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Above- and below-ground response to soil water change in an alpine wetland ecosystem on the Qinghai-Tibetan Plateau, China

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ABSTRACT

The reduction of soil water content induced by global warming is expected to affect plant communities worldwide. However, less is known about the consequences of global warming-induced decreases of soil water on alpine wetland ecosystems on the Qinghai-Tibetan Plateau. To determine the responses of a natural alpine wetland community to decreases in soil moisture, we conducted a gradient analysis of soil water using a sequence space-series variation. We used the sequence space-series variation of soil water contents to reflect potential time-series variations by examining the effects of spatial heterogeneity on soil water, as well as determining the changes that would occur in above- and below-ground properties of an alpine wetland community. We found that vegetation aboveground biomass, vegetation cover and height all significantly increased along soil moisture, but species richness decreased. Soil organic carbon, total nitrogen, available nitrogen, total phosphorus and available phosphorus all significantly increased along soil moisture, but soil pH, total potassium and available potassium significantly decreased. Species richness was significantly and negatively correlated to aboveground biomass, vegetation cover and height. Aboveground biomass, vegetation cover and height were all significantly and positively related to soil organic carbon, total N and P, and available N and P, but were negatively related to total K. Conversely, species richness was significantly and negatively related to soil organic carbon, total N and P, and available N and P, but positively related to total K. Our observations indicate that decreased soil water would potentially have a negative influence on the alpine wetland plant communities and soil properties.

1. Introduction

Information on responses of ecosystems to warming-induced changes of soil water content can improve our understanding about its functions and potential succession direction during global warming-induced changes of soil water content. The mean global temperature has increased by approximately 0.74 °C in recent decades and is expected to continue increasing (IPCC, 2007) and (IPCC) predicted a 1.4–5.8 °C average increase in the global surface temperature over the period 1990–2100 (Houghton et al., 2001). Warming-induced changes of soil water content is expected to have a major impact on ecosystems worldwide (Rosenzweig et al., 2008), affecting both above- and below-ground properties, e.g., biodiversity, productivity. Some studies reported that warming-induced changes of soil water content has an important impact on changes in species composition at the regional level (biogeographic regions or political entities) or at local scales (e.g., site or ecosystem) in Europe and North America for various types of ecosystems (Rosset et al., 2010). These studies mainly focused on the description and prediction of changes affecting species distribution, phenology and functional groups composition (Walther et al., 2002; Parmesan and Yohe, 2003; Hickling et al., 2006; Parmesan, 2006; Lenoir et al., 2008; Morin and Thuiller, 2009). Some research indicated that warming tends to significantly increase ecosystem species richness in terrestrial environments (Pauli et al., 2007; Vittoz et al., 2009; Rosset et al., 2010). Other studies reported that warming has already led to dramatic changes in plant functional groups (e.g., C_3 litter with high quality and C_4 litter with low quality), and suggested that this may cause appreciable changes in soil chemical properties by altering the quantity and quality of plant material entering into the soil (Day et al., 2008; Fissore et al., 2008).

Relatively few studies have explored the effect of warming-induced decrease of soil water content on soil chemical traits (Brinkman and Sombroek, 1996; Díaz et al., 1997; Wang et al., 2004). Water is the most important factor potentially affecting wetland ecosystems and plant communities. Even if precipitation

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may increase in some places, the tendency towards aridity may still occur because of increasing evaporation that accompanies the rise in temperatures due to warming. This has important impacts on regional environments and local ecosystems. It is therefore important to conduct investigations across a range of soil water gradients to ascertain the impact of warming-induced decrease of soil water content on wetland ecosystems. Understanding the effects of warming-induced changes of soil water content at the local scale is currently one of the main challenges of ecological study (Rosset et al., 2010). The Qinghai-Tibetan Plateau may be more strongly impacted than the average at the global scale since Nogues-Bravo et al. (2007) predicted that temperature increases will be particularly high in mountain regions. Alpine wetland ecosystem studies are rarer than those covering other terrestrial environments and existing work tends to describe species composition of assemblages rather than local species richness.

Warming-induced changes of soil water content is likely to affect above- and below-ground properties of alpine wetland communities by altering key habitat factors (Engel et al., 2009). Ecological science deals with the complex interactions between ecosystems and their environment, particularly interconnections that allow ecosystems to change their properties to adapt to a variable environment. These interconnections involve 'potential responses' when a change in environmental conditions affects ecosystems in ways whereby the ecosystem can then make potential contributions to environmental change. An important role of ecological research is to provide accurate information on the probability that global change will have impacts on ecosystems. Warming-induced changes of soil water content and soil chemical traits may regulate the availability of soil C, N and P to vegetation growth and ultimately influence the net primary productivity and community structure of grassland ecosystems. Hence, it is imperative for us to understand how warming-induced decrease of soil water content will affect soil chemical dynamics.

The specific objectives of this study were to: (1) evaluate the impact of decreases of soil water on the aboveground vegetation biomass, cover, height and richness of a natural alpine wetland community; (2) evaluate the impact of decreases of soil water on soil organic carbon (SOC), pH, total nitrogen, available N, total phosphorus, available P, total potassium and available K of a natural alpine wetland community in a natural alpine wetland ecosystem on the Qinghai-Tibetan Plateau.

