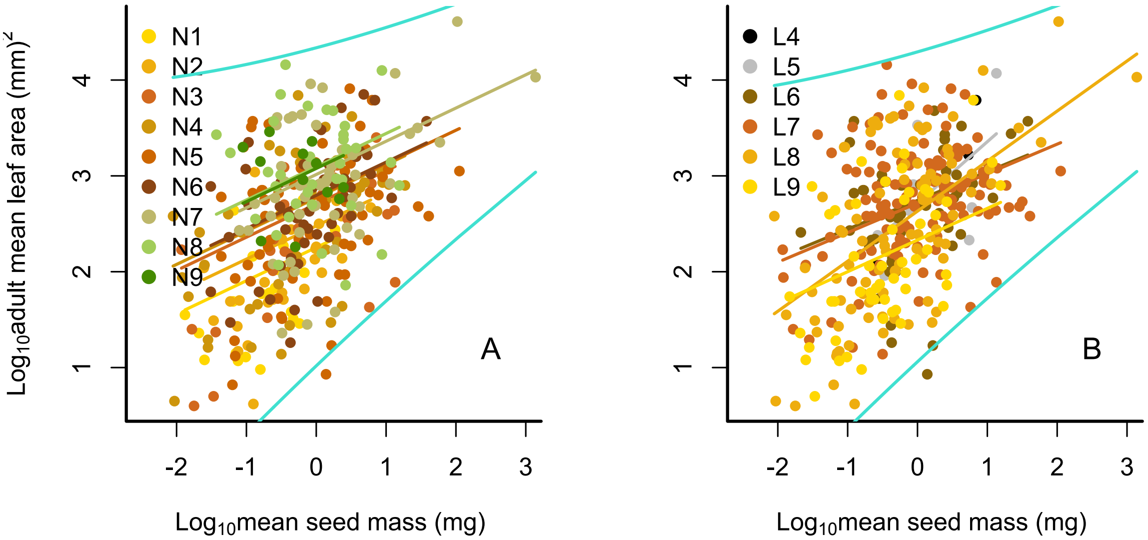

Figure 1. Log_{10} adult leaf area in relationship to $\log_{10}$ seed mass at different: A) EIV-N and B) EIV-L levels. The blue lines are the fitted variance function for each model, calculated as the fitted mean ± 1.96 × $\sqrt{Var}(y)$, where *Var (y)* is given by equation [1]. Values for EIV-N (N1-N9)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

