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Critical role of water conditions in the responses of autumn phenology of marsh wetlands to climate change on the Tibetan Plateau

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Abstract:

The Tibetan Plateau, housing 20% of China's wetlands, plays a vital role in the regional carbon cycle. Examining the phenological dynamics of wetland vegetation in response to climate change is crucial for understanding its impact on the ecosystem. Despite this importance, the specific effects of climate change on wetland vegetation phenology in this region remain uncertain. In this study, we investigated the influence of climate change on the end of the growing season (EOS) of marsh wetland vegetation across the Tibetan Plateau. Utilizing satellite-derived Normalized Difference Vegetation Index (NDVI) data and observational climate data, we observed a significant delay in the regionally averaged EOS of marsh vegetation by 4.10 days/decade from 2001 to 2020. Warming preseason temperatures were found to be the primary driver behind the delay in the EOS of marsh vegetation, whereas preseason cumulative precipitation showed no significant impact. Interestingly, the responses of EOS to climate change varied spatially across the plateau, indicating a regulatory role for hydrological conditions in marsh phenology. In the humid and cold central regions, preseason daytime warming significantly delayed the EOS. However, areas with lower soil moisture exhibited a weaker or reversed delay effect, suggesting complex interplays between temperature, soil moisture, and EOS. Notably, in the arid southwestern regions of the plateau, increased preseason rainfall directly delayed the EOS, while higher daytime temperatures advanced it. Our results emphasize the critical role of hydrological conditions, specifically soil moisture, in shaping marsh EOS responses in different regions. Our findings underscore the need to incorporate hydrological factors into terrestrial ecosystem models, particularly in cold and dry regions, for accurate predictions of marsh vegetation phenological responses to climate change. This understanding is vital for informed conservation and management strategies in the face of current and future climate challenges.

KEYWORDS Marsh vegetation, autumn phenology, climate change, water condition, Tibetan Plateau

1 Introduction

Vegetation phenology refers to the seasonal timing of life cycle events in plants and reflects the dynamic responses of terrestrial ecosystems to global climate change (Chen et al., 2017; Peñuelas et al., 2001; Piao et al., 2007, 2008, 2019; Richardson et al., 2013; Wu et al., 2022). Several studies have demonstrated that autumn phenology, signaling the end of the growing season (EOS), reflects the vegetation's growing period better than spring phenology and has a significant effect on carbon sequestration in terrestrial ecosystems (Bao et al., 2020; Fu et al., 2018; Garonna et al., 2014; Zhu et al., 2012).

Global climate change has significantly changed the autumn phenology worldwide, affecting the regional and global energy balance, water flux, and carbon budget (Che et al., 2014; Estiarte et al., 2015; Kelsey et al., 2021; Richardson et al., 2013; Yang et al., 2021). Although the variations in the autumn phenology of vegetation and its response to regional and global climate changes have been extensively analyzed, most studies have focused on grassland or forest ecosystems, with few investigations of wetland ecosystems (Coleman et al., 2022; Ge et al., 2015; Ma et al., 2022; Rice et al., 2018; Yang et al., 2015). Due to the unique environmental conditions in wetlands, climate change may have different effects on the autumn phenology of vegetation compared to other ecosystems (Keppeler et al., 2021; Ma et al., 2022; Molino et al., 2022; Shen et al., 2022). Such differences must be considered if we are to better understand the responses of the global carbon cycle and ecosystem vegetation to climatic variation in the context of global climate change.

As the highest plateau in the world, the Tibetan Plateau is highly sensitive to climate change. And yet the roles of temperature or precipitation in determining the vegetation phenology of the Tibetan Plateau appear contradictory; Some studies assert that temperature plays a dominant role in determining vegetation phenology (Yu et al., 2010), while others argue that precipitation is critical to the vegetation phenology of the region (Shen et al., 2014, 2015a). Known as the “water tower of Asia”, the Tibetan Plateau features a large area of marsh wetlands with relatively high water content (Che et al., 2014; Shen et al., 2011; Shen et al., 2021a) that provide an ideal opportunity for clarifying the dominant effects of temperature and precipitation on the phenology of the vegetation of the Tibetan Plateau.

Recent studies have analyzed the effects of climate change on autumn phenology in various ecosystems of the region (Shen et al., 2022b), reported the phenology of grassland vegetation as positively correlated with precipitation and negatively correlated with daytime maximum temperature. Increased precipitation can enhance the water use efficiency of grassland vegetation, potentially delaying the EOS (Shen et al., 2015b; Wu et al., 2018). However, an increase in daytime maximum temperature also promotes evaporation, reducing water use efficiency and consequently advancing the EOS. Clearly, an improved understanding of the influence of climate variation on the autumn phenology of marsh vegetation in this region can greatly improve our knowledge of the relationships between the vegetation of ecosystems and climate change.

This study utilizes data from 2001 to 2020, incorporating the Normalized Difference Vegetation Index (NDVI) and observational climate data. The aim is to explore spatiotemporal variations in the end of the growing season (EOS) and vegetation responses to climatic variations in the marshes of the Tibetan Plateau. The objective is to enhance our understanding and predictive capabilities regarding phenological changes in marsh vegetation. By illuminating the intricate relationship between vegetation and climate change in this ecologically significant area, our study's findings can offer valuable new insights for ecological management and conservation efforts.

2 Material and method

2.1 Study region

The Tibetan Plateau is located in southwestern China at an altitude of 3,000–5,000 m (average altitude > 4,000 m) and is characterized by a semi-arid and cold climate (Figure 1) (Shen et al., 2022). The annual precipitation exceeds 1,000mm in the southeastern region and is < 100mm in the northwestern region (Cheng et al., 2021; Gao et al., 2013; Piao et al., 2006a). The average temperature in the northwestern and southeastern areas is approximately −6°C and 20°C, respectively (Qin et al., 2022).

