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Effect of Long-term Experimental Warming on the Nutritional Quality of Alpine Meadows in the Northern Tibet

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Abstract: The nutritional quality of grasslands is closely related to recruitment of young and population dynamics of livestock and wild herbivores. However, the response of nutritional quality to climate warming has not been fully understood in the alpine meadow on the Tibetan Plateau, especially in the Northern Tibet. Here, we investigated the effect of experimental warming (beginning in 2008) on nutritional quality in three alpine meadows (site A: 4313 m, B: 4513 m and C: 4693 m) in the Northern Tibet. Crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), crude ash (Ash), ether extract (EE) and water-soluble carbohydrate (WSC) were examined in 2018–2019. Experimental warming only increased the content of CP by 27.25%, ADF by 89.93% and NDF by 41.20%, but it decreased the content of Ash by 57.76% in 2019 at site B. The contents of CP and WSC both increased with soil moisture (SM). The content of CP decreased with vapor pressure deficit (VPD). The combined effect of SM and VPD was greater than air temperature (T_a) in controlling the variations of the CP content, ADF content and nutritional quality. Compared to T_a, VPD explained more of the variation in NDF and Ash content. All of these findings suggest that warming effects on nutritional quality may vary with site and year, and water availability may have a stronger effect on the nutritional quality than temperature in the alpine meadow of the Northern Tibet.

Key words: acid detergent fiber; crude ash; crude protein; ether extract; neutral detergent fiber; water-soluble carbohydrate

1 Introduction

With the intensification of various human activities, the earth's surface is continuing to undergo a series of changes (e.g. climate change and desertification) (Arft et al., 1999; Lu et al., 2011; Dumont et al., 2015). Research shows that as one of the most significant features of global change, warming strongly affects ecosystem biodiversity, structure, function, and carbon and nutrient cycles at various spatial and temporal scales (Rustad et al., 2001; Klein et al., 2004; Yu et al., 2019a). Nutritional quality of herbage is an important indicator of the status of grassland health and degradation (Birnie-Gauvin et al., 2017; Baranova et al., 2019). Changes in nutritional quality of herbage can directly affect recruitment of young, growth and population dynamics of herbivorous livestock (e.g. yak and sheep) and wild herbivores (e.g. *Equus kiang* and *Pantholops hodgsoni*), and so these changes can indirectly affect the reproduction, growth and maintenance of consumers at higher trophic levels (e.g. humans) (Birnie-Gauvin et al., 2017; Augustine et al., 2018). Low nutritional quality of herbage can lead to higher mor-

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tality, lower pregnancy rates and fewer offspring for livestock and wild herbivores, and also higher predation risks from wild animals at higher trophic levels (Proffitt et al., 2016). Therefore, understanding the response of nutritional quality of grasslands to climatic warming is very important for predicting future changes in the ecosystem services provided by those grasslands and the protection of wild herbivores.

The Tibetan Plateau, as one of the world's most sensitive regions, continues to attract extensive attention from domestic and overseas scientists (Klein et al., 2008; Zhang et al., 2015a). More than 300 publications on the response of alpine ecosystems (e.g. alpine meadows, alpine steppes and forests) to experimental warming on the Tibetan Plateau have been produced. However, only a few of them have examined the effects of experimental warming on the nutritional quality in alpine grasslands on the Tibetan Plateau (Li and Liu, 2017; Li et al., 2018; Xu et al., 2018). Moreover, these previous studies related to the response of nutritional quality in alpine grasslands to experimental warming were conducted during only one growing season, although the effect of experimental warming on nutritional quality can vary among years (Augustine et al., 2018). Therefore, the response of nutritional quality to climate warming in alpine grasslands on the Tibetan Plateau remains unclear.

As an important region of the National Ecological Safety Construction, the Northern Tibet is mainly occupied by alpine grasslands, which are crucial components of global alpine ecosystems (Piao et al., 2006; Dorji et al., 2013). The surface temperature of the Northern Tibet has increased by approximately 0.45 ℃ from 2001 to 2015 (Sun et al., 2019), and will continue warming (Diffenbaugh and Field, 2013). Several studies conducted in the Damxung County (Fu et al., 2019; Yu et al., 2019b), the Xainza County (Lu et al., 2013; Ma et al., 2017), the Baingoin County (Ganjurjav et al., 2016; Zhang et al., 2019) and the Nagqu City (Cui et al., 2017; Wu et al., 2020) have investigated the responses of localized alpine grasslands to climate warming under controlled warming conditions in the Northern Tibet. However, to our best knowledge, no studies have examined the response of nutritional quality to warming in the alpine grasslands of the Northern Tibet. Therefore, here we report the effect of experimental warming on nutritional quality in the alpine meadow in the Northern Tibet to better understand how climate warming will affect it in the future.

