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Soil moisture determines the effects of climate warming on spring phenology in grasslands

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ABSTRACT

Spring vegetation phenology is highly sensitive to global change. However, the effects of ongoing climate warming and N deposition on grassland spring phenology and how abiotic and biotic factors modulate such effects remain unclear. Here, we conducted a factorial field experiment of warming and N addition in three types of grasslands with varying aridity indices (0.20–0.39) in Inner Mongolia, China. Our results showed that warming and the combination of warming plus N addition had similar effects on start of season (SOS). These treatments delayed SOS by 3–5 weeks in low-, moderate and high-aridity grasslands in both wet (2018) and dry (2019) years, except that they advanced SOS by ~1 week in low-aridity grassland in the wet year. N addition alone slightly advanced or delayed SOS by 2–5 days depending on the grassland type. The magnitude and direction of SOS response to warming and warming plus N addition were closely and linearly correlated to grassland soil moisture, but not to air temperature or soil N availability. Warming-induced reduction in soil moisture drove SOS by affecting species richness and/or functional group composition. By contrast, N addition–induced changes in species richness and functional group composition did not alter the SOS. These combined results indicate that temperature and soil water availability are primary factors regulating SOS in semiarid grasslands. Our findings suggest that annual variation and spatial distribution in soil moisture should be considered in future studies of climate warming and environmental effects on grassland phenology.

1. Introduction

Spring vegetation phenology [the start of season (SOS)] is a sensitive bio-indicator of global change and it plays a crucial role in regulating terrestrial carbon, water, and energy balance (Cleland et al., 2007; Xu et al., 2020). As two of the most prominent parameters of global changes, global temperature is predicted to rise 1.0–3.7 °C by the end of 21st century compared to that of 1986–2005, while terrestrial nitrogen (N) input from anthropogenic activity is projected to increase approximately 6-fold by 2050 compared to preindustrial rates (Collins et al., 2013; Galloway et al., 2008). Ongoing climate warming and N deposition have shifted SOS (Piao et al., 2019). Previous studies generally focused on the effects of global changes in SOS of forest ecosystems (Fu et al., 2015; Wenden et al., 2020). Grassland ecosystems account for ~30% of global land surface and are crucial for the provision of biological products and services to human populations (John et al., 2014; Sala and Maestre, 2014). However, the response of SOS to climate warming and N deposition and their underlying mechanisms remain unclear in grassland ecosystems (Piao et al., 2019).

Temperature is a dominant factor driving plant phenology changes, but the SOS in grasslands shows varied responses to climate warming. Some studies reported that rising temperature advanced spring phenology (Cleland et al., 2007; Zhou et al., 2014), whereas other studies reported that warming either did not affect or delayed spring phenology (Wang et al., 2019; Yu et al., 2010). Temperature, precipitation and/or nutrients are the primary limiting factors for plant growth in grassland ecosystems (Bharath et al., 2020; Fu et al., 2021; Liu et al., 2020); thus, the inconsistent responses of SOS to warming suggest that the effects of warming on SOS in grasslands may depend on other environmental conditions (Montgomery et al., 2020; Wang et al.,

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2020b). Soil moisture reflects simultaneous changes in temperature and precipitation (Seneviratne et al., 2010). Slight changes in soil moisture generally have large influences on plant growth (Green et al., 2019; Zhang et al., 2020). For example, recent research indicates that increasing precipitation 140% (60 mm) in the dormant season only increases early spring soil moisture ~2% (absolute value), but significantly advances plant growth and boosts biomass (Ganjurjav et al., 2021). However, it remains unclear how abiotic factors (e.g., temperature, soil water and N) regulate grassland spring phenology responses to climate warming and N deposition.

Mounting evidence indicates that global warming and increased N deposition are threatening plant diversity (Harpole et al., 2016; Klein et al., 2004). Plant diversity changes result in community-scale changes in phenology. For example, some studies indicate that species loss advances plant growing period (Du et al., 2019; Wolf et al., 2017), but increasing species richness prolongs plant growing period (Oehri et al., 2017; Rheault et al., 2015). Moreover, warming and N addition may exacerbate competitive exclusion and lead to shifts in plant functional groups (Liu et al., 2018; Strain et al., 2017). These shifts can affect SOS; for example, changes in functional group composition from forbs to grasses can advance SOS (Wang et al., 2020a). However, few studies have investigated whether changes in SOS of grasslands induced by warming and N enrichment could be attributed to changes in species richness and functional group composition.

In this study, we investigated how climate warming and N addition affected spring vegetation phenology via abiotic factors (temperature, soil water, and nutrients) and biotic factors (plant diversity and functional groups) in three grasslands with different aridity and species composition in Inner Mongolia, China. The purposes of this study were: (1) to analyze the impacts of warming, N addition, and warming plus N addition on SOS in three types of grasslands with different aridity indices; (2) to examine how changes in SOS relate to abiotic factors such as temperature, soil moisture and nutrients under warming and N addition; and (3) to determine whether changes in species richness and functional group composition induced by warming and N addition affected SOS.

Two hypotheses were tested. (1) The effects of warming and N addition on SOS depend on soil water availability, but warming will have greater effects on SOS than N addition. This hypothesis builds on the fact that water is one of the main limiting factors for plant growth in arid and semiarid grassland ecosystems (Green et al., 2019). Warming exacerbates soil water stress in habitats with low soil moisture, leading to delayed plant growth. Low water availability might attenuate the positive effects of nitrogen addition on plant growth (Bharath et al., 2020), resulting in non-significant changes in plant phenology (Fig. 1a). Conversely, grassland habitats with high soil moisture may display

