

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	59	4	741–751	2011
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Regular research paper

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## RESPONSE OF ALPINE PLANT COMMUNITY TO SIMULATED CLIMATE CHANGE: TWO-YEAR RESULTS OF RECIPROCAL TRANSLOCATION EXPERIMENT (TIBETAN PLATEAU)

**ABSTRACT:** The great sensitivity of the response of alpine plant community to climate change makes the identification of these responses important. In 2007, we conducted a reciprocal translocation experiment on 100 × 100 × 40 cm coherent turf and soil along an elevation gradient of 3200–3800 m on the south slope of Qilian Mountains northeast of the Qinghai-Tibetan Plateau. The aim was to understand the warming/cooling effects on the alpine ecosystem where treatments were simulated by donor elevations below/above receptors. Translocated vegetation comprised the *Kobresia* meadow at 3200 m, deciduous shrub meadow at 3400 m, forbs meadow at 3600 m, and sparse vegetation at 3800 m. The 5 × 5 cm grid method (50 × 50 cm, 100 grids) was used for surveying plant species absolute abundance in translocated quadrats. Results showed that species richness and Shannon-Weaver index of *Kobresia* meadow increased significantly ( $P < 0.05$ ) when translocated to 3400 m. Shannon-Weaver index of shrub meadow declined, while shrub species abundance responded slightly both to warming and cooling treatments. Both species richness and Shannon-Weaver index of forbs meadow and sparse vegetation were enhanced evidently at 3200 m and 3400 m. Four groups were identified by non-metric multidimensional scaling based on receptor elevation. Responses of the alpine plant community and the function group appeared to be specific to climate magnitude and specific to

function type, respectively. Correlation indicated that climatic factors played a much more important role than soil in the response of the alpine plant community. Four vegetation types were sensitive to climate change, while *Kobresia* meadow behaved flexibly. Global warming would depress sedges but favor legumes and graminoids.

**KEY WORDS:** species richness, Shannon-Weaver index, function group, non-metric multidimensional scaling

### 1. INTRODUCTION

Climate change influences the structure and function of terrestrial ecosystems, especially in alpine region (Klanderud *et al.* 2005, Walker *et al.* 2006, IPCC 2007). Alterations in the composition and distribution of plant communities have important effects on ecosystem processes, including net primary production, biodiversity, and nutrient cycling, which in turn affect climate change (Walther *et al.* 2002, Eviner *et al.* 2003, Hart 2006). The tundra undergoes a much more dramatic climate change than other regions, and its flora is predicted to be very sensitive to such changes (Lesica *et al.* 2004, Klanderud 2008). Moreover, conclusions

of studies involving the tundra have implications in other terrestrial ecosystems (Bruehlheide 2003). Results from previous studies vary depending on the research sites or simulative methods, so that the direction and amplitude of plant response at individual, community, and ecosystem levels in the alpine region remain unclear (Dunne *et al.* 2004). Thus, further studies on alpine ecosystem response to climate change, particularly plant community and species distribution, are still necessary (Hollister *et al.* 2005, Wookey *et al.* 2009).

Experimental manipulation of climate conditions provides a powerful tool for exploring how plant community responds to climate change (Dunne *et al.* 2004). The tundra is an appropriate biome for examining the response of plant community with higher plant species density and more vegetation types (Körner 1999, Li *et al.* 2009). Previous studies reported that species richness either declined or increased, and shrubs either expanded or contracted (Klein *et al.* 2004, Jónsdóttir *et al.* 2005, Wahren *et al.* 2005). Climate warming-induced plant species loss and dominant vegetation alteration were either irreversible (Harte *et al.* 1995, Cross and Harte 2007) or reversible under climate change (Melick and Seppelt 1997). However, most conclusions are based on theoretical models or warming chambers, which are unable to obtain complete information on the alpine plant community (Dunne *et al.* 2004).

The reciprocal translocation method is an integrating experiment using natural gradients and simulating technique that is advantageous for understanding ecological responses to natural climate change (Ineson *et al.* 1998, Bruehlheide 2003, Dunne *et al.* 2004). It has been adopted for exploring the response of alpine meadow ecosystems in the Tibetan Plateau to climate change.

The short- and long-term response of the alpine community to simulated experiments has been proven to be different (Chapin *et al.* 1995, Epstein *et al.* 2000, Hollister *et al.* 2005), while the tundra ecosystem responded to climate change in a quick and flexible manner (Cannone *et al.* 2007). Hence, we used the two-year results of translocation experiment to study the initial response of an alpine community. Based on the conclusions of

other manipulation experiments, we hypothesize that the different alpine vegetation types will respond quickly and specifically and that plant function group responses will be specific to function type. This study aims to understand the response of an alpine plant community and function group, and determine the role of climatic factors and soil nutrient in alpine plant community variations under simulated climate change. Specifically, we will compare the community characteristics of *Kobresia* meadow under cooling treatment with the historical survey results of similar temperature conditions to test whether variations of the *Kobresia* meadow are irreversible.

