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Varying responses of vegetation activity to climate changes on the Tibetan Plateau grassland

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Abstract Vegetation activity on the Tibetan Plateau grassland has been substantially enhanced as a result of climate change, as revealed by satellite observations of vegetation greenness (i.e., the normalized difference vegetation index, NDVI). However, little is known about the temporal variations in the relationships between NDVI and temperature and precipitation, and understanding this is essential for predicting how future climate change would affect vegetation activity. Using NDVI data and meteorological records from 1982 to 2011, we found that the inter-annual partial correlation coefficient between growing season (May–September) NDVI and temperature (R_{NDVI-T}) in a 15-year moving window for alpine meadow showed little change, likely caused by the increasing R_{NDVI-T} in spring (May–June) and autumn (September) and decreasing R_{NDVI-T} in summer (July–August). Growing season R_{NDVI-T} for alpine steppe increased slightly, mainly due to increasing R_{NDVI-T} in spring and autumn. The partial correlation coefficient between growing season NDVI and precipitation (R_{NDVI-P}) for alpine meadow increased slightly, mainly in spring and summer, and R_{NDVI-P} for alpine steppe increased, mainly in spring. Moreover, R_{NDVI-T} for the growing season was significantly higher in those 15-year windows with more precipitation for alpine steppe. R_{NDVI-P} for the growing season was significantly higher in those 15-year windows with higher temperature, and this tendency was stronger for alpine meadow than for alpine steppe. These results indicate that the impact of warming on vegetation activity of Tibetan Plateau grassland is more positive (or less negative) during periods with more precipitation and that the impact of increasing precipitation is more positive (or less negative) during periods with higher temperature. Such positive effects of the interactions between temperature and precipitation indicate that the projected warmer and wetter future climate will enhance vegetation activity of Tibetan Plateau grassland.

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Introduction

Grassland covers more than 60% of the area of the Tibetan Plateau (TP), including mainly alpine steppe and alpine meadow (Wang et al. 2015a). Changes in TP grassland vegetation could therefore affect regional carbon and energy balances, ecosystem services to local society, and water resources of the TP and surrounding regions by modifying the water balance as well as play a significant role in the Asian Monsoon by altering the surface heat source (Yin et al. 2013; Zhu et al. 2013; Li et al. 2015; Shen et al. 2015c; Wu et al. 2015). Understanding the responses of vegetation activity to climatic warming is thus important for predicting how the TP grassland will change in response to future climate change and for

improving assessments of the role of the TP in the regional climate system.

Previous studies investigated the impacts of climate change on vegetation activity on the TP, which are mainly measured by satellite observation of vegetation greenness (i.e., the normalized difference vegetation index, NDVI). Those studies generally revealed positive correlations between growing season (May–September) NDVI and temperature on the TP (Xu et al. 2011; Tao et al. 2015; Wang et al. 2015b), particularly for the alpine meadow (Shen et al. 2015d). Yet, the correlations exhibited spatio-temporally varying strength, likely due to the differences in plant functional traits, the effects of other environmental factors such as precipitation, and the different periods over which the correlations were calculated (Zhou et al. 2007; Hu et al. 2011; Xu et al. 2011; Zhang et al. 2013, 2014; Wang et al. 2015b). Such findings were also reproduced by simulations with both empirical and process-based vegetation production models (Piao et al. 2006, 2012; Chen et al. 2014). These studies suggested that the climatic warming over the past few decades enhanced vegetation activity on the TP. However, it is unknown whether the projected warming (Su et al. 2013) would continue to stimulate vegetation activity in the future, because the relationships between vegetation activity and temperature could vary among different periods and areas of the TP. The magnitudes of such spatio-temporal variations on the TP grassland, however, remain unclear.

Observations have revealed a more prominent climatic warming during the past few decades in the northern high latitudes as compared to the middle and low latitudes (Hansen et al. 2010). In response, the Arctic vegetation activity in the 1980s and 1990s was substantially enhanced, as revealed by in situ observations, satellite images, and simulation of process-based ecosystem models. Such a stimulating effect of increasing temperature, however, was found to be weakening in the Arctic region during the past three decades in a recent study (Piao et al. 2014). The authors attributed the weakening response of Arctic vegetation activity to the nonlinear response of photosynthesis to temperature, the increasing number of extremely hot days, and the increased abundance of shrubs. Similar to the cold grasslands of dry tundra regions of the Arctic, the TP has a cold climate and is covered by cold-adapted grasslands. However, it remains unclear whether the findings for the Arctic ecosystems apply to the TP grassland.

The grassland of the TP is mostly distributed in arid and semi-arid regions, so the vegetation activity may be simultaneously controlled by temperature and precipitation. For instance, a recent study found that both increasing temperature and precipitation could advance vegetation spring phenology (Shen et al. 2015b), and another study found that a decline in precipitation likely caused the delay in vegetation spring phenology and depressed spring vegetation activity observed between 2000 and 2011 in the southwestern TP (Shen et al.

2014b). Hence, vegetation activity on the TP is probably affected by both temperature and precipitation. Previous studies have documented the responses of TP vegetation activity to temperature and precipitation. However, little is known about the effects of interactions between temperature and precipitation on vegetation activity in the TP grasslands, although the response of plant activity to temperature was suggested to be modified by variation in precipitation (Shen et al. 2015b). Moreover, the spatially heterogeneous temporal trends in temperature and precipitation (Chen et al. 2013) might result in complex responses of vegetation activity.

In this study, we investigated the temporal changes in vegetation activity responses to climate change for alpine meadow and alpine steppe on the TP. We tested the hypotheses that vegetation activity is more responsive to temperature during periods with more precipitation and that it is more responsive to precipitation during periods with higher temperature.

Materials and methods

Study area

The TP (76° 7′–105° 5′ E, 25° 10′–39° 2′ N) is well known as "roof of the world" and "the third pole" with an average altitude over 4000 m above sea level and an area of about 2,500,000 km². The plateau is mainly characterized by lower temperature relative to the same latitude area, with annual mean temperature ranging from −15–10 °C (You et al. 2013) and growing season (May–September) mean temperature from lower than 0 to higher than 20 °C (Fig. S1A), spatially descending from south to north in addition to altitudinal decrease. The precipitation mainly concentrates in the growing season. Mean growing season precipitation ranges from lower than 200 mm to more than 1000 mm and spatially descending from south to north (Fig. S1B). Here, the temperature and precipitation were mapped using the Climate Research Unit (CRU) data (Mitchell and Jones 2005). Alpine meadow and alpine steppe cover more than 60% area of the plateau (Zheng et al. 2000) (Fig. S1C).

