Morphological plasticity and adaptation level of distylous *Primula nivalis* in a heterogeneous alpine environment

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A B S T R A C T

Plant populations at high elevation face extreme climatic conditions and resource limitations. The existence of distylous species at different elevations can help us investigate their adaptation to high altitudes, the evolution of their morphological characteristics, as well as their responses to limited resources. Here, 17 populations of *Primula nivalis* at different elevations were evaluated regarding variations in plant morphological characteristics, biomass allocation, and morphological plasticity in a heterogeneous environment. Our results demonstrate that heterogeneous environments can affect plant morphological characteristics and resource allocation in each sexual morph of these plants. Moreover, environmental variations reduced morphological plasticity in the two plant morphs, and the plasticity of long style (LS) plants was greater than that of short style (SS) plants. There were significant negative correlations between morphological characteristics and elevation, rainfall, temperature, and sunshine, and these are the main variables that affect morphological characteristics and resource allocation of both morphs of *P. nivalis* plants in heterogeneous environments. The morphological characteristics of *P. nivalis* plants transplanted from high to lower elevations were not significantly different in either population. LS plants had greater morphological plasticity and adaptability in heterogeneous environments than SS plants. Elevational gradients and heterogeneous environments differentiated both morphs of *P. nivalis* plants with regards to morphology as well as adaptations. LS plants showed a higher level of adaptability than SS plants.

1. Introduction

Plant life history traits (growth, reproduction, and seeding) and adaptation (plasticity or differentiation) are influenced by the biotic and/or abiotic factors in heterogeneous environments (Miner et al., 2005; Matesanz et al., 2010). Spatial or temporal variation of ecological variables and/or microhabitat heterogeneity can affect plant morphological characteristics (plasticity) or differentiation of plant traits (Shen et al., 2008; Tétard-Jones et al., 2011; Herrera and Bazaga, 2013). Changes in plant traits are signals of plant adaptation and evolution in heterogeneous environments (Matesanz et al., 2010; Scheiner, 2013; Anderson et al., 2014; Leingärtner et al.,

2014). Therefore, previous studies have focused on the effects of climate change on the abundance of species in heterogeneous environments (Valladares et al., 2007; Shimizu et al., 2011). Spatial-temporal variation in climatic variables (temperature, soil fertility, sunshine, rainfall, etc.) and resource limitation (Dorken and Barrett, 2004; Millal and Reich, 2011; Goh et al., 2013; Mou et al., 2013) in highly heterogeneous environments affect plant morphological characteristics and growth rates (Gómez-Aparicio et al., 2005). The limitations of ecological variables can play an important role in plant morphological, physiological, and anatomical trait development and adaptation under low resource conditions among different populations (Puijalon and Bornette, 2006; Gianoli and Valladares, 2010; Wang et al., 2014; Nascimbene and Marini, 2015). For instance, increasing elevation leads to limiting effects of multiple ecological variables (i.e. those related to soil, water, and temperature) which affect morphological plasticity and the level of

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adaptation of alpine species; however, this phenomenon has previously been poorly understood.

Significant variations in plant morphological traits (plasticity) is an important adaptation response for successful plant performance (Huber et al., 2009; Nicotra et al., 2010; Godoy et al., 2011) and natural selection for plant growth in a harsh environment (Richards et al., 2006; Nicotra et al., 2010). Morphological plasticity can be important in predicting population dynamics and plant evolutionary adaptations to different novel environments (Nicotra et al., 2010). Variation in climatic variables (temperature, light, rainfall, and other variables) along elevation gradients may be associated with enhanced life history characteristics of plants and their evolutionary responses (Aragon et al., 2012; Guerin et al., 2012; Leingärtner et al., 2014). This is because variation or limited resources (ecological variables) can be crucial for plant performance and survival (Nicotra et al., 2010). However, most previous research on plant morphological plasticity and survival has been carried out in controlled environments (Goh et al., 2013). Furthermore, to the best of our knowledge, no previous studies have focused on both morphological variation and adaptation of the both morph of plants in populations of distylous species at an elevational gradient that experience variations in climatic and ecological variables.

Primula nivalis is a spring-flowering herbaceous perennial distylous species, which grows in grassland and forest habitats at elevations of 1600—3000 m a.s.1. It has a wide distribution that includes Kazakhstan, Kyrgyzstan, Mongolia, Russia, Tajikistan, Turkmenistan, Uzbekistan and the northeastern and northwestern regions of the Xinjiang Uyghur Autonomous Region of China (Abdusalm, 2018). Plants flower from early May to late July, and fruits mature from July to mid-August, depending on elevation, with flowering and fruiting occurring later in high compared to low elevation populations.

Data from herbaria suggest that plant morphological traits differ significantly among specimens collected at different points along the elevational gradient, and plant height and leaf size decreases with increasing elevation. We hypothesized that elevational variation, climate change, and resource availability affects the morphological plasticity of both morph plants, and that this leads to adaptation in populations that occur at different elevations. To test this hypothesis, we used *P. nivalis* to address three questions: (1) Do morphological traits and biomass allocation of both morphs of *P. nivalis* plants differ at different elevations? (2) What is the relationship between ecological variables and morphological characteristics and the level of biomass allocation to both sexual morphs in each population? (3) What is the effect of a heterogeneous environment on the morphological plasticity of both morph plants at different elevations?

