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The evolutionary correlation associated with seed mass and altitude on nutrient allocation of seeds

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Abstract

Seed reserves play vital roles in seed germination and seedling growth and their variation may be related to various environment factors, plant traits and phylogenetic history. Here, the evolutionary correlation associated with seed mass and altitude and carbon (C), nitrogen (N) and phosphorus (P) allocation of seeds among 253 alpine herbaceous plants was tested. In this study, phylogeny had strong limitations on nutrient allocation of seeds across species, and species from younger phylogenetic groups tended to have higher N and P contents, which might be considered as the evolutionary selection of seed plants. Higher seed N and P content would help seedlings to gain more survival chance and stronger competitive capacity, and their progeny would be more likely to be preserved. When phylogeny was considered, altitude only had a significant positive effect on P content, but the negative effects on seed mass were all expressed. The independent effects of altitude and seed mass suggest that the nutrient allocation of seeds might be affected by both environment and plant traits. In addition, altitude and seed mass displayed partial overlapping effects on nutrient allocation of seeds. The negative effects of seed mass were affected slightly by altitude, whereas altitude only had a significant positive effect on P content when seed mass was controlled. Above all, seed P content showed obvious and general correlations with seed mass, altitude and age of clade, which indicated that higher seed P content might be an adaptive selection of species associated with growth and survival of progeny.

Introduction

Seed reserves play vital roles in seed germination, seedling growth and survival of individuals which directly determine if the population can regenerate successfully (Lamont and Groom, 2013; Cheng *et al*., 2015). The physiological and morphological processes of seed germination depend highly on seed reserves (Soltani *et al*., 2006; Bewley *et al*., 2013; Cheng *et al*., 2015). Carbon (C), nitrogen (N) and phosphorus (P) are indispensable elements for plant growth (Bu *et al*., 2018). C is the main element to form dry matter and energetic materials, N is strongly associated with protein content, and P is an indication of the level of nucleic acids (McGinley and Charnov, 1988; Elser *et al*., 2000; Soriano *et al*., 2011). C, N and P allocation of plant roots, stems and leaves have been widely investigated (Jackson *et al*., 1997; Kerkhoff *et al*., 2006; Reich *et al*., 2008; Rong *et al*., 2015), but has been rarely studied in seeds (Lamont and Groom, 2013; Bu *et al*., 2018).

As another important trait associated with nutrient allocation of seeds, seed mass has been associated with germination strategy, soil seed bank composition, seedling growth, etc. (Peco *et al*., 2003; Kidson and Westoby, 2000; Turnbull *et al*., 2012; Zhang *et al*., 2014). In many studies it has been argued that smaller seeds germinate more rapidly, have higher percentage of germination, represent a larger proportion in the permanent soil bank, and produce smaller seedlings with rapid relative growth but lower survival rate (Susko and Lovettdoust, 2000; Poorter and Rose, 2005; Turnbull *et al*., 2012). Thus, seed mass and seed reserves might influence seed germination and early seedling growth with different nutrient elements playing parts in it. The question then arises if the differences in seedling growth and survival between larger and smaller seeds are caused by differences in C, N and P allocation of seeds.

The accumulation of C, N and P in seeds is influenced by diverse environmental factors, such as CO_2 (He *et al*., 2005), drought (Dornbos and Mullen, 1992), light (Mathew *et al*., 2000), temperature (Nayyar *et al*., 2010; Xu *et al*., 2016), and latitude (Frenne *et al*., 2011). The environment at different altitudes varies strongly in temperature, light, precipitation, and CO_2 concentration (Li and Yuan, 2012). This environmental variation will exert selective pressure on plant growth, survival, physiological regulation, and result in adaptive evolution (Lord, 1994). In our previous studies, seeds collected from the study site in this paper showed a decreasing tendency in weight with increasing altitude (Bu *et al.*, 2007). Baker (1972) suggested that the lighter seeds might be the result of a short growing season at high altitude which provides inadequate time for plants to produce and stock nutrient materials. Thus, nutrient allocation of seeds across species might be influenced by altitude and seed mass for their close connection with plant growth and survival.

