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Reproductive allometry in *Pedicularis* species changes with elevation

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Summary

1. Plants produce biomass and then allocate some of it to reproductive structures, so the relationship between reproductive (R) and vegetative (V) mass is a fundamental aspect of a plant's reproductive strategy.

2. Differences among populations or taxa in the allometric relationship between R and V have been attributed to environmental conditions. We hypothesize that populations and taxa living at high elevations should exhibit a lower log R vs. log V slope than those in more benign environments, because the environmental limits on size in alpine environments should favour a relatively large reproductive allocation at smaller sizes and a smaller investment in reproduction per additional unit of biomass accumulated.

3. We investigated variation in the allometric relationship between R and V among 44 naturally occurring populations representing 24 species of *Pedicularis* in the Tibetan Plateau, to test the hypothesis that the slope of the relationship declines with increasing elevation.

4. There was a significant negative relationship between the slope of the log R vs. log V relationship and elevation among populations, although the relationship among populations within species varied. We interpret this in terms of abiotic limitations on size and decreasing efficiency of resource allocation to reproduction with increasing plant size (measured as vegetative biomass) at high elevations. We also found a significant positive relationship between the *y*-intercept of the regression of log R on log V and elevation across species, but the relationship was not significant among populations within species. The combination of the lower slopes and the higher *y*-intercepts for high-elevation populations means that plants growing at high elevations allocate proportionately more biomass to reproduction at smaller sizes and less at larger sizes than plants growing at lower elevations.

5. *Synthesis*. The allometric slope (exponent) of the R–V relationship decreases with increasing elevation among *Pedicularis* populations and species, reflecting fundamental changes in the costs and benefits of increased vegetative biomass with elevation.

Key-words: alpine plants, elevation, *Pedicularis*, plant development and life-history traits, reproductive allometry

Introduction

The way a plant allocates its biomass to different structures is a fundamental aspect of its biology (Begon, Harper & Townsend 2006). Allocation implies trade-offs, because resources allocated to one function are unavailable for other functions. Patterns of allocation reflect evolved strategies that are the results of different selection pressures and constraints (Weiner 2004). Life-history theory has put special emphasis on allocation to reproduction (Gadgil & Bossert 1970; Abrahamson & Gadgil 1973).

Allocation patterns have usually been described and analysed as ratios, such as reproductive effort (defined as the percentage of total biomass in reproductive structures), but plant allocation is usually allometric in the broad sense:

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*Correspondence authors. E-mails: guozdu@lzu.edu.cn, hui.guo325@gmail.com it changes with plant size (Weiner 2004). Given that plant size is the most important determinant of reproductive output, allocation patterns can be better understood through analysing and interpreting allometric relationships [e.g. reproductive (R) vs. vegetative (V) biomass, or log R vs. log V]. The allometric relationship between reproductive and vegetative investment within populations has been the focus of many previous studies (Samson & Werk 1986; Ohlson 1988; Thompson, Weiner & Warwick 1991; Sugiyama & Bazzaz 1998; Weiner *et al.* 2009a,b).

How do environmental factors influence the relationship between R and V? In studies of R–V relationships within populations, differences among populations in reproductive allometry have been attributed to soil properties (Ohlson 1988), disturbance (Welham & Setter 1998) and pH (Méndez & Karlsson 2004), but there are alternative explanations for these observations. From the perspective of developmental constraints, plants in favourable environments might grow faster than those in less favourable environments, but this does not necessarily imply that the relationship between R and V will be altered. It has been argued that the relationship between R and V is not very plastic (Weiner *et al.* 2009a), but natural selection under different abiotic conditions could affect reproductive allometry, particularly for perennial plants in which vegetative biomass contributes to year-to-year survival. For example, populations adapted to more favourable environments may exhibit a more positive slope for the R vs. V (or log R vs. log V) relationship, because under benign conditions, relatively large plants can maximize reproductive effort with little risk to longer-term survival. For perennial plants living under certain types of stress, on the other hand, high reproductive allocation at small sizes may be advantageous if mortality is so high that delaying reproduction and maintaining high allocation to growth is too risky. Decreasing reproductive allocation with increasing size may reflect adaptations to increase longer-term survival or may be the result of environmental limitations on size and/or reproduction (e.g. if larger individuals suffer increased damage to buds and meristems). In other words, in populations living in extreme environments, individuals may allocate more of their biomass to reproduction when small, but natural selection may favour the conversion of a smaller proportion of additional biomass into reproductive biomass as they grow than in populations growing in more benign environments. If this is the case, populations adapted to such unfavourable environments will exhibit lower R–V slopes.

