Contents lists available at ScienceDirect



Agricultural and Forest Meteorology

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Increased precipitation has stronger effects on plant production of an alpine meadow than does experimental warming in the Northern Tibetan Plateau



Gang Fu*, Zhen-Xi Shen, Xian-Zhou Zhang

Lhasa Plateau Ecosystem Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

ARTICLE INFO

Keywords: Normalized difference vegetation index Soil-adjusted vegetation index Gross primary production Aboveground biomass Climatic change Alpine grassland

ABSTRACT

The Tibetan Plateau is overall getting warmer and wetter, whereas the relative responses of plant growth to warming and increased precipitation are not fully understood. Therefore, a field warming (control, low- and high-level) and increased precipitation (control, low- and high-level) experiment was conducted to compare the relative effects of warming and increased precipitation on the normalized difference vegetation index (NDVI), soil-adjusted vegetation index (SAVI), aboveground biomass (AGB) and gross primary production (GPP) in an alpine meadow in the Northern Tibetan Plateau since June 2014. The low- and high-level experimental warming significantly decreased soil moisture (SM) by $0.02 \text{ m}^3 \text{ m}^{-3}$ and $0.04 \text{ m}^3 \text{ m}^{-3}$, but significantly increased air temperature (T_a) by 1.91 °C and 3.51 °C, respectively, across the three growing seasons in 2014–2016. The low- and high-level warming did not significantly affect NDVI, SAVI, AGB and GPP across the three growing seasons in 2014–2016. The low- and high-level increased precipitation did not significantly affect T_a , but significantly increased SM by $0.02 \text{ m}^3 \text{ m}^{-3}$, respectively, across the three growing seasons in 2014–2016. The high-level increased precipitation did not significantly affect T_a , but significantly increased SM by $0.02 \text{ m}^3 \text{ m}^{-3}$, respectively, across the three growing seasons in 2014–2016. The high-level increased precipitation only tended to increase NDVI by 9.8%, SAVI by 8.2%, AGB by 1.2% and GPP by 25.0%, whereas the low-level increased precipitation only tended to increase NDVI by 9.8%, SAVI by 8.2%, AGB by 6.2% and GPP by 12.9%. Therefore, increased precipitation had stronger effects on NDVI, SAVI, AGB and GPP than did experimental warming in this alpine meadow site of the Northern Tibetan Plateau.

1. Introduction

Global surface temperature will increase by 1.0-3.7 °C at the end of 21 century (IPCC, 2013) and global annual precipitation increases by 2% since 2000 (Hulme et al., 1998). The Tibetan Plateau is overall getting warmer and wetter (Diffenbaugh and Field, 2013; Lu and Liu, 2010). The warming magnitude on the Tibetan Plateau is much greater than the global average and increases with increasing elevation (Kuang and Jiao, 2016; Yao et al., 2000). Precipitation has increased by 0.67 mm a^{-1} during 1961–2010 on the Tibetan Plateau (Li et al., 2016) and will continue to increase in the 21 century (Ji and Kang, 2013). Many warming and/or increased precipitation experiments have been conducted to quantify responses of alpine ecosystems to the warming and wetting trends on this Plateau (Ganjurjav et al., 2016; Klein et al., 2007; Li et al., 2011; Liu et al., 2011; Shi et al., 2012; Wang et al., 2012; Xu et al., 2010; Xue et al., 2015). However, warming and increased precipitation experiments are fewer than warming experiments or increased precipitation experiments (Dorji et al., 2013; Heng et al., 2011). The responses of alpine ecosystems to warming or increased

precipitation can most likely overestimate or underestimate those to warming and increased precipitation. For example, the main effect of experimental warming and interactive effect of experimental warming and increased precipitation on temperature sensitivity of soil respiration was not significant, whereas increased precipitation increased significantly temperature sensitivity of soil respiration in an alpine meadow of the Northern Tibetan Plateau (Shen et al., 2015). Therefore, more in situ warming and increased precipitation experiments are needed to better understand the effects of climatic changes on alpine ecosystems on the Tibetan Plateau (Shen et al., 2014).

There are various alpine ecosystems, including forests, shrublands, alpine meadows and alpine steppes, on the Tibetan Plateau. These alpine ecosystems are representative terrestrial ecosystems in alpine regions at both Asian and global scales. The alpine meadow on the Tibetan Plateau is one of the most typical vegetation types and one of the most sensitive grassland types to climatic change (Zhao et al., 2012). There are only a few warming and increased precipitation studies in alpine meadows on the Tibetan Plateau, and these studies mainly focus on the responses of soil carbon, nitrogen, respiration and

* Corresponding author.

E-mail addresses: fugang@igsnrr.ac.cn, fugang09@126.com (G. Fu).

https://doi.org/10.1016/j.agrformet.2017.11.017

Received 30 May 2017; Received in revised form 14 September 2017; Accepted 15 November 2017 0168-1923/ © 2017 Elsevier B.V. All rights reserved.

plant phenology (Dorji et al., 2013; Heng et al., 2011; Shen et al., 2015). Normalized difference vegetation index (NDVI), soil-adjusted vegetation index (SAVI), aboveground biomass (AGB) and gross primary production (GPP) are four vital indicators of plant production. They are important components of global carbon cycling. However, to our knowledge, no studies have reported their responses to warming and increased precipitation in alpine meadows under controlled warming and increased precipitation conditions on the Tibetan Plateau. On the other hand, several previous studies have analyzed the relationships between satellite-based vegetation indices and climatic variables (e.g. air temperature and precipitation) (Chu et al., 2007; Sun et al., 2013) or the effects of climatic change on ground-based AGB along an environmental (e.g. precipitation or elevation) gradient (Wang et al., 2013; Wu et al., 2014). However, satellite-based vegetation indices are simultaneously affected by climatic change and human activities (e.g. grazing). Grazing can alter warming effects on plant production in alpine grasslands on the Tibetan Plateau (Klein et al., 2007; Wang et al., 2012). Along an environmental gradient, not only climatic variables but also vegetation types and soil characteristics (e.g. soil nitrogen availability) most likely change. Changes in vegetation types and soil characteristics can disturb the effects of climatic variables on plant production (Ganjurjav et al., 2016; Wang et al., 2013). In situ warming and increased precipitation experiments can minimize these disturbed factors mentioned above (Rustad et al., 2001). Third, several previous studies have indicated that precipitation rather than air temperature predominate variations of satellite-based vegetation indices on the Tibetan Plateau (Chu et al., 2007; Sun et al., 2013), no studies have focused on the relative responses of plant production to warming and increased precipitation under controlled warming and increased precipitation conditions. Distinguishing the relative strengths of warming and increased precipitation on plant production plays an vital effect on grassland use management and livestock husbandry sustainable development under future climatic change. Therefore, it remains unclear how climatic warming and increased precipitation will influence plant production in alpine meadows on the Tibetan Plateau. More in situ warming and increased precipitation experiments under controlled warming and increased precipitation conditions are needed to investigate their relative effects of warming and increased precipitation on plant production in alpine meadows on the Tibetan Plateau.