2. Material and methods

Field experiments were conducted in the flowering season of 2014 in populations of *P. nivalis* at 17 different elevations (1650 m to 2704 m a.s.l.). The *P. nivalis* populations were natural populations growing in forests and grasslands in the Tianshan Mountains of the Kunas area of northwestern Xinjiang, China (Fig. 1). A transplanting experiment was carried out at an elevation of 1650 m a.s.l. during the flowering period in 2014 and 2015 (see below).

2.1. Variation in plant morphological characteristics and resource allocation at different elevations

To determine effects of elevational variation on morphological characteristics of *P. nivalis* during the flowering season of each population, in 2014, 30 individuals of long style (LS) and short style (SS) plants were randomly selected from 17 populations. The height of the above-ground part of the each individuals, the number of leaves, maximum leaf length, and length of scape in both the morph plants were recorded. To investigate the effects of elevational variations on resource allocation in LS and SS plants at each population were collected, and the root, scape, leaf, and inflorescence were separated, and oven-dried to constant mass at 80 °C for 48 h. After drying, each part of both morphs was weighed using a Sartorius BS210S electronic-balance (accurate to 0.0001 g). The sum of the weight of all individual parts was considered the total plant total biomass; and biomass allocation to each part (roots, scape, leaves and inflorescence) was calculated as T = (biomass of plant each part/plant total biomass) × 100%.

2.2. Transplantation experiment

To investigate the effects of variations in multiple ecological variables on plant morphological characteristics, we conducted transplanting experiments using *P. nivalis* populations at four different elevations (2,704, 2,423, 2,013, and 1657 m a.s.l.). Thirty individual plants (both LS and SS morphs) were selected in each population, and dug out along the soil and placed in plastic bags to be transferred to lower elevations (1657 m a.s.l.) in 2014. In order to ensure the survival of the plants at the lower elevation (at which temperatures were higher), the plants were watered every second day. One year after plants were transplanted to the lower elevation, the plant height, number of leaves, and maximum leaf length was measured. The morphological plasticity and environmental adaptability of both sexual morph plants were also evaluated at the site of transplantation. The morphological plasticity index (MPI) was calculated following the formula from Ceplick (1995): $MPI = (X_{maximum} - X_{minimum})/X_{maximum}$; where $X_{maximum}$ and $X_{minimum}$ is the maximum or minimum measurement of each organ before and after transplanting both morph plants.

2.3. Data on ecological variables

In this experiment, the data regarding climate variables included elevation, and geographic data (latitude and longitude), and this data was determined at each site using an electronic GPS. The climate variable data of temperature, precipitation, and annual sunshine were downloaded from http://www.worldclim.org. Soil samples were collected from each elevation site at a depth of 20 cm. The soil nutrient composition was evaluated at the Biogeochemical Laboratory of the Kunming Division of the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences. Soil pH (1:2.5 v/v soil/water mixture; LY/T 1239—1999) for each population was measured using a digital pH meter (PHS-3C, Shanghai Leici Equipment Factory, China). Total N and C were measured using an elemental analyzer (Vario MAX CN, Elementar Analysensysteme GmBH, Germany). Concentrations of total potassium (K), total phosphorus (P), and full magnesium (Mg) were determined by digestive as well as inductively coupled plasma—atomic emission spectrometry, LY/T (1254—1999 ICP-AES). The soil was extracted using $HF-HClO_4$, and total nitrogen (N) concentrations were measured using molybdenum-antimony colorimeters. The concentrations of microelements (zinc (Zn), total copper (Cu), total iron (Fe), total manganese (Mn), and boron (B)) were investigated using the methods described by Zhang et al. (2011).

