

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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1 Critical role of water conditions in the responses of autumn phenology

2 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 27 the regional carbon cycle. Examining the phenological dynamics of wetland vegetation 28 in response to climate change is crucial for understanding its impact on the ecosystem. 29 Despite this importance, the specific effects of climate change on wetland vegetation 30 phenology in this region remain uncertain. In this study, we investigated the influence of 31 climate change on the end of the growing season (EOS) of marsh wetland vegetation 32 across the Tibetan Plateau, utilizing satellite-derived Normalized Difference Vegetation 33 Index (NDVI) data and observational climate data. We observed that the regionally 34 averaged EOS of marsh vegetation across the Tibetan Plateau was significantly (P <35 0.05) delayed by 4.10 days/decade from 2001 to 2020. Warming preseason temperatures 36 37 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, 38 the responses of EOS to climate change varied spatially across the plateau, indicating a 39 regulatory role for hydrological conditions in marsh phenology. In the humid and cold 40 central regions, preseason daytime warming significantly delayed the EOS. However, 41 areas with lower soil moisture exhibited a weaker or reversed delay effect, suggesting 42 complex interplays between temperature, soil moisture, and EOS. Notably, in the arid 43 southwestern regions of the plateau, increased preseason rainfall directly delayed the 44 EOS, while higher daytime temperatures advanced it. Our results emphasize the critical 45 46 role of hydrological conditions, specifically soil moisture, in shaping marsh EOS responses in different regions. Our findings underscore the need to incorporate 47

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.

52

KEYWORDS marsh wetlands, vegetation, autumn phenology, climate change, water
 condition, Tibetan Plateau

55

56 **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 69 ecosystems (Coleman et al., 2022; Ge et al., 2015; Ma et al., 2022; Rice et al., 2018; 70 Yang et al., 2015). Due to the unique environmental conditions in wetlands, climate 71 change may have different effects on the autumn phenology of vegetation compared to 72 other ecosystems (Keppeler et al., 2021; Ma et al., 2022; Molino et al., 2022; Shen, 73 Wang, et al., 2022). Such differences must be considered if we are to better understand 74 the responses of the global carbon cycle and ecosystem vegetation to climatic variation 75 in the context of global climate change. 76

As the highest plateau in the world, the Tibetan Plateau is highly sensitive to 77 climate change. And yet the roles of temperature or precipitation in determining the 78 vegetation phenology of the Tibetan Plateau appear contradictory; Some studies assert 79 that temperature plays a dominant role in determining vegetation phenology (Yu et al., 80 2010), while others argue that precipitation is critical to the vegetation phenology of the 81 region (Shen et al., 2014; Shen, Piao, Cong, et al., 2015). Known as the "water tower of 82 Asia", the Tibetan Plateau features a large area of marsh wetlands with relatively high 83 water content (Che et al., 2014; Shen et al., 2011; Shen, Jiang, et al., 2021) that provide 84 an ideal opportunity for clarifying the dominant effects of temperature and precipitation 85 on the phenology of the vegetation of the Tibetan Plateau. 86

Recent studies have analyzed the effects of climate change on autumn phenology
in various ecosystems of the region (Shen, Wang, et al., 2022), reported the phenology
of grassland vegetation as positively correlated with precipitation and negatively

correlated with daytime maximum temperature. Increased precipitation can enhance the 90 water use efficiency of grassland vegetation, potentially delaying the EOS (Shen, Piao, 91 Dorji, et al., 2015; Wu et al., 2018). However, an increase in daytime maximum 92 temperature also promotes evaporation, reducing water use efficiency and consequently 93 advancing the EOS. Clearly, an improved understanding of the influence of climate 94 variation on the autumn phenology of marsh vegetation in this region can greatly 95 improve our knowledge of the relationships between the vegetation of ecosystems and 96 climate change. 97

