

The community-level effect of light on germination timing in relation to seed mass: a source of regeneration niche differentiation

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Summary

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- Within a community, species may germinate at different times so as to mitigate competition and to take advantage of different aspects of the seasonal environment (temporal niche differentiation). We illustrated a hypothesis of the combined effects of abiotic and biotic competitive factors on germination timing and the subsequent upscale effects on community assembly.
- We estimated the germination timing (GT) for 476 angiosperm species of the eastern Tibetan Plateau grasslands under two light treatments in the field: high (i.e. natural) light and low light. We also measured the shift in germination timing (SGT) across treatments for all species. Furthermore, we used phylogenetic comparative methods to test if GT and SGT were associated with seed mass, an important factor in competitive interactions.
- We found a significant positive correlation between GT and seed mass in both light treatments. Additionally, small seeds (early germinating seeds) tended to germinate later and large seeds (late germinating seeds) tended to germinate earlier under low light vs high light conditions.
- Low light availability can reduce temporal niche differentiation by increasing the overlap in germination time between small and large seeds. In turn, reduced temporal niche differentiation may increase competition in the process of community assembly.

Introduction

The timing of germination can determine subsequent plant performance and success (Baskin & Baskin, 2001; Fenner & Thompson, 2005). Germinating earlier in the growing season, for instance, might permit a plant to grow larger and acquire more resources for reproduction (Verdú & Traveset, 2005; Donohue *et al.*, 2010). Germinating too early, however, might put a plant at risk of adverse environmental conditions, such as late spring frosts (Inouye, 2008). Thus, there is the potential for selection to act on germination to optimize its timing with respect to environmental conditions. Germination timing can also be mediated by species interactions (Dyer *et al.*, 2000; Geber & Griffen, 2003). Within a community, species may germinate at different times so as to mitigate competition and to take advantage of different aspects of the seasonal environment: this is known as temporal niche differentiation (De Luis *et al.*, 2008; Donohue *et al.*, 2010; Roscher *et al.*, 2011).

How species partition temporal niche space through germination timing will depend on the nature of competitive interactions between species. Both abiotic and biotic factors can influence

competition. For instance, resource limitation, such as low light, can modify competition dynamics and thereby influence temporal niche differentiation. Resource limitation can either directly intensify competitive interactions or act as an indirect cue of increased competition (Miller *et al.*, 1994). Earlier germination to avoid competition is therefore one expectation under limited resource conditions – especially among small, less competitive seeds. With regard to light availability, previous studies have found a general shift toward earlier germination under low light or crowded conditions for several species (Miller *et al.*, 1994; Dyer *et al.*, 2000; Weinig, 2000). However, studies of how germination timing shifts in response to light availability on a community-wide level are rare.

Biotic interactions might also affect germination timing by constraining competition along alternative niche axes (Geber & Griffen, 2003). For example, seed mass is a major biotic factor in plant competition (Rees, 1995; Coomes & Grubb, 2003; Muller-Landau, 2003). Larger seeds have a competitive advantage over smaller seeds because of their surplus resources (Turnbull *et al.*, 1999; Volis & Bohrer, 2013). Germinants from small seeds, therefore, may require a head start in growth in order to be

competitive with germinants from larger seeds (Winn & Miller, 1995). One might predict then that small seeds should germinate earlier than large seeds.

The interaction between competition and germination can have upscale effects on community assembly. The abiotic and biotic factors that influence germination time are also known to be important factors in community assembly in general. For instance, light availability can act as a filter that excludes species based on their tolerance of low or high light (Connell & Slatyer, 1977; Nevo, 1997; Fenner & Thompson, 2005; Hautier *et al.*, 2009; Willis *et al.*, 2010), with this filtering process often mediated at the germination and seedling stage (Van Couwenberghe *et al.*, 2013). By contrast, biotic interactions between species can limit the co-occurrence of ecologically or functionally similar species (Weiher & Keddy, 2001; Cavender-Bares *et al.*, 2004). As with abiotic filtering, the effects of biotic interactions are often mediated at the germination and seedling stage (Dyer *et al.*, 2000; Geber & Griffen, 2003). For instance, differential germination times may permit the co-existence of species that vary in seed mass – a proxy for competitive ability – over several orders of magnitude (Silvertown, 1981; Leishman & Westoby, 1994). How these abiotic and biotic factors might interact to effect germination timing and the subsequent implications for community assembly, however, remains largely unknown.

Given what we know about the effects of light availability and seed mass on germination timing, we have illustrated a hypothesis of the combined effects of these two competitive factors on germination timing and the subsequent upscale effects on community assembly (Fig. 1). The growing season in most seasonal communities is bounded by unfavorable conditions before the beginning of the season. Thus, if resource limitation (e.g. reduced light availability) causes a general shift toward earlier germination across all species, it will reduce the time available for temporal niche differentiation. The result will be greater overlap in germination timing among small and large seeds. This will increase biotic interactions that favor large seeds over small seeds, and ultimately reduce community diversity. The process is analogous to the loss of alpine habitat on mountaintops due to climate change (Gottfried *et al.*, 2012; Pauli *et al.*, 2012). As climate change permits low-elevation species to grow at higher altitudes, the available niche space of high-elevation species will be compressed, bounded by competition with low-elevation species on one edge and the top of the mountain on other. In the same way, we hypothesize that low light will compress the available temporal space for niche differentiation by ‘pushing’ the germination time of all species up against the being of the growing season.

