



Germination time, other plant traits and phylogeny in an alpine meadow on the eastern Qinghai-Tibet plateau

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Abstract: In this paper, 633 species (involving 10 classes, 48 families, 205 genera) collected from the alpine meadow on the eastern Qinghai-Tibet plateau were studied. We tested potential factors affecting variation in mean germination time (MGT), i.e., plant traits (adult longevity, dispersal mode and seed size) or phylogeny, to evaluate if these factors were independent or they had interaction. Nested ANOVA showed that taxonomic membership accounted for the majority of MGT variation (70%), and in the generalized linear model, family membership could explain independently the largest proportion of MGT variation (29%). The strong taxonomic effect suggests that MGT variation within taxonomic membership is constrained. The other plant traits could also explain MGT variation independently (1% by adult longevity and dispersal mode, respectively, and 2% by seed size). Thus, the phylogeny was an important constraint to maintain the stability of species, and we could simplify the question if we regarded the phylogeny as an individual factor, but we could not negate the adaptive significance of the relationship between other plant traits and seed MGT. In addition, a large percentage of the variance remained unexplained by our model, thus important selective factors or parameters may have been left out of this analysis. We suggest that other possible correlates may exist between seed germination time and additional ecological factors (for example, altitude, habitat and post-dispersal predation) or phylogenetic related morphological and physiological seed attributes (e.g., endosperm mass) that were not evaluated in this study.

Abbreviations: MGT — Mean Germination Time, GLM — Generalized Linear Model.

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 germination time varies extensively. For example, viviparous seeds (e.g., mangrove trees) often germinate inside the ripe fruit, while still on the mother plant (Figuroa 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). Variation in seed germination time is a functional response of a plant in its most vulnerable stage to the predictability of its abiotic and biotic environment (Angevine and Chabot 1979). Venable and Brown (1988) examined the selective interactions among seed mass, dormancy, and dispersal and predicted that trade-offs should exist between these variables. It has

also been argued that, because seedling establishment rarely occurs in the vicinity of long-lived species (Waller 1988), seeds of long-lived species should have longer survival in soil than short-lived species. Thompson (1987) suggested that perennials which usually had larger seeds than annuals tended to have more non-dormant seeds to avoid predation by herbivores. Thus, it is clear there is no consensus on the effect of adult longevity on the evolution of dormancy. Germination time may also correlate with dispersal mode. For example, seeds dispersed by frugivores must survive the passage through the digestive tracts of the animals, and they should delay germination longer than their abiotically dispersed relatives. Early germination would reduce progeny survival in biotically dispersed species (Garwood 1983).

Additional evidence about the factors controlling delayed germination derives from studies of taxonomically related species. According to recent studies, it is reasonable to expect that, within a family or a genus, reproduc-

tive characters, such as seed mass and germination, could be affected by phylogenetic constraints and developmental allometries that limit segregation (Kochmer and Handel 1986, Feinsinger 1987, Herrera 1992, Baskin et al. 1993, Jordano 1995, Baskin and Baskin 1998, Smith-Ramírez et al. 1998, Figueroa and Armesto 2001, Zhang et al. 2004). These examples support the hypothesis that germination strategies can be stable evolutionary traits, thus constraining interspecific variation in germination behavior.

Despite the quite large number of empirical studies on seed germination, very few studies have been addressed to test seed germination in an entire plant community (Garwood 1983, Westoby et al. 1992, Leishman et al. 1995, Lord et al. 1995, Jurado and Flores 2005). However, the study of germination of seeds collected from one community at the same time may provide important information to understand the dynamics of a community. Therefore, we expect to advance our understanding on phylogenetic and ecological factors regulating seed germination times in plant communities. In this study, we build up a database of 633 species (involving 10 classes, 48 families, 205 genera) collected from the alpine meadows on the eastern Qinghai-Tibet plateau. The following questions were addressed: (1) To what extent could seed germination time be correlated with phylogenetic membership and other plant traits: adult longevity, seed mass and dispersal mode? (2) Was the seed MGT variation constrained by the plant traits or phylogeny background? Were these factors independent or there was interaction among them?

Methods

Study site

The region of this study is located on the eastern Qinghai-Tibet plateau (101-103° E, 34-35°70' N). The altitude ranges from 2800 m 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 with -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 monocots, for example, Gramineae, Cyperaceae, and various dicots, such as Ranunculaceae, Polygonaceae, Saxifragaceae, Compositae, Scrophulariaceae, Gentianaceae, and Leguminosae.