In this study, an in-situ warming and increased precipitation experiment was conducted in an alpine meadow of the Northern Tibetan Plateau. The main objectives of this study were to (1) examine the effects of experimental warming and increased precipitation on NDVI, SAVI, AGB and GPP; and (2) investigate whether increased precipitation had stronger effects on NDVI, SAVI, AGB and GPP than did experimental warming.

2. Materials and methods

2.1. Study area and experimental design

The study area (30°30′N, 91°04′E) was located at the Damxung Grassland Observation Station, Tibet Autonomous Region of China. Detailed description on climatic, soil and vegetation characteristics are given in our previous studies (Shen et al., 2015).

The field experiment was based on a complete factorial design with three replicates of nine treatments: control (C), low-level experimental warming (LW), high-level experimental warming (HW), low-level increased precipitation (LP), low-level experimental warming plus low-level increased precipitation (LW + LP), high-level experimental warming plus low-level increased precipitation (HW + LP), high-level increased precipitation (HW + LP), high-level increased precipitation (LW + HP), and high-level experimental warming plus high-level increased precipitation (HW + HP). There were a total of 27 experimental plots. Two heights (40 cm and 80 cm) of open top chambers (OTC), which were hexagonal in shape

Table 1

Repeated-measures analysis of variance was used to estimate the main and interactive effects of experimental warming (W), increased precipitation (IP), measuring year (Y) and month (M) on the normalized difference vegetation index (NDVI), soil-adjusted vegetation index (SAVI), aboveground biomass (AGB) and gross primary production (GPP).

Model	NDVI	SAVI	AGB	GPP
W	1.96	1.77	1.97	1.72
IP	4.19*	2.85	3.85*	6.32**
Y	79.84***	70.42***	62.16***	107.47***
М	165.51***	78.29***	126.09***	319.67***
$W \times IP$	0.15	0.27	0.14	0.23
$W \times Y$	2.92*	3.53*	3.56*	1.54
$W \times M$	1.35	1.89	1.37	2.76*
$IP \times Y$	0.74	1.04	0.90	0.67
$IP \times M$	0.50	0.84	0.15	0.39
$Y \times M$	31.94***	50.98***	20.06***	73.89***
$W \times IP \times Y$	0.43	0.29	0.43	0.66
$W \times IP \times M$	0.19	0.33	0.19	0.40
$W \times Y \times M$	0.72	0.95	0.73	0.58
$IP \times Y \times M$	0.42	0.31	0.38	0.55
$W \times IP \times Y \times M$	0.24	0.29	0.24	0.36

*, ** and *** indicates significance at p < 0.05, p < 0.01 and p < 0.001, respectively.

with 60° inwardly inclined sides, were installed to obtain the two magnitudes of warming in early June 2014. All the top opening of the two heights of OTCs was 60 cm and left in place year round. These OTCs were similar with those of (Li et al., 2011). Two diameters (approximately 44 cm and 62 cm) of precipitation collection funnels with rubber tubing (2 cm inner diameter) were installed to obtain the two magnitudes (15% and 30%) of increased precipitation in early June 2014. These increased precipitation devices were similar with those of some previous studies (Blankinship et al., 2010; Ma et al., 2012). The increased magnitudes of precipitation was comparable to previous studies (i.e. 6–50%) (Chimner et al., 2010; Huang et al., 2015; Niu et al., 2008; Shen et al., 2015) and the predicted values in the 21 century (10–25%) (Ji and Kang, 2013).

2.2. Microclimate measurements

Meteorological stations (HOBO weather station, Onset Computer, Bourne, MA, USA) continuously auto-monitored soil moisture at a depth of 0.10 m (SM), air temperature (T_a) and relative humidity (RH) at a height of 0.15 m during growing season (June–September) in 2014–2016. Measured T_a and RH was used to calculate vapor pressure deficit (VPD). Growing season accumulated temperature (AccT) was the sum of \geq 5 °C daily air temperature during June–September. Growing season precipitation (GSP) was obtained from the Damxung County meteorological station. The ratio of GSP to AccT (GSP/AccT) was used as a synthesized factor of air temperature and precipitation (Wang et al., 2013).

2.3. NDVI, SAVI, AGB and GPP

During the growing season in 2014–2016, photographs in a $0.50 \text{ m} \times 0.50 \text{ m}$ subplot in the center of each plot were taken by a Tetracam Agricultural Digital Camera (ADC, Tetracam Inc., Chatsworth, CA, USA). NDVI and SAVI values were obtained from these photographs using a PixelWrench2 software (Liu et al., 2012; Yi et al., 2011).

A non-destructive method was used to estimate aboveground biomass (AGB). That is, NDVI data were used to estimate AGB (AGB = $10.33e^{3.28NDVI}$) (Fu and Shen, 2016). Moderate Resolution Imaging Spectroradiometer (MODIS) GPP algorithm was used to estimate GPP. The MODIS GPP algorithm was validated by our previous study (Fu et al., 2017) which conducted in the same alpine meadow as this study. Detailed descriptions on the MODIS GPP algorithm are given in previous studies (Fu et al., 2017).