This study utilizes data from 2001 to 2020, incorporating the Normalized 98 Difference Vegetation Index (NDVI) and observational climate data, to explore 99 100 spatiotemporal variations in the end of the growing season (EOS) and their responses to climatic variations in the marshes of the Tibetan Plateau. The objective is to enhance 101 102 our understanding and predictive capabilities regarding phenological changes in marsh vegetation. By illuminating the intricate relationship between vegetation and climate 103 change in this ecologically significant area, the findings of our study can offer valuable 104 new insights for ecological management and conservation efforts. 105

106

107 2 Material and method

108 2.1 Study region

109 The Tibetan Plateau is located in southwestern China at an altitude of 3,000–5,000 m
110 (average altitude > 4,000 m) and is characterized by a semi-arid and cold climate

(Figure 1) (Shen, Liu, 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). The average temperature in the northwestern and southeastern areas is
approximately -6°C and 20°C, respectively (Qin et al., 2022).

As the highest plateau in the world, the Tibetan Plateau is extremely sensitive to 115 climate change (Dong et al., 2012; Zhang et al., 2013). Changes in vegetation 116 phenology in this region serve as crucial indicators of global climate change (Chen et al., 117 2015). Large wetland areas characterized by marshes are distributed on the Tibetan 118 Plateau and are important for the ecological security of the region and the major river 119 systems that originate there, including the Yangtze, Yellow, and Lancang rivers (Liu et 120 al., 2021; Shen et al., 2023). The main species of marsh plants distributed on the Tibetan 121 Plateau are Phragmites australis, Blysmus sinocompressus, Carex pseudosupina, and 122 123 Kobresia littledalei (Shen, Jiang, et al., 2021).

124

125 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 \times 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). In order to exclude the impact of land use or cover change on the results, we used the marsh distribution data for two specific years (2000 and 2015) to extract the unchanged marsh distribution as the study area (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 2001 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 \times 250 m to maintain consistency with the spatial resolution of the NDVI data (Shen, Liu, et al., 2021).

151

152 2.3 Methods

153 Considering that snow cover decreases the NDVI value, consequently affecting the accuracy of satellite-derived phenology data, we replaced the snow-contaminated NDVI 154 values with the median value of the uncontaminated winter NDVI values between 155 November and the following March for each pixel (Shen et al., 2014; Shen, Piao, Cong, 156 et al., 2015). This preprocessing of data has been validated and included in numerous 157 previous studies (Ganguly et al., 2010; Shen, Piao, Cong, et al., 2015; Wang et al., 158 2021). In addition, we removed the pixels with long-term (2001-2020) mean NDVI 159 averaged from May to September ≤ 0 to exclude the impact of non-vegetation pixels on 160 the results (Shen, Jiang, et al., 2021). In general, with increasing Julian day, the NDVI 161 value for a vegetation pixel gradually increases and then declines after reaching its 162 163 maximum. Consistent with many previous studies (e.g. Ma et al., 2022; Piao et al., 2011; Shen et al., 2018, 2019; Su et al., 2022; Wu & Liu, 2013; Zhang et al., 2013), this study 164 165 used the Polyfit-Maximum method (Piao et al., 2006, 2011) to represent the seasonal changes in NDVI as a function of Julian day and extract phenological information. 166 Because of the impact of some nonvegetation effects of cloud, atmosphere, solar zenith 167 angle, and other factors, some NDVI values are lower than their two adjacent ones. 168 Evidently, the polynomial function fitting a smooth NDVI seasonal curve as a function 169 of time can help smooth these abnormal values (Piao et al., 2006; 2011). For the 170 Polyfit-Maximum method, it is proved that a sixth-degree polynomial function is better 171 172 to fit the NDVI time series and applicable in most cases (Kafaki et al., 2009; Piao et al., 2006, 2011; Su et al., 2022; Yang et al., 2015). This method has been demonstrated to be 173

