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Seed weight increases with altitude in the Swiss Alps between related species but not among populations of individual speciesReceived: 31 August 2004 / Accepted: 2 February 2005 / Published online: 11 May 2005
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Abstract Seed weight is a crucial plant life history trait, determining establishment success and dispersal ability. Especially in stressful environments, larger seeds may be selected at the expense of seed number, because larger seeds have a better chance of giving rise to an established offspring. We tested the hypotheses that between related species-pairs and among populations of single species a similar trend for increasing seed weight with increasing altitude should be present. Firstly, we measured seed weights from 29 species-pairs, with one species occurring in lowland areas and a congeneric species from high altitudes. Seeds of the alpine species were $28 \pm 8\%$ larger than seeds from lowland species ($P < 0.01$). Compared to the related lowland species, 55% of the alpine species had heavier seeds, 3% (one species) had lighter, and 41% had seeds of approximately equal weight. Secondly, we compared seed weights among populations of four species from different habitats and with different life histories. Seeds from between 11 and 34 populations per species were sampled along altitudinal gradients of 800–1,500 m (ca. 800 m in *Scabiosa lucida*, ca. 1,000 m in *Saxifraga oppositifolia*, ca. 1,000 m in *Epilobium fleischeri*, and ca. 1,500 m in *Carex flacca*). In all the four species, we found no indication for heavier seeds at higher altitudes. Our results indicate a selection pressure for species with heavier seeds at higher altitude, but the trend does not seem to operate across all cases. Phylogenetic constraints may limit the correlation among altitude and seed weight, operating particularly against selection for larger seed size, the closer populations and species are related to each other.

Keywords Seed size · *Carex flacca* · *Epilobium fleischeri* · *Saxifraga oppositifolia* · *Scabiosa lucida*

Introduction

Seed weight is a critical character of a plant's life history. Particularly in adverse conditions or with high competition pressure, larger seeds can have a higher establishment success, as they provide more reserves for seedlings (see references in Moles and Westoby 2004; Westoby et al. 1997). If resources are limited, a plant may allocate them into fewer, larger seeds or into many, smaller ones (Harper et al. 1970; Smith and Fretwell 1974). As seed number is related directly to fitness, a selection pressure for more but smaller seeds should operate similarly for all species. However, under stressful environmental conditions, selection pressure for larger seeds might override selection pressure for more but smaller seeds (Westoby et al. 1992), because large-seeded species are known to have higher survivorship during establishment than small-seeded species (Westoby et al. 1997).

Here, we ask if seed weight changes along altitudinal gradients in the Alps, as favourable conditions for seed recruitment decrease continuously from low altitude to the top of mountains (Jolls and Bock 1983) where short and cold summers, long snow cover, and soil instability constrain seedling establishment (Bliss 1971; Urbanska and Schütz 1986; Rusterholz et al. 1993; Chambers 1995a, b; Stöcklin and Bäumler 1996). The compromise between seed size and number may be resolved differently at different elevations. Indeed, variation in seed size among populations living in different environmental conditions has been reported (Winn 1988).

However, seed weight within species was considered for a long time to be relatively constant (Harper 1977), and selection was predicted to produce one optimal seed weight within mother plants (Smith and Fretwell 1974). More recently, many studies have emphasised

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that seed size does vary within species and that at the same time heritability of seed size in populations of wild plants can be low (e.g. Schaal 1980; Wolfe 1995). Frequently, a large part of the variation in seed weight is among seeds of the same plant (Winn 1991; Stöcklin and Favre 1994; Wolfe 1995), whereas differences in seed sizes within genera or even families are small (e.g. Hodgson and Mackey 1986; Mazer 1990; Lord et al. 1995). The low variation within genera or families is explained by phylogenetic constraints or niche conservatism (Lord et al. 1995). Adaptive changes may be restricted by a species' evolutionary history, i.e. complex patterns of covariation among functionally related traits (Pigliucci 2003).

In the most detailed across-species study of variation in seed weight with environmental conditions, seed weight of herbaceous species of the Californian flora decreased with increasing altitude as well as with decreasing soil moisture (Baker 1972). As differences in altitude and moisture availability are confounded in the Mediterranean climate of California, the conclusions were questioned (Körner 2003). Phylogenetic relationships among species are important but were not considered by Baker (1972), whereas Landolt (1967) compared seed weight in pairs of congeneric lowland and alpine species in Switzerland. Qualitatively measured seed size tended to increase rather than decrease with higher altitude (Landolt 1967). A number of studies, dealing with single species and focussing on several aspects of plant life history, reported variation in seed weight with increasing altitude, but a consistent picture is not apparent. Most of these studies observed an increase (Mariko et al. 1993; Oyama 1993; Holm 1994; Lord 1994; Piano et al. 1996; Ayana and Bekele 2000; Boulli et al. 2001; Blionis and Vokou 2002), some others a decrease (Totland and Birks 1996) or no alteration (Holm 1994; Kaya and Temerit 1994; Gera et al. 2000) in seed weight with increasing altitude.