Fig. 1. Comparison of normalized difference vegetation index (NDVI), soil-adjusted vegetation index (SAVI), aboveground biomass (AGB) and gross primary production (GPP) under different experimental warming and increased precipitation treatments in 2014 (a, d, g, j), 2015 (b, e, h, k) and 2016 (c, f, i, l).

2.4. Statistical analyses

A repeated-measures analysis of variance was used to estimate the main and interactive effects of experimental warming, increased precipitation and measuring year on T_{a} , AccT, VPD, SM and GSP/AccT. A repeated-measures analysis of variance was used to estimate the main and interactive effects of experimental warming, increased precipitation, measuring year and month on NDVI, SAVI, AGB and GPP. Duncan multiple comparisons were performed among the three warming or increased precipitation treatments. Single variable linear regressions between NDVI, SAVI, AGB and GPP, and daily T_{a} , AccT, VPD, SM, GSP and GSP/AccT were conducted. Multiple linear regressions between NDVI, SAVI, AGB and GPP, and daily T_a , VPD, SM and GSP were also conducted. For each year, response ratio (*R*) was used as the effect size (Hedges et al., 1999),

$$R = \overline{X_t} / \overline{X_c} \tag{1}$$

For warming effect (R_w), $\overline{X_c}$ and $\overline{X_t}$ is plant production variables (i.e. NDVI, SAVI, AGB and GPP) in 'C' and 'LW', 'C' and 'HW', 'LP' and 'LW + LP', 'LP' and 'HW + LP', 'HP' and 'LW + HP', or 'HP' and 'HW + HP', respectively. For increased precipitation effect ($R_{\rm IP}$), $\overline{X_c}$ and $\overline{X_t}$ is plant production variables (i.e. NDVI, SAVI, AGB and GPP) in 'C' and 'LP', 'C' and 'HP', 'LW' and 'LW + LP', 'LW' and 'LW + HP', 'HW' and 'HW + LP', or 'HW' and 'HW + HP', respectively. All the statistical analyses were performed using the SPSS software (version 16.0; SPSS Inc., Chicago, IL).

3. Results

3.1. Effects of warming and increased precipitation on microclimates

There were significant main effects of experimental warming on T_a , AccT, VPD, SM and GSP/AccT, main effects of increased precipitation



Fig. 2. Relationships (a) between normalized difference vegetation index (NDVI) and growing season precipitation (GSP), (b) between NDVI and soil moisture (SM), (c) between NDVI and the ratio of GSP to accumulated temperature (GSP/AccT), (d) between soil-adjusted vegetation index (SAVI) and GSP, (e) between SAVI and SM, (f) between SAVI and GSP/AccT, (g) between aboveground biomass (AGB) and GSP, (h) between AGB and SM, (i) between AGB and GSP/AccT, (j) between gross primary production (GPP) and GSP, (k) between GPP and SM, and (l) between GPP and GSP/AccT.

on VPD, SM and GSP/AccT, and an interactive effect of experimental warming and increased precipitation on VPD (Table S1). Across the three growing seasons, the low- and high-level experimental warming significantly decreased SM by $0.02 \text{ m}^3 \text{ m}^{-3}$ and $0.04 \text{ m}^3 \text{ m}^{-3}$, and GSP/AccT by $0.05 \text{ mm} \text{°C}^{-1}$ and $0.07 \text{ mm} \text{°C}^{-1}$, but significantly increased daily T_a by 1.91 °C and 3.51 °C, daytime T_a by 3.10 °C and 5.50 °C, nighttime T_a by 0.65 °C and 1.36 °C, AccT by 239.71 °C and 435.42 °C, and VPD by 0.20 kPa and 0.40 kPa, respectively (Table S1, Fig. S1). The low- and high-level increased precipitation significantly increased SM by $0.02 \text{ m}^3 \text{ m}^{-3}$ and 0.03 m^{-3} , and GSP/AccT by 0.04 mm °C⁻¹ and 0.08 mm °C⁻¹, but significantly decreased VPD by 0.05 kPa and 0.09 kPa, respectively (Table S1, Fig. S1).

3.2. Effects of warming and increased precipitation on NDVI, SAVI, AGB and GPP

There were significant main effects of increased precipitation rather than experimental warming on NDVI, AGB and GPP (Table 1). Across the three growing seasons, the high-level increased precipitation significantly increased NDVI by 18.7% (0.03), SAVI by 18.4% (0.02), AGB by 11.4% (2.13 g m⁻²) and GPP by 25.0% (0.16 g C m⁻² d⁻¹), respectively.

The comparison of NDVI, SAVI, AGB and GPP among experimental warming and increased precipitation treatments were illustrated in Fig. 1. The high-level increased precipitation significantly increased NDVI in 2014 by 20.5% (0.04), NDVI in 2016 by 19.6% (0.03), SAVI in 2014 by 19.7% (0.03), SAVI in 2016 by 21.2% (0.03), AGB in 2014 by



Fig. 3. Relationships (a) between normalized difference vegetation index (NDVI) and daytime mean air temperature (daytime T_a), (b) between soil-adjusted vegetation index (SAVI) and daytime T_a , (c) between aboveground biomass (AGB) and daytime T_a , (d) between gross primary production (GPP) and daytime T_{av} (e) between NDVI and nighttime mean air temperature (nighttime T_a), (f) between SAVI and nighttime T_a , (g) between GPP and nighttime T_a , and (h) between GPP and nighttime T_a

14.0% (2.81 g m⁻²) and AGB in 2016 by 11.7% (2.16 g m⁻²), respectively. The low- and high-level increased precipitation significantly increased GPP by 15.6% (0.11 g C m⁻² d⁻¹) and 28.3% (0.19 g C m⁻² d⁻¹) in 2016, respectively.