2. Materials and methods

2.1. Study area

This study was conducted in an alpine wetland ecosystem at an elevation of on average 3500 m a.s.l. in the Maqu Wetland Protection Area, which is 98.03×10^4 ha in area. A typical zone was selected extending from N33°66′ to 33°95′, E101°67′ to 102°16′ in Gansu Province, PR China, which is located on the eastern Qinghai-Tibetan Plateau (Wu et al., 2010a,b). The mean daily air temperature is 1.2 °C, ranging from −10 °C in January to 11.7 °C in July. Mean annual precipitation is 620 mm, mainly falling during the short and cool summer. The monthly mean temperature, monthly mean precipitation, annual accumulated temperature of $\geqslant 0$ °C and the mean precipitation from 1969 to 2005 in this protected area were reported in Wu et al. (2009), who predicted that the annual accumulated temperature is increasing and that the regional climate has been getting warmer for decades in association with warming-induced changes of soil water content. The annual cloud-free solar radiation is about 2580 h. The potential natural vegetation of the majority of the study area is alpine wetland and is dominated by clonal *Kobresia tibetica* Maxim., *Kobresia humilis* (C. A. Mey. ex Trautv.) Sergiev, *Blysmus sinocompressus* Tang et Wang, *Deschampsia caespitosa* (Linn.) Beauv. and *Carex atrofusca* Schkuhr.

2.2. Experiment design and sampling

In this study, a sequence space-series variation of soil water was used to reflect potential time-series variations of soil water in an alpine wetland community by examining the effects of spatial heterogeneity of soil water on the wetland community as well as by determining the changes occurring in the above- and below-ground properties of the community. We hypothesized that decreases of soil water could have a significantly negative impact on above- and below-ground properties of alpine wetland ecosystems. To test this hypothesis, we studied the relationships between the soil water gradient and community above- and below-ground properties. Fifteen sampling sites, which had the same alpine meadow soil, a typical Cryrendoll (USDA soil classification), and a similar history of wetland vegetation, were selected for this study carried out in September, 2009. The selected sites and aboveground vegetation characteristics of the studied meadows are shown in Table 1. All the sample sites were in an open, flat, wetland area where there were practically no slopes. Livestock was entirely excluded from all of the sites during the plant growth-season from April to October to avoid grazing; however, some low-level grazing was allowed during the hay-stage during the winter under the Chinese Government's "Return Livestock Production to Grassland Ecology Project" from 2001 onwards. In this study, we selected three plots (each plot was about 5×10^3 m^2) at each selected site with three diagonal sampling quadrats (1 m^2) per plot. The nine quadrats were examined and sampled at each study site in early September, when the biomass was at its greatest. We determined the aboveground dry biomass of each quadrat by weighing after drying at 80 °C for 48 h to constant weight. Vegetation cover, mean height, productivity based on aboveground biomass, and richness of plant community were measured by the methods of Wu et al. (2009). The Richness index (*R*) was determined from the total species numbers of each community using the methods of Wu et al. (2009).

The top-soil water content was determined gravimetrically. Soil samples were also collected from two soil depths (0–10 and 10–20 cm) using a bucket auger (diameter, 5 cm; length, 10 cm) from three places chosen at random within each quadrat. The three soil samples collected from a given depth were then mixed. The nine mixed soil samples for a given depth, 18 in total, from each plot were used in the laboratory analyses. All soil samples were air-dried and then passed through a 0.14 mm sieve. Soil pH was determined using a soil–water ratio of 1:5. Soil organic carbon content in the soil samples was measured using the $K_2Cr_2O_7$ method (Nelson and Sommers, 1982). Total N, available N, total P, available P, total K and available K contents in the soil were determined using the methods of Miller and Keeney (1982). The contents of each nutrient trait were calculated as the proportions of soil organic matter, total N, available N, total P, available P, total K and available K per unit soil dry weight (Wu et al., 2009).

2.3. Data analysis

All vegetation and soil data were expressed as mean ±1 standard error in Tables 1 and 2. The soil sample data for the 0–10-cm and 10–20-cm soil layers were used to analyze the changes in soil chemical properties in the study area. A general linear model (GLM) procedure with two-way ANOVA was used to examine the between-subjects effects of the studied sites and the two soil depths on the soil properties. All data were assessed for homogeneity of variance and normality. One-way ANOVA analyses were

Table 1
Selected sites and aboveground vegetation characteristics of studied meadows. Values are means (± standard error, n = 9). AL altitude; PD productivity; dominant species show species which covers over 10% in the community.