2.4. Data analysis

Data analyses were carried out using SPSS 16.0 software (SPSS Inc., Chicago, IL, USA). The data on morphological characteristics and biomass allocation were arcsine transformed before statistical analysis to ensure homogeneity of variance. Non-linear data were
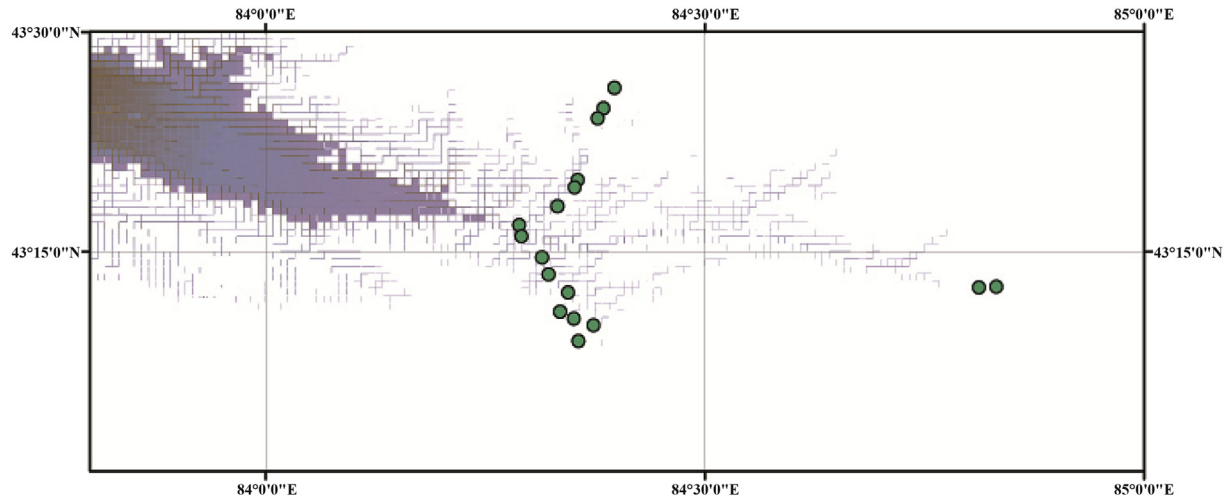
Fig. 1. The observed population geographical distribution characteristics of *Primula nivalis*.

square-root transformed. The relationships between elevation, morphological traits, and biomass of LS and SS plants were analyzed using bivariate correlations and linear models as $y = b_0 + b_1 \times x$. The effect of multiple correlations of all the climatic variables (14 variables) on morphology and biomass allocation in both morph plants was evaluated by RDA (redundancy analysis) using R software. Generalized linear models (GLM) were used to analyze morphological characteristics, morphological plasticity indexes, and variation in different organs of LS and SS plants before and after plants were transplanted. Independent sample *t*-tests

were used to compare differences in plant morphological characteristics and biomass of each part in both morph plants.

3. Results

3.1. Effects of elevation on plant morphological characteristics and resource allocation

There were significant variations in morphological characteristics of both morph plants at different elevations. Plant height and
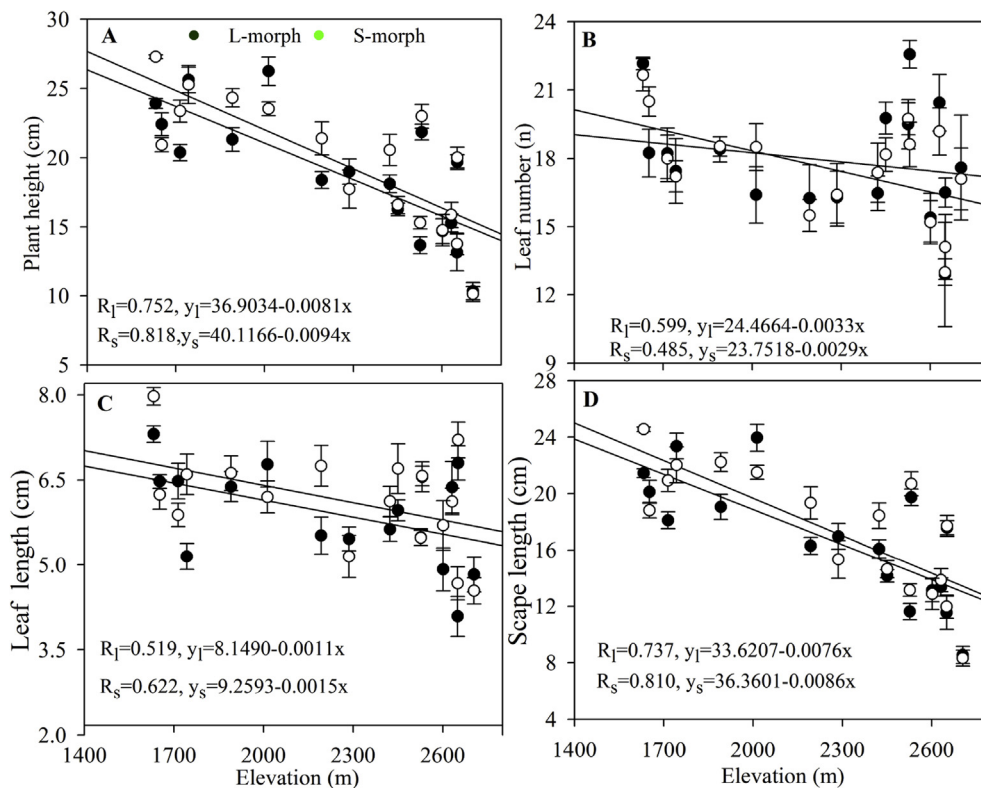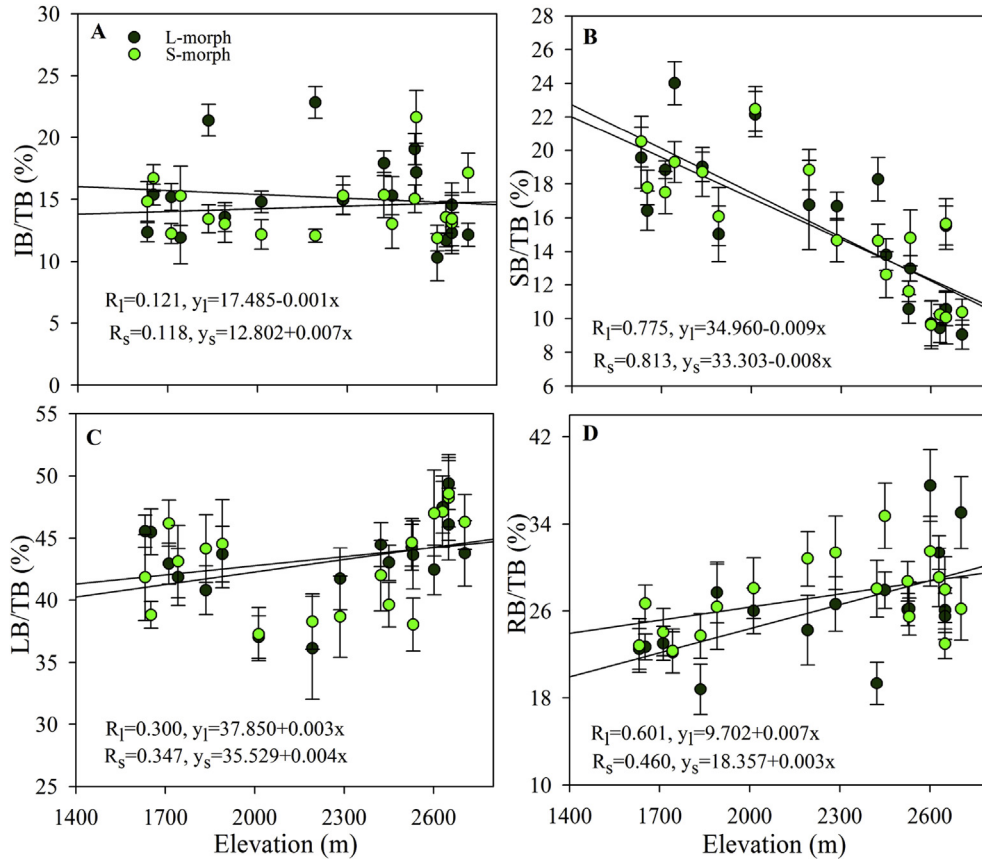