2 Materials and methods

2.1 Study area and experimental design

Three sites (site A: 30°30′N, 91°04′E, 4313 m; site B: 30°31′N, 91°04′E, 4513 m; site C: 30°32′ N, 91°03′E, 4693 m), are located in the Damxung County, were set up in July 2008 (Fu and Shen, 2017). Comparing precipitation and temperature data for 1963–2019, 2018 was a warm and wet year, and 2019 was a warm and dry year (Table 1). The HOBO stations were used to monitor soil temperature (T_s), soil moisture (SM), air temperature (T_a) and relative humidity (RH). Vapor pressure deficit (VPD): $VPD=0.6108\exp\left(\frac{17.27\times T_a}{T_a+237.3}\right)\times(1-RH)$ was derived from T_a and RH (Fu and Shen, 2017). The environmental temperature decreases, while the environmental moisture increases, from site A to site C (Fu and Shen, 2017). The four treatments included control, warming, clipping and warming + clipping at each meadow site. Each treatment had three replicates. The warming and warming + clipping treatments were warmed by open top chambers (OTCs). Only the clipping and warming + clipping treatments were used in this study. The clipping and warming + clipping treatments had the vegetation clipped at a height of 0.01 m above the ground three times (in June, July and September) in each growing season beginning in 2009. The clipped aboveground biomass was weighed after being oven-dried (65 ℃ for 48 h). The clipped aboveground biomass of the three sampling times were mixed into a single sample for each plot in 2018 and 2019. Then these mixed samples were then used for analysis of several nutritional components at the whole community level, including crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), crude ash (Ash), ether extract (EE) and water-soluble carbohydrate (WSC).

Table 1 Annual mean temperature (AT) and precipitation (AP), and growing season (June–September) temperature (GST) and precipitation (GSP) in 1963–2019, 2018 and 2019 in the Damxung County, Lhasa City, Tibet, China

Year	AT (℃)	AP (mm)	GST (℃)	GSP (mm)
1963–2019	1.96±0.80	476.36±96.69	10.02±0.62	400.45±86.83
2018	2.67	667.00	10.82	589.10
2019	3.08	426.20	11.14	372.40

2.2 Nutritional content analyses

The Kjeldahl method was used to obtain total nitrogen, which was multiplied by 6.25 to determine CP (Lithourgidis et al., 2006). The Van Soest method was used to determine ADF and NDF (Van Soest et al., 1991). The complete combustion method, Soxhlet extraction method and anthrone-based method were used to determine Ash, EE (Cui et al., 2016) and WSC (Yemm and Willis, 1954), respectively.

2.3 Statistical analyses

A repeated analysis of variance (ANOVA) was used to determine the main and interactive effects of experimental warming and measurement year on T_s, SM, T_a, VPD, CP, ADF, NDF, Ash, EE and WSC for each site. A *t*-test was used to examine the differences in T_s, SM, T_a, VPD, CP, ADF, NDF, Ash, EE and WSC between non-warming and warming treatments. The permutational multivariate analysis of variance and nonmetric multi-dimensional scaling

(NMDS) were used to investigate the nutritional quality, which was determined by the matrix of CP, ADF, NDF, Ash, EE and WSC. Correlation analyses were used to examine the correlations between nutritional content parameters (i.e. CP, ADF, NDF, Ash, EE and WSC) and environmental variables (i.e. T_s, SM, T_a and VPD). When the correlations were statistically significant, univariate regression analyses were then used to examine the relationships between those correlated nutritional content and environmental variables. That is, only the significant relationships between the nutritional content and environmental variables were illustrated. Variation partitioning analyses (vegan) were used to examine the shared and exclusive effects of T_s, SM, T_a and VPD on the content of CP, ADF, NDF, Ash, EE and WSC, and the overall nutritional quality. Repeated ANOVA, *t*-test and univariate regression analyses were performed by SPSS 16.0. The permutational multivariate analysis of variance, NMDS(labdsv package)(https://cran.r-project.org/web/packages/labdsv/index.html) and variation partitioning analyses were performed using R 3.6.1.

