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REGULAR ARTICLE

Linking thaw depth with soil moisture and plant community composition: effects of permafrost degradation on alpine ecosystems on the Qinghai-Tibet Plateau

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Abstract
Background and aims The warming of the planet in recent decades has caused rapid, widespread permafrost degradation on the Qinghai–Tibet Plateau. These changes may significantly affect soil moisture content and nutrient supply, thereby affecting ecosystem structure and function. This study aimed to describe the dynamic changes in thaw depth, assess the relationship between thaw depth and soil moisture content, and analyze the changes in species composition and water-use efficiency in response to permafrost degradation.
Methods We surveyed species composition, thaw depth, ground temperature, soil moisture, nutrient content, and foliar stable carbon isotope compositions to gain insights into the response of alpine grassland ecosystems to permafrost degradation on the Qinghai-Tibet Plateau.
Results Moisture content of the surface layer decreased with increasing thaw depth. The correlation between thaw depth and surface soil moisture content was strongest in June and decreased in July and August. The strongest correlation occurred at a depth of 20 cm to 30 cm. The dominant species shifted from Cyperaceae in alpine meadow to mesoxerophytes in alpine steppe before finally shifting to xerophytes in alpine desert steppe. Thaw depth correlation was significantly negative with organic C content ($r=-0.49$, $P<0.05$) and with total N content ($r=-0.62$, $P<0.01$). The leaf δ^{13}C of *Carex moorcroftii* increased with increasing thaw depth and followed a linear relationship ($R^2=0.85$, $P=0.008$).
Conclusions Permafrost degradation decreases surface soil moisture and soil nutrient supply capacity. Increasing permafrost degradation decreases the number of plant families and species, with hygrophytes and mesophytes gradually replaced by mesoxerophytes and xerophytes. The water-use efficiency of plants improved in response to increasing water stress as surface layers dried during permafrost degradation. Permafrost on the Qinghai–Tibetan Plateau is expected to further degrade as global warming worsens. Therefore, more attention should be dedicated to the response of alpine ecosystems during permafrost degradation.

Keywords Permafrost · Thaw depth · Soil moisture · Species composition · Water-use efficiency · Qinghai–Tibet Plateau

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Introduction

Permafrost, which is defined as subsurface materials that remain below 0 °C for two consecutive years (Washburn 1979; Schuur et al. 2008), is widespread in the Arctic and boreal regions of the Northern Hemisphere as well as at high elevations in many alpine ecosystems. The area of all soils in the northern permafrost region is approximately 16 % of the global soil area (Tarnocai et al. 2009). Therefore, permafrost is a key component of terrestrial ecosystems in cold regions, and is extremely sensitive to environmental change (Cheng and Zhao 2000). A potential increase in global average temperatures of up to 7 °C to 8 °C will warm high-latitude areas by the end of the 21st century and dramatically impact regions underlain by permafrost (IPCC 2007). Changes in permafrost conditions will significantly impact surface and subsurface hydrology, land surface energy budget, carbon exchange between land and atmosphere, ecosystems, landscapes, geomorphological processes, and engineering construction projects (Cheng and Wu 2007; Lemke et al. 2007; Wu et al. 2010). Therefore, understanding the response of permafrost to climatic change is important in the study of global change.

Permafrost plays an active role in determining vegetation growth and production in alpine ecosystems (Li et al. 2005; Camill et al. 2001). Related studies in the Arctic permafrost region have verified that permafrost degradation will potentially change vegetation communities located in these ecosystems (Nicholas and Hinkel 1996; Rovansek et al. 1996; Osterkamp et al. 2000). Rising ground temperatures and improvements in soil drainage and oxygen availability may increase C mineralization rates, thus increasing greenhouse gas emissions (Goulden et al. 1998). Alpine ecosystems in the fragile altitudinal permafrost regions of the Qinghai–Tibet Plateau are more sensitive to natural and anthropogenic disturbances (Wu et al. 2003a). However, quantifying the response of alpine ecosystems to permafrost degradation on the Qinghai–Tibet Plateau has garnered little attention.

Permafrost on the Qinghai–Tibet Plateau comprises the largest permafrost region at mid and low latitudes, and covers an estimated $1.5\times10^6 \mathrm{km}^2$, accounting for 69.8 % of the total permafrost area in China (Jin et al. 2000). Permafrost on the plateau mainly occur in the plateau's interior between the Kunlun Mountains and the Tanggula Range, with Xidatan (north of the Kunlun Mountains) as the northern limit and Anduo (south of the Tanggula Range) as the southern limit. The permafrost area extends about 550 km from south to north along the Qinghai-Tibet highway. Significant permafrost degradation has occurred in most of the region's permafrost. Observations along the Qinghai–Tibet highway showed that the southern lower limit of permafrost has moved 12 km northward, whereas the northern lower limit has moved 3 km southward since the 1970s (Wang and Mi 1993; Jin et al. 2006). Observations since the 1970s have shown that the lower limit of the permafrost have risen 25 m to 80 m in elevation (Wang et al. 2000). At Xidatan, the northern part of the permafrost area, the lowest elevation at which permafrost occurred increased by 25 m from 1975 to 2002 (Nan et al. 2003). The temperature in the permafrost areas (at 6 m below the surface) has been increasing at rates of 0.05 and 0.02 $°\mathrm{C\,yr}^{-1}$ in the low- and high-temperature permafrost areas, respectively, of the plateau (Wu et al. 2005). Mean annual permafrost temperatures at a depth of 6.0 m increased by 0.12 °C to 0.67 °C (averaging approximately 0.43 °C) from 1996 to 2006 (Wu and Zhang 2008). Permafrost on the Qinghai–Tibet Plateau continues to degrade because of global warming. Results obtained from an altitude-adjusted model using climatic forcing from the HADCM2 general circulation model scenario for climate change (Viner 1996) indicate that the areal extent of permafrost in the plateau will decrease by as much as 19 % from 2020 to 2050 and by around 58 % by 2099, resulting in complete permafrost degradation in the southern and eastern parts of the Plateau (Li and Cheng 1999).