## 2. STUDY AREA

The translocation experiment was conducted at the Haibei Alpine Meadow Research Station, Chinese Academy of Sciences (101°19'E, 37°35'N, elevation 3200 m), located in the northeast of the Qinghai-Tibetan Plateau. Annual mean air temperature and rainfall amount is at -1.7°C and 570 mm, respectively. Soil is abundant with organic matter but nitrogen-poor (Zhou and Wu 2006, Zhang *et al.* 2009).

The four translocated regions are along the altitude gradient and comprise the *Kobresia* meadow at 3200 m, deciduous shrub meadow at 3400 m, forbs meadow at 3600 m, and sparse vegetation at 3800 m. *Kobresia humilis* (C. A. Mey.) Serg., *Elymus nutans* Griseb., *Stipa aliena* Keng, *Taraxacum dissectum* (Ledeb) Ledeb, *Anaphalis lactea* Maxim., and *Potentilla anserina* L. Sp. Pl. are the dominant species in *Kobresia* meadow at 3200 m (Zhou and Wu 2006). Its soil is a clay loam and high in organic matter (7%, 0–10 cm), which is classified as Mat Cry-gelic Cambisols (Zhou and Wu 2006).

The shrub meadow at 3400 m has a two-layer structure of taller deciduous shrub and lower herb stratum. The former is occupied by *Potentilla fruticosa* L. Sp. Pl., while the latter is inhabited by *Elymus nutans*, *Stipa aliena*, *Aster flaccidus* Bge., and *Saussurea nigrescens* Maxim. (Zhou *et al.* 2006). Forbs meadow at 3600 m consists of *Polygonum viviparum* L. Sp. Pl., *Galium verum* Linn., *Thalictrum alpinum* L. Sp. Pl., *Carex pachyrrhiza* Franch., and *Kobresia humilis* (Zhou *et al.* 2006). It is

inhabited by only a few species but plant coverage is as high as 40%. Sparse vegetation at 3800 m consists of only few species without a clear dominant species. Bare ground occupies approximately 80% of the area. *Leontopodium nanum* (Hook. et Thomas.) Hand. -Mazz., *Galium verum*, and *Corydalis melanochlora* Maxim. is the common species in sparse vegetation (Zhou *et al.* 2006). Soil in shrub meadow, forbs meadow, and sparse vegetation is classified as Mollic-Gryic Cambisols with high organic matter (14%, 0–15 cm) and low nitrogen content (0.7%, 0–15 cm) (Zhou and Wu 2006).

### 3. MATERIAL AND METHODS

#### 3.1. Experiment design

The experiment was completed in early May 2007 when most alpine plants were dormant. We selected four flat (aspect  $<3^\circ$ ) and homogenous plots of each vegetation types, with each plot having an area of  $7 \times 9$  m, and divided each plot into twelve ( $3 \times 4$ ) quadrats of  $100 \times 100$  cm (Fig. 1). Three quadrats were kept at original elevation, while nine were translocated to the three other elevations. Twelve quadrats were semi-randomly distributed at each elevation.

The four sides of the translocated quadrats were wrapped with plastic sheets to prevent the exchange of soil nutrients between quadrats and the surroundings and to minimize root invasion and edge effects (Bruehlheide 2003). All gaps that appeared during translocation were filled with the donor's subsoil. Experimental blocks were then enclosed with wire-netting to eliminate grazing influence (Fig. 1).

#### 3.2. Environmental factors

Air temperature (at 1.5 m), soil temperature (at 20 cm), and soil water content (SWC at 20 cm) were automatically recorded in 30-minute average values. At 3200 and 3400 m, they were measured by temperature probe (HMP45C, Vaisala, Finland), copper-constantan thermocouples, and time-domain reflectometry (CS-615, Campbell, USA), which were equipped with eddy covariance observation system. Simple-weather stations (HOBO Weather Station) were built at 3600 and 3800 m. SWC and temperature were monitored by ECH<sub>2</sub>O Soil Moisture Smart Sensor (SMA-M005, Onset, USA) and HOBO-U23 Temp Probe (TMB-M006, Onset, USA), respectively. Since the lowest temperature was below  $-40^\circ\text{C}$  and the data logger could not

