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Does seed mass drive the differences in relative growth rate between growth forms?

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The idea that herbaceous plants have higher relative growth rates (RGRs) compared with woody plants is fundamental to many of the most influential theories in plant ecology. This difference in growth rate is thought to reflect systematic variation in physiology, allocation and leaf construction. Previous studies documenting this effect have, however, ignored differences in seed mass. As woody species often have larger seeds and RGR is negatively correlated with seed mass, it is entirely possible the lower RGRs observed in woody species is a consequence of having larger seeds rather than different growth strategies. Using a synthesis of the published literature, we explored the relationship between RGR and growth form, accounting for the effects of seed mass and study-specific effects (e.g. duration of study and pot volume), using a mixed-effects model. The model showed that herbaceous species do indeed have higher RGRs than woody species, and that the difference was independent of seed mass, thus at all seed masses, herbaceous species on average grow faster than woody ones.

1. Introduction

Relative growth rate (RGR) varies widely between species [1,2]. In a large screening experiment, Grime & Hunt [3] grew 130 species in standardized, 'optimal' conditions (no competition, plentiful light and nutrients), and found that even in this environment there was a sixfold variation in maximum RGR between species. As a result of this variation, RGR is considered to be a useful metric for separating species into functional groups. For example, in Grime's CSR theory, RGR is a central parameter determining a species' strategy, with fast-growing species being classified as ruderals (R) or competitors (C), and slow-growing species as stress tolerators (S) [4,5]. Similarly, RGR is also a key trait in Tilman's theories [6], and he argued that differences in allocation determine RGR. Thus, both theories predict a link between RGR and growth form, with woody species having lower RGRs than herbaceous species (see also [2,7]). The link between RGR and growth form is therefore central to many of the most influential ideas in plant ecology, and has been found repeatedly in experimental studies [2,8].

In addition to growth form, RGR is associated with several other traits. In particular, seed mass is often negatively correlated with RGR, so large-seeded species tend to have lower RGRs [9–11]. A meta-analysis of six studies [12] demonstrated the generality of the negative relationship between RGR and seed mass, suggesting that it is robust to differences in experimental protocol and the pool of species used. Like RGR, seed mass is linked with growth form, with herbaceous species usually having smaller seed masses than woody species [13]. As a result of this, it is possible that the relationship between RGR and growth form is a consequence of variation in seed mass, rather than the differences in growth strategy. Recently, Turnbull *et al.* [14] have re-evaluated the seed mass–RGR relationship by calculating RGR at a common seedling mass so allowing comparison between species of different masses. We were unable to use this approach with published estimates of RGR, and so compare growth forms at a common seed mass.

To do this, we built a database of published studies that contained measures of RGR, and augmented this with additional information on life history,