3 Results

3.1 Environmental variables

The main and interactive effects of experimental warming and measurement year on T_s, SM, T_a and VPD are shown in Table 2. The main effect of experimental warming was the significant alteration of T_s at sites A, B and C, VPD at sites B and C, and T_a at site C. The main effect of year was the significant alteration of T_s at site A, VPD at sites B and C, and SM at site C. There was a significant interactive effect of experimental warming and year on VPD at site C. The effects of experimental warming on T_s, SM, T_a and VPD are illustrated in Fig. 1. Experimental warming significantly increased T_s by 1.26 ℃ in 2018 and by 1.31 ℃ in 2019 at site A, by 1.34 ℃ in 2019 at site B and by 1.50 ℃ in 2019 at site C. Experimental warming significantly increased T_a by 1.42 ℃ at site B and by 1.22 ℃ at site C in 2018; and it increased VPD by 0.16 kPa in 2019 at site B, and by 0.05 kPa in 2018 and 0.14 kPa in 2019 at site C.

Table 2 Repeated analysis of variance for the main and interactive effects of experimental warming (W) and measurement year on soil temperature (T_s), soil moisture (SM), air temperature (T_a) and vapor pressure deficit (VPD)

Site	Model	T_s		SM		T_a		VPD	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
A	W	**25.01**	**0.007**	1.22	0.331	0.95	0.385	0.14	0.731
	Y	**12.11**	**0.025**	1.60	0.275	0.09	0.774	5.29	0.083
	W×Y	0.02	0.891	0.11	0.753	0.02	0.897	0.79	0.425
B	W	**215.52**	**<0.001**	3.41	0.139	4.33	0.106	**17.07**	**0.014**
	Y	5.00	0.089	6.62	0.062	0.42	0.554	**81.01**	**0.001**
	W×Y	1.93	0.237	0.00	0.952	0.02	0.883	2.90	0.164
C	W	**43.26**	**0.003**	1.78	0.253	**10.09**	**0.034**	**149.08**	**<0.001**
	Y	0.19	0.683	**14.93**	**0.018**	0.15	0.718	**379.35**	**<0.001**
	W×Y	5.49	0.079	1.21	0.334	1.10	0.355	**25.49**	**0.007**

Note: *F*: *f* values; *P*: significance probability.

3.2 Nutritional content and nutritional quality

The main and interactive effects of experimental warming and measurement year on the content of CP, ADF, NDF, Ash, EE and WSC are shown in Table 3. The main effect of experimental warming only significantly changed the content of CP, NDF and Ash at site B. The main effect of measuring year showed significant alterations in the content of CP and NDF at all the three sites, WSC at site B, and ADF at site C. The interactive effect of experimental warming and measurement year only had a significant influence on the content of WSC at site B.

The effects of experimental warming on the content of CP, ADF, NDF, Ash, EE and WSC are illustrated in Fig. 2. Experimental warming increased the content of CP by 27.25%, ADF by 89.93% and NDF by 41.20%, but significantly reduced the content of Ash by 57.76% in 2019 at site B. Regardless of experimental warming, at sites A, B and C the contents of CP and NDF in 2019 were lower than those in 2018 by 37.62%, 25.25% and 24.01%, and by 34.62%, 23.98% and 25.48%, respectively. The content of ADF in 2019 was 50.20% lower than that in 2018 at site C. The content of WSC in 2019 was 32.75% greater than that in 2018 at site B.

Experimental warming and measurement year had significant effects on the nutritional quality (Table 4). The stress of the NMDS was 0.10, indicating that the NMDS was acceptable (Fig. 3). The nutritional quality levels between the non-warming and warming treatments in 2019 at site B were separated by the first axis of the NMDS (i.e. NMDS1) (P=0.010). The nutritional quality levels between 2018 and 2019 under warming conditions at site A were separated by the NMDS1 axis (P=0.004). The nutritional quality levels between 2018 and 2019 under non-warming