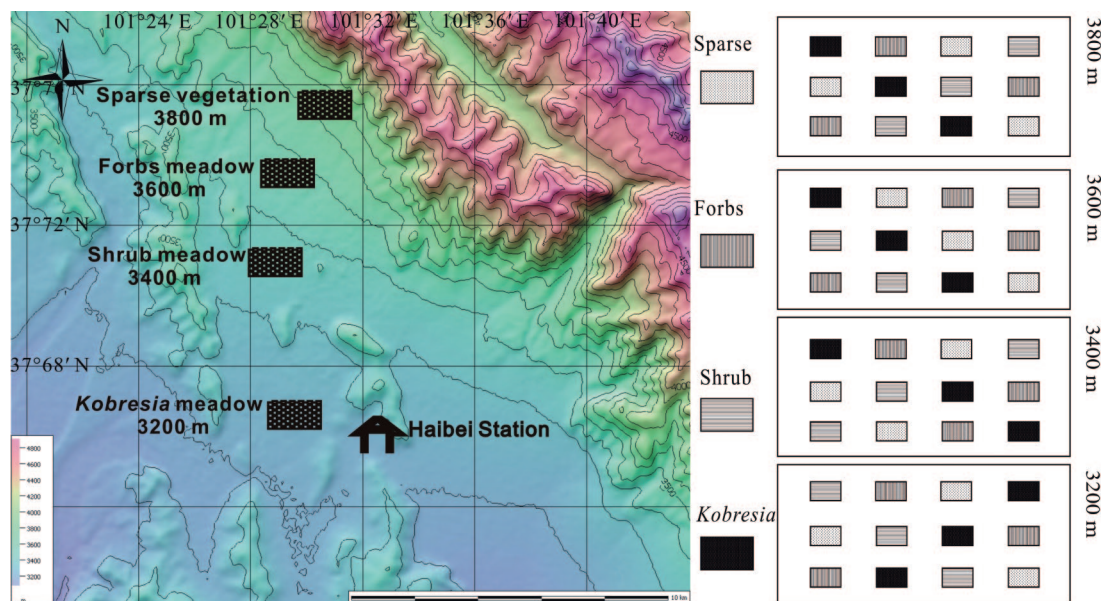


Fig. 1. Location map of the four vegetation types (left) and the diagram of reciprocal translocation experiment (right).

work above 3600 m, there were wide data gaps during non-growing season from October to May. Thus, climate factors were calculated and assumed to be equal at the same elevation during growing season from June to September.

Soil organic matter (SOM) and total nitrogen (Total N) were sampled in August 2007 and 2008. In the first year, we sampled five soil cores at the depths of 0–10, 10–20, and 20–30 cm using a soil sampler with diameter of 7 cm at the studied elevations, while a soil sampler with diameter of 3 cm was used in all translocated quadrats in 2008. SOM and Total N were determined by oil bath- $K_2CrO_7$  titration method and  $K_2CrO_7 + H_2SO_4$  digestion, respectively (Ineson *et al.* 1998).

### 3.3. Species diversity and function groups

Grid method of  $5 \times 5$  cm (frame of  $50 \times 50$  cm, total 100 points) was used to survey the absolute coverage of each plant species. The occurrence of each plant species within 100 grids was recorded and used to calculate the coverage of each plant species in every translocated quadrat in August, during which alpine plants flourish. Species diversity was measured based on the coverage of each plant species. Species richness ( $D$ , Eq (1)), Shannon-Weaver index ( $H'$ , Eq (2)), and species evenness (Pielou index,  $E$ , Eq (3)) were calculated as following equations:

$$D = S \quad (1)$$

$$H' = -\sum_{i=1}^s P_i \ln(P_i) \quad (2)$$

$$E = \frac{H'}{\ln(S)} \quad (3)$$

Where  $S$  is the sum of species number in the frame and  $P_i$  is the absolute coverage of species  $i$ . Similar to other studies (Walker *et al.* 2006), four plant function groups were identified: sedges, graminoids, legumes, and forbs.

### 3.4. Non-metric multidimensional scaling (NMDS)

Non-metric multidimensional scaling (NMDS) is one of the most powerful ordination methods (Clarke 1993) and used to examine the variations of species community and function group. We used PC-ORD 4.2 (MjM Software, USA) for NMDS ordination of full species cover  $\times$  (treatment + year) matrix ( $51 \times 32$ ) and function group abundance  $\times$  (treatment + year) matrix ( $4 \times 32$ ). In the NMDS set-up, autopilot mode (slow and thorough) was applied, and Sorensen (Bray-Curtis) was chosen for measuring distance.