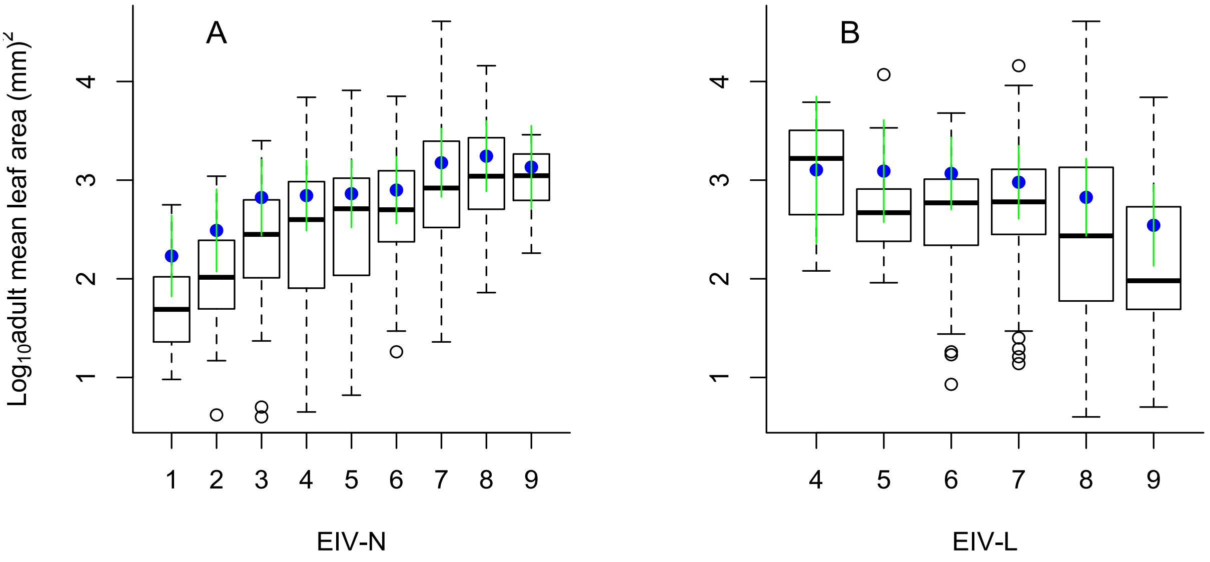

Figure 2. Relationship between log$_{10}$ adult leaf area and: A) EIV-N and B) EIV-L levels. Blue points are the fitted values and 95% confidence intervals are shown in green.

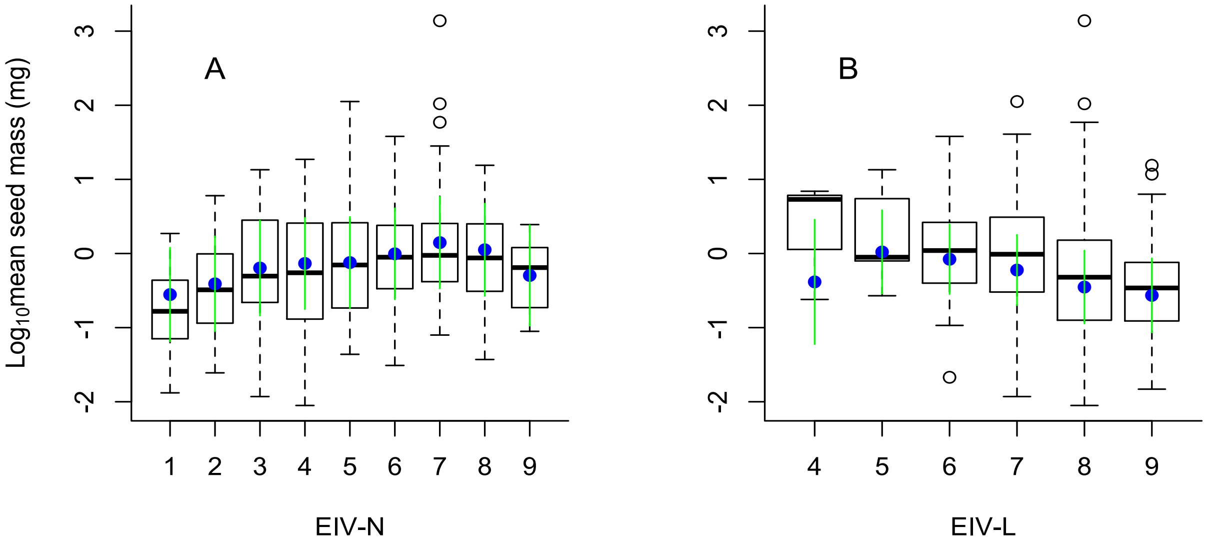

Figure 3. Relationship between log$_{10}$ seed mass and: A) EIV-N and B) EIV-L levels. Blue points are the fitted values and 95% confidence intervals are shown in green.