Widespread permafrost degradation in the plateau has already caused environmental deterioration, including changes in surface hydrology, acceleration of desertification, and destabilization of human infrastructures. During the process of permafrost degradation, the deepening active layer and decreasing soil moisture content near the surface cause shifts from alpine wetlands to alpine meadows and from alpine meadows to alpine steppes (Jin et al. 2008). The area of alpine meadows decreased by 8.0 %, while the area of alpine swamps decreased by 28.1 % as a result of permafrost degradation from 1986 to 2000 (Wang et al. 2006). These changes, which are predicted to become irreversible under the projected climate warming, will cause further degradation of the permafrost. A previous study investigated the spatial distributions of vegetation cover and dynamic changes in the source areas of the Yangtze and Yellow rivers between 1982 and 2001 (Yang et al. 2006). These authors concluded that vegetation cover (represented by the normalized-difference vegetation index in their study) is very sensitive to changes in soil temperature at a depth of 40 cm, and that freezing and thawing processes play an important role in plant growth. These and other results indicate a strong correlation between the depth of seasonal thawing and vegetation cover (Liang et al. 2007). The increasing thickness of active layer corresponds to the significant decrease of vegetation cover and biomass in the alpine cold meadows, the exponential decrease of soil organic matter content of alpine meadow ecosystems, and the coarsening and gravelling of surface soil materials (Wang et al. 2006). These studies were mainly conducted at a regional scale based on remote sensing data. To increase our understanding of the mechanistic relationship between permafrost degradation on the Qinghai–Tibet Plateau and vegetation change, detailed investigations into ecological changes in permafrost regions are needed.

In the present study, we investigated the relationships among thaw depth, soil moisture content, and plant species composition. We aimed to describe the dynamic changes in thaw depth, assess the relationship between thaw depth and soil moisture content, and analyze the changes in species composition and water-use efficiency in response to permafrost degradation. This study will provide significant insights into the mechanism of alpine grassland ecosystem degradation in permafrost region on the Qinghai–Tibet Plateau.

Materials and methods

Study area and sampling sites

The area between Xidatan (at the foot of the Kunlun Mountains) and the southern slope of the Tanggula Range comprises the main part of the permafrost on the Qinghai–Tibet Plateau. The climate in this area is semi-arid (Lin and Wu 1981), with an average annual air temperature ranging from −3 °C in the east to −7 °C in the west. The average monthly air temperature remains below 0 °C outside the growing season. Annual mean precipitation varies widely, decreasing from 300 mm to 400 mm in eastern regions to <100 mm in western regions (84 % of the total annual mean precipitation occurs from June to September). Annual mean precipitation at Anduo and Qingshuihe was more than 400 and 500 mm, respectively. Soils are also variable, and include alpine meadow soils (also called felty soils, which are comparable to cambisols in the Food and Agricultural Organization of the United Nations' [FAO] taxonomy), alpine steppe soils (also called frigid calcic soils, which are comparable to cambisols), and cold desert and frigid frozen soils (comparable to gelic arenosols in the FAO taxonomy).

The use of long-term study plots that allow researchers to monitor the relationship between changes in vegetation and permafrost conditions is ideal in the study of the effects of permafrost degradation on vegetation succession. Unfortunately, such plots are rare, and none currently exist on the Qinghai–Tibet Plateau. When such plots are lacking, it is often possible to use a spatial sequence as a proxy for a chronosequence. In this study, we used a sequence based on the typical depth of the active layer, which decreased in the following order: Wuli >66Daoban > Kunlun Mountains pass > Wudaoliang > Beiluhe > Fenghuoshan (Fig. 1).

The area between Kunlun Mountains pass and Tuotuohe was selected as our study area. According to the climatic data recorded at existing stations and the distribution trend of climatic elements at the Qinghai–Tibet Plateau, the precipitation in the selected area is estimated to be 260 mm to 290 mm. Three main vegetation types are present in this area: alpine steppes, alpine meadows, and alpine swamps. Sparse *Myricaria germanica* shrubs can be found in river valleys, polsters on the huge mountain body, and sparse vegetation on talus slopes. We selected an area with flat terrain and good drainage in typical alpine ecosystems, and established a 10 m× 10 m fixed plots in Kunlun Mountains pass, 66Daoban, Wudaoliang, Beiluhe, Fenghuoshan, and Wuli (Fig. 1). The dominant species at Fenghuoshan and Beiluhe are *Kobresia pygmaea* and *Kobresia capilifolia*, *Poa* spp., *Kobresia humilis*, *Lagotis brevituba*, and *Kobresia tibetica*. In other plots, the dominant species are *Carex moorcroftii* and *Stipa purpurea*, and secondary species mainly include *Androsace tapete, Saussurea arenaria, Arenaria kansuensis, Kobresia robusta, Oxytropis falcata, Leontopodium pusillum*, and *Potentilla bifurca.* Table 1 summarizes information on sampling sites and the soil nutrient contents (0 cm to 10 cm) in each plot.