The database

In this study, we build up a database of 633 species (involving 10 classes, 48 families, 205 genera) collected

from the alpine meadows of the study site. The sample represented 65% of the species, 50% of the genera, and 50% of the families reported from the area. Seeds were gathered from July to October in 2004, and species included not only native but also introduced ones. Seeds were collected in paper bags at the start of natural dispersal. Harvested seeds were transported to the laboratory, and spread on tables and allowed to air-dry at room temperature (approximately 15°C), then weighed. Structures supporting seed dispersal (like wings, pappus, etc) were removed prior to weighing. Seeds were pooled per species, and then three subsamples, each formed by randomly selected 100 seeds were separated. The average weight of the 3 subsamples was used as seed mass variable. The germination experiment was started on the middle of March (starting season of germination in the study area), in 2005. Seeds were placed in Petri dishes (9 cm diameter) on double layers of moistened filter paper, and then placed in climate chambers (made in Canada) under conditions of 20 °C, 12 h / 5 °C, 12 h with continuous darkness and a relative humidity of about 70%. The temperature regime of the germination tests resembled natural conditions prevailing in the soil at 5 cm depth in April and May. All of the species had three replicates of 50 seeds. Every day, the percentage of seeds germinated was recorded, newly emerged seedlings were removed from the Petri dishes and seeds were regularly watered with distilled water. A seed was considered germinated when the radicle was visible. The experiment of seed germination lasted 60 days.

Statistical analyses and comparative method

The following analyses were performed using the data set generated by laboratory assays. Mean germination time (MGT) was estimated as follows:

$$MGT = \frac{\sum_i G_i \times i}{\sum_i G_i}$$

(Figueroa and Armesto 2001), where i is the number of days of germination elapsed since the day of sowing (day 0) and G_i is the number of seeds germinated on day i . Seeds that did not germinate at the end of the assay were not considered in this calculation.

For multifactorial ANOVAs of MGT, we grouped these species into various major categories, defined as follows:

(1) *Phylogenetic groups*. Since much of the seed trait variation among species is associated with family membership (Mazer 1989, Rees 1993, Lord et al. 1995), we grouped species by family. Families were considered according to the Angiosperm Phylogeny Group (2003). Data for 40 families were used in the

Table 1. Total amount of seed germination time variation explained by a nested model including all taxonomic levels above species; component R^2 , seed germination time variation explained by class, order within class, family within order, and genus within family. P values were not computed because of the unbalanced data set. Number of species is 567.

Source of variance	df	Sum of squares	Component R^2
Total	566	36.91	100
Classes	9	4.54	0.12
Orders	12	6.21	0.17
Families	17	3.94	0.11
Genera	151	11.04	0.30
Error	377	11.18	0.30

analysis because species of the further 8 families did not germinate. A total of 66 species had no germination at the end of the essay and were not considered in this calculation. Then, the number of species was 567.

(2) *Plant trait categories.* (a) Adult longevity – species in the flora were grouped into two classes: annual (168 species, including a few biennials) and perennial (465 species). (b) Seed size – seeds were sorted by weight into 8 size classes conformed to that 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), 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 bards), wind-adapted (108 species, with wings, hairs or a pappus) and vertebrate-adapted (27 species, with an aril or flesh).

To examine the taxonomic pattern of MGT variation, a nested ANOVA model was fitted to the data set, and component R^2 values were calculated by the proportion of Type I sums of squares (SS) explained by each taxonomic level. This characterized the amount of MGT variation correlated with each level nested within the previous level. Next, in order to examine divergence within, versus among, taxonomic groups, one-way ANOVA models were fitted to the data set using membership at the order level, at the family level with the model fitted separately to each order, and at the genus level with the model fitted separately to each family.

Furthermore, we conducted a series of ANOVAs to assess the significance of these factors in determining MGT variation. The Type III sum of squares was used to establish the significance level of each effect because the data were unbalanced. Firstly, one-way ANOVAs estimated the main effect of each factor on the variance of

MGT. In addition, to test the independent effect of each factor, we used analysis of deviance. When we compared the full model (e.g., families + adult longevity + seed mass + dispersal mode) with different reduced models (adult longevity + seed mass + dispersal mode), the difference between the proportion of the total sum of squares (SS) explained by the full model (its R^2) and the R^2 of the reduced model explained the independent effect by the deleted variable.

In addition, MGT was log-transformed before statistical analysis to ensure homogeneity of variance. All analyses were performed with SPSS 12.0.

Results

Seed germination time variation associated with phylogeny

When we considered all taxonomic levels from class to genus together, taxonomic membership accounted for 70% of MGT variation (Table 1). Thus, it is clear that MGT is strongly related to phylogeny. Most seed germination variation was generally associated with differences among orders within classes and differences among genera within families (Component R^2 values; Table 1). Variation among families within orders contributed less possibly because there were fewer families per order than genera per family or orders per class (Lord et al. 1995).