174	capable of depicting the seasonal patterns of NDVI time series in northern mid and high
175	latitudes well (e.g. Jeong et al., 2011; White et al., 2009; Wu & Liu, 2013). It is
176	generally considered that the end date of growing season represents the period when
177	vegetation growth begins to decline rapidly (Lee et al., 2002; Reed et al., 1994; Yu et al.,
178	2003; Zhang et al., 2003). This date indicates when the NDVI annual cycle transitions
179	from one stage to another, and this transition date corresponds to the times at which the
180	rate of change in curvature in the NDVI shows local maximums (Piao et al., 2006;
181	Zhang et al., 2003). Therefore, in the Polyfit-Maximum approach, the EOS date is set to
182	correspond to the time of the largest decrease in NDVI at the end of the growth period
183	(Piao et al., 2006). The Polyfit-Maximum method has been widely used to extract
184	vegetation phenology owing to its excellent performance (e.g. Cong et al., 2013; Fu et
185	al., 2014; Jeong et al., 2011; Kafaki et al., 2009; Li et al., 2023; Liu et al., 2016; Liu et
186	al., 2023; Ma et al., 2022; Piao et al., 2015; Shen et al., 2018, 2019, 2023; Su et al.,
187	2022; Wang et al., 2016; Wang et al., 2018; Wu & Liu, 2013; Yang et al., 2015; Yang et
188	al., 2021; Zhang et al., 2013; Zhou et al., 2020) 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., 2006). The following equation was used to calculate the rate of NDVI variation:

192
$$NDVI_{ratio}(t) = \frac{NDVI(t+1) - NDVI(t)}{NDVI(t)}$$
(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 195 NDVI(t+1) is the NDVI value for period t+1.We detected the time t with the minimum 196 NDVI_{ratio} and used the corresponding NDVI(t+1) at time (t+1) as the NDVI threshold 197 for the EOS.

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

201 NDVI =
$$a + a_1 x^1 + a_2 x^2 + a_3 x^3 + a_4 x^4 + a_5 x^5 + a_6 x^6$$
 (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., 2006). 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):

211
$$\theta_{slope} = \frac{\left(n \times \sum_{i=1}^{n} i \times x_i\right) - \left(\sum_{i=1}^{n} i \sum_{i=1}^{n} x_i\right)}{n \times \sum_{i=1}^{n} i^2 - \left(\sum_{i=1}^{n} i\right)^2} \quad (3)$$

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 variable) for each pixel; and x_i is the EOS (or climatic variable) during the *i* year. A negative θ_{slope} implies that the temporal variation shows an advancing (or a decreasing) trend, whereas a positive θ_{slope} implies a delaying 216 (or increasing) trend.

To investigate the seasonal changes in the EOS in response to climate variations, 217 we analyzed the simple correlation coefficients between monthly and seasonal climate 218 factors and the EOS in previous winter (November to February of the following year), 219 220 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 221 between climate variables and the EOS. Through this analysis, it was possible to 222 determine the relationship between two parameters after removing the influence of other 223 factors (Peng et al., 2013; Shen et al., 2016). 224

The partial correlation coefficient between the time series of the EOS and daytime 225 226 maximum temperature (or nighttime minimum temperature) was calculated to assess the effect of maximum temperature (or minimum temperature) on the EOS, with 227 228 precipitation and minimum temperature (or maximum temperature) as the controlling variables. In line with previous studies, the duration of the preseason was calculated for 229 the maximum temperature (or minimum temperature) based on the period preceding the 230 long-term average date of the EOS. When the maximum temperature (or minimum 231 temperature) had the highest absolute value for the partial correlation coefficient with 232 the EOS, this period is referred to as the preseason for the maximum temperature (or the 233 minimum temperature) (Shen et al., 2016; Wu et al., 2018). In this study, an interval of 234 235 10 days was adopted to determine the duration of the preseason period and smooth out potential extreme values (Shen, Piao, Cong, et al., 2015). 236