3.3. Relationships between NDVI, SAVI, AGB and GPP, and microclimates

The NDVI, SAVI, AGB and GPP significantly increased with increasing GSP, SM and GSP/AccT (Fig. 2). GPP significantly decreased with increasing VPD (p = 0.012). The NDVI, SAVI, AGB and GPP

significantly increased with increasing nighttime T_a rather than daytime T_a (Fig. 3). GSP and daily T_a explained 81% and 8%, 76% and 10%, and 77% and 9% variations of NDVI, SAVI and AGB, respectively (Table 2). GSP, daily T_a and VPD explained 83%, 3% and 5% variation of GPP, respectively (Table 2).

Table 2

Multiple linear regressions between the normalized difference vegetation index (NDVI), soil-adjusted vegetation index (SAVI), aboveground biomass (AGB) and gross primary production (GPP), and daily air temperature (T_a), soil moisture (SM), vapor pressure deficit (VPD) and growing season precipitation (GSP).

Variable		Coefficient	R^2	Partial correlation	р
NDVI	Constant	-0.03			0.187
	GSP	0.00	0.81	0.94	< 0.001
	T_a	0.01	0.08	0.65	< 0.001
SAVI	Constant	-0.04			0.050
	GSP	0.00	0.76	0.93	< 0.001
	T_a	0.01	0.10	0.66	< 0.001
AGB	Constant	5.37			0.004
	GSP	0.02	0.77	0.92	< 0.001
	T_a	0.38	0.09	0.61	< 0.001
GPP	Constant	-0.59			< 0.001
	GSP	0.00	0.83	0.82	< 0.001
	T_a	0.08	0.03	0.70	< 0.001
	VPD	-0.50	0.05	-0.63	< 0.001

4. Discussion

4.1. Warming

Our findings implied that experimental warming-induced soil drying magnitude increased with warming magnitude (Fig. 4). This result was in line with several previous studies (Li et al., 2011; Wang et al., 2014a; Xu et al., 2013; Zhong et al., 2016). For example, a 3.10 °C and 1.30 °C increase in soil temperature significantly caused 0.05 m³ m⁻³ and 0.02 m³ m⁻³ decline in soil moisture, respectively, in an alpine meadow in the Northern Tibetan Plateau (Shen et al., 2016b). A 2.2 °C, 2.8 °C, 3.2 °C and 3.6 °C increase in T_a resulted in 3.1%, 4.4%, 7.2% and 8.7% decline in soil moisture in an alpine meadow in the Northern Tibetan Plateau, respectively (Zhu, 2016).

Our findings implied that responses of plant production to warming showed quadratic relationships with warming magnitudes (Fig. 4). The optimum warming magnitudes of daily T_a was approximately 3.00 °C (NDVI: 3.07 °C; SAVI: 3.18 °C; AGB: 3.00 °C; GPP: 2.91 °C). Similarly, the increased magnitude in AGB under 2.7 °C warming conditions tended to greater than those under 1 °C and 4 °C warming conditions in an old-field herbaceous community (Hoeppner and Dukes, 2012). This finding implied that climatic warming may not always increase plant productivity in alpine regions. For example, experimental warming decreased AGB and GPP (Fu and Shen, 2016; Hu et al., 2013) or did not affect AGB (Natali et al., 2012).

There were no obvious differences in NDVI, SAVI, AGB and GPP between the low- and high level experimental warming. This could be attributed to the following mechanisms. First, the increased magnitudes of T_a under the low- and high-level experimental warming were 1.91 °C and 3.51 °C in 2014-2016, respectively. That is, they both deviated from the optimum warming magnitudes, although the deviated magnitude under the low-level experimental warming was greater than that under the high-level experimental warming. Second, the high-level experimental warming resulted in greater environmental drying (i.e. the greater decline in SM and increase in VPD) (Fig. 4), which in turn dampened the high-level warming effects on plant production to a greater extent, compared to the low-level experimental warming. High VPD can result in stomatal closure and suppress plant photosynthesis (Broeckx et al., 2014). Third, greater warming resulted in a greater decline in GSP/AccT, and NDVI, SAVI, AGB and GPP showed positive relationships with GSP/AccT (Figs. 3 and 4).

Our findings suggested that plant production had different sensitivities to daytime and nighttime T_a (Fig. 3). Therefore, the asymmetry of daytime and nighttime warming may result in asymmetric effects of daytime and nighttime temperature on plant production in alpine regions. Similarly, daily minimum T_a had stronger effects on green-up date than daily maximum T_a on the Tibetan Plateau (Shen et al., 2016a). Summer vegetation greenness showed positive correlation with summer daily minimum T_a , but negative correlation with summer daily maximum T_a on the Tibetan Plateau (Shen et al., 2016a). The NDVI showed positive partial correlation with daily maximum T_a in most wet and cool ecosystems, but negative partial correlation with daily minimum T_a in boreal regions (Peng et al., 2013). Daytime T_a had stronger effects on leaf unfolding dates than nighttime T_a in the northern hemisphere (Piao et al., 2015).

Low-temperature is a more vital limiting factor in plant growth at higher latitudes and altitudes than at lower latitudes and altitudes (Pan et al., 2015). Warming magnitudes are expected to be greater at higher latitudes and altitudes than at lower latitudes and altitudes (Root et al., 2003). These previous studies suggested that plant production may have greater responses to warming at higher latitudes and altitudes than at lower latitudes and altitudes. However, our findings implied that the low- and high-level warming did not significantly affect plant production in 2014–2016. This finding was not in line with some previous studies which demonstrated that warming significantly increased or decreased plant production in sub-tropical and tropical regions (Clark et al., 2003; Wu et al., 2016). Therefore, plant production may not always have greater response to warming in alpine regions than tropical regions.

4.2. Increased precipitation

Our findings implied that responses of plant production to increased precipitation varied with years (Fig. 1). Likewise, a 50% increase in precipitation increased significantly AGB in June 2004 rather than June 2003 and 2005 in a mixed-grass prairie, Wyoming, USA (Chimner et al., 2010). Increased precipitation increased AGB in August 2011 rather than August 2012 in a typical steppe (Xu et al., 2016b). A 30% increase in precipitation increased GPP by 6.6% in 2005 and 33.8% in 2006 in a temperate steppe (Niu et al., 2008).