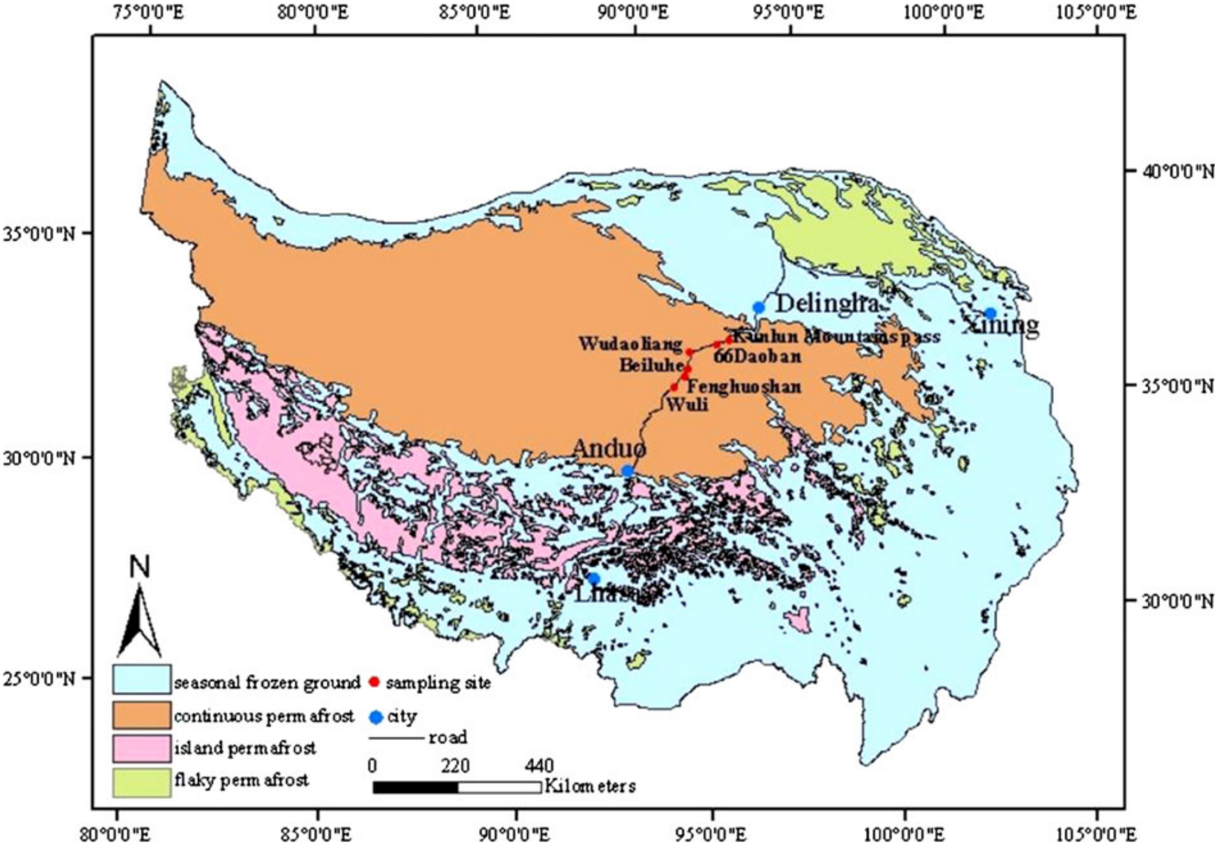

Fig. 1 Location of the sampling site on the Qinghai–Tibetan Plateau

Thaw depth and ground temperature

Surveying was performed on about the 20th of each month (June, July, and August) in 2008. In June, the thaw depth was shallow; thus, we measured the thaw layer by inserting a thaw-depth probe into the ground until it reached the freezing layer. When a compact mattic epipedon is present at the sample point, we removed the layer with a shovel before inserting the thaw-depth probe. In July and August, when the permafrost depth was deeper, we dug pits before inserting the thaw-depth probe to reach the freezing layer. When the thaw depth could not be measured using the thaw-depth probe, we used shovels to dig until we reached the top of the freezing layer. Ground temperatures at depth of 50 cm were measured using an automatic permafrost temperature monitoring system.

Plant species composition

We randomly established five 20 m×20 m plots at each site for vegetation surveys. We randomly established six 1 m×1 m quadrats in each plot and counted and identified individuals of all vascular plant species. We then determined the percent of the total vegetation cover, height, and density of these vascular plant species. We calculated an importance value (IV) for each species based on the height, cover, and density of its individuals using the following equations (Jiang et al. 2003):

$$R_{Hi} = \frac{H_i}{\sum H} \tag{1}$$

$$R_{Ci} = \frac{C_i}{\sum C} \tag{2}$$

$$R_{Di} = \frac{D_i}{\sum D} \tag{3}$$

$$IV_i = \frac{R_{Hi} + R_{Ci} + R_{Di}}{3} \tag{4}$$

Table 1 Description of sampling plots, soil nutrient contents and pH (0–10 cm)

Plot	Coordinate	Altitude (m asl)	Vegetation cover (%)	Active layer thickness (m)	Soil type	Total P (g/kg)	Available P (mg/kg)	Available K (mg/kg)	Inorganic N(mg/kg)	pH
Fenghuoshan	34.67°N 92.90°E	4899	> 90	2.5	Clay	0.25	3.78	102.30	14.91	7.55
Beiluhe	34.34°N 93.92°E	4636	30–70	2.4	Clay	0.37	2.89	128.22	11.78	7.50
Wudaoliang	35.19°N 93.07°E	4656	30–60	3.0	Sandy clay	0.35	2.47	78.74	7.62	7.72
Kunlun Mountains pass	35.63°N 93.46°E	4753	5–8	2.8	Clay	0.47	2.12	158.63	5.41	7.34
66Daoban	35.52°N 93.78°E	4560	15–30	3.3	Gravelly soil	0.39	1.86	82.65	4.03	7.83
Wuli	34.39°N 92.66°E	4623	40–65	> 3.3	Sandy clay	0.20	2.08	88.21	4.97	7.76

where $R_{\mathrm{H}i}$ means the relative height of species i; $R_{\mathrm{C}i}$ means the relative vegetation cover by species i; $R_{\mathrm{D}i}$ means the relative density of species i; H_i is the height of individuals of species i; C_i means the individual cover by species i; D_i means the density of individuals of species i; $\sum H$ is the sum of the height of all species; $\sum C$ is the sum of the cover of all species; $\sum D$ denotes the sum of the density of all species; and IV_i is the importance value of species i.

Content measurement of soil moisture, soil organic C, and total N

We measured the volumetric soil water content of three soil layers (0 cm to 10 cm, 10 cm to 20 cm, and 20 cm to 30 cm) in the quadrats using frequency-domain reflectometry (ML2x Theta probe, Delta T Devices Ltd., Cambridge, UK) on the 20th of June, July, and August. The sensor rods of the Theta probe are 6 cm in length and have a diameter of 2.5 cm. The probe measured the integrated moisture content in the cylindrical volume spanned by the rods. The rods were inserted vertically into the soil profile and centered on the midpoint of each depth interval. Soil moisture was obtained from the measured signal using the built-in calibration curve, which agreed well with independent moisture measurements conducted in the field. The probe was calibrated for the permafrost region based on the measurements, and the accuracy was ±2 %. In each layer, soil moisture was measured three times.

