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Authors: Bu, HaiYan, Du, GuoZhen, Chen, XueLin, Wang, Yifeng, Xu, XiuLi, et al.

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The Evolutionary Significance of Seed Germinability in an Alpine Meadow on the Eastern Qinghai-Tibet Plateau

HaiYan Bu†

GuoZhen Du‡

XueLin Chen§

Yifeng Wang¶

XiuLi Xu# and

Kun Liu$

*Department of Ecology, Lanzhou University, South Tianshui Road 222, Lanzhou 730000, P. R. China
†bohy@lzu.edu.cn
‡Corresponding author: guozdu@lzu.edu.cn
§chenxuelin63@yahoo.com.cn
¶wangyifeng6481@yahoo.com.cn
#xxl5188@163.com
$liukun01@st.lzu.edu.cn

Abstract

In this study, we created a database of 633 species collected from alpine meadows on the eastern Qinghai-Tibet Plateau, and considered the correlation of interspecific seed germinability variation with ecological, life-history, and phylogenetic background. We found that taxonomic membership accounted for the majority of the weighted germination index (WGI) variation (71%). The strong taxonomic effect suggests that WGI variation within taxonomic membership is constrained, and a large proportion of WGI variation is explained by life-history traits also correlated with taxonomic membership. The overlap does not negate the adaptive significance of the relationship between these life-history traits and germinability. In addition, the altitudes and habitats when considered first had no significant effect on seed germinability variation, but we found that there were significant interactions between altitudes (or habitats) and some phylogenetic groups. Although their interactions were all less than the main effects of phylogenetic groups, they could explain that the effect of phylogenetic constraint on seed germination was also impacted by environmental factors. Thus, we could not exclude the effect of longtime selection by environmental factors on seed germination, and we think interspecific seed germinability variation was affected by phylogenetic, life-history, and ecological factors together.

Introduction

Seeds are a critical component of the life history of higher plants, providing the main opportunity for a species to disperse to new habitats and escape from adverse conditions in space and time. Given that seeds perform a similar function in all plants, it is remarkable that seed germinability varies extensively. For example, viviparous seeds (e.g. mangrove trees) often germinate inside the ripe fruit, while still on the mother plant (Figueroa and Armesto, 2001); however, seeds of many desert plants remain dormant and viable, while buried in the soil for years or decades after dispersal (Venable and Lawlor, 1980).

It has been argued theoretically that low germinability would be associated with life history attributes such as seed size (Thompson and Grime, 1979; Venable and Lawlor, 1980; Grime et al., 1981; Venable and Brown, 1988; Rees, 1993, 1994; Cater and Ungar, 2003), seed dispersal mode (Garwood, 1983), longevity of plant (Thompson, 1987), and life form (Figueroa and Armesto, 2001).

Additional evidence about factors controlling seed germination derives from studies of taxonomically related species. According to recent studies, it is reasonable to expect that, within a family or a genus, seed germination could be affected by phylogenetic constraints and developmental allometries that limit segregation (Baskin et al., 1993; Baskin and Baskin, 1998, 2004; Figueroa and Armesto, 2001; Nikolaeva, 1999; Smith-Ramírez et al., 1998). These examples lend support to the hypothesis that germination strategies can be stable evolutionary traits, thus constraining interspecific variation in germination behavior.

In addition, with differences in precipitation and temperature, geographically related variation in germination response is common among widespread plants (Lord, 1994), and populations in different environments may have experienced different selection pressures on germination behavior (Lord, 1994). Altitude is a likely factor to be associated with seed germination variation among populations, and variations in germination of different species have been observed in relation to altitude (Miller and Cummins, 1987; Holm, 1994; Vera, 1997). Seed germination has also been found to be influenced by other growth conditions such as moisture and temperature (Moles and Westoby, 2004; Jurado and Flores, 2005).