The effect of preseason cumulative precipitation on the EOS was similarly 237 analyzed, and preseason precipitation was determined by setting the maximum and 238 minimum temperatures as the controlling variables (Shen et al., 2016). We did not 239 constrain the duration of preseason precipitation to be equal to that of preseason 240 temperature. In addition, to further analyze the influences of climatic variations on the 241 EOS, we compared the partial correlation coefficients between the EOS and preseason 242 precipitation and between the EOS and maximum and minimum temperatures at 243 different levels of temperature and soil moisture. 244

245

246 **3 Results**

247 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 TibetanPlateau, while the latter was concentrated in the central regions (Figure 1a,c).

260

261 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 267 268 variables. Across the Tibetan Plateau, the regionally averaged EOS showed a weak negative correlation with preseason cumulative precipitation but a significant positive 269 270 correlation with preseason maximum and minimum temperatures (Figure 2). Spatially, the proportion of pixels displaying a negative correlation between EOS and preseason 271 cumulative precipitation was approximately 52.1%, and that with a significant negative 272 relationship was approximately 7.6% (Figure 3a). The proportions of pixels showing a 273 274 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 275 significant (P < 0.05) positive relationship were 19.5% and 34.0%, respectively (Figure 276 277 3c,e).

279 The partial correlations between EOS and preseason climatic variables indicated spatial heterogeneity across the Tibetan Plateau. In the southwestern region, the EOS 280 showed a positive and negative partial correlation with preseason cumulative 281 precipitation and preseason maximum temperature, respectively; however, in the central 282 283 area, it exhibited a significant negative and positive partial correlation with these two parameters, respectively (Figures 2, 3a,c). The partial relationships between EOS and 284 preseason minimum temperature were positive in most of the study area, and the 285 positive relationships were extremely significant (P < 0.01) in the western and eastern 286 regions (Figure 3e). 287

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).

294

295 **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, Liu, et al., 2021), 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, Wang, et al., 2022), which showed a total 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, Wang, 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 (Lin et al., 2020; Zhou et al., 2020), 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, Liu, 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.

331

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

333 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). Plant available water is important for the growth of vegetation and it is usually not sufficient in arid or semi-arid regions due to high soil salinity and low water content (Wang et al., 2022). Our results indicated that, in the southwestern Tibetan Plateau, higher preseason precipitation significantly delayed the EOS although this was 342 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 343 low (Figure 4), an increase in preseason precipitation can alleviate water stress, 344 enhancing water use efficiency (Liu et al., 2016; Munné-Bosch et al., 2004) and 345 delaying the EOS. At the same time, an increase in maximum temperature would 346 increase hydrological losses through evaporation and reduce the amount of available 347 water (Kelsey et al., 2021; Shen et al., 2016), inhibiting the growth of marsh vegetation 348 (Shen, Liu, et al., 2021). These dynamics fit well with our results, indicating that the 349 EOS was primarily affected by precipitation in the southwestern arid regions of the 350 study area. For the first time, our results indicate that, even in marsh ecosystems with 351 352 their relatively high water contents, available water may be insufficient for vegetation growth in the drier regions of the Tibetan Plateau. 353

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.

361 An increase in maximum temperature can decelerate the process of chlorophyll 362 degradation (Shi et al., 2017) and retard the progression of leaf senescence (Estiarte et 363 al., 2017). In addition, high preseason nighttime temperatures reduce the occurrence of frost damage (Shen, Liu, et al., 2022). By calculating the number of the frost days, we 364 confirmed that warming preseason nighttime temperatures had the most notable 365 negative effect on the frost days in the central Tibetan Plateau, the coldest region of the 366 study area (Figure S2). This could account for the role of increasing minimum 367 temperature in delaying the EOS in the central Tibetan Plateau. In contrast, increased 368 preseason precipitation could retard the growth of marsh vegetation due to the 369 accompanying cooling effect, which would advance the EOS in the already cold and 370 humid areas of the central Tibetan Plateau. 371