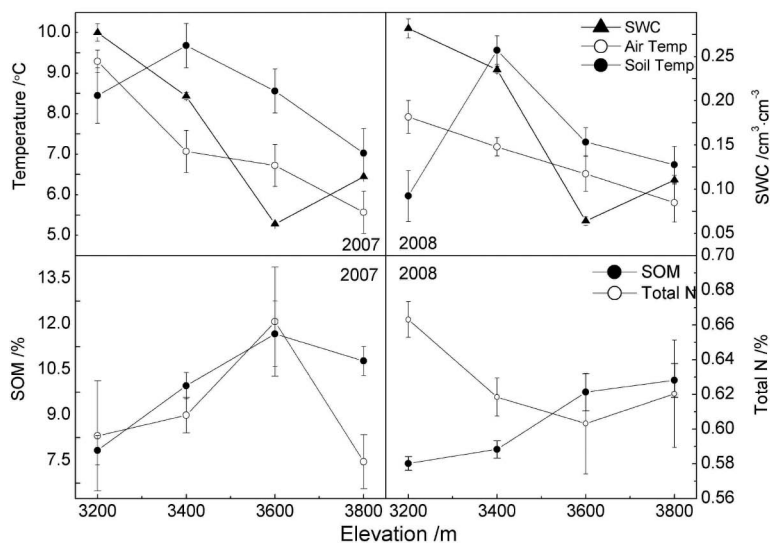


Fig. 2. Variations of temperature, soil water content (SWC), soil organic matter (SOM), soil total nitrogen (Total N) of translocated quadrats in 2007 and 2008.

Environmental factors and soil nutrient  $\times$  (treatment + year) were treated as second matrix ( $5 \times 32$ ) for describing their influence on community variations. One-way ANOVA and LSD-multiple comparisons were performed in SPSS 13.0 (SPSS Inc, USA) for means and multiple comparisons of plant community diversity and function groups abundance.

#### 4. RESULTS

##### 4.1. Microclimate and soil nutrients

During the growing seasons of 2007 and 2008, mean air temperature ranged from 9.8°C at 3200 m to 6.1°C at 3800 m (Fig. 2), which decreased by 0.98°C/200 m with elevation hoist ( $R^2 = 0.91$ ,  $P < 0.001$ ). The maximum value of 20 cm-soil temperature for 2007 and 2008 both appeared at 3400 m, and was 10.2 and 10.9°C, respectively. There was a little difference of soil temperature between the two years. For example, soil temperature at 3200 m was 8.9°C in 2007 and 6.7°C in 2008, and this difference may be attributed to rainfall. Precipitation was 236.4 mm in 2007 and 290.2 mm in 2008. The two years variations of 20 cm-SWC showed a similar “V” trend, with the minimum value ( $0.09 \text{ cm}^3 \cdot \text{cm}^{-3}$ )

at 3600 m for both years. The peak value of SWC occurred at 3200 m with values of 0.35 and  $0.31 \text{ cm}^3 \cdot \text{cm}^{-3}$  in 2007 and 2008, respectively. SWC at 3400 m was greater compared with that at 3800 m, with the two-year average values equal to 0.26 and  $0.15 \text{ cm}^3 \cdot \text{cm}^{-3}$ , respectively. SOM and total N showed similar unimodal fluctuation in 2007. Their values were 9.01% and 1.81% at 3200 m, reaching maximum values of 12.8% and 0.77% at 3600 m and decreasing to 8.21% and 0.89% at 3800 m, respectively. In 2008, data were averaged by quadrats with the same receptor elevations, such that soil nutrient displayed different changes compared with 2007. SOM increased by 0.5% /200 m with elevation rising ( $R^2 = 0.92$ ,  $P < 0.05$ ). Minimum and maximum values of total N were 0.60% at 3600 m and 0.66% at 3200 m, respectively.

##### 4.2. Plant community and function groups

In our survey, 51 plant species were found in translocated quadrats and all remained for ordination. For *Kobresia* meadow, species richness ( $D$ , Eq (1)) increased significantly by 15% in corresponding cooler quadrats at 3400 m and decreased by 25% in the coldest quadrats at 3800 m. Shannon-Weaver index ( $H'$ , Eq

Table 1. Comparison of two-year average for species richness ( $D$ , Eq(1)), Shannon-Weaver index ( $H'$ , Eq(2)), and species evenness ( $E$ , Eq(3)), and the percent increase of absolute abundance of function groups among different quadrats with the same donor elevations.