Soil samples from each layer were collected using a soil auger when soil moisture was measured. Samples were air-dried and finely ground to pass a 0.5-mm sieve. The samples were then analyzed for organic C (by means of oxidization with potassium dichromate in the presence of H_2SO_4, heated at 180 °C for 5 min), and for total N (by means of the Kjeldahl method) following the procedures of ISSCAS (1978).

Analysis of the stable C isotope composition

Plant samples from the dominant species at the six study sites were collected in late July 2008, when the plants were actively growing. We randomly selected three to five healthy and fully expanded leaves from five individual plants of each species. The plant samples were ultrasonically washed with distilled water, air-dried, and then oven-dried at 65 °C for more than 48 h. All the leaves from the same species were combined to produce a single composite sample. The composite sample was then ground in a ball mill (MM200, Retsch, Düsseldorf, Germany) into a uniformly fine powder.

We then weighed 3 mg to 5 mg of the sample into tin capsules and determined the foliar stable C isotope composition using a MAT-253 mass spectrometer (Thermo Finnigan, Waltham, MA, USA). The accuracy of the stable C isotope composition was <0.02‰ based on comparisons with the Vienna PeeDee Belemnite standard. The ratios were calculated as follows:

$$\delta^{13}C(‰) = \frac{\left({}^{13}C/{}_{12}C\right)_{sample} - \left({}^{13}C/{}_{12}C\right)_{s\tan dard}}{\left({}^{13}C/{}_{12}C\right)_{s\tan dard}} \times 1000 \quad (5)$$

Data analysis

We used one-way analysis of variance (ANOVA) to assess the difference in soil nutrient content between study sites. We tested for homogeneity of variances among the site data using Levene's test. We used leastsignificant-difference (LSD) tests for multiple comparisons when the variances were homogeneous; otherwise, we used Tamhane's T2 test. We used Pearson's correlation coefficient to evaluate the relationships among the variables. All data analyses were conducted using version 13.0 of the SPSS software (SPSS Inc., Chicago, IL, USA).

Results

Thaw depth and belowground temperature

The minimum thaw depth at all sites occurred in June and the maximum occurred in August, with the depth increasing from June to August (Fig. 2). The deepest thaw occurred at Wuli, whereas the shallowest was recorded at Fenghuoshan. Thaw depths at Fenghuoshan and Beiluhe were 0.71 and 0.99 m in June, respectively. Thaw depth in June was more than 2 m at 66Daoban and Wuli, deeper than that of other sites. The order of the thaw depths among sites was similar in June and July. Thaw depth at Kunlun Mountains pass in August was 2.16 m, which was shallower than at Wudaoliang (2.44 m). Trends for the belowground temperature at 50 cm were similar to those of thaw depth. Fenghuoshan had higher belowground temperatures than Wudaoliang in both July and August; however, thaw depth was deeper at Wudaoliang in these months.

Richness of major taxonomical groups

Table 2 summarizes the species composition at the study sites. Gramineae, Cyperaceae, and Compositae were present at all sites; Gramineae was typically the dominant family. The genus and family composition for the alpine ecosystems in the permafrost region on the plateau were similar and appear to be closely linked. There were 11 families at Fenghuoshan comprising 20 genera and 28 species, which was the highest number in all plots, suggesting a more complex species composition. Sites in the Kunlun Mountain pass and 66Daoban had the fewest species (22 and 16, respectively).

The dominant species at Fenghuoshan was *Kobresia pygmaea* (Table 3), and the dominant species at Beiluhe were *Kobresia pygmaea* and *Kobresia humilis.* At Fenghuoshan and Beiluhe, the dominant species were mainly mesophytes. Xerophytes were the dominant and secondary species at Kunlun Mountains pass, Wudaoliang, 66Daoban, and Wuli sites due to the relatively low surface soil moisture content. Wudaoliang was dominated by *Leontopodium pusillum*, *Carex moorcroftii*, and *Poa annua*. Wuli was dominated by *Stipa purpurea* and *Leontopodium pusillum.* The soil environment at Kunlun Mountains pass and 66Daoban sites was much drier, leading to widespread distribution of cushion plants.

The importance value can reflect a synthesis of the abundance and other characteristics of individual species in plant communities. Table 3 lists only the species with importance value greater than 4. At Fenghuoshan, 7 species had an importance value greater than 4; *Kobresia pygmaea* had the highest importance value (34.6), followed by *Kobresia humilis, Oxytropis glabra*, and *Thalictrum alpinum*. At Beiluhe, *Kobresia pygmaea* had the highest importance value (21.3), followed by *Kobresia humilis, Littledalea racemosa*, and *Poa annua.* The

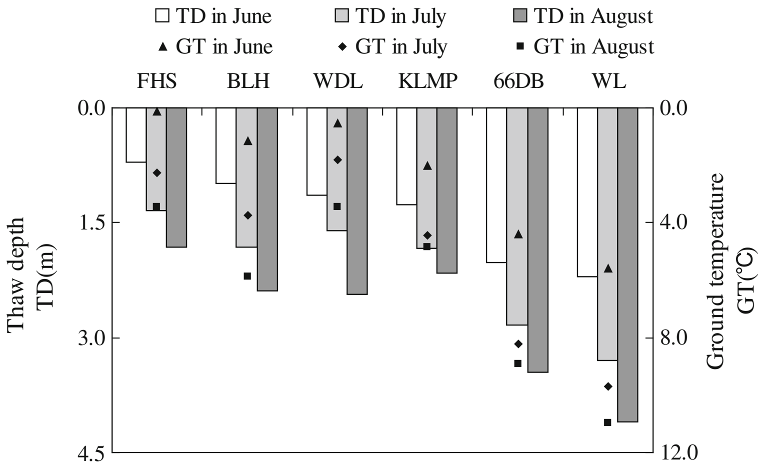

Fig. 2 Thaw depth (TD) and belowground temperature (GT, at a depth of 50 cm) at the study sites. *FHS* Fenghuoshan, *BLH* Beiluhe, *WDL* Wudaoliang, *KLMP* Kunlun Mountain pass, 66DB 66Daoban, *WL* Wuli