In addition, Lord *et al.* (1995) hypothesized that species from the same ancestor tend to have similar attributes and appear at similar habitats. Phylogenetic history has a strong limitation on the variation of plant traits to adapt independently to the environment (Lord, 1994). Many studies have addressed the constraint of phylogeny on plant traits, such as seed mass, fleshy-fruit traits, seed germinability and flowering phenology (Grime *et al.*, 1981; Jordano, 1995; Jia *et al.*, 2011; Qi *et al.*, 2014). However, few studies have addressed the phylogenetic limitation on C, N and P allocation of seeds (Bu *et al.*, 2018). Many studies have indicated that the nutrient allocation of seeds might be controlled by phylogenetic history. For example, seeds from Brassicaceae have higher oil content and those from Fabaceae have higher protein content (Salisbury *et al.*, 2018; Dornbos and Mullen, 1992). Thus, the variation in nutrient allocation of seeds collected from an alpine meadow was predicted to be controlled by the phylogenetic groups. In view of the fact that plants within a lineage might be shaped by diverse environmental factors during evolution, the evolutionary direction of nutrient allocation of seeds across species with different clade age should be considered.

Here, the evolutionary correlation between seed mass and altitude on C, N and P allocation of seeds from 253 species was tested. The following questions were addressed: (1) Do seed mass, altitude and phylogenetic history influence nutrient allocation of seeds? (2) If yes, are the effects of altitude and seed mass affected by phylogenetic history? Do altitude and seed mass have independent and interactive effects on nutrient allocation of seeds?

Materials and methods

Study area

The study area is situated on the northeastern edge of Qinghai-Tibet plateau in China (100°44′–104°45′ E, 33°06′–35° 34′). The main vegetation types include alpine meadow, shrub and forest, where it is altitudinal (altitude: 2000 to 4200 m) and cold (annual average temperature of 1.2°C and annual average 270 frost days) with annual precipitation of 450–780 mm and short growing season (from late May to late September) (Zhang *et al.*, 2014; Bu *et al.*, 2016).

Data set

Mature seeds of 253 species (40 families) were all collected from an alpine meadow from August to September in 2015. Seeds of all species were collected randomly and seeds from over 30 plants (at site within 50 m altitude difference) of each species were mixed. Intact seeds were screened out and stored in envelopes and oven-dried to constant weight after which seed mass and nutrient content were measured. Seed mass of each species was defined as the average hundred-seed weight of three samples from the same site. Dry combustion was used to measure C and N content whereas the molybdenum blue method was used to measure P content as described in Bu *et al.* (2018). The C, N and P contents (percentage) were used to estimate the nutrient allocation of seeds.

Table 1. Correlations between the C, N and P allocation of seeds and altitude (or seed mass), and partial correlations between them when altitude or seed mass was kept constant among 253 species

Variables	Control variables	C (%)	N (%)	P (%)
Seed mass	–	−0.209**	−0.102	−0.289***
	Altitude	−0.202**	−0.087	−0.272***
Altitude	–	0.113	0.160*	0.217**
	Seed mass	0.056	0.107	0.144*

*Significant at $P < 0.05$, **significant at $P < 0.01$, ***significant at $P < 0.001$, unmarked is not significant.

Table 2. Phylogenetic signals of the C, N and P allocation of seeds across 253 species; three of the 253 species (only at family level) were not considered in the analysis

Source	Pagel's lambda	*P*
C (%)	0.6655	<0.0001
N (%)	0.8346	<0.0001
P (%)	0.8358	<0.0001

Statistical analysis

Altitude, seed mass and C, N and P contents were log-transformed. Bivariate correlations were used to estimate if nutrient allocation of seeds changed with increasing altitude (Spearman's correlation coefficient) and seed mass (Pearson's correlation coefficient). The partial correlations were used to determine the interactions or associations between seed mass and altitude on nutrient allocation.

Considering phylogenetic limitations on seed mass and nutrient allocation, Pagel's lambda (Pagel, 1999) was used to test the phylogenetic signals in C, N and P allocation of seeds. Phylogenetically independent contrasts (Felsenstein, 1985) were conducted to assess the net correlations between C, N and P allocation and seed mass (or altitude). Lambda values were tested using likelihood ratio tests, *P* values showing maximum likelihood values of lambda were significantly greater than 0. Furthermore, the linear correlation between C, N and P allocation and age of clade (genus-level age) calculated by PICs (log-transformed) was determined to evaluate the evolutionary history of nutrient allocation of seeds.