Because of lower temperatures, the shorter growing season and soil instability, the overall conditions for plant growth and reproduction are less favourable at very high elevations. Here, we investigated the effects of altitude on the allometric relationship between reproductive and vegetative biomass within populations of species in the genus *Pedicularis* in the eastern portion of the Tibetan Plateau. The large number of *Pedicularis* species and populations growing at different elevations in this region provides a good opportunity to look at the effects of elevation on reproductive allometry within and among species at different elevations. Focusing on closely related species in a single genus allows us to focus on ecologically and morphologically similar taxa while investigating sources of variation in reproductive allometry. The specific questions addressed are as follows:

1 What are the relationships between reproductive and vegetative biomass within populations and among species of *Pedicularis* growing at different elevations?

2 How do the slope and intercept of the log R–log V relationship change with increasing elevation among populations and among species?

Materials and methods

STUDY SITES AND SAMPLING METHODS

Our investigations were conducted in the eastern Tibetan Plateau, considered to be the geographical centre of the origin and evolution of the genus *Pedicularis* Linn. (Li 1951). In this region, *Pedicularis* species are distributed across a large range of elevations, from 1600 to 5000 m a.s.l. In this study, we focused on 44 populations of 24 species, sampled in 2006 from different elevations located in the eastern Tibetan Plateau, Gansu Province, China. All the species are monocarpic. *Pedicularis chinensis*, *Pedicularis kansuensis* and *Pedicularis semitorta* are biennial, and the remaining species are perennial. All of the species are hemi-parasitic, have self-compatible breeding systems and bumblebees as primary pollinators. For 16 of the species, we collected data on only one population, while the other species are represented by at least two populations (information about the populations and species are presented in Appendix S1 in Supporting Information).

In 2006, we sampled wild populations at the fruiting stage, after all flower production had ceased. In each population, we randomly collected 11–52 individuals (see Appendix S1 for sample sizes) by cutting the stem at the soil surface. Each plant was placed in a paper envelope until processed. From each infructescence on every plant, we removed 3–5 mature but unopened fruits from different positions. To reduce potential effects of fruit position on seed mass, we chose fruits at basal, middle and distal positions on each sampled infructescence. These fruits were dissected, and the seeds were removed and examined. Fully developed seeds were counted and oven-dried for a minimum of 48 h at 60 °C. We weighed the dry mass of all of the fully developed seeds in a given fruit to the nearest 0.1 mg. Reproductive output (R) of each plant was estimated as total seed mass per plant (mean total seed mass per fruit multiplied by fruit number; Klinkhamer *et al.* 1992). Vegetative biomass (V) was determined by weighing the above-ground parts of each sampled individual, including stem, fruit, stalks and leaves, to the nearest 0.1 mg. Population means for reproductive and vegetative mass were based on values for all individuals.

STATISTICAL ANALYSES

We analysed the R–V relationship using the classical allometric model: $R = aV^b$, usually fit as $\log R = \log a + b \log V$ (Klinkhamer *et al.* 1992). Parameter a is usually referred to as the 'allometric coefficient' and b the 'allometric exponent'. An exponent significantly different from 1.0 indicates an allometric (non-isometric) relationship. Several researchers (Henry & Aarssen 1999; Niklas 2006) have argued that model II regression, e.g. standardized major axis (SMA), is more appropriate than traditional least squares for fitting allometric data and estimation of the parameters, so we used SMA.

We tested whether the slope of each population statistically differed from one. We tested whether the slopes and y-intercepts of the regressions from higher elevations differed from lower ones by running multiple *post hoc* comparisons. All of the SMA analyses were conducted using the software package 'Standardised Major Axis Tests and Routines (SMATR)' (Falster, Warton & Wright 2006). The significance level for testing slope heterogeneity and difference from slope = 1 was $P < 0.05$.