Finally, the extent to which germination timing exhibits phylogenetic signal can influence broader patterns of phylogenetic community structure. Phylogenetic signal is the tendency for closely related species to share similar traits or niche preferences (Losos, 2008). The extent to which these shared traits or niche preferences underlie community assembly processes can shape patterns of phylogenetic relatedness within communities that is, phylogenetic community structure (Cavender-Bares *et al.*, 2009). Evidence for phylogenetic signal in both functional traits and niche preference in plants is now fairly common at broad phylogenetic scales

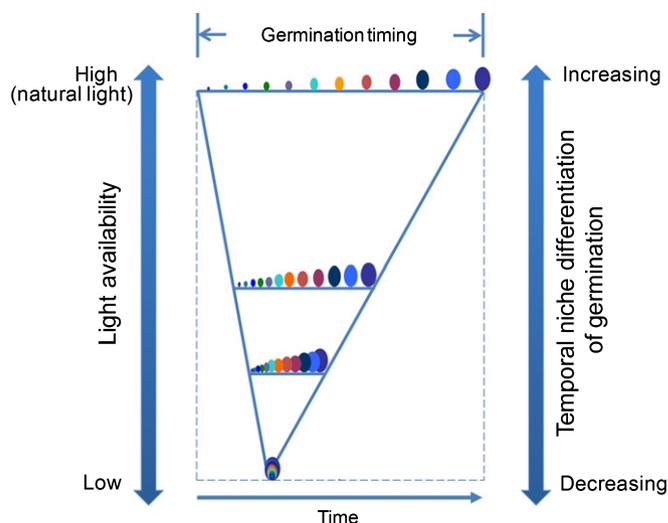


Fig. 1 Illustrated hypothesis of how light availability can influence temporal niche differentiation and subsequent biotic interactions. The ellipses represent seeds, different colors represent different species, and the ellipse size indicates seed mass. The x-axis represents time during a single growing season. As light availability decreases (left y-axis), so does the available temporal niche space (right y-axis). The consequence is greater overlap in germination timing between small and large seeds (bottom of y-axes). This will result in greater competitive interactions under low light conditions in favor of large seeds, as they tend to have a competitive advantage over small seeds.

(Prinzing, 2001; Crisp *et al.*, 2009; Norden *et al.*, 2009; Davies *et al.*, 2013; Cornwell *et al.*, 2014). These broad-scale patterns have been linked to patterns of phylogenetic community structure (Cavender-Bares *et al.*, 2006). In the only large-scale phylogenetic study of germination timing, Norden *et al.* (2009) reported that mean germination time for tropical trees exhibited significant phylogenetic signal across multiple tropical forest communities. Thus, at least to some extent, germination timing via temporal niche differentiation may have permitted greater phylogenetic diversity in these tropical forest communities than otherwise might have been expected. The extent to which additional competitive factors, such as resource limitation, might alter these dynamics, however, remains poorly understood.

In this study, we investigate how abiotic (light availability) and biotic (seed mass) competitive factors – both independently and in combination – affect germination timing across 476 species from the eastern Tibetan Plateau grassland. We interpret these results with regard to their impact on community assembly and phylogenetic community structure. Specifically, we address the following three questions. How does light availability affect the germination timing (GT) of species? Is seed mass correlated with GT and SGT? Finally, do GT, SGT and seed mass exhibit phylogenetic signal?

Materials and Methods

Study region

The study area is located on the northeastern verge of the Tibetan Plateau in China (101°05′–104°40′E, 32°60′–35°30′N, *c.*

40 000 km², see Fig. 2). The altitude ranges from 1200 to 4800 m a.s.l., and the climate is mainly alpine with a mean annual precipitation of 450–780 mm (mainly in summer and autumn) and a mean annual temperature of -4 – 9°C . The growing season general ranges from late April–late May to late October–early November. The grassland types are mainly alpine meadow and temperate/subalpine steppe, which are dominated by native monocotyledons (predominately species in the families Poaceae and Cyperaceae) and by native dicotyledons (predominately species in the families Ranunculaceae, Polygonaceae, Saxifragaceae, Asteraceae, Scrophulariaceae, Gentianaceae and Fabaceae). Sheep and yak have grazed these grasslands for centuries.

Seed collection

The 476 species (see species list in Supporting Information Table S1) used in this study included most of the common and dominant species found in the region. Seeds were collected from the field at the start of natural dispersal, in 2008. Seeds were collected from 20+ unique individual plants for the majority of species, and from all available unique individual plants for the remaining rare species. The collected seeds were allowed to air-dry to a constant mass at room temperature (*c.* 15°C) and were pooled across individuals of a species before being weighed and planted. Seeds were stored for 9–12 months to minimize the effects of primary dormancy (Holdsworth *et al.*, 2008). Körner (2003) documented that several months of quiescence (at room temperature) was sufficient to reduce dormancy and increased germination rates among many alpine and sub-alpine species.