Despite the large number of empirical studies on seed germination, very few studies have been conducted to test seed germination in a whole plant community. Furthermore, these studies mainly focused on vegetation in tropical (Garwood, 1983) and temperate zones (Figueroa and Armesto, 2001), and the seed germinability of plants in alpine meadows remains poorly understood. We believe the study of germination of seeds collected from one community at the same time could provide important information that would improve our understanding of community dynamics. Therefore, we expect to advance our understanding on phylogenetic, life-history, and ecological factors regulating seed germinability in plant communities. In this study, we created a database of 633 species (involving 10 classes, 48 families, and 205 genera) collected from alpine meadows on the eastern Qinghai-Tibet Plateau. The following questions were addressed: (1) To what extent could seed germinability be correlated with phylogenetic membership, life-history traits (life form, seed size, and dispersal mode), and environmental factors (altitude and habitat)? (2) To what extent were correlations between seed germinability and taxonomic membership also correlated with sets of niche-

related traits? (3) Was interspecific germinability variation constrained by environmental factors, life-history traits, or phylogenetic background? Were these factors independent or did they interact?

Materials and Methods

STUDY SITE

The study was conducted on the eastern Qinghai-Tibet Plateau (34°–35°70′N, 101°–103°E). The altitude ranges from 2800 to 4200 m, and the climate is cold Humid-Alpine with mean annual rainfall of 450–780 mm. Mean annual temperature is 1.2°C, –10.7°C in January and 11.7°C in July, and there are on average 270 frost days a year. The grassland type mainly belongs to alpine meadow (59.32%), which is dominated by many monocotyledons, for example, Poaceae and Cyperaceae, and various dicotyledons, such as Ranunculaceae, Polygonaceae, Saxifragaceae, Asteraceae, Scrophulariaceae, Gentianaceae, and Fabaceae.

THE DATABASE

In this study, we built up a database of 633 species that included 10 classes, 48 families, and 205 genera collected from alpine meadows on the eastern Qinghai-Tibet Plateau (Appendix [available free of charge at MetaPress: http://instaar.metapress.com/content/120707 or at BioOne: http://www.bioone.org/perlserv/?request=get-archive&issn=1523-0430]). The sample represented 65% of the species, 50% of the genera, and 50% of the families reported from the area. Species collected included not only native but also introduced ones. Seeds were collected at the start of natural dispersal for each species from July to October in 2004. Enveloped seeds were spread on tables and allowed to air-dry at room temperature (approximately 15°C) before being weighed. Seed mass was defined as that of the embryo and endosperm, plus the seed coat. Structures having the function of contributing to dispersal (appendages, fruit coat in some cases) were not included as part of the seed mass. Seeds were pooled by species, and we randomly selected 3 subsamples of 100 seeds from the pooled samples. The average weight of the 3 subsamples was used as seed size variable. The germination experiment was started on the middle 10 days of March (starting season of field germination) in 2005. Seeds were placed in covered Petri dishes (9 cm diameter) on double layers of moistened filter paper, and then placed in temperature chambers (made in Canada) at a diurnal fluctuation of 15°C (20°C day/5°C night; 12 h/12 h) with 24-h darkness (the effect of light was not considered) and a relative humidity of about 70%. The temperature of the germination trial resembled natural conditions for April and May: it approximated the daily maximum and minimum temperatures at the 5-cm depth in soil. Three replicates of 50 seeds were incubated for each species. Every day, the number of germinated seeds was recorded, newly emerged seedlings were removed from the Petri dishes, and the seeds were regularly watered with distilled water. A seed was considered germinated when the radicle was visible. Germination was counted for 60 days.

STATISTICAL ANALYSES AND COMPARATIVE METHOD

A weighted germination index (WGI) as described by Reddy et al. (1985) was calculated with maximum weight given to the seeds germinating early and less to those germinating late. Larger WGI values mean early percentage.

$$WGI = [60 \times n_1 + 59 \times n_2 + \ldots + 1 \times n_{60}]/(60 \times N) \quad (1)$$

where n_1, n_2, …, n_{60} are the number of seeds that germinated on 1st, 2nd, and subsequent days until the 60th day, respectively; 60, 59, ……, 1 are the weights given to the seeds germinated on 1st, 2nd, and subsequent days until the 60th days. N is the total number of seeds placed in incubation.