We combined two approaches to assess differences in seed weight with altitude. We hypothesized that between related species and among populations within a species, a similar trend for increasing seed weight with increasing altitude should be observed. Firstly, we selected 29 related species-pairs from the Alps, with one species occurring at low altitude and a corresponding species from a higher elevation. We quantified mean individual seed weight using seed samples from the seed collection of the Botanical Institute at the University of Basel, Switzerland. We considered each species-pair in this across-species comparison as a phylogenetically independent replicate of seed weight and altitude. Secondly, we selected four species occurring over a large altitudinal gradient, and having large differences in seed weight and seed dispersal capacities (*Carex flacca* Schreber, *Epilobium fleischeri* Hochstetter, *Saxifraga oppositifolia* L., *Scabiosa lucida* Vill.). Seeds were collected from populations along an altitudinal gradient. The relationship between altitude and seed weight was tested for each of the four species separately.

Materials and methods

Comparison of seed weight between related species from low and high altitude

We randomly selected 29 species-pairs (Table 1) from a list of 53 lowland and 38 related alpine plants published by Landolt (1967). The list was initially compiled for a comparison of morphological characteristics between lowland and alpine species-pairs of open habitats in Switzerland. Species of each pair grow on similar soils and have in most cases (20 out of 29) the same moisture indicator values (Landolt 1977). The indicator value has five levels and differs by one between the species-pairs in nine cases. Therefore, differences in elevation are primarily due to decreasing temperature and decreasing growing period with increasing altitude. The lowland species occur mainly below the lower montane region. The alpine species occur mainly in the subalpine/alpine region. The two species within a pair are not only from the same genus, but are closely related sister species and may occasionally even hybridise (Landolt 1967). The list of pairs in our study includes species from 14 families and 27 genera: 25 genera were represented by one species-pair and only two genera are represented by two species-pairs (*Helianthemum* and *Plantago*). The nomenclature for plant species follows Hess et al. (1976).

For all 58 species, we measured mean individual seed weight using seed samples from the seed collection of the Botanical Institute at the University of Basel, Switzerland. A seed sample in this collection includes seeds from plants of a single local population. For lowland species, between two and ten seed samples from different locations were available. For most alpine species, seeds from between one and six populations were available and for two species more population samples were available (*E. fleischeri* and *S. lucida*). From each seed sample, batches of at least 20 or, if available, 50 air-dried seeds were weighed. Mean weight per seed of a species was calculated using all available seed samples of this species. Values from the literature (Salisbury 1942; Lhotska and Chrtkova 1978; Grime et al. 1981; Müller-Schneider 1983; Bakker et al. 1997; Cerletti 1997; Akinola et al. 1998; Milberg et al. 2000; VanAssche et al. 2002) complemented our measurements of 14 species (see Table 1). The age of the seed samples from the collection of the Botanical Institute (Basel, Switzerland) had no significant influence on seed weight (regression analysis with 47 seed samples from 11 randomly chosen species).

For the comparison of seed weights between lowland and alpine species, we used a *t*-test in which the unit of replication was the species-pair. Data were log-transformed prior to analysis. We tested whether the difference in weight between the pairs was significantly different from zero. Tests for seed weight differences within single species-pairs were not possible, because in 21 of the 58 species seeds of only one or two populations

Table 1 Mean weight per seed of 29 lowland and 29 related alpine species, as well as the percentage-increase or percentage-decrease of seed weight of the alpine compared to the lowland species