Field germination experiment

The germination experiment was carried out at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University in the eastern Tibetan plateau, in Hezuo ($34^{\circ}55'\text{N}$, $102^{\circ}53'\text{E}$, see Fig. 2), Gansu, China, on a broad, flat site at 2980 m a.s.l. At the site specifically, the mean annual temperature is 2.0°C , ranging from -10°C in January to 11.7°C in July; the maximum temperature of the growing season is 23.6 – 28.9°C (see annual temperature of 2009 in Fig. S1). Mean annual precipitation over the previous 35 yr has been 532 mm, characterized by a short, cool summer. The area has 2294 h of sunshine and > 270 frost days per year. The vegetation is dominated by *Elymus* sp., *Roegneria* sp., *Scirpus* sp. and *Festuca* sp.

We tested germination under two light treatments: high light (100% unfiltered light, i.e. natural light) and a low light treatment manipulated with a plastic shade net. Based on the photosynthetic active radiation (PAR) at 1 cm above the soil surface under and outside the plastic shade net, light availability under low light treatment (mean PAR = $40675.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, SE = 3997.9) was only *c.* 2.9% of that of high light (mean PAR = $112946.8 \mu\text{mol m}^{-2} \text{s}^{-1}$, SE = 6419.7). PAR was recorded with a Decagon Sunfleck Ceptometer (Decagon, Pullman, Washington, DC, USA).

The temperature under the different light treatments differed by an average of 1.3°C (paired *t*-test: $t=11.00$, $df=110$, $P<0.0001$; noonday means with standard error for 111 d in June–September: high light, $17.9 \pm 0.46^{\circ}\text{C}$; low light $16.6 \pm 0.37^{\circ}\text{C}$). Furthermore, we have known that temperature can effect germination time (Baskin & Baskin, 2001). Thus, we recognize that temperature is a possible confounding effect on

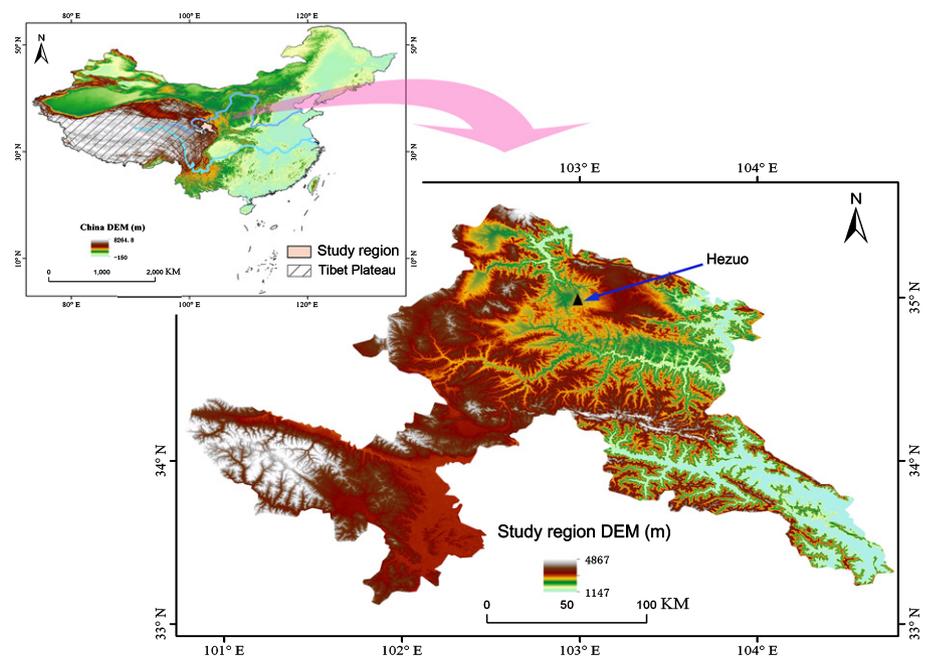


Fig. 2 Digital Elevation Map (DEM) of study region and China. The map in the upper left-hand corner highlights the complete range of the Tibetan plateau. The call-out in the lower right-hand corner highlights the study region. Hezuo, indicated with a blue arrow, is the site where the field germination experiment was carried out (2980 m a.s.l.).

our estimates of germination timing. Most studies, however, have found that germination was earlier under increased temperature (e.g. Bierhuizen & Wagenvoort, 1974; Garcia-Huidobro *et al.*, 1982). In our study, we found that germination was relatively later under the high light (higher temperature) treatment (see the Results section), suggesting that the effects of temperature on germination timing were minimal with respect to the effects of light availability in our experiment.