Site	Geographic location	AL (m)	Covers (%)	PD (g m^{-2})	Height (cm)	Richness	Dominant species
1	E102°01′ 79 N33°94′ 92	3524	95.0 ± 1.0	339.9 ± 13.8	21.0 ± 1.5	12.0 ± 0.3	*Kobresia tibetica* Maxim., *Blysmus sinocompressus. Tang et Wang*, *Deschampsia caespitosa* (Linn.) *Beauv.*, *Carex atrofusca Schkuhr*
2	E102°01′ 82 N33°95′ 08	3521	92.2 ± 1.7	263.5 ± 7.5	20.3 ± 1.4	11.6 ± 0.5	*Deschampsia caespitosa* (Linn.) *Beauv.*, *Carex limosa* Linn., *Blysmus sinocompressus Tang et Wang*, *Caltha palustris* Linn
3	E101°67′ 35 N33°78′ 41	3521	85.6 ± 1.6	281.8 ± 11.5	10.4 ± 0.6	9.4 ± 0.5	*Batrachium bungei (Steud.) L. Liou*, *Halerpestes sarmentosa* (Adams) Kom, *Potentill aanserina* Linn
4	E101°67′ 36 N33°78′ 41	3507	90.4 ± 1.6	287.8 ± 6.4	13.0 ± 0.4	12.4 ± 0.4	*Kobresia tibetica* Maxim., *Kobresia macrantha Bocklr.*, *Blysmus sinocompressus Tang et Wang*, *Carex atrofusca Schkuhr*
5	E101°67′ 33 N33°78′ 43	3504	78.4 ± 1.4	298.9 ± 7.8	8.4 ± 0.5	12.4 ± 0.5	*Carex atrofusca Schkuhr*, *Kobresia macrantha Bocklr.*, *Kobresia tibetica* Maxim
6	E101°71′ 49 N33°76′ 57	3502	91.6 ± 1.5	344.5 ± 8.8	9.4 ± 0.8	16.0 ± 0.3	*Kobresia tibetica* Maxim., *Potentill aanserina* Linn., *Ranunculus tanguticus* (Maxim.) *Ovcz*, *Cremanthodium lineare* Maxim
7	E101°71′ 49 N33°76′ 60	3506	59.0 ± 2.9	249.9 ± 9.5	6.6 ± 0.5	9.6 ± 0.5	*Descuminia sophia* (L) webb. Ex Prantl, *Potentill aanserina* Linn., *Sedum ulricae* Froed
8	E101°71′ 44 N33°76′ 71	3512	78.0 ± 2.5	260.5 ± 4.6	6.8 ± 0.4	10.0 ± 0.3	*Potentill aanserina* Linn., *Kobresia macrantha Bocklr.*, *Carex atrofusca Schkuhr*, *Deschampsia caespitosa* (Linn.) Beauv
9	E101°76′ 62 N33°77′ 16	3510	62.0 ± 2.0	245.6 ± 12.3	5.7 ± 0.3	13.8 ± 0.6	*Potentill aanserina* Linn., *Halenia corniculata* (L.) Cornaz, *Gentiana leucomelaena* Maxim
10	E101°76′ 65 N33°77′ 16	3434	67.6 ± 1.1	243.5 ± 13.3	4.8 ± 0.4	16.2 ± 0.5	*Kobresia tibetica* Maxim., *Elymus nutans Griseb.*, *Kobresia humilis* (C. A. Mey. ex Trautv.) Sergiev, *Pedicularis szetschuanica* Maxim
11	E101°76′ 74 N33°77′ 34	3435	58.0 ± 2.5	144.5 ± 12.2	4.2 ± 0.4	15.4 ± 0.5	*Kobresia humilis* (C. A. Mey. ex Trautv.) Sergiev, *Polygonum viviparum* Linn., *Deschampsia caespitosa* (Linn.) *Beauv.*, *Taraxacum officinale* F. H. Wigg
12	E102°15′ 73 N33°72′ 10	3433	80.2 ± 3.8	271.3 ± 3.9	4.0 ± 0.3	16.6 ± 0.5	*Ligularia virgaurea* Maxim., *Kobresia macrantha Bocklr.*, *Elymus nutans Griseb*
13	E102°16′ 02 N33°71′ 99	3438	44.0 ± 2.9	114.6 ± 7.6	3.9 ± 0.3	16.6 ± 0.9	*Kobresia macrantha Bocklr.*, *Pedicularis kansuensis* Maxim., *Potentill aanserina* Linn.
14	E102°16′ 21 N33°71′ 69	3449	49.0 ± 1.9	126.5 ± 10.5	3.0 ± 0.3	20.0 ± 0.7	*Ligularia virgaurea* Maxim., *Leontopodium alpinum*, *Stipa aliena Keng*, *Kobresia pygmaea (C. B. Clarke) C. B. Clarke*
15	E102°08′ 06 N33°66′ 98	3433	75.2 ± 2.7	138.4 ± 14.5	6.1 ± 0.3	15.2 ± 0.9	*Anemone rivularis Buch.-Ham.*, *Scirpus pumilus Vahl*, *Herba heteropappi* Altaici

Table 2
Soil properties of selected sites in the studied meadows. Values (± standard error) are means of 9 squares (n = 135).