Data sets

Vegetation activity was represented by NDVI produced by the Global Inventory Modeling and Mapping Studies (GIMMS) group based on observations of the Advanced Very High Resolution Radiometer (Tucker et al. 2005). The NDVI has been validated as an effective indicator of vegetation activity and is widely used to infer vegetation dynamics (Tucker et al. 1986; Myneni et al. 1997; Jeong et al. 2011; Shen et al. 2008, 2011, 2012, 2014a, 2015a; Xu et al. 2013). The third generation of the GIMMS NDVI data, covering the period from 1982 to 2011, was used in this study. This data set was

produced using improved calibration procedures, unlike its previous counterpart (Xu et al. 2013; Pinzon and Tucker 2014). The spatial resolution was 8 × 8 km, and the temporal resolution was 15 days. The data have been calibrated for atmospheric effects, scan angle effects, cloud contamination, and effects of varying solar zenith angle at the time of measurement (Pinzon and Tucker 2014).

Daily temperature and precipitation data for the meteorological stations located in the alpine meadow and alpine steppe (Editorial-Board-of-Vegetation-Map-of-China 2001) were provided by the China Meteorological Administration. The stations with continuous daily temperature and precipitation observations during the growing season (May–September) for the period 1982–2011 were included. As a result, there were 32 and 19 stations located in the alpine meadow and alpine steppe (Fig. S1C), respectively. We did not use the CRU temperature and precipitation data for analyses because of their low quality over the TP.

Analyses

Prior to analysis, we first excluded the pixels for sparse vegetation, with an annual mean NDVI <0.1. Because NDVI occasionally decreased suddenly from early May to the time of annual maximum in August, we replaced such NDVI value with the mean of its two nearest values. Likewise, a sudden drop of NDVI value from late September to the time of annual maximum in August was treated similarly.

Next, to determine the temporal changes in the relationships between vegetation activity and climate, we first calculated the partial correlation coefficients between growing season averaged NDVI ($NDVI_{GS}$) and temperature ($R_{NDVI-GT}$), with the growing season sum of precipitation as the control variable, and between $NDVI_{GS}$ and precipitation ($R_{NDVI-GP}$), with temperature as the control variable, for each of the 15-year moving windows from 1982–1996 to 1997–2011. Consequently, there were a total of 16 moving windows centered from 1989 to 2004 and correspondingly 16 $R_{NDVI-GT}$ and 16 $R_{NDVI-GP}$ values, respectively. $R_{NDVI-GT}$ and $R_{NDVI-GP}$ were then regressed against the centers of the moving windows to determine their respective temporal trends. Moreover, to investigate whether the inter-window variations in $R_{NDVI-GT}$ are related with precipitation, we calculated the partial coefficient between the time series of $R_{NDVI-GT}$ (16 $R_{NDVI-GT}$ values) and the series of mean precipitation of each of 16 moving windows (16 precipitation values), while controlling for the mean temperature of each moving window (16 temperature values). A positive partial coefficient between $R_{NDVI-GT}$ and window average of precipitation indicates that higher temperature trends to enhance vegetation activity more strongly in the 15-year window with more precipitation. The temporal relationship between $R_{NDVI-GP}$ and temperature was analyzed similarly. Such analyses were also performed for

spring (May–June), summer (July–August), and autumn (September), respectively.

Here, the width of the moving window (15 years) was determined considering the sample size (number of years in this case) for partial correlation analysis within each window. A window with small sample size may be not appropriate for partial correlation analysis. Using a wider window may miss temporal changes in the partial correlation coefficient. Of course, the partial correlation coefficient could vary among windows with different widths (e.g., Fig. S2). This partial correlation was conducted at two levels including regional and meteorological station levels. For the regional level analysis, the NDVI and climatic variations averaged over all the 51 meteorological station in grassland were used. At the level of vegetation type (alpine meadow or steppe), the NDVI and climatic variations averaged over all the meteorological station in alpine meadow and alpine steppe were used, respectively. For station-level analysis, the partial correlation coefficients were calculated for each station. The NDVI for the 3 × 3 pixels with the station in the center was used.

Results

Changes in correlations between vegetation activity and climatic factors

The partial correlation coefficients ($R_{NDVI-GT}$) between the regionally averaged $NDVI_{GS}$ and growing season temperature (GT) showed substantial temporal evolution during the past 30 years (Fig. 1a). $R_{NDVI-GT}$ was about 0.29 for the window 1984–1998 (the 15-year window centered at 1991), decreased to about −0.02 for the window 1988–2002, and then increased to about 0.27 for the windows 1996–2010 and 1997–2011. On the other hand, $R_{NDVI-GP}$ increased from about −0.26 for the window 1983–1997 to about 0.26 for the window 1988–2002 and was between 0.00 and 0.12 for later windows. The alpine meadow $NDVI_{GS}$ showed the opposite correlations with GT and growing season precipitation (GP) compared with those of the alpine steppe (Fig. 1b, c). The $R_{NDVI-GT}$ for the alpine meadow fluctuated between 0.20–0.40 for most of the 15-year windows, but it was between −0.45 and −0.20 for the alpine steppe for the windows with centers from 1990 to 2000. The $R_{NDVI-GP}$ for the alpine meadow was −0.32 and −0.47 for the earliest two windows, respectively, and then gradually increased toward 0.00 onward. In contrast, the $R_{NDVI-GP}$ for the alpine steppe was between 0.16–0.37 for the first four windows and fluctuated between 0.46–0.67 for the remaining windows.