For each treatment, we germinated 300 seeds of each species, distributed over three replicate pots per species (i.e. for each species there were: 100 seeds \times 3 pots \times 2 treatments). Seeds were placed on gray cotton fabric on top of local soil (see soil information in Table S2) in plastic pots. Seeds were germinated on cotton fabric because it made scoring of germination easier, prevented the germination of contaminated seeds within the soil, and kept seeds from becoming buried which may have biased germination timing measurements. The pots were kept in plastic pools (see photographs of experimental facilities in Fig. S2). Germination at high elevation is restricted mainly to short periods in late spring and early summer, with many species germinating as soon as conditions are suitable (Bliss, 1971; Körner, 2003). To match the growing season, we began our germination trials as soon as conditions and practicality allowed (9 June 2009) and monitored seeds for germination time through late fall (30 September 2009) for a total of 114 d. Every day, the number of germinated seeds was recorded and newly emerged seedlings were removed from the pots. The pools were regularly watered and always full of water to keep the soil and grey cotton fabric wet. A seed was considered germinated when the radicle was visible. In addition, to avoid seeds being washed out by rain, we covered the plots with tarpaulins at night and on rainy days. Before the conclusion of the experiment, we tested the viability of seeds (three replicates of 50 seeds for each species) using a tetrazolium test (Hendry & Grime, 1993). Final germination proportion (GP, or 'germination fraction') for each species was calculated as the number of germinates divided by the total number of viable seeds (Fig. S3). Germination proportion is an estimate of dormancy within a species, and thus corrects for the bias dormancy might have on our estimate of germination timing.

Seed mass, germination timing and shift

Seed mass was defined as the weight of the embryo, endosperm and seed coat or fruit coat (e.g. Asteraceae seeds of which we cannot separate fruit coat from seed coat). Accessories (e.g. wings, comas, pappus, elaiosomes, fruit flesh) were not included in measures of seed mass (Cornelissen *et al.*, 2003). We weighed 100 seeds from pooled collections three times for each species, and then took the mean divided by 100 as seed mass.

We calculated germination timing (GT, days post planting) using the following formula:

$$GT = \sum (G_i \times i) / \sum G_i$$

(i , number of days between seed sowing (day 0) and seed germination; G_i , number of seeds germinated on day i). As calculated,

GT corresponds to the mean germination time of the fraction of seeds that germinated, and does not factor in seeds that failed to germinate. We calculated GT for all species within each light treatment (GT_{low}, germination timing under low light treatment; GT_{high}, germination timing under high light treatment).

We calculated germination timing shift (SGT) between the above two treatments as the value of GT_{low} – GT_{high} for each species. For SGT, values below 0 indicate earlier germination under low light conditions whereas values above 0 indicate earlier germination under high light.

Before analyses, seed mass (mg) and GT (days) were log-transformed to optimize normality of frequency distributions. The final GP was logit-transformed $\{\log_{10}[x/(1-x)]\}$ (Warton & Hui, 2011).

Phylogeny construction

A composite phylogeny of all species was constructed with Phylo-matic v3 (Webb & Donoghue, 2005) based on the angiosperm megatree (R20091120.new). This tree was further resolved based on the Angiosperm Phylogeny Website v12 (Stevens, 2001 onwards). Branch lengths were made proportional to time using the 'bladj' function in the program Phylocom 4.0 (Webb *et al.*, 2008) and divergence time estimates based on fossil data (Bell *et al.*, 2010; Smith *et al.*, 2010).

Correlations of GT and SGT with seed mass

We used both standard linear regression and phylogenetic generalized linear models (PGLM) to test if GT and SGT were correlated with seed mass. Standard linear regression was conducted using the 'lm' functions of the R package 'stats' (R Core Team, 2013). Phylogenetic generalized linear models control for the effects and degree phylogenetic signal in the dependent variable (Revell & Harrison, 2008). Phylogenetic generalized linear models were conducted using the 'plgs' functions of the R package 'caper' v0.5 (Orme *et al.*, 2012). For the PGLM, λ was estimated for the dependent variable using a maximum likelihood framework.

Seed mass and germination time are both associated with a suite of life-history traits such as life form, dispersal mode, adult plant height and flower timing (Mazer, 1989; Leishman & Westoby, 1994; Bu *et al.*, 2008; Chiang *et al.*, 2009), as well as with maternal habitat (Donoghue, 2009; Guo *et al.*, 2010). These associations can potentially confound the relationship between seed mass and germination time. Therefore, when examining the relationship of GT or SGT with seed mass, we controlled for variation in life-history traits (life form, plant height, dispersal mode, onset of flowering and duration of flowering; see description in Notes S1) or maternal habitats (elevation, water in maternal habitat and light in maternal habitat; see description in Notes S1) by using residuals. For example, the residuals of GT on life form and the residuals of seed mass on life form were used in bivariate regressions to examine the relationship between GT and seed mass, independent of variation in life form, using standard linear regression.

Additionally, we also controlled for the effect of final GP on germination timing. Similar to how we controlled for life-history traits above, the residuals of GT on GP were used in regression analysis of the effects of seed mass on $GT_{\text{residuals}}$.

Finally, we also used both standard linear regression and PGLM to test if SGT was correlated with GT in both the high light and low light treatments.