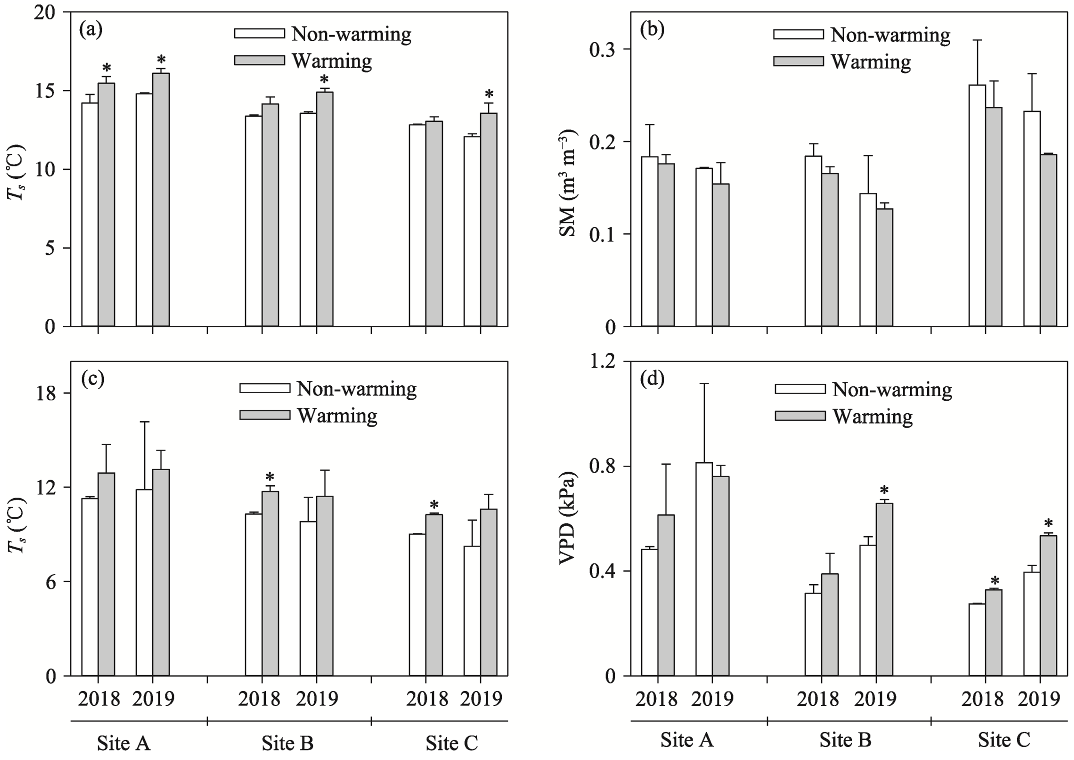

Fig. 1 Comparisons of (a) soil temperature (T_s), (b) soil moisture (SM), (c) air temperature (T_a) and (d) vapor pressure deficit (VPD) between non-warming and warming treatments at sites A, B and C in 2018 and 2019

Note: * indicates $P<0.05$.

Table 3 Repeated analysis of variance for the main and interactive effects of experimental warming (W) and measurement year on the content of crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), crude ash (Ash), ether extract (EE) and water-soluble carbohydrate (WSC)

Site	Model	CP		ADF		NDF		Ash		EE		WSC	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
A	W	2.40	0.197	6.71	0.061	0.15	0.716	0.25	0.645	0.01	0.919	0.11	0.761
	Y	**32.37**	**0.005**	5.86	0.073	**8.59**	**0.043**	3.86	0.121	2.75	0.172	1.36	0.308
	W×Y	0.85	0.410	2.29	0.205	0.05	0.841	0.03	0.870	2.12	0.220	0.21	0.670
B	W	**79.22**	**0.001**	4.99	0.089	**23.00**	**0.009**	**24.52**	**0.008**	5.73	0.075	0.85	0.409
	Y	**24.56**	**0.008**	1.61	0.273	**15.18**	**0.018**	0.65	0.467	0.44	0.545	**10.49**	**0.032**
	W×Y	0.00	0.975	0.08	0.793	2.38	0.198	2.78	0.171	1.07	0.360	**9.33**	**0.038**
C	W	0.21	0.668	3.98	0.117	0.77	0.429	1.14	0.346	0.06	0.813	0.79	0.423
	Y	**77.38**	**0.001**	**17.92**	**0.013**	**41.27**	**0.003**	1.00	0.373	0.53	0.506	1.38	0.306
	W×Y	4.21	0.109	0.01	0.926	1.33	0.313	2.96	0.161	0.64	0.470	0.18	0.690

Note: *F*: *f* values; *P*: significance probability.

(P=0.031) and warming conditions (P=0.027) were separated by the second axis of the NMDS (i.e. NMDS2) at site B.

3.3 Relationships between nutritional content and environmental variables

The contents of both CP and WSC increased with SM (Fig. 4). The content of CP decreased with VPD (Fig. 4). The SM, T_a and VPD independently explained 10%, 18% and 29% of the variation of the CP content, respectively (Fig. 5a). The SM and VPD co-explained 23% of the variation of the CP content, whereas the SM, T_a and VPD co-explained 10% of

Table 4 The permutational multivariate analysis of variance of experimental warming (W), measurement year (Y) and measurement site (S) on nutritional quality

Model	*F*	*P*
W	4.59	0.028
Y	21.71	0.001
S	1.52	0.231
W×Y	1.75	0.173
W×S	0.76	0.542
Y×S	1.51	0.214
W×Y×S	1.29	0.287