In addition, we used tetrazolium chloride (0.1% TTC) to test seed viability. We computed the percent of alive seeds of each species that were used to amend the value of WGI. Then the final WGI value was the product of experimental value of WGI and the percent of alive seeds of each species.

For multifactorial ANOVAs of seed germinability, we grouped these species in various major categories, defined as follows:

(1) Phylogenetic groups: Several phylogenetic classifications of flowering plants based on molecular and morphological traits are available. We used the Angiosperm Phylogeny Group II (2003) to assign the affiliation of each species to higher levels because it is the most complete and updated molecular phylogeny available. The species in the studied flora were grouped into the following ten groups: 1. monocots (2 families, 3 genera, and 16 species); 2. commelinids (3 families, 25 genera, and 73 species); 3. eudicots (3 families, 17 genera, and 63 species); 4. core eudicots (6 families, 20 genera, and 82 species); 5. rosids (2 families, 6 genera, and 9 species); 6. eurosids I (10 families, 31 genera, and 99 species); 7. eurosids II (3 families, 14 genera, and 28 species); 8. asterids (3 families, 5 genera, and 14 species); 9. euasterids I (10 families, 36 genera, and 119 species); and 10. euasterids II (6 families, 48 genera, and 130 species).

(2) Life-history categories: (a) Life form_species in the flora were grouped into three classes: annuals (168 species, including a few biennials), perennial herbs (417 species), and woody plants (48 species). (b) Seed size_seeds were sorted by weight into eight size classes conformed to those of Baker (1972): 0.010–0.031 mg (14 species), 0.032–0.099 mg (74 species), 0.100–0.315 mg (111 species), 0.316–0.999 mg (163 species), 1.000–3.161 mg (162 species), 3.162–9.999 mg (72 species), 10.000–31.611 mg (32 species), and 31.612–99.999 mg (5 species). (c) Dispersal mode_species in the flora were classified into the following five large groups according to the morphological features of their seeds (Leishman et al., 1995): unassisted (441 species, no obvious morphological structure), ant-adapted (34 species, with an elaiosome), adhesion-adapted (23 species, with hooks, spines or barbs), wind-adapted (108 species, with wings, hairs, or a pappus), and vertebrate-adapted (27 species, with an aril or flesh).

(3) Environmental factors: (a) The altitudes as the categorical variable were divided into five classes: <2500 m, 2501–2850 m, 2851–3350 m, 3351–3700 m, and >3700 m. (b) The habitats were classified into four categories: bottomland, shrub, north slope, and south slope.

WGI was arcsine square root transformed before statistical analysis to ensure homogeneity of variance. Both phylogenetic and ecological correlates of seed germination were taken into account in the present study. All analyses were performed with SPSS 12.0.

First, one-way ANOVAs estimated the main effect of each factor on the variance of seed germinability. Second, two-way

TABLE 1

The effects of phylogenetic groups, life-history traits, and environmental factors on variation in mean WGI.

Source of variation	d.f.	F	P	R^2
Phylogenetic groups				
Class	9	5.53	<0.001	0.07
Order	21	6.31	<0.001	0.19
Family	47	7.52	<0.001	0.38
Genus	204	4.77	<0.001	0.71
Life-history traits				
Life form	2	4.80	0.009	0.02
Seed dispersal mode	4	20.78	<0.001	0.12
Seed size	7	7.72	<0.001	0.08
Environment factors				
Altitude	4	1.01	0.40	0.01
Habitat	3	1.36	0.26	0.01