In the low altitude humid regions in the east and high-altitude cold permafrost 372 regions in the west, the EOS showed a significant positive correlation with preseason 373 minimum temperature (Figure 3), indicating that an increase in this parameter delayed 374 375 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 376 these two areas. On one hand, increased nighttime temperatures cause a greater loss of 377 organic matter due to enhanced respiration, but on the other hand it can also stimulate 378 accumulation of more organic matter via the overcompensation effect (Shen, Liu, et al., 379 2021, 2022), a phenomenon through which the vegetation recovers and exceeds its 380 original state by promoting photosynthesis the day after the enhanced respiration (Peng 381 382 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, Liu, et al., 2022). 383

384 In cold high-altitude regions, the physiological processes causing vegetation senescence are typically determined by low temperatures during cold nights (Tang et al., 385 386 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 387 preseason minimum temperature would delay the EOS by alleviating frost damage and 388 retarding vegetation senescence (Cong et al., 2017). In contrast, in the low altitude area 389 of the eastern Tibetan Plateau, the climate is relatively warm and humid (Figure 4) and 390 marsh vegetation has access to sufficient water (Shen, Liu, et al., 2022). Therefore, 391 although organic matter may be depleted through the respiration of marsh vegetation 392 due to nighttime warming, increased temperatures can also promote photosynthesis, 393 394 leading to accumulation of more organic matter the following day via the over compensation effect (Belsky et al., 1986; Shen, Liu, et al., 2021, 2022). This would 395 396 contribute to delaying the EOS in the eastern region as a consequence of the increased preseason minimum temperatures. 397

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 405 became gradually stronger (Figure 5). Based on our results, we propose that the effects 406 of climate variations on the EOS differ depending on the hydrological constraints on 407 soil moisture in the marshes within the Tibetan Plateau. As such, we further compared 408 the partial correlations between EOS and climatic factors for preseason soil moisture 409 gradients of $0.03 \text{ m}^3/\text{m}^3$. The results showed that as soil moisture increased, the delaying 410 effect of increased preseason precipitation on the EOS gradually weakened (Figure 3), 411 while the delaying effects of higher preseason maximum and minimum temperatures 412 became gradually stronger (Figure 3). This finding supports the proposal that increased 413 precipitation and warming temperatures significantly delayed the EOS for marsh 414 415 vegetation in the arid southwestern Tibetan Plateau and the humid central and eastern areas, respectively. In contrast, increasing daytime temperatures and precipitation 416 417 advanced the EOS in the arid southwestern and humid central areas due to the reduced soil moisture and cooling effect, respectively (Figure 3). 418

419

420 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 minimum temperature exhibited increasing trends (0.52 mm/a and 0.05 C/a, respectively), and the increase in the minimum temperature was significant 426 (*P* < 0.05). Because the EOS showed a significant positive relationship with preseason
427 minimum temperature, the increase in this parameter may partly account for the delayed
428 EOS on the Tibetan Plateau (Figure 1 and Table 1).
429 Table 1 Temporal trends of preseason and seasonal precipitation (mm/a), maximum

430 temperature (\mathcal{C}/a), and minimum temperature (\mathcal{C}/a) in marshes of the Tibetan Plateau

431 from 2001 to 2020.