Lowland species	Mean weight per seed (mg) ^a	Alpine species	Mean weight per seed (mg)	Percentage difference of alpine vs. lowland species ^b
<i>Achillea collina</i> Becker	0.16	<i>A. stricta</i> Schleicher	0.22	+38 ^c
<i>Anthoxanthum odoratum</i> L.	0.60 ³	<i>A. alpinum</i> Löve et Löve	0.51	-15
<i>Anthyllis macrocephala</i> Wenderoth	2.71	<i>A. alpestris</i> (Kit.) Rchb./Hegetschw.	5.33	+97 ^c
<i>Arenaria leptoclados</i> (Rchb.) Guss.	0.04	<i>A. marschlinii</i> Koch	0.08	+90 ^c
<i>Artemisia campestris</i> L.	0.12	<i>A. borealis</i> Pall.	0.22	+76 ^c
<i>Campanula rotundifolia</i> L.	0.06 ^{3,4,5}	<i>C. scheuchzeri</i> Vill.	0.09	+43 ^c
<i>Centaurea scabiosa</i> L.	7.49 ^{3,4}	<i>C. alpestris</i> Hegetschw.	8.82	+18
<i>Cerastium caespitosum</i> Gilib.	0.09	<i>C. fontanum</i> Baumg.	0.13	+48 ^c
<i>Chrysanthemum leucanthemum</i> L.	0.42	<i>C. montanum</i> All.	0.62	+49 ^c
<i>Epilobium dodonaei</i> Vill.	0.30 ³	<i>E. fleischeri</i> Hochst.	0.17	-42 ^c
<i>Erigeron acer</i> L.	0.13 ³	<i>E. angulosus</i> Gaud.	0.11	-12
<i>Galium pumilum</i> Murray	0.50	<i>G. anisophyllum</i> Vill.	0.48	-4
<i>Helianthemum canum</i> (L.) Baumg.	0.39 ³	<i>H. alpestre</i> (Jacq.) DC.	0.60	+54 ^c
<i>Helianthemum nummularium</i> (L.) Miller	0.94 ⁵	<i>H. grandiflorum</i> (Scop.) Lam.	1.59	+70 ^c
<i>Herniaria incana</i> Lam.	0.14	<i>H. alpina</i> Vill.	0.21	+47 ^c
<i>Juniperus communis</i> L.	12.29	<i>J. nana</i> Willd.	10.54	-14
<i>Lotus corniculatus</i> L.	1.42 ^{1,2,3,4,5,7}	<i>L. alpinus</i> (DC.) Schleicher	1.98	+39 ^c
<i>Onobrychis arenaria</i> (Kit.) DC.	7.53	<i>O. montana</i> DC.	11.72	+56 ^c
<i>Phleum boeheimeri</i> Wib.	0.12	<i>P. hirsutum</i> Honck.	0.30	+150 ^c
<i>Plantago lanceolata</i> L.	1.96 ^{3,4,5,6,7}	<i>P. atrata</i> Hoppe	1.52	-22
<i>Plantago serpentina</i> All.	1.00	<i>P. alpina</i> L.	0.84	-16
<i>Rumex acetosa</i> L.	0.97 ^{7,8,9}	<i>R. arifolius</i> All.	1.42	+46 ^c
<i>Sagina subulata</i> (Schwarz) Presl	0.02	<i>S. linnaei</i> Presl	0.02	+40 ^c
<i>Satureja acinos</i> L. Scheele	0.28	<i>S. alpina</i> (L.) Scheele	0.26	-7
<i>Scabiosa columbaria</i> L.	1.73 ⁵	<i>S. lucida</i> Vill.	1.53	-12
<i>Scrophularia canina</i> L.	0.34	<i>S. juratensis</i> Schleicher	0.43	+28 ^c
<i>Silene vulgaris</i> (Moench) Garcke	0.85 ^{3,4}	<i>S. willdenowii</i> Sweet	0.98	+16
<i>Trifolium pratense</i> L.	1.54 ⁶	<i>T. nivale</i> Sieber	1.33	-13
<i>Veronica serpyllifolia</i> L.	0.08 ⁴	<i>V. tenella</i> All.	0.06	-23

Main data sources are seed samples from the seed collection of the Botanical Institute at the University of Basel, Switzerland

^aNumbers refer to included data from the literature: ¹Salisbury (1942); ²Lhotska and Chrtkova (1978); ³Grime et al. (1981); ⁴Müller-Schneider (1983); ⁵Bakker et al. (1997); ⁶Cerletti (1997); ⁷Akinola et al. (1998); ⁸Milberg et al. (2000); ⁹VanAssche (2002)

^bMean weight per seed among species-pair is considered different (indicated by ^c) based on a threshold value of $\pm 25\%$ (see [Materials and methods](#) for explanation)

were available. We used the following approach to assess how many alpine species have heavier, equal, or lighter seed weights compared to the congeneric lowland species. We designated the seed weight of the lowland species as 100%. The seed weight of the alpine species was calculated as a percentage of the seed weight of the corresponding lowland species. Seed weights of the alpine species were considered to be different from the corresponding lowland species when they exceeded a threshold value. A threshold value was used because of the large among-population variation in seed weight within many species. The mean coefficient of variation (CV) of 24 randomly chosen species with seed samples from at least three populations was $19.9 \pm 2.0\%$ (corrected for different sample numbers according to the procedure described in Sokal and Rohlf (1995)). Based on this mean CV, we set the threshold value to $\pm 25\%$.