Fig. 2. Variation in plant height (A), leaf number (B), leaf length (C), and scape length (D) for L- and S-morph individuals from 17 populations of *Primula nivalis* at different elevations.

Fig. 3. Variation in IB/TB (A), SB/TB (B), LB/TB (C), and RB/TB (D) for L- and S-morph individuals from 17 populations of *Primula nivalis* at different elevations. IB: inflorescence biomass; SB: scape biomass; LB: leaf biomass; RB: root biomass; and TB: total biomass.

the length of the scape and leaves in both morph plants were significantly negatively correlated with elevation (Fig. 2). Plant height and the length of the scape and leaves decreased with increasing elevation. The size of each part of LS plants was larger than that of SS plants, and plant height ($t = 3.380$; $P < 0.05$), scape length ($t = 4.423$; $P < 0.01$), and leaf length ($t = 4.233$; $P < 0.01$) differed significantly between LS and SS plants.

The biomass allocation in some components of both morph plants was significantly affected by changes in elevation. The resource allocation to reproductive organs and inflorescence biomass was not significantly correlated with elevation in either morph plant. The leaf biomass and root biomass of both morph plants were more strongly positively correlated with elevation, but scape biomass was negatively correlated with elevation (Fig. 3).
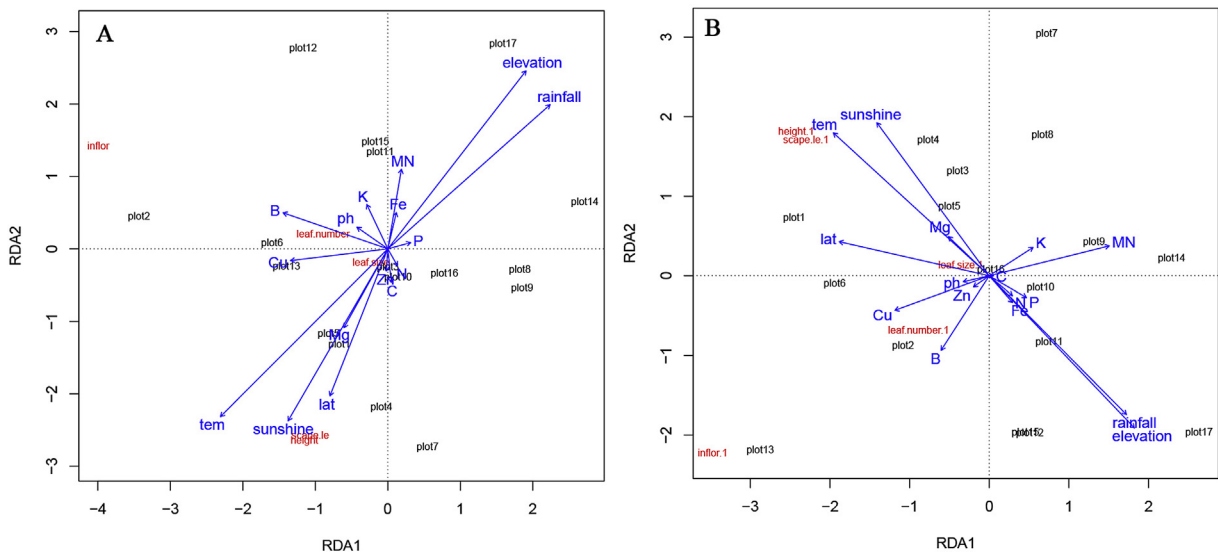
Fig. 4. RDA analysis of plant morphological characteristics and ecological structure of 17 populations of *Primula nivalis* at different elevations. Analysis is based on variation among 16 ecological factors for (A) L-morph and (B) S-morph individuals.