To determine whether the regressions were consistent with the assumptions of regression analysis, we inspected graphs of residuals vs. predicted Y values first. Thirty-seven of the 44 populations had good error structure, but we included even those that did not (populations 3, 16, 26, 28, 38, 39 and 43) because the results were similar (see Appendix S1). To determine whether allometric relationships changed with elevation, we investigated the relationship between the estimated parameters (y-intercept and slope) and elevation with least-square regressions. We analysed the data in two ways. For species with only one sampled population, we looked at variation in the y-ntercept and slope among species with increasing elevation. This analysis was conducted to detect evidence for divergence among species that may reflect evolutionary change in allometric relationships with increasing elevation. For species with two or more populations, we examined variation among conspecific populations growing at different elevations. We predicted that changes in allometry with elevation exhibited among species would also occur within species. As the range of elevations occupied by conspecific populations was less than the range occupied across species, we predicted that the relationships between the slope (and the y-intercept) and elevation would be weaker within than across species.

To examine the effect of elevation and species membership on the y-intercept and slope, we used the data set that included species with at least two populations and performed two-way ANCOVA in which species membership was treated as fixed factors and elevation as a covariate. Given that, within species, only one population was sampled at a given elevation, we could not test simultaneously for variation in our focal traits because of both population identity and elevation. The inclusion of multiple populations per species, however, provided replication that enabled us to factor out the variation because of species membership when detecting other sources of variation in y-intercept and slope in the analyses of covariance described earlier. Within the model, the default type III sums of squares were used to test for significant effects of each of the included factors independent of the other given the unbalanced sample sizes. We performed a linear regression using the complete data set, which included both species with only one population and species with two or more populations. To examine the bivariate relationships across species and among conspecific populations, we also performed a linear regression (and analysis of variance) to detect whether elevation affected the y-intercept and the slope within each species and among species with only one population. The analyses of least-square regression and ANCOVA were conducted using JMP 7.0 (SAS Institute 2007).

Results

LOG R VS. LOG V WITHIN POPULATIONS

There were significant positive relationships between log reproductive biomass and log vegetative biomass within all populations (Appendices S1 and S2). Four populations had slopes significantly < 1 (populations 3, 28, 31 and 43; altitudes 3500, 3550, 3500 and 4100); five populations had slopes significantly > 1 (populations 20, 27, 38, 39 and 41; altitudes 3600, 3000, 2100, 2100 and 3150).

THE EFFECT OF ELEVATION ON ALLOMETRIC SLOPE

There was a highly significant negative relationship between the estimated allometric slope and elevation among species (Fig. 1a). The *post hoc* multiple comparisons of slopes among the 16 species for which only one population was sampled showed that most of the slopes for populations at high elevations were significantly lower than those at low elevations (Appendix S3a).

Among all populations, a significant negative relationship between the allometric slope and elevation also existed (Fig. 2a). Moreover, the effect of elevation on slope was significantly independent of species identity (Table 1). Within each species, however, the *post hoc* comparisons detected no consistent altitudinal change in slope for most species. Nevertheless, two species (*Pedicularis lasiophrys* and *Pedicularis szetschuanica*) – represented by multiple populations – exhibited significantly lower slopes at high elevations (Appendix S1). Six of the eight species from which two or more populations were sampled showed a negative trend (Fig. 2a).