At the regional scale, both R_{NDVI-T} and R_{NDVI-P} showed distinct patterns among spring, summer, and autumn (Fig. 2). The R_{NDVI-T} for spring gradually increased from low values in the first two 15-year windows centered on 1989 and 1990 to about 0.38 in the
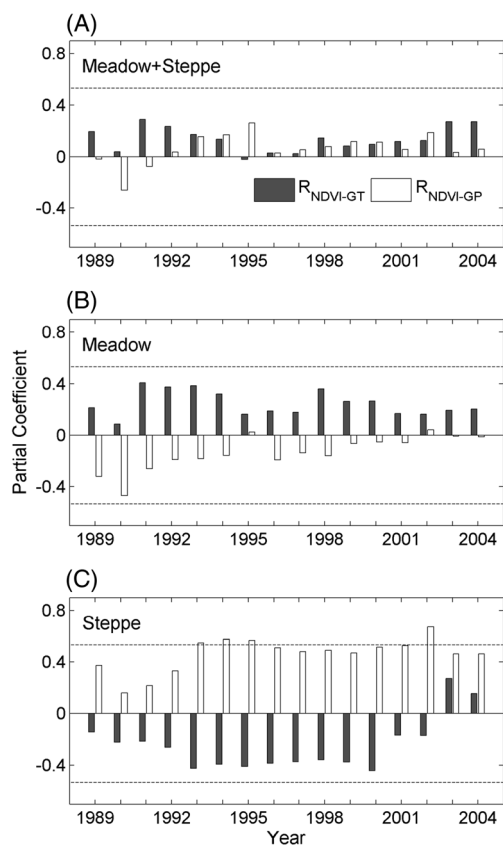
Fig. 1 **a** Temporal variations in partial correlation coefficients between regionally averaged growing season (May–September) NDVI and temperature ($R_{NDVI-GT}$) and precipitation ($R_{NDVI-GP}$) for each 15-year moving window. **b**, **c** Similar to (**a**) but for NDVI averaged for the alpine meadow and alpine steppe, respectively. The partial correlation coefficient was calculated between NDVI and temperature (precipitation), while controlling for precipitation (temperature). The *horizontal axis* indicates the central year of each 15-year moving window. The *dashed line* indicates partial R value corresponding to significance at $P = 0.05$ level

last windows centered on 2003 and 2004 (Fig. 2a). In contrast, the R_{NDVI-T} for summer dropped from between 0.45 and 0.63 in the first five windows to between −0.30 and 0.08 for the other windows (Fig. 2b). R_{NDVI-T} for autumn was between 0.10 and 0.33 for the earlier nine windows and then increased to about 0.50 for the latest window (Fig. 2c). With regard to the response to precipitation, R_{NDVI-P} for spring was between −0.30 and 0.00 for the first four windows, increased to about 0.44 for the windows centered in 1998 and 1999, gradually decreased to about 0.40 for the window centered in 2002, and at last, dropped to about −0.12 for the latest two windows (Fig. 2a). R_{NDVI-P} for summer was between −0.43 and −0.53 for the first two windows and then increased to about −0.20 for the window centered in 2004 (Fig. 2b). R_{NDVI-P} for autumn was between 0.40 and 0.44 for the first two

windows and then decreased to about −0.26 for the window centered in 2004 (Fig. 2c).

At the level of vegetation type, the R_{NDVI-T} and R_{NDVI-P} for alpine meadow (Fig. 2d–f) showed similar temporal variations as those for the regional average but with greater magnitudes of the correlation coefficients. The correlation coefficients for alpine steppe differed greatly from those for the alpine meadow with regard to both sign and magnitude and the temporal changes (Fig. 2g–i). For the alpine steppe, in general, the R_{NDVI-T} for spring increased gradually from about −0.26 in the window centered on 1990 to about 0.18 in the windows centered on 2001 and 2002, that for summer was mostly between −0.09 and 0.25 and that for autumn was between 0.16 and 0.30 for the earlier 12 windows and between 0.49 and 0.65 for the rest 4 windows. Compared with R_{NDVI-T}, R_{NDVI-P} for the steppe showed a different pattern. R_{NDVI-P} for spring in general showed increasing pattern in the earlier 14 windows. It was between 0.19 and 0.41 for the earliest four windows and was about 0.63 in the window 2002 but was about 0.17 and −0.10 for the windows centered in 2003 and 2004, respectively. R_{NDVI-P} for summer also increased slightly, from −0.27 for the window centered in 1989 to 0.20 in the window centered in 2003. R_{NDVI-P} for autumn was between 0.33 and 0.42 in the earlier 6 windows and between 0.16 and 0.36 for the other 10 windows, showing a slightly decreasing pattern.

In terms of the spatial pattern across the TP, $R_{NDVI-GT}$ showed positive temporal trends at 26 of the 51 meteorological stations, mostly in the eastern and central parts of the TP (Fig. 3a), and 18 of the positive temporal trends were significant ($P < 0.05$). Negative trends of $R_{NDVI-GT}$ were found at the other 25 stations, with 15 being significant ($P < 0.05$). On the other hand, 26 stations had positive temporal trends for $R_{NDVI-GP}$, of which 18 were significant ($P < 0.05$), and these were mainly distributed in the southeastern and central parts of the TP (Fig. 3b). Negative trends of $R_{NDVI-GP}$ were found at the other 25 stations, with 18 being significant ($P < 0.05$).