Although the GSP in 2015 was the lowest among the three years (Fig. S2), there were significant increases in plant production in 2014 and 2016 rather than in 2015. This finding suggested that plant production was not always more responsive to increased precipitation in drier years in alpine regions. Similarly, a previous meta-analysis showed that the response of AGB to increased precipitation was not correlated with mean annual precipitation (Wu et al., 2011). This finding could be attributed to the following mechanisms. First, the lower limit of soil moisture was 11.8% for alpine grassland growth (Ma et al., 2004), whereas the soil moisture in the 'HP' plots was only 11.3% in 2015 rather than in 2014 and 2016. Second, the responses of NDVI, SAVI, AGB and GPP to increased precipitation showed positive relationships with the increased magnitudes of GSP caused by increased precipitation treatments (Fig. 5). The low- and high-level increased precipitation increased GSP by 65.6 mm and 131.2 mm in 2014, by 45.0 mm and 90.1 mm in 2015, and by 57.0 mm and 114.1 mm in 2016, respectively (Fig. S2). Third, the responses of NDVI, SAVI, AGB and GPP to increased precipitation showed positive correlations with the increased magnitudes of GSP/AccT caused by increased precipitation treatments (Fig. 6). The low- and high-level increased precipitation resulted in increases of GSP/AccT by 0.05 mm °C⁻¹ and 0.09 mm °C⁻¹ in 2014, 0.03 mm $^{\circ}C^{-1}$ and 0.06 mm $^{\circ}C^{-1}$ in 2015, and 0.04 mm $^{\circ}C^{-1}$ and 0.08 mm $^{\circ}C^{-1}$ in 2016, respectively.

Compared to the natural precipitation conditions, the increased magnitudes of GSP under the high-level increased precipitation conditions were approximately twice than those under the low-level increased precipitation conditions (i.e. 55.9 mm) across the three growing seasons in 2014–2016 (Fig. S2). NDVI, SAVI, AGB and GPP did not change under the low-level increased precipitation, but was significantly increased under the high-level increased precipitation across the three growing seasons in 2014–2016. These findings implied that a



Fig. 4. Relationships (a) between the response ratio of normalized difference vegetation index to experimental warming (R_{w NDVI}) and increased magnitude of air temperature (ΔT_a) , (b) between the response ratio of soil-adjusted vegetation index (SAVI) to experimental warming ($R_{w SAVI}$) and ΔT_{a} , (c) between the response ratio of aboveground biomass to experimental warming (R_{wAGB}) and ΔT_a , (d) between the response ratio of gross primary production to experimental warming ($R_{\rm w GPP}$) and ΔT_a , (e) between the decreased magnitude of soil moisture caused by experimental warming (Δ SM) and ΔT_a , (f) between the increased magnitude of vapor pressure deficit caused by experimental warming (Δ VPD) and Δ T_a, and (g) between the decreased magnitude of the ratio of growing season precipitation to accumulated air temperature caused by experimental warming $(\Delta GSP/AccT)$ and ΔT_a

55.9 mm increase in precipitation may be invalid in resulting in significant changes of plant production in alpine regions. In other words, the no obvious changes of plant production under the low-level increased precipitation conditions may be attributed to the relative low increase in GSP.

Our findings implied that there were no significant differences in NDVI, SAVI, AGB and GPP between the low- and high-level increased precipitation across the three growing seasons in 2014–2016 (Fig. 1). Likewise, although AGB under a low water availability conditions was lower than those under a medium and high water availability conditions, there were no obvious differences in AGB between the medium

and high water availability in semiarid grasslands (Köchy and Wilson, 2004). The GSP difference between the no extra precipitation and the low-level increased precipitation (i.e. 55.9 mm) was completely equivalent to that between the low- and high-level increased precipitation across the three growing seasons in 2014–2016 (Fig. S2). The GSP/AccT difference between the no extra precipitation and the low-level increased precipitation was nearly equivalent to that between the low- and high-level increased precipitation across the three growing seasons in 2014–2016 (i.e. $0.039 \text{ mm}^{\circ}\text{C}^{-1}$ vs. $0.038 \text{ mm}^{\circ}\text{C}^{-1}$). Therefore, the no obvious differences of NDVI, SAVI, AGB and GPP between the two levels increased precipitation could be most likely



Fig. 5. Relationships (a) between the response ratio of normalized difference vegetation index to increased precipitation (RIP NDVI) and increased magnitude of growing season precipitation (Δ GSP), (b) between the response ratio of soil-adjusted vegetation index to increased precipitation $(R_{\rm IP SAVI})$ and Δ GSP, (c) between the response ratio of aboveground biomass to increased precipitation $(R_{IP AGB})$ and Δ GSP, (d) between the response ratio of gross primary production to increased precipitation ($R_{IP GPP}$) and Δ GSP. (e) between the increased magnitude of soil moisture caused by increased precipitation treatments (Δ SM) and Δ GSP, (f) between the change magnitude of vapor pressure deficit caused by increased precipitation treatments (Δ VPD) and Δ GSP, and (g) between the increased magnitude of the ratio of growing season precipitation to accumulated air temperature caused by increased precipitation treatments (Δ GSP/AccT) and Δ GSP.

attributed to their relative low differences in GSP and GSP/AccT.

