

# The ecological and evolutionary significance of seed shape and volume for the germination of 383 species on the eastern Qinghai-Tibet plateau

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**Abstract** Seed shape and seed volume are functionally important traits which are associated with seed germination. To study the ecological and evolutionary significance of seed shape and volume in relation to germination, a database comprising seed information for 383 species within 50 families from an alpine meadow on the eastern Qinghai-Tibet plateau was compiled. The independent and interactive effects of seed traits on germination and whether these effects are controlled by phylogeny are discussed. The results show the following: (1) Elongated seeds had higher percentage and faster speed of germination than compact seeds whereas smaller seeds tended to have higher germinability compared to larger ones; (2) Seed volume and shape evolved together but had independent effects on seed germination. Seed volume had no significant influence on seed germination among species with compact seeds, but had a significant effect on those among species with elongated seeds; seed germination of larger seeded species was affected by seed shape, but not by seed volume. These results might be related to their predation pressure and ability to germinate from deeper soil layers. Lastly,

(3) Phylogenetic conservation plays an important role in the co-evolution of seed traits and germination characteristics. Species with similarly shaped seeds on a large scale might reflect a common selective pressure, but related species within a family might be more dependent on phylogenetic conservation.

**Keywords** alpine meadow · phylogeny · seed germination · seed shape · seed volume

## Introduction

Seeds are a critical component of the life history of higher plants, which helps species to disperse to vacant or new habitats and escape from adverse conditions in space and time (Lord et al. 1995). Seed germination and the early stage of seedlings are the most vulnerable periods in a plant's life cycle, and their successes are directly related to population recruitment, the preservation of species and the construction of communities (Jiménez-Alfaro et al. 2016). The food reserves in seeds, which increase with seed volume (Tripathi and Khan 1990; Khan and Shankar, 2011), provide the primary energy and minimal nutrition for seed germination and earlier growth of seedlings. Thus, seed volume plays an important role in the establishment of earlier life stages, principally under poor soil (Grubb and Coomes 1997; Grubb and Burslem 1998; Meyer and Carlson 2001).

Conflicting reports exist on the relationship between seed volume (weight, mass or size) and germination. For example, some studies suggested that smaller seeds

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were more likely to show delayed germination than larger seeds and might be more persistent in the soil seed bank (Thompson and Grime 1979; Venable and Brown 1988; Rees 1994); large-seeded species are expected to have higher post-dispersal predation than small-seeded species (Janzen 1971; Louda 1989; Blate et al. 1998) and should therefore show prompt seed germination to avoid the risk of predation (Kumar et al. 2016). However, some hypotheses argued that smaller seeds germinated more rapidly than larger seeds, which could give them a competitive advantage in time and space (Hendrix 1984), and germination speed of larger seeds would not be too fast because of their usual opacity of thick and hard seed coats (Pearson et al. 2002). Of course, some other studies showed no significant relationship (Mckersie et al. 1981; Piper 1986; Eriksson 1999).

Seed shape is another functionally important trait which is associated with persistence in the seed bank, seed germination and dispersal (Thompson et al. 1993; Kos and Poschold 2010; Reynolds and Cumming 2016). For instance, Thompson et al. (1993) showed that smaller and compact seeds tended to be persistent in the soil, while larger, flattened or elongated seeds were transient in the soil among 97 species of the British flora. This means that small and compact seeds might escape from germination, predation or secondary dispersal, and thus generally tend to live longer (Bekker et al. 1998). However, Grime et al. (1981) showed that many small- and elongated- or conical-seeded species were able to germinate immediately after collection in the flora of Sheffield.

Seed shape is a trait related to surface area that provides contact with the external environment, whereas seed volume (weight, mass or size) gives a measure of resource availability. Each of them might influence the response of seeds to burial depth in a different way, and then the success of seeds germination and seedlings establishment. Generally, heavier seeds will have larger volume than lighter ones. Larger seeds will have more nutrient reserves for seed germination and earlier seedling growth than smaller seeds. If, however, two species have seeds with the same volume but different shape, do their seed germination strategies differ?

In addition, seed shape, volume and germination characteristics are traits which are closely related to phylogeny. For example, many studies documented that

phylogenetic relatedness of plant species could account for a significant proportion of interspecific variation in seed volume (Rees 1993; Leishman et al. 1995) and seed germination rates (Grime et al. 1981). Species within each family normally have similarly shaped seeds, such as caryopses in the Poaceae, achenes in the Asteraceae. However, seed shape, volume and germination characteristics also show significant difference among species within taxa. Then, does phylogenetic conservatism play a role on the co-evolution between seed traits and germination characteristics?