ANOVAs were performed on the same data to assess the interactions between phylogeny groups and environmental factors. The phylogeny groups used for two-way ANOVAs included classes and families within classes (the number of families was over three). Finally, the GLM procedure was used to examine the independent effects of taxonomic membership and life-history traits on variation in seed germinability. We fitted a series of general linear models to the data set. A GLM on a categorical variable is equivalent to a one-way ANOVA. The type III sum of squares was used to establish the significance level of each effect because the data were unbalanced. Variables can be fitted sequentially, where R^2 measures the proportion of seed germinability accounted for by that variable when considered first, when considered after each other variable, and when considered last after all other variables, while the F-ratio tests the significance of the variation accounted for. If a variable has significant explanatory power even when fitted after other variables, it can be said to be independently associated with seed germinability. On the other hand, a case in which a variable has explanatory power when fitted first, but none when fitted after other variables is consistent with an interpretation whereby the first variable's association with seed germination arises from a secondary correlation via the third variable (Lord et al., 1995; Leishman et al., 1995). Four kinds of GLM were used in our analysis: the first included family membership, life form, and seed dispersal mode; the second included family membership, life form, and seed size; the third included family membership, seed size, and dispersal mode; the last included life form, seed size, and dispersal mode.

Results

SEED GERMINABILITY VARIATION ASSOCIATED WITH PHYLOGENY

When we considered all taxonomic levels from class to genus, taxonomic membership had significant effects on the arcsine square root transformation of WGI (Table 1). Genus membership could account for 71% of seed germinability variation. Thus, it is clear that seed germinability is strongly related to phylogeny.

Differences between classes were statistically significant; however, class membership could account for only 7% of the arcsine square root WGI variation (Table 2). Thus the majority (93%) of WGI variation took the form of variation within classes. At the level of family, strong divergence between families was evident within classes of core eudicots, eurosids I, euasterids I, and

TABLE 2

Results from one-way ANOVA models examing divergence within versus among taxonomic groups. We listed only classes with more than three families and families with more than five genera. Seventeen families that were not listed had no significant effect. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $^{ns}P > 0.05$.

Source	No. of groups	No. of species	R^2	F
Class	10	633	0.07	5.53***
Families within				
Core eudicots	6	82	0.26	5.32***
Eurosids I	9	97	0.18	2.35*
Euasterids I	10	119	0.21	3.29**
Euasterids II	6	130	0.37	14.81***
Families	48	633	0.38	7.52***
Genus within				
Caryophyllaceae	8	37	0.40	2.74*
Asteraceae	26	78	0.52	2.27**
Poaceae	21	43	0.73	2.96**
Brassicaceae	13	24	0.76	2.82*
Lamiaceae	15	26	0.89	6.54**
Fabaceae	13	51	0.53	3.60**
Ranunculaceae	13	48	0.29	1.21^{ns}
Rosaceae	10	27	0.96	51.37***
Apiaceae	17	32	0.80	3.73**

euasterids II (26%, 18%, 21%, and 37%, respectively). However, overall, differences between families accounted for less WGI variation (Table 2; $R^2 = 0.38$) than divergence within families. At the level of genus, most variation in WGI (71%) could be accounted for by genus membership (Table 1). Strong divergence between genus, rather within genus, was evident within almost all families in the list (Table 2), for example, Asteraceae, Poaceae, Brassicaceae, Lamiaceae, Fabaceae, Rosaceae, and Apiaceae.

SEED GERMINABILITY VARIATION ASSOCIATED WITH OTHER LIFE-HISTORY ATTRIBUTES

The life-history groups had significant effects on arcsine square root WGI (Table 1). Life form, seed dispersal mode, and seed size could account for 2%, 12%, and 8% of seed germinability variation, respectively. Given that WGI shows a strong phylogenetic pattern, do other life-history attributes account for WGI independently, or are patterns of trait correlation a product of phylogenetically conservative suites of traits? Much of the seed traits variation between species is associated with family membership (Lord et al., 1995; Mazer, 1989; Rees, 1993), so we grouped species by family (total 48 families). Table 3 lists R^2 values derived from Type III sums of squares for family membership, life form, seed size, and seed dispersal mode as an indication of the power of these terms to independently and jointly explain variation in log seed WGI.