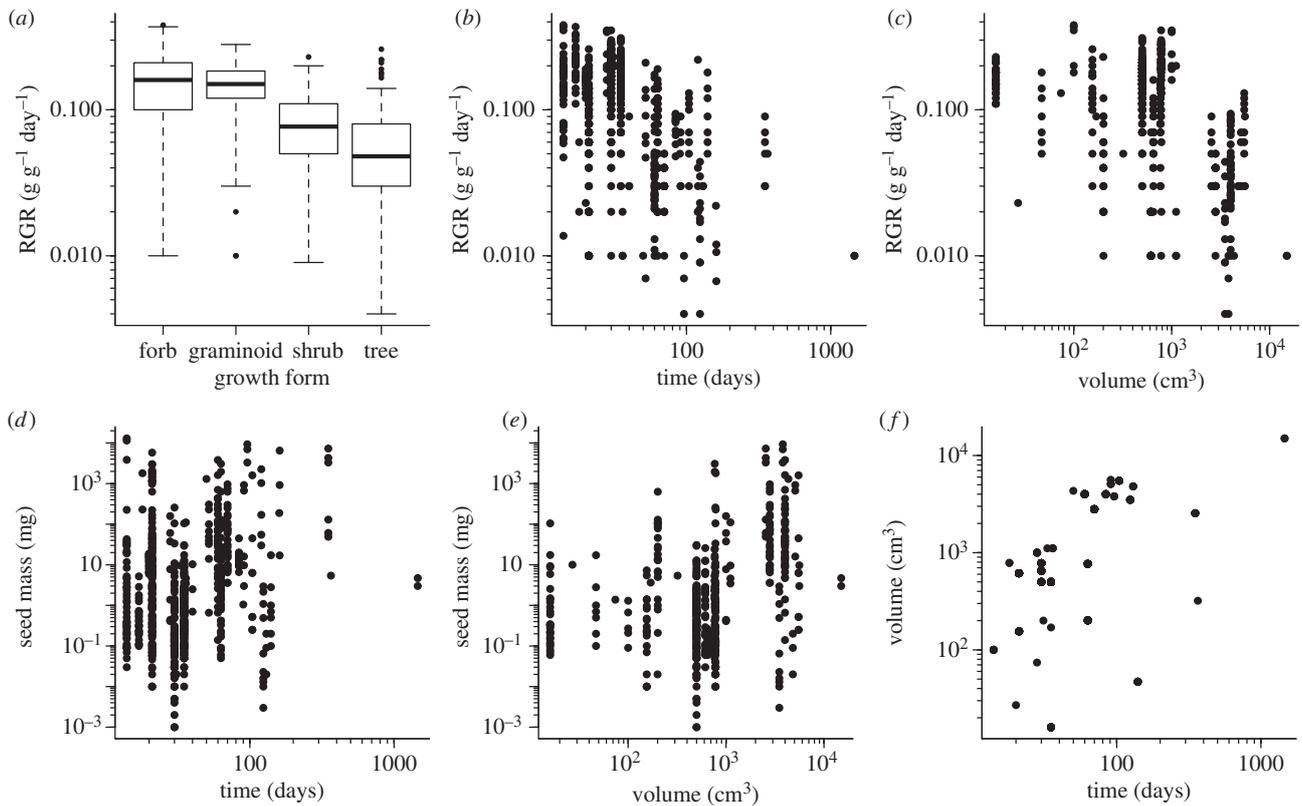


Figure 1. The relationships between the experimental variables. (a) RGR and growth form ($p < 0.0001$), (b) RGR and duration ($p < 0.0001$), (c) RGR and pot volume ($p < 0.0001$), (d) seed mass and duration ($p < 0.001$), (e) seed mass and volume ($p < 0.0002$) and (f) volume and duration ($p < 0.0001$). All variables except growth form are displayed on the log scale. p -values generating a sample from the posterior distribution of the parameters of the fitted model using Markov chain Monte Carlo methods; see text for details.

Köppen–Geiger climate classification and seed mass. Comparing the results of different studies is problematic due to differences in experimental protocols (e.g. duration of the study and the pot volume) and other unmeasured factors. In order to account for this, we used a mixed modelling approach incorporating study-specific covariates and random effects.

2. Material and methods

(a) Data collection

The ‘Web of Knowledge’ (Thomson Reuters, 2012 Web of Science) and ‘Scopus’ (Elsevier BV, 2012 SciVerse Scopus) databases were searched for papers containing the words ‘seed mass’ or ‘seed size’ and ‘relative growth rate’ or ‘growth rate’ on 20 January 2012. The following variables were recorded per species per study:

- the relative growth rate. This was either calculated using linear regression or as:

$$\text{RGR} = \frac{\log W_t - \log W_0}{t},$$

- where W_0 is the initial plant mass, W_t is the final plant mass and t is the number of days between the two measurements [15]. All measurements were expressed as $\text{g g}^{-1} \text{d}^{-1}$;
- seed mass, in mg. Where the seed mass was not presented in the original paper, the average seed mass for the species was obtained from either the Ecoflora database [16], the KEW seed information database [17] or Grime *et al.* [18];
- the duration of the study was measured as the number of days between germination and the final harvest;
- pot volume was recorded in cubic centimetre;

- the growth forms of each species (forb, graminoid, shrub or tree) were recorded, using data from: the original paper, Grime *et al.* [18] or the PLANTS database [19]; and
- studies were assigned to the Köppen–Geiger climate classification (continental, dry, moderate or tropical) based on their location [20];

Where studies had multiple treatment groups (e.g. multiple light levels), only the results from the control treatments (i.e. plentiful light, nutrients and water) were recorded. The final dataset consisted of 761 species from 45 studies (see the electronic supplementary material, S1 for details).