In this study, we compiled a database comprising 383 species of an alpine meadow on the eastern Qinghai-Tibet plateau. The ecological and evolutionary significance of seed shape and volume associated with germination characteristics is discussed, and the following questions are addressed: (1) Do species with smaller seeds have higher percentage germination and faster germination speed compared to larger seeded species? (2) Do species with elongated seeds have higher percentage germination and faster germination speed compared to compact-seeded species? (3) Do seed shape and volume show interactions in seed germination? (4) Are the effects of seed traits on germination characteristics affected by phylogeny?

## Material and methods

### Study site and seeds collections

We compiled a database comprising seed information for 383 species within 50 families from an alpine meadow on the eastern Qinghai-Tibet plateau (101–103° E, 34–35°70' N). The altitude of the collection sites ranges from 1,700 m to 4,100 m. In the alpine meadow, the climate is cold and humid with mean annual rainfall of 450–780 mm, mean annual temperature of 1.2°C and mean annual number of frost days of 270 (Bu et al. 2008). Seeds of all species were collected from more than 10 individual plants at the start of natural dispersal from July to October in 2012. Seeds were air-dried at room temperature (approximately 15°C) and were stored in laboratory located in study area (elevation 2,950 m a.s.l.) with ambient temperature for 6 months, which replaced the cold-stratified treatment to affect the dormancy level of seeds and could make seeds obtain the similar natural germination situation in the next year.

## The measurement of seed volume and shape

Ten seeds without appendages of each species were scanned by Epson Expression 10000XL, then WinSEEDLE 2011a software was used to measure the length and width of the seeds, but their depth was measured using a digital vernier caliper with an accuracy of 0.01 mm. According to the parameters of the three seed dimensions, seeds being assumed to be oval, seed volume (SV) was calculated using WinSEEDLE 2011a. Variance of seed dimensions (VSD) was used to reflect seed shape by dividing length, width and depth by length and then calculating the variance of these three values by dividing the summed squared deviation from the mean by three (as in Thompson et al. 1993 and Bekker et al. 1998). This way shape becomes dimensionless and can vary between 0 (spherical) and 0.2 (flattened or elongated).

## Germination experiments

We conducted a germination experiment to determine the speed of germination and germination success rate. The germination experiment was started on 10th April 2013 (the beginning of germination season in the field). Fifty seeds of each species were placed in covered Petri dish (9 cm diameter) on a double layer of moistened filter paper in temperature chambers. Each species has three replicates. The germination conditions were set at a diurnal fluctuation of 15°C (20°C day, 12 h light; 5°C night, 12 h dark) and a relative humidity of approximately 70 %. The temperature and light conditions of the germination trial were approximated to conditions at 5 cm soil depth in May and June. A seed was considered germinated when the radicle was visible. The number of germinated seeds were recorded daily and the seeds were regularly watered with distilled water. In view of the short growth season in the alpine meadow and the speed of germination across species, the experiment was terminated after 40 days.

## Statistical analyses

The following analyses were performed for the dataset generated by the laboratory assays described above:

Two germination characteristics were used to assess germination strategies: germination percentage and speed of germination. Before the germination experiment, tetrazolium tests were used to measure the

viability of seeds. The results showed that nearly all the seeds used in the experiment were alive. Thus, the germination indexes were calculated without considering the seed survival rate. Germination percentage (GP) was defined as the final germination success rate. Speed of germination (SG) was estimated with a modified Rozema index (see Zheng et al. 2003) as follows:  $\sum (100 \times G_i) / (n \times i)$ , where  $n$  was the number of sown seeds,  $G_i$  was the number of germinated seeds on day  $i$  ( $i = 1, 2, 3 \dots$ ), and higher values of SG indicated faster speed of germination.

In this study, seed volume (SV) and seed shape (VSD) were considered as seed traits. Seed volume was used to measure the relative size of seed contacted with external environment. Seed volume and speed of germination were log transformed, and germination percentage was arcsine square root transformed before statistical analysis to ensure homogeneity of variance. The data of seed shape were not transformed due to their homogeneity of variance.