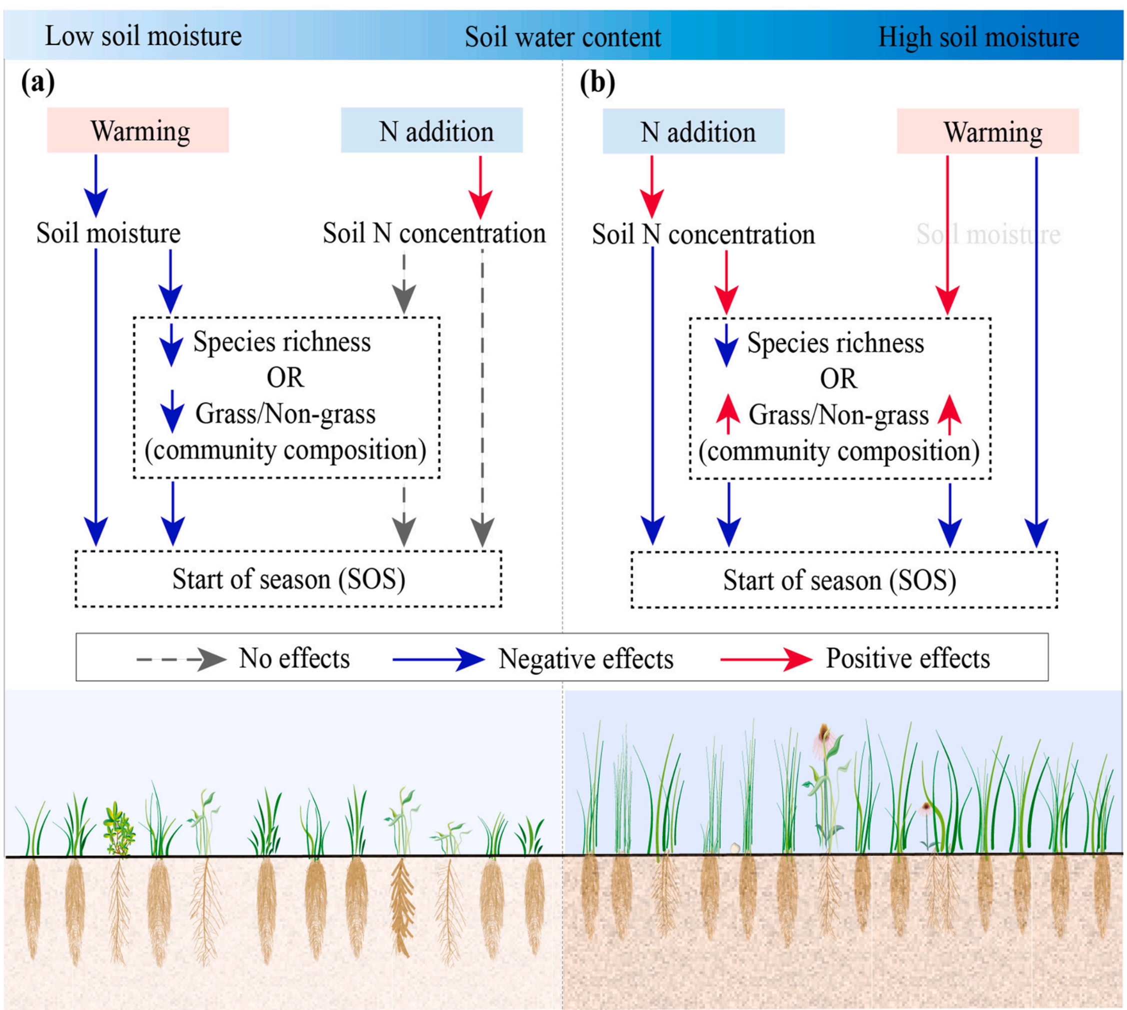

Fig. 1. Illustration of two hypotheses in this study. (a) Warming, but not N addition, exacerbates soil water stress in habitats with low soil moisture, and/or reduces species richness or alters functional group composition, leading to delayed plant growth; because water is the main limiting factor for plant growth, and plant diversity changes result in community-scale changes in phenology. (b) Warming and N addition increase temperature and nutrients, respectively, and/or favor grasses in grasslands with high soil water availability, resulting in advanced SOS; because temperature and nutrients become the main limiting factors for plant growth.

greater responses to nutrient limitation because nutrients become the main limiting factor instead of water (Wang et al., 2017). Warming and N addition advance plant growth, but changes in the SOS may be more sensitive to warming than N addition because temperature is critical for plant growth during the early growing season (Fig. 1b). (2) Warming and N addition-induced changes in species richness and community composition drive the SOS. This hypothesis centers on vegetation phenology being altered by changes in plant diversity and functional group composition (Oehri et al., 2017; Wang et al., 2020a). Warming may delay SOS by reducing species richness or altering functional group composition, because it can exacerbate plant water stress in grasslands with low soil water availability. By contrast, warming and N addition may advance SOS by favoring grasses in grasslands with high soil water availability (Liu et al., 2018; Wang et al., 2020a).

2. Materials and methods

2.1. Site selection and characteristics

To explore whether the effects of warming and N addition on SOS depended on environmental conditions, we selected three types of grasslands with varying abiotic and biotic factors in Inner Mongolia, China (Tables S1, S2). The low-aridity grassland was located in Ewenke (48.93°N, 119.69°E), received an average precipitation of ~350 mm year^{-1}, and had a mean annual temperature of –0.30 °C and aridity index (AI) of 0.39. The moderate-aridity grassland was located in Hangjinqi (39.78°N, 108.66°E), received an average precipitation of ~305 mm year^{-1}, and had a mean annual temperature of 6.40 °C and AI of 0.27. The high-aridity grassland was located in Xilinhot (43.94°N, 115.86°E), received an average precipitation of ~263 mm year^{-1}, and had a mean annual temperature of 2.35 °C and AI of 0.20. The AI is the ratio of mean annual precipitation to potential evapotranspiration (Thornthwaite, 1948). All three types of grasslands belonged to semi-arid climate (AI: 0.2–0.5) based on Thornthwaite aridity classification. These definitions of low-, moderate- and high-aridity grasslands were relative rankings based on the AI. Mean annual precipitation, temperature, and potential evapotranspiration data were extracted for 2002–2016 from 45 climate stations across Inner Mongolia using a kriging method in ArcGIS software (Environmental Systems Research Institute, Redlands, CA, USA). Background N deposition rate was ~4 g m^{-2} year^{-1} in this region (Xu et al., 2015). Precipitation began earlier in the year during 2018 than 2019 in the three grasslands (Fig. S1).

Species richness was highest in the low-aridity grassland and lowest in the high-aridity grassland (Table S2). The dominant species in the low-aridity grassland were *Leymus chinensis* (Trin.) Tzvel., *Cleistogenes squarrosa* (Trin.) Keng, *Potentilla acaulis* Linn., *Klasea centauroides* (L.) Cass., and *Carex korshinskyi* (Kom.) Malyschev, and most of these species belonged to mesoxerophytes. Xerophytes and mesoxerophytes such as *Stipa krylovii* Roshev., *Lespedeza caraganae* Bunge, *C. squarrosa, Heteropappus altaicus* (Willd.) Novopokr., and *Salsola collina* Pall. formed the dominant species in the moderate-aridity grassland. The dominant species in the high-aridity grassland comprised more xerophytes and included *S. krylovii, C. squarrosa, Convolvulus ammannii* Desr., and *Dysphania aristate* (L.) Mosyakin & Clemants.