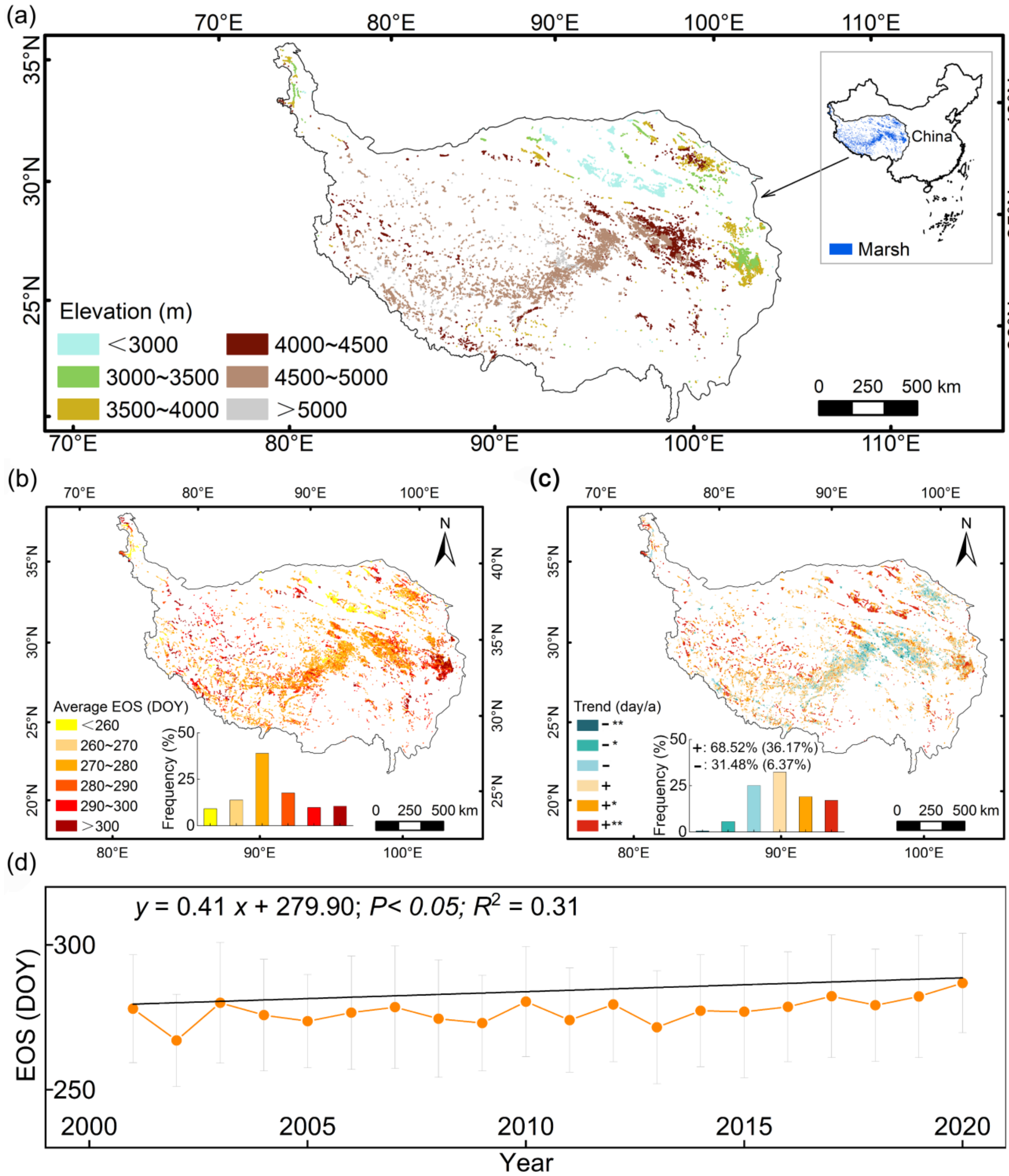

FIGURE 1 Spatiotemporal change of the end of the growing season (EOS) in the marshes of the Tibetan Plateau from 2001 to 2020. (a) Distribution of marshes at different altitudes on the Tibetan Plateau. (b) Spatial patterns of regionally averaged EOS. (c) Temporal trends in EOS. (d) Temporal variations of regionally averaged EOS. The inset histograms at the bottom of (b) and (c) describe the frequency distributions of the average EOS and EOS trend. - and + in C show the negative (advancing) and positive (delaying) trend, respectively; * and ** indicate the trend is significant ($P < 0.05$) and extremely significant ($P < 0.01$), respectively. The error bar and bold black line in D show standard error and linear trend of the regionally averaged EOS, respectively.

As the highest plateau in the world, the Tibetan Plateau is extremely sensitive to climate change (Dong et al., 2012; Zhang et al., 2013). Changes in vegetation phenology in this region serve as crucial indicators of global climate change (Chen et al., 2015). Large wetland areas characterized by marshes are distributed on the Tibetan Plateau and are important for the ecological security of the region and the major river systems that originate there, including the Huanghe (Yellow), Changjiang (Yangzi), and Brahmaputra rivers. The main species of marsh plants distributed on the Tibetan Plateau are *Phragmites australis, Blysmus sinocompressus, Carex pseudosupina, and Kobresia littledalei* (Shen et al., 2021a).

2.2 Data

Satellite-derived NDVI data covering the 2001−2020 period were obtained from the

MOD13Q1 NDVI dataset, with temporal and spatial resolutions of 16 d and 250 m, respectively (Shen et al., 2023). This dataset was provided by the Earth Science Data Systems of the National Aeronautics and Space Administration.

The distribution of marshes in the study area was obtained from the wetland distribution datasets for China for years 2000 and 2015 at a resolution of 30 m × 30 m (Mao et al., 2020). These digital maps were available from the National Earth System Science Data Center. The accuracy of datasets had been verified through field observations, and the producer's and user’s accuracies were over 95% and 98%, respectively (Mao et al., 2020). We used the marsh distribution data for two specific years (2000 and 2015) to extract the unchanged marsh distribution (Shen et al., 2023).

The soil moisture data used in this study were extracted from a 1-km daily soil moisture dataset of in situ measurements conducted in China from 2000 to 2020 (Li et al., 2022). These dataset was produced using spatially dense in situ observations and machine learning, and was obtained from the National Tibetan Plateau Scientific Data Center.

The Climate Change Research Center of the Chinese Academy of Sciences provided the daily gridded climate data from more than 2400 meteorological stations distributed across China. These included daily precipitation as well as the minimum, maximum, and mean temperatures with a spatial resolution of 1 km from 2001 to 2020. Marsh distribution, soil moisture, and climatic data were resampled at a resolution of 250 m × 250 m to maintain consistency with the spatial resolution of the NDVI data (Shen et al., 2021b).