Based on the Phylomatic tree R20120829 for plants with APG III (2009), PICs were conducted by Phylocom version 4.2 (Webb *et al.*, 2008). Phylogenetic signal and analysis was conducted through the package 'picante' of R statistical software v3.3.1 (R Development Core Team, 2016). The bivariate and partial correlations were analysed by SPSS 17.0.

Results

In this study, we observed great variations in C, N and P allocation of seeds among species and even among families (seed supplement file). C, N and P contents of seeds across 253 species

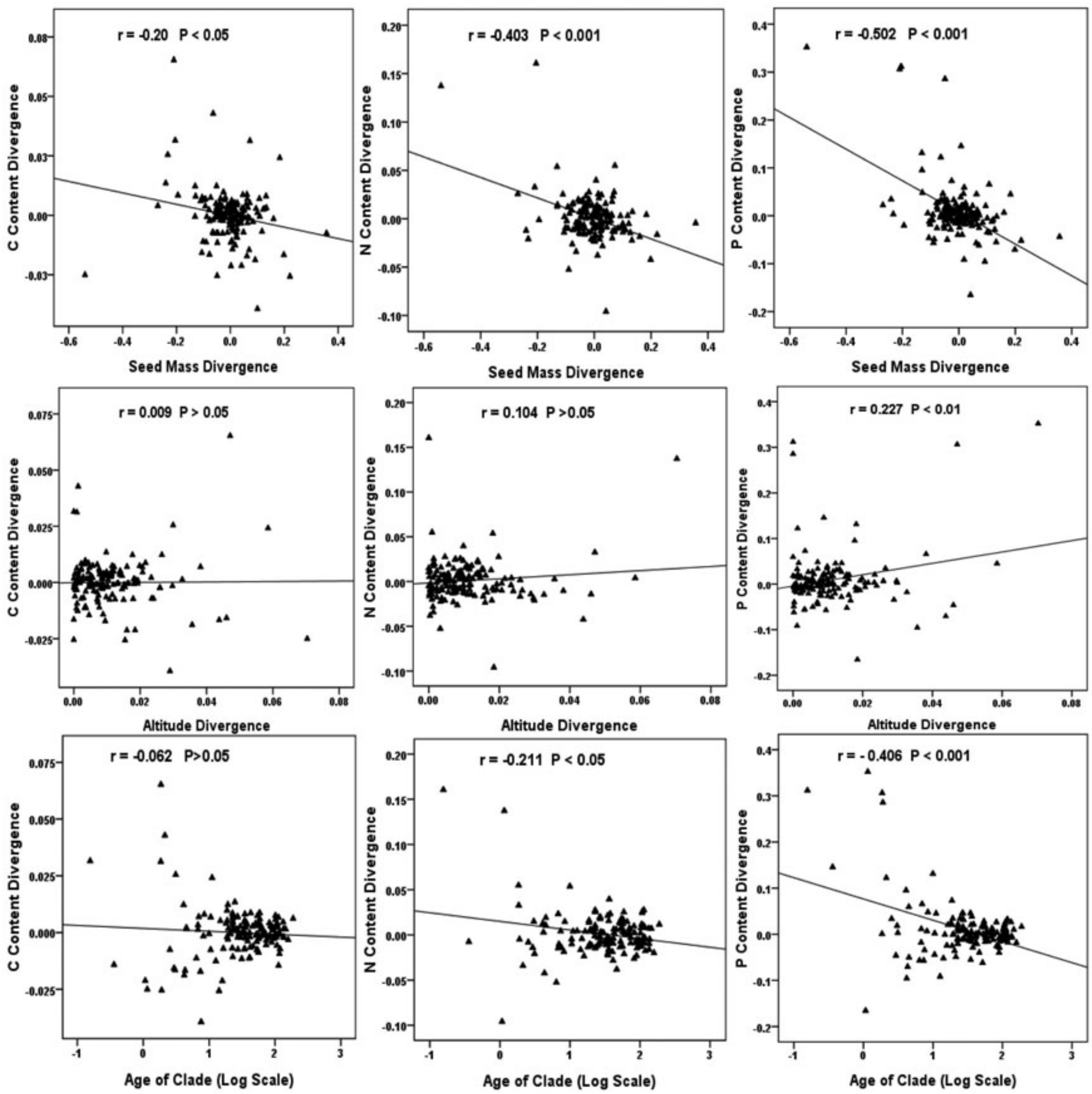

Fig. 1. Divergence in C, N and P contents (log scale) correlated with divergence in seed mass, altitude and age of clade (log scale) for 148 nodes produced by PIC analysis. Three of the 253 species (only at family level) were not considered in PIC analyses.

varied from 39.46 to 76.68%, from 1.25 to 9.49% and from 0.09 to 1.47%, respectively. The coefficients of variation in C, N and P contents among species were 12.3, 35.2 and 42.9%, and those among families were 12.2, 26.3 and 37.0%, respectively.

The smaller seeds tended to have higher C and P contents, and seeds from higher altitude tended to have higher N and P contents (Table 1). The partial correlations indicate that altitude and seed mass had interactive effects on the contents of C, N and P (Table 1). When altitude was kept constant, the correlation coefficients between nutrient contents (C, N and P) and seed mass decreased by 3.3, 14.7 and 5.9%, whereas the correlation associated with altitude decreased by 50.4, 33.1 and 33.6% when seed mass was kept constant (Table 1).

Significant phylogenetic signals in nutrient allocation of seeds were found (Table 2). PIC analyses produced 148 nodes. Pearson's correlations between the standardized independent contrasts of each node indicated that the influence of altitude and seed mass on nutrient allocation of seeds was independent of phylogeny (Fig. 1). When phylogeny was taken into consideration, C and N contents had no significant variation tendency with altitude, but a significant positive correlation between P content and altitude was found (Fig. 1). Interestingly, the effect of seed mass on C, N and P allocation was greater when the effect of phylogeny was removed. C, N and P allocation of seeds all correlated significantly negatively with seed mass. In addition, the N and P contents correlated significantly negatively with age of clade, whereas the C contents displayed no significant correlation.