Phylogeny signal

We tested for phylogenetic signal in GT, SGT and seed mass by estimating Pagel's λ with the 'fitContinuous' function in the R package 'geiger' v1.99-3 (Harmon *et al.*, 2013), which uses a maximum likelihood framework to estimate the parameter λ . Pagel's λ can vary from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal) (Pagel, 1999; Freckleton *et al.*, 2002). We tested for the significance of phylogenetic signal against the assumption of no signal ($\lambda = 0$) using a likelihood ratio test.

In order to visualize the distribution of GT, SGT and seed mass across their community phylogeny, we use the 'contMap' function in the R package 'phytools' v0.3-10 (Revell, 2012). The function estimates the ancestral states of each internal node using maximum likelihood, and subsequently interpolates these states along branch.

Sensitivity analyses

In order to test the robustness of our results to uncertainties associated with branch-length estimates, we ran our analyses on the same composite tree, but with different node age estimates from Wikström *et al.* (2001). Also we tested the sensitivity of our results to phylogenetic uncertainty in topology (Donoghue & Ackerly, 1996). All of our analyses were run across a set of 50 trees with polytomies from the main tree randomly resolved. Polytomies were resolved using the program Mesquite v2.75 (Maddison & Maddison, 2011).

Results

Under the high light treatment, GT ranged from 2.9 to 92.5 d, while under the low light treatment, GT ranged from 2.6 to 95.3 d (Fig. 3a). The resulting SGT ranged from -44.9 to 23.6 d (Fig. 3b). Seed mass varied from 1.1×10^{-2} to 37.6 mg (Fig. 3c). On average, across all species, the low light treatment significantly accelerated GT by a mean of 4.8 d (paired *t*-test: $t = 16.05$, $df = 475$, $P < 0.0001$, Fig. 3a).

For both standard linear regression and PGLM analyses, GT was significantly positively associated with seed mass in both light treatments (Fig. 4a,b; Table 1). Those relationships were also significant when controlling for variation in life-history traits, maternal habitats or final GP that are known to affect germination timing (see detail in Figs S4, S5).

Shift in germination timing and seed mass were significantly negatively correlated for both standard linear regression (Fig. 4c) and PGLM analyses (Table 1); that is, small seeds tend to germinate later under low light vs high light conditions, while large

seeds tend to germinate earlier (Fig. 5). This relationship was significant even when controlling for life-history traits and maternal habitats that are known to affect germination timing (see detail in Fig. S4).

For both standard linear regression and PGLM analyses, SGT was significantly negatively correlated with GT under the high light treatment (Table S3); that is, under high light, early germinating seeds tend to germinate later, while late germinating seeds tend to germinate earlier when grown under low-light conditions. However, SGT was significantly positively correlated with GT under the low light treatment only when using PGLM analyses (Table S3).

There was significant phylogenetic signal in GT under both light treatments (Table 2, Figs S6, S7). There was significant phylogenetic signal in SGT (Table 2, Fig. S8) and seed mass (Table 2, Fig. S9).

In general, our results were robust to phylogenetic sensitivity analyses (Tables S4–S7).

Discussion

We investigated the combined effects of abiotic and biotic competitive factors on germination timing across 476 angiosperm plants from the eastern Tibetan Plateau grassland. We found that germination timing (GT) was dependent on abiotic competitive environment (high light vs low light), with species generally germinating earlier under resource-limited (low light) conditions. We also found that GT was positively associated with seed mass, as predicted under conditions where seed mass positively correlates with competitive ability. In combination, the effect of low light appears to conflict with the effect of seed mass on germination timing, restricting the available temporal niche space and likely increasing biotic competition among species. We found significant phylogenetic signal in GT, SGT and seed mass. The phylogenetic distribution of GT, SGT and seed mass in combination with the effects of competition on germination timing is likely to have upscale effects on patterns of community structure.

As predicted, we found that germination was earlier under conditions of low resource availability (low light). Earlier germinants will not only have a head start in terms of growth, but also a head start in accessing the limited resources available (Kalisz, 1986). Under conditions of limited resources, that advantage of early germination will likely be exaggerated (Ross & Harper, 1972; Stanton, 1985; Wallre, 1985; Wilson, 1988; Streng *et al.*, 1989; Jones *et al.*, 1994; Miller *et al.*, 1994; Dyer *et al.*, 2000; Verdú & Traveset, 2005). Thus, early germination has evolved in part to reduce competition for limited resources for individuals, but it may have increase interspecies competition at the community level (see later discussion).

The positive correlation of GT with seed mass we found is consistent with several previous studies (Silvertown, 1981; Norden *et al.*, 2009). It is well documented that seed mass can mediate competitive interactions, where large seeds tend to have a competitive advantage over small seeds (Turnbull *et al.*, 1999; Volis & Bohrer, 2013). One explanation for the positive