Differences between orders were statistically significant; however, order membership could account only for 29% of log mean MGT variation (Table 2). Thus, the majority (71%) of MGT variation took the form of variation within orders. At the level of family, strong divergence between families was evident within Malpighiales (90%). However, overall, no significant difference was found between families in 4 of 21 orders testable (10 orders that had only one family were not listed), and 7 of the 21 orders in which a significant family effect was found, differences between families accounted for less MGT variation (Table 2, $R^2 = 0.40$) than divergence within families. At the level of genus, most variation in MGT (70%) could be accounted for by genus membership (Table 2). 14

Table 2. Results from one-way ANOVA models examining divergence within versus among taxonomic groups, for all data sets pooled. 10 orders which had only one family are not listed, and 14 families which had only one genus are not listed. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Number of species is 567.

Source	df	No of species	MS	R^2	F
Orders	20	567	0.53	0.29	10.97***
Families within					
Asterales	1	87	0.39	0.09	8.21**
Caryophyllales	3	59	0.21	0.17	3.76*
Dipsacales	1	7	0.002	0.02	0.07 ^{ns}
Ericales	1	13	0.17	0.39	6.92*
Gentianales	1	38	0.18	0.09	3.63 ^{ns}
Lamiales	4	64	0.09	0.16	2.71*
Malpighiales	3	8	0.14	0.90	11.79*
Poales	2	65	0.75	0.48	28.56***
Ranunculales	1	47	0.003	0.002	0.08 ^{ns}
Rosales	1	19	0.22	0.18	0.07 ^{ns}
Saxifragales	1	22	0.45	0.29	8.28*
families	39	567	0.38	0.40	9.16***
Genus within					
Boraginaceae	2	5	0.13	0.90	8.67 ^{ns}
Campanulaceae	3	11	0.02	0.45	1.90 ^{ns}
Caryophyllaceae	7	36	0.10	0.42	2.89*
Amaranthaceae	2	11	0.26	0.67	8.14*
Asteraceae	22	76	0.09	0.51	2.52**
Brassicaceae	12	26	0.07	0.67	2.17 ^{ns}
Cyperaceae	3	14	0.01	0.03	0.10 ^{ns}
Gentianaceae	5	34	0.06	0.19	1.30 ^{ns}
Geraniaceae	1	5	0.12	0.48	2.77 ^{ns}
Poaceae	18	44	0.04	0.64	2.46*
Crassulaceae	1	9	0.29	0.92	76.51***
Lamiaceae	12	22	0.09	0.86	4.64*
Fabaceae	12	51	0.10	0.51	3.25**
Liliaceae	1	13	0.08	0.15	1.95 ^{ns}
Onagraceae	1	5	0.004	0.06	0.20 ^{ns}
Papaveraceae	1	4	0.02	0.11	0.26 ^{ns}
Polygonaceae	2	11	0.15	0.46	3.35 ^{ns}
Primulaceae	2	12	0.02	0.12	0.60 ^{ns}
Ranunculaceae	10	43	0.08	0.58	4.38**
Rosaceae	9	16	0.10	0.79	4.28*
Rubiaceae	1	4	0.06	0.37	1.17 ^{ns}
Saxifragaceae	4	13	0.06	0.30	0.82 ^{ns}
Scrophulariaceae	4	36	0.02	0.12	1.02 ^{ns}
Apiaceae	12	27	0.02	0.49	1.14 ^{ns}
Urticaceae	1	3	0.09	0.95	18.77 ^{ns}
Valerianaceae	2	5	0.04	0.74	2.78 ^{ns}
Genus	188	567	0.14	0.70	4.62***

Table 3. Power of each factor to explain log MGT variation in GLM containing a categorical variable. * = $P < 0.05$, ** = $P < 0.01$, ns = $P > 0.05$. Number of species is 567.

Source	df	MS	F	R^2
Family	39	0.38	9.16***	0.40
Adult longevity	1	1.89	30.56***	0.05
Dispersal mode	3	0.90	14.87***	0.07
Seed mass	7	0.34	5.41***	0.06

Table 4. Multifactorial ANOVAs for the independent effects of each factor. To calculate the proportion of the variance explained by only one of the main factors, we subtracted the R^2 of the incomplete ANOVA with that factor removed, from the R^2 of the complete model. * = $P < 0.05$, ** = $P < 0.01$, ns = $P > 0.05$. Number of species is 567.