2.2. Experimental design

Each experimental field (50 $m \times$ 50 m) was fenced in 2016 to prevent large animal grazing. During the early growing season of 2017, we created 12 plots (3 $m \times$ 3 m) at each site using a Latin square design. Four treatments with three replicates per treatment were arranged into four rows and three columns, and any two adjacent plots had a 2-m buffer zone. The factorial treatments included control, warming, nitrogen (N) addition, and warming plus N addition. The warming treatment was performed using an open-top chamber (OTC) with >90% transparency and a 4.39 m^2 basal area. Each open-top chamber was firmly stabilized and mounted 10 cm above the ground to facilitate air flow. Passive warming via OTC is a common and well-documented method for simulated climate warming (Marion et al., 1997; Prevey et al., 2017). The method is well-suited to our circumstances of highly variable plant heights, limited electricity supply, and strong wind (Zhu et al., 2020). N addition involved broadcast of urea on the soil surface by hand in August at a rate of 20 g N m^{-2} year^{-1}. This N addition rate was five times higher than the average annual N deposition rate typically seen in this region (Xu et al., 2015). We selected this rate because it represented the use of N fertilizer to improve pasture yield or restore degraded grasslands (Xu et al., 2021), and was used in previous studies in this region to assess the effect of N deposition on grassland ecosystems (Hasi et al., 2021).

We selected one permanent 0.75 $m \times$ 0.75 m subplot in each of the 3 $m \times$ 3 m plots to study the effects of warming and N addition on SOS during the early growing season in 2018. The four corners of the 0.75 $m \times$ 0.75 m subplot were marked by PVC to ensure the same and comparable field of view for successive photograph. We placed a PVC frame of 0.75 $m \times$ 0.75 m at the center of each subplot, and divided the subplot into nine small observation plots of 0.25 $m \times$ 0.25 m to accurately identify phenological metrics. We defined the nine 0.25 $m \times$ 0.25 m small observation plots as the photographic field-of-view areas of a smartphone camera in each subplot (Fig. S2). The observation plots were photographed at weekly intervals during two growing-season years (2018 and 2019). The observation plots were photographed from fixed points to ensure similar views for each photograph (Hufkens et al., 2019; Liu et al., 2022). The photographer held the smartphone ~0.5 m above the ground for each photograph of the 0.25 $m \times$ 0.25 m small observation plots (Liu et al., 2022). Photographs were taken from 8:00 am to 12:00 noon, depending on weather conditions. The default smartphone settings were used. To ensure image quality for later analysis, all images of experimental plots were immediately examined after photography. If an image was anomalous (e.g., blurred or distorted), it was deleted and another retaken until all images were satisfactory.

2.3. Plant sampling and meteorological data

In August 2018 and 2019, a subplot (0.75 $m \times$ 0.75 m; not part of the imagery sub-plots) was randomly selected for plant sampling within each 3 m x 3 m experimental plot. Species richness and individual species abundance were measured and recorded in the selected subplots. After recording these data, all aboveground parts of plants in the selected subplot were clipped at the soil surface. The previous year's litter was segregated. The collected plants were weighed after oven-drying at 65 °C until they reached a constant weight. Two soil cores were extracted from the subplot using a soil auger (7-cm inner diameter) at 0–10 cm depth. We composited the two soil cores and these soil samples from each subplot were used for further analysis. The soil samples were sieved by passing through a 2-mm screen and then air dried. Soil N concentration was determined using the Kjeldahl acid-digestion method and a flow analyzer [Auto Analyzer 3 (AA3), SEAL, Germany] (Bremner and Mulvaney, 1982).

Site-specific meteorological data were obtained by installing automatic meteorological towers within the experimental field at each study site to monitor air temperature, precipitation and soil moisture during the study period. Each meteorological tower measured air temperature 10 cm and precipitation 2.5 m above the ground, and soil moisture (volumetric water content) 10 cm below the ground. The air temperature and soil moisture of each plot were automatically measured at 30-min intervals via sensor probes which connected to meteorological towers (FY-QBX).

Soil moisture and aridity index both reflect simultaneous changes in temperature and precipitation (Seneviratne et al., 2010; Vicente-Serrano et al., 2010). Additional climatological information might help verify whether changes in soil moisture represented the aridity conditions between years, and whether treatments affected soil moisture and subsequently SOS. We calculated the Standardised

Precipitation-Evapotranspiration Index (SPEI) of each study site using temperature and precipitation data (2010–2019) which derived from our study data and interpolation data (Vicente-Serrano et al., 2010). The SPEI is a normalized metric that standardizes water availability against the climate history of the site (Bharath et al., 2020). To test whether the effects of warming and N addition on SOS varied with soil moisture along a temperature and precipitation gradient, we also calculated Köppen aridity index ($AI_{Köppen}$) using our study data as follows: $AI_{Köppen}$ = precipitation / (temperature + 33) (Köppen, 1923; Quan et al., 2013). Here, lower $AI_{Köppen}$ values correspond to more arid climate conditions and vice versa. The 1-month SPEI and $AI_{Köppen}$ that represent the climatic water conditions in the current month were estimated, respectively. Moreover, the 6-month SPEI and $AI_{Köppen}$ (e.g., in April) represent the accumulated climatic water balance for the half year (e.g., from November to April). We calculated the cumulative effects of 6-month SPEI and $AI_{Köppen}$ on SOS before spring season (March, April and May) (Fu et al., 2015; Zeng et al., 2021). In order to correspond to spring soil moisture, mean spring 1- and 6-month SPEI and $AI_{Köppen}$ were calculated, respectively.