2.3 Methods

Considering that snow cover decreases the NDVI value, consequently affecting the accuracy of satellite-derived phenology data, we replaced the snow-contaminated NDVI values with the median value of the uncontaminated winter NDVI values between November and the following March for each pixel (Shen et al., 2014, 2015). This preprocessing of data has been validated and included in numerous previous studies (Ganguly et al., 2010; Shen et al., 2015a; Wang et al., 2021). Based on previous research (Cong et al., 2013; Liu et al., 2016; Ma et al., 2021; Piao et al., 2006b; Shen et al., 2016; Su et al., 2022), we used the poly fit-maximum approach to extract phenological information (Piao et al., 2006b). In this method, the growth curve of the growing season is fitted with a daily temporal resolution in order to remove abnormal NDVI values (Piao et al., 2006b, 2011), and the EOS date is set to correspond to the time of the largest decrease in NDVI at the end of the growth period. The polyfit-maximum method has been widely used to extract vegetation phenology owing to its excellent performance (Fu et al., 2014; Ma et al., 2022; Piao et al., 2006b, 2011; Shen et al., 2018, 2019, 2023; Su et al., 2022) and consists in a number of steps.

First, we calculated the annual and multiyear average rates of NDVI variation to obtain the corresponding day of the year (DOY) for the vegetation's EOS (Piao et al., 2006b). The following equation was used to calculate the rate of NDVI variation:

$$\mathrm{NDVI}_{\mathrm{ratio}}(\mathrm{t}) = \frac{\mathrm{NDVI}(\mathrm{t}+1) - \mathrm{NDVI}(\mathrm{t})}{\mathrm{NDVI}(\mathrm{t})} \quad (1)$$

where t is time (temporal resolution of 16 days), $NDVI_{ratio}(t)$ is the rate of NDVI change corresponding to period t, NDVI(t) is the NDVI value for period t, and NDVI(t+1) is the NDVI value for period t+1.We detected the time t with the minimum NDVIratio and used the corresponding NDVI(t+1) at time (t+1) as the NDVI threshold for the EOS.

Then, we used the maximum value method of multivariate fitting to construct a unary sixth-degree polynomial function (Piao et al., 2006b) and fitted the annual and multiyear average daily NDVI fitting curve by pixel. The formula used was:

$$\mathrm{NDVI} = \mathrm{a} + \mathrm{a}_1\mathrm{x}^1 + \mathrm{a}_2\mathrm{x}^2 + \mathrm{a}_3\mathrm{x}^3 + \mathrm{a}_4\mathrm{x}^4 + \mathrm{a}_5\mathrm{x}^5 + \mathrm{a}_6\mathrm{x}^6 \qquad (2)$$

where x is the day of each year (DOY); and a_1, a_2, a_3, ... a_6 are the regression coefficients determined by least-squares regression.

Finally, we substituted the DOY into the fitting curve of the multiyear average daily NDVI to obtain the NDVI threshold corresponding to the EOS (Piao et al., 2006b). We applied the NDVI threshold values to the daily NDVI fitting curve of each year to obtain the corresponding EOS values for marsh vegetation in that year.

To analyze the EOS trend and climatic variables on the Tibetan Plateau from 2001 to 2020, we performed a linear regression analysis using the following equation (Piao et al., 2011):

$$\theta_{slope} = \frac{(n\times\sum_{i=1}^{n} i\times x_i) - (\sum_{i=1}^{n} i \sum_{i=1}^{n} x_i)}{n\times\sum_{i=1}^{n} i^2 - (\sum_{i=1}^{n} i)^2} \qquad (3)$$

where n is the number of years analyzed (i.e., 20 years for this study); θ_{slope} indicates the trend (of the EOS or climatic variables) for each pixel; and x_i is the climate variable (or EOS) during the i year. A negative θ_{slope} implies that the temporal variation shows an advancing (i.e., decreasing) trend, whereas a positive θ_{slope} implies a delaying (i.e., increasing) trend.

To investigate the seasonal changes in the EOS in response to climate variations, we analyzed the simple correlation coefficients between monthly and seasonal climate factors and the EOS in previous winter (November to February of the following year), spring (March to May), summer (June to August), and autumn (September to October). In addition, we carried out a partial correlation analysis to further examine correlations between climate variables and the EOS. Through this analysis, it was possible to determine the relationship between two parameters after removing the influence of other factors (Peng et al., 2013; Shen et al., 2016).

The partial correlation coefficient between the time series of the EOS and daytime maximum temperature (or nighttime minimum temperature) was calculated to assess the effect of maximum temperature (or minimum temperature) on the EOS, with precipitation and minimum temperature (or maximum temperature) as the controlling variables. In line with previous studies, the duration of the preseason was calculated for the maximum temperature (or minimum temperature) based on the period preceding the long-term average date of the EOS. When the maximum temperature (or minimum temperature) had the highest absolute value for the partial correlation coefficient with the EOS, this period is referred to as the preseason for the maximum temperature (Shen et al., 2016; Wu et al., 2018) (or the minimum temperature). In this study, an interval of 10 days was adopted to determine the duration of the preseason period and smooth out potential extreme values

(Shen et al., 2015a).

The effect of preseason cumulative precipitation on the EOS was similarly analyzed, and preseason precipitation was determined by setting the maximum and minimum temperatures as the controlling variables (Shen et al., 2016). We did not constrain the duration of preseason precipitation to be equal to that of preseason temperature. In addition, to further analyze the influences of climatic variations on the EOS, we compared the partial correlation coefficients between the EOS and preseason precipitation and between the EOS and maximum and minimum temperatures at different levels of soil moisture.

3 Results

3.1 Spatial and temporal variations in the EOS

The multiyear mean EOS on the Tibetan Plateau occurred primarily between 260th and 300th day of year (DOY), with a regional average of 277th DOY (October 4, or October 3 in leap years) (Figure 1b). The EOS was later in the low altitude (below 4,000 m) humid areas of the eastern Tibetan Plateau and earlier in the high-altitude (above 4,000 m) central areas (Figure 1a,b).

The regionally averaged EOS from 2001 to 2020 across the Tibetan Plateau exhibited a significant delay of 4.10 days per decade ($P < 0.05$) (Figure 1d). The percentage of pixels showing a trend of delayed EOS (68.5%, with a significant proportion of 36.2%, $P < 0.05$) was higher than that showing a trend of advanced EOS

(31.5%, with a significant proportion of 6.4%, $P < 0.05$). The former trend was more evident in the northern and western (high altitude permafrost areas) of the Tibetan Plateau, while the latter was concentrated in the central regions (Figure 1a,c).

3.2 Relationships between the EOS and climate variables

We first analyzed partial correlations between seasonal climate variables and the EOS without using pre-seasons. In autumn, the EOS showed a significant positive correlation with temperatures ($P < 0.05$) but a weak negative correlation with precipitation ($P > 0.05$) across the Tibetan Plateau (Figure S1). The partial correlations between EOS and climatic variables in other seasons were not statistically significant ($P > 0.05$).