4.3. Interactive effects of warming and increased precipitation

The NDVI and AGB in the 'HW + LP' and 'HW + HP' plots in 2014 was 33.6% and 41.9%, and 23.6% and 28.6% greater than that of the 'C' plots, respectively (Fig. 1). The GPP in the 'HW + HP' plots in 2014 was 46.1% higher than that of the 'C' plots (Fig. 1). The NDVI, SAVI, AGB and GPP in the 'LW + HP' plots in 2016 was 34.6%, 39.3%, 21.3% and 38.0% higher than that of the 'C' plots, respectively (Fig. 1). In contrast, the NDVI, AGB and GPP in the 'HW', 'LP' and 'HP' plots in

2014, and the NDVI, SAVI, AGB and GPP in the 'LW' and 'HP' plots in 2016 was not significant different from that of the 'C' plots (Fig. 1). These results suggested that the single effect of warming or increased precipitation on plant production may underestimate the interactive effect of warming and increased precipitation. There may be a positive interactive effect of warming and increased precipitation on plant production in alpine regions. However, this positive interactive effect did not occur in 2015. The GSP in 2014, 2015, 2016 and 1963–2016 and was 437.3 mm, 300.2 mm, 380.2 mm and 398.3 mm, respectively. The high-level increased precipitation significantly increased SM by 23.2% in 2015, which remained lower than the minimum value of SM



Fig. 6. Relationships (a) between the response ratio of normalized difference vegetation index to increased precipitation $(R_{IP NDVI})$ and the increased magnitude of the ratio of growing season precipitation to accumulated air temperature caused by increased precipitation treatments (Δ GSP/AccT), (b) between the response ratio of soil-adjusted vegetation index to increased precipitation (RIP SAVI) and Δ GSP/AccT, (c) between the response ratio of aboveground biomass to increased precipitation $(R_{\rm IP AGB})$ and $\Delta GSP/AccT$, (d) between the response ratio of gross primary production to increased precipitation ($R_{IP GPP}$) and $\Delta GSP/AccT$, (e) between $R_{\rm IP \ NDVI}$ and the increased magnitude of soil moisture caused by increased precipitation treatments (Δ SM), (f) between $R_{\text{IP SAVI}}$ and Δ SM, (g) between $R_{\text{IP AGB}}$ and Δ SM, and (h) between $R_{\text{IP}_{GPP}}$ and Δ SM.

(11.8%) for alpine grassland growth (Ma et al., 2004). The SM change magnitudes were positively correlated with those of GSP (Fig. 5). Therefore, the negligible interactive effects of warming and increased precipitation on plant production in 2015 may be mainly attributed to its low GSP and SM. Water availability may regulate the interactive effects of warming and increased precipitation on plant production in alpine regions. The lack of significant interactive effects of warming and increased precipitation on plant production across the three growing seasons (Table 1) was in line with some previous studies (Xu et al., 2016a). This may result largely from the low precipitation

(372.6 mm) across the three growing seasons.

Our findings were in line with several previous studies which demonstrated that warming effects on plant production were regulated by water availability in alpine regions (Fu and Shen, 2016; Wang et al., 2013) and tropical regions (Clark, 2004; Wang et al., 2014b). Therefore, water availability may be a vital limit factor in affecting warming effects on plant production in both alpine and tropical regions.

4.4. Stronger effects of increased precipitation on plant production than those of experimental warming

Our results implied that increased precipitation had stronger effects on plant production than did experimental warming across the three growing seasons in 2014–2016. This finding was supported by several previous studies. For example, satellite-based yearly maximum NDVI was more responsive to precipitation than temperature during 1982-2006 on the Tibetan Plateau (Sun et al., 2013). Precipitation had a more profound effect on satellite-based NDVI than temperature during 1985–1999 in the Lhasa area, Tibetan Plateau (Chu et al., 2007). AGB was more responsive to precipitation fluctuation than temperature variation in Tibetan alpine grasslands (Shi et al., 2014). AGB responded more quickly to GSP than T_a in alpine grasslands in the Northern Tibetan Plateau (Wu et al., 2014). AGB was more responsive to GSP than T_a in the alpine meadow along an elevation gradient in the Northern Tibetan Plateau (Wang et al., 2013). Water addition significantly increased GPP, whereas experimental warming did not affect GPP in an Arctic polar semidesert ecosystem (Sharp et al., 2013). Increased precipitation markedly increased aboveground biomass, whereas experimental warming had no obvious effects on AGB in a typical steppe in August 2011 and in a desert steppe in August 2011 and 2012 (Xu et al., 2016b).

This finding could be attributed to the following mechanisms. First, experimental warming could result in significant environmental drying and declines in GSP/AccT. The optimum GSP/AccT could be 0.80-0.84 for AGB in alpine meadows on the Tibetan Plateau (Wang et al., 2013). The NDVI, SAVI, AGB and GPP showed positive relationships with environmental humidity and GSP/AccT (Fig. 2). These findings implied that effects of experimental warming-induced increases in T_a on plant production can be dampened by experimental warming-induced negative effects on environmental humidity and GSP/AccT. Second, increased precipitation did not affect T_a and AccT, which suggested that increased precipitation did not indirectly affect plant production by changing temperature. Increased precipitation significantly increased environmental humidity and GSP/AccT, which was beneficial to plant growth (Fig. 2). In general, experimental warming can result in indirect and negative effects on plant production, whereas increased precipitation had negligible indirect and negative effects on plant production.

5. Conclusions

In this study, we examined responses of NDVI, SAVI, AGB and GPP to experimental warming and increased precipitation in an alpine meadow of the Northern Tibetan Plateau in 2014–2016. The high-level increased precipitation increased NDVI in 2014 by 20.5%, NDVI in 2016 by 19.6%, SAVI in 2014 by 19.7%, SAVI in 2016 by 21.2%, AGB in 2014 by 14.0% and AGB in 2016 by 11.7%, respectively. The low-and high-level increased precipitation increased GPP by 15.6% and 28.3% in 2016, respectively. The low-level and high-level experimental warming did not affect NDVI, SAVI, AGB and GPP. The response ratios of NDVI, SAVI, AGB and GPP to experimental warming showed quadratic relationships with warming magnitudes. The response ratios of NDVI, SAVI, AGB and GPP to increased precipitation showed positive and linear relationships with increased magnitudes of precipitation.

Acknowledgements

We thank the editor and reviewers for their insightful and valuable comments, which greatly improved the quality of this manuscript. This work was supported by the National Natural Science Foundation of China [Nos. 31600432, 41571042], the National Key Research Projects of China [No. 2016YFC0502005], and the Youth Innovation Research Team Project of Key Laboratory of Ecosystem Network Observation and Modeling [No. LENOM2016Q0002].