2.4. Plant phenology

Fractional coverage represents the vegetation cover on the ground surface expressed as fraction or percent of the reference area. This parameter is closely related to vegetation indices and biomass production (Purevdorj et al., 1998; Sanaei et al., 2018). According to our previous study, fractional coverage was a robust and reliable indicator that tracks grassland phenology under various ambient light conditions and translates across different smartphones (Liu et al., 2022). All collected images were processed by geometric correction and cropping using Photoshop CS6 (Adobe Systems Incorporated, San Jose, CA, USA) (Fig. S2). Then, fractional coverage was determined from the processed images using the green pixels and the Otsu algorithm in MATLAB (Xu et al., 2021). We confirmed the accuracy of the computed fractional coverage value by visually comparing each original image with the binary image using the methods described above. Specifically, the original and it's binary image were magnified from 100 to 300% of default canvas size in Photoshop CS6. If all and only green plants in the original image were detected in the binary image by visual comparison on the 300% of default canvas size, the fractional coverage was determined from binary images. However about 20% of 13,662 total images needed visual classification. For this process we checked if green pixels (e.g., incomplete green leaves or plants) were omitted or non-green pixels (e.g., litter) were over-identified in the binary image. If these pixels were infrequent and could be selected directly in the original image using the Magic Wand Tool, the fractional coverage was the sum or difference of the binary image and interpreted original image. Otherwise, the green pixels of the original image underwent complete visual interpretation using the Magic Wand Tool and Select Similar Command.

Plant community phenology was measured by smartphone photography which is a near-surface remote sensing technique (Hufkens et al., 2019). The process can integrate the species-specific differences in plant phenology (Wang et al., 2020a). The SOS was determined from fractional coverage in three steps (Liu et al., 2022). First, we selected the fractional coverage data from the start to the end of season. Then, the time-series fractional coverage of each subplot was fitted using a loess curve with a fixed span of 0.4, and the daily interpolated smoothed data were fitted using a spline model. Finally, a previous study established that grazing behavior in this region of Inner Mongolia generally began in early May when fractional coverage reached 30% of the annual maximum coverage (Wang et al., 2021). To explore the effects of warming and N addition on grazing time, the SOS was defined as the date on which the fractional coverage reached 30% of the annual maximum coverage. In the current study, we also examined the differences between setting SOS as the 30% threshold value (Trs method) and using other methods to set SOS, such as Derivatives, Klosterman, and Gu (Filippa et al., 2016). The calculated responses of SOS to warming and N addition were similar among all four methods (Fig. S3).

2.5. Data analyses

To explore whether changes in functional group composition caused by warming and N addition affect SOS, plants were divided into three groups: annual and biennial plants, perennial forbs, and perennial grasses (Table S2) (Bai et al., 2004). Perennial grasses (e.g., *L. chinensis, S. krylovii*, and *C. squarrosa*) grow quickly at the start of the growing season. Annual and biennial plants (e.g., *Chenopodium glaucum, Tribulus terrestris*, and *D. aristata*) and perennial forbs (e.g., *Potentilla bifurca, L. caraganae*, and *C. ammannii*) generally begin growing somewhat later. The response of SOS, species richness and functional group composition to warming and warming plus N addition in high-aridity grassland in 2019 were not conducted in the subsequent analysis due to the lack of relevant data.

Data were analyzed using a three-step protocol and R version 4.1.1 (The R Project for Statistical Computing, https://www.r-project.org/). First, a repeated-measures ANOVA was conducted using the *aov* function to examine the effects of warming, N addition, site, year, and their interactions on all variables. We conducted two-way ANOVA to test the effects of warming, N addition and their interactions on all variables at each site. We conducted multiple comparisons using the least significant difference test to determine differences among treatments for each variable with *agricolae* package. Variables included mean spring air temperature, soil moisture, 1-month SPEI and 6-month SPEI, and soil N concentration, SOS, species richness, plant productivity and the relative abundance of annual and biennial plants, perennial forbs, and perennial grasses. The SPEI was calculated using Thornthwaite method with *SPEI* package. All data were log-transformed to meet homogeneity and normality assumptions of ANOVA before further analysis.

Second, to explore whether the effects of warming and N addition on SOS depended on environmental conditions, we calculated the natural log-transformed response ratio of SOS by comparing values for control and experimental plots treated with warming and N addition (Yuan and Chen, 2015). The mean spring air temperature, soil moisture, 1-month $AI_{Köppen}$ and 6-month $AI_{Köppen}$, and soil N concentration relative to the SOS response ratio were fitted by linear models ($y = a*x + b$; $y = a*x^2 + b*x + c$; $y = a*\ln(x) + b$) and nonlinear models ($y = a*\exp^{(b*x)}$; $y = a*\exp^{(b*x)} + c$; $y = a*x^b$; $y = a*x^b + c$), respectively. We also examined the relationship between soil moisture and spring 1-month or 6-month $AI_{Köppen}$, because of the large differences in temperature among three sites. The best fitting functions were selected using Akaike's Information Criterion (AIC). All statistical analyses were performed using *ggtrendline* package.

Third, we used the *psych* package to compute correlation coefficients and significance between any two variables under warming and N addition. Direct and indirect effects of warming and N addition on SOS were quantified using a structural equation model (SEM) based on theoretical and empirical knowledge. Partial least squares structural equation modeling (PLS-SEM) has high predictive accuracy and wide tolerance for small sample sizes without normal distributions (Hair et al., 2011). The PLS-SEM analysis was performed using SmartPLS 3 ver. 3.2.8 (SmartPLS GmbH, Boenningstedt, Germany).

3. Results

3.1. Changes in microenvironment of climate and soil

The mean spring (March–May) air temperature in low-, moderate-, and high-aridity grasslands was 11.4, 12.3, and 10.7 ℃ in 2018, and 9.6, 11.0, and 10.5 ℃ in 2019, respectively, under ambient conditions (Fig. S4). The mean spring soil moisture in low-, moderate-, and high-aridity grasslands was 11.4, 8.9, and 8.3% in 2018, and 8.5, 7.8, and 6.9% in 2019, respectively, under ambient conditions (Fig. S5).

Similarly, the plant productivity and mean spring 1-month SPEI in 2018 were higher by 30–57% and 90–435% than that in 2019, respectively, under ambient conditions (Figs. S6, S7). Thus, 2018 was a wetter year than 2019 across all three grasslands. The soil N concentration in low-, moderate-, and high-aridity grasslands was 1.9, 0.7, and 1.8 g kg^{-1} in 2018 and 1.8, 0.5, and 1.7 g kg^{-1} in 2019, respectively, under ambient conditions (Fig. S8). Thus, the soil N concentration was highest in the low-aridity grassland and lowest in the moderate-aridity grassland.