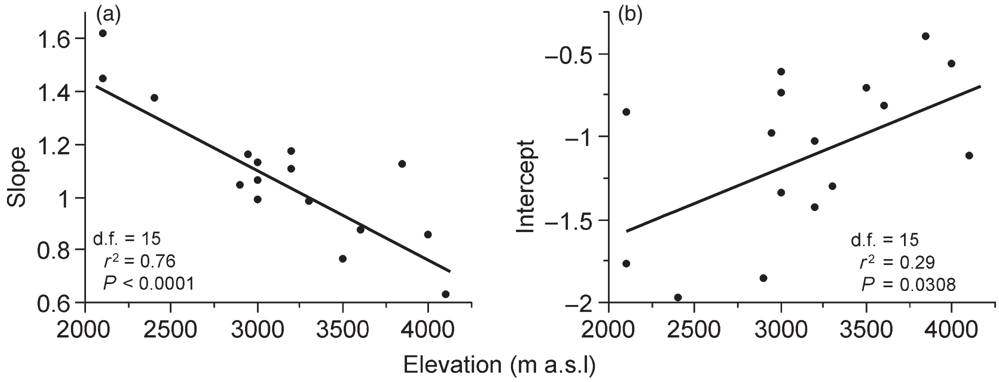

Fig. 1. Estimates of slope (a) and intercept (b) for log R–log V regressions vs. elevation within populations of *Pedicularis* species growing in the Tibetan Plateau. Sixteen species, for which only one population was sampled in the study area, are included. Solid lines show significant regression relationships.

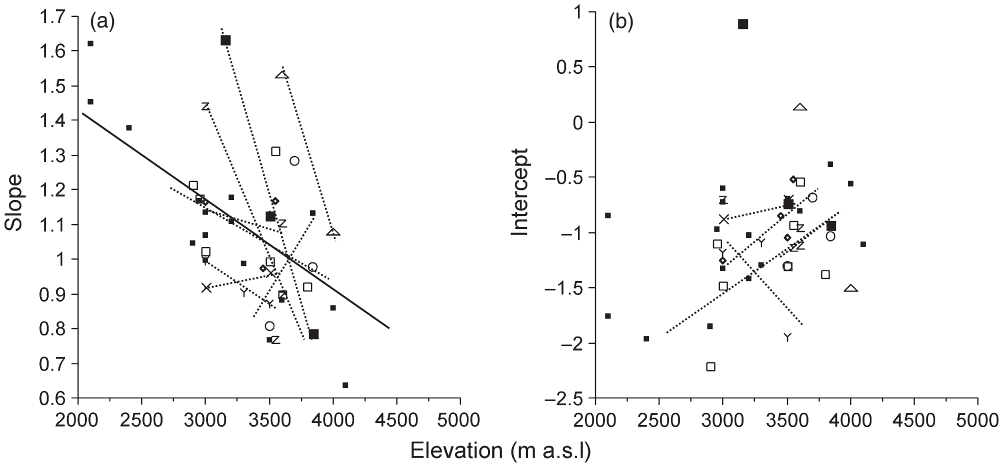

Fig. 2. (a) Slope of log R–log V regression vs. elevation for all populations. The solid line shows the significant negative relationship between slope and elevation ($r^2 = 0.32$, $P < 0.0001$); the dotted lines across different symbols represents the regression lines between slope and elevation among two or more populations within each species. Six of the eight species, from which two or more populations were sampled, show a negative trend. (b) The *y*-intercept of the log R–log V regression vs. elevation for all populations. There is no significant relationship between the intercept and elevation across all populations; the dotted lines across different symbols represent the regression line between *y*-intercept and elevation among two or more populations within each species for which slopes are not significantly different. Three of the four species (*Pedicularis longiflora*, *Pedicularis semitorta*, *Pedicularis chinensis* and *Pedicularis kansuensis*) show a positive relationship (The solid circles represent different species where only a single population was sampled. Species where multiple populations were sampled are each represented by a different symbol, i.e. □: *P. chinensis*; ◇: *P. kansuensis*; △: *Pedicularis lasiophrys*; Y: *P. longiflora*; Z: *Pedicularis polyodonta*; ○: *Pedicularis rhinanthoides*; ×: *P. semitorta*; ■: *Pedicularis szetschuanica*).

Table 1. ANCOVA to test the effects of species and elevation on *y*-intercept and slope

		Intercept			Slope		
Source	d.f.	Sum of squares	*F* ratio	*P*	Sum of squares	*F* ratio	*P*
Species	7	4.90	4.33	**0.0130**	0.41	2.26	0.1025
Elevation	1	0.55	3.39	0.0906	0.16	6.01	**0.0305**
Species × elevation	7	3.98	3.51	**0.0274**	0.40	2.20	0.1105
Model	15	6.97	2.8728	**0.0361**	0.97	2.48	0.0599
Error	12	1.94			0.31		
Total	27	8.92			1.28		

Boldfaced *P*-values are statistically significant at the $P < 0.05$ level. This data set included eight species for which two or more populations were sampled.