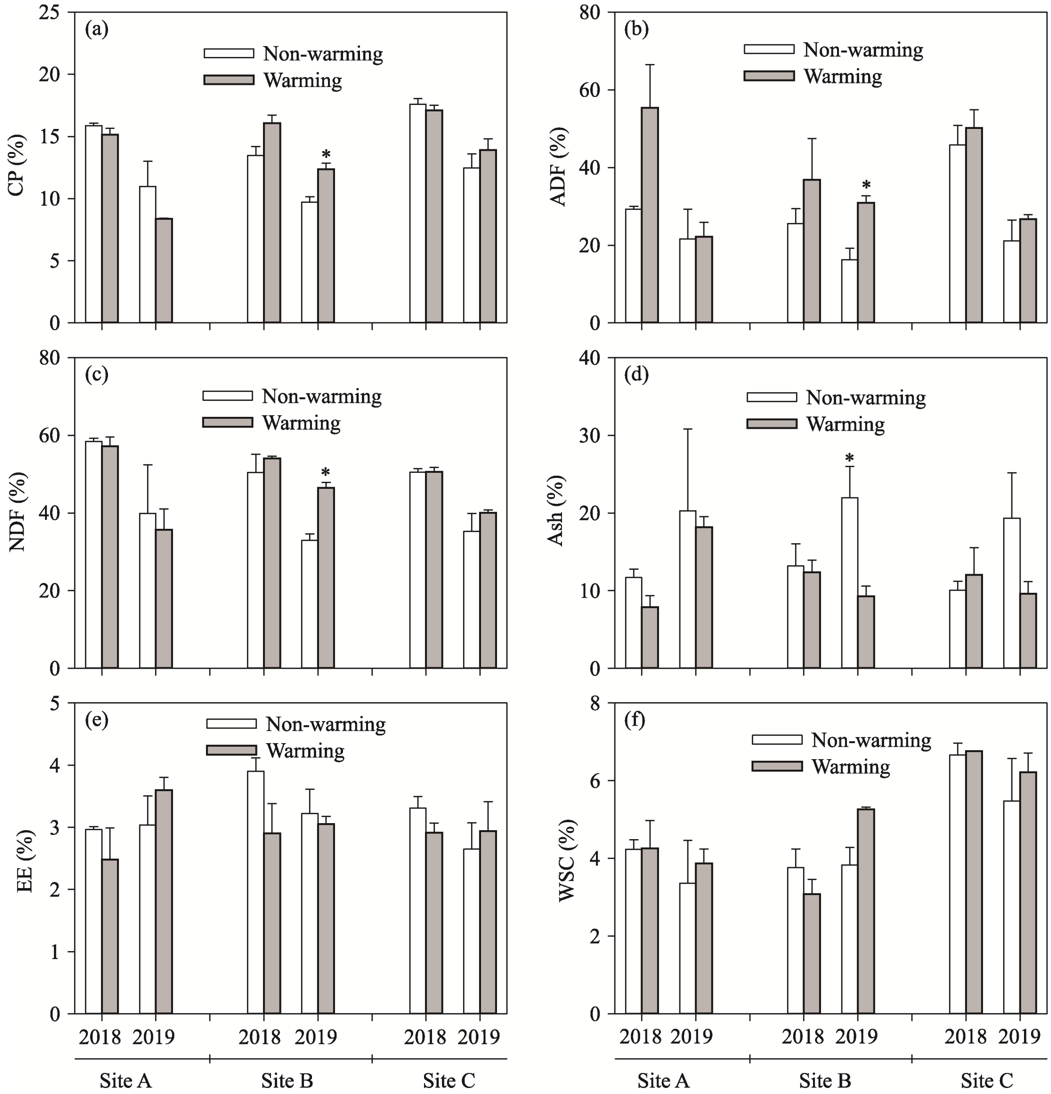

Fig. 2 Comparisons of (a) crude protein (CP), (b) acid detergent fiber (ADF), (c) neutral detergent fiber (NDF), (d) crude ash (Ash), (e) ether extract (EE) and (f) water-soluble carbohydrate (WSC) between non-warming and warming treatments at sites A, B and C in 2018 and 2019

Note: * indicates $P<0.05$.

the variation of the CP content (Fig. 5a). The SM, T_a and VPD independently explained 21%, 47% and 11% of the variation of the ADF content, respectively, whereas the SM and VPD co-explained 22% of the variation of the ADF content (Fig. 5b). The T_a and VPD independently explained 49% and 56% of the variation of the NDF content, respectively (Fig. 5c), and 22% and 26% of the variation of the Ash content, respectively (Fig. 5d). The SM, T_a and VPD independently explained 11%, 47% and 21% of the variation of the nutritional quality, respectively, whereas the SM and VPD co-explained 19% variation of the nutritional quality (Fig. 5e).