Warming and warming plus N addition increased mean spring air temperature by 1.4–1.8 ℃ (Table 1 and Fig. S4). These treatments reduced mean spring soil moisture by ~10% of control moisture level in 2018 and 2019 across all three grasslands (Table 1 and Fig. S5). N addition alone affected neither mean spring air temperature nor soil moisture (Table 1 and Figs. S4, S5). Warming generally did not affect soil N concentration except for boosting soil N in the moderate-aridity grassland in 2019 (Fig. S8). N addition and warming plus N addition increased soil N concentration by 15–35% (Table 1 and Fig. S8). No significant warming × N addition interaction was detected on mean spring air temperature, mean spring soil moisture, or soil N concentration (Tables 1, S3). Moreover, the effects of warming and N addition on soil moisture resembled the effects on spring 1- and 6-month SPEI (Table S3). Soil moisture was related to 1- and 6-month $AI_{Köppen}$ with $R^2 > 0.85$ (Fig. S9). Therefore, we only present the effects of warming and N addition on SOS under diverse soil moisture across three grasslands.

3.2. Effects of warming and N addition on spring phenology

Warming, but not the N addition, affected SOS (Tables 1, S4 and Fig. 2). In the low-aridity grassland, warming advanced SOS by ~1 week during the wet year (2018), but delayed SOS by ~3 weeks during the dry year (2019) (Fig. 2a, b). However, warming delayed SOS by 3–5 weeks in the moderate- and high-aridity grasslands (Fig. 2c–e). N addition slightly advanced or delayed SOS by 2–5 days in all three grasslands (Fig. 2). Warming and warming plus N addition had similar effects on SOS. No significant interactions between warming and N addition were detected for SOS (Tables 1, S4).

The response of SOS to warming and N addition depended on environmental conditions (Fig. 3). The SOS response ratios were not correlated with mean spring air temperature or soil N concentration under warming, N addition, and warming plus N addition (Fig. 3a–c, g–i). By contrast, the SOS response ratios decreased with increasing mean spring soil moisture ($R^2 > 0.83$, $P < 0.001$) under warming and warming plus N addition (Fig. 3d, f).

3.3. Effects of warming and N addition on species richness and functional group composition

Warming and N addition affected species richness and functional composition differently in all three grasslands during the wet and dry years (Tables 1, S4 and Figs. 4, 5). Warming and warming plus N addition reduced species richness by 15–35% in low- and moderate-aridity grasslands (Fig. 4a–d). N addition reduced species richness by 15–45% in the low-aridity grassland, whereas N addition reduced species richness in the moderate-aridity grassland only in the wet year (Fig. 4a–c). Warming and N addition slightly affected species richness in the high-aridity grassland (Table S4 and Fig. 4e, f).

Warming and N addition had similar effects on functional group composition (Fig. 5). In the wet year, warming, N addition and warming plus N addition reduced the relative abundance of perennial forbs by 20–30%, but increased the relative abundance of perennial grasses by 75–115% in low-aridity grassland (Fig. 5b, c). All treatments increased the relative abundance of annual and biennial plants in the moderate-aridity grassland (Fig. 5d), and increased the relative abundance of perennial forbs in the high-aridity grassland (Fig. 5h). In the dry year, none of the three treatments significantly altered the functional group composition in low-, moderate-, and high-aridity grasslands (Table S4 and Fig. 5j–r).

3.4. Relationships among microenvironment, species richness, functional group composition, and spring phenology

Warming and warming plus N addition had similar effects on SOS, air temperature, soil moisture, species richness, and functional group composition. However, these effects differed from those of N addition alone. Therefore, we present data pooled across warming and warming plus N addition separately from those of N addition alone in the following analyses.

Pearson correlation and SEM analyses of warming and warming plus N addition indicated that they reduced soil moisture ($R^2 = 0.85$), reduced the relative abundance of perennial forbs ($R^2 = 0.32$), and increased the relative abundance of perennial grasses ($R^2 = 0.95$), thus leading to an advanced SOS ($R^2 = 0.90$) in the low-aridity grassland in the wet year (Figs. 6a, S10a). By contrast, warming and N addition reduced soil moisture ($R^2 = 0.84$), reduced species richness ($R^2 = 0.48$), and increased the relative abundance of annual and biennial plants ($R^2 = 0.71$), thus resulting in a delayed SOS ($R^2 = 0.89$) in the moderate-aridity grassland in the wet year (Figs. 6b, S10b). Increased air

Table 1
Repeated measures ANOVA for the effects of warming (W), N addition (N), site (S), year (Y), and their interactions on mean spring air temperature (AT), mean spring soil moisture (SM), soil N concentration (SN), start of season (SOS), species richness (SR), and the relative abundance of annual and biennial plants (ABP), perennial forbs (PF), and perennial grasses (PG). *F* values are presented.

Variable	AT	SM	SN	SOS	SR	ABP	PF	PG
W	110***	53.8***	2.21	21.9***	3.06	6.03*	0.705	4.68*
N	0.236	0.406	8.67**	0.066	4.62*	0.132	1.65	1.10
S	0.060	304***	4.84*	35.4***	9.63**	112***	24.3***	0.974
Y	45.6***	298***	0.184	6.72*	14.5***	65.2***	1.36	10.8**
$W \times N$	0.076	1.40	2.53	0.117	4.82*	0.017	0.307	0.220
$W \times S$	0.156	0.012	0.012	0.000	0.480	3.34	0.888	0.007
$W \times Y$	0.000	0.213	0.044	2.24	0.449	1.67	1.17	3.10
$N \times S$	0.044	0.168	3.00	0.002	1.47	0.568	5.64*	3.60
$N \times Y$	0.022	0.024	2.51	9.29**	5.94*	4.19*	1.48	5.32*
$S \times Y$	18.2***	31.9***	0.012	62.1***	0.636	33.7***	2.50	2.68
$W \times N \times S$	0.001	0.243	3.00	0.031	6.04*	0.475	0.025	0.283
$W \times N \times Y$	0.000	0.074	0.010	0.014	0.002	0.320	0.998	0.439
$W \times S \times Y$	0.290	0.021	0.012	42.8***	6.36*	0.613	0.149	0.003
$N \times S \times Y$	0.013	0.057	0.014	0.698	0.403	0.285	0.030	0.015
$W \times N \times S \times Y$	0.026	0.002	0.060	0.044	0.215	0.077	4.88*	4.00