Plot	Treatment	$D$	$H'$	$E$	Sedges	Graminoids	Legumes	Forbs
P32→32	Control	20 <sup>b</sup>	3.45 <sup>c</sup>	0.81	13% <sup>b</sup>	66% <sup>a</sup>	22% <sup>a</sup>	87% <sup>b</sup>
P32→34		23 <sup>a</sup>	3.84 <sup>a</sup>	0.85	3% <sup>c</sup>	24% <sup>b</sup>	5% <sup>b</sup>	128% <sup>a</sup>
P32→36	Cooling	21 <sup>ab</sup>	3.49 <sup>b</sup>	0.80	43% <sup>a</sup>	16% <sup>b</sup>	2% <sup>b</sup>	88% <sup>b</sup>
P32→38		15 <sup>c</sup>	3.09 <sup>c</sup>	0.79	18% <sup>b</sup>	28% <sup>b</sup>	2% <sup>b</sup>	55% <sup>c</sup>
P34→32	Warming	19 <sup>ab</sup>	3.45 <sup>b</sup>	0.83 <sup>ab</sup>	7% <sup>c</sup>	63% <sup>a</sup>	20% <sup>a</sup>	70% <sup>b</sup>
P34→34	Control	24 <sup>a</sup>	3.91 <sup>a</sup>	0.86 <sup>a</sup>	8% <sup>c</sup>	34% <sup>b</sup>	4% <sup>b</sup>	108% <sup>a</sup>
P34→36		19 <sup>ab</sup>	3.46 <sup>b</sup>	0.82 <sup>b</sup>	47% <sup>a</sup>	18% <sup>b</sup>	1% <sup>b</sup>	79% <sup>b</sup>
P34→38	Cooling	16 <sup>b</sup>	3.15 <sup>b</sup>	0.79 <sup>b</sup>	29% <sup>b</sup>	32% <sup>b</sup>	2% <sup>b</sup>	54% <sup>b</sup>
P36→32		21 <sup>a</sup>	3.65 <sup>a</sup>	0.84 <sup>ab</sup>	15% <sup>b</sup>	44% <sup>a</sup>	17% <sup>a</sup>	93% <sup>a</sup>
P36→34	Warming	21 <sup>a</sup>	3.79 <sup>a</sup>	0.87 <sup>a</sup>	9% <sup>c</sup>	19% <sup>bc</sup>	1% <sup>b</sup>	103% <sup>a</sup>
P36→36	Control	17 <sup>b</sup>	3.35 <sup>b</sup>	0.82 <sup>ab</sup>	40% <sup>a</sup>	14% <sup>c</sup>	1% <sup>b</sup>	66% <sup>b</sup>
P36→38	Cooling	17 <sup>b</sup>	3.22 <sup>b</sup>	0.80 <sup>b</sup>	31% <sup>a</sup>	25% <sup>b</sup>	2% <sup>b</sup>	48% <sup>b</sup>
P38→32		23 <sup>a</sup>	3.84 <sup>a</sup>	0.85 <sup>b</sup>	12% <sup>b</sup>	40% <sup>a</sup>	14% <sup>a</sup>	90% <sup>a</sup>
P38→34	Warming	22 <sup>ab</sup>	3.93 <sup>a</sup>	0.89 <sup>a</sup>	10% <sup>c</sup>	20% <sup>bc</sup>	0% <sup>b</sup>	80% <sup>a</sup>
P38→36		19 <sup>b</sup>	3.47 <sup>b</sup>	0.82 <sup>b</sup>	43% <sup>a</sup>	13% <sup>c</sup>	1% <sup>b</sup>	64% <sup>b</sup>
P38→38	Control	15 <sup>c</sup>	3.23 <sup>b</sup>	0.83 <sup>b</sup>	29% <sup>b</sup>	27% <sup>b</sup>	3% <sup>b</sup>	34% <sup>c</sup>

Note: 1) Values with the same superscript letter indicate no significant difference ( $P > 0.05$ ) and *vice versa*; 2) Legend for the first column: P = plot; numbers beside P = donor elevation abbreviation; → = direction of translocation; bold numbers = receptor elevation abbreviation (32, 34, 36, and 38 for 3200 m, 3400 m, 3600 m, and 3800 m, respectively)

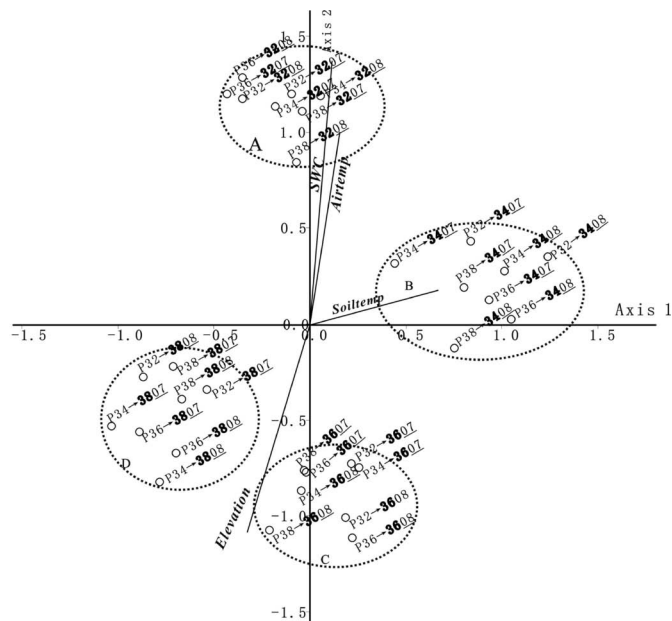


Fig. 3. Results of non-metric multidimensional scaling analysis of the alpine plant community under reciprocal translocation experiment.