	Precipitation	Maximum	Minimum
	recipitation	temperature	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

432 **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 cumulative 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 440 minimum temperature may contribute to the delayed EOS in these regions (Figures 1 441 and 6). In the northeastern area of the plateau, the EOS appeared to occur earlier 442 throughout the study period (Figure 1), possibly due to the rise in preseason minimum 443 temperature (Figures 3 and 6). Previous studies have shown that the Tibetan Plateau will 444 become warmer and wetter in the future (Shen, Liu, et al., 2022), therefore the EOS of 445 marsh may continue to be delayed to some extent in the future, especially in the 446 southwestern Tibetan Plateau. 447

448

449 **5** Conclusions

450 Our study reveals several crucial findings regarding the end of the growing season (EOS) in marsh vegetation across the Tibetan Plateau. Firstly, we observed a significant delay 451 452 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, 453 warmer preseason temperatures led to a significant delay in the average EOS of marsh 454 vegetation. Notably, the delaying effect of higher nighttime temperatures on the 455 456 regionally averaged EOS was more pronounced than that of daytime temperatures. This asymmetric response to diurnal temperature variations can be attributed to the 457 widespread delaying effect of nighttime warming and the spatially diverse relationship 458 459 between EOS and daytime temperature, influenced by water conditions. Furthermore, our evidence indicates that hydrological factors influencing soil water content play a 460

461 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 462 and even reversed, while the delaying effect of increased preseason precipitation was 463 strengthened. In the humid, cold regions of the central Tibetan Plateau, higher preseason 464 maximum temperatures significantly delayed the EOS, whereas increased precipitation 465 advanced it, potentially due to a cooling effect. In the low altitude, humid regions in the 466 east, higher minimum temperatures delayed the EOS, possibly due to an 467 overcompensation effect. In the arid southwestern area, increased precipitation directly 468 and significantly delayed the EOS, whereas higher daytime temperatures advanced it, 469 likely due to limited water availability. These findings suggest that the EOS in these 470 471 regions is constrained by water conditions, even within marsh ecosystems. As the marsh in the Tibetan Plateau is a typical alpine freshwater marsh, our findings can provide 472 473 some implications for other studies of alpine freshwater marsh. Overall, this study highlights the asymmetric influences of daytime and nighttime temperatures on the EOS 474 of marsh vegetation, particularly in the context of global diurnal asymmetric warming 475 (stronger warming during nighttime than during daytime). It underscores the importance 476 477 of considering water conditions in EOS simulations conducted by terrestrial ecosystem models in cold and dry regions worldwide. 478

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480 Author contributions

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Acquisition; Investigation; Methodology; Resources; Validation; Visualization; Writing 482 - Original Draft Preparation; Writing - Review & Editing. Miaogen Shen: 483 Conceptualization; Data Curation; Formal Analysis; Investigation; Methodology; 484 Resources; Validation; Visualization; Writing – Original Draft Preparation; Writing – 485 Review & Editing. Chaoyang Wu: Data Curation; Formal Analysis; Methodology; 486 Resources; Visualization; Writing - Original Draft Preparation; Writing - Review & 487 Editing. Josep Peñuelas: Formal Analysis; Funding Acquisition; Writing - Review & 488 Editing. Philippe Ciais: Formal Analysis; Writing – Review & Editing. Jiaqi Zhang: 489 Data Curation; Formal Analysis; Investigation; Validation; Visualization; Writing -490 Original Draft Preparation; Writing – Review & Editing. Chris Freeman: Formal 491 Analysis; Writing – Review & Editing. Paul I. Palmer: Formal Analysis; Writing – 492 Review & Editing. Binhui Liu: Methodology; Writing – Review & Editing. Mark 493 494 Henderson: Formal Analysis; Writing – Review & Editing. Zhaoliang Song: Writing - Review & Editing. Shaobo Sun: Writing - Review & Editing. Xianguo Lu: 495 Conceptualization; Formal Analysis; Methodology; Resources; Writing - Review & 496 Editing. Ming Jiang: Conceptualization; Formal Analysis; Funding Acquisition; 497 Methodology; Project Administration; Resources; Supervision; Writing - Review & 498 Editing. 499

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509 **Conflict of interest statement**

The authors declare no conflict of interest. 510

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512 Data availability statement