THE EFFECT OF ELEVATION ON ALLOMETRIC INTERCEPT

A significant positive relationship between the *y*-intercept of the log R–log V regression and elevation was found among 16 species represented by only one population (Fig. 1b). The *post hoc* multiple comparisons among the 16 species showed that most of the *y*-intercepts of populations at high elevations were higher than those at low elevations (Appendix S3b).

Among all 44 populations, however, there was no significant relationship between the *y*-intercept and elevation (Fig. 2b). Species membership (but not elevation) had a significant effect on the intercept of the log R–log V regression. In addition, the ANCOVA detected a significant effect of the species × elevation interaction (Table 1), indicating that the effect of elevation on the *y*-intercept depended on the species identity.

The *post hoc* multiple comparisons among the 16 species represented by only one population showed variable relationships between the *y*-intercept and elevation. Among the species represented by multiple populations where slopes differ ignificantly (*Pedicularis longiflora*, *P. semitorta*, *P. chinensis* and *P. kansuensis*), a positive relationship between the *y*-intercept and elevation was found within three species, i.e. *P. chinensis*, *P. semitorta* and *P. kansuensis* (Appendix S1). Only *P. longiflora* exhibited a negative relationship between the *y*-intercept and elevation (Fig. 2b).

Discussion

SIZE-DEPENDENT REPRODUCTIVE BIOMASS

Not surprisingly, our results showed strong positive relationships between log R and log V within all populations: larger plants produced more reproductive biomass than smaller plants. This relationship can be interpreted as a result of plants' modular architecture. Within a population, larger individuals have more vegetative and reproductive modules (Weiner 1988; Niklas 1993). However, the slopes of regressions of log R on log V varied greatly among populations and among species (from 0.63 to 1.63). In populations or taxa with regression slopes < 1.0, larger plants invest a lower fraction of their biomass into reproduction than smaller plants. In contrast, in populations or taxa where the slope is > 1.0, larger individuals allocate proportionally more biomass to reproduction than smaller ones. A recent review of R–V relationships within plant populations found no populations in which a log R–log V slope was significantly > 1 (Weiner *et al.* 2009a). Unlike the results reported previously, in the present study, we found nine populations with a slope significantly different from one, of which five populations at the relatively low elevations had a slope > 1, and four populations at relatively high elevations exhibited slopes significantly < 1. These contrasting results may be due to the environments and taxa in our samples. They suggest that there is more variation among populations and taxa in their allometric slopes than previously thought.

THE EFFECT OF ELEVATION ON THE ALLOMETRIC SLOPE AND INTERCEPT

The change in the R–V allometric slope and intercept with increasing elevation differed within vs. among *Pedicularis* species. Among species represented by only one population, there was a significant negative relationship between the slope of the log R vs. log V regression and elevation and a significant positive relationship between the *y*-intercept and elevation (Fig. 1a,b). There was also a negative relationship between log R–log V slope and elevation among all populations across species (Fig. 2a), but the relationship between *y*-intercept and elevation was not significant (Fig. 2b). Among populations within species, however, there was no consistent relationship between the slope or the *y*-intercept and elevation (Appendix S1).

From an allocation perspective, the slope reflects how efficiently vegetative biomass is converted into reproductive biomass across plant sizes within the population (Weiner *et al.* 2009b). The lower R–V slope at high altitudes reflects high conversion efficiency at lower sizes and lower efficiency at larger sizes when compared with lower altitudes. Thus, low altitude plants have relatively high reproductive allocation at larger sizes, while high altitude plants have relatively high reproductive allocation at smaller sizes (the R–V lines cross). The differences in size-dependent reproductive allocation may be an adaptive response to limits imposed on plant growth and survival by high elevation (e.g. lower temperatures at higher elevations may reduce photosynthetic rates and lower rates of cell division, and shorter growing seasons may reduce the time for development of reproduction parts). Plants at high elevations are generally smaller than their conspecific counterparts at lower elevations because some of the adverse conditions plants face at high elevations are less extreme close to the ground such that plant growth is restricted to the boundary layer (Körner 2003).