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

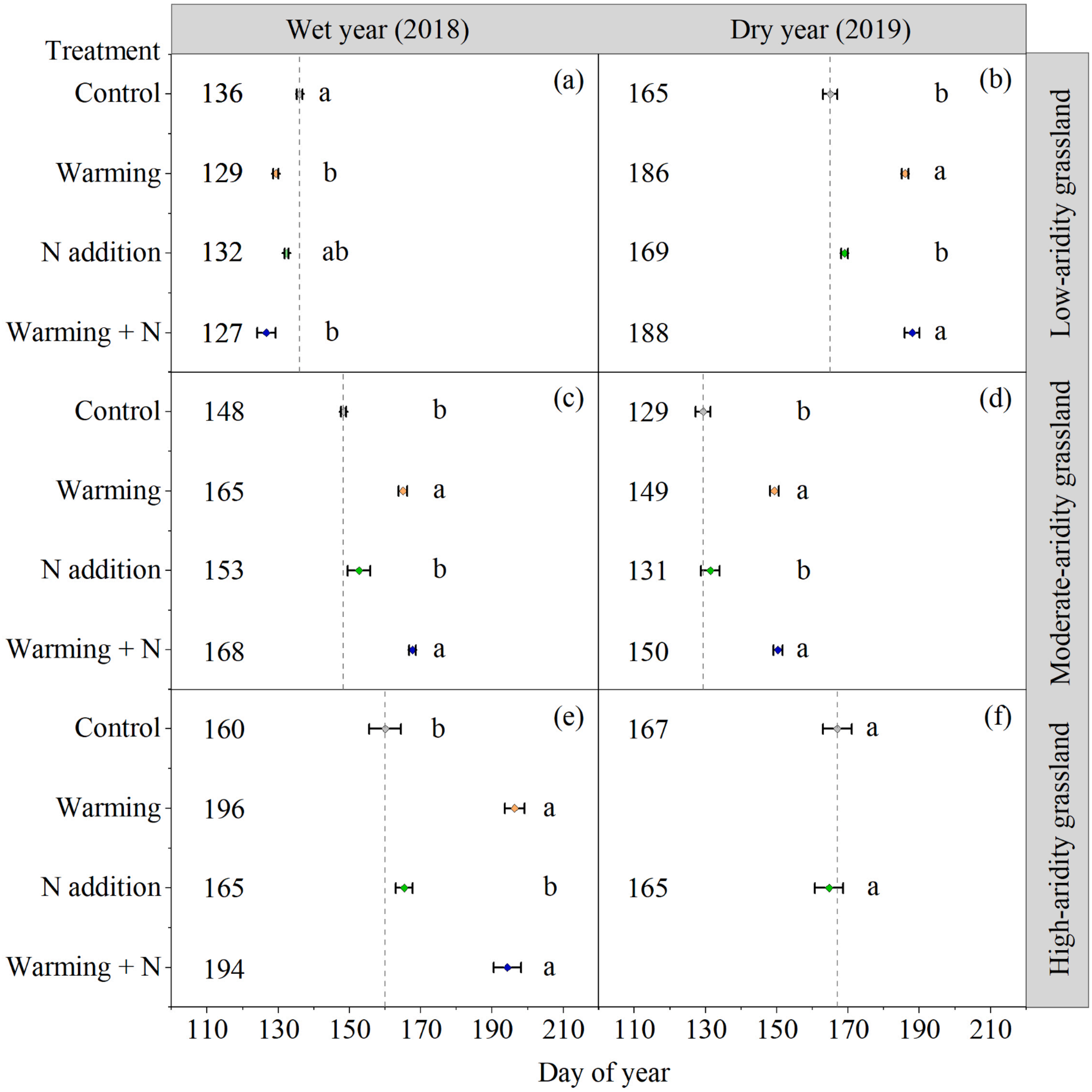

Fig. 2. Effects of warming, N addition, and warming plus N addition on the start of season (SOS) in low- (a, b), moderate- (c, d), and high- (e, f) aridity grasslands in a wet year (2018) and a dry year (2019). Values represent mean ± S.E. Dashed gray line indicates the mean value under control conditions. Different lowercase letters indicate significant differences among treatments ($P < 0.05$).

temperature in the high-aridity grassland in the wet year reduced soil moisture ($R^2 = 0.57$) and improved the relative abundance of perennial forbs ($R^2 = 0.63$), thereby delaying SOS ($R^2 = 0.79$) (Figs. 6c, S10c). However, reduced soil moisture ($R^2 = 0.81$) in the low- and moderate-aridity grasslands in the dry year directly or indirectly affected species richness ($R^2 = 0.79$) and then delayed SOS ($R^2 > 0.69$) (Figs. 6d–e, S10d–e).

N addition alone did not significantly affect SOS in all three grasslands (Fig. S11). Therefore, the direct and indirect effects of N addition on SOS were not analyzed using SEM. The relative abundances of perennial forbs and grasses decreased and increased, respectively, with increasing soil N concentration in the low-aridity grassland in the wet year (Fig. S11a). Soil N concentration was negatively correlated to soil moisture in the moderate-aridity grassland in the wet year (Fig. S11b). Species richness and the relative abundance of annual and biennial plants declined with increasing soil N concentration in the low-aridity grassland in the dry year (Fig. S11d).

4. Discussion

Our results support the first hypothesis that the effects of warming and warming plus N addition on SOS depend on grassland soil water availability but N addition alone does not significantly affect SOS in all three types of grasslands. Warming had greater effects on SOS than N addition. The results indicate that soil moisture modulated the effects of warming on SOS in grassland ecosystems. Consistent with our second hypothesis, warming and warming plus N addition reduced soil moisture and drove SOS via species richness and functional group composition. By contrast, changes in species richness and functional group composition induced by N addition alone did not alter SOS. This suggests that temperature and soil water availability were the primary drivers for SOS in semiarid grasslands.