(b) Statistics

A linear mixed-effects model for variation in RGR was developed in R [21] using the lme4 package [22]. These models allow the dependence on covariates and unmeasured study-specific factors to be explored. Specifically, in this case, different studies were performed using different protocols and under different environmental conditions, and so study-specific random effects were included in the models. In addition to these, we also included study-specific covariates (e.g. duration and pot volume). Information on pot volume was not available for ≈ 25 per cent of the species, and so we initially developed models ignoring pot volume. The conclusions from models with and without pot volume were, however, similar, and so we only present analyses ignoring pot volume; see the electronic supplementary material, S2 for models including pot volume. All continuous variables were log transformed (base 10).

The statistical significance of the relationships between RGR and the study-specific covariates, and between the covariates was assessed using a mixed model with a study-specific random intercept. We then generated a sample from the posterior distribution of the parameters from the fitted model using

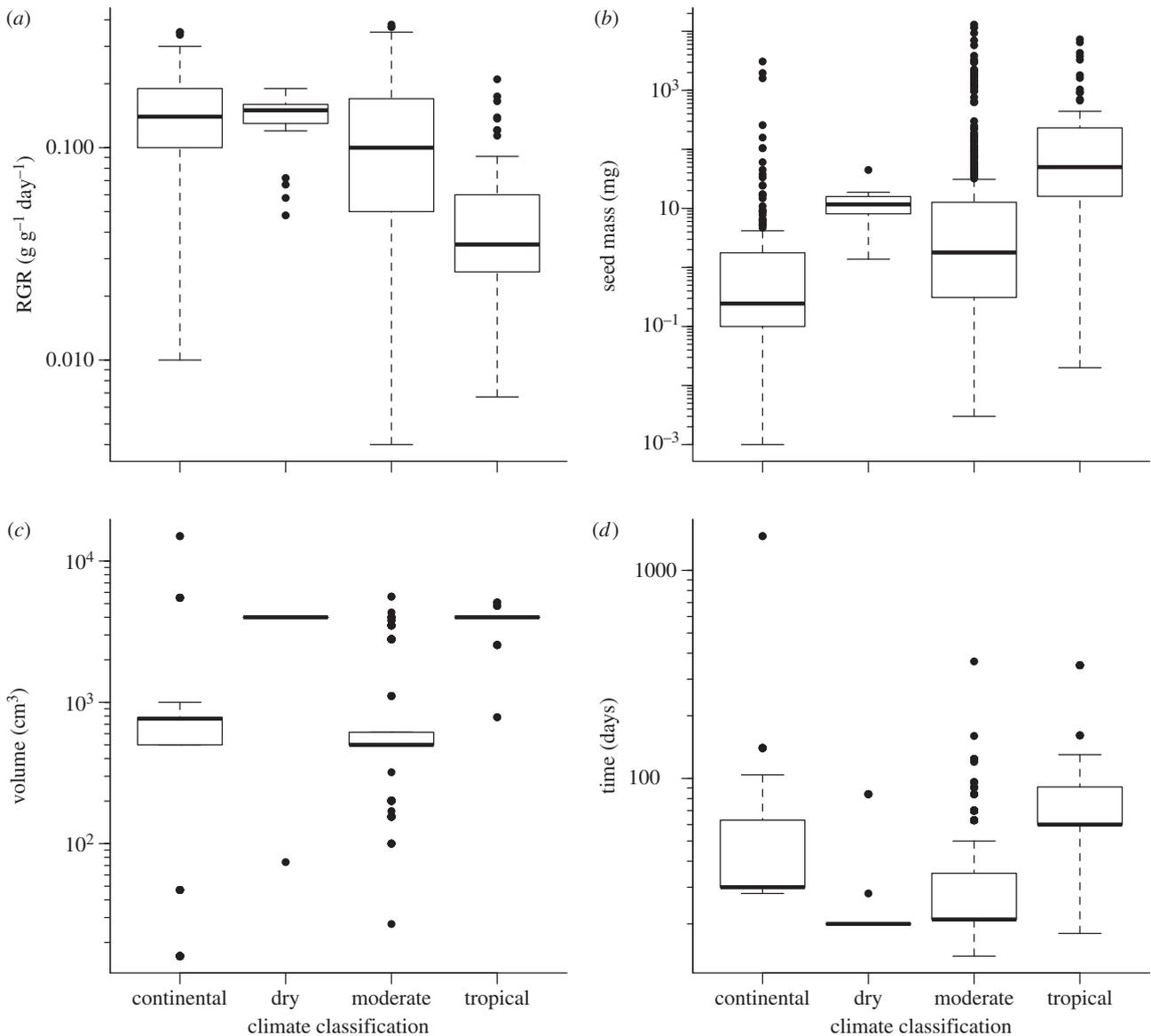


Figure 2. The relationships with climate classification for (a) RGR, (b) seed mass, (c) pot volume and (d) duration. In all cases $p < 0.0001$, using p -values generated using Markov chain Monte Carlo methods; see text for details.