Site	Soil depth (cm)	Soil water	pH value	SOC	TN	AN	TP	AP	TK	AK
1	0–10	103.31 ± 7.48	5.18 ± 0.02	25.53 ± 1.24	1.99 ± 0.05	473.55 ± 57.40	0.16 ± 0.01	16.21 ± 0.06	1.02 ± 0.03	123.23 ± 11.29
	10–20	113.12 ± 6.75	5.57 ± 0.04	18.06 ± 0.17	1.43 ± 0.04	342.97 ± 30.14	0.12 ± 0.01	15.66 ± 0.44	1.33 ± 0.02	60.86 ± 1.56
2	0–10	93.96 ± 3.43	5.65 ± 0.05	19.91 ± 0.61	1.40 ± 0.11	390.51 ± 21.42	0.26 ± 0.03	23.04 ± 4.58	1.82 ± 0.04	182.02 ± 7.27
	10–20	81.45 ± 3.23	5.56 ± 0.05	17.12 ± 0.22	1.07 ± 0.11	266.91 ± 40.07	0.23 ± 0.02	12.12 ± 0.32	1.83 ± 0.05	73.06 ± 12.79
3	0–10	86.19 ± 2.75	5.61 ± 0.15	8.26 ± 0.38	0.68 ± 0.05	285.57 ± 33.81	0.14 ± 0.04	7.29 ± 1.51	2.11 ± 0.09	145.21 ± 23.28
	10–20	69.93 ± 4.29	5.65 ± 0.05	5.88 ± 0.32	0.48 ± 0.03	174.64 ± 4.13	0.10 ± 0.04	4.56 ± 0.50	2.26 ± 0.08	55.96 ± 4.58
4	0–10	83.63 ± 2.69	6.28 ± 0.10	19.87 ± 0.91	1.64 ± 0.05	471.04 ± 46.70	0.15 ± 0.02	20.82 ± 1.84	1.39 ± 0.04	142.94 ± 41.69
	10–20	80.28 ± 1.82	6.10 ± 0.23	17.97 ± 5.04	1.17 ± 0.07	351.14 ± 16.40	0.31 ± 0.19	14.32 ± 1.61	1.50 ± 0.13	52.62 ± 5.31
5	0–10	79.35 ± 2.10	5.93 ± 0.20	15.57 ± 2.32	1.05 ± 0.13	354.45 ± 37.99	0.17 ± 0.01	11.48 ± 0.59	1.65 ± 0.04	65.51 ± 17.79
	10–20	77.41 ± 3.13	5.97 ± 0.14	19.43 ± 0.32	1.16 ± 0.10	324.17 ± 25.48	0.16 ± 0.01	10.31 ± 0.85	1.61 ± 0.05	44.00 ± 8.86
6	0–10	77.93 ± 4.80	5.65 ± 0.04	17.38 ± 1.40	1.26 ± 0.05	437.68 ± 4.31	0.21 ± 0.04	19.14 ± 8.28	1.69 ± 0.07	150.27 ± 27.78
	10–20	61.58 ± 4.12	5.69 ± 0.13	9.05 ± 1.19	0.68 ± 0.12	260.45 ± 36.89	0.23 ± 0.05	10.72 ± 6.30	1.89 ± 0.05	45.28 ± 9.95
7	0–10	49.93 ± 7.87	7.90 ± 0.04	6.55 ± 0.10	0.64 ± 0.01	190.42 ± 4.17	0.09 ± 0.01	14.33 ± 2.16	2.61 ± 0.03	196.51 ± 13.97
	10–20	40.22 ± 0.88	8.04 ± 0.02	6.63 ± 0.18	0.59 ± 0.01	162.63 ± 4.84	0.08 ± 0.01	11.17 ± 0.81	2.54 ± 0.08	119.79 ± 4.77
8	0–10	46.87 ± 1.73	5.34 ± 0.05	13.53 ± 1.14	1.12 ± 0.10	418.30 ± 37.50	0.20 ± 0.01	25.46 ± 2.69	2.00 ± 0.10	210.88 ± 18.05
	10–20	34.04 ± 0.98	5.69 ± 0.04	6.34 ± 0.28	0.46 ± 0.04	175.07 ± 14.21	0.14 ± 0.01	16.72 ± 2.81	2.32 ± 0.06	106.75 ± 11.15
9	0–10	41.21 ± 3.55	6.44 ± 0.20	8.19 ± 1.48	0.74 ± 0.16	276.48 ± 56.03	0.08 ± 0.01	6.24 ± 1.59	1.97 ± 0.11	74.96 ± 26.23
	10–20	37.98 ± 1.33	6.54 ± 0.15	7.05 ± 0.85	0.61 ± 0.08	217.35 ± 41.73	0.08 ± 0.01	4.49 ± 1.23	2.01 ± 0.03	48.51 ± 13.07
10	0–10	58.43 ± 1.89	7.72 ± 0.05	5.56 ± 0.35	0.46 ± 0.03	153.11 ± 11.10	0.10 ± 0.01	11.63 ± 3.55	3.22 ± 0.06	112.56 ± 9.35
	10–20	39.03 ± 0.81	6.89 ± 0.09	14.79 ± 0.93	1.13 ± 0.10	366.64 ± 21.99	0.13 ± 0.01	17.42 ± 6.59	2.18 ± 0.11	89.46 ± 3.11
11	0–10	36.23 ± 1.96	7.35 ± 0.02	7.46 ± 0.56	0.70 ± 0.03	228.02 ± 21.13	0.11 ± 0.01	16.38 ± 3.90	2.88 ± 0.06	294.16 ± 20.08
	10–20	33.63 ± 1.53	7.88 ± 0.09	4.83 ± 0.42	0.44 ± 0.02	161.44 ± 7.42	0.09 ± 0.01	9.59 ± 3.93	2.92 ± 0.12	116.22 ± 11.91
12	0–10	30.95 ± 1.43	6.58 ± 0.13	7.40 ± 0.21	0.61 ± 0.01	207.43 ± 5.58	0.10 ± 0.01	17.35 ± 0.54	2.80 ± 0.03	607.89 ± 32.80
	10–20	24.06 ± 2.23	6.59 ± 0.01	4.73 ± 0.55	0.33 ± 0.03	115.01 ± 7.22	0.08 ± 0.01	12.37 ± 1.50	2.88 ± 0.14	372.95 ± 27.77
13	0–10	23.14 ± 0.27	7.97 ± 0.10	1.89 ± 0.36	0.15 ± 0.03	63.86 ± 12.41	0.06 ± 0.01	6.46 ± 0.36	2.70 ± 0.03	41.44 ± 5.70
	10–20	19.29 ± 0.06	8.25 ± 0.02	0.96 ± 0.15	0.07 ± 0.01	40.18 ± 6.73	0.06 ± 0.01	5.53 ± 0.16	2.64 ± 0.06	34.21 ± 8.95
14	0–10	18.80 ± 0.09	6.48 ± 0.15	5.29 ± 0.49	0.49 ± 0.03	189.85 ± 11.92	0.08 ± 0.01	5.39 ± 1.05	1.92 ± 0.10	102.61 ± 10.11
	10–20	16.53 ± 0.21	7.54 ± 0.13	3.13 ± 0.11	0.32 ± 0.01	125.42 ± 4.62	0.08 ± 0.01	4.78 ± 1.80	1.95 ± 0.04	58.01 ± 1.99
15	0–10	17.61 ± 0.33	6.21 ± 0.03	3.59 ± 0.18	0.33 ± 0.01	153.65 ± 8.34	0.07 ± 0.01	9.76 ± 0.89	2.52 ± 0.11	313.42 ± 51.74
	10–20	16.45 ± 0.22	6.11 ± 0.05	3.18 ± 0.24	0.31 ± 0.03	126.15 ± 7.01	0.06 ± 0.01	8.65 ± 0.73	2.47 ± 0.14	329.24 ± 57.22

Soil water (%), the soil water values were determined on a gravimetric basis; SOC soil organic carbon content (%); TN soil total nitrogen content (%); AN soil available nitrogen content (mg/kg); TP soil total phosphorus content (%); AP soil available phosphorus content (mg/kg); TK soil total potassium content (%); AK soil available potassium content (mg/kg).