For evaluating, if the relative change in seed weight was related to the absolute seed weight of the lowland or the alpine species, we used a parametric Pearson's product-moment (*R*) test.

Altitudinal variation in seed weight among populations of four species

To assess the variation in seed weight among populations, we selected four species with different seed sizes, different dispersal capacities, and occurrence in different alpine habitats, but with similar distributions over a large altitudinal gradient. *C. flacca* and *S. oppositifolia* have seeds without particular structures to assist seed dispersal, while seeds of *E. fleischeri* and *S. lucida* are adapted for wind dispersal. *E. fleischeri* and *S. oppositifolia* are species from alpine scree and moraines, while *C. flacca* and *S. lucida* occur preferentially in grasslands. The altitudinal gradient covered ca. 800 m in *S. lucida*, ca. 1,000 m in *S. oppositifolia*, ca. 1,000 m in *E. fleischeri*, and ca. 1,500 m in *C. flacca* (Table 2). In late summer 2000 and 2001, as well as in 1996 for *S. oppositifolia*, we collected seeds in 34 populations of *E. fleischeri*, in 14 populations of *S. oppositifolia*, and in 11 populations of *S. lucida*. Each population was visited once and seeds were sampled from 15 to 25 plants

Table 2 Number and altitudinal range of sampled populations, mean individual seed weight ($\bar{x} \pm \text{SD}$), and coefficient of variation (CV) among and within populations in four species from the Swiss Alps

Species	No. of populations	Altitudinal range (m a.s.l.)	Weight per seed (mg) ($\bar{x} \pm \text{SD}$)	CV among populations (%)	CVs within populations (%)
<i>Carex flacca</i> Schreber	32	430–2,100	0.77 \pm 0.13	17	–
<i>Epilobium fleischeri</i> Hochstetter	34	1,500–2,500	0.17 \pm 0.02	12	11–31
<i>Saxifraga oppositifolia</i> L.	14	2,040–3,020	0.07 \pm 0.02	29	20–36
<i>Scabiosa lucida</i> Vill.	11	1,650–2,400	1.53 \pm 0.28	19	24–51

CVs within populations are missing for *Carex flacca* as seeds were not sampled per individual due to extensive clonal growth in this species

separately. Per plant 10–30 air-dried seeds were weighed. Mean seed sizes of single plants were averaged per population. In *C. flacca*, we used bulk samples with seeds from different individuals or ramets from 32 populations collected either in late summer 2000 in the Alps or taken from samples in the seed collection of the Botanical Institute at the University of Basel, Switzerland. Samples from the seed collection included mostly populations from low altitudes. In *C. flacca*, population means were calculated from 50 air-dried seeds per population. We calculated CV for individual seed weights per species based on population means. For each population, CV was calculated based on means for individual plants, except in the case of *C. flacca*, where we have no means for individual plants due to the extensive clonal growth of this species. All CVs were corrected for different sample numbers using the procedure described in Sokal and Rohlf (1995).

With a parametric Pearson's product-moment (R) test, we analysed the relationship between altitude and population means of seed weight for each of the four species. All calculations were done with JMP (version 3.1; SAS Institute, Cary, NC, USA, 1995).

Results

Comparison of seed weight between related species from low and high altitude

Seeds of alpine species were $28 \pm 8\%$ larger than seeds of the related lowland species ($df = 28$, $t = 2.76$, $P < 0.01$). The 29 species-pairs included 16 pairs (55%) with heavier, 1 pair (3%) with lighter, and 12 pairs (41%) with equal seed weights for alpine species (Table 1). When the *Phleum* species-pair, where the seeds of the alpine species were $2.5\times$ heavier than the seeds of the lowland species, was excluded, the significant difference among lowland and alpine species remained ($df = 27$, $t = 2.48$, $P < 0.05$). If only those species-pairs with the same moisture indicator values were tested, the relationship of seed weight remained the same ($df = 19$, $t = 2.31$, $P < 0.05$).