Biomass allocation to roots, scapes, and leaves was significantly different between the two sexual morphs (Fig. 3). The biomass of each part of the LS plants was greater than that of each part of the SS plants.
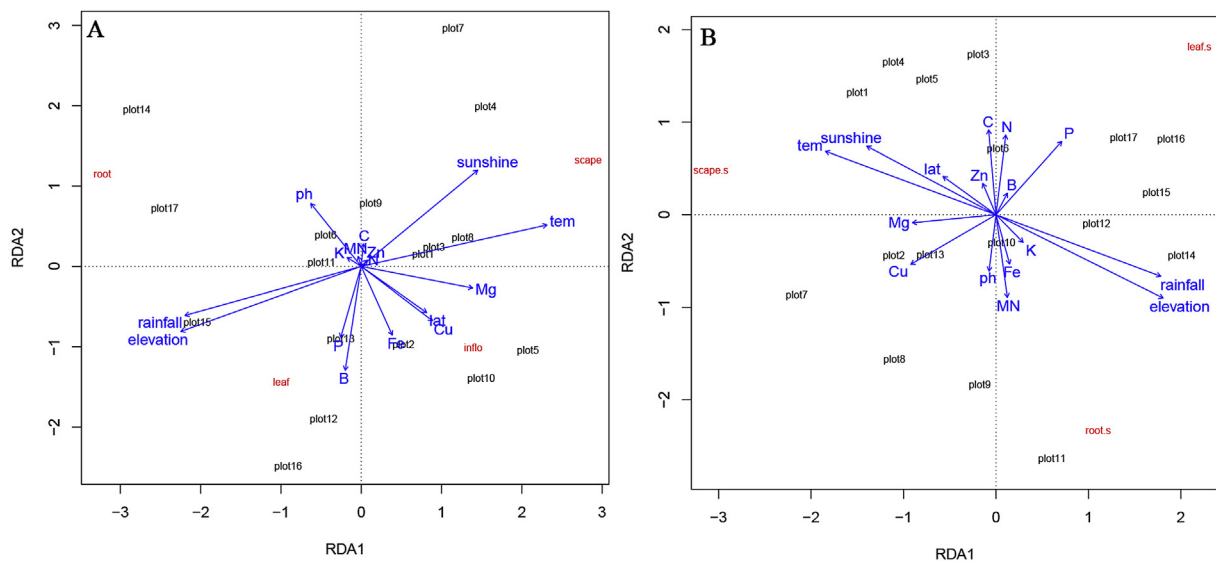
3.2. Relationships between ecological variables and plant morphological characteristics

RDA results suggest that ecological variables can significantly affect plant morphological characteristics of both morph plants at different elevations. Almost all ecological variables examined affected the morphological characteristics of both morph plants. Mean temperature, annual sunshine, and rainfall were major variables which affected the plant morphological characteristics of LS plants (Fig. 4). Latitude was also a major variable for the differences in morphological characteristics of LS and SS plants. Soil characteristics, however, did not significantly affect the morphological characteristics of both morph plants (Fig. 4, Table 1).

RDA analysis results suggest that all the evaluated variables, with the exception of soil characteristics, significantly affected resource allocation in both morph plants. Soil elements were only important with regard to the quality of resource allocation to individual components of both morph plants (Fig. 5, Table 2).

3.3. Effects of transplanting P. nivalis from higher to lower altitudes on plant morphological characteristics

GLM results indicate that, before transplanting, the plant height, number of leaves, maximum length of leaves, and scape length in both morph plants were affected by elevation and sexual morph, but not by the interaction between elevation and sexual morph (Fig. 6 and Table 3). After transplanting P. nivalis plants from higher elevations (2,704, 2,423, 2013 m a.s.l.) to a lower elevation (and 1657 m a.s.l.), plant morphological characteristics were not significantly affected by elevation, sexual morph, nor the interaction between elevation and sexual morph (Fig. 6 and Table 3). However, the heterogeneous environment affected plant

Table 1
RDA analysis for L- and S-morph individuals separately using the correlation matrix among ecological factors and plant morphological characters from 17 populations of *Primula nivalis* at different elevations.