conducted for vegetation community characteristics among different study sites to assess the effect of sites differences on aboveground properties. Significant differences for all statistical tests were evaluated at the level of $P \leqslant 0.05$. Correlations between soil water and the various soil chemical and community properties were calculated from the log-transformed data from all sample quadrats using a linear mixed-effects model. All statistical analyses were performed using the software program SPSS, ver. 13.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Aboveground vegetation changes to soil water gradient

ANOVA indicated significant differences for vegetation cover ($F = 33.64$, $P < 0.001$), height ($F = 20.27$, $P < 0.001$), aboveground biomass ($F = 20.07$, $P < 0.001$) and species richness ($F = 16.28$, $P < 0.001$) among sampling sites with different soil moisture. Vegetation cover ranged from 44.0% to 95.0%, aboveground productivity ranged from 114.6 to 344.5 g m^{-2}, vegetation height ranged from 3.0 to 20.3 cm, and species richness ranged from 9.4 to 20.0 for different sampling sites with different dominant species (Table 1). Sampling sites with higher soil water contents were dominated by typical constructive species occurring in local alpine wetland communities, such as *Kobresia tibetica* Maxim., *Blysmus sinocompressus* Tang et Wang, *Deschampsia caespitosa* (Linn.) Beauv., *Carex atrofusca Schkuhr*, *Halerpestes sarmentosa* (Adams) Kom and *Batrachium bungei* (Steud.) L. Liou. Some companion species were also dominant species, such as *Kobresia macrantha* Bocklr., *Kobresia humilis* (C. A. Mey. ex Trautv.) Sergiev, *Ranunculus tanguticus* (Maxim.) *Ovcz*, *Deschampsia caespitosa* (Linn.) *Beauv.* (Linn.) *Beauv.* and *Potentilla anserine* Linn., found at the sampling sites with moderate soil water contents; these were transitive wetland communities. Communities dominated by some drought-resistant species, such as *Stipa aliena* Keng, *Pedicularis kansuensis* Maxim., *Elymus nutans* Griseb., *Kobresia pygmaea* (C. B. Clarke) C. B. Clarke, *Stipa aliena* Keng, *Leontopodium alpinum*, *Anemone rivularis* Buch.-Ham., *Scirpus pumilus* Vahl and *Ligularia virgaurea* Maxim. occurred in the sampling sites with lower soil water contents (Table 1).

Correlation analysis showed that vegetation aboveground biomass, cover and height all significantly increased with soil water content. In contrast, species richness significantly decreased with soil water content at the two soil depths (Fig. 1).

3.2. Belowground soil chemical changes to soil water gradient

ANOVA tests of between-subjects effects showed that there were significant differences of soil water content among the different sampling sites ($F = 56.57$, $P < 0.001$) and between the soil depths ($F = 11.97$, $P < 0.01$), as well as a significant interaction effect ($F = 14.02$, $P < 0.001$). Gravimetric soil water content ranged from 17.6% to 103.3% in the upper layer (0–10 cm) and from 113.1% to 16.5% in the lower layer (10–20 cm) at the 15 sampling sites. The upper layer always had a higher soil water content than the lower layer except at site 1 (Table 2). Soil pH ($F = 20.38$, $P < 0.001$), SOC ($F = 8.45$, $P < 0.001$), total N ($F = 6.88$, $P < 0.001$), available N ($F = 4.38$, $P < 0.01$), total P ($F = 5.79$, $P < 0.01$), available P ($F = 5.64$, $P < 0.01$), total K ($F = 11.54$, $P < 0.001$) and available K ($F = 12.83$, $P < 0.001$) varied significantly among the sample sites, probably as a result of differences in other soil properties. Soil pH ranged from 5.18 to 7.97 in the upper layer and from 5.56 to 8.25 in the lower layer. Soil organic carbon ranged from 1.89% to 25.53% in the upper layer and from 0.96% to 19.43% in the lower layer; total N ranged from 0.15% to 1.99% in the upper layer and from 0.07% to1.43% in the lower layer; available N ranged from 63.86 to 473.55 mg kg^{-1} in the upper layer and from 40.18 to 366.64 mg kg^{-1} in the lower layer; total P ranged from 0.06% to 0.26% in the upper layer and from 0.06% to 0.31% in the lower layer; available P ranged from 5.39 to 25.46 mg kg^{-1} in the upper layer and from 4.49 to 17.42 mg kg^{-1} in the lower layer; total K ranged from 1.02% to 3.22% in the upper layer and from 1.33% to 2.88% in the lower layer; available K ranged from 41.44 to 313.42 mg kg^{-1} in the upper layer and from 34.21 to 329.24 mg kg^{-1} in the lower layer (Table 2). Additionally, soil depth significantly affected soil total N ($F = 5.43$, $P < 0.05$), available N ($F = 7.80$, $P < 0.05$), available P ($F = 10.18$, $P < 0.01$), and available K ($F = 20.37$, $P < 0.001$).

Correlation analysis found that SOC, total N, available N, total P and available P all significantly increased with soil water content for the two soil depths, although at different rates depending on the soil depth (Fig. 2). In contrast, soil pH, total K and available K significantly decreased with increases of soil water content for the two soil depths, although at different rates depending on the soil depth (Fig. 2).

3.3. Relationships among above- and below-ground properties

Results showed that aboveground biomass, vegetation cover and height were all significantly and positively related to SOC, total N and P, and available N and P, but were negatively related to total K. In contrast, species richness was significantly and negatively related to SOC, total N and P, and available N and P, but was positively related to total K. Furthermore, species richness showed significantly positive correlations with aboveground biomass, vegetation cover and height. Additionally, there are some other positive or negative correlations among aboveground properties or below-ground properties in these natural wetland communities (Table 3).