Source of variation	df	MS	F	R^2	df	MS	F	R^2
	Full model				Family removed			
Family	39	0.27	6.71***	0.34	1	1.27	22.49***	0.04
Adult longevity	1	0.15	3.82*	<0.01	3	0.67	11.87***	0.06
Dispersal mode	3	0.13	3.23*	0.02	7	0.19	3.36**	0.04
Seed size	7	0.07	1.84 ^{ns}	0.02	11	0.52	9.15***	0.15
Corrected model	50	0.32	8.06***	0.44				
	Adult longevity removed				Dispersal mode removed			
Family	39	0.30	7.39***	0.36	39	0.31	7.65***	0.37
Adult longevity	1	0.17	4.27*	<0.01	1	0.17	4.27*	<0.01
Dispersal mode	3	0.14	3.39*	0.02	3	0.14	3.39*	0.02
Seed size	7	0.07	1.82 ^{ns}	0.02	7	0.10	2.50*	0.03
Corrected model	49	0.34	8.10***	0.43	47	0.34	8.26***	0.43
	Seed size removed							
Family	39	0.29	7.15***	0.35				
Adult longevity	1	0.15	3.67 ^{ns}	<0.01				
Dispersal mode	3	0.20	4.81**	0.03				
Seed size								
Corrected model	43	0.36	8.97**	0.42				

families that had only one genus were not listed. There was no significant difference within 17 families. Strong divergence between genera, rather than within genus, was evident within some families in the list (Table 2), for example, Amaranthaceae, Asteraceae, Poaceae, Crassulaceae, Lamiaceae, Fabaceae, Ranunculaceae and Rosaceae.

Seed germination time variation associated with other plant traits

The plant traits had significant effects on log MGT (Table 3). Adult longevity, seed dispersal mode and seed size could account for 5%, 7% and 6% of MGT variation, respectively. Given that MGT shows a strong phylogenetic pattern, the question arises whether other plant attributes account for MGT independently, or are patterns of traits correlation a product of phylogenetic conservative suites of traits.

In our GLM, when taxonomic family was used as the first explanatory variable, it accounted for the larger proportion of the variation in MGT (40%, Table 3). However, when we compared the full model with different reduced models, we found that the percentage of variance in MGT explained by family membership independently decreased to 29% when removing the effects of the other factors (see methods) (Table 4), and the other plant traits could only account for independently 1% (adult longevity and dispersal mode) and 2% (seed size).

Discussion

A growing number of studies have documented that phylogenetic relatedness of plant species within a com-

munity 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 inhabiting 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 MGT is correlated with taxonomic membership. The strong taxonomic effect on MGT suggests that MGT variation within taxonomic membership is limited. 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, McKittrick 1993, Miles and Dunham 1993, Yokoyama 1994, Ackerley and Donoghue 1995).

However, our data suggested that MGT was also correlated with plant longevity, seed mass and dispersal mode, traits obviously showing the apparent conservation of sets of traits within lineages. The observation that MGT is correlated with a number of other plant attributes could be interpreted as adaptations to different life histories (Lord et al. 1995). The overlap between family member-

ship, plant longevity, seed mass and dispersal mode does not negate the adaptive significance of the relationship between adult longevity (or seed mass and dispersal mode) and seed germination time. Furthermore, the association within a lineage between traits and the environment can be maintained by selection; descendant species will be most successful if they show only minor variations of the ancestral set of traits (Lord et al. 1995). For example, selection against departure from the ancestral condition had been suggested as a factor maintaining characteristic seed dispersal syndromes within lineages of Neotropical plants (Lord et al. 1995).

In this study, the full model (family + adult longevity + dispersal mode + seed size) could only account for 44% variation in MGT, and even if we considered all taxonomic levels from class to genus together, taxonomic membership could account for but 70% of seed MGT variation. The variance accounted for by genus was in doubt because many genera had only one or two species. Thus, a large percentage of the variance remained unexplained by our model, and important selective factors or parameters may have been left out of this analysis. Then we suggest that other possible correlates may exist between seed germination time and additional ecological factors (for example, altitude, habitat and post-dispersal predation) or phylogenetic related morphological and physiological seed attributes (e.g., endosperm mass) that were not evaluated in this study.

In summary, when we considered the effect of phylogenetic and other plant traits on seed MGT in the alpine meadow on the eastern Qinghai-Tibet plateau, we found that the phylogenetic constraint was the strongest, the other plant traits also accounted independently for partial variation of seed MGT. Thus, the phylogeny was an important constraint to maintain the stability of species, and we could simplify the question if we regarded the phylogeny as an individual factor, but we could not negate the adaptive significance of the relationship between other plant traits and seed germination time. The smaller proportion accounted for by other plant traits might be the result of the shorter history of the alpine meadow on the eastern Qinghai-Tibet plateau, which was not enough longer to form a stronger evolution of adaptation.

