SEED MASS INCREASE ALONG ALTITUDE WITHIN FOUR SAUSSUREA (ASTERACEAE) SPECIES IN TIBETAN PLATEAU

ABSTRACT: Seed mass is a critical life-history character in seed evolutionary ecology. Plant species can present responses in seed mass to environmental stresses. We tested the hypotheses that seed mass was positively correlated with altitude within species. We selected four congeneric Saussurea species as study objects, and collected their seeds along altitudinal gradients (2100–4200 m a.s.l.) in the alpine area of the Qinghai-Tibetan Plateau, China. Results showed that mean seed mass of the four species were significantly affected by altitude ($P <0.001$). There was a general trend of an increase in seed weight with altitude among the populations of the four species. In addition, mean seed mass of four species were not significantly different, but all presented a bigger coefficients of variation within species along altitude gradients. Our results indicate selection pressure within species, with larger seeds occurring at higher altitudes.

KEY WORDS: adaptation strategy, altitude, Qinghai-Tibetan Plateau, Saussurea sp., seed mass

Seed mass is a critical life-history character in seed evolutionary ecology (Fenner and Thompson 2005, Moles et al. 2005). Seed mass can affect community structure and succession directly or indirectly (Westoby et al. 1992, Rees et al. 2001, Muller-Landau 2003). Seed mass within species was considered for a long time to be relatively constant (Harper 1977, Moles et al. 2005, Wu et al. 2010a). However, plants produced larger or smaller seeds to adapt to environmental pressure (Baker 1972) or escape predation (Gomez 2004). Seed mass often varies among individuals within plant species. It was thought to maintain a range of seed mass, because of resource heterogeneity (Janzen 1982, Venable 1992, Seiwa 2000), conflicting selective forces of the ability to escape pathogens and predators (Moegenburg 1996, Seiwa 2000, Gomez 2004), or evolution of life-history strategy to germinate and become successfully established (Leishman et al. 2000).

Many studies have emphasized that seed mass does vary within species (Schaal 1980, Wolfe 1995), but differences in seed mass within species are small in comparison to differences within genera or even families (Hodgson and Mackey 1986, Mazer 1990, Lord et al. 1995). Most studies have reported an increase in seed mass with increasing altitude (Boulli et al. 2001, Blionis and Vokou 2002). However, a decrease in seed mass was recorded with increasing altitude for Ranunculus acris in an alpine area of Norway (Totland and Birks 1996). Variation in seed mass among populations living in dif-
Different environmental conditions has been reported (L andolt 1967, W inn 1988, Pluess et al. 2005, Wu and Du 2009). L andolt (1967) compared seed weight in pairs of congeneric lowland and alpine species in Switzerland and concluded that seed mass tended to increase rather than decrease with higher altitude. Wu and Du (2009) found that seed mass increased and decreased half and half with altitude within 44 species studied in two alpine Kobresia-dominated communities. There has been no consistent view on seed mass with increasing altitude within species. Pluess et al. (2005) proposed that phylogenetic relationships among species are important for seed mass variation. Thus, we selected four Saussurea species as our study group. Seeds were collected from populations along an altitudinal gradient. The relationship between altitude and seed mass was tested for the four species separately.

In the present study, we examined altitude as one of the factors affecting geographic variation in seed mass among and within species of Saussurea species in an alpine area of the Qinghai-Tibetan Plateau. This study was conducted on the eastern side of the Qinghai-Tibetan Plateau where there is a short and cold summer and a long winter (Gannan plateau, Gansu Province). It is about $3.8 \times 10^4 \text{ km}^2$ in area. Its geographical location is $100^\circ35'–104^\circ50'\text{N}, 33^\circ05'–35^\circ35'\text{E}$. The climate is Humid-Alpine with a mean annual rainfall of $350 ~ 880 \text{ mm}$, mainly falling in summer and increasing with altitude from east to west. Mean annual air temperature is $<3.0^\circ\text{C}$ with $-12^-18^\circ\text{C}$ in December and January and $18^-20^\circ\text{C}$ in July and August, and with an average of more than 200 days of frost annually. The dominant vegetation is typical of alpine meadows and subalpine meadows, which were dominated by graminoids such as Poa, Kobresia, Elymus and Stipa, and by dicots such as Trollius, Anemone, Aconitum, Ligularia, Saussurea, Pedicularis, Potentilla, and Gentiana (Wu et al. 2010b).