To estimate the effect of seed shape on germination within smaller and larger seed groups, considering the distribution of SV value and the number of species, the 383 species in this study were divided into two groups:  $SV < 1 \text{ mm}^3$  (smaller seeds, 198 species) and  $SV > 1 \text{ mm}^3$  (larger seeds, 185 species); to estimate the effect of seed volume on seed germination within compact and elongated seed groups, according to the distribution of VSD and the number of species, the 383 species in this study were divided into two groups:  $VSD < 0.085$  (compact seeds, 185 species) and  $VSD > 0.085$  (elongated seeds, 198 species).

Spearman's correlation coefficient was used to examine the relationships between germination characteristics and seed traits. Partial correlations were used to test the net effect of one trait after the effect of other trait was removed (when the other trait was controlled). Both of these analyses were considered among all species and species within groups.

Considering seed traits and germinability might be controlled by phylogeny, the phylogenetic signal in seed traits and germination characteristics were tested by estimating Pagel's lambda (Pagel 1999) in the package 'picante' of R statistical software v. 3.3.1 (R Development Core Team, 2016), the correlations between germination characteristics and seed traits were also assessed by phylogenetically independent contrasts (PICs – Felsenstein, 1985). The standardized independent contrasts across all nodes calculated by PICs were

integrated to produce an ordinary least square linear regression through the origin, and it returns a Pearson's correlation coefficient (PIC  $r$ ). The 'Analysis of Traits (AOT)' module in Phylocom version 4.0 (Webb et al. 2008) was used to conduct PIC analyses based on the angiosperm megatree (tree R20091110.new) with Angiosperm Phylogeny Group III (2009).

Except phylogenetic signal and PIC analyses, the other analyses were performed in SPSS 16.0.

## Results

Of the 383 herbaceous plant species, seed volume ranged from 0.023 mm<sup>3</sup> to 17.156 mm<sup>3</sup>; the variance of seed dimensions ranged from 0.002 to 0.189; the seed germination percentage ranged from 0.67 % to 100 %; speed of germination ranged from 0.02 to 48.93 except one singular value (SG = 93) from seeds of *Salsola collina* which got 96 % germination on the first day.

If all of 383 species were considered, there were significant positive correlations between germination characteristics and VSD (Table 1). In other words, elongated seeds had a higher percentage and faster speed of germination than compact seeds. Similarly, germination characteristics showed significant negative correlations with seed volume. That is, smaller seeds had higher percentage and faster speed of germination than larger ones. The partial correlations showed that seed shape and volume had interactive effect on seed germination (Table 1). When one variable was controlled, the correlations between germination indexes and the other variable were decreased or increased slightly (Table 1). However, the effect of each variable was still significant correlated with germination indexes after the effect of another variable was removed.

If we divided the 383 species into two groups: smaller seeded species (SV < 1 mm<sup>3</sup>) and larger seeded species (SV > 1 mm<sup>3</sup>), species with elongated seeds (VSD > 0.08) and species with compact seeds (VSD < 0.08), respectively, the results were different in correlations between germination characteristics and seed traits within each of the groups (Table 2). Whether within smaller-seeded species or larger-seeded ones, the effects of seed shape on seed germination were consistent with those when all species were considered. Even after the effect of VSD was removed, the significant effect of SV on seed germination was still reflected in germination percentages among species with smaller seeds; however, seed germination characteristics within larger-seeded species were irrelevant to SV in all cases. For species with compact seeds, no significant correlations were found between germination characteristics and seed traits; for species with elongated seeds, seed germinability decreased with increasing SV whether SV was considered alone or after the effect of VSD was removed; however, the effect of seed shape was significant only when the effect of SV was removed.

No significant correlations between germination characteristics and seed traits among species within most of the families were found in the present study (Table 3). There were significant phylogenetic signals in seed shape, volume, germination percentage and speed of germination (Table 4). Thus, considering the strong phylogeny control, PIC analyses were used to test the effect of seed shape and volume on seed germination characteristics without the limit of phylogeny. Among the phylogenetic contrasts, 147 nodes were produced, and standardized independent contrasts across all nodes were calculated. Pearson's correlation between these contrasts showed that there were no significant responses of germination characteristics to seed shape or

**Table 1** Results of correlation analysis between germination characteristics and seed traits, and partial correlation when one variable was controlled among 383 species.