P = plot; numbers beside P = donor elevation abbreviation;  $\rightarrow$  = direction of translocation; bold numbers after  $\rightarrow$  = receptor elevation abbreviation (32, 34, 36, and 38 for 3200 m, 3400 m, 3600 m, and 3800 m, respectively); underlined numbers = surveying year abbreviation (07 and 08 for 2007 and 2008, respectively).

(2)) was enhanced maximally at 3400 m (11%) and recorded 1.2% rise at 3600 m. There was no significant difference ( $P = 0.07$ ,  $N = 6$ ) in Shannon-weaver index ( $H'$ , Eq (2)) between 3200 and 3800 m. Species evenness ( $E$ , Eq (3)) fluctuated insignificantly ( $P = 0.28$ ,  $N = 6$ ). The coverage of graminoids and legumes declined more significantly by 50% at the other three elevation quadrates (Table 1). The peak abundance of sedges and forbs occurred at 3600 and 3400 m, respectively. In shrub meadow, species richness ( $D$ , Eq (1)) declined by 33% only at 3800 m, and Shannon-Weaver index ( $H'$ , Eq (2)) decreased at the other three altitudes. The value of species evenness ( $E$ , Eq (3)) fell in cooler quadrates at 3600 and 3800 m. The abundance of graminoids and legumes increased at 3200 m but did not change at the other two elevations. Sedge abundance clearly increased the most at 3600 m (487%) and recorded 262% increase at 3800 m. Forbs abundance evidently declined by 37% at the other three elevations (Table 1).

Species richness ( $D$ , Eq (1)) and Shannon-Weaver index ( $H'$ , Eq (2)) of forbs meadow increased by 10% when translocated to 3200 m

and 3400 m, whereas species evenness ( $E$ , Eq (3)) did not significantly vary with elevations. The coverage of sedges decreased by 62% when transferred to lower elevation from 3600 m, while abundance of the other three function types increased along with elevation decreasing. Sparse vegetation was very sensitive to translocation. Values of species richness ( $D$ , Eq (1)), Shannon-Weaver index ( $H'$ , Eq (2)), and species evenness ( $E$ , Eq (3)) increased along with altitude decreasing, with rates of 2.7 ( $R^2 = 0.94$ ,  $P < 0.01$ ), 0.23 ( $R^2 = 0.82$ ,  $P < 0.05$ ), and 0.013 ( $R^2 = 0.29$ ,  $P = 0.46$ ) per 200 m, respectively. Sedge coverage increased by 48% at 3600 m and declined afterwards. The abundance of graminoids, legumes, and forbs was enhanced along with the decline in elevation.

#### 4.3. Non-metric multidimensional scaling (NMDS)

Results of non-metric multidimensional scaling (NMDS) were shown in Figs. 3 and 4. Final solutions for species and function group coverage were achieved after 55 and 80 iterations, respectively.

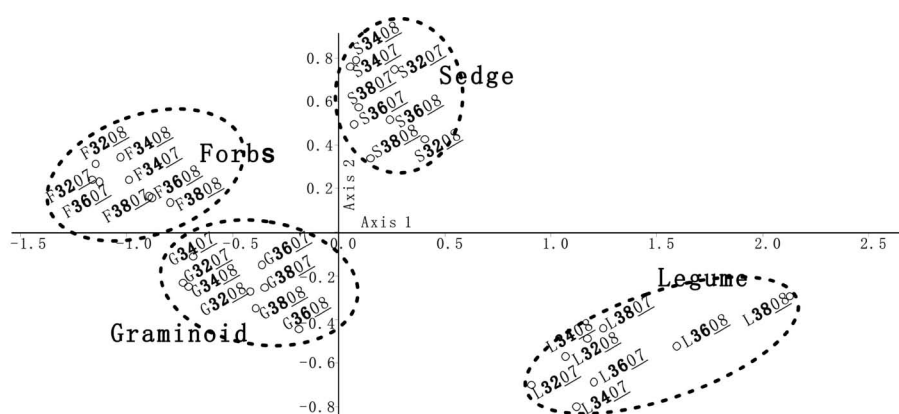


Fig. 4. Results of non-metric multidimensional scaling analysis of function groups under translocation experiment.

S = sedges; G = graminoids; L = legumes; F = forbs; the first two numbers after community = donor elevation abbreviation (32, 34, 36, and 38 for 3200 m, 3400 m, 3600 m, and 3800 m, respectively); underlined numbers = surveying year abbreviation (07 and 08 for 2007 and 2008, respectively).