The lower slopes at high altitudes may also have evolved by natural selection if the low efficiency of reproduction is a consequence of life adapted to environments at high altitudes. There are clearly high costs and risks associated with being tall in an alpine environment, so many plants have evolved a prostrate habit. If stressful conditions for plant growth and survival at the apical meristems intensify as plants get larger, the ability to produce, maintain and mature reproductive structures would also decrease as plants get larger, resulting in a lower log R–log V slope in populations at high elevations.

Our data suggest that plants growing at lower elevations 'invest' more in vegetative biomass when they are small, whereas at higher elevation the 'returns' on such investment are lower, such that at high elevations, plants invest relatively more in reproduction when they are small (reflected in the higher *y*-intercept for these populations) and relatively less when they are large (accounting for the lower allometric slope of these populations). Aarssen (2008) explained the advantage of being small using the concept of 'reproductive economy' and suggested that smaller plants, within a species, may have a greater efficiency of space use and higher fecundity per unit resource uptake per unit time compared with larger plants. If the environment prevents large individuals from producing proportionally more offspring than smaller individuals because additional tissues are damaged by the extreme environment, the log R–log V slope will be lower because of this damage. In this case we would expect populations or species to evolve a log R–log V relationship with a relatively low slope in such environments. In other words, if the environment dictates that plants pay a big penalty for being large, then plants will evolve strategies that improve their performance at smaller sizes at the expense of performance at larger, disadvantaged sizes: a decrease in the allometric slope (Fig. 3). In this sense, a change in allometric slope represents a trade-off of performances at larger vs. at smaller sizes.

Variation in the R–V allometric slope among conspecific populations has been documented in several studies (Ohlson 1988; Hartnett 1990; Sugiyama & Bazzaz 1998; Welham & Setter 1998; Méndez & Karlsson 2004), but trends across environmental gradients have not yet been documented. In the present study, we found a trend of decreasing slope with increasing elevation among populations within species, similar to the relationship among species represented by single populations (Fig. 2a). The slope often differed among conspecific populations and was not always similar to the interspecific altitudinal pattern (Appendix S1). With the results obtained here, we cannot predict that an interspecific pattern will consistently apply to populations within a species. Because our data are from field populations, we cannot say to what degree differences among populations of the same species are attributed to genetic vs. environmental effects. It has been argued that reproductive allometry itself is not very plastic for a given genotype, but that growth and developmental rates are highly plastic (Weiner *et al.* 2009a). Differences among species are likely to be in large part genetic, whereas differences within species may be more

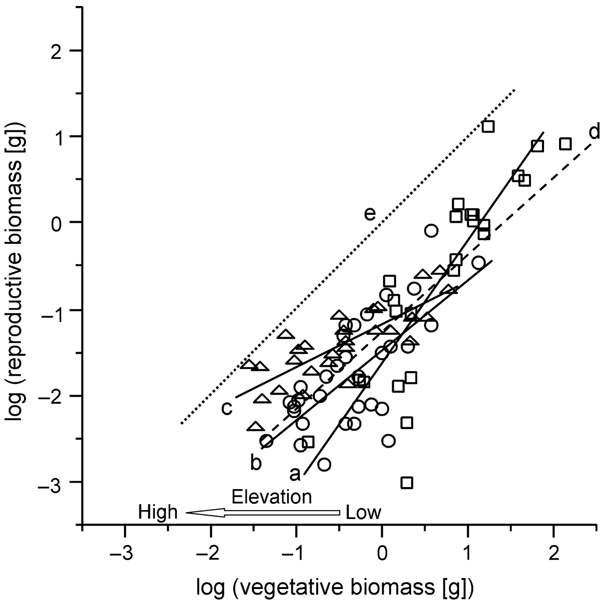

Fig. 3. Examples showing the change in reproductive allometry in *Pedicularis* species growing at different elevations on the Tibetan Plateau. The allometric relationship between log reproductive biomass and log vegetative biomass in one population (code: 39) growing at 2100 m a.s.l (solid line a; squares; *Pedicularis striata*), one population (code: 13) at 3000 m a.s.l. (solid line b; circles; *Pedicularis curvituba*) and one (code: 43) at 4100 m a.s.l. (solid line c; triangles; *Pedicularis ternata*). 'Elevation Low to High' on the figure refers to the relative elevations of the populations represented by lines a, b and c. Dashed line d is the regression relationship across the three populations (slope = 1.09, $P < 0.0001$). The dashed line e is the diagonal line with slope = 1. The means of slopes and intercepts and the multiple comparisons among these three species were shown in Appendices S1 and S2.

influenced by the direct effect of the environment on a genotype's allometric growth. As the number of species was high and the number of populations per species was low, with most species represented by only one population, our intraspecific data have low statistical power.