Study species Saussurea DC. is one of the largest genera, comprising over 300 species in the Asteraceae (Bremer 1994) and the Qinghai-Tibetan Plateau is a major distribution centre of species of Saussurea DC (Lipschitz 1979, Wang and Liu 2004). These Saussurea species occur mainly in the subalpine/alpine region of the Qinghai-Tibetan Plateau and are perennial herbaceous broad-leaf species and dominant species in this area. They had visible convergent evolution in their morphology under the different selective pressure of the Qinghai-Tibetan Plateau (Shi and Jin 1999, Wang and Liu 2004). Four Saussurea species (S. epilobioides, S. iodostegia, S. minuta and S. subulisquama) with similar distributions over a large altitudinal gradient were selected for this study. The nomenclature for plant species follows Wu (1995).

In the study area, we collected the seeds of four Saussurea species from different populations along altitudinal gradients by the methods outlined by Pluess et al. (2005), during July to October 2005. Differences in seed mass are expected to be mainly due to decreasing temperature and growing period with increasing altitude. We collected the seeds separately from more than ten individual plants from three to five subsampled populations in each altitude site. All seeds of the same species from three subsampled populations in an altitude site were combined, and

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of altitude-sites</th>
<th>Altitudinal range (m a.s.l)</th>
<th>Coefficients of variation (C.V)</th>
<th>Mean seed mass (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. epilobioides</td>
<td>9</td>
<td>3100–4200</td>
<td>0.27</td>
<td>1.841</td>
</tr>
<tr>
<td>S. iodostegia</td>
<td>8</td>
<td>3100–3900</td>
<td>0.14</td>
<td>2.742</td>
</tr>
<tr>
<td>S. minuta</td>
<td>13</td>
<td>2100–3420</td>
<td>0.20</td>
<td>1.739</td>
</tr>
<tr>
<td>S. subulisquama</td>
<td>8</td>
<td>3200–4400</td>
<td>0.21</td>
<td>3.018</td>
</tr>
</tbody>
</table>
the mean seed mass of each species within a population at an altitude was determined. Seeds were divided into batches of 100 air-dried (three months) seeds, and three batches per species per altitude site were weighed. The altitudinal gradient covered ca. 1100 m (3100, 3300, 3420, 3520, 3600, 3650, 3680, 4100 and 4200 m a.s.l.) in *Saussurea epilobioides*, 800 m (3100, 3200, 3300, 3400, 3420, 3700, 3850 and 3900 m a.s.l.) in *S. iodostegia*, 1,320 m (2100, 2150, 2450, 2500, 2600, 2780, 2830, 2900, 3100, 3200, 3300, 3350 and 3420 m a.s.l.) in *S. minuta*, and 1,200 m (3200, 3300, 3420, 3450, 3500, 3850, 4000 and 4400 m a.s.l.) in *S. subulisquama* (Table 1).

We log-transformed the data and analysed the relationship between altitude and mean seed mass of population for each of the four species with a parametric Pearson’s product–moment (r) test. An ANOVA analysis was done to test for significance (*P* <0.05) of species and altitude on seed mass. Coefficients of variation (C.V.) of seed mass were calculated by C.V. = Standard deviation of seed mass (S.D.) × 100 /mean (Wu and Du 2009). All calculations were done with the Statistical Package for the Social Sciences version 11.0 (SPSS, Inc., Chicago, USA).

There was a general trend of seed weight variation with altitude among the populations for the four species (*P* <0.001). Seed mass increased positively with increasing altitude in *S. epilobioides* (*r* = 0.34, *P* <0.001), *S. iodostegia* (*r* = 0.62, *P* <0.001), *S. minuta* (*r* = 0.72, *P* <0.001), and *S. subulisquama* (*r* = 0.82, *P* <0.001) (Fig. 1). In addition, mean seed mass of the four species were not significantly different, but all presented a bigger coefficients of variation within species along altitude gradients (Table 1). Meanwhile, there

Fig. 1. Relationships of seed mass and altitude for the four study species, *Saussurea epilobioides* (*n* = 9), *S. iodostegia* (*n* = 8), *S. minuta* (*n* = 13), and *S. subulisquama* (*n* = 8). Populations were sampled along altitudinal gradients (see Table 1).
was different slope among species and clear deviations from a general trend, especially for *S. epilobioides* (Fig. 1).