Table 2 Vegetation composition at the study sites

Family	Fenghuoshan		Beiluhe		Wudaoliang		Kunlun Mountains Pass		66Daoban		Wuli	
	Genera number	Species number	Genera number	Species number	Genera number	Species number	Genera number	Species number	Genera number	Species number	Genera number	Species number
Gramineae	6	6	3	3	5	5	4	4	2	4	5	5
Scrophulariaceae	1	1	1	1	1	1	1	1	—	—	1	1
Primulaceae	1	1	1	1	—	—	1	1	—	—	—	—
Compositae	2	2	2	2	3	4	1	2	1	1	4	4
Leguminosae	2	3	—	—	2	3	2	4	2	4	2	4
Labiatae	—	—	2	2	—	—	1	1	—	—	—	—
Cruciferae	2	2	1	1	2	2	3	3	—	—	—	—
Cyperaceae	2	6	2	4	2	3	1	1	2	4	2	4
Umbelliferae	—	—	—	—	1	1	2	2	1	1	—	—
Caryophyllaceae	1	1	1	1	2	2	2	2	1	1		
Euphorbiaceae	—	—	—	—	—	—	1	1	—	—	1	1
Iridaceae	—	—	1	1	—	—	—	—	1	1	—	—
Rosaceae	1	1	1	1	1	1	—	—	—	—	1	2
Gentianaceae	1	3	1	1	1	1	—	—	—	—	—	—
Papaveraceae	—	—	—	—	1	1	—	—	—	—	1	1
Liliaceae	—	—	—	—	1	1	—	—	—	—		
Polygonaceae	1	2	1	3	—	—	—	—	—	—	1	1
Boraginaceae	—	—	1	1	—	—	—	—	—	—	1	1
Ranunculaceae	—	—	1	1	—	—	—	—	—	—	—	—
Chenopodiaceae	—	—	1	1	—	—	—	—	—	—	—	—
Total	20	28	20	24	22	25	19	22	10	16	19	24

dominance of *Kobresia pygmaea* at Fenghuoshan was higher than at Beiluhe. However, *Kobresia humilis* was less dominant at Fenghuoshan than at Beiluhe, and Gramineae were less dominant based on their importance values. At Wudaoliang, *Leontopodium pusillum* had the highest importance value (22.2), followed by *Poa annua, Astragalus ellipsoideus,* and *Carex moorcroftii,* which were all meso-xerophytes. At Wuli and 66Daoban, *Stipa purpurea* had the highest importance values (20.6 and 29.2, respectively). At Kunlun Mountains pass, *Carex moorcroftii* had the highest importance value (24.5), followed by *Saussurea arenaria,* and *Littledalea racemosa*. The dominant species shifted from Cyperaceae at Fenghuoshan and Beiluhe to mesoxerophytes at Wudaoliang and Wuli, then shifted to xerophytes at Kunlun Mountains pass and 66Daoban, indicating that the dominance of mesoxerophytes and xerophytes increased gradually along the permafrost degradation sequence.

Soil nutrient contents

The total N and organic C contents decreased with soil depth at Kunlun Mountains Pass, Beiluhe and Fenghuoshan (Table 4). No significant differences were found in soil nutrient contents between Wuli and Wudaoliang in all depths. The total N and organic C contents at 10 cm to 20 cm at 66Daoban, Wudaoliang and Wuli were significantly higher than that at 0 cm to 10 cm ($P<0.05$); corresponding difference between 10 cm to 20 cm and 20 cm to 30 cm was not significant ($P>0.05$; Table 4). Total N and organic C contents at Fenghuoshan and Beiluhe were significantly higher than those of other sites in all depths. Soil nutrient contents at Fenghuoshan were highest in all three depths (Table 4). Fenghuoshan had higher available P (3.78 mg/kg) but lower total P (0.25 g/kg) than Kunlun Mountains pass (Table 1). The highest available K (158.63 mg/kg) in the 0 cm to 10 cm depth

Table 3 Importance values (calculated using Eq. 4) for the dominant plants at the study sites

Species	Fenghuoshan	Beiluhe	Wudaoliang	Kunlun Mountains Pass	66Daoban	Wuli
Carex moorcroftii	4.06	—	8.44	24.52	7.54	4.77
Kobresia pygmaea	34.63	21.31	—	—	—	—
Oxytropis glabra	6.17	5.12	—	—	—	—
Kobresia tibetica	4.73	—	7.00	—	—	4.55
Kobresia humilis	6.34	18.01	—	—	—	—
Aster flaccidus	4.01	—	—	—	—	—
Thalictrum alpinum	5.21	—	—	—	—	—
Leontopodium pusillum	—	4.05	22.19	—	—	11.89
Poa annua	—	5.50	8.78	4.59	—	—
Littledalea racemosa	—	7.15	5.75	10.61	—	—
Hedinia tibetica	—	5.45	—	—	—	—
Pedicularis alaschanica	—	—	—	4.41	—	—
Saussurea gnaphalodes	—	—	—	4.77	—	—
Oxytropis falcata	—	—	—	7.91	4.70	—
Oxytropis stracheyana	—	—	—	5.90	—	4.69
Saussurea arenaria	—	—	—	10.66	12.65	—
Potentilla bifurca	—	—	5.24	—	—	7.26
Stipa purpurea	—	—	—	—	29.20	20.58
Heteropappus hispidus	—	—	—	—	—	6.16
Koeleria litvinowii	—	—	—	—	—	4.79
Kengyilia thorodiana	—	—	—	—	—	4.53
Carex spp.	—	—	—	—	8.63	4.39
Astragalus ellipsoideus	—	—	8.61	—	—	—
Roegneria kokonorica	—	—	4.30	—	—	—
Astragalus coeruleus	—	—	—	—	7.75	—
Astragalus tanguticus	—	—	—	—	7.09	—
Iris potaninii	—	—	—	—	4.77	—
Kobresia robusta	—	—	—	—	5.44	—

occurred in Kunlun Mountains pass. Inorganic N (0 cm to 10 cm) in Fenghuoshan was the largest (14.91 mg/kg) and the second largest content (11.78 mg/kg) was in Beiluhe. Soil pH value (0 cm to 10 cm) was between 7.34 and 7.86 and decreased in the following order: 66Daoban > Wuli > Wudaoliang > Fenghuoshan > Beiluhe > Kunlun Mountains pass (Table 1).