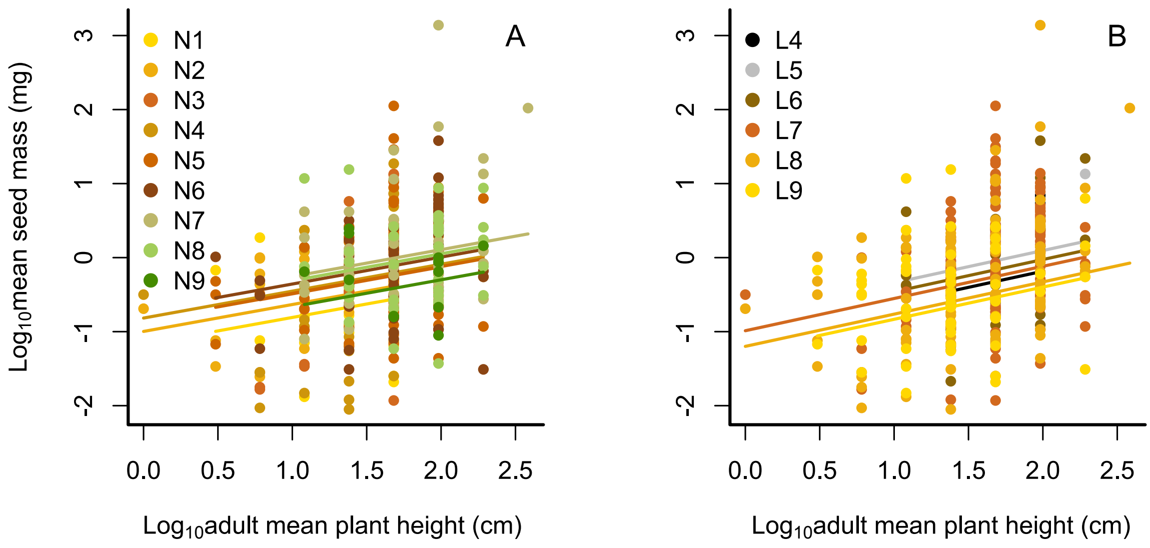

Figure 4. Relationship between $\log_{10}$ seed mass and $\log_{10}$ adult plant height at different values for A) EIV-N and B) EIV-L levels. Only lines with significant slopes are shown. The predicted relationships for EIV-N (N1-N9) and EIV-L (L4-L9) are indicated by different colors, and represent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

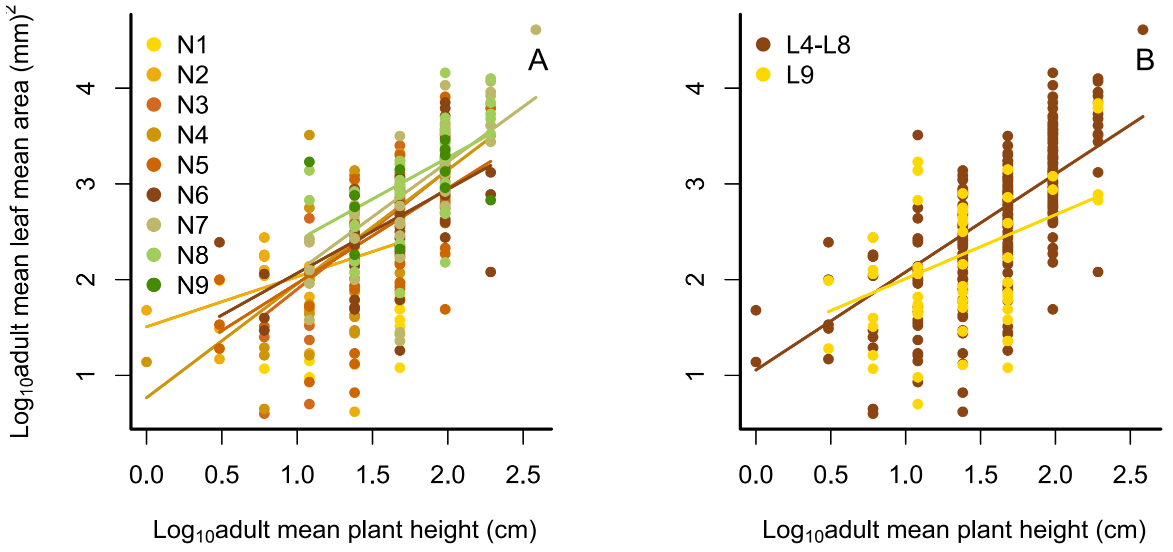

Figure 5. Log_{10} leaf area in relationship $\log_{10}$ plant height depending on: A) EIV-N and B) EIV-L levels (from the reduced model). Only lines with significant slopes are shown. Values for EIV-N (N1-N9) and EIV-L (L4-L9) are indicated by different colors, and represent a different line.