R_{NDVI-T} for spring showed 37 positive trends, with 27 being significant ($P < 0.05$), the largest among the three seasons (Fig. 4a–e). In contrast, R_{NDVI-T} for summer showed decreasing trends at 31 stations, mostly across a transect from south edge to east edge of TP. The positive trends of R_{NDVI-T} for summer were observed for only 20 stations. The positive trends of R_{NDVI-T} for autumn were observed for 33 stations, across a transect from south edge to east edge of TP. R_{NDVI-P} for spring showed positive trends at 36 stations (21 significant, $P < 0.05$), mostly distributed in the northern half and southeastern region (Fig. 4b). Compared with spring, fewer (27) stations had positive trends in R_{NDVI-P} (with 15 significant, $P < 0.05$) for summer, mostly distributed in the southeastern and central regions (Fig. 4d). For autumn, negative trends of R_{NDVI-P} were found at 31 stations, and 23 of them were significant ($P < 0.05$, Fig. 4f).
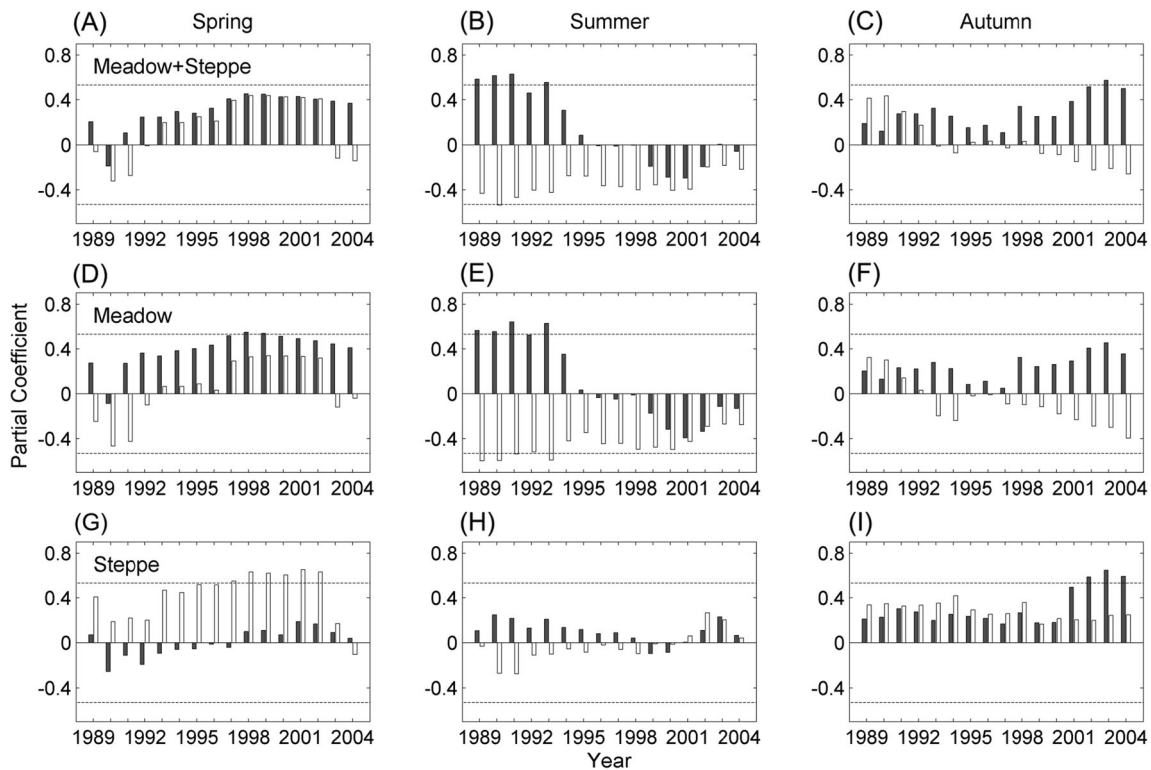
Fig. 2 Temporal variations in partial correlation coefficients between regionally averaged seasonal NDVI and temperature (R_{NDVI-T}) and precipitation (R_{NDVI-P}) for each 15-year moving window for spring (**a**), summer (**b**), and autumn (**c**), respectively. (**d–f**) and (**g–i**) are similar to (**a–c**) but for alpine meadow and alpine steppe, respectively. The partial correlation coefficient was calculated between NDVI and temperature (precipitation), while controlling for precipitation (temperature). The *horizontal axis* indicates the central year of each 15-year moving window. The *dashed line* indicates partial R value corresponding to significance at $P = 0.05$ level
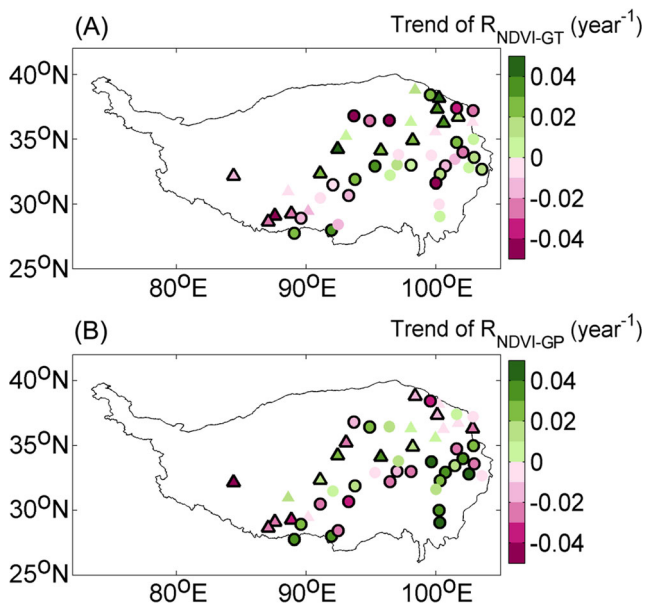
Fig. 3 Spatial distribution of the temporal trends of the partial coefficients between growing season NDVI and temperature ($R_{NDVI-GT}$) or precipitation ($R_{NDVI-GP}$). The trends were obtained between the time series of partial coefficients and the series of the central year of each 15-year moving window. The *black outlines* indicate significance at $P < 0.05$. *Circles* and *triangles* indicate alpine meadow and alpine steppe, respectively

Effects of interactions between temperature and precipitation on the correlations between vegetation activity and climatic factors