Our analysis revealed a strong significant positive correlation (r>0.72) between soil moisture and both organic C and total N contents (P<0.01), and moderate but significant negative correlations (r<−0.47) with ground temperature and thaw depth (P<0.05; Table 5). A previous study in the arctic indicated that the main driving factor responsible for soil organic matter storage was the thickness of the active layer (Rodionov et al. 2007). In the present study, the thaw depth was significantly negatively correlated with the organic C content (r=−0.54, P<0.05) and with the total N content (r=−0.62, P<0.01). Significantly negative correlations also existed between ground temperature and organic C content (r=−0.49, P<0.05) as well as total N content (r=−0.58, P<0.05).

Foliar stable carbon isotope compositions

The foliar carbon isotope (δ^{13}C) of a given species differed among the study sites. The δ^{13}C of *Carex moorcroftii* at the six sites was ranked in the following order: Wuli >66Daoban > Kunlun Mountains pass >

Table 4 Soil total nitrogen and organic carbon contents at the study sites

	Total N ($g.kg^{-1}$)			Organic C ($g.kg^{-1}$)		
	0–10 cm	10–20 cm	20–30 cm	0–10 cm	10–20 cm	20–30 cm
Kunlun Mountains Pass	0.76±0.03^{a}	0.65±0.08^{a}	0.50±0.04^{a}	7.08±0.39^{a}	5.83±0.33^{a}	4.52±0.71^{a}
66Daoban	0.35±0.04^{b}	0.69±0.09^{a}	0.41±0.01^{b}	3.78±0.35^{b}	5.68±0.22^{a}	4.91±0.80^{a}
Wudaoliang	0.46±0.04^{b}	0.69±0.06^{a}	0.47±0.01^{a}	4.30±0.57^{b}	6.61±0.75^{a}	4.73±0.15^{a}
Wuli	0.39±0.05^{b}	0.54±0.09^{a}	0.48±0.01^{a}	4.09±0.47^{b}	5.26±0.83^{a}	5.05±0.52^{a}
Beiluhe	1.07±0.01^{c}	1.05±0.01^{b}	0.79±0.01^{c}	13.37±0.90^{c}	10.87±2.37^{b}	7.12±1.06^{b}
Fenghuoshan	1.26±0.26^{d}	1.10±0.25^{b}	0.86±0.08^{d}	13.95±3.60^{c}	11.21±1.84^{b}	8.74±0.57^{c}

Values in a column followed by different letters differ significantly (LSD test, $P<0.05$).

Wudaoliang > Fenghuoshan > Beiluhe (Table 6). The $\delta^{13}C$ values for *Carex moorcroftii, Kobresia tibetica*, and *Stipa purpurea* were lower (more negative) at 66Daoban than at Wuli (Table 6). *Kobresia pygmaea* was the dominant species at Beiluhe and Fenghuoshan, and the $\delta^{13}C$ values were −26.42‰ and −25.86‰, respectively (Table 6). *Leontopodium pusillum* had a lower foliar $\delta^{13}C$ value at Fenghuoshan (−27.98‰) than at Wudaoliang (-27.05‰) (Table 6).

Discussion

Effects of active-layer depth on soil moisture and soil nutrient contents

Changes in the active layer thickness as a result of permafrost thawing alter the soil's water-holding capacity and moisture distribution within the soil (Wu et al. 2003b). Negative correlations between soil moisture and thaw depth suggested the surface soil moisture content (to a depth of 30 cm) decreased with increasing thaw depth in all months (Table 7). When the ground surface begins to thaw, it thaws from the surface downward, and meltwater is maintained above the frozen layer, where it remains available to the root system. This process creates a stronger correlation between thaw depth and soil moisture in June than in July or August at all depths. As the thaw depth increases, a small amount of the meltwater near the thawing front is transferred upward as a result of transpiration pressure and capillarity action of the soil. However, most of the meltwater moves downward along with the thawing front, thereby lowering the water table and decreasing moisture contents in the surface soil. As a result, the correlation between thaw depth and surface soil moisture decreased in July and August. The correlation between thaw depth and soil moisture was strongest at the depth of 20 cm to 30 cm, with values of −0.97, −0.92, and −0.85 in June, July and August, respectively. Thaw depth was more strongly correlated with soil moisture content in the deeper layers because the zone of wet soil moves gradually downward as the thawing front moves deeper into the soil.

Permafrost appears to be extremely sensitive to global warming. From 1995 to 2002, the active layer of the soil above the permafrost has increased in depth

Table 5 Pearson correlation coefficients for the relationships among soil nutrient and permafrost condition variables

	Soil moisture	Thaw depth	Ground temperature	Organic C	Total N
Soil moisture	1	—	—	—	—
Active-layer depth	−0.478*	1	—	—	—
Ground temperature	−0.554*	0.967**	1	—	—
Organic C	0.729**	−0.544*	−0.494*	1	—
Total N	0.780**	−0.622**	−0.584*	0.983**	1

*significant at $P<0.05$ (two-tailed); **, significant at $P<0.01$ (two-tailed)

Table 6 Foliar stable carbon isotope compositions (δ^{13}C) (‰) of the most common species

	Beiluhe	Fenghuoshan	Wudaoliang	Kunlun Mountains pass	66Daoban	Wuli
Kobresia pygmaea	−26.42	−25.86	—	—	—	—
Carex moorcroftii	−26.33	−26.30	−26.13	−26.06	−25.67	−24.75
Leontopodium pusillum	—	−27.98	−27.05	—	—	—
Kobresia tibetica	—	—	—	—	−27.47	−26.59
Stipa purpurea	—	—	—	—	−26.41	−25.99

by 0.8 cm to 8.4 cm per year based on records at several ground temperature monitoring sites between the Kunlun and Fenghuoshan (Wu and Liu 2004). Based on the relationship between thaw depth and surface soil moisture in the present study, we predict that deepening of the active layer as a result of continuing permafrost degradation on the Qinghai–Tibet Plateau will cause the zone of wet soil to move deeper. Simultaneously, water vapor will migrate downwards and condense at the permafrost table as a result of a vapor pressure gradient, leading to decreased moisture in the surface soil, which will gradually decrease water availability to vegetation and increase the risk of drought (Cao et al. 2006).