The relative amount of change in seed weight was not related to the absolute seed weight of the alpine nor the lowland species ($R = 0.01$, $P = 0.96$; $R = -0.13$, $P = 0.49$, respectively).

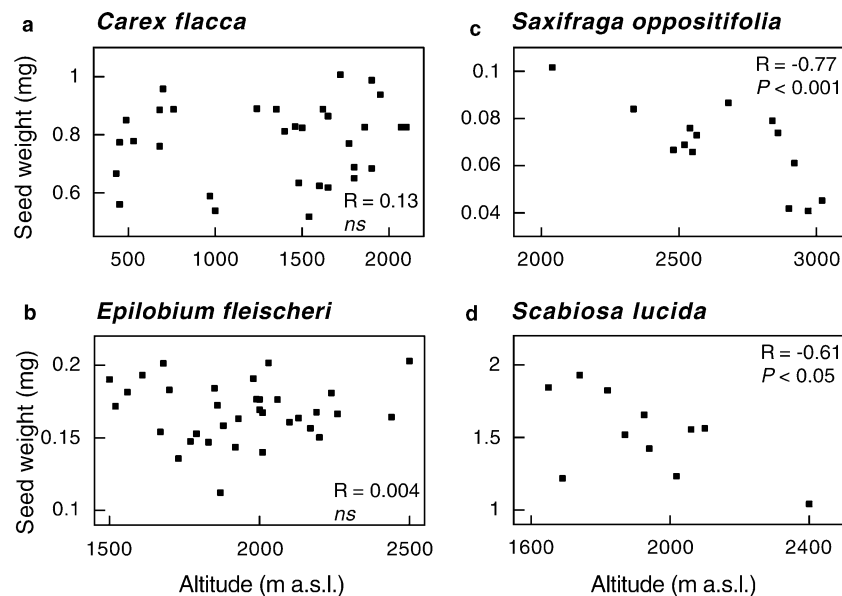


Fig. 1 Population means for weight per seed of **a** *Carex flacca* ($N = 32$), **b** *Epilobium fleischeri* ($N = 34$), **c** *Saxifraga oppositifolia* ($N = 14$), and **d** *Scabiosa lucida* ($N = 11$). Populations were sampled along altitudinal gradients of ca. 800–1,500 m

Altitudinal variation in seed weight among populations of four species

There was no general pattern of seed weight variation with altitude among the populations of the four species. In *C. flacca* and *E. fleischeri*, we found no correlation of seed weight with altitude ($R=0.13$, $P=0.6$, Fig. 1a; $R=0.004$, $P=0.98$; Fig. 1b; respectively), whereas seed weight decreased significantly with altitude in *S. oppositifolia* and *S. lucida* ($R=-0.77$, $P<0.001$, Fig. 1c; $R=-0.61$, $P<0.05$, Fig. 1d; respectively).

Seed weight variation among population means was relatively high with coefficients of variation of 17% in *C. flacca*, 12% in *E. fleischeri*, 29% in *S. oppositifolia*, and 19% in *S. lucida* (Table 2). Variation among seed families within populations was between moderate and high with coefficients of seed weight variation between 11% and 51% (Table 2). The coefficients of seed weight variation within populations did not correlate with the altitude of the populations in *E. fleischeri*, *S. oppositifolia*, and *S. lucida* (data not shown).

Discussion

Seed weights of related species

In the overall comparison of seed weight differences of lowland vs. alpine species, we observed significantly heavier seeds in alpine species. This result suggests that selection tends to favour the formation of larger seeds in species from higher altitudes, or that species with larger seeds are favoured at higher altitude because environmental conditions for seedling establishment are more severe and larger seedlings are at an advantage. At any given stage during development, seedlings of larger-seeded species should have more reserves available to compensate for various environmental stresses (Leishman et al. 2000).

However, alpine plants do not generally have large seeds. A considerable number of species-pairs (41%) did not differ much in seed weight. Functional, developmental, or genetic co-variation among traits impose constraints that keep changes in size and shape of seeds within narrow limits inside a taxonomic lineage (Hodgson and Mackey 1986; Pigliucci 2003). Furthermore, the ancestors of a particular species-pair may have acquired a combination of traits enabling them to succeed in a particular habitat type (Lord et al. 1995). The descendants within the same lineage could have migrated to higher altitudes, following climatic warming, where they still occupy similar habitats and, thereby, may have preserved the characteristic trait combination. Selection for larger seeds may also be constrained because of a shortage of carbon due to the short duration of the growing season at high altitude. An overall reduction in plant size is the most conspicuous structural alteration in plants observed along elevational gradients (Körner et al. 1989). However, in

a recent study it was found that, despite a reduction in shoot mass of alpine species, biomass of reproductive structures did not change with altitude suggesting that alpine plant species often invest relatively more in reproductive structures compared to lowland species (Fabbro and Körner 2004).