We further analyzed the partial correlations between EOS and preseason climatic variables. Across the Tibetan Plateau, the regionally averaged EOS showed a weak negative correlation with preseason cumulative precipitation but a significant positive correlation with preseason maximum and minimum temperatures (Figure 2). Spatially, the proportion of pixels displaying a negative correlation between EOS and preseason cumulative precipitation was approximately 52.1%, and that with a significant negative relationship was approximately 7.6% (Figure 3a). The proportions of pixels showing a positive relationship between EOS and preseason maximum and minimum temperatures were approximately 65.2% and 89.4%, respectively, and the proportions of pixels with a significant ($P < 0.05$) positive relationship were 19.5% and 34.0%, respectively (Figure 3c,e).

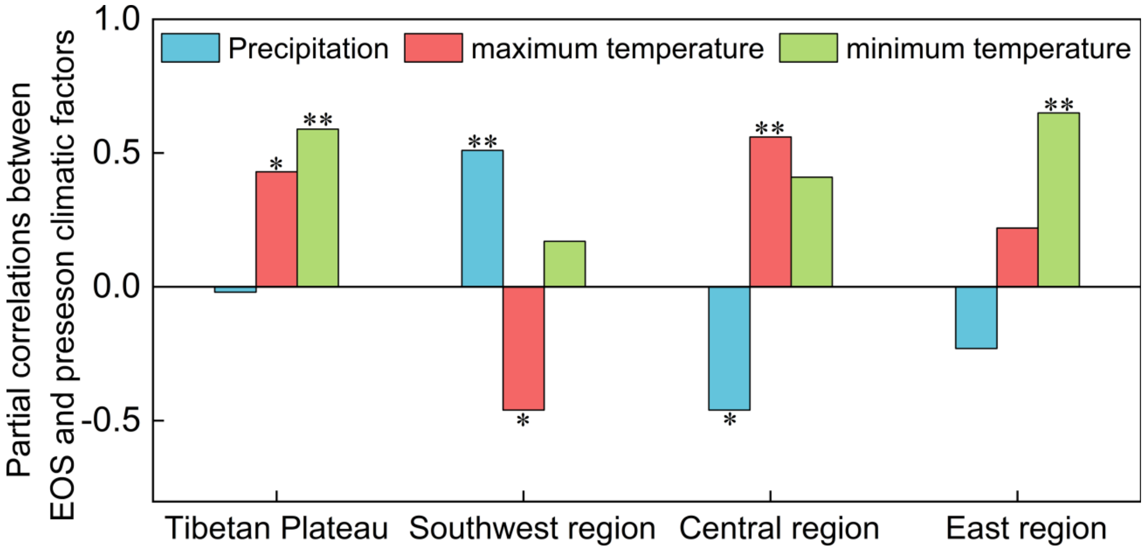

FIGURE 2 Partial correlation coefficients between preseason climatic factors and EOS of marsh vegetation on the Tibetan Plateau. *$P < 0.05$; **$P < 0.01$. Correlations lacking an asterisk are non-significant ($P > 0.05$).

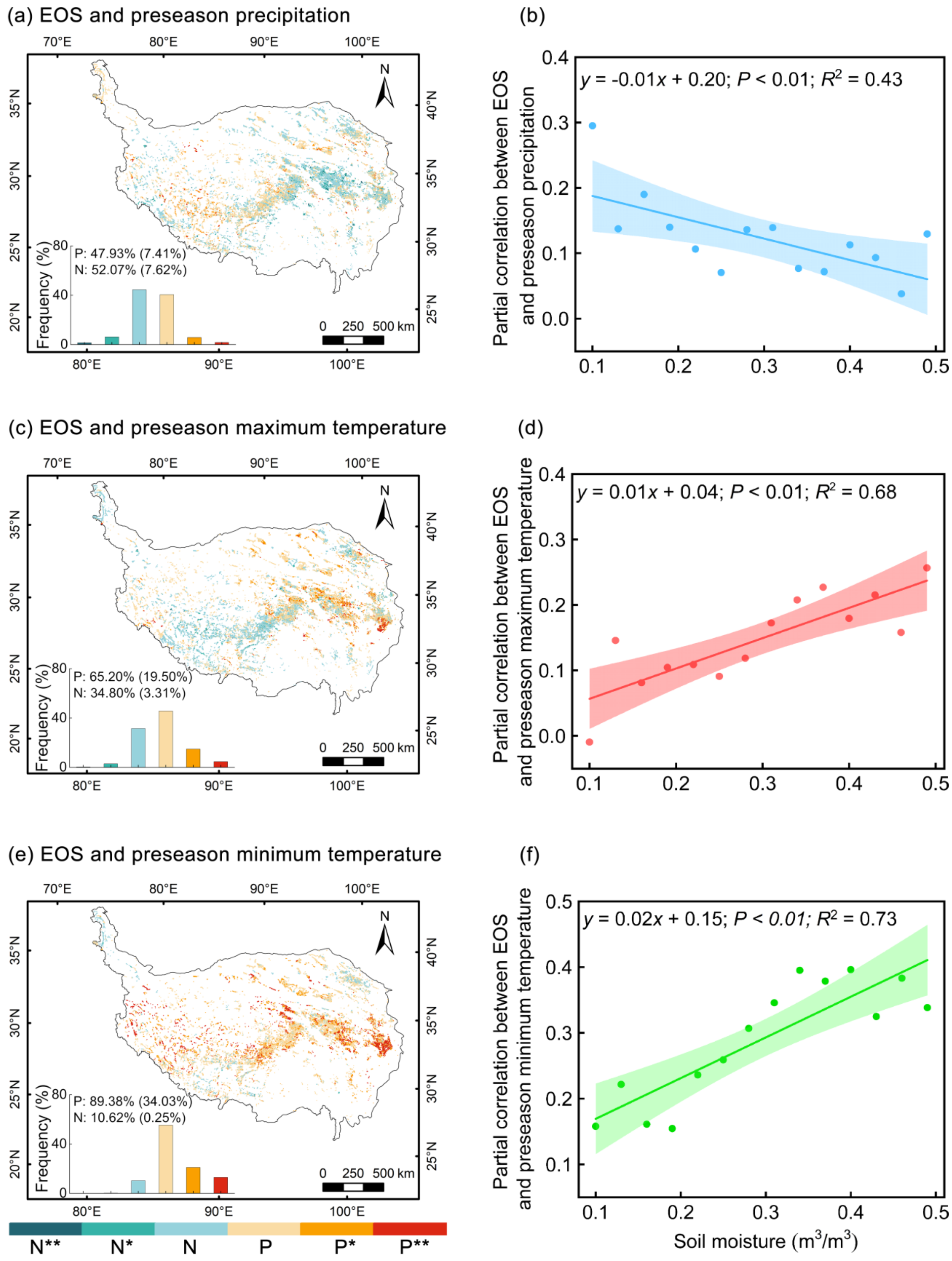

FIGURE 3 Relationship between EOS and preseason climate variables for the marshes on the Tibetan Plateau from 2001 to 2020. Spatial patterns of partial correlation coefficients between EOS and preseason cumulative precipitation (a), maximum