	L-morph				S-morph			
	PC1	PC2	R^2	Pr(>r)	PC1	PC2	R^2	Pr(>r)
Elevation	0.6127	0.7903	0.5874	**0.005****	0.6903	−0.7235	0.648	**0.002****
Latitude	−0.3665	−0.9304	0.2880	0.101	−0.9752	0.2215	0.347	0.056
Temperature	−0.7063	−0.7079	0.6484	**0.002****	−0.7368	0.6762	0.653	**0.001****
Sunshine	−0.5017	−0.8650	0.4561	**0.009****	−0.5914	0.8064	0.529	**0.007****
Total rainfall	0.7472	0.6646	0.5445	**0.007****	0.7030	−0.7112	0.558	**0.006****
Soil pH	−0.8182	0.5749	0.0164	0.893	−0.9748	−0.2232	0.010	0.933
Total carbon	0.1021	−0.9948	0.0132	0.913	0.9994	−0.0347	0.001	0.999
Total nitrogen	0.4929	−0.8701	0.0044	0.978	0.7590	−0.6510	0.014	0.919
Total phosphorus	0.9647	0.2633	0.0064	0.955	0.8629	−0.5054	0.027	0.823
Total potassium	−0.4284	0.9036	0.0278	0.820	0.8398	0.5430	0.040	0.756
Full magnesium	0.1680	0.9858	0.0754	0.576	0.9704	0.2415	0.224	0.166
Total iron	0.2270	0.9739	0.0160	0.907	0.6571	−0.7538	0.019	0.860
Total Mn	−0.4871	−0.8734	0.0940	0.517	−0.7220	0.6919	0.047	0.710
Copper	−0.9928	−0.1196	0.1110	0.457	−0.9392	−0.3433	0.148	0.315
Zinc	−0.0712	−0.9975	0.0057	0.960	−0.8180	−0.5753	0.005	0.962
Boron	−0.94541	0.32589	0.1418	0.335	−0.5430	−0.8397	0.1152	0.408

The * and ** is significantly difference at the 0.05 level and 0.05 level, respectively.

Fig. 5. RDA analysis of plant biomass allocation and ecological structure of 17 populations of *Primula nivalis* at different elevations. Analysis is based on variation among 16 ecological factors for (A) L-morph and (B) S-morph individuals.

Table 2
RDA analyses for L- and S-morph individuals separately using the correlation matrix among ecological factors and plant each part biomass from 17 populations of *Primula nivalis* at different populations.

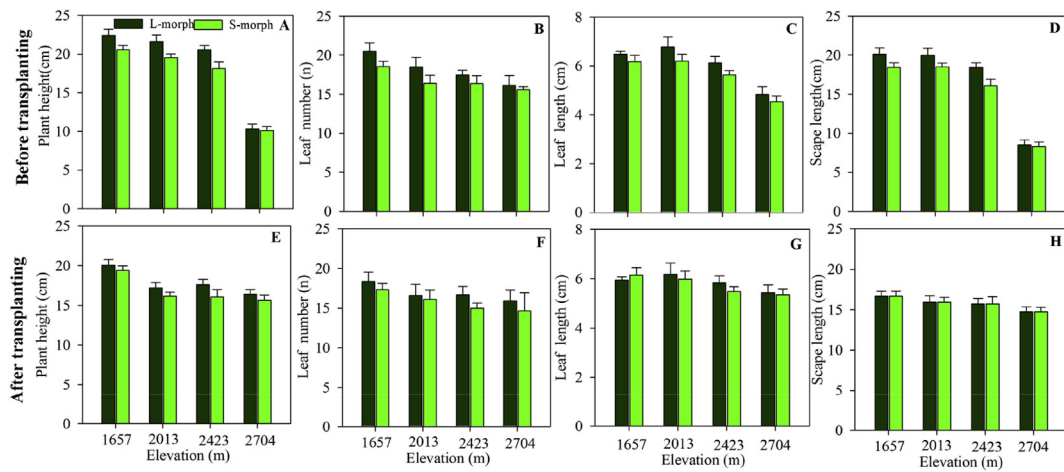|	L-morph				S-morph			
	PC1	PC2	R^2	$Pr(>r)$	PC1	PC2	R^2	$Pr(>r)$
Elevation	−0.9408	−0.3390	0.564	**0.002****	0.8951	−0.4460	0.7310	**0.001****
Latitude	0.8171	−0.5765	0.099	0.484	−0.8107	0.5855	0.0894	0.529
Temperature	0.9762	0.2175	0.557	**0.005***	−0.9373	0.3486	0.6938	**0.001****
Sunshine	0.7711	0.6367	0.353	**0.035***	−0.8836	0.4683	0.4481	**0.019***
Total rainfall	−0.9635	−0.2677	0.513	**0.007****	0.9368	−0.3499	0.6475	**0.001****
Soil ph	−0.6256	0.7802	0.100	0.477	−0.1226	−0.9925	0.0674	0.613
Total carbon	0.0982	0.9952	0.008	0.951	−0.0863	0.9963	0.1515	0.297
Total nitrogen	0.8872	0.4613	0.001	1.000	0.1218	0.9926	0.1346	0.353
Total phosphorus	−0.2772	−0.9608	0.084	0.520	0.6683	0.7439	0.2030	0.206
Total potassium	−0.8466	0.5323	0.004	0.970	0.7001	−0.7141	0.0314	0.808
Full magnesium	−0.2943	0.9557	0.002	0.986	0.1365	−0.9906	0.1459	0.322
Total iron	0.4126	−0.9109	0.087	0.536	0.2673	−0.9636	0.0548	0.679
Total Mn	0.9816	−0.1908	0.198	0.214	−0.9954	−0.0961	0.1477	0.321
Copper	0.7952	−0.6063	0.124	0.419	−0.8643	−0.5030	0.2034	0.192
Zinc	0.7183	0.6958	0.001	0.994	−0.3896	0.9210	0.0241	0.850
Boron	-0.1522	-0.9883	0.169	0.279	0.4677	0.8839	0.0124	0.930