In our GLM, when taxonomic family was used as the first explanatory variable, it accounted for the largest proportion of the variation in WGI (38%; Table 3). Moreover, family membership also accounted for most of the variation in WGI after the addition of the other variables (32%–38%). Other life-history attributes, such as life form, seed size, and dispersal mode, are also significantly correlated with WGI (account for 2%, 8%, and 12%, respectively). However, when family membership was taken into account first, the amount of WGI variation explained by dispersal mode dropped to 6% and by seed size dropped to 4% (Table 3). This means that 50% of the variance in log WGI explained by dispersal mode and 50% by seed size was correlated

TABLE 3

Power of family, life form, seed size, and dispersal mode to explain mean WGI variation alone and with two or three terms in linear models.

Sources	R^2	d.f.	F	P
Family first	0.38	47	7.52	<0.001
Family after dispersal mode	0.34	47	6.27	<0.001
Family after life form	0.38	47	7.51	<0.001
Family after seed size	0.35	47	6.51	<0.001
Family after dispersal mode and life form	0.36	47	6.80	<0.001
Family after life form and seed size	0.35	47	6.73	<0.001
Family after dispersal mode and seed size	0.32	47	5.63	<0.001
Dispersal mode first	0.12	47	20.78	<0.001
Dispersal mode after family	0.06	4	9.30	<0.001
Dispersal mode after life form	0.12	4	21.24	<0.001
Dispersal mode after seed size	0.09	4	15.05	<0.001
Dispersal mode after family and seed size	0.05	4	6.81	<0.001
Dispersal mode after life form and seed size	0.10	4	17.37	<0.001
Dispersal mode after family and life form	0.09	4	14.14	<0.001
Life form first	0.02	2	4.80	0.009
Life form after family	0.02	2	4.71	0.009
Life form after dispersal mode	0.02	2	5.72	0.003
Life form after seed size	0.01	2	1.82	0.16
Life form after family and dispersal mode	0.05	2	13.99	<0.001
Life form after family and seed size	0.02	2	5.34	0.005
Life form after dispersal mode and seed size	0.02	2	6.15	0.002
Seed size first	0.08	7	7.72	<0.001
Seed size after family	0.04	7	2.97	<0.05
Seed size after life form	0.07	7	6.80	<0.001
Seed size after dispersal mode	0.05	7	4.66	<0.001
Seed size after family and dispersal mode	0.02	7	1.63	0.12
Seed size after life form and dispersal mode	0.05	7	4.79	<0.001
Seed size after family and life form	0.04	7	3.17	0.003

with family membership. But the amount of WGI variation accounted for by life form did not change significantly. There was no significant correlation between life form and dispersal mode (the variation in WGI explained by one did not change with the addition the other), and significant correlation between seed size and life form (or dispersal mode). Seed size, life form, and dispersal mode themselves covaried independently. But the covariance of seed size and dispersal mode was not independent of family membership ($P > 0.05$; Table 3).

SEED GERMINABILITY VARIATION ASSOCIATED WITH ENVIRONMENTAL FACTORS

The altitudes and habitats when considered first had no significant effect on seed germinability variation (Table 1), but we found that there were significant interactions between altitudes (or habitats) and some phylogenetic groups (including class, and family within four classes: core eudicots, eurosids I, euasterids I,

and euasterids II) (Tables 4 and 5), which involved more than three families.

Discussion

A growing number of studies have documented that phylogenetic relatedness of plant species within a community could account for a significant proportion of interspecific variation in reproductive traits. For example, seed germination rates of species belonging to the same plant families in Sheffield, England, were more similar than those of species in different families (Grime et al., 1981); seven species of *Alstroemeria* that grow in different mountain and lowland habitats in South America exhibited similar germination strategies, regardless of their habitat of origin (Figueroa and Armesto, 2001); Baskin et al. (1993) reported analogous results when dormancy types were compared among species in the family Asteraceae. Species belonging to the Arcto-Tertiary flora presently inhab-

TABLE 4

Tests for significant interactions between altitudes and taxonomic groups. We listed only the classes containing at least three families. The altitude ranges from 2000 to 4200 m, and was divided into 5 groups: <2500 m, 2501–2850 m, 2851–3350 m, 3351–3700 m, and >3700 m. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $^{ns}P > 0.05$.