Discussion

Seed mass correlations

Storage materials of seeds play a crucial role in a plant's history because seeds must provide sufficient nutrients for seed germination and primary growth until seedlings become autotrophic and established (Suda and Giorgini, 2000; Ichie *et al.*, 2001; Soltani *et al.*, 2006; Bewley *et al.*, 2013; Cheng *et al.*, 2015). Here, C and P contents decreased with seed mass irrespective of altitude and phylogeny (Table 1). This result was consistent with that of Grubb and Burslem (1998). Carbohydrates, lipids and proteins are three main nutrient components of seeds (Soriano *et al.*, 2011). The C content of the three nutrients are in the order: carbohydrates, proteins and lipids. Thus, the higher C content in smaller seeds might represents higher contents of lipids which contain more than twice the energy of non-structural carbohydrates or proteins (Soriano *et al.*, 2011). A higher lipid content may provide more energy for primary growth which is especially important to species with smaller seeds. Compared with larger-seeded species, smaller-seeded species have a weaker competitive capacity because the primary growth of seedlings completely relies on seed reserves (Soriano *et al.*, 2011). Many studies report a negative correlation across species of seedling relative growth rate and seed mass (Paz and Martínezramos, 2003; Poorter *et al.*, 2008). Thus, the rapid growth of seedlings from smaller seeds was expected to be caused by the difference in nutrient contents compared with larger seeds. In addition, as an essential material for cell differentiation and plant growth, P content reflects nucleic acid content but is also important for the synthesis of sugar-phosphate intermediates of photosynthesis and respiration (Slot *et al.*, 2013). Many studies also implicate that higher P content in smaller seeds could provide sufficient ribosomes for fast seed germination and rapid initial growth (Nedel *et al.*, 1996; Elser *et al.*, 2003; Soriano *et al.*, 2011). Therefore, higher C and P content in smaller seeds may point to adaptive selection of species for survival and preservation.