At the regional scale, $R_{NDVI-GT}$ was higher in the 15-year windows with higher averaged GP, as revealed by the partial correlation analysis (partial $R = 0.71$, $P = 0.003$, Fig. 5a). Such tendency was stronger for alpine steppe (partial $R = 0.79$, $P < 0.001$) than for alpine meadow (partial $R = 0.27$, $P = 0.331$, Fig. 5c, e). Across the plateau, positive partial correlation coefficients between $R_{NDVI-GT}$ and window average of GP were found in 37 stations (Fig. 5g), and 18 correlation coefficients were significantly positive ($P < 0.05$), while significantly negative correlation coefficients between them were found in only 3 stations. On the other hand, we observed slightly higher $R_{NDVI-GP}$ for the windows with higher window average of GT (partial $R = 0.49$, $P = 0.063$, Fig. 5b). Particularly for alpine meadow, the temporal variations in $R_{NDVI-GP}$ were strongly related with window average of GT (partial $R = 0.85$, $P < 0.001$, Fig. 5d). For alpine steppe, the partial correlation between $R_{NDVI-GP}$ and window average of GT was weak (partial $R = 0.45$, $P = 0.096$, Fig. 5f). Spatially, positive partial correlations between $R_{NDVI-GP}$ and window
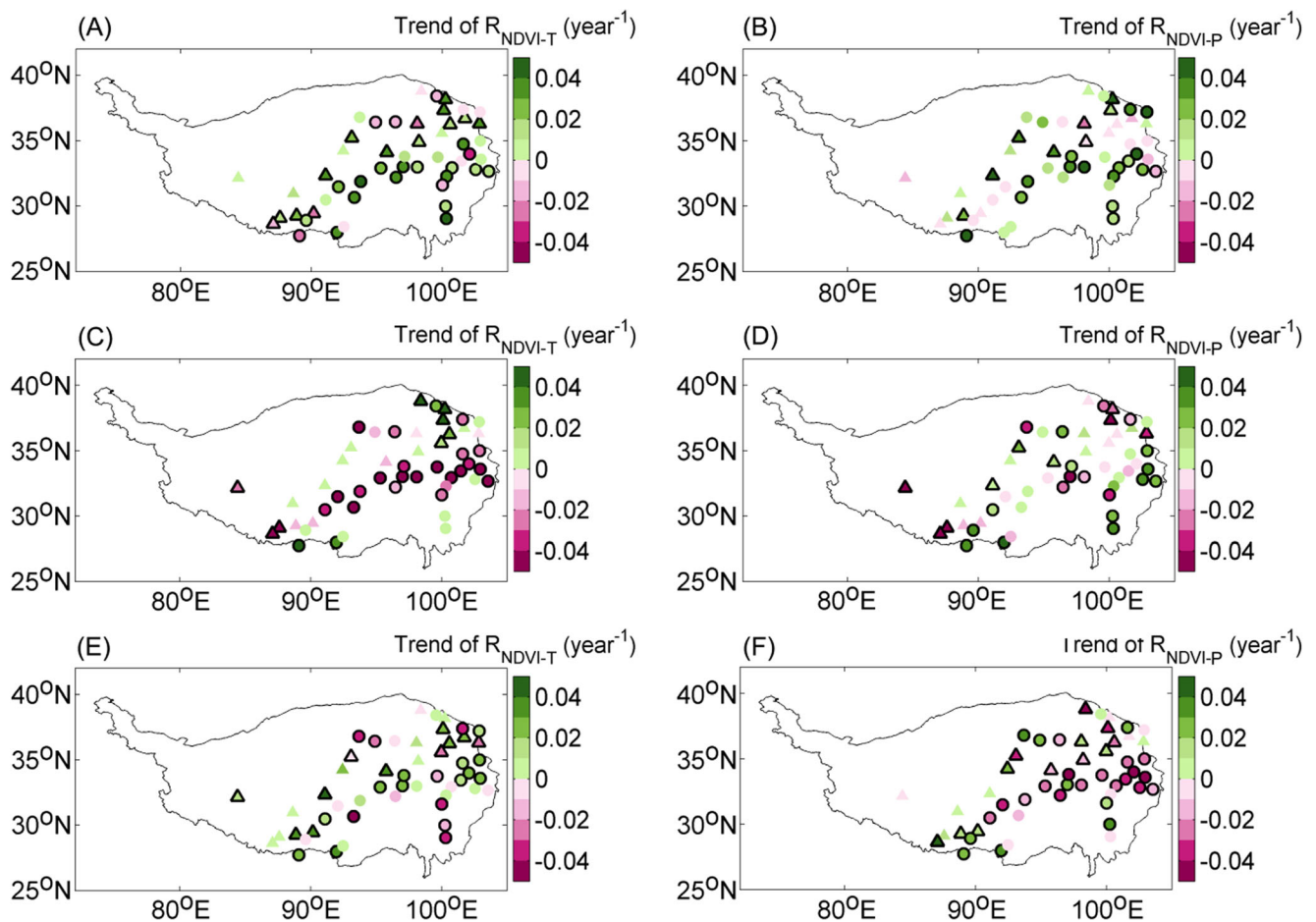
Fig. 4 Spatial distribution of the temporal trends of the partial coefficients between NDVI and temperature (R_{NDVI-T}) or precipitation (R_{NDVI-P}) for different seasons. The trends were obtained between the time series of partial coefficients and the series of the central year of each 15-year moving window. The *black outlines* indicate significance at $P < 0.05$. *Circles* and *triangles* indicate alpine meadow and alpine steppe, respectively

average of GT were mainly in the east half of the TP and negative correlation between them mainly in central and western areas of the TP (Fig. 5h).

Regarding seasonal pattern, for summer, the partial correlation between the R_{NDVI-T} and the window average of summer precipitation was significantly positive ($R = 0.52$, $P = 0.046$, Fig. 6b), while for spring and autumn, the partial correlation between them was insignificant ($P > 0.10$, Fig. 6a, c). Similar patterns were also observed at the level of vegetation type (Fig. 6d–i). Consistent with the results for the regional average, for spring, we observed inter-window positive partial correlations between the R_{NDVI-T} and the window average of precipitation at 31 of the 51 stations, mainly in the southern half of the TP, and the positive correlations were significant ($P < 0.05$) at 10 stations (Fig. 6j). For summer, there were inter-window positive partial correlations between the R_{NDVI-T} and the window average of precipitation at 31 of the 51 stations (significantly positive at nine stations),

and most of those stations were in the southern half of the TP (Fig. 6k). Less than those for spring and summer, at 28 stations, there were inter-window positive partial correlations between the R_{NDVI-T} and the window average of precipitation for autumn, and most of those stations are in the northern area of TP (Fig. 6j).

On regional average, the inter-window variations in R_{NDVI-P} were not significantly related with window average of temperature in either spring or summer (Fig. 7a, b), and the partial correlation between them was significantly negative for autumn (Fig. 7c). In the level of vegetation type, R_{NDVI-P} for alpine meadow was significantly positively, significantly negatively, and not significantly related with window average of temperature for summer, for autumn, and for spring, respectively (Fig. 7d–f). For alpine steppe, R_{NDVI-P} was positively related with window average of temperature for all the three seasons, but only the partial correlation for spring was significant (Fig. 7g–i). Regarding spatial variations, positive partial correlation