4. Discussion

4.1. Implications of decreased soil water content on aboveground vegetation

Soil water is crucial to agriculture and is an important part of the agricultural drought outlook in many areas of the world. Climatic warming increases soil temperature, which exacerbates soil water losses by increasing evapotranspiration (Rustad et al., 2001; Fontaine et al., 2004; Niu et al., 2008), and accelerates the global hydrological cycle in general (Milly et al., 2002; Bosilovich et al., 2005).

Many studies reported that plant species and vegetation change would result from relatively small degrees of warming in terrestrial ecosystems (Hollister and Webber, 2000; Hollister et al., 2005; Oberbauer et al., 2007). Warming-induced changes of soil water content have profound influences on community structure and composition (Yang et al., 2010). Variations in the mean annual precipitation and air temperatures show that in this area (the Maqu Wetland Protection Area) there has been an overall decrease in rainfall and an increase in temperature, resulting in increased aridity in recent decades. Local vegetation and soil water balances were confronted with a situation where soil water would gradually become less over time (Yao et al., 2007). It was suggested that a climatic warming-induced potential decrease of soil water would significantly decrease aboveground biomass, vegetation cover and height in alpine wetland ecosystems, which is consistent with many other reports (Klein et al., 2004; Keryn and Mark, 2009; Kardol et al., 2010; Yang et al., 2010).

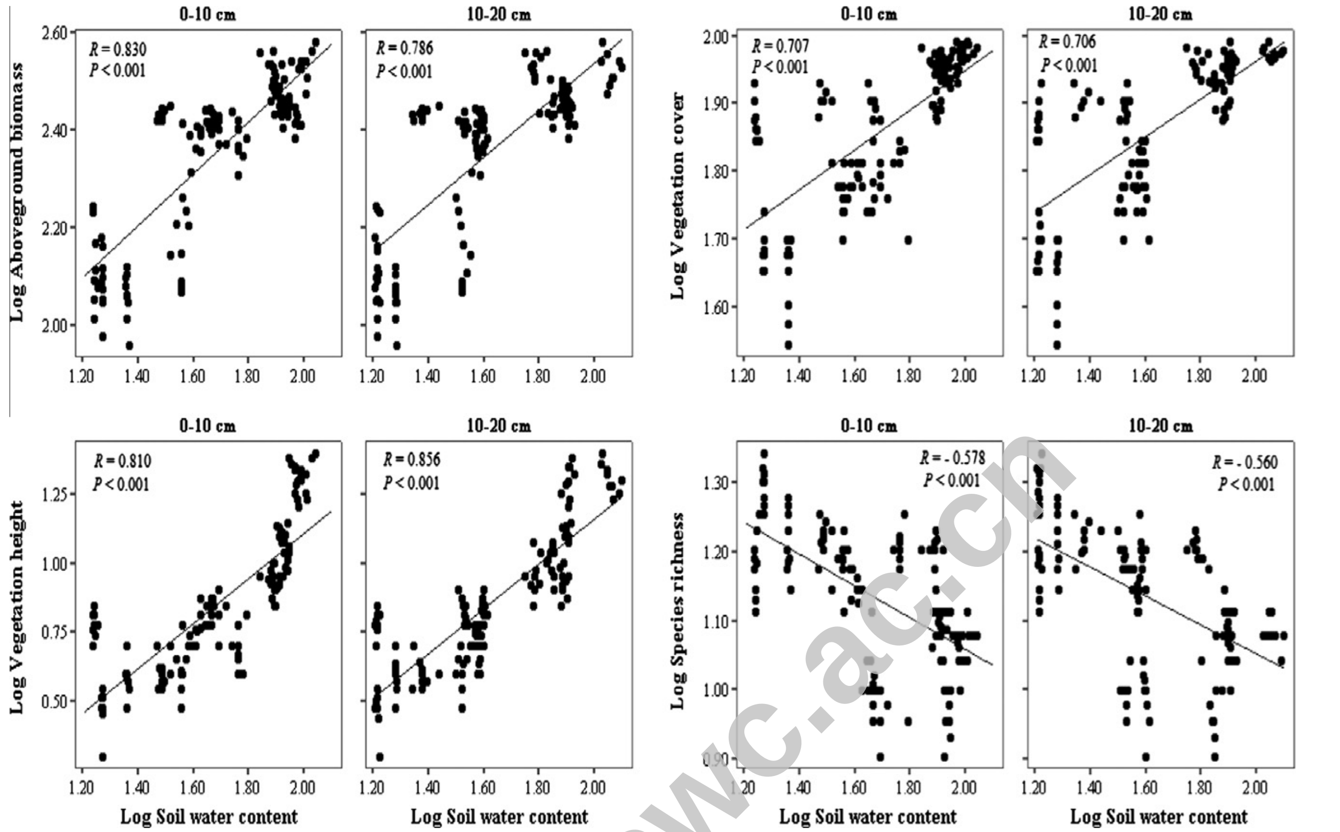

Fig. 1. Relationship of soil water at two soil depths (0–10 and 10–20 cm) to aboveground biomass, vegetation cover, vegetation height, and species richness in studied meadows.