temperature (c), and minimum temperature (e). The changes in partial correlation coefficients between EOS and preseason cumulative precipitation (b), maximum temperature (d), and minimum temperature (f) along the spatial gradient of long-term preseason soil moisture on the Tibetan Plateau from 2001 to 2020. The inset histograms at the bottom of left figures (a, c, e) display the frequency distributions of partial correlation coefficients. - and + show the negative and positive correlation, respectively; * and ** indicate the correlation is significant ($P < 0.05$) and extremely significant ($P < 0.01$), respectively. The body lines in the right figures (b, d, f) indicate the linear fit for the partial correlation coefficients, and the shading represents the 95% confidence band of the fits.

The partial correlations between EOS and preseason climatic variables indicated spatial heterogeneity across the Tibetan Plateau. In the southwestern region, the EOS showed a positive and negative partial correlation with preseason cumulative precipitation and preseason maximum temperature, respectively; however, in the central area, it exhibited a significant negative and positive partial correlation with these two parameters, respectively (Figure 3a,c). The partial relationships between EOS and preseason minimum temperature were positive in most of the study area, and the positive relationships were extremely significant ($P < 0.01$) in the western and eastern regions (Figure 3e).

Subsequently, we examined the partial correlations between EOS and preseason climatic variables under different soil moisture levels in the study region (Figure 3). The results showed that as the preseason soil moisture increased, the positive relationships between EOS and preseason cumulative precipitation gradually weakened, whereas those between EOS and preseason maximum and minimum temperatures became gradually stronger (Figures 3 and 4).

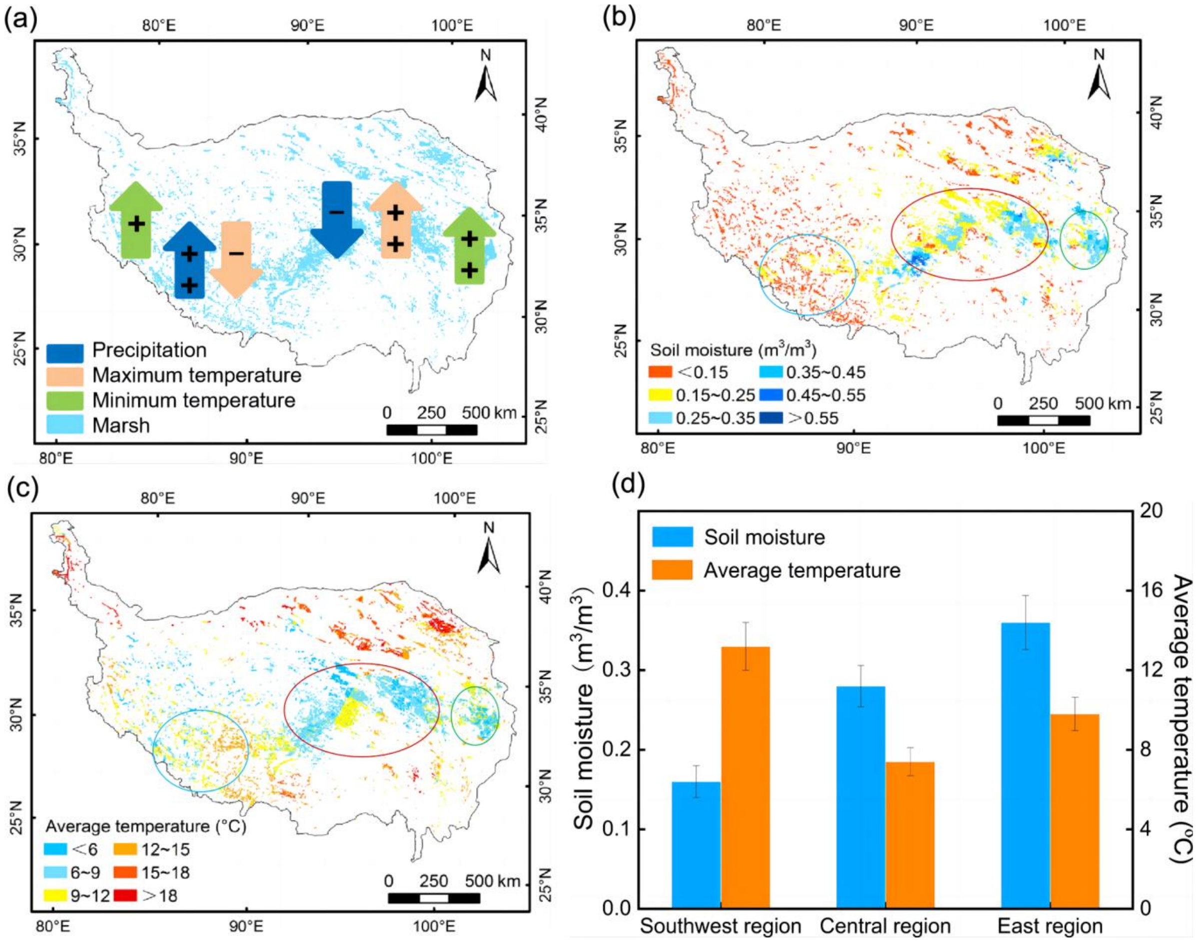

FIGURE 4 Impact of climate change on marsh EOS in different regions of the marshes on the Tibetan Plateau. (a) Conceptual diagrams showing the effects of climate change on the EOS. (b) Spatial distribution of long-term average preseason soil moisture (m^3/m^3). (c) The long-term average preseason temperature (°C) for marsh vegetation on the Tibetan Plateau. (d) long-term average preseason soil moisture (m^3/m^3) and preseason temperature (°C) in different regions of the Tibetan Plateau. “+” and “–” indicate that the

climatic variable had a significant positive and negative effect on the EOS, respectively (P < 0.05). "++" indicates an extremely significant positive effect (P < 0.01). In the southwestern Tibetan Plateau (circled in blue), increased preseason precipitation can significantly delay the EOS, while a higher preseason maximum temperature will advance it. In contrast, in the central Tibetan Plateau (circled in red), a higher preseason maximum temperature significantly delayed the EOS, while an increased preseason precipitation advanced it. In the eastern Tibetan Plateau (circled in green), a higher preseason minimum temperature significantly delayed the EOS.