Fig. 5 Temporal relationships between $R_{NDVI-GT}$ and 15-year moving-window average of growing season precipitation for NDVI averaged for all (**a**), alpine meadow (**c**), and alpine steppe stations (**e**). In each plot, R indicates the partial correlations between the $R_{NDVI-GT}$ and the moving window average of growing season precipitation over the 16 windows with moving window average of growing season temperature being the control variable. (**b**, **d** and **f**) Similar to (**a**, **c** and **e**) but for the relationships between $R_{NDVI-GP}$ and 15-year moving window average of growing season temperature. Spatial distribution of the temporal partial correlations between $R_{NDVI-GT}$ and moving-window average of precipitation, with the moving window average of temperature as the control variable (**g**). Spatial distribution of the temporal partial correlations between $R_{NDVI-GP}$ and moving window average of temperature, with the moving-window average of precipitation as the control variable (**h**). The *black outlines* in (**g**) and (**h**) indicate significance at $P < 0.05$. *Circles* and *triangles* indicate alpine meadow and alpine steppe, respectively
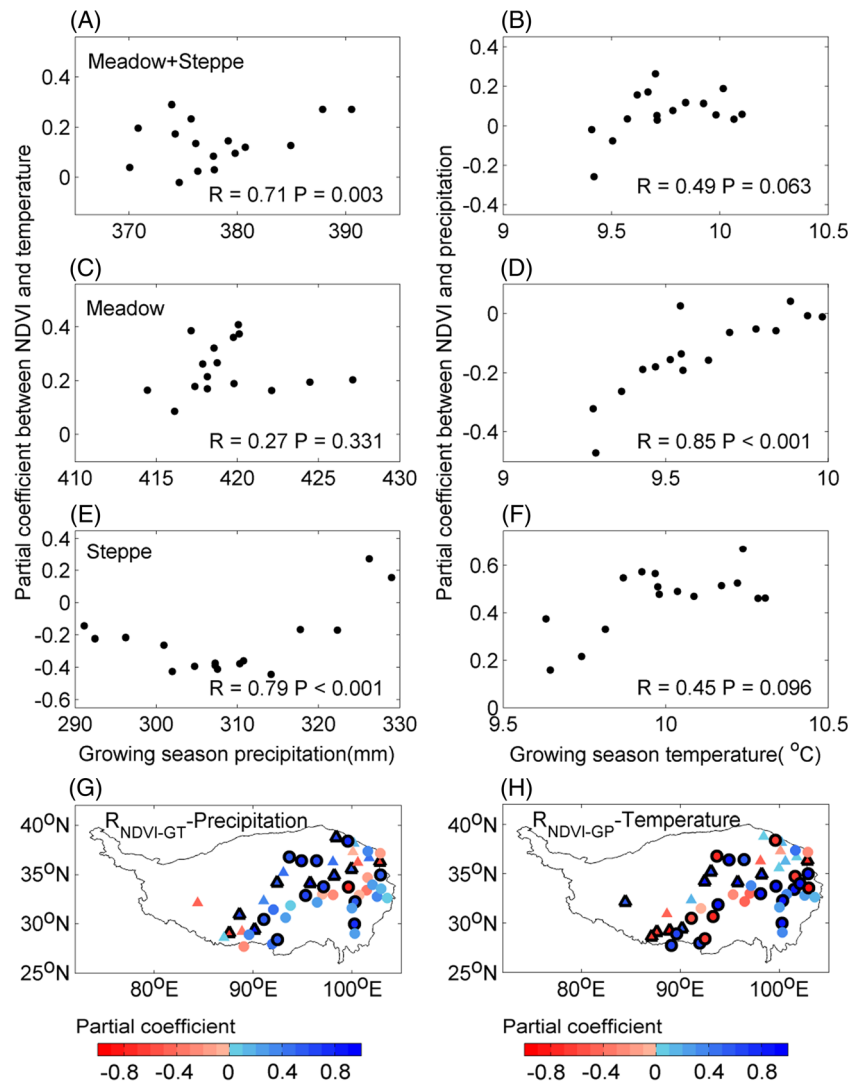

between R_{NDVI-P} and window average of temperature for spring was mainly in the central region and southeastern areas, and negative correlation between them was mainly in the northeastern and south areas (Fig. 7j). There were more stations (31) with positive correlations between R_{NDVI-P} and window average of temperature (12 significant) than stations (20) with negative correlations between them (5 significant). For summer, positive correlations between R_{NDVI-P} and window average of temperature were observed at 27 stations (11 significant at $P < 0.05$), mostly in the eastern regions, and negative correlations between R_{NDVI-P} and temperature were observed in 24 stations (Fig. 7k). For autumn, there were 26 stations at which positive correlations between R_{NDVI-P} and window average of temperature were observed (10 significant at $P < 0.05$), mainly in the west half and northern region of the TP, and negative correlations between R_{NDVI-P} and temperature were observed mainly in the central and east half of the TP (Fig. 7l).