Rapid losses of plant species under climate warming have been observed widely on the Tibetan Plateau (Klein et al., 2004), and in temperate steppes (Yang et al., 2010), salt marshes (Keryn and Mark, 2009) and Mediterranean shrubland (Prieto et al., 2009). However, our study found that species richness was significantly increased in warmer soils with lower water contents in the alpine wetland ecosystems. This could be due to the change of soil water altering the growth and relative superiority of dominating species, which are distributed in higher-moisture habitats, resulting in decreased height and cover of these species, thereby presenting an opportunity for invasion and coexistence by other species. Warming-induced changes of soil water content indirectly affects subdominant species by altering competitive interactions with the dominant species (Engel et al., 2009; Kardol et al., 2010). Additionally, elevated temperatures and decreased soil water can indirectly influence the plant community by altering species interactions (Niu and Wan, 2008; Yang et al., 2010). Changes in interspecific relationships under warming conditions (Klanderud and Totland, 2007; Niu and Wan, 2008) can also affect the plant community composition since, because of their intrinsic thermal sensitivity, plant species and functional groups can have different responses to warming, contributing to changes in competitive ability and relative dominance among species and functional groups (Walker et al., 2006; Post and Pedersen, 2008). In addition, our results suggested that dominant species within the communities were changed from typical constructive species with lower richness in local alpine communities – "wetland species" – to some drought-resistant species with higher richness, which accompanied the climatic warming-induced decrease in soil moisture. Hence, soil water plays an important role in regulating the response of plant community structure and composition to climatic warming (Walker et al., 2006; Niu and Wan, 2008; Yang et al., 2010). All these results and studies showed that the climatic warming-induced decreases of soil water also play an important role in regulating plant community composition and species richness in the alpine wetland community.

4.2. Implications of decrease of soil water on soil chemical properties

Our results showed that a climatic warming-induced potential decrease of soil water significantly decreased SOC, total N, available N, total P and available P, but increased soil pH and total K in the studied alpine wetland ecosystem. Warming-induced changes of soil water may regulate the availability of soil N and P for vegetation growth and that would then affect plant community composition and species richness. Xue et al. (2010) reported that the losses of soil C and N were significantly correlated with climatic warming-induced decreases of soil water in a tallgrass prairie. Hence, it is imperative for us to understand how warming-induced changes of soil water content will affect soil chemical dynamics.

Results showed that there is a significantly lower SOC, total N, available N, total P and available P in studied meadow soil with lower soil moisture. There are a number of reasons why this occurs: first, in our study and many others, warming leads to decreases in soil C and N because of large decreases in biomass, vegetation cover and height in the plant communities (Klein et al., 2004; Keryn and Mark, 2009; Kardol et al., 2010; Yang et al., 2010), and this is consistent with our finding that SOC, N and P were all significantly and positively related to aboveground biomass, cover and height. Second, warming-induced decrease of soil water content increases organic matter decomposition rates and affect net N mineralization across different biomes; and the warming effects on soil N mineralization are dependent on soil

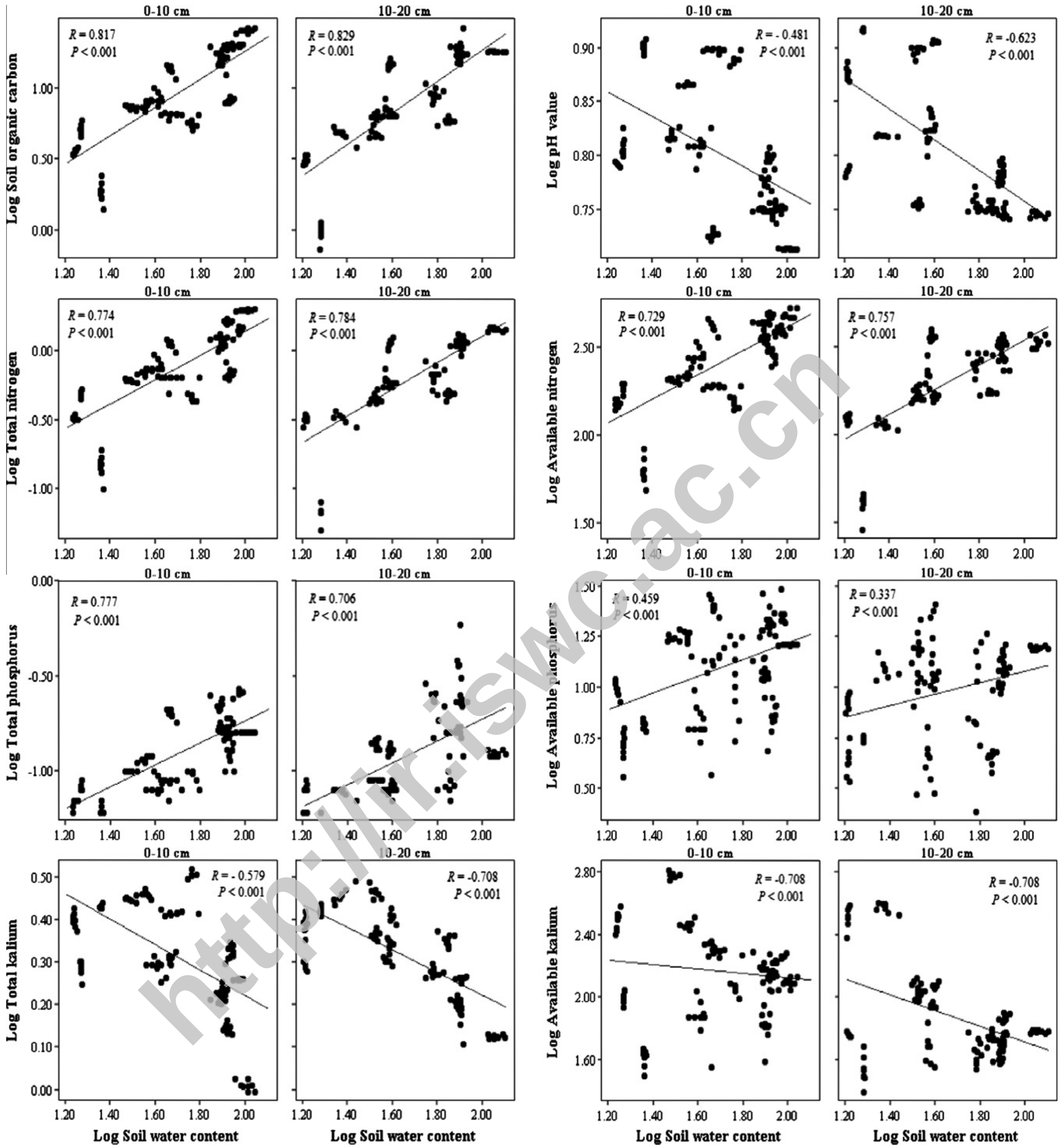

Fig. 2. Relationship of soil water to soil organic carbon, soil pH value, total nitrogen, available nitrogen, total phosphorus, available phosphorus, total potassium and available potassium at two soil depths (0–10 and 10–20 cm) in studied meadows.