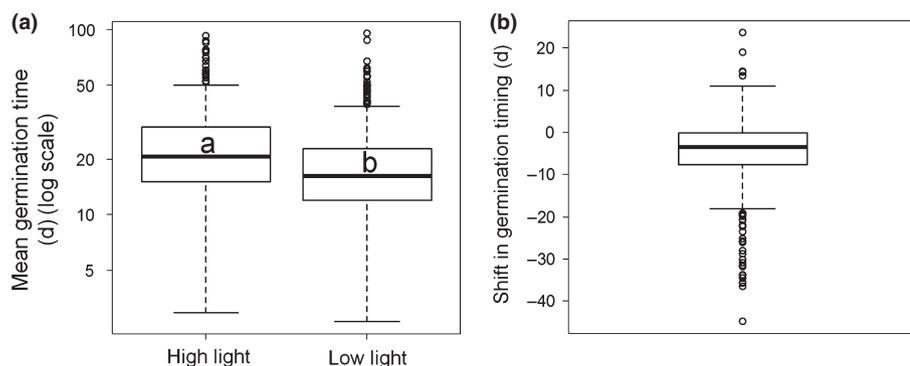


Fig. 3 Box plot of the variation in (a) germination timing under high light and low light treatments, (b) shift in germination timing across treatments, and (c) seed mass. The ends of the box represent the first and third quartiles and the middle line represents the median. The error bars indicate 1.5-fold the interquartile range. The different lowercase letters in (a) indicate significant differences of germination timing in the high light and low light treatment. The significance was tested using the paired *t*-test.

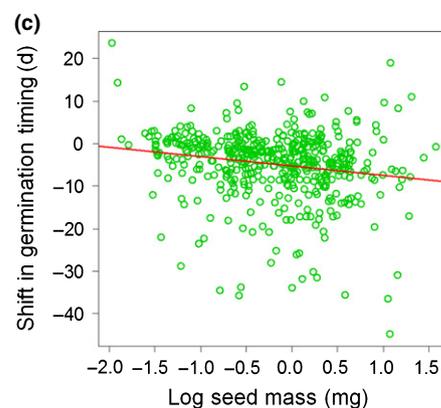
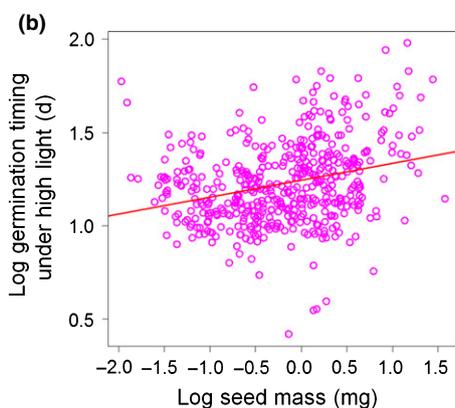
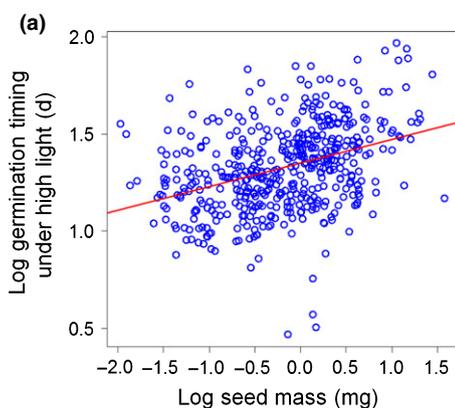
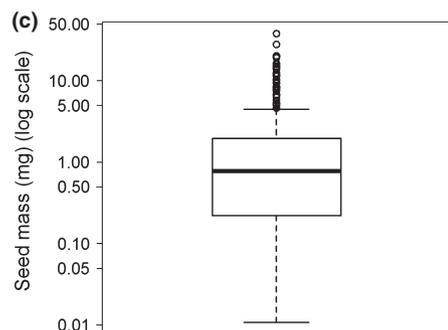


Fig. 4 Linear regression analysis of germination timing and shift in germination timing with seed mass across 476 species. (a) Germination timing under high light treatment and seed mass ($\beta = 0.12$, $R^2 = 0.14$, $P < 0.0001$); (b) germination timing under low light treatment and seed mass ($\beta = 0.090$, $R^2 = 0.078$, $P < 0.0001$); (c) shift in germination timing and seed mass ($\beta = -2.2$, $R^2 = 0.03$, $P < 0.0001$). The red line indicates the slope estimate (β) for each regression. See Table 1 for phylogenetic linear regression results.

association between seed mass and GT, then, is that small seeds germinate earlier to either avoid competition with or get a head-start over large seeds. There are alternative explanations for the pattern we observed that do not necessarily invoke direct competition. Norden *et al.* (2009) suggested that the positive relationship between germination timing and seed mass is the result of biophysical constraints and proposed several possible mechanisms that could account for this pattern.

Another possible explanation is that small seeds have limited ability to 'escape' from the soil, and thus need to germinate early to avoid being buried. Small seeds generally need more light to germinate and have limited ability to emerge from deep layers of soil (Harper & Obeid, 1967; Wallre, 1985; Maun & Lapierre, 1986; Wulff, 1986; Milberg *et al.*, 2000; Pons & Fenner, 2000; Fenner & Thompson, 2005), and also can be easily lost in the

cracks or deep layers of soil following disturbance (Thompson *et al.*, 1993; Bekker *et al.*, 1998). Additionally, there is evidence that smaller seeds have relatively low viability in the soil and post-dispersal seed survivorship (Lee *et al.*, 1991; Osunkoya, 1994; Blate *et al.*, 1998; Moles *et al.*, 2003; Yu *et al.*, 2007), contrary to the traditional view (Harper *et al.*, 1970; Janzen, 1971; Harper, 1977; Louda, 1989). Thus, on the one hand, selection may favor a strategy of rapid or early germination in small seeds to avoid being buried in deep layers of soil from which they cannot emerge. On the other hand, the fact that small seeds easily move into, but have difficulty emerging from, deep soil layers may also select for the ability of small seeds to survive for long periods in the soil seed bank.