Markov chain Monte Carlo methods (based on the `mcmc` function in `lme4` and `pvals.fnc` in `languageR`).

3. Results

(a) Relationships between experimental variables

In agreement with previous research, woody plants do appear to have lower RGRs than herbaceous species (figure 1*a*). There were also associations with the study-specific covariates: study duration and pot volume. RGR was negatively correlated with both the duration of the study and pot volume (figure 1*b,c*). Similarly, seed mass was also correlated with these covariates, with studies of longer duration, in larger pots, typically using larger seeded species (figure 1*d,e*). As expected, studies using larger pots were usually of longer duration (figure 1*f*). In tropical studies, RGR is lower, and these studies typically use larger seeded species (figure 2*a,b*). Tropical studies are also typically performed in large pots and are of long duration (figure 2*c,d*). Consistent with expectations from the literature [23], woody species (trees and shrubs) had higher seed masses than the herbaceous species (forbs and graminoids, figure 3), which could potentially bias comparisons between growth forms.

(b) Model selection

A linear mixed-effects model was developed to explain the effects of growth form and seed mass on RGR, using: seed mass, growth form, duration of the study, Köppen–Geiger climate classification and study (which groups the data by their original paper). The initial model assumed that variation in RGR was explained by seed mass, growth form, Köppen–Geiger climate classification and duration, with study-specific correlated intercepts and seed mass slopes (table 1: model 1). Removing the duration of the study from the model improved the fit (table 1: model 1 versus 2), possibly because the effect of duration was confounded with the study random effect. Likewise, removal of the Köppen–Geiger climate classification improved the fit of the models (table 1: model 2 versus 3); therefore both variables were removed from the model. Inspection of the fitted parameters suggested there was little difference between the forbs and graminoids, and between the shrubs and trees, and so they were combined into two groups, the herbaceous and woody species. This grouping improved both the Akaike information criterion (AIC) and Bayesian information criterion (BIC) (table 1: model 3 versus 4). Including an

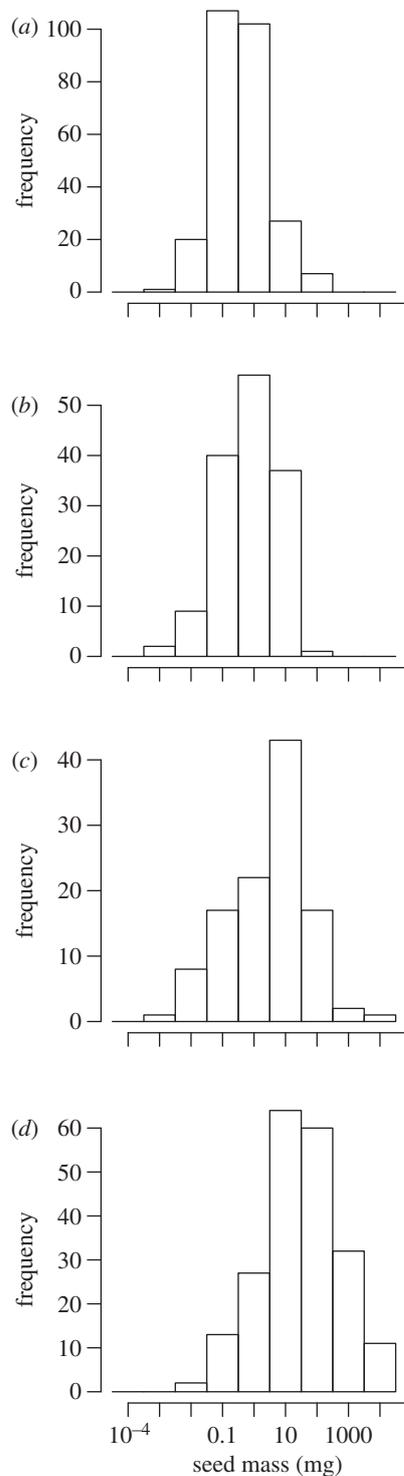


Figure 3. Histogram of seed mass, subdivided into (a) forbs, (b) graminoids, (c) shrubs and (d) trees ($p < 0.0001$); p -value generated using Markov chain Monte Carlo methods, see text for details.

interaction between herbaceous and woody, and seed mass did not improve the fit of the model (table 1: model 4 versus 5), however, making the study-specific intercepts and seed mass slopes independent did (table 1: model 4 versus 6).