water content and vegetation type (Shaw and Harte, 2001), which leads to losses of soil C and N (Rustad et al., 2001; Fontaine et al., 2004). Warming-induced changes in the soil water content is also likely to combine with other human-induced stresses to further increase the vulnerability of ecosystems to above- and below-ground properties (Hollister and Flaherty, 2010). Climatic warming increases soil temperatures and microhabitats and hence accelerate soil water evaporation and organic matter decomposition rates, leading to loss of soil C and N (e.g., Rustad et al., 2001; Fontaine et al., 2004). Additionally, human disturbances can also significantly affect above- and below-ground properties of an alpine wetland ecosystem (Wu et al., 2009, 2010a,b). Grazing could also enhance carbon loss to the atmosphere in the region by decreasing the litter biomass and increasing dung production and would increase with the stocking rate under future warmer conditions (Luo et al., 2010). Conversely, some studies have reported warming-induced changes of microhabitats (moisture, temperature, pH value and aeration) leads to increases in soil C and N because of large increases in biomass production and litter inputs in tundra ecosystems (e.g., Welker et al., 2004; Day et al., 2008). Nutrients in soil are strongly affected by soil pH due to reactions with soil particles and other nutrients, so in fact the availability of many nutrients has been determined as a function of soil pH. Fissore et al. (2008) suggested thatlower pH and cation exchange capacity

Table 3
Pearson's correlation coefficients (*R*) among soil water, soil chemical properties and vegetation properties of studied meadows (*n* = 270).

Pearson's correlation coefficients (*R*)	AN	TP	AP	TK	AK	Height	Richness	SOC	Cover	Aboveground biomass
SWC	0.772**	0.749**	0.421**	−0.656**	−0.131*	0.858**	−0.587**	0.856**	0.733**	0.769**
TN	0.974**	0.732**	0.563**	−0.692**	0.113 ns	0.667**	−0.375**	0.982**	0.684**	0.716**
AN		0.746**	0.536**	−0.682**	0.124 ns	0.617**	−0.340**	0.954**	0.680**	0.692**
TP			0.505**	−0.565**	−0.078 ns	0.640**	−0.331**	0.782**	0.665**	0.623**
AP				−0.213**	0.455**	0.399**	−0.271**	0.566**	0.482**	0.439**
TK					0.322**	−0.692**	0.221**	−0.714**	−0.519**	−0.492**
AK						−0.127 ns	0.004 ns	0.048 ns	0.201*	−0.016 ns
Height							−0.572**	0.705**	0.763**	0.642**
Richness								−0.381**	−0.421**	−0.470**
SOC									0.723**	0.757**
Cover										0.740**

SWC soil water content; SOC soil organic carbon content (%); TN soil total nitrogen content (%); AN soil available nitrogen content (mg/kg); TP soil total phosphorus content (%); AP soil available phosphorus content (mg/kg); TK soil total potassium content (%); AK soil available potassium content (mg/kg).
ns not significant.
* Correlation significant at the 0.05 level.
** Correlation significant at the 0.01 level (2-tailed).

have advantages to stabilize SOC. Altland et al. (2008) also reported that N and P concentration were higher at low pH condition within a certain range.

Warming-induced changes of microhabitats potentially stimulates nutrient mineralization and lengthens growing seasons, which consequently increases plant growth, and this can affect the biospheric metabolism because it can lead to greater releases of heat-trapping gases to the atmosphere (Jenkinson et al., 1991) and/or increases in carbon sequestration (Schimel et al., 1996). Additionally, Warming-induced changes of microhabitats can improve N and P translocation and allocation from stem to leaves (Sardans et al., 2008), which may be translated from soil subsystem by livestock grazing, because aboveground biomass and litter removal can significantly reduce C inputs to soil (Wan and Luo, 2003). However, our results show that total K increased in soils with lower moisture contents. From the above, it can be concluded that Warming-induced changes of soil water significantly affect soil chemical traits.

Additionally, we found that species richness was significantly and negatively related to SOC, total N and P, and available N and P, but was positively related to total K. Richness can also be affected by the spatial heterogeneity of soil resources (Grace et al., 2000; Fernandez-Lugo et al., 2009). Plant–soil feedbacks play an important role in determining and potentially affecting species coexistence by influencing plant community structure (Kardol et al., 2006). Plant species richness is significantly influenced by soil organic matter and N content, and there is a variety of direct and indirect processes whereby mineral soil properties could influence richness and diversity (Stohlgren et al., 1999; Bashkin et al., 2003). Soil properties can therefore impact directly and indirectly on the diversity of local species in plant communities and this is crucial for understanding the consequences of above- and belowground trophic interactions on ecosystem functioning (Ettema and Wardle, 2002).

5. Conclusions

Our study predicted the potential effects of warming-induced changes of soil water content on above- and below-ground properties by using a sequence space-series soil water gradient analysis to reflect a potential time-series variation of soil water in an alpine wetland community. First, warming-induced changes of soil water content have a significant negative impact on the above- and below-ground properties, it decrease aboveground productivity, vegetation cover and height. Second, warming-induced changes of soil water content adversely affect belowground chemical properties in the alpine wetland community. Finally, these results were expected to reveal the response of an alpine wetland community to warming-induced decreases of soil water. Long-term field experiments should be conducted to improve our understanding of ecosystem responses to climatic warming over time.

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