Based on correlation coefficients between soil nutrients and thaw depth ($r<-0.54$, $P<0.05$) as well as soil nutrients and ground temperature ($r<-0.49$, $P<0.05$; Table 5), we concluded that decreasing soil moisture contents and increasing ground temperature, which were caused by increased active-layer depth during permafrost degradation on the Qinghai–Tibet Plateau, would decrease soil organic C and total N, thereby decrease the soil nutrient supply capacity. Several recent studies of permafrost on the plateau have shown that the permafrost degradation process was accompanied by significant decreases in soil organic matter. For example, the soil organic matter content in an alpine marsh meadow was five and seven times the value of that in an alpine steppe meadow and an alpine desert steppe, respectively (Jin et al. 2000; Guo et al. 2007). In addition, the melting of permafrost decreased the content of hydrolyzable nitrogen, available potassium, and available phosphorus (Wang et al. 2007).

Table 7 Pearson correlation coefficients for the relationships among soil moisture content (0 cm to 30 cm) and thaw depth (June–August)

	June	July	August
0 cm to 10 cm	−0.90*	−0.69	−0.78
10 cm to 20 cm	−0.94**	−0.78	−0.77
20 cm to 30 cm	−0.97**	−0.92**	−0.85*

*significant at $P<0.05$ (two-tailed); **, significant at $P<0.01$ (two-tailed)

Changes in water and heat conditions in the soil as a result of permafrost degradation on the Qinghai–Tibet Plateau appear to have decreased the soil nutrient content and altered nutrient availability, thereby decreasing the soil's nutrient supply capacity and driving retrogressive succession of the alpine ecosystems in the study area. Our analysis suggests a possible mechanism for the alpine ecosystem deterioration that is occurring as a result of permafrost degradation on the plateau. First, permafrost degradation leads to downward migration of soil moisture, thereby decreasing soil moisture availability in the rooting zone near the surface (Table 7). This, in turn, drives a change in species composition towards species capable of surviving with more limited soil moisture availability. Second, the changes in water and heat transport during permafrost degradation alter the availability of soil nutrients and decrease the soil's nutrient supply capacity (Table 5). This, in turn, causes the alpine grassland communities, which are already limited by soil nutrient availability (Jiang et al. 2012; Xu et al. 2006), to degrade towards communities capable of tolerating even lower soil nutrient contents. Although this hypothesis seems reasonable, it should be validated further. Future studies should focus on diagnosing soil nutrient limitations in alpine grassland ecosystems and confirming the hypothesized trends in nutrient availability as a result of permafrost degradation on the plateau.

Permafrost thawing has the potential to significantly affect plant communities, ecosystem processes and soil properties in Qinghai–Tibet Plateau permafrost regions. These multiple direct and indirect effects of permafrost thawing are difficult to simulate in experimental approaches, which often manipulate only one or two factors. Generally, a natural gradient approach was used usually to represent stages in the process of permafrost thawing. Although, our results strongly support the theoretical understanding about alpine ecosystems response to permafrost degradation on the Qinghai–Tibet Plateau, our analysis is bounded by some key issues. This study could not fully take into account differences in soil physicochemical properties amongst six sampling sites; therefore, to what extent change in active layer depth affects soil moisture and nutrient content was unknown. Differences between soil properties before and after permafrost thawing could not be considered adequately, which would weaken reliability of findings in this study. Thaw depth, soil moisture and nutrient contents and species composition were surveyed in only one growth season. If sampling and monitoring were continued in several consecutive growing seasons, the results would be more convincing because more data would decrease the effect of random factors. Consequently, we proposed, to improve creditability and integrality of findings in this study, the long-term and located field observations plots with different permafrost conditions and similar climate conditions, topography and soil properties should be constructed, based on which predict ecosystem dynamic in permafrost degradation.

Effects of permafrost degradation on plant species

The degradation of permafrost can lead to large changes in ecosystems (Jorgenson et al. 2001; Liang et al. 2007). Several arctic studies showed that communities dominated by tall woody vegetation expanded in response to permafrost degradation (e.g., Nicholas and Hinkel 1996; Rovansek et al. 1996). Regressive succession during permafrost degradation on the Qinghai–Tibet Plateau followed a sequence from alpine marsh meadow to alpine meadow, then to alpine steppe and alpine desert steppe (Guo et al. 2007). In the present study, the ecosystem types at Fenghuoshan and Beiluhe were alpine meadow, which had higher soil moisture content than the alpine steppe site at Wudaoliang. Soil moisture content at Kunlun Mountains pass and 66Daoban sites was much lower than those at Wudaoliang. Lower soil moisture always accompanied a thicker active layer. Based on the vegetation communities, soil moisture levels, and active layer thickness, the permafrost condition deteriorated, leading to regressive succession, along the sequence from Fenghuoshan to Beiluhe, Wudaoliang, Kunlun Mountains pass, and 66Daoban.