4 Discussion

The content of CP (8.37%–17.59%) in this study was greater than the CP requirement for livestock maintenance (7%–9.5%) (Soussana and Luscher, 2007; Roukos et al., 2011; Koidou et al., 2019). The content of NDF (32.93% –58.42%) in this study was lower than the upper limit of dietary intake (60%– 65%) for most animals (Roukos et al., 2011; Samuil et al., 2018). Therefore, the CP and NDF contents may not only meet maintain requirements of livestock, but also indicate a relatively high nutritive value of the vegetation. The content of CP, ADF (16.26%–55.39%), NDF, EE (2.48%–4.38%), Ash (7.89%–21.95%) and WSC (3.08%–6.76%) in this study were equivalent to the results (CP: 2.71%–19.21%; ADF: 9.06%–48.30%; NDF: 12.16%–76.23%; EE: 0.64%–10.90%; Ash: 3.49%–12.47%; WSC: 1.24%–17.27%) observed in alpine meadows on the Tibetan Plateau by previous studies (Xu et al., 2002; Shi et al., 2013; Sun et al., 2015; Zhang et al., 2015b; Fan et al., 2017; Li and Liu, 2017; Zhang et al., 2017; Li et al., 2018).

Increased water availability may have increased the content of CP in this study, which was in line with the results

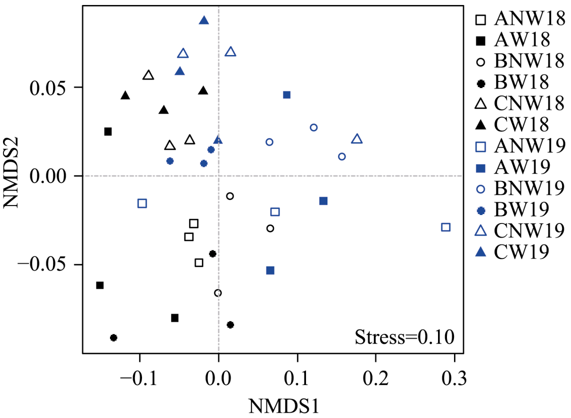

Fig. 3 Nonmetric multidimensional scaling (NMDS) analysis of the nutritional quality

Note: Legend abbreviations: ANW18: site A of non-warming treatment in 2018; AW18: site A of warming treatment in 2018; BNW18: site B of non-warming treatment in 2018; BW18: site B of warming treatment in 2018; CNW18: site C of non-warming treatment in 2018; CW18: site C of warming treatment in 2018; ANW19: site A of non-warming treatment in 2019; AW19: site A of warming treatment in 2019; BNW19: site B of non-warming treatment in 2019; BW19: site B of warming treatment in 2019; CNW19: site C of non-warming treatment in 2019; CW19: site C of warming treatment in 2019.

observed in the steppes of Inner Mongolia Autonomous Region, China (Schönbach et al., 2012; Ren et al., 2016a), a C4 tropical grass in Brazil (Habermann et al., 2019), mountain side grasslands in North-West Greece (Roukos et al., 2011) and alpine meadows on the Tibetan Plateau (Yao et al., 2019). This finding may be related to several mechanisms. First, increased water availability may accelerate soil nitrogen mineralization and in turn increase the availability of nitrogen to plants (Austin et al., 2004; Miao et al., 2015). Second, increased water availability may increase the capacity of plants to assimilate nitrogen by affecting the activities of nitrogen anabolism, net photosynthetic rate and/or stomatal conductance (Xu and Zhou, 2006; Habermann et al., 2019). Third, increased water availability may promote new tissues generation and delay the maturation of the plants (Schönbach et al., 2012; Ren et al., 2016a). Fourth, higher precipitation may be accompanied by dimming of the solar radiation, which may result in a greater CP content (Lenart et al., 2002).

Our findings implied that water availability may have stronger effects than temperature on the nutritional quality of alpine grasslands. This finding was in line with the results of several previous studies (Schönbach et al., 2012; Ren et al., 2016b; Scocco et al., 2016), and may be attributed to one or more of the following mechanisms. First, forage nutritional quality can be negatively correlated with aboveground plant production (White, 1986; Shi et al., 2013). Water availability can play a more important role in the variation of forage production than air temperature in the same alpine meadows used in this study (Fu et al., 2018). Second, water availability may have a stronger relationship with soil available nitrogen than temperature in the same alpine meadows used in this study (Yu et al., 2014).