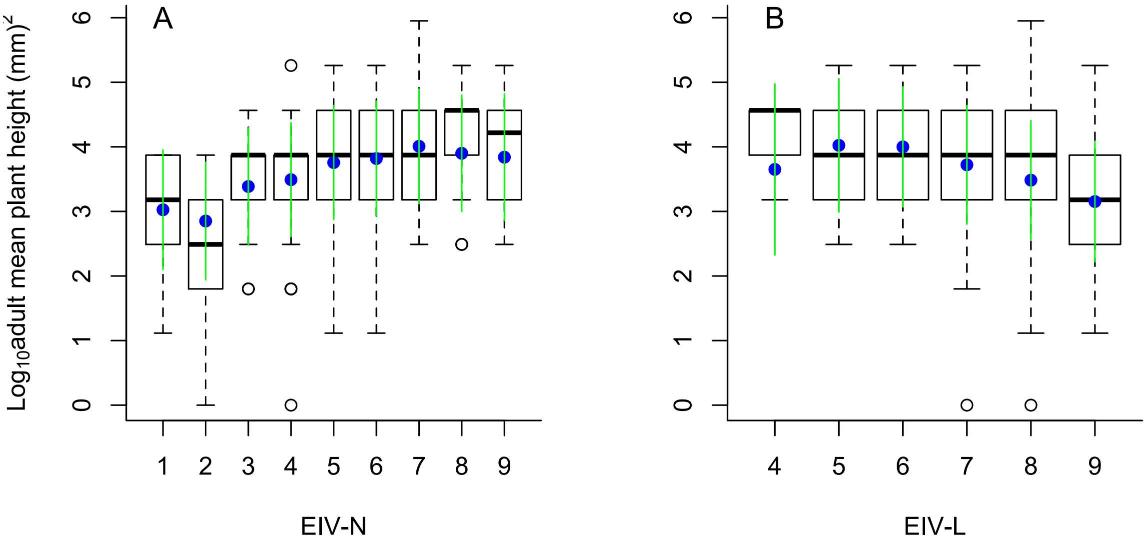

Figure 6. Relationship between $\log_{10}$ adult plant height and: A) EIV-N and B) EIV-L levels. Blue points are the fitted values and 95% confidence intervals are shown in green.

Tables

Table 1. Families and number of species per family used in the analysis. Mean seed mass (mg) and mean leaf area (mm^2) per family are shown; mean values were calculated as the back transformed 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

Malvaceae	7	3.98	1942.38
Montiaceae	3	0.55	202.61
Orobanchaceae	8	0.91	158.03
Papaveraceae	14	0.86	1057.51
Plantaginaceae	13	0.27	128.09
Poaceae	64	1.54	399.15
Polygonaceae	12	2.01	896.40
Portulacaceae	1	0.08	269.15
Primulaceae	2	0.46	118.85
Ranunculaceae	9	1.38	569.58
Resedaceae	1	1.15	275.42
Rosaceae	2	0.20	48.98
Rubiaceae	6	2.59	38.61
Saxifragaceae	2	0.02	61.66
Scrophulariaceae	1	0.02	25.12
Solanaceae	4	1.58	1688.50
Urticaceae	1	0.51	512.86
Valerianaceae	5	0.79	348.74
Violaceae	2	0.56	213.80

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 $\log_{10}$ transformed for the analysis.

Plant trait	EIVs	*Intercept* (C.I.)	*P*	*Slope* (C.I.)	*P*

Leaf area vs seed mass	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**
	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
Seed mass vs plant height	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
	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
Leaf area vs plant height	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