In our survey, species numbers decreased along the sequence from alpine meadow to alpine steppe and alpine desert steppe. The number of genera and species in the most common families (i.e. the Cyperaceae and Gramineae) were highest in the alpine meadow and lowest in the alpine steppe, and based on these changes, we can describe the decreases in numbers of genera and species along this sequence of permafrost degradation. Based on water ecological groups, the communities at Fenghuoshan and Beiluhe were mainly mesophytes as a result of the relatively high soil moisture levels, and included hygrophytes locally where surface soils were continuously moist or even saturated. At the drier alpine steppe site at Wudaoliang, xeromesophytes and xerophytes were widespread, including *Stipa purpurea, Leontopodium pusillum, Potentilla bifurca, Carex moorcroftii*, and *Poa annua*. Xerophytes were more abundant at 66Daoban because of the harsher growing environment, which was characterized by coarser soils (with high gravel content), a low water-holding capacity, and much drier soils. At Kunlun Mountains pass site, the shallow ground temperature was lower, the active layer was thinner, and the soil moisture content was higher compared with that at 66Daoban. However, the soil parent materials at Kunlun Mountains pass site were mainly composed of lake sediments, which were not suitable for plant growth, and dwarf cushion plants were widely distributed (Wu et al. 2003b). During permafrost degradation that has occurred on the Qinghai–Tibet Plateau, the number of families and species has decreased, and hygrophytes and mesophytes were gradually replaced by mesoxerophytes and xerophytes.

The response of permafrost to climate change is a long-term and gradual process. Changes in permafrost conditions could have far-reaching consequences for future alpine ecosystems such as those of the plateau (e.g. greenhouse gas emission, nutrient cycling, and vegetation structure). At present, we lack long-term observations of the successional dynamics of alpine ecosystem during ongoing permafrost degradation. Thus, spatial sequences, such as the one used in this study, have mostly been used instead of chronosequence approaches. To investigate the mechanisms responsible for alpine grassland degradation in permafrost regions of the plateau, initiating long-term studies at appropriate locations in the field are necessary.

Water-use efficiency of plants during permafrost degradation

Plant carbon isotope composition ($\delta^{13}C$) can comprehensively integrate the effects of the growing environment on CO_2 and H_2O exchange during the process of plant photosynthesis. Thus, it could theoretically serve as a potential indicator of long-term changes in the water-use efficiency (WUE) of plants (Warren et al. 2001; Zhao et al. 2004; Song et al. 2008).

Figure 3 shows the relationship between thaw depth and $\delta^{13}C$. The leaf $\delta^{13}C$ of *Carex moorcroftii* increased with increasing thaw depth following a linear relationship (R^2=0.85, P=0.008). *Kobresia pygmaea*, the dominant species at Fenghuoshan and Beiluhe, had a higher $\delta^{13}C$ value at Fenghuoshan than at Beiluhe (Table 6). A previous study on the plateau showed that leaf $\delta^{13}C$ values of *Kobresia pygmaea* were negatively correlated with annual precipitation along a water gradient (Song et al. 2008). Fenghuoshan and Beiluhe had the same rainfall (an average of 290.9 mm per year); therefore, differences in precipitation could not explain the difference in leaf $\delta^{13}C$ values between Beiluhe and Fenghuoshan. Permafrost condition and vegetation cover at Fenghuoshan were better than those at Beiluhe; however, the water-holding capacity was lower at Fenghuoshan due to the looser soil structure. As a result, soil moisture at Fenghuoshan was lower than at Beiluhe. The higher soil moisture at Beiluhe caused a lower leaf $\delta^{13}C$ value than at Fenghuoshan.

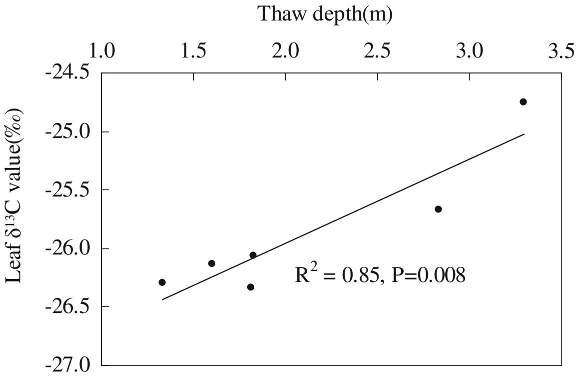

Fig. 3 Relationship between thaw depth and plant carbon isotope composition for *Carex moorcroftii*

Stipa purpurea is the dominant species at 66Daoban and Wuli, and had leaf $\delta^{13}C$ values of -26.41‰ and −25.99‰, respectively (Table 6). This suggests that the leaf $\delta^{13}C$ value of *Stipa purpurea* increased with increasing thaw depth (Fig. 3). The leaf $\delta^{13}C$ values of *Kobresia tibetica* at 66Daoban and Wuli showed a similar trend as that of *Stipa purpurea*. *Leontopodium pusillum* had $\delta^{13}C$ values of −27.98‰ and −27.05‰ at Fenghuoshan and Wudaoliang, respectively, which indicated higher water-use efficiency at Wudaoliang. The difference in leaf $\delta^{13}C$ of *Leontopodium pusillum* between Fenghuoshan and Wudaoliang was consistent with the difference in Carex moorcroftii $\delta^{13}C$ values, which increased with increasing thaw depth. In general, the leaf $\delta^{13}C$ values of the most common species at all study sites increased with increasing thaw depth. The thaw depth increased as a result of permafrost degradation on the Qinghai–Tibet Plateau, leading gradually to decreasing soil moisture availability. Therefore, we deduce that plant water-use efficiency improved as an adaptation to water stress as soil moisture levels gradually decreased during permafrost degradation on the plateau.

Conclusions

In this study, we analyzed the relationships among thaw depth, soil moisture content, and species composition in a permafrost region of the Qinghai–Tibet Plateau. The correlation between thaw depth and surface soil moisture content was strongest in June and decreased in July and August. The surface soil moisture at depths of 20 cm to 30 cm was stronger than the correlations at shallower depths. As the active layer increased in thickness during permafrost degradation, the surface soil moisture decreased, gradually increasing water stress. These changes would decrease soil organic C and total N contents, thereby decreasing the soil's nutrient supply capacity. During the process of permafrost degradation on the plateau, the number of families and species decreased, and hygrophytes and mesophytes were gradually replaced by mesoxerophytes and xerophytes. Leaf $\delta^{13}C$ values suggest that improved plant water-use efficiency represents an adaptation to water stress that results from a gradual decrease in soil moisture content caused by permafrost degradation. If global warming persists, the permafrost on the Qinghai–Tibetan Plateau is expected to further degrade. Hence, the response of alpine ecosystems to permafrost degradation should receive more attention.

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