Variable	Controlled variable	Germination percentage		Speed of germination	
		$r$	$P$	$r$	$P$
VSD		0.274	***	0.215	***
VSD	SV	0.280	***	0.208	***
SV		-0.123	*	-0.149	**
SV	VSD	-0.149	**	-0.132	**

VSD variance of seed dimensions, SV seed volume.

\* – significant at  $P < 0.05$ , \*\* – significant at  $P < 0.01$ , \*\*\* – significant at  $P < 0.001$ .

**Table 2** Results of correlation analysis between germination characteristics and seed traits, and partial correlation when one variable was controlled among species in different groups.

Groups	Variable	Controlled variable	Germination percentage		Speed of germination	
			<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
SV < 1 ( <i>N</i> = 198)	VSD		<b>0.256</b>	***	<b>0.220</b>	**
	VSD	SV	<b>0.251</b>	***	<b>0.205</b>	**
	SV		<b>-0.157</b>	*	<b>-0.181</b>	*
	SV	VSD	<b>-0.14</b>	*	-0.111	ns
SV > 1 ( <i>N</i> = 185)	VSD		<b>0.314</b>	***	<b>0.243</b>	***
	VSD	SV	<b>0.305</b>	***	<b>0.211</b>	**
	SV		-0.066	ns	-0.070	ns
	SV	VSD	-0.053	ns	-0.044	ns
VSD < 0.085 ( <i>N</i> = 185)	VSD		0.016	ns	-0.005	ns
	VSD	SV	-0.022	ns	-0.038	ns
	SV		-0.126	ns	-0.115	ns
	SV	VSD	-0.106	ns	0.067	ns
VSD > 0.085 ( <i>N</i> = 198)	VSD		0.112	ns	0.095	ns
	VSD	SV	<b>0.187</b>	**	<b>0.172</b>	*
	SV		<b>-0.158</b>	*	<b>-0.206</b>	**
	SV	VSD	<b>-0.215</b>	**	<b>-0.238</b>	***

VSD variance of seed dimensions, SV seed volume, ns non-significant. The significant correlations were indicated in bold font.

\* – significant at  $P < 0.05$ , \*\* – significant at  $P < 0.01$ , \*\*\* – significant at  $P < 0.001$ .

surface area / volume (Fig. 1). The effect of seed shape or surface area / volume on seed germination was strongly controlled by phylogeny.

## Discussion

### Seed germination in relation to seed volume

An increasing number of studies has focused on the relationship between seed germination and seed volume. For example, seed volume has been found to affect speed of germination and germination success rate (Mckersie et al. 1981; Piper 1986; Wulff 1986; Winn 1988; Counts and Lee 1991; Vera 1997; Eriksson 1999). However, different researches draw inconsistent conclusions from different populations (Counts and Lee 1991; Vera 1997) or communities (Grime et al. 1981; Piper 1986; Jurado and Westoby 1992; Pearson et al. 2002). Studies on intraspecific variation among populations

**Table 3** Correlations between germination characteristics and seed traits within families. Families containing less than eight species in this study are not listed.

Family ( <i>N</i> )	Germination percentage		Speed of germination	
	VSD	SV	VSD	SV
Amaranthaceae (9)	-0.767 <sup>ns</sup>	-0.150 <sup>ns</sup>	-0.700 <sup>ns</sup>	0.033 <sup>ns</sup>
Apiaceae (21)	0.204 <sup>ns</sup>	-0.216 <sup>ns</sup>	0.249 <sup>ns</sup>	-0.112 <sup>ns</sup>
Asteraceae (86)	<b>-0.183*</b>	<b>-0.343**</b>	<b>-0.211*</b>	<b>-0.314*</b>
Brassicaceae (16)	-0.232 <sup>ns</sup>	-0.068 <sup>ns</sup>	-0.209 <sup>ns</sup>	0.124 <sup>ns</sup>
Caryophyllaceae (8)	-0.071 <sup>ns</sup>	-0.286 <sup>ns</sup>	0.048 <sup>ns</sup>	-0.381 <sup>ns</sup>
Fabaceae (23)	-0.082 <sup>ns</sup>	0.312 <sup>ns</sup>	0.037 <sup>ns</sup>	0.192 <sup>ns</sup>
Gentianaceae (12)	0.524 <sup>ns</sup>	-0.098 <sup>ns</sup>	0.427 <sup>ns</sup>	-0.133 <sup>ns</sup>
Lamiaceae (15)	-0.221 <sup>ns</sup>	-0.132 <sup>ns</sup>	0.196 <sup>ns</sup>	-0.221 <sup>ns</sup>
Primulaceae (9)	<b>-0.561<sup>ns</sup></b>	-0.067 <sup>ns</sup>	-0.467 <sup>ns</sup>	-0.033 <sup>ns</sup>
Poaceae (42)	-0.112 <sup>ns</sup>	0.247 <sup>ns</sup>	-0.242 <sup>ns</sup>	0.144 <sup>ns</sup>
Ranunculaceae (13)	0.498 <sup>ns</sup>	-0.066 <sup>ns</sup>	0.280 <sup>ns</sup>	-0.269 <sup>ns</sup>
Rosaceae (8)	0.357 <sup>ns</sup>	0.143 <sup>ns</sup>	0.119 <sup>ns</sup>	0.001 <sup>ns</sup>
Scrophulariaceae (20)	0.398 <sup>ns</sup>	-0.346 <sup>ns</sup>	0.429 <sup>ns</sup>	<b>-0.529*</b>