Plant species altered their morphological traits to advance their success in survival and reproduction in special rigorous physical and biological habitats (Harper 1977). Seed mass has been regarded as an important plant trait since the pioneering studies of Salisbury (1942). The number of studies on the evolutionary and ecological significance of seed mass has increased greatly in recent years (Westoby *et al.* 1996, Leishman *et al.* 2000, Fenner and Thompson 2005). Variation in seed mass is common among individual plants in the same population (Westoby *et al.* 1992) and is an evolutionarily adaptive strategy to environmental heterogeneity (Rees and Westoby 1997, Geritz *et al.* 1999).

Based on the comparison of seed mass response to increasing altitude of four congeneric *Saussurea* species, we observed that seed mass presented an increasing with altitude in alpine area of the Qinghai-Tibetan. The potential reasons should be included: Firstly, individuals with larger seed may have greater offspring recruitment success, because of advantages of seed germination (Wu and Du 2007), hazards of earlier seedling performance, seedling establishment, resisting environment stresses (Westoby *et al.* 1996, Leishman *et al.* 2000, Eriksson 2005). Study in the Swiss Alps had indicated that selection favours larger seeds at higher altitudes (Pluess *et al.* 2005). It is well known that offspring from large seeds are better competitors and have a higher survival than offspring from small seeds (Geritz *et al.* 1999). Secondly, there was a lower predation hazard at high altitude than at low altitude. There was severe overgrazing in low-altitude alpine meadow of the Qinghai-Tibetan Plateau, but less grazing pressure in the high-altitude sites because of upland topography. Meanwhile, there were a few birds, sheep and yak in high-altitude alpine area of the Qinghai-Tibetan Plateau. Besides, many studies around the world have documented reduced insect diversity, abundance, and activity in alpine ecosystems (Bingham and Orthner 1998). High-intensity grazing is an important selective pressure for plants existing in low-altitude alpine meadow, resulting in that plant tends to produce the smaller seed to escape predation hazard (Gomez 2004). Thirdly, there was lower temperature and later plant phenology at high altitude than low altitude. The individuals at high altitude undergo a longer growth and assimilation period and accumulated much available resources (Johann 2000), because under cooler temperatures, the seeds ripen more slowly and the longer falling period allows for greater total assimilation (Fenner and Thompson 2005). Thus, these plants produced larger seeds at higher altitudes. In addition, there was an increase in rainfall at higher altitude in the eastern Qinghai-Tibetan Plateau. All these indicated that it was more favorable to produce larger seeds within species with increasing altitude, which brought more inclement habitats for plants in alpine area of the Qinghai-Tibetan Plateau. Under specific conditions, plants form the optimal reproductive strategy through the optimal life history characteristics. The altitudinal gradient becomes a significant aspect of the gradient of seed mass, because it includes rainfall, temperature, humidity and radiation (Gaston 2000). Thus, increasing seed mass is an important ecological and evolutionary strategy to higher altitude for these four *Saussurea* species. It suggested that natural selection promotes the formation of larger seeds within populations at higher altitudes. Additionally, a consistent aspect of seed mass and altitude and low variation in seed mass among these four species were found, which can be explained by phylogenetic constraints (Lord *et al.* 1995), because adaptive changes may be restricted by a species’ evolutionary history, i.e. complex patterns of covariation in the same genera among functionally-related traits (Pigliucci 2003, Pluess *et al.* 2005). The closer populations and species in phylogenetic levels had the similar correlation among altitude and seed weight. Additionally, our results showed clear deviations from a general trend, especially for *S. epilobioides*. It may be resulted from different habitats where plant produced different-size seeds because of resource heterogeneity (e.g. light, water and soil nutrient).

In summary, there are many factors affecting seed mass variances, e.g. climate
change, resource competition, predators, habitat disturbance, artificial disturbances and ecological evolution reason. Thus, seed mass variance of within populations at different altitudes is very complex. Seed mass variance can also be one of the population dynamic strategies because seed mass is one reason for changes in vegetation dynamics (Rees et al. 2001). Our results indicate selection pressure within species with larger seeds at higher altitude. Meanwhile, our results suggest that selection for larger seeds within species with altitude show consistent aspect within this genus. To confirm our results, examinations similar to the present study must be conducted for more species in relation to more altitudinal sites.

ACKNOWLEDGEMENTS: This study was supported by Projects of Natural Science Foundation of China (NSFC30900177) and Project of West Light Foundation (2009) of CAS, and NWSUAF (Z111020903). We thank William D. Bowman, Masakado Kawatafor and David Ward for their valuable comments on this manuscript.

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Received after revision July 2010