Table 2. Correlation coefficients between environmental factors and the two non-metric multidimensional scaling axes.

	SOM	Total N	Elevation	Air temp	Soil temp	SWC
Axis 1	-0.182	-0.075	-0.465	0.320	0.666	0.279
Axis 2	-0.328	-0.217	-0.847	0.819	0.346	0.957

The ordination final stress, which reflects the goodness of ordination on species coverage matrix, was 11.12 for two-dimensional solution, and its final instability was 0.00001, suggesting that a appropriate ordination with greater reliance (Clarke 1993). The variability of the first and second axes was 24% and 65%, respectively. The first axis combined the effect of soil temperature and elevation (Table 2), with soil temperature providing more positive effect than negative effect in terms of elevation. The second axis illustrated the impact of SWC, elevation, and air temperature. SWC and air temperature had positive influences, whereas elevation had a negative effect. In addition, SOM had little influence ( $R^2 = 0.09$ ) on the second axis (Table 2).

Ordination revealed good separation of treatments. Four groups were easily determined in the non-metric multidimensional scaling (NMDS) graph primarily based on receptor elevations (Fig. 3), suggesting that the plant community responded to climate specifically. Group A was in the district with the lowest altitude, and the highest SWC and air temperature at 3200 m. Group B could be found at the area with the highest soil temperature, moderate SWC and air temperature, and lower elevation at 3400 m. Since

the negative influence of air temperature and SWC offset the positive effect of elevation, there was minimal difference between group C and D except for soil temperature (Fig. 3).

The ordination final stress on function group abundance was 3.03 for two-dimensional solution, with final instability at 0.00001. Variability of the first and second axes was 85% and 11%, respectively, with orthogonality of 80.1%. Four groups were identified clearly by function type. Responses of each function group to simulated climate change were specific to function type at any treatments (Fig. 4).

## 5. DISCUSSION AND CONCLUSIONS

### 5.1. Plant community

Some studies have shown that experimental warming caused loss of species richness in the arctic plant community (Klein *et al.* 2004, Walker *et al.* 2006, Wookey *et al.* 2009). Nevertheless, we found that suitable cooling evidently improved the values of species richness ( $D$ , Eq (1)) and Shannon-Weaver index ( $H'$ , Eq (2)). For example, species richness ( $D$ , Eq (1)) and Shannon-Weaver index ( $H'$ , Eq (2)) of *Kobresia* meadow significantly

increased when transferred from 3200 m to 3400 m. However, the coverage of sedges, graminoids, and legumes declined, indicating that edible forage by animals (mostly sedges and graminoids in our sites) decreased and resulted in lower quality of *Kobresia* meadow. Klein *et al.* (2007) found that experimental warming also worsened rangeland quality as less-digestible shrubs replaced more-digestible graminoids in the same region. This suggested that slight temperature fluctuations might have negative consequences on *Kobresia* meadow. Periodic analysis of Guliya ice core of the Qinghai-Tibet Plateau hinted that temperature fluctuations would last for long periods in the future (Yao *et al.* 1996), indicating that alpine grassland management must be more cautious. Although dwarf shrub *Potentilla fruticosa* was not pinned in our two-year survey quadrates at 3200 and 3800 m, it played an important role in alpine biome under climate change (Walker *et al.* 2006, Wookey *et al.* 2009). Shrub species coverage was 6% at 3400 m and 3% at 3600 m, showing an insignificant decreasing trend ( $P = 0.18$ ) with altitude hoist. Shrub canopy height was measured in all quadrats; this revealed that there was no evident difference between canopy height at 3200 m (21.8 cm) and 3400 m (20.6 cm). However, cooling depressed shrub canopy height significantly (9.3 cm at 3600 m and 9.8 cm at 3800 m,  $P < 0.01$ ). Our initial results were different from previous reports that found shrub expansion caused by warming in alpine ecosystem (Chapin *et al.* 1995, Klanderud 2008). Results of manipulative experiments depended on duration (Epstein *et al.* 2000, Hollister *et al.* 2005), and differences might be because our experiment was of short duration only.

After testing the stability of *Kobresia* meadow ecosystem in temporal scale, we found that the growing season temperature was  $7.4 \pm 0.3^\circ\text{C}$  from 1983 to 1986. This was consistent with  $7.4 \pm 0.5^\circ\text{C}$  at 3600 m, indicating that responses of the plant community during 1983 to 1986 were comparable with that of our cooling treatment at 3600 m. The community of *Kobresia* meadow showed that pioneer sedge coverage was twofold of the dominant graminoid coverage in 1985 (Zhang and Zhou 1992). Similar results were observed in *Kobresia* meadow quad-

rats translocated to 3600 m from 3200 m (Table 1). Cooling treatments could revert the community of *Kobresia* meadow at present into that in the 1980s in terms of dominant species. This suggested that the alpine meadow was stable to some extent, which concurred with results of temporal analysis of biomass, temperature, and rainfall (Zhou *et al.* 2006, Zhang *et al.* 2009). Comparison results indicated that variations in the alpine meadow community induced by climate change may be reversible to some extent. This was consistent with findings that the alpine ecosystem was reversible under climate change (Melick *et al.* 1997), which was in contrast to findings of other reports (Harte and Shaw 1995, Cross and Harte 2007). Since ecosystem evenness was the key factor in preserving stability (Wittebolle *et al.* 2009), the insignificant fluctuations of evenness of *Kobresia* meadow also hinted that it was stable.