Discussion

Temporal changes in responses of vegetation activity to climate change

Our results show considerable temporal variability in the partial correlation coefficients between NDVI and temperature or precipitation on the TP. This variability indicates temporal changes in the responses of vegetation activity to climate change. The differential responses of vegetation activity to climate change can be also found between the results in previous studies focusing on different periods on the TP (Zhang et al. 2013; Wang et al. 2015b). Therefore, the correlation calculated based on observations in one period could not be simply applied to another period. It is also worthy to note that the temporal changes found in this study based on 30 years may not necessarily reflect long-term transition in the relationship between vegetation activity and climate, which may require longer observations to be addressed.
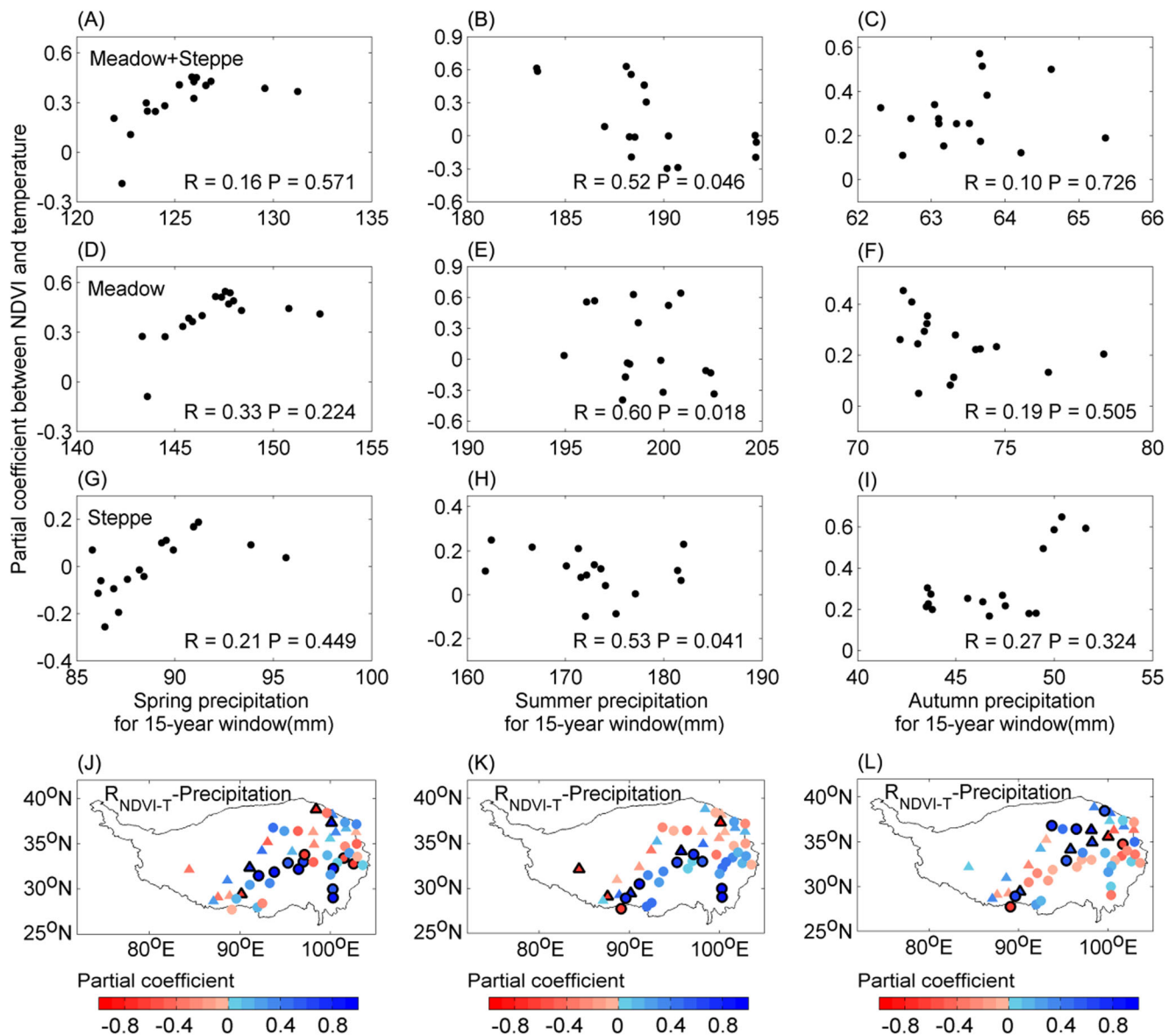
Fig. 6 Temporal relationships between spring R_{NDVI-T} and 15-year moving window average of spring precipitation for NDVI averaged for all (**a**), alpine meadow (**d**), and alpine steppe stations (**g**). In each plot, R indicates the partial correlations between the R_{NDVI-T} and the moving window average of spring precipitation with moving window average of spring temperature being the control variable (**j**). Spatial pattern of the temporal partial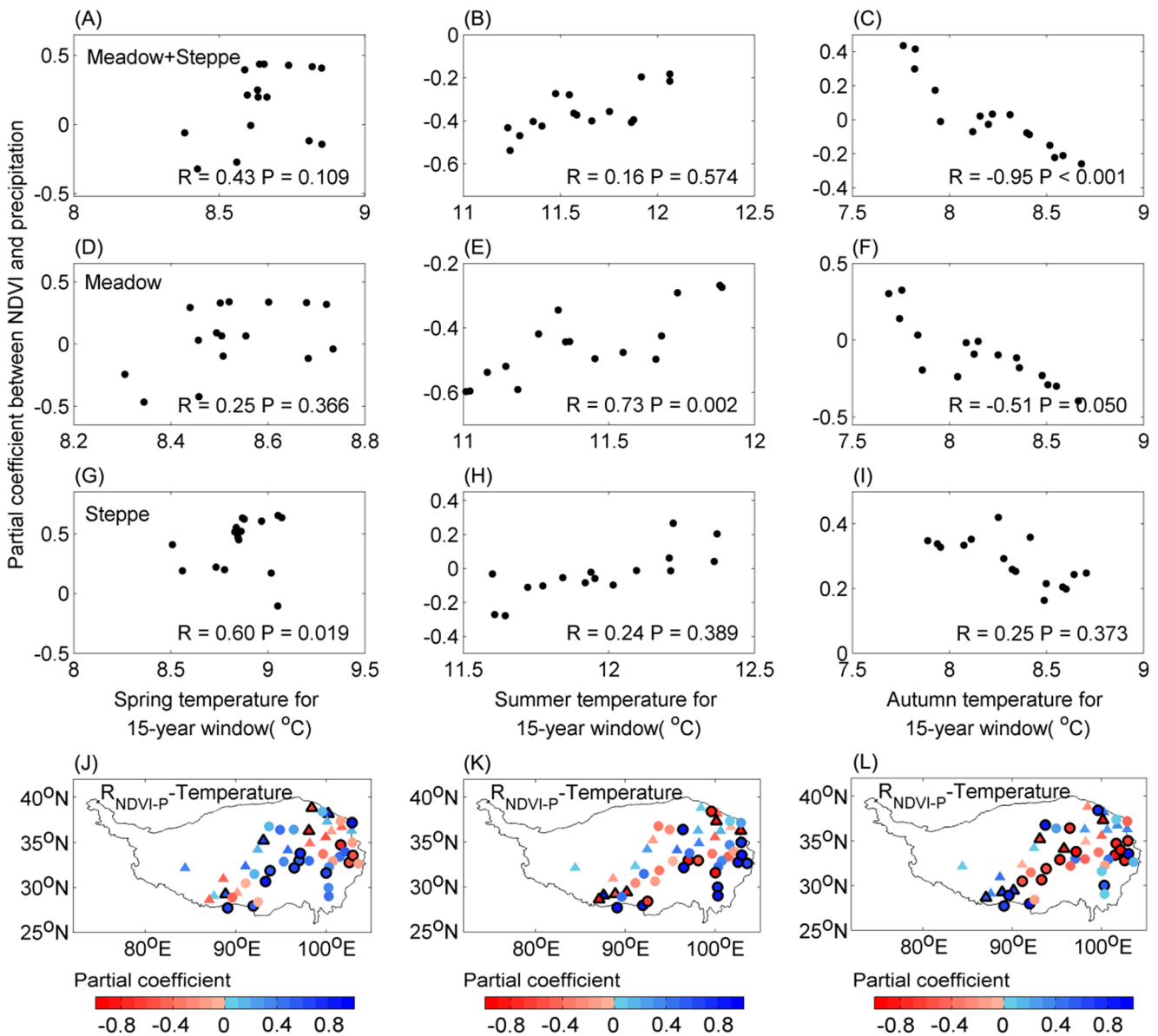 correlation between spring R_{NDVI-T} and 15-year moving-window average of spring precipitation, with 15-year moving-window average of spring temperature being the control variable (**j**). (**b**, **e**, **h** and **k**) and (**c**, **f**, **l** and **l**) are similar to (**a**, **d**, **g** and **j**) but for summer and autumn, respectively. The *black outlines* in (**j**–**l**) indicate significance at $P < 0.05$. *Circles* and *triangles* indicate alpine meadow and alpine steppe, respectively

Interactive effects of temperature and precipitation on vegetation activity

Temperature is often suggested as a constraint on vegetation growth on the TP, and thus, recent climatic warming was deemed to be a major driver of the growth enhancement (Kato et al. 2006; Chu et al. 2007; Hu et al. 2011; Xu et al. 2011). However, there was little explanation available for the differences in the NDVI–temperature relationship among previous studies (Zhou et al. 2007; Hu et al. 2011; Xu et al. 2011;

Zhang et al. 2013, 2014; Wang et al. 2015b). Our analyses showed substantial inter-decadal variations in the response of growing season vegetation activity to temperature on the TP grassland, and such variations were statistically explained by the precipitation. For the alpine meadow, positive responses of vegetation activity were stronger in the 15-year windows with more precipitation. This trend was stronger for the alpine steppe located in the arid region of the TP. The vegetation activity–temperature correlation was negative in the 15-year windows with less precipitation but was positive in the