4.1. Effects of warming and N addition on spring vegetation phenology

Many environmental factors affect vegetation phenology, including temperature, precipitation, and soil nutrient availability (Montgomery et al., 2020; Wang et al., 2020b). The mechanisms driving these

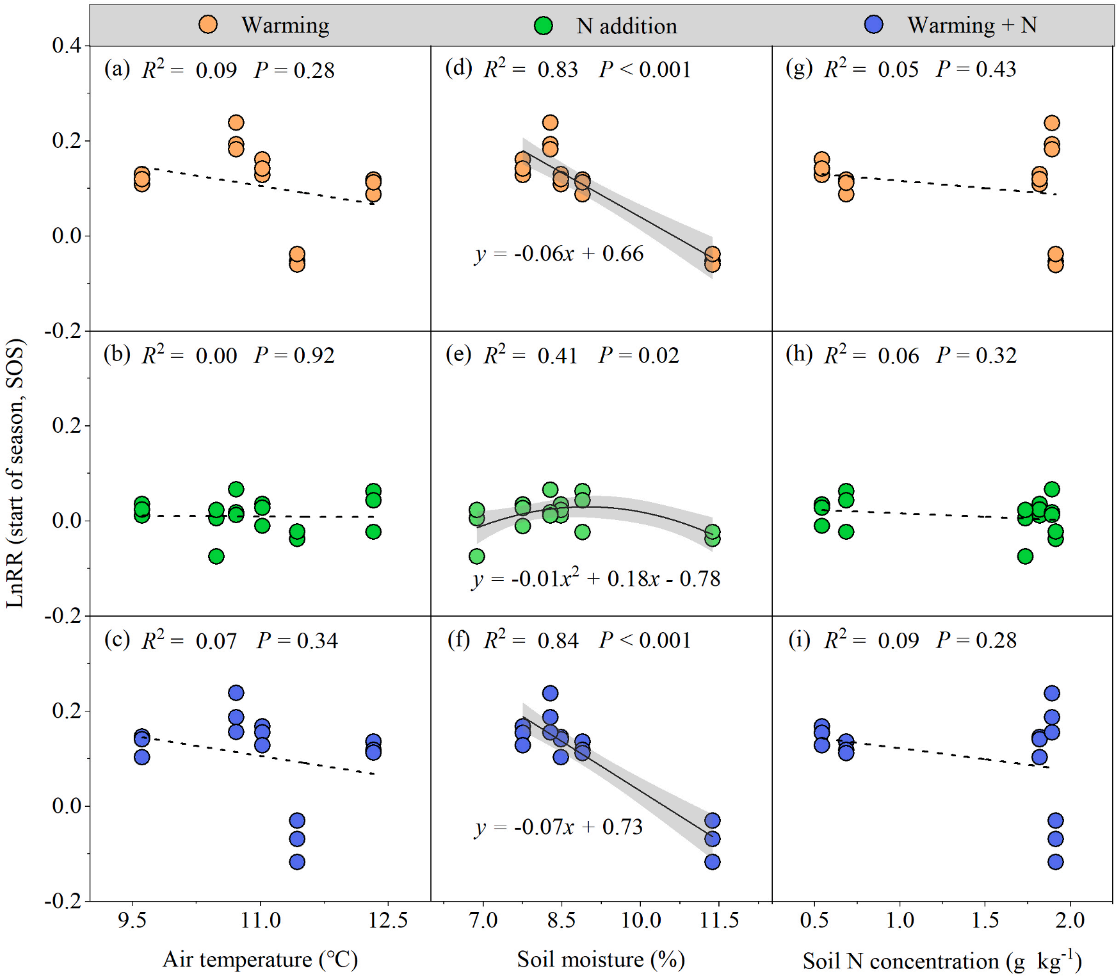

Fig. 3. Natural log response ratios (LnRR) of start of season (SOS) relative to mean spring air temperature (a–c), mean spring soil moisture (d–f), and soil N concentration (g–i) under warming, N addition, and warming plus N addition. R^2 and P values of linear regression analyses are shown. Black solid line indicates significant linear relationship with $P < 0.05$, gray areas are the 95% confidence intervals. Black dotted line indicates non-significant linear relationship with $P > 0.05$.

relationships can be evaluated by conducting experiments that manipulate the parameters because the effects of a single factor on plant phenology can be masked by other factors in time-series and remote-sensing studies (Hanninen et al., 2019). In this study, we examined experimentally induced warming in three types of grasslands that differed in soil water availability. Previous studies reported that experimental warming affects plant growth (i.e., plant biomass) within several months after treatment in this region (Wu et al., 2020; Yang et al., 2017). The dominant timescales were 1–6 months for the lagged and cumulative effects of environmental changes on SOS (Fu et al., 2015; Zeng et al., 2021). To reduce the potential residual effects in this field experiment, we conducted our warming experiment during the early growing season of 2016, and measured the effects of warming on SOS in 2017. We found that warming advanced spring phenology in the low-aridity grassland during a year with high soil water availability. This result is consistent with those of previous studies that employed remote sensing in this region. Thus, rising temperatures and sufficient water can advance plant growth in early spring (Fu et al., 2021; Zhou et al., 2014).

Interestingly, we also found that warming delayed SOS in grasslands with low soil moisture. This likely happened because warming reduced soil moisture levels by ~10% of control water moisture (Fig. S5), and then led to a delayed SOS in grasslands (Tao et al., 2020). The SOS response ratios were negatively correlated to soil moisture under warming and warming plus N addition (Fig. 3), which suggests that soil moisture is a primary driver that modulates the spring phenology response to climate warming in semiarid grasslands. This corroborates why long time-series and remote sensing study in this region reports that SOS exhibits high interannual variability but no significant trends across years under climate warming (Fu et al., 2021; Wang et al., 2019). Our empirical studies indicate that soil moisture that reflects precipitation availability should be considered when investigating and predicting the effects of climate warming on grassland phenology.

Nitrogen is an essential element that has an important role in plant growth (Bharath et al., 2020; Harpole et al., 2007). Previous research indicates that N enrichment acts quickly to affect plant growth within several months after N addition in this region (Lu et al., 2018; Ma et al., 2020b). We tested the effect of N enrichment on SOS in the second growing season after N addition. Our study showed that N addition only slightly affected SOS in three grasslands with varied aridity during the wet and dry years (Fig. 2), although the effects of N enrichment on plant productivity depended on soil water availability in arid and semiarid grasslands (Ma et al., 2020b; Wang et al., 2017). These results are consistent with previous studies in a Mediterranean ecosystem that received ~650 mm year^{-1} precipitation (Luo et al., 2020), and in a temperate continental climate that received 400 mm year^{-1} precipitation (Xu et al., 2021). A possible explanation could be that temperature and/or water are the primary limiting factors for plant growth during the early growing season, despite adequate nutrients (Fu et al., 2021; Prevey et al., 2017). In general, our results suggest that N addition alone had little effect on SOS in semiarid grasslands.