VSD variance of seed dimensions, SV seed volume, *N* = number of species, ns – non-significant. The significant correlations were indicated in bold font.

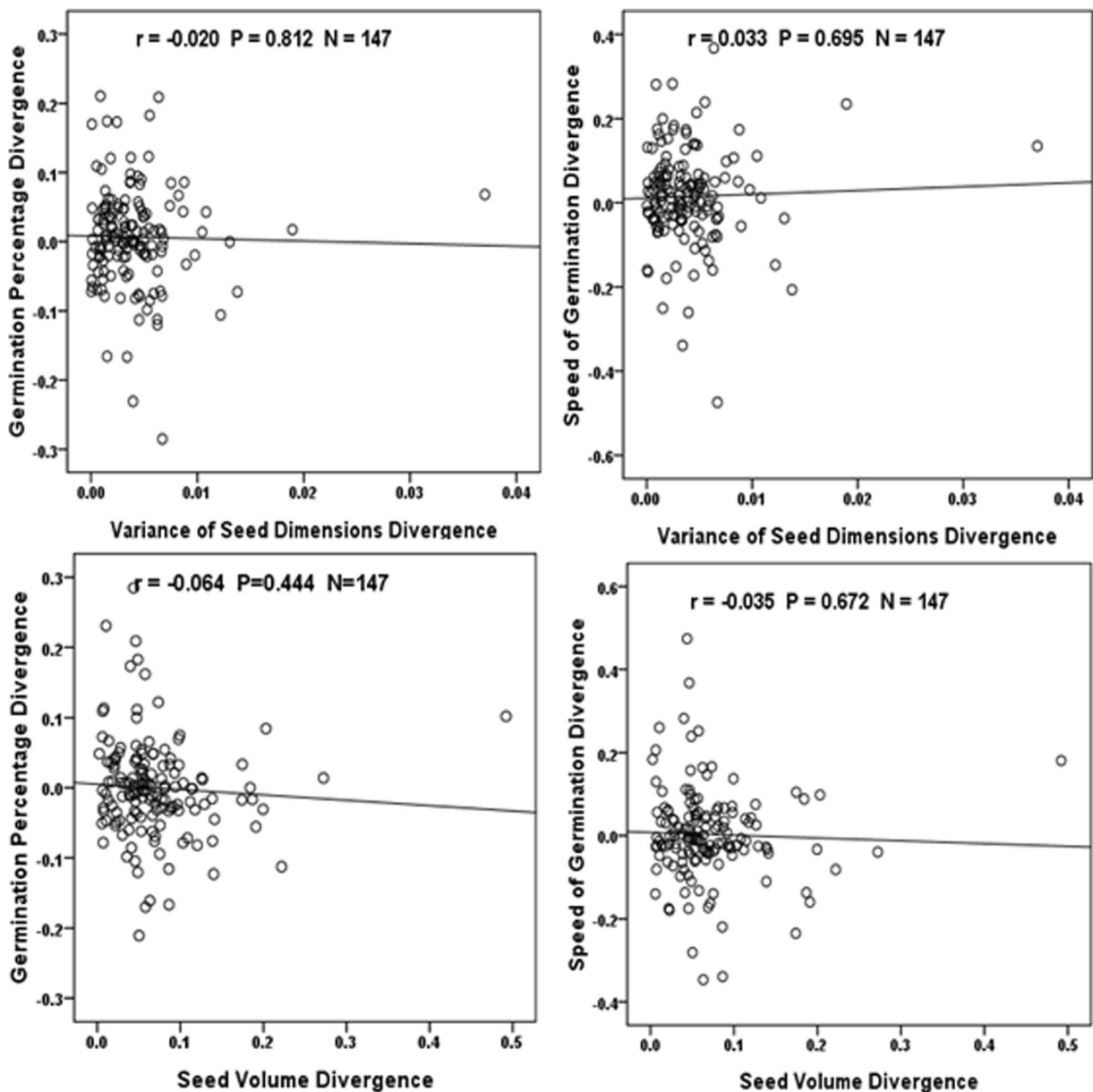
\* – significant at  $P < 0.05$ , \*\* – significant at  $P < 0.01$ .