Taxonomic group	Group d.f.	Group F	Altitudes d.f.	Altitudes F	Group × Altitudes d.f.	Group × Altitudes F
Class	9	5.53***	4	1.01^{ns}	47	2.14***
Family within						
Core eudicots	5	5.32***	4	1.11^{ns}	21	2.43**
Eurosids I	8	2.35*	4	2.60*	20	3.83**
Euasterids I	9	3.29**	4	2.28^{ns}	27	1.59*
Euasterids II	5	14.81***	4	1.72^{ns}	21	4.46***

TABLE 5

Tests for significant interactions between habitats and taxonomic groups. We listed only the classes containing at least three families. According to the environmental conditions in which species were collected, the habitat was divided into 4 groups: bottomland, south slope, north slope, and shrub. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, [ns]$P > 0.05$.

Taxonomic group	Group d.f.	Group F	Habitats d.f.	Habitats F	Group×Habitats d.f.	Group×Habitats F
Class	9	5.53***	3	1.36[ns]	36	2.04***
Family within						
Core eudicots	5	5.32***	3	0.47[ns]	16	3.08**
Eurosids I	8	2.35*	3	3.05*	18	2.73**
Euasterids I	9	3.29**	3	1.04[ns]	24	1.89*
Euasterids II	5	14.81***	3	0.22[ns]	17	4.70***

iting deciduous North American forests had germination strategies that matched those of congeneric species presently occurring in East Asia (Baskin and Baskin, 1998). This study has confirmed that a large proportion of between-species variation in WGI is correlated with taxonomic membership. The strong taxonomic effect on WGI suggests that WGI variation within taxonomic membership is limited, which may be a general pattern. The biological and evolutionary interpretation of the close association between seed germinability and phylogenetic affinity in the alpine meadow is complex. One possible interpretation is that phylogeny imposes limits to variability in reproductive traits within a clade, because of similar developmental and design constraints in related species (Lanyon, 1993; McKitrick, 1993; Miles and Dunham,1993; Yokoyama, 1994; Ackerley and Donoghue, 1995).

However, our data suggested life-history attributes (life form, seed size, and dispersal mode) also significantly correlated with WGI when family membership was considered; that is, the effects of life-history attributes on seed germinability were independent of phylogeny. There was significant difference in seed germinability when a life form was considered as the first explanatory variable, but not significant when seed size was also considered (Table 3). Thus, the effect of life form on seed germinability arises from a secondary correlation via seed size. WGI was correlated with a number of other life-history attributes that could be interpreted as adaptations to different life histories (Lord et al., 1995). The overlap in seed germinability variation accounted by seed size and family membership (4%) or dispersal mode and family membership (6%) (Table 3) does not negate the adaptive significance of the relationship between seed size (or dispersal mode) and germinability.

Many studies have concluded that altitude or other habitat conditions had significant effects on seed germination; for example, Vera (1997) found that germination percentage could be influenced by the altitude at which seeds were collected, and Holm (1994) found that seed germinability decreased or increased with altitude according to species and between years. These studies tested the effect of environmental factors on one or several species. Do environmental factors also impose stress on interspecific seed germinability variation in a larger geographical scale? In this study, we found that the altitudes and habitats when considered first had no significant effect on interspecific seed germinability variation, but we could not consider interspecific seed germinability variation as irrelevant to environmental factors. We found that there were significant interactions between altitudes (or habitats) and some phylogenetic groups. Although their interactions were all less than the main effects of phylogenetic groups, they could account for at least the effect of phylogenetic constraint on seed germination relative to altitudes or habitats. Thus, we

could not exclude the effect of longtime selection of environmental factors on seed germination.

In summary, when we considered the effect of phylogenetic, life-history, and ecological factors on seed germinability in alpine meadows of the eastern Qinghai-Tibet Plateau, we found that the phylogeny was the most important constraint to maintain the stability of species, and its constraints tended to be correlated with life-history and ecological factors. Thus, we think interspecific seed germinability variation was affected by phylogenetic, life-history, and ecological factors together.

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