4 Discussions

4.1 Autumn phenology of marsh vegetation on the Tibetan Plateau

The long-term average EOS for marsh vegetation occurred later in the eastern Tibetan Plateau than in the central and southwestern regions (Figure 1b). This aligns with observations that the eastern area has a lower altitude and a warmer climate (Shen et al., 2021b), thus allowing the growing season to continue for longer. This result is consistent with the findings of (Liu et al., 2021), which showed that the combined EOS for all vegetation types occurred earlier in the central Tibetan Plateau and later in the eastern regions. From 2001 to 2020, the average EOS was delayed by 4.10 days per decade across the plateau (Figure 1c), a trend consistent with the results of Shen et al. (Shen et al., 2022), which showed a delay of 8.2 days in the EOS for vegetation on the plateau over the same period.

4.2 Climatic effects on the regionally averaged EOS for marsh vegetation

The regionally averaged EOS exhibited significant positive partial correlations with preseason daytime maximum and nighttime minimum temperatures but a weak negative correlation with preseason cumulative precipitation across the Tibetan Plateau. The phenology of marsh vegetation on the plateau observed in this study differed from that of grasslands reported in previous studies (Dorji et al., 2013; Shen et al., 2022; Yang et al., 2021).

Previous studies have shown that in the grassland vegetation of the Tibetan Plateau, increased precipitation significantly enhances water use efficiency, delaying the EOS. In these relatively arid systems, the higher maximum temperatures increase evaporation and reduce water use efficiency, thus advancing the EOS (Dorji et al., 2013; Yang et al., 2021). In contrast, the marshes examined in the present study contained far more water (Ganjurjav et al., 2022; Shen et al., 2022), making it less likely that preseason precipitation would affect the regionally averaged EOS for their vegetation, and explain how the abundance of water allowed the EOS to be delayed by the increased preseason temperatures on the Tibetan Plateau.

Our results indicate that preseason temperature is a key factor affecting the EOS, and an increase in this parameter significantly delayed the EOS on the Tibetan Plateau (Figure 3). It is known that increased preseason maximum temperature can promote photosynthesis by enhancing the daytime photosynthetic activity of enzymes (Piao et al., 2007; Turnbull et al., 2022). This increased photosynthesis, together with raised nighttime minimum temperatures that reduce frost and low-temperature constraints (Shen et al., 2016), would further delay the EOS on the plateau.

4.3 Elucidating spatial variations in the effects of climatic change on the EOS

We identified 3 characteristic areas within the Tibetan Plateau, which exhibited differing primary drivers of the changes in EOS; south western, central and eastern.

In the relatively arid areas of the southwestern Tibetan Plateau, the EOS exhibited a significant positive partial correlation with preseason cumulative precipitation but a significant negative correlation with preseason maximum temperature (Figure 3a, c). This indicated that, in this region, higher preseason precipitation significantly delayed the EOS although this was constrained by preseason maximum temperatures tending to significantly advance the EOS. As the climate in this southwestern region is dry and the preseason soil moisture is low (Figure 4), an increase in preseason precipitation can alleviate water stress, enhancing water use efficiency (Liu et al., 2016; Munné-Bosch et al., 2004) and delaying the EOS. At the same time, an increase in maximum temperature would increase hydrological losses through evaporation and reduce the amount of available water (Kelsey et al., 2021; Shen et al., 2016), inhibiting the growth of marsh vegetation. These dynamics fit well with our results, indicating that the EOS was primarily affected by precipitation in the southwestern arid regions of the study area. For the first time, our results indicate that, even in marsh ecosystems with their relatively high water contents, available water may be insufficient for vegetation growth in the drier regions of the Tibetan Plateau.

In the central Tibetan Plateau, a higher preseason temperature delayed the EOS, while increased preseason precipitation advanced it (Figure 3). In the humid and cold areas of the central Tibetan Plateau, soil moisture and temperature are higher and lower, respectively, than those in the southwestern region (Cong et al., 2017) (Figure 4). In light of these conditions, our results indicate that water was not the key factor affecting the growth of marsh vegetation in the central Plateau, although temperature remained a limiting factor.

An increase in maximum temperature can decelerate the process of chlorophyll degradation (Shi et al., 2017) and retard the progression of leaf senescence (Estiarte et al., 2017). In addition, high preseason nighttime temperatures reduce the occurrence of frost damage (Shen et al., 2022). By calculating the number of the frost days, we confirmed that warming preseason nighttime temperatures had the most notable negative effect on the frost days in the central Tibetan Plateau, the coldest region of the study area (Figure S2). This could account for the role of increasing minimum temperature in delaying the EOS in the central Tibetan Plateau. In contrast, increased preseason precipitation could retard the growth of marsh vegetation due to the accompanying cooling effect, which would advance the EOS in the already cold and humid areas of the central Tibetan Plateau.

In the low altitude humid regions in the east and high-altitude cold permafrost regions in the west, the EOS showed a significant positive correlation with preseason minimum temperature (Figure 3), indicating that an increase in this parameter delayed the EOS in the marshes distributed in these regions of the Tibetan Plateau. However, the mechanisms through which minimum temperature affects the EOS may differ between these two areas. On one hand, increased nighttime temperatures cause a greater loss of organic matter due to enhanced respiration, but on the other hand it can also stimulate accumulation of more organic matter via the overcompensation effect (Shen et al., 2021b, 2022), a phenomenon through which the vegetation recovers and exceeds its original state by promoting photosynthesis the day after the enhanced respiration (Peng et al., 2013). It has been reported that the occurrence of this effect is favored by the presence of sufficient water and nutrients (Peng et al., 2013; Shen et al., 2022).

In cold high-altitude regions, the physiological processes causing vegetation senescence are typically determined by low temperatures during cold nights (Tang et al., 2016). In the high-altitude cold permafrost regions of the western Tibetan Plateau, nighttime minimum temperature is generally low (Nan et al., 2005), and an increase in preseason minimum temperature would delay the EOS by alleviating frost damage and retarding vegetation senescence (Cong et al., 2017). In contrast, in the low altitude areas of the eastern Tibetan Plateau, the climate is relatively warm and humid (Figure 4) and marsh vegetation has access to sufficient water (Shen et al., 2022). Therefore, although organic matter may be depleted through the respiration of marsh vegetation due to nighttime warming, increased temperatures can also promote photosynthesis, leading to accumulation of more organic matter the following day via the over compensation effect (Belsky et al., 1986; Shen et al., 2021b, 2022). This would contribute to delaying the EOS in the eastern region as a consequence of the increased preseason minimum temperatures.