had found a positive or non-significant relationship between seed volume and germination characteristics (Wulff 1986; Winn 1988; Vera 1997), which, it had been suggested, was due to environmental heterogeneity. Similarly, studies among species in different habitats had found positive correlations between seed volume and speed of germination. For example, pioneer species in tropical rainforest tended to produce a mass of small seeds and were typically associated with delayed germination (Vázquez-Yanes et al. 1990), which maximized the chances to colonize gaps or to be incorporated in the soil bank until optimal light conditions enable seeds

**Table 4** Phylogenetic signal of germination characteristics and seed traits for 378 species; five species that were determined only at the family level were excluded from the analysis.

Source	Pagel's lambda	<i>P</i>
Variance of seed dimensions	0.9439	< 0.0001
Seed volume	0.9626	< 0.0001
Germination percentage	0.5621	< 0.0001
Speed of germination	0.5327	< 0.0001





**Fig. 1** Relationship between divergence in germination characteristics (arcsine square root germination percentage, log speed of germination) and divergence in seed traits (variance of seed

dimensions, log seed volume) for 383 species when PIC was used; PICr and *P* values are reported.

germination. Shade-tolerant species were more likely to produce larger seeds and were expected to germinate fast to reduce predation risks (Foster and Janson 1985). In an arid-zone study, the larger-seeded species had faster speed of germination and higher success rate than smaller-seeded species (Easton and Kleindorfer 2008). In this study, significant negative correlations were observed between germination characteristics

(germination percentage and speed of germination) and seed volume among 383 species (Table 1, 2). That is, smaller seeded species tended to have higher germinability compared to larger-seeded ones. In accordance with our results, Grime et al. (1981) concluded that there was a progressive decline in representation of rapid-germinating species with increasing seed weight among 403 species in the Sheffield flora. One possible reason

was that smaller seeds had a relatively larger seed surface to volume ratio. If a seed can absorb sufficient water to germinate, it must absorb water across the soil-seed interface faster than it loses it across the atmosphere-seed interface (Harper et al. 1970). Thus, larger seeds might have difficulty in obtaining sufficient water for germination from temporarily available water supplies because of their low ratio of surface to volume, which declined with increasing seed volume (provided shape remains constant). The other idea was that might be due to the natural conditions of the study site. The alpine meadow in this study has low and open vegetation, a short growth season and an adverse climate which is cold, humid and windy. When there was selection pressure for rapid germination (due to short time period of favourable conditions), it was likely to result in a shift towards smaller seeds as seedlings from smaller seeds might be able to be deployed more quickly. Furthermore, if smaller seeds germinated more rapidly than larger seeds, it could give them a competitive advantage in time and space (Hendrix 1984), especially in the changeable alpine environment.

#### Seed germination in relation to seed shape

Seed shape, which was considered to be important in determining seed bank behaviour (Thompson 1987; Grime 1989; Bekker et al. 1998), might be another factor to affect seed germination. For example, small, compact seeds were expected to live longer and be dormant for their ease of burial (Thompson and Grime 1979; Grime et al. 1988; Thompson et al. 1993; Rees 1993), while large, flattened or elongated seeds were expected to live shorter and germinate more for their pressure of predation (Fenner 1983; Thompson 1987), advantage in early establishment (Burke and Grime 1996) and ability to germinate from deeper soil layers (Hutchings and Booth 1996). In this study, the success rate and speed of germination increased with increasing variance of seed dimensions (Tables 1, 2). In other words, species with elongated seeds had higher speed and success rate of germination compared to those with compact seeds. Thus, seeds of similar shape might be under some common pressure and therefore exhibit similar germination strategies. Of the 383 species from the alpine meadow, the fast germination of elongated or flattened seeds in the present study was consistent with the result of Grime et al. (1981) and the expectations of earlier theoretical works. This result might be explained

by the hypothesis that elongated seeds expedite their germination in response to increased predation risk due to their lower likelihood of being buried.