The y-intercept reflects the location of the log R–log V relationship in bivariate space, which can be interpreted in turn as the overall density or concentration of the relationship. For example, if reproductive structures or tissues increase in biomass across all sizes, this would be reflected in an increased y-intercept: an overall shift in the efficiency of conversion of vegetative into reproductive biomass given the same vegetative size. Our results showed a positive relationship between the intercept of the log R–log V regressions and elevation among 16 species each represented by a single population (Fig. 1b). The species at high elevations tended to have larger intercepts (Appendices S1 and S3a). Among conspecific populations, a significant increase in the intercept in populations at higher elevations was also found within three species: *P. chinensis*, *P. semitorta* and *P. kansuensis* (Appendix S1). This suggests that some species or populations of *Pedicularis* at higher elevations may be generally more efficient in converting vegetative into reproductive biomass given the same vegetative size (Fig. 4a). Although the combination of lower slopes and higher y-intercepts in high-elevation populations does not necessarily indicate a higher conversion efficiency of biomass into reproductive structures at smaller plant sizes (e.g. if the lines do not cross: Fig. 4b), our results suggest that this is the case in *Pedicularis*, as the allometric lines of different species often crossed (Appendix S4).

The variation of intercept with increasing elevation may also result from differences in the geographical distribution of specific species rather the direct effect of elevation (Table 1). Because of the environmental limits at high elevations, vegetative size is usually smaller than at low elevations. The increasing y-intercept or allometric coefficient may be part of an adaptive strategy characterized by an increase in reproductive output at smaller vegetative size.

Our results show clearly that plant species growing at higher elevations showed different patterns of size-dependent resources allocation than closely related species growing in more favourable environments and that these differences can be interpreted in terms of allometric strategies. A comparative allometric approach can provide insights and testable hypotheses for the study of life-history strategies (Weiner *et al.* 2009a). Plant attributes associated with growth at high elevations have been well described in the seminal work by Körner (2003). We suggest that a lower reproductive allometric exponent should be added to the list.

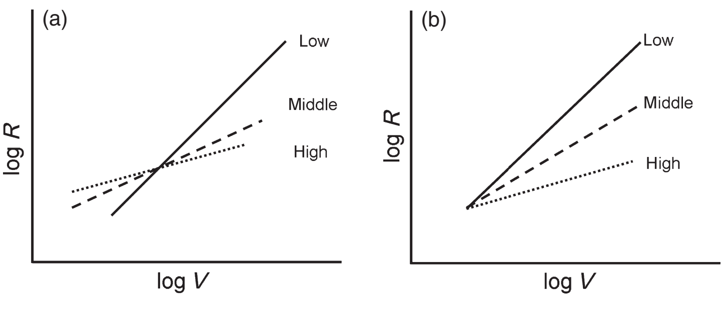

Fig. 4. Two scenarios in which both slopes and y-intercepts of the allometric V–R relationship differ among populations of a species or among taxa along an elevation gradient. 'Low', 'middle' and 'high' refer to the relative elevations of the three populations or taxa. Only in case 'a' there is strong evidence for increased reproductive allocation at smaller sizes at high elevation; in case 'b' there is greater allocation to reproduction at low elevation across all observed sizes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Information on species, populations, locations, elevation and population means of standardised Major Axis regression scaling exponents (slope), allometric constants (intercept), and their respective 95% confidence intervals for the allometric model: log (seeds mass) = log $a + b$ log (vegetative mass); results of zero hypothesis test: slope = 1.

Appendix S2. Bivariate plots of log reproductive biomass vs. log vegetative biomass within populations.

Appendix S3. *Post hoc* multiple comparison of (a) slopes and (b) intercepts among 16 species, for which only one population was sampled in the study area.

Appendix S4. Linear regression lines of log V-log R for 16 species, for which only one population was sampled in the study area.