Our findings suggested that warming may not always change the nutritional quality of alpine meadows on the Tibetan Plateau. This finding strengthened the results obtained in alpine meadows on the Tibetan Plateau by several previous studies. For example, experimental warming altered the content of CP (Li and Liu, 2017), EE, Ash, ADF and NDF (Li and Liu, 2017; Xu et al., 2018) in alpine meadows of the Haibei station. The effects of experimental warming on the content of CP, EE and ADF varied with soil water availability in alpine meadows of the Beiluhe experimental station (Li et al., 2018). These findings may be attributed to one or more of the following mechanisms. First, although the increased soil temperature in this study was lower than those in at least two of the three previous studies (Li et al., 2018; Xu et al., 2018), increased soil temperature may not be correlated with the effect of experimental warming on the content of CP in leaves (Lu et al., 2011). Second, the effect of experimental warming on the content of CP in leaves can decrease with an increasing duration of experimental warming (Bai et al., 2013). The warming duration was less than nine years for at least two of the three previous studies (Li et al., 2018; Xu et al., 2018), whereas the duration was greater than ten years in this study. Third, experimental warming may accelerate soil nitrogen and phosphorus mineralization and the plant's capacity to assimilate nitrogen

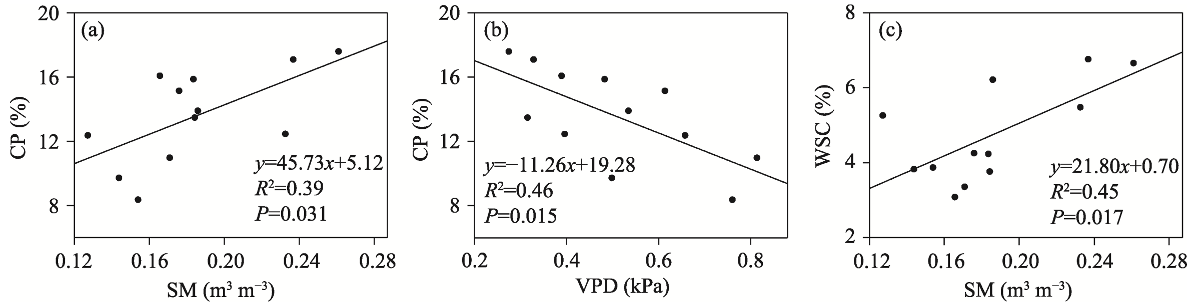

Fig. 4 Univariate regression analysis between the contents of (a) crude protein (CP) and soil moisture (SM), (b) CP and vapor pressure deficit (VPD), and (c) water-soluble carbohydrate (WSC) and SM