Fig. 7 Temporal relationships between spring R_{NDVI-P} and 15-year moving window average of spring temperature for NDVI averaged for all (**a**), alpine meadow (**d**), and alpine steppe stations (**g**). In each plot, R indicates the partial correlations between the R_{NDVI-P} and the moving window average of spring temperature with moving window average of spring precipitation being the control variable. Spatial pattern of the temporal partial correlation between spring R_{NDVI-P} and 15-year windows with more precipitation. Our results suggest that the response of vegetation activity to climatic warming on the TP is regulated by precipitation. In periods with little precipitation, water may be a factor that limits vegetation growth and its response to higher temperature, because a higher metabolic rate requires more water, whereas in wetter periods, greater water availability allows a more sensitive response to temperature. This regulatory effect of precipitation on the vegetation response to temperature was stronger for alpine steppe in the more arid region. Therefore, the variations in the relationships moving window average of spring temperature, with 15-year moving-window average of spring precipitation being the control variable (**j**). (**b**, **e**, **h** and **k**) and (**c**, **f**, **l** and **l**) are similar to (**a**, **d**, **g** and **j**) but for summer and autumn, respectively. The *black outlines* in (**j**–**l**) indicate significance at $P < 0.05$. *Circles* and *triangles* indicate alpine meadow and alpine steppe, respectively

between NDVI and temperature among different periods in previous studies on the TP could be partly explained by variation in the amounts of precipitation among the periods. Moreover, our results suggested that the variations in the partial correlation coefficient between growing season vegetation greenness and temperature over the period from 1982 to 2011 (Fig. 1) should to be partly caused by the changes in precipitation (Figs. S3ACE and Fig. 5). Such effect was stronger for alpine steppe than for alpine meadow (Fig. 5c, e). This is different from the case of Arctic region, where the positive

effect of increasing temperature on vegetation activity was weakening during this period (Piao et al. 2014). Other reasons in addition to the regulatory effect of precipitation on the response of vegetation activity to temperature should be further explored.

The positive effect of greater precipitation on vegetation activity response to temperature revealed here indicates that the projected increasing precipitation and temperature in the twenty-first century (Su et al. 2013) are likely to enhance vegetation growth on the TP grassland. However, attention should be given to severe declines in precipitation and drought that occur on the TP (Gao and Yang 2009; Yao et al. 2012; Mohammat et al. 2013). When precipitation is insufficient, increasing temperature may not enhance vegetation activity but may result in vegetation browning on the TP. For the steppe, where a negative NDVI–temperature relationship was observed, if precipitation did not increase, the vegetation coverage could continue to decline as temperature increases, which could result in land degradation as well as desertification in addition to net carbon release. Therefore, precipitation must be included when assessing the vegetation dynamics on the TP, particularly in field-warming experiments that alter the water conditions (Klein et al. 2007; Wang et al. 2012).

Because climatic warming is the major characteristic of climate change and because vegetation growth in cold regions such as the TP is assumed to be temperature limited, most studies have focused on the direct effects of temperature on NDVI. Less research has focused on the impact of precipitation on vegetation dynamics, and no studies have addressed temperature regulation of the vegetation response to precipitation. Similar to the correlations between NDVI and temperature, however, there were also considerable differences in the correlations between NDVI and precipitation among previous studies. For example, Wang et al. (2015b) found that NDVI for the TP steppe and meadow was not significantly ($P > 0.10$) correlated with precipitation from 1982 to 2006, whereas for the period 2000–2009, Zhang et al. (2013) observed a widespread significantly ($P < 0.10$) positive correlation between NDVI and precipitation on the alpine meadow. Consistent with those studies, we also observed increasing correlation coefficients between NDVI and precipitation for both the alpine steppe and the meadow during the past three decades. We further found that such an increase was strongly associated with the temperature increase (Fig. 5 and Fig. S3BDF). This suggests that the response of vegetation activity to precipitation is stronger in the warmer decades and, thus, provides further evidence that low temperature limits the vegetation growth. The negative or weak correlations between NDVI and temperature in this study and previous studies (e.g., Zhang et al. 2013) were not likely caused by a direct negative effect of higher temperature on vegetation growth; it is more likely that higher temperatures increased evaporative demand and that the consequences for plant

growth then depended on whether enough soil water was available to compensate for the increased evapotranspiration. Moreover, higher temperature could result in a stronger positive response of vegetation activity to precipitation. This result provides the first evidence of the regulatory effect of temperature on the vegetation response to precipitation in the TP grassland, and it gives extra support to the proposal that a warmer and wetter climate could result in more flourishing vegetation on the TP.

In addition to temperature and precipitation, there might be other factors that affect vegetation growth. Permafrost is distributed across the TP, and thus, its degradation in some areas might play a potential role (Yang et al. 2004, 2010). During the past few decades, dramatic increases in soil temperature have deepened the active layer and enhanced soil water infiltration and runoff on the TP, thereby reducing water availability in the upper soil layers (Cheng and Wu 2007; Jin et al. 2009) and likely influencing vegetation growth adversely. Changes in nitrogen availability on the TP (Yang et al. 2007; Lu et al. 2012) may also have affected vegetation growth. Moreover, human activities have induced severe grassland degradation, deforestation, and desertification in some areas across the TP (Cui and Graf 2009). Further research is needed to clarify the influences of these changes, particularly to distinguish true biological responses from changes in NDVI values induced directly by human activities. Besides, most meteorological stations are located in the eastern and southern parts of the TP, although we tried to include as many stations as possible. Our result thus should not be directly applied to western areas. More stations with operational metrological observations are needed on the TP.

Conclusions

Detection and attribution of the varying responses of vegetation activity to climate change help us to predict how future climate change will influence the TP grassland ecosystems. This study showed inter-decadal variation in the responses of growing season averaged vegetation activity to inter-annual variations in temperature, and such temperature responses were strongly affected by the inter-decadal changes in the amount of precipitation. On the other hand, growing season-averaged vegetation activity of the alpine steppe showed increasing positive responses to inter-annual variations in precipitation, and the negative inter-annual relationship between growing season-averaged vegetation activity and precipitation for the alpine meadow was weakened over the past three decades. Both changes were explained by the increasing temperature over the past 30 years. Our findings suggest that the responses of growing season averaged vegetation activity to temperature are positively regulated by precipitation, and the positive responses to precipitation could be

strengthened by higher temperature. Given such positive effects of the interactions between temperature and precipitation, the projected warmer and wetter climate in the future may enhance growing season-averaged vegetation activity on the TP grassland.

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