The * and ** is significantly difference at the 0.05 level and 0.05 level, respectively.

Table 3
General liner modeling (GLM) of morphological characters prior to and following transplantation of two morphs of *Primula nivalis* from populations at different elevations.

	Plant height		Leaf number		Leaf length		Scape length	
	MS	F	MS	F	MS	F	MS	F
Before transplanting								
Elevation (E)	798.671	**104.626****	44.624	**2.426***	15.430	**13.263****	878.651	**107.103****
Sexual morph (S)	37.424	**4.903***	12.411	.675	4.956	**4.260***	80.697	**9.836****
E×S	10.481	1.373	19.105	1.039	.145	.124	6.205	.756
Error	7.634		18.391		1.163		8.204	
After transplanting								
Elevation (E)	3.402	.584	38.058	2.024	2.540	2.360	8.519	1.437
Sexual morph (S)	3.503	.601	.026	.001	.103	.096	2.784	.470
E×S	7.629	1.309	12.358	.657	.390	.362	4.304	.726
Error	5.829		18.803		1.076		5.927	

The * and ** is significantly difference at the 0.05 level and 0.05 level, respectively.


Fig. 6. Variation in plant morphological characters (plant height, leaf number, leaf length, and scape length) for both sexual morphs of *Primula nivalis* plants from populations at different elevations. (A—D) Before transplanting; (E—H) after transplanting.

morphological characteristics in both morph plants. There was a significant difference between the morphological characteristics of the two sexual morphs before transplanting, but after transplanting, these differences became non-significant. This suggests that environmental heterogeneity is the main variable causing differences in plant morphology.

3.4. Morphological plasticity index (MPI) of both plant morphs

The MPI of individual plants of both morphs was positively affected by elevation ($F_{3,32} = 4.580$, $P < 0.01$) and sexual morph ($F_{1,32} = 2.080$, $P < 0.05$). The MPI of both morph plants increased with increasing elevation (Fig. 7A). The MPI of individual
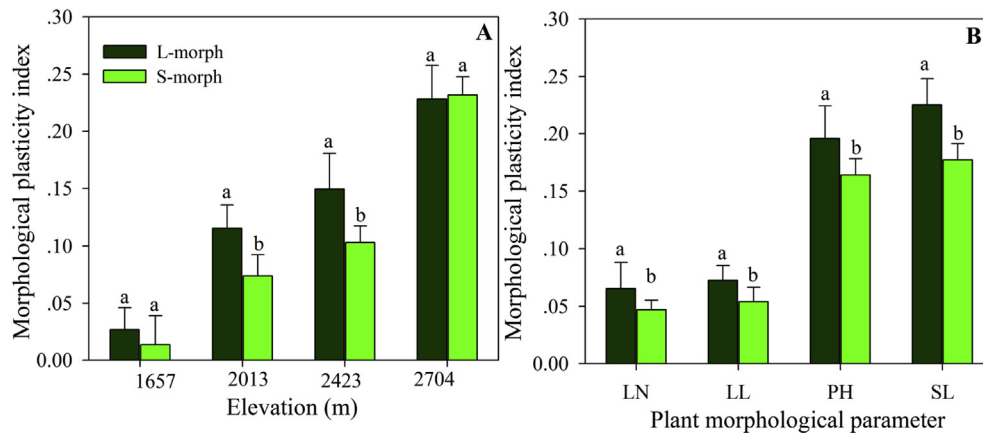
Fig. 7. Variation of morphological plasticity index for both sexual morph of *Primula nivalis* individuals at the population (A) and plant organ (B) level. LN: leaf number; LL: leaf length; PH: plant height; SL: scape length.

components of the plants of both sexual morphs was affected by plant organs ($F_{1,32} = 5.669$, $P < 0.01$) and sexual morph ($F_{1,32} = 2.069$, $P < 0.05$). In both sexual morphs of *P. nivalis*, the MPI of plant height and scape length was higher than that of the number and length of leaves (Fig. 7B). However, the MPI of LS plants was higher than that of SS plants (see Fig. 7).