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.11.017.

References

- Blankinship, J.C., Brown, J.R., Dijkstra, P., Allwright, M.C., Hungate, B.A., 2010. Response of terrestrial CH₄ uptake to interactive changes in precipitation and temperature along a climatic gradient. Ecosystems 13, 1157–1170.
- Broeckx, L.S., et al., 2014. The effect of a dry spring on seasonal carbon allocation and vegetation dynamics in a poplar bioenergy plantation. Global Change Biol. Bioenergy 6, 473–487.
- Chimner, R.A., Welker, J.M., Morgan, J., LeCain, D., Reeder, J., 2010. Experimental manipulations of winter snow and summer rain influence ecosystem carbon cycling in a mixed-grass prairie Wyoming, USA. Ecohydrology 3, 284–293.
- Chu, D., Lu, L., Zhang, T., 2007. Sensitivity of normalized difference vegetation index (NDVI) to seasonal and interannual climate conditions in the Lhasa area Tibetan plateau, China. Arct. Antarct. Alp. Res. 39, 635–641.
- Clark, D.A., Piper, S.C., Keeling, C.D., Clark, D.B., 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proc. Natl. Acad. Sci. U. S. A. 100, 5852–5857.
- Clark, D.A., 2004. Tropical forests and global warming: slowing it down or speeding it up? Front. Ecol. Environ. 2, 73–80.
- Diffenbaugh, N.S., Field, C.B., 2013. Changes in ecologically critical terrestrial climate conditions. Science 341, 486–492.
- Dorji, T., et al., 2013. Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. Global Change Biol. 19, 459–472.
- Fu, G., Shen, Z.X., 2016. Environmental humidity regulates effects of experimental warming on vegetation index and biomass production in an alpine meadow of the Northern Tibet. PLoS One 11. http://dx.doi.org/10.1371/journal.pone.0165643.
- Fu, G., et al., 2017. Validation of collection of 6 MODIS/Terra and MODIS/Aqua gross primary production in an alpine meadow of the Northern Tibetan Plateau. Int. J. Remote Sens. 38, 4517–4534.
- Ganjurjav, H., et al., 2016. Differential response of alpine steppe and alpine meadow to climate warming in the central Qinghai-Tibetan Plateau. Agric. For. Meteorol. 223, 233–240.
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.
- Heng, T., Wu, J.G., Xie, S.Y., Wu, M.X., 2011. The responses of soil C and N: microbial biomass C or N under alpine meadow of Qinghai-Tibet Plateau to the change of temperature and precipitation. Chi. Agric. Sci. Bull. 27, 425–430.
- Hoeppner, S.S., Dukes, J.S., 2012. Interactive responses of old-field plant growth and composition to warming and precipitation. Global Change Biol. 18, 1754–1768.
- Hu, J., Hopping, K.A., Bump, J.K., Kang, S.C., Klein, J.A., 2013. Climate change and water use partitioning by different plant functional groups in a grassland on the Tibetan Plateau. PLoS One 8. http://dx.doi.org/10.1371/journal.pone.0075503.
- Huang, G., Li, Y., Su, Y.G., 2015. Effects of increasing precipitation on soil microbial community composition and soil respiration in a temperate desert, Northwestern China. Soil Biol. Biochem. 83, 52–56.
- Hulme, M., Osborn, T.J., Johns, T.C., 1998. Precipitation sensitivity to global warming: comparison of observations with HadCM2 simulations. Geophys. Res. Lett. 25, 3379–3382.
- IPCC, 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, M., Tignor, S.K., Allen, J., Boschung, A., Nauels, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press Cambridge, United Kingdom and New York, NY, USA.
- Ji, Z.M., Kang, S.C., 2013. Double-nested dynamical downscaling experiments over the Tibetan Plateau and their projection of climate change under two RCP Scenarios. J. Atmos. Sci. 70, 1278–1290.
- Köchy, M., Wilson, S.D., 2004. Semiarid grassland responses to short-term variation in water availability. Plant Ecol. 174, 197–203.
- Klein, J.A., Harte, J., Zhao, X.Q., 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. Ecol. Appl. 17, 541–557.
- Kuang, X.X., Jiao, J.J., 2016. Review on climate change on the Tibetan Plateau during the last half century. J. Geophys. Res.-Atmos. 121, 3979–4007.
- Li, N., Wang, G.X., Yang, Y., Gao, Y.H., Liu, G.S., 2011. Plant production, and carbon and nitrogen source pools: are strongly intensified by experimental warming in alpine ecosystems in the Qinghai-Tibet Plateau. Soil Biol. Biochem. 43, 942–953.
- Li, X.Y., Yao, Z.Y., Xiao, J.H., Wang, H.W., 2016. Analysis of the spatial-temporal variation characteristics of precipitation over the Tibetan Plateau from 1961 through 2010. J. Glaciol. Geocryol. 38, 1233–1340.
- Liu, Q., et al., 2011. Belowground responses of *Picea asperata* seedlings to warming and nitrogen fertilization in the eastern Tibetan Plateau. Ecol. Res. 26, 637–648.
- Liu, W.J., et al., 2012. Storage, patterns, and control of soil organic carbon and nitrogen in the northeastern margin of the Qinghai-Tibetan Plateau. Environ. Res. 7. http://dx. doi.org/10.1088/1748-9326/7/3/035401.
- Lu, H.L., Liu, G.F., 2010. Trends in temperature and precipitation on the Tibetan Plateau, 1961–2005. Clim. Res. 43, 179–190.
- Ma, K.M., et al., 2004. Multiple-scale soil moisture distribution and its implications for ecosystem restoration in an arid river valley, China. Land Degrad. Dev. 15, 75–85.
- Ma, L., Huang, W., Guo, C., Wang, R., Xiao, C., 2012. Soil microbial properties and plant

G. Fu et al.

growth responses to carbon and water addition in a temperate steppe: the importance of nutrient availability. PLoS One 7. http://dx.doi.org/10.1371/journal.pone. 0035165.