From the 29 species-pairs, only the alpine *E. fleischeri* produced markedly smaller seeds than the related lowland species (*E. dodonaei*). Stöcklin and Favre (1994) studied the variation in reproductive components of these two species in detail and reported a similar number of seeds per stem. However, they found a lower fruit number per stem of the alpine plant, due to an increase in the number of seeds per fruit and a reduction in seed weight. The combination of a lower seed weight with a higher seed number per fruit in *E. fleischeri* probably results from selection for better dispersal ability in this early successional plant from glacier foreland (Stöcklin and Favre 1994). In the island nature of the alpine landscape, the small and efficiently dispersed seeds of *E. fleischeri* have a better chance of colonising new sites, while a reduced probability of seed establishment is compensated for by clonal growth, an ability absent in the lowland *E. dodonaei*. The case of *Epilobium*, though an exception among the 29 species-pairs, illustrates that selection for high dispersal ability of seeds may counteract the suggested selection pressure for larger seeds in adverse conditions.

Intra-specific differences in seed weights

In the comparison of seed weights among populations of the four species studied, we found no indication of larger seed size with increasing altitude. There are several possible reasons for this result. Firstly, in the comparison among related species the increase of seed size with altitude is not general. Coincidence may explain the lack of evidence for larger seeds at higher altitudes among populations within single species, even though we selected species with different life history traits and from different habitats. Secondly, within a species high gene flow among populations by pollen and seeds may homogenise the gene pool and thereby counteract selection pressures among populations at different altitudes. Phenotypic variation in seed weight was mostly much higher within populations than between populations (Table 2). This variation may be due to random variation in the abiotic environment (Wolfe 1995), or random variation during the course of the vegetation period (Winn 1991), thereby counteracting the selection strength towards heavier seeds and causing a low heritability of this trait. Thirdly, a change of seed weight can affect several other traits and phylogenetic constraints may operate against changes in a single trait such as seed weight (Hodgson and Mackey 1986; Pigliucci 2003). Such constraints may become less of a driving force with decreasing relatedness, which

might explain why we found an increase in seed weight between but not within species. Indeed, seed weight has been characterised as one element of a co-evolving complex of characters including dispersal, seed dormancy, plant biomass, niche specialisation, and competition ability (Venable and Brown 1988; Rees 1997). Consequently, an increase in seed size at higher altitude may involve changes of several traits causing a change of the taxonomic status of the plants concerned. For instance, Mariko et al. (1993) reported larger seeds at higher altitude in *Reynoutria japonica* on Mt Fuji. However, they classified the studied populations into two distinct ecotypes, with the larger-seeded ecotype growing at higher altitude. Blionis and Vokou (2002) reported a similar observation for *Campanula spatulata*. Elevation played a primary role in subspecies formation in this species. The subspecies showed a marked divergence in morphological and phenological characters beside the larger seeds in the subspecies from higher altitude. In our study, for the assessment of intraspecific differences in seed weight, we carefully avoided choosing species with a taxonomic differentiation at the subspecies level. This may not only be a reason for the absence of an intraspecific increase in seed weight but also why the altitudinal gradient covered by the four species does not exceed 1,000 m, or in the case of *C. flacca* 1,500 m.

Instead of an increase, we found a decrease of seed weight with altitude in *S. oppositifolia* and *S. lucida*, which can most likely be explained by the climatic conditions at higher sites. Weather conditions, like temperature and season length as well as resource availability are suggested to be important in determining the reproductive output of single plants (Totland and Birks 1996). It is expected that plants from the upper part of their altitudinal distribution may face limiting conditions for producing and filling up seeds. Therefore, in the absence of a selection towards heavier seeds, a negative elevational trend in the weight of seeds collected at field sites is not surprising.

In summary, our results indicate a selection pressure for species with heavier seeds at higher altitude. Moreover, our results suggest that selection for heavier seeds with altitude does not seem to operate across all cases, because phylogeny may constrain the correlation among altitude and seed weight. The trend for increasing seed weight was not found among populations within a single species probably because such constraints are particularly strong within species and because a change in seed weight would also affect other plant traits.

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