By building a multi-variable regression for each pixel, we showed spatially which preseason variable is the most important for affecting the EOS. The results confirmed that preseason cumulative precipitation and minimum temperature played a crucial role in the relatively arid southwestern and humid eastern Tibetan Plateau, respectively (Figure S3). By comparing the partial correlation coefficients between EOS and climatic factors in different regions, we confirmed that as annual mean temperature increased, the delaying effects of higher preseason maximum and minimum temperatures on the EOS gradually weakened, while the delaying effect of increased preseason precipitation became gradually stronger (Figure 5). Based on our results, we propose that the effects of climate variations on the EOS differ depending on the hydrological constraints on soil moisture in the marshes within the Tibetan Plateau. As such, we further compared the partial correlations between EOS and climatic factors for preseason soil moisture gradients of 0.05 m3/m3. The results showed that as soil moisture increased, the delaying effect of increased preseason precipitation on the EOS gradually weakened (Figure 3), while the delaying effects of higher preseason maximum and minimum temperatures became gradually stronger (Figure 3). This finding supports the proposal that increased precipitation and warming temperatures significantly delayed the EOS for marsh vegetation in the arid southwestern Tibetan Plateau and the humid central and eastern areas, respectively. In contrast, increasing daytime temperatures and precipitation advanced the EOS in the arid southwestern and humid central areas due to the reduced soil moisture and cooling effect, respectively (Figure 3).

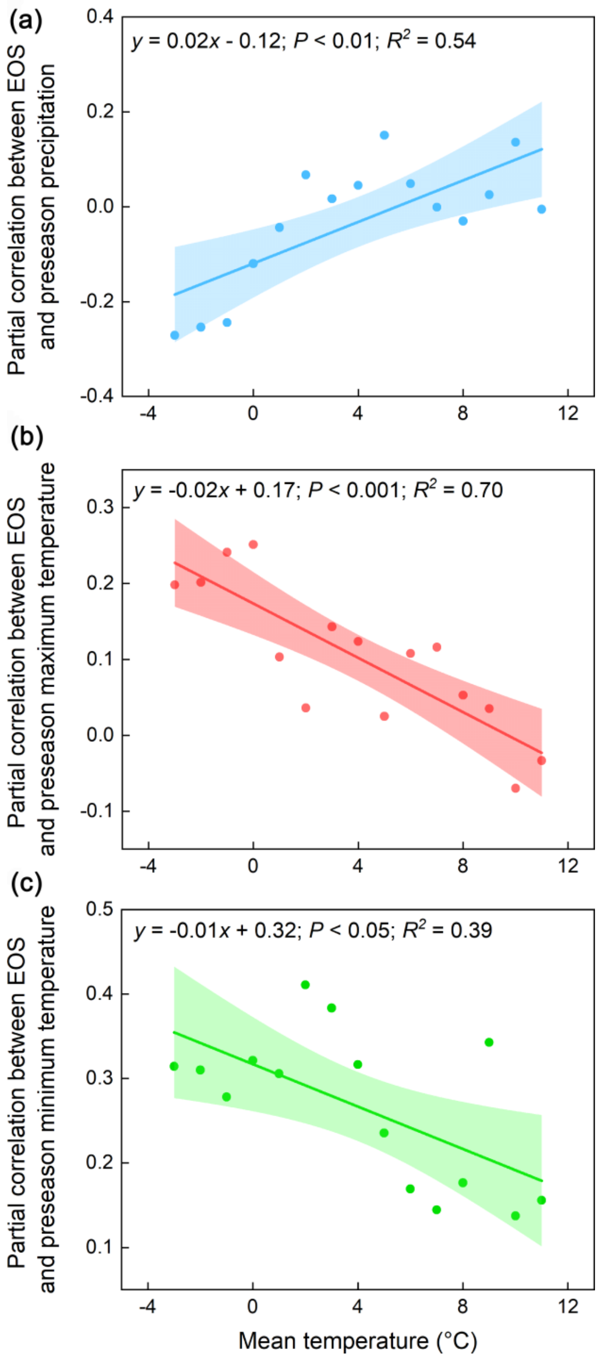

FIGURE 5 The changes in partial correlation coefficients between EOS and preseason cumulative precipitation, maximum temperature, and minimum temperature along the spatial gradient of long-term annual mean temperature on the Tibetan Plateau from 2001 to 2020. The body lines in the figures indicate the linear fit for the partial correlation

coefficients, and the shading represents the 95% confidence band of the fits.

4.4 Attribution of temporal changes in the EOS

To further explain the temporal and spatial variations in the EOS, we calculated the rates at which precipitation and maximum and minimum temperatures varied on the plateau from 2001 to 2020 (Figure 6 and Table 1). The preseason cumulative precipitation and maximum and minimum temperatures exhibited increasing trends (0.52 mm/a, 0.02 °C/a, and 0.05 °C/a, respectively), but only the increase in the minimum temperature was significant ($P < 0.05$). Because the EOS showed a significant positive relationship with preseason minimum temperature, the increase in this parameter may partly account for the delayed EOS on the Tibetan Plateau (Figure 1 and Table 1).