In the final mixed-effects model, $\log(\text{RGR})$ declined linearly with $\log(\text{seed mass})$, but the herbaceous and woody species had different intercepts, so woody species had a consistently lower average RGR (figure 4a). There was no evidence for an interaction between seed mass and growth form (table 1: model 4 versus 5), suggesting that RGR declines with seed mass at the same rate in both groups. Importantly, this means that at any common seed mass, woody species

do indeed grow more slowly than herbaceous species. All study-specific slopes were negative (figure 4b).

4. Discussion

(a) Seed mass and relative growth rate

There was a highly significant overall negative relationship between RGR and seed mass (table 2 and figure 4a), and all the study-specific slopes were negative (figure 4b), which supports the majority of the literature (for example [9,24]) and agrees with the results of the only other published comparative analysis on the relationship between RGR and seed mass [12].

Herbaceous species had consistently higher average RGRs than woody species at all seed masses, and growth form does not alter the slope of the relationship between RGR and seed mass. As a result, conclusions from previous research that have compared RGR across growth forms, ignoring seed mass, may not be qualitatively affected by not accounting for seed mass. However, because seed mass is correlated with RGR, and seed mass varies between growth forms, failure to account for the effects of seed mass will bias comparisons.

(b) Growth forms

The RGRs of forbs and graminoids were similar, as were the RGRs of shrubs and trees (figure 1a). However, herbs had significantly higher RGRs than woody species (figure 4), consistent with the widely accepted view that different growth forms have different RGRs [3,25]. As this difference holds even when species are compared at a common seed mass, we must consider other causes of variance in seedling RGR between growth forms.

The differing RGR between growth forms has previously been linked to growth components, where RGR is decomposed into: specific leaf area (SLA; leaf area per unit of leaf biomass), leaf mass ratio (LMR; ratio of leaf biomass to total plant biomass) and net assimilation rate (NAR; increase in biomass per unit of leaf area per time). Herbaceous species tend to have higher SLAs than woody species [7,8], providing greater light absorption per unit of leaf mass, which may contribute to their higher RGR. SLA is often found to account for most of the variance in RGR in studies of herbaceous species [1,26]. In woody species, however, while a major contribution of SLA is supported by some studies [27,28], others find that NAR explains more of the variance in RGR [29]. The meta-analysis by Shipley [30] found that NAR was generally the best predictor of RGR, but that as light intensity decreased, the importance of NAR declined and the importance of SLA increased, at least in herbaceous species. The relationship between LMR and RGR is inconsistent, with many a non-significant relationships [31,32]. Therefore, explanations for the variance in RGR between growth forms using the components of RGR are currently contradictory and require further research using approaches that accounts for the effects of plant mass [33].

(c) Environmental variables

Although plants in longer studies had lower RGRs (figure 1b), duration did not improve the model for RGR (table 1), likewise pot volume was also removed from the model (see the electronic supplementary material, S2). There was a negative relationship between pot volume and RGR (figure 1c) possibly