## 5.2. Function groups

Our translocation experiments revealed that sedges favored cooling, while graminoids and legumes preferred warmer environments (Table 1). Sedge species had high metabolic rates in abnormally warm environments (Körner 1999), with their optimum region elevating together with future climate warming (Walther *et al.* 2002, Lesica and McCune 2004). Sedge coverage in our study was enhanced from 13% at 3200 m to 48% at 3600 m in the cooling treatment, confirming sedges contraction and observations that warming depressed sedges and favored graminoids (Bruehlheide 2003, Walker *et al.* 2006, Klein *et al.* 2007). This might be attributed to mycorrhizal symbioses. The alpine ecosystem was nutrient-limited, and competition was predicted to have determined influence on the response of vegetation to climate change. Graminoids and legumes had mycorrhizal fungi (arbuscular or ecto-mycorrhizal) that allowed their partner plants to absorb the nutrients they produced and outcompete other species. Since sedge species were predominantly non-mycorrhizal (Read *et al.* 2004), they would have difficulty in surviving in nutrient-limited environments in future warming scenarios. Results partially confirmed that alpine plant species initially



adapted to climate change *via* emigration instead of evolution (Walther *et al.* 2002).

The responses of plant function groups to climate change were proven to be specific to function type and common in the alpine ecosystem (Walther *et al.* 2002, Walker *et al.* 2006). The compensatory effect was found among plant species and function groups (Cross and Harte 2007, Klanderud 2008). Sedges and graminoids, as well as legumes and forbs, were located in opposite quadrants (Fig. 4), indicating that the alpine community responded to climatic change through interaction and compensation (Cross and Harte 2007, Klanderud 2008). However, results of the ANOVA method from Cross and Harte (2007) showed a weak abundance compensation ( $N = 76$ ,  $P = 0.15$ ) only between legumes and forbs.

### 5.3. Non-metric multidimensional scaling (NMDS)

The plant community was divided into four groups in terms of receptor elevations, indicating that the alpine ecosystem was susceptible to climate change and responded in a climate-specific manner. Variations of climate factors accounted for most of those changes in the non-metric multidimensional scaling (NMDS) axes. However, their respective contributions were not distinguished using ordination axis rotation. The correlation between environmental factors and non-metric multidimensional scaling (NMDS) axes indicates that soil nutrients did not play an important role in plant community response. This concurred with findings that the alpine ecosystem community responded directly to climate change and was less influenced by soil nutrient alterations induced by climate change. In addition, this was also in line with results showing that climate factors were an important determinant in community response to climate change (Walker *et al.* 2006, Wookey *et al.* 2009).

After a two-year reciprocal translocation experiment, initial results revealed that species richness ( $D$ , Eq (1)) and Shannon-Weaver index ( $H'$ , Eq (2)) of *Kobresia* meadow increased when transferred to 3400 m from 3200 m and that shrub species cover-

age did not change significantly in cooling treatments. Sedges thrived at 3600 m, while graminoids and legumes favored the warmest quadrates at 3200 m. A comparison of results with a historical survey of the plant community in the mid-1980s and the fluctuation of ecosystem evenness suggested that the *Kobresia* meadow was susceptible and flexible. Results of ordination indicated that the response of alpine vegetation type and function group were specific to climate magnitude and specific to function type, respectively. Climate variations played a much more important role than soil in plant community response. The effects of abiotic and biotic factors and their interaction were masked to some extent in the translocation experiment, thus indicating the need for long-term studies.

**ACKNOWLEDGMENTS:** We sincerely thank Prof. Anna Hillbricht-Ilkowska and the anonymous reviewer for their valuable comments. This work was financially supported by the following: Foundation of Institute of Plateau Meteorology, China Meteorological Administration, Chengdu (LPM2008011); Action-Plan for West Development of the Chinese Academy of Sciences (KZCX2-XB2-06-01); Knowledge Innovation Project of the Chinese Academy of Sciences (KJCX2-YW-432-1h and KSCX2-YW-Z-1020); and 100 Talents Program of the Northwest Institute of Plateau Biology, CAS.

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*Received after revision September 2010*