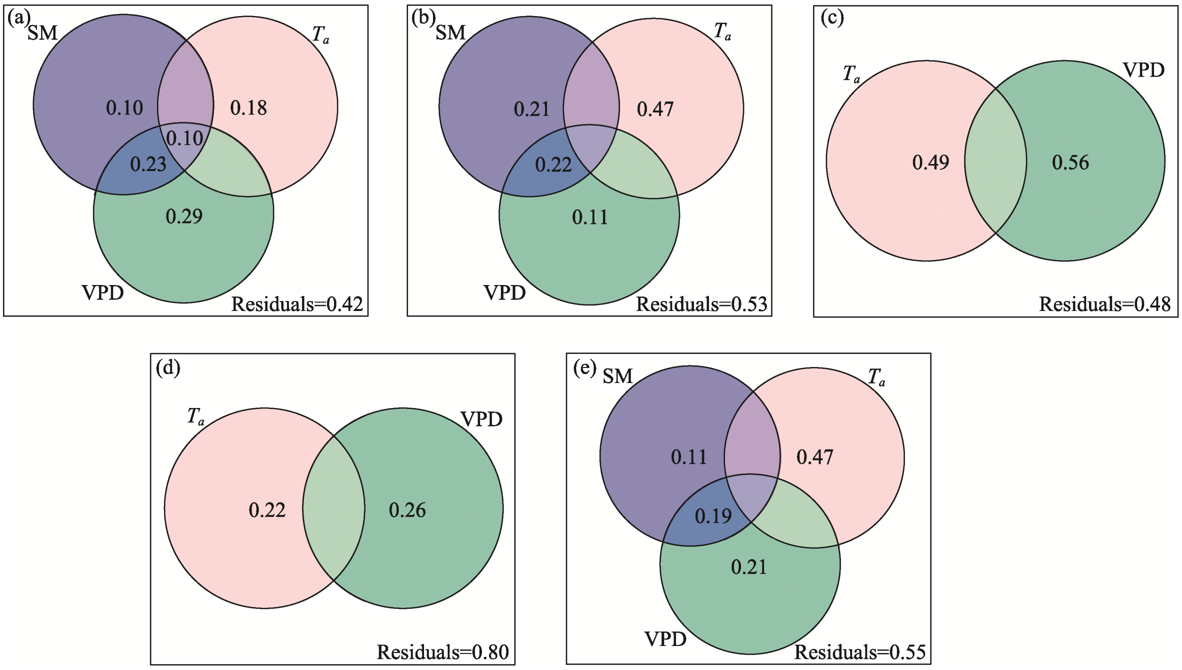

Fig. 5 Variation partitioning analysis (VPA), showing the shared and exclusive effects of soil moisture (SM), air temperature (T_a) and vapor pressure deficit (VPD) on (a) crude protein (CP), (b) acid detergent fiber (ADF), (c) neutral detergent fiber (NDF), (d) crude ash (Ash), and (e) the nutritional quality

Note: The fractions of unexplained variation are not illustrated.

and phosphorus, but the drying effect that is induced by experimental warming may suppress soil nitrogen and phosphorus mineralization and the plant's capacity to assimilate nitrogen and phosphorus (Gauly et al., 2013; Dumont et al., 2015). However, the probability of this occurring may be low considering the non-significant change in SM in the current study. Fourth, warming may have contrasting effects on plant production and nutritional quality (Li et al., 2018). For example, warming could decrease plant production only when it was a dry growing season at site A, but not at B or C (Fu and Shen, 2016). Warming had significant effects on herbaceous biomass only when the mean annual temperature was no more than –2 ℃ (Lin et al., 2010). The temperature decreased from site A to C (Fu and Shen, 2016), and the mean annual temperature in this study was greater than those in the three previous studies (Li and Liu, 2017; Li et al., 2018; Xu et al., 2018). Fifth, the nutrient content may change under experimental warming conditions when precipitation is near a certain threshold but not above/below a certain threshold (Augustine et al., 2018). Precipitation increased from site A to C (Fu and Shen, 2016). The mean annual precipitation in this study was lower than those in two of the three previous studies (Li and Liu, 2017; Xu et al., 2018), but greater than that for the third previous study (Li et al., 2018).

5 Conclusions

In summary, experimental warming only significantly altered the content of CP, ADF, NDF, Ash and the nutritional quality in one (i.e. Site B with an elevation of 4513 m) of the three alpine meadow sites during a dry year. Water availability had stronger effects than temperature on the content of CP, ADF, NDF, Ash, WSC and the nutritional quality, and it had positive effects on the content of CP and WSC. Therefore, understanding the effect of climate warming on nutritional quality may need to consider water availability, which may vary with site and year, in the alpine meadow on the Tibetan Plateau.

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长期实验增温对藏北高寒草甸群落营养品质的影响

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摘　要：草地营养品质与家畜和野生草食动物的幼畜补充和种群动态密切相关。然而，在青藏高原特别是藏北高原，高寒草甸营养品质对气候变暖的响应还没有得到充分的认识。本研究调查了藏北三个高寒草甸样地(A: 4313 m、B: 4513 m和C: 4693 m，实验从 2008 年开始)的长期实验增温对群落营养品质的影响。基于 2018–2019 年的粗蛋白(CP)、中性洗涤纤维(NDF)、酸性洗涤纤维(ADF)、粗灰分(Ash)、粗脂肪(EE)和水溶性碳水化合物(WSC)含量，发现实验增温仅使样地B 2019 年的CP含量增加了 27.25%，ADF 增加了 89.93%，NDF 增加了 41.20%，Ash 含量减少了 57.76%。CP 和 WSC 的含量均随土壤含水量(SM)的增加而增加，CP含量随饱和水汽压差(VPD)的增加而降低。SM 和 VPD 对 CP 含量、ADF 含量和营养品质变异的总的解释度大于气温。与气温相比，VPD 更能解释 NDF 和 Ash 的变化。因此，气候变暖对藏北高原高寒草甸群落营养品质的影响随着地点和年份的不同而不同；与温度相比，水的有效性对藏北高原高寒草甸群落营养品质的影响更大。

关键词：酸性洗涤纤维；粗灰分；粗蛋白；粗脂肪；中性洗涤纤维；水溶性碳水化合物