Whether the positive relationship between seed mass and germinating timing is the result of biotic competitive interactions or

Table 1 Linear regression analysis of germination timing and shift in germination timing with seed mass across 476 species using phylogenetic generalized linear models

Dependent variable	Predictor variable	β	P	F	R^2
Log GT_{high}	Log seed mass	0.094	< 0.0001	35.6	0.070
Log GT_{low}	Log seed mass	0.059	< 0.00016	14.6	0.030
SGT	Log seed mass	-2.46	< 0.00050	12.3	0.025

GT_{high} , germination timing under high light treatment; GT_{low} , germination timing under low light treatment; SGT, shift in germination timing. Significant P -values are indicated in bold type. See Fig. 4 for nonphylogenetic linear regression results.

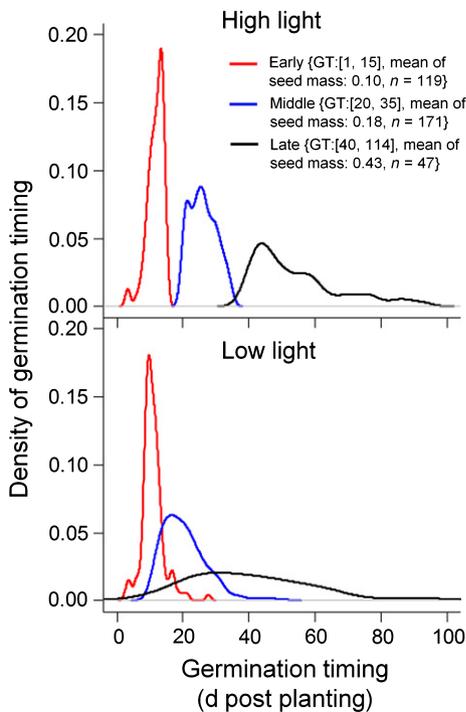


Fig. 5 The effect of high light and low light treatments on the overlap of germination timing in relationship to seed mass. Based on germination timing (GT, see Supporting Information Table S1) under the high light treatment, species were categorized into three groups: early germinates (red), middle germinates (blue) and late germinates (black). The range of germination timing for each group is included in the key in brackets. The mean seed mass of each group is also included in the key. Under low light, larger seeds germinated earlier, compressing the temporal niche. These results support the hypothesis illustrated in Fig. 1. n , number of species within each group.

other evolutionary or ecological factors, it nonetheless has the effect of mitigating competition between small and large seeds. Consequently, it is a mechanism that permits greater diversity in a community and, therefore, is important for understanding community assembly.

Our results support our hypothesis (Fig. 1) that abiotic competitive factors reduce the available temporal niche space and increase the potential for biotic competition in favor of large seeds. In both light conditions, small seeds germinated earlier than large seeds, indicating that species were sorting along

Table 2 Phylogenetic signal of germination timing traits and seed mass

Trait	n	λ	$Log_e L_{obs}$	$Log_e L_0$	$Log_e L_1$	λ 95% CI
Log GT_{high}	476	0.83	151.6	40.9***	116.7***	0.75, 0.92
Log GT_{low}	476	0.85	175.0	47.6***	147.1***	0.77, 0.93
SGT	476	0.82	-1638.0	-1673.7***	-1662.7***	0.73, 0.93
Log seed mass	476	0.98	-302.5	-488.0***	-305.8*	0.97, 1.00

n , number of species; $Log_e L_{obs}$, log-likelihood estimate of observed λ ; $Log_e L_0$, log-likelihood estimate with λ set to 0 (no phylogenetic signal); $Log_e L_1$, log-likelihood estimate with λ set to 1 (maximum phylogenetic signal); GT_{high} , germination timing under high light treatment; GT_{low} , germination timing under low light treatment; SGT, shift in germination timing. Phylogenetic signal was estimated as Pagel's λ using a maximum likelihood framework.

*, $P < 0.05$; ***, $P < 0.0001$.

temporal niche axis partly due to seed mass (Figs 1, 5). However, small seeds (early germinating seeds) tended to germinate later and large seeds (late germinating seeds) tended to germinate earlier under low light vs high light conditions (Fig. 5). That is to say, under low light conditions, the temporal niche space was compressed, with small seeded species and large seeded species shifting toward each other with respect to their germination time (Fig. 5). Because large seeds have a competitive advantage – an advantage that may be even more intense in conditions of low resource availability (reviewed in Leishman *et al.*, 2000 and Volis & Bohrer, 2013) – the net effect is that the compressed temporal niche space will likely favor species with large seeds.