Altitude correlations

Storage materials of seeds may vary temporally and spatially with the environmental conditions experienced by the mother plant (Oluwatosin, 1997; Soriano *et al.*, 2011; Xu *et al.*, 2016). For example, Dornbos and Mullen (1992) found that drought and high temperature increased protein content and decreased oil content of soybean; Sakla *et al.* (1988) found that soybean from lower altitude had higher content of carbohydrates and lower protein content; Wardlaw and Dunstone (1984) suggested that drought and low temperature induced seeds to accumulate soluble sugar. Here, altitude had an indistinct impact on C content but displayed significant positive effects on the contents of N and P, but especially on the variation of P content. Irrespective of phylogeny and seed mass, seeds from higher altitude tended to have higher P content (Table 1, Fig. 1). With increasing altitude, the climate becomes more adverse and unstable, which is risky for plant growth and survival, especially for initial growth (Giménez-Benavides *et al.*, 2008; Poll *et al.*, 2009). Furthermore, the short growth season of high altitude areas causes species to have less chance of population regeneration and higher risk of discontinuing their life cycle (Zhang *et al.*, 2004). If species from high altitude areas had rapid initial growth, they would take the opportunity to recruit seedlings and, subsequently, spread population. Hence, the high content of P in seeds of species from high altitude areas might be the result of natural selection for rapid initial growth.

In the present study, partial correlations between altitude and seed mass showed overlapping effects on nutrient allocation of seeds (Table 1). The relationship between nutrient allocation and seed mass were affected only slightly by altitude. Whether the effect of altitude was considered or not, seed mass correlated significantly negatively with seed C and P contents (Table 1). Thus, higher C and P contents in smaller seeds might be more important to plant growth than alteration of the environment caused by altitude. Furthermore, when the effect of seed mass was considered, the relationship between seed N contents and altitude became indistinct, yet altitude had a significant positive effect on P content (Table 1). Therefore, the higher P content might be an adaptive selection to species from higher altitude.

Phylogenetic history correlations

Here, C, N and P allocation across species showed significant phylogenetic signals that suggest strong effects of ancestors (Table 2). In other words, lineage history forced limitations on variability in nutrient allocation of seeds within a clade. However, C, N and P allocation showed large variation across species among families and even within a family. For example, the seed N content of Ranunculaceae ranged from 1.52 to 5.17%, the C content from 52.12 to 72.58%, and the P content from 0.09 to 0.82%. Similarly, seeds from other families also showed significant variation in nutrient contents (see supplementary material). One possible reason for the large variation in nutrient contents across species might be due to natural selective pressure and co-evolution of traits. Although progeny of each species tends to maintain their ancestral traits (Lord *et al.*, 1995), many studies found that plant traits, such as seed germination, flowering phenology and seed size, may be shaped by habitat conditions (Jordano, 1995; Giménez-Benavides *et al.*, 2008; Qi *et al.*, 2014) and co-evolve with other traits (Grime *et al.*, 1981; Zhang *et al.*, 2004; Jia *et al.*, 2011; Qi *et al.*, 2014). In this study, when the effect of phylogeny was removed (PIC analyses), contents of C and N were indistinct but P content was still significantly affected by altitude (Fig. 1), whereas the effects of seed mass on C, N and P contents were all enhanced significantly. Hence, adaptive selection or coevolution of characteristics played a part in the variation of nutrient allocation of seeds although phylogeny imposed strong constraints to maintain the traits inherited from ancestors. In addition, N and P contents showed significant negative correlations with age of clade among the 253 species. In other words, species from younger phylogenetic groups had higher N and P contents. As mentioned earlier, higher N and P contents are beneficial to improve the vigor, growth rate and survival of seedlings (Elser *et al.*, 2003). Thus, species with higher N and P contents of seeds might be more likely to be preserved because they have a better chance of survival and stronger competitive capacity. However, each nutrient is irreplaceable and each is important to seed germination and seedling growth, thus there should be a trade-off among various nutrients. The optimal C:N:P ratio of seeds will be investigated in future studies.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0960258518000387.

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