#### The evolutionary and ecological significance of seed volume and shape in relation to germination

Seed germination characteristics showed a significant correlation with seed volume (or seed size) and variance of seed dimensions (or seed shape) when the variables of seed traits were considered alone (Table 1). However, if seeds were very small, differences in shape would not affect their incorporation into the soil. By contrast, if seeds were large and heavy, round seeds would penetrate the soil more easily than awkward-shaped seeds. So does the effect of seed shape on seed germination change with seed volume variation? In the present study, the partial correlations showed that there were significant combined effects of seed shape and volume on the success rate and speed of germination (Table 1). The correlation coefficient between germination characteristics and seed traits fluctuated slightly and were still significant after the effect of one variable was removed. In other words, seed volume and shape evolved together but had an independent effect on seed germination.

Table 2 shows that seed volume had no significant influence on seed germination among species with compact seeds, but had a significant effect on those among species with elongated seeds, and seed germination of larger seeded species was affected by seed shape, but not by seed volume. These might be resulted from a common selective pressure. For example, compact seeds, be it larger or smaller, all easily became buried in soil or litter, while larger and elongated seeds might be more likely to stay on the soil surface and become prey. In natural habitats, larger and elongated seeds less easily drop into litter or soil cracks, and then might be difficult to be buried and gain insufficient water for germination and seedling growth than smaller or round ones.

Considering seed shape, volume and germination characteristics are traits closely related to phylogeny, the control of phylogenetic conservation on the co-evolution between seed traits and germination characteristics was analysed. In contrast to seed traits, germination characteristics were affected less, yet still significantly, by phylogenetic groups in this study (Table 4). Within most of families, no significant correlations between germination characteristics and seed traits were found (Table 3). Of the 383 species from the alpine

meadow, germination characteristics had significant correlations with seed shape and volume, but non-significant when phylogeny was considered (Fig. 1). That is, phylogenetic conservatism played an important role in the co-evolution of seed traits and germination characteristics. For example, most species of the Poaceae and Asteraceae used in this study had higher germination percentage, both large and small seeds, but members of the Gentianaceae, Ranunculaceae and Primulaceae showed the opposite results. Lord et al. (1995) considered that descendant species would be most successful if they showed only minor variations of their ancestral traits. The association within a lineage between traits might be more likely to reflect some special selective pressure, dormancy mechanism, inhibition of seed coat and so on. For example, many species of the Fabaceae had lower germination percentages, which might be caused by their hard and tight seed coat.

However, the strong phylogenetic control over the co-evolution of seed traits and germination characteristics in this study also indicated a lack of a predominant mechanism that could be responsible for seed traits in germination strategy. The conflict between correlation and PIC analyses might be caused by species in this study which had strong phylogenetic dependence or uneven distribution of species numbers in different taxa (Du and Qi 2010). For example, germination characteristics were all significantly correlated with seed trait variation among species in the Asteraceae (86 species), which included more species than other taxa, and only one or a few species were absorbed within most of the families in the present study. Thus, the effect of long-time selection of environmental factors on co-evolution between seed traits and seed germination could not be excluded absolutely. Furthermore, the correlations between germination characteristics and seed shape among the 383 species were positive in this study, but those among species within a family were not always. For example, in this study, most species of the Asteraceae tended to have smaller and oval-shaped seeds or larger and elongated seeds, while smaller and oval-shaped seeds tended to have higher success rates and speed of germination, but larger and elongated seeds showed lower and slow germination, which might be caused by their thick coat. Thus, species with similarly shaped seeds on a large scale might reflect a common selective pressure, but related species within a family might be more dependent on phylogenetic conservatism.

In addition, the variation in seed germination might be affected by external factors which caused by seed volume or shape directly or indirectly, such as pressure from predation and seedling establishment (Fenner 1983; Thompson 1987; Burke and Grime 1996). Besides suitable germination conditions, which are considered in the present study, other special requirements might exist in some species. For example, dormancy might be considered another control factor affecting the final results. Therefore, as a integrated trait, seed germination could be shaped by various factors in long-term evolution. The effects of many unknown, possible and co-evolved factors on seed germination will be considered in our future study.

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