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References

- Ackerley, D.D. and M.J. Donoghue. 1995. Phylogeny and ecology reconsidered. *Journal of Ecology* 83: 727-734.
- Angevine, M.V. and B.F. Chabot. 1979. Seed germination syndromes in higher plants. In: O. Solbrig, S. Jain, G. Johnson and P. Raven (eds.), *Topics in Plant Population Biology*. Columbia University Press, New York. pp. 188-206.
- Angiosperm Phylogeny Group. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141:399-436.
- Baker, H.G. 1972. Seed mass in relation to environmental conditions in California. *Ecology* 53:997-1010.
- Baskin, C.C. and J.M. Baskin. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, California, USA.
- Baskin, C.C., J.M. Baskin and M.A. Leek. 1993. Afterripening pattern during cold stratification of achenes of ten perennial Asteraceae from eastern North America, and evolutionary implications. *Plant Species Biology* 8:61-65.
- Feinsinger, P. (1987) Effects of plants species on each other's pollination: is community structure influenced? *Trends. Ecol. Evol.* 2: 123-126.
- Figuerola, J.A. and J.J. Armesto. 2001. Community-wide germination strategies in a temperate rainforest of Southern Chile: ecological and evolutionary correlates. *Aust. J. Bot.* 49:411-425.
- Garwood, N.C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* 53:159-181.
- Grime, J.P., G. Mason, A.V. Curtis, J. Rodman, S.R. Bond, M. Mowforth, A.M. Neal and S. Shaw. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69:1017-1059.
- Herrera, C. 1992. Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents. *Ecology* 73:1832-1841.
- Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist* 145:163-191.
- Jurado, E. and J. Flores. 2005. Is seed dormancy under environmental control or bound to plant traits? *Journal of Vegetation Science* 16:559-564.
- Kochmer, J.P. and S.N. Handel. 1986. Constraints and competition in the evolution of flowering phenology. *Ecol. Monographs* 56:303-325.
- Lanyon, S.M. 1993. Phylogenetic frameworks: towards a firmer foundation for the comparative approach. *Biological Journal of the Linnean Society* 49:45-61.
- Leishman, M.R., M. Westoby and E. Jurado. 1995. Correlates of seed size variation: a comparison among five temperate floras. *Journal of Ecology* 83:517-530.
- Lord, J., M. Westoby and M. Leishman. 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. *American Naturalist* 146: 349-364.
- Mazer, S.J. 1989. Ecological, taxonomic, and life history correlates of seed mass among Indiana dune angiosperms. *Ecol. Monographs* 59:153-175.
- McKittrick, M.C. 1993. Phylogenetic constraint in evolutionary theory: has it any explanatory power? *Annual Review of Ecology and Systematics* 24:307-330.
- Miles, D.B. and A.L. Dunham. 1993. Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analyses. *Annual Review of Ecology and Systematics* 24: 587-619.

- Rees, M. 1993. Trade-offs among dispersal strategies in British plants. *Nature* 366:150-152.
- Smith-Ramírez, C., J.J. Armesto and J.A. Figueroa. 1998. Flowering, fruiting and seed germination in Chilean rain forest myrtaceae: ecological and phylogenetic constraints. *Plant Ecology* 136:119-131.
- Thompson, K. 1987. Seed and seed banks. *New Phytologist* 106 (Supplement): 23-34.
- Venable, D.L. and J.S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131:360-384.
- Venable, D.L. and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* 46: 272-282.
- Waller, D.M. 1988. Plant morphology and reproduction. In: J.L. Doust and L.L. Doust (eds.), *Plant Reproductive Ecology Patterns and Strategies*. Oxford University Press, Oxford, pp. 203-207.
- Westoby, M., E. Jurado and M. Leishman. 1992. Comparative evolutionary ecology of seed mass. *Trends. Ecol. Evol.* 7:368-372.
- Yokoyama, J. 1994. Molecular phylogeny and coevolution. *Plant Species Biology* 9: 163-167.
- Zhang, S.T., G.Z. Du and J.K. Chen. 2004. Seed size in relation to phylogeny, growth form and longevity in a subalpine meadow on the east of the Tibetan Plateau. *Folia Geobotanica* 39:129-142.

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Appendix

The longevity of adult plants, dispersal mode, seed mass and mean germination time of 633 species in the alpine meadow on the eastern Qinghai-Tibet plateau. The Angiosperm Phylogeny Group II (2003) was used to assign the affiliation of each species to higher taxonomic levels.

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