- Natali, S.M., Schuur, E.A.G., Rubin, R.L., 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. J. Ecol. 100, 488–498.
- Niu, S.L., et al., 2008. Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. New Phytol. 177, 209–219.
- Pan, S.F., et al., 2015. Impacts of climate variability and extremes on global net primary production in the first decade of the 21 st century. J. Geogr. Sci. 25, 1027–1044.
 Peng, S., et al., 2013. Asymmetric effects of daytime and night-time warming on Northern
- Hemisphere vegetation. Nature 501 (88-+). Piao, S., et al., 2015. Leaf onset in the northern hemisphere triggered by daytime tem-
- perature. Nat. Commun. 6. Root, T.L., et al., 2003. Fingerprints of global warming on wild animals and plants. Nature
- 421, 57–60. Rustad, L.E., et al., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.
- Sharp, E.D., Sullivan, P.F., Steltzer, H., Csank, A.Z., Welker, J.M., 2013. Complex carbon cycle responses to multi-level warming and supplemental summer rain in the high Arctic. Global Change Biol. 19, 1780–1792.
- Shen, M.G., et al., 2014. Increasing altitudinal gradient of spring vegetation phenology during the last decade on the Qinghai-Tibetan Plateau. Agric. For. Meteorol. 189, 71–80.
- Shen, Z.X., Li, Y.L., Fu, G., 2015. Response of soil respiration to short-term experimental warming and precipitation pulses over the growing season in an alpine meadow on the Northern Tibet. Appl. Soil Ecol. 90, 35–40.
- Shen, M.G., et al., 2016a. Strong impacts of daily minimum temperature on the green-up date and summer greenness of the Tibetan Plateau. Global Change Biol. 22, 3057–3066.
- Shen, Z.X., et al., 2016b. The soil drying along the increase of warming mask the relation between temperature and soil respiration in an alpine meadow of Northern Tibet. Pol. J. Ecol. 64, 125–129.
- Shi, F.S., Chen, H., Chen, H.F., Wu, Y., Wu, N., 2012. The combined effects of warming and drying suppress CO₂ and N₂O emission rates in an alpine meadow of the eastern Tibetan Plateau. Ecol. Res. 27, 725–733.
- Shi, Y., et al., 2014. Field-based observations of regional-scale, temporal variation in net primary production in Tibetan alpine grasslands. Biogeosciences 11, 2003–2016.
- Sun, J., Cheng, G.W., Li, W.P., Sha, Y.K., Yang, Y.C., 2013. On the variation of NDVI with the principal climatic elements in the Tibetan Plateau. Remote Sens. 5, 1894–1911. Wang, S.P., et al., 2012. Effects of warming and grazing on soil N availability, species
- composition, and ANPP in an alpine meadow. Ecology 93, 2365–2376.

- Wang, Z., Luo, T.X., Li, R.C., Tang, Y.H., Du, M.Y., 2013. Causes for the unimodal pattern of biomass and productivity in alpine grasslands along a large altitudinal gradient in semi-arid regions. J. Veg. Sci. 24, 189–201.
- Wang, X., et al., 2014a. Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration. Global Change Biol. 20, 3229–3237.
- Wang, X., et al., 2014b. A two-fold increase of carbon cycle sensitivity to tropical temperature variations. Nature 506 (212-+).
- Wu, Z.T., Dijkstra, P., Koch, G.W., Penuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biol. 17, 927–942.
- Wu, J.S., et al., 2014. Effects of livestock exclusion and climate change on aboveground biomass accumulation in alpine pastures across the Northern Tibetan Plateau. Chin. Sci. Bull. 59, 4332–4340.
- Wu, Y.Z., et al., 2016. Effects of reduced water and diurnal warming on winter-wheat biomass and soil respiration. Environ. Sci. 37, 280–287.
- Xu, Z.F., et al., 2010. Initial soil responses to experimental warming in two contrasting forest ecosystems, Eastern Tibetan Plateau, China Nutrient availabilities, microbial properties and enzyme activities. Appl. Soil Ecol. 46, 291–299.
- Xu, W.F., et al., 2013. A meta-analysis of the response of soil moisture to experimental warming. Environ. Res. 8. http://dx.doi.org/10.1088/1748-9326/8/4/044027.
- Xu, X., et al., 2016a. Unchanged carbon balance driven by equivalent responses of production and respiration to climate change in a mixed-grass prairie. Global Change Biol. 22, 1857–1866.
- Xu, Z.Z., Hou, Y.H., Zhang, L.H., Liu, T., Zhou, G.S., 2016b. Ecosystem responses to warming and watering in typical and desert steppes. Sci. Rep.-Uk 6. http://dx.doi. org/10.1038/srep34801.
- Xue, X., Peng, F., You, Q.G., Xu, M.H., Dong, S.Y., 2015. Belowground carbon responses to experimental warming regulated by soil moisture change in an alpine ecosystem of the Qinghai-Tibet Plateau. Ecol. Evol. 5, 4063–4078.
- Yao, T.D., Liu, X.D., Wang, N.L., Shi, Y.F., 2000. Amplitude of climatic changes in Qinghai-Tibetan Plateau. Chin. Sci. Bull. 45, 1236–1243.
- Yi, S.H., et al., 2011. Effects of permafrost degradation on alpine grassland in a semi-arid basin on the Qinghai-Tibetan Plateau. Environ. Res. 6. http://dx.doi.org/10.1088/ 1748-9326/6/4/045403.
- Zhao, W.L., Qi, J.G., Sun, G.J., Li, F.M., 2012. Spatial patterns of top soil carbon sensitivity to climate variables in northern Chinese grasslands. Acta Agric. Scand. B-S. P. 62, 720–731.
- Zhong, Z.M., Shen, Z.X., Fu, G., 2016. Response of soil respiration to experimental warming in a highland barley of the Tibet. SpringerPlus 5. http://dx.doi.org/10. 1186/s40064-016-1761-0.
- Zhu, J.T., 2016. Effects of experimental warming on plant reproductive phenology in Xizang alpine meadow. Chin. J. Plant Ecol. 40, 1028–1036.