Species with relatively large seeds are often associated with low light habitats (reviewed in Guo *et al.*, 2010). Light availability usually decreases along the succession gradient, with shade-tolerant, large-seeded species appearing in later succession stages (Connell & Slatyer, 1977). In the Tibetan Plateau grassland specifically, Chu *et al.* (2007) found that large-seeded species were more abundant than small-seeded species in the late phase of succession. Light availability also decreases with eutrophication (Hautier *et al.*, 2009; Yang *et al.*, 2012). Again, large-seeded species have been documented as more common in heavily fertilized communities of the Tibetan Plateau grasslands (X. Zhou *et al.*, unpublished). Previous studies have often attributed the absence of small seeds in shade habitats to the lack of seed resources sufficient to support their post-germination success (reviewed in Leishman *et al.*, 2000). Our results suggest, however, that the absence of small seeds in shade habitats may have resulted from low light compressing the temporal niche space and increasing biotic competition among species in favor of those with large seeds.

In the Tibetan Plateau grassland, we found that closely related species share similar temporal niche preferences (i.e. germination times) and competitive ability at germination (i.e. seed mass). These results confirm previous findings of phylogenetic signal in both germination timing (Norden *et al.*, 2009) and seed mass

(Moles *et al.*, 2005). We also report the novel result that shift in germination time in response to light availability exhibits significant phylogenetic signal. That this response to light is shared among closely related species suggests that, at some level, the genetic or physiological mechanisms that regulate germination response to light may themselves be phylogenetic conserved. With regard to community assembly, temporal niche differentiation in germination timing may permit greater phylogenetic diversity in the Tibetan Plateau grassland. By contrast, the compression of temporal niche space under low light might result in the phylogenetically biased exclusion of species with small seeds, resulting in reduced phylogenetic diversity and greater phylogenetic clustering. It is not clear, however, if patterns of phylogenetic community structure at the germination stage will translate into similar patterns of phylogenetic community structure at the adult stage. For instance, Webb *et al.* (2006) found that among Bornean rain forest tree communities, phylogenetic structure at the seedling stage did not necessarily carry over to the sapling stage. Whether similar dynamics apply to the eastern Tibetan Plateau grasslands, which are dominated not by trees, but by grasses and herbs, will require further long-term investigation.

Conclusions

We found that there are significant effects of abiotic (light availability) and biotic (seed mass) competitive factors on germination time (GT) across 476 angiosperm plant species from the Tibetan Plateau grasslands. These effects remained even after accounting for additional life-history traits, maternal habitats and phylogenetic signal. When considered in combination, by examining the shift in germination timing across light environments (SGT), we found that limited resources (i.e. low light availability) reduce temporal niche differentiation by increasing the overlap in germination time between small and large seeds. In turn, the reduced temporal niche differentiation may increase competition in the process of community assembly. Interpreting plant community composition and ecosystem function from plant traits is a major research challenge and focus in ecology (Shipley, 2010; Webb *et al.*, 2010). Seed mass is one of a core list of plant traits for functional ecology (Westoby, 1998; Weiher *et al.*, 1999; Westoby *et al.*, 2002). Thus, it will be valuable to examine temporal germination niche differentiation in relation to seed mass along other environment gradients (e.g. rainfall and soil fertility) in future studies. They, together with this study, will increase our ability to understand the vegetation construction and phylogenetic community structure as a function of germination, a major component of a plant's life cycle. Additionally, this study is the first to show that shift in germination timing in response to light availability exhibits significant phylogenetic signal.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Mean temperature, maximum temperature and minimum temperature during each month of 2009 for the experimental location.

Fig. S2 Photographs of experimental facilities.

Fig. S3 Box plot of final germination proportion for each treatment.

Fig. S4 Bivariate regression analysis across 476 species using standard linear regression.

Fig. S5 Relationship between germination timing and seed mass independent of variation in germination proportion using standard linear regression.

Fig. S6 Visualization of distribution of germination timing under high light treatment (GT_{high}) across community phylogeny.

Fig. S7 Visualization of distribution of germination timing under low light treatment (GT_{low}) across community phylogeny.

Fig. S8 Visualization of distribution of shift in germination timing (SGT) across community phylogeny.

Fig. S9 Visualization of distribution of seed mass across community phylogeny.

Table S1 Species list and dataset

Table S2 Soil properties of the soil used in this study

Table S3 Linear regression analysis of germination timing with shift in germination timing across 476 species using standard linear regression and phylogenetic generalized linear model (PGLM)

Table S4 Phylogenetic signal of germination timing traits and seed mass using a phylogeny with branch lengths adjusted using

alternative estimated divergence times from Wikström *et al.* (2001)

Table S5 Phylogenetic signal of germination timing traits and seed mass over 50 trees with randomly resolved polytomies

Table S6 Results for bivariate regression analysis using phylogenetic generalized linear model (PGLM) using a phylogeny with branch lengths adjusted using alternative estimated divergence times from Wikström *et al.* (2001)

Table S7 Results for bivariate regression analysis using phylogenetic generalized linear model (PGLM) over 50 trees with randomly resolved polytomies

Notes S1 Characterization of life-history traits and maternal habitats.

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