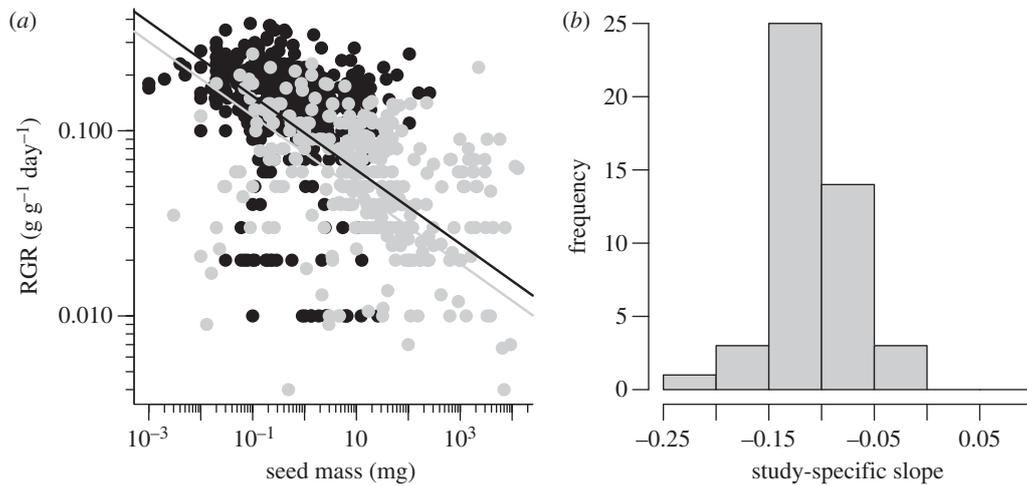


Figure 4. (a) Relationship between RGR and seed mass. Herb, black; woody, grey. The solid lines use the fixed effects from the final mixed-effects model (model 6, table 1). (b) Study-specific slopes for the log(RGR) versus log (seed mass) regressions.

Table 1. Model selection, for the linear mixed-effects model of RGR. RGR, seed mass and duration were all log transformed (base 10), KG, Köppen–Geiger climate classification. The terms in brackets indicate study-specific random effects. The (1|study) term specifies study-specific intercepts, the (seed mass|study) term specifies study-specific correlated slopes and intercepts, while (0 + seed mass|study) specifies study-specific uncorrelated slopes and intercepts. AIC and BIC are both measures of model fit, with different penalties on model complexity (the number of parameters estimated).

no.	model	AIC	BIC
1	RGR ~ seed mass + duration + growth form + KG + (seed mass study)	-275.3	-215.6
2	RGR ~ seed mass + growth form + KG + (seed mass study)	-277.2	-222.1
3	RGR ~ seed mass + growth form + (seed mass study)	-279.4	-238.1
4	RGR ~ seed mass + herb or woody + (seed mass study)	-293.4	-261.2
5	RGR ~ seed mass × herb or woody + (seed mass study)	-288.0	-251.2
6	RGR ~ seed mass + herb or woody + (1 study) + (0 + seed mass study)	-295.2	-267.7

Table 2. Parameters of the final mixed-effects model for variation in RGR (table 1; model 6).

fixed effects	estimate	s.e.	t-value
woody	-1.211	0.053	-23.052
herb	-1.012	0.054	-18.732
seed mass	-0.107	0.015	-7.084
random effects	variance	s.e.	
study	0.100	0.317	
seed mass	0.004	0.060	
residual	0.030	0.172	

because plants in large pots tend to be woody species in long-term experiments, which have a lower RGR (figure 1a). The effects of pot volume are unlikely to be a consequence of plants becoming pot bound, as study duration is typically too short for this to occur [34]. The lack of significant pot volume and duration effects is largely a consequence of these factors varying at the level of the study. Where there is within-study variation in pot volume, large effects are often found [34]. The regressions between pot volume, duration and other covariates indicate, unsurprisingly, that they are not independent, making it difficult to separate their effects (figure 1).

(d) Study

RGR varied between studies, for reasons beyond differences in species, seed mass and growth form. This suggests that details of the experimental protocol are important. Previous studies have also shown that other factors that vary between studies, for example light [35] and nutrients [36], also affect RGR, but that even after these variables are accounted for (as far as they can be), substantial variation remains [30]. To fully understand the physiological effects of the variables studied here and the relations between them, the development of a standardized experimental design should be considered. Standardized growth conditions would improve the integrity of comparisons between experiments and produce a clearer outcome across studies and species groups. This would enable more clear and specific conclusions to be drawn from comparative and meta-analyses. However, this may prove difficult on the global scale, as conditions that are optimal for one species may be very suboptimal for others. Encouraging the ecological community to adopt the same design, which may be difficult or expensive to implement in some environments, may also prove to be an insurmountable challenge.

5. Conclusion

RGR varied between growth forms, even at a given seed mass, particularly between the herbaceous and woody species.

However, there was little difference between the forbs and graminoids, and between the shrubs and trees. The slopes of the regressions between seed mass and RGR was the same for both herbaceous and woody growth forms, suggesting a consistent difference between the groups. Further work is required to understand why RGR has a common scaling in

these different groups, and to explain the magnitude of the difference between them.

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