4. Discussion

4.1. Variation in morphological characteristics of both plant morphs

Our study revealed that the morphological characteristics of *P. nivalis* plants varied between the sexual morphs and different elevational gradients. The morphological characteristics of both morphs of *P. nivalis* plants are crucial for predicting changes in different populations because inter-population (elevation) variation in ecological variables (climate change) decrease growth rates and adaptation (Hudson et al., 2011; Anderson et al., 2012). We found that an increase in elevation and associated shifts in ecological variables bring about changes in plant morphological traits. However, there are indications that SS plants have a higher adaptation potential than LS plants.

The growth–differentiation balance hypothesis (GDBH) suggests that there is a physiological trade-off between growth and secondary metabolism, and it predicts that more resources will be allocated to growth (Pizarro and Bisigato, 2010), or that related processes will differentiate over a range of environmental conditions (Xie et al., 2007; Frei et al., 2014). Although limiting ecological variables such as reduced resource allocation and soil nutrient heterogeneity in the different populations did not affect plant morphological adaptation, limiting ecological variables did influence biomass allocation to the different components of *P. nivalis*. Moreover, above-ground biomass was measured as an indication of overall plant growth and performance and found to be strongly influenced by the geographic distribution of *P. nivalis*. There was a consistent (and often strong) positive response of N to P ratios to increasing elevation in short style plant morphs. This is likely because improved nutrient availability leads to increases in leaf area growth and photosynthetic capacity (Wu et al., 2004).

4.2. Relationships between elevational climate variation and morphological plasticity

Varying climatic conditions along elevational gradients also results in different selection pressures that shape inter-morph traits so that plants can adapt to a particular elevation. Previous

studies have shown that different genotypes are found in locations that experience different annual weather conditions (Fusco and Minelli, 2010). *P. nivalis*, which has a large distribution in Xinjiang, may have adapted to short growing seasons at high elevations, and is likely to have evolved different morphological traits (Gugger et al., 2015). The adaptive hypothesis suggests that there is a strong correlation between plant morphological characteristics and fitness (adaptive significance) under different habitat environments (Dudley and Schmitt, 1996). For example, results from a previous transplant experiment suggest that there was no difference in plasticity between high and low elevation populations of three grassland species (Frei et al., 2014). Our transplanting data emphasized that specific maternal families of *P. nivalis* have growth benefits in low elevation populations. The ability to change their morphological characteristics is the most important adaptive strategy for *P. nivalis* in a heterogeneous environment.

We found evidence that indicates that the plasticity of morphological traits is greater in LS plants than in SS plants in response to environmental heterogeneity, and the LS plants were better adapted to high elevations (harsh environments) than SS plants. Trait plasticity is an advantage for plants experiencing great spatial habitat heterogeneity, and allows plants to maximize their fitness (Frei et al., 2014). In response to climate change and novel conditions, these plants responded through morphological plasticity and adapted through natural selection (Frei et al., 2014). Higher plasticity of plant height and scape length would be an advantage for *P. nivalis* experiencing greater spatial habitat heterogeneity under different environmental conditions. Therefore, environmental resource limitations in high elevation populations induced morphological plasticity, and this plasticity may be a critical component of the response of *P. nivalis* to changing environments.

4.3. Adaptations of both plant morphs and populations

Alpine systems have extreme temperature and water availability gradients associated with elevation, and adaptive plasticity is predicted to evolve when a species is subjected to environmental heterogeneity within the life span of the plants (Valladares et al., 2002). The plastic response to four ecological variables was adaptive for both morph plants in our experiment. The decreased plant size under increased elevation resulted in efficient use of available resources. Plasticity of morphological traits, such as height or biomass, may play a role in competitive interactions (Navas and Richard, 2005). The LS plants were significantly more plastic than SS plants in populations of *P. nivalis* located at different elevations. With the exception of plant height, morphological traits (scape

length, root, and leaf biomass) were more plastic than other parameters in both plant morphs. The phenotypic variation among populations of *S. candolleana* along its distribution range was pointed out by Ramírez-Valiente et al. (2015). Our results support the idea that resource availability is limited in high elevation environments, and results in greater phenotypic plasticity (Bradshaw and Holzapfel, 2006; Gianoli and Valladares, 2010). Variation in ecological variables (resource limitation) can affect plant traits and the adaptive nature of morphological plasticity of *P. nivalis*; moreover, variation of plasticity in both plant morphs could be subjected to evolution by natural selection (Richards et al., 2006). Although several studies have shown that climate change can increase phenotypic plasticity within populations, we demonstrated the importance of environmental heterogeneity for distylous species, which can result in morphological plasticity mainly because of climate change, and rarely includes intra-specific differences (Lenoir and Svenning, 2013; Valladares et al., 2014).

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2018.11.003.

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