513 The NDVI dataset (MOD13Q1) was provided by the Earth Science Data Systems of the National Aeronautics Space Administration 514 and (https://ladsweb.modaps.eosdis.nasa.gov). The distribution dataset of marshes was 515 obtained from the wetland distribution datasets for China (30 m wetland distribution 516 thematic data in China) (http://www.geodata.cn). The soil moisture data (1 km daily soil 517 moisture dataset over China) were obtained from the National Tibetan Plateau Scientific 518 519 Data Center (https://data.tpdc.ac.cn/en/data/49b22de9-5d85-44f2-a7d5-a1ccd17086d2/). Metadata that support the findings of this study are available from Zenodo 520 at https://doi.org/10.5281/zenodo.10258355. 521

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832 **Figure legends**:

FIGURE 1 Spatiotemporal change of the end of the growing season (EOS) in the 833 marshes of the Tibetan Plateau from 2001 to 2020. (a) Distribution of marshes at 834 different altitudes on the Tibetan Plateau. (b) Spatial patterns of long term average EOS. 835 (c) Temporal trends in EOS. (d) Temporal variations of regionally averaged EOS. The 836 inset histograms at the bottom of (b) and (c) describe the frequency distributions of the 837 average EOS and EOS trend. - and + in (c) show the negative (advancing) and positive 838 (delaying) trend, respectively; * and ** indicate the trend is significant (P < 0.05) and 839 extremely significant (P < 0.01), respectively. The error bar and bold black line in (d) 840 show standard error and linear trend of the regionally averaged EOS, respectively. Map 841 842 lines delineate study areas and do not necessarily depict accepted national boundaries.

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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).

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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 853 preseason soil moisture on the Tibetan Plateau from 2001 to 2020. The inset histograms 854 at the bottom of left figures (a, c, e) display the frequency distributions of partial 855 correlation coefficients. - and + show the negative and positive correlation, respectively; 856 857 * and ** indicate the correlation is significant (P < 0.05) and extremely significant (P < 0.05) 0.01), respectively. The body lines in the right figures (b, d, f) indicate the linear fit for 858 the partial correlation coefficients, and the shading represents the 95% confidence band 859 of the fits. Map lines delineate study areas and do not necessarily depict accepted 860 national boundaries. 861

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863 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 864 on the EOS. (b) Spatial distribution of long-term average preseason soil moisture 865 (m^3/m^3) . (c) The long-term average preseason temperature (°C) for marsh vegetation on 866 the Tibetan Plateau. (d) Long-term average preseason soil moisture (m^3/m^3) and 867 preseason temperature (°C) in different regions of the Tibetan Plateau. "+" and "-" 868 indicate that the climatic variable had a significant positive and negative effect on the 869 EOS, respectively (P < 0.05). "++" indicates an extremely significant positive effect (P870 < 0.01). In the southwestern Tibetan Plateau (circled in blue), increased preseason 871 872 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 873

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. Map
lines delineate study areas and do not necessarily depict accepted national boundaries.

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FIGURE 5 The changes in partial correlation coefficients between EOS and preseason cumulative precipitation, maximum temperature, and minimum temperature along the spatial gradient of 1 °C for 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.

FIGURE 6 Preseason climate change in the marshes of the Tibetan Plateau. Spatial 885 886 patterns of temporal trends in preseason cumulative precipitation (a), maximum temperature (b), and minimum temperature (c) in the marshes of the Tibetan Plateau 887 from 2001 to 2020. The inset histograms at the bottom of figures display the frequency 888 distributions of the trends. - and + show the negative and positive trend, respectively; * 889 and ** indicate the variation trend is significant (P < 0.05) and extremely significant (P890 < 0.01), respectively. Map lines delineate study areas and do not necessarily depict 891 accepted national boundaries. 892









(c)EOS and preseason maximum temperature





 $= -0.01x + 0.20; P < 0.01; R^{2} = 0.43$



898

899



(b)

0.4





FIGURE 4



FIGURE 5



(b) Trend of preseason maximum temperature (°C/a)





FIGURE 6