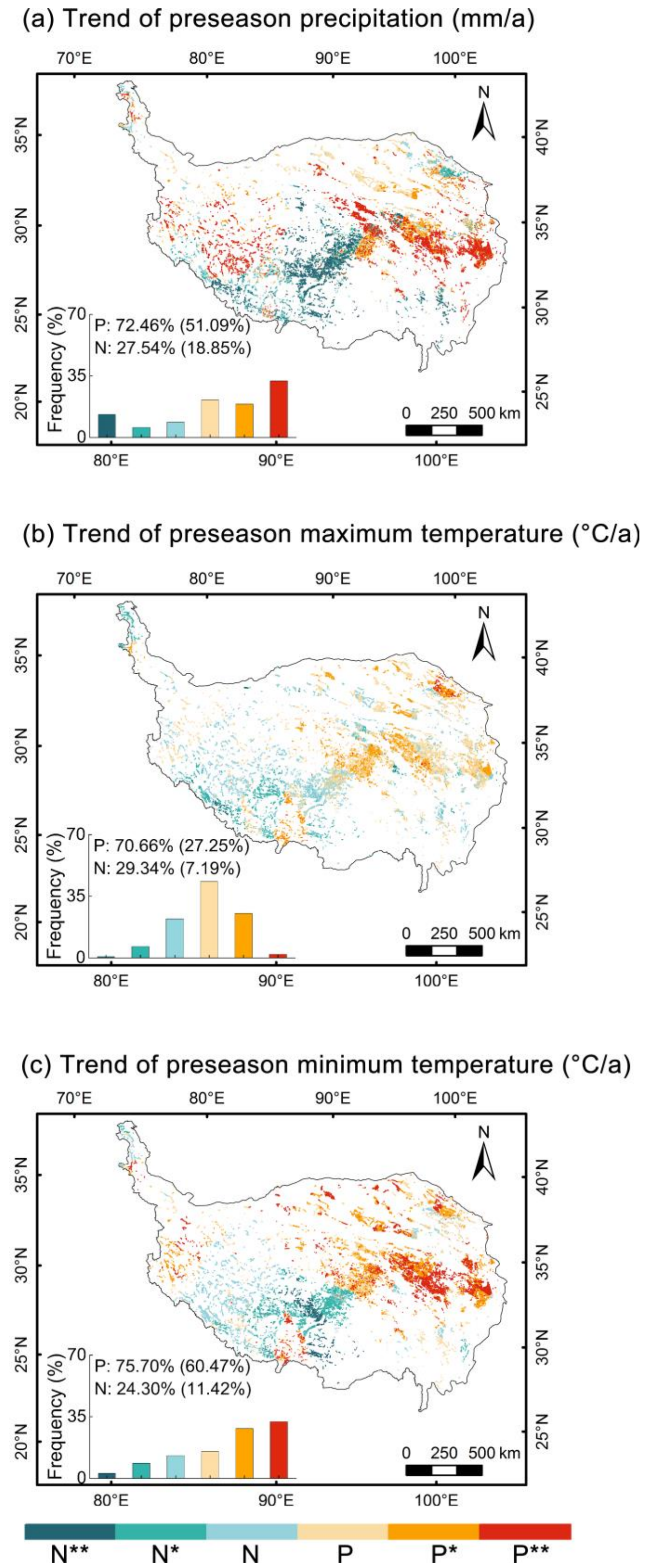

FIGURE 6 Preseason climate change in the marshes of the Tibetan Plateau. Spatial patterns of temporal trends in preseason cumulative precipitation (a), maximum

temperature (b), and minimum temperature (c) in the marshes of the Tibetan Plateau from 2001 to 2020. The inset histograms at the bottom of figures display the frequency distributions of the trends. - and + show the negative and positive trend, respectively; * and ** indicate the variation trend is significant ($P < 0.05$) and extremely significant ($P < 0.01$), respectively.

Table 1 Temporal trends of preseason and seasonal precipitation (mm/a), maximum temperature (°C/a), and minimum temperature (°C/a) in marshes of the Tibetan Plateau from 2001 to 2020.

	Precipitation	maximum temperature	minimum temperature
Preseason	0.52*	-0.02	0.05*
Spring	0.22	0.01	0.05**
Summer	0.31	0.05*	0.06*
Autumn	0.14	0.05	0.08**
Winter	0.79	-0.03	0.03

$^{**}P < 0.01$; $^{*}P < 0.05$.

In the high-altitude arid area of the southwestern Tibetan Plateau, the EOS was positively correlated with preseason cumulative precipitation (Figure 3). As preseason cumulative precipitation showed significant increasing trends in the high-altitude arid area of the southwestern Tibetan Plateau (Figure 6), the increase in preseason precipitation may partly account for the delayed EOS in this region (Figure 1). In the low altitude humid areas in the east and high-altitude cold permafrost areas in the west, the EOS was positively correlated with preseason minimum temperature (Figure 3). Therefore, we deduce that the extremely significant increases of preseason minimum temperature may contribute to the delayed EOS in these regions (Figures 1 and 6). In the northeastern area of the plateau, the EOS appeared to occur earlier throughout the study period (Figure 1), possibly due to the rise in preseason minimum temperature (Figures 3 and 6).

5 Conclusions

Our study uncovers several crucial findings regarding the end of the growing season (EOS) in marsh vegetation across the Tibetan Plateau. Firstly, we observed a significant delay in the EOS by 4.10 days/decade during the study period. Secondly, while average preseason cumulative precipitation did not notably impact the regionally averaged EOS, warmer preseason temperatures led to a significant delay in the average EOS of marsh vegetation. Notably, the delaying effect of higher nighttime temperatures on the regionally averaged EOS was more pronounced than that of daytime temperatures. This asymmetric response to diurnal temperature variations can be attributed to the widespread delaying effect of nighttime warming and the spatially diverse relationship between EOS and daytime temperature, influenced by water conditions. Furthermore, our evidence indicates that hydrological factors influencing soil water content play a regulatory role in the impact of climate change on the EOS. As soil moisture decreased, the delaying effect of increasing preseason maximum temperatures gradually weakened and even reversed, while the delaying effect of increased preseason precipitation was strengthened. In the humid, cold regions of the central Tibetan Plateau, higher preseason maximum temperatures significantly delayed the EOS, whereas increased precipitation advanced it, potentially due to a cooling effect. In the low altitude, humid regions in the east, higher minimum temperatures delayed the EOS, possibly due to an overcompensation effect. In the arid southwestern area, increased precipitation directly and significantly delayed the EOS, whereas higher daytime temperatures advanced it, likely due to limited water availability. These findings suggest that the EOS in these regions is constrained by water conditions, even within marsh ecosystems. Overall, our study highlights the asymmetric influences of daytime and nighttime temperatures on the EOS of marsh vegetation, particularly in the context of global diurnal asymmetric warming (stronger warming during nighttime than during daytime). It underscores the importance of considering water conditions in EOS simulations conducted by terrestrial ecosystem models in cold and dry regions worldwide.

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Conflict of interest statement

The authors declare no conflict of interest.

Data availability statement

The MOD13Q1 NDVI dataset was provided by the Earth Science Data Systems of the National Aeronautics and Space Administration (https://ladsweb.modaps.eosdis.nasa.gov). The distribution of marshes was obtained from the wetland distribution datasets for China (http://www.geodata.cn). The climate data was available from the National Meteorological Information Center of China (http://data.cma.cn/data). The soil moisture data were obtained from the National Tibetan Plateau Scientific Data Center (https://data.tpdc.ac.cn).

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