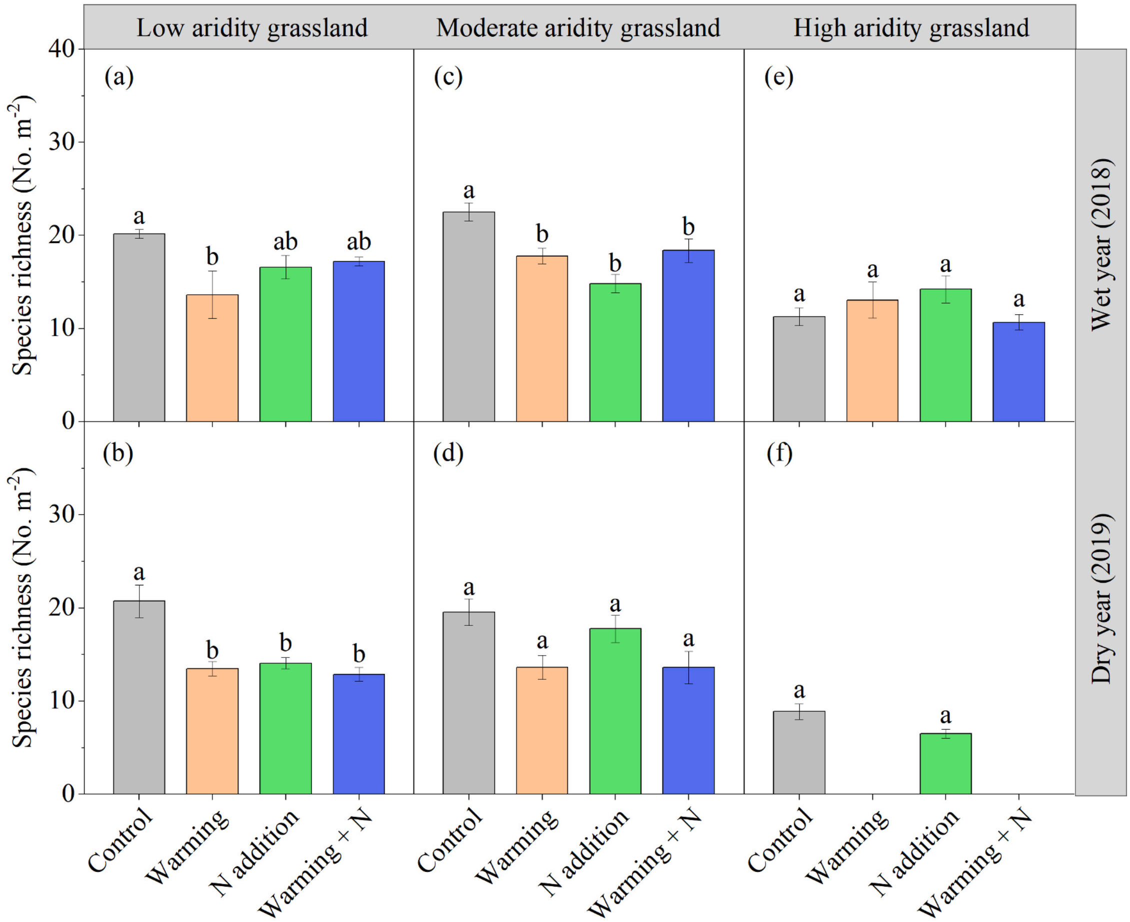

Fig. 4. Effects of warming, N addition, and warming plus N addition on species richness in low- (a, b), moderate- (c, d), and high- (e, f) aridity grasslands in a wet year (2018) and a dry year (2019). Values represent mean ± S.E. Different lowercase letters indicate significant differences among treatments ($P < 0.05$). The effects of warming and warming plus N addition on species richness in high-aridity grassland in 2019 were not conducted due to the lack of relevant data.

4.2. Warming and N addition independently affect spring vegetation phenology

Recent studies report that N availability alters the effects of climate warming on plant phenology; for example, SOS is less sensitive to climate warming in areas with high N deposition than in area with low N deposition (Wang et al., 2020b; Zhu et al., 2016). Our study showed that N addition did not modulate the effects of warming on spring phenology in three types of grasslands (Tables 1, S4). There were three possible explanations for this observation. First, warming can directly or indirectly accelerate litter decomposition through microbial activity and thereby increase soil N availability (Bork et al., 2019). Second, the endogenous soil N levels may be sufficient for plant growth in the early growing season (Harpole et al., 2007). Third, high N deposition attenuated SOS sensitivity to climate warming in areas with annual precipitation >500 mm year^{-1} (Wang et al., 2020b). Our results are consistent with a previous study in this region, which showed that the effects of warming and N addition on plant reproductive phenology were independent (Xia and Wan, 2013). In general, our results were reconcilable with previous studies, and further showed that soil N availability did not alter the response of SOS to climate warming in semiarid grasslands.

Our results also revealed that the effects of warming and N addition on SOS were not related to air temperature or soil N concentration in the three types of grasslands. As discussed before, this may be because soil water was the primary limiting factor for plant growth in arid and semiarid grasslands (Green et al., 2019). In our study, warming altered soil water availability and then shifted SOS. We also observed that N addition did not affect SOS, possibly because the grasslands had sufficient soil N to support early plant growth (Harpole et al., 2007). Therefore, warming and its combination with N addition, advanced SOS in grasslands with high soil moisture and delayed SOS in grasslands with low soil moisture, rather than N treatment alone. We also found that spring 6-month SPEI was significantly reduced by warming and warming plus N addition treatments, rather than N treatment alone (Figs. S10, S12). The effects of warming and warming plus N addition on SOS correlated to spring 6-month $AI_{Köppen}$ (Fig. S13). This indicated the importance of cumulative effects of preseason temperature and precipitation on SOS (Zeng et al., 2021). Soil moisture had significant correlation with spring 1-month $AI_{Köppen}$ ($R^2 = 0.86$) or spring 6-month $AI_{Köppen}$ ($R^2 = 0.85$) (Fig. S9) suggesting that soil moisture was an effective metric reflecting meteorological aridity conditions and preseason cumulative effects (Zeng et al., 2021). Our results of short-term experiments indicate that ongoing climate warming, rather than N deposition, significantly shifted SOS in grasslands, and the magnitude and direction of change in SOS depended on soil water availability. Whether these short-term results could be translated to longer temporal scales with multiple 'wet' and 'dry' years needs to be tested, because grassland biotic factors (e.g., diversity and functional group) may differ among various dry/wet years.

4.3. Effects of species richness and functional group composition on spring phenology

Changes in species richness and community composition can affect plant community phenology due to species-specific differences in growth time (Oehri et al., 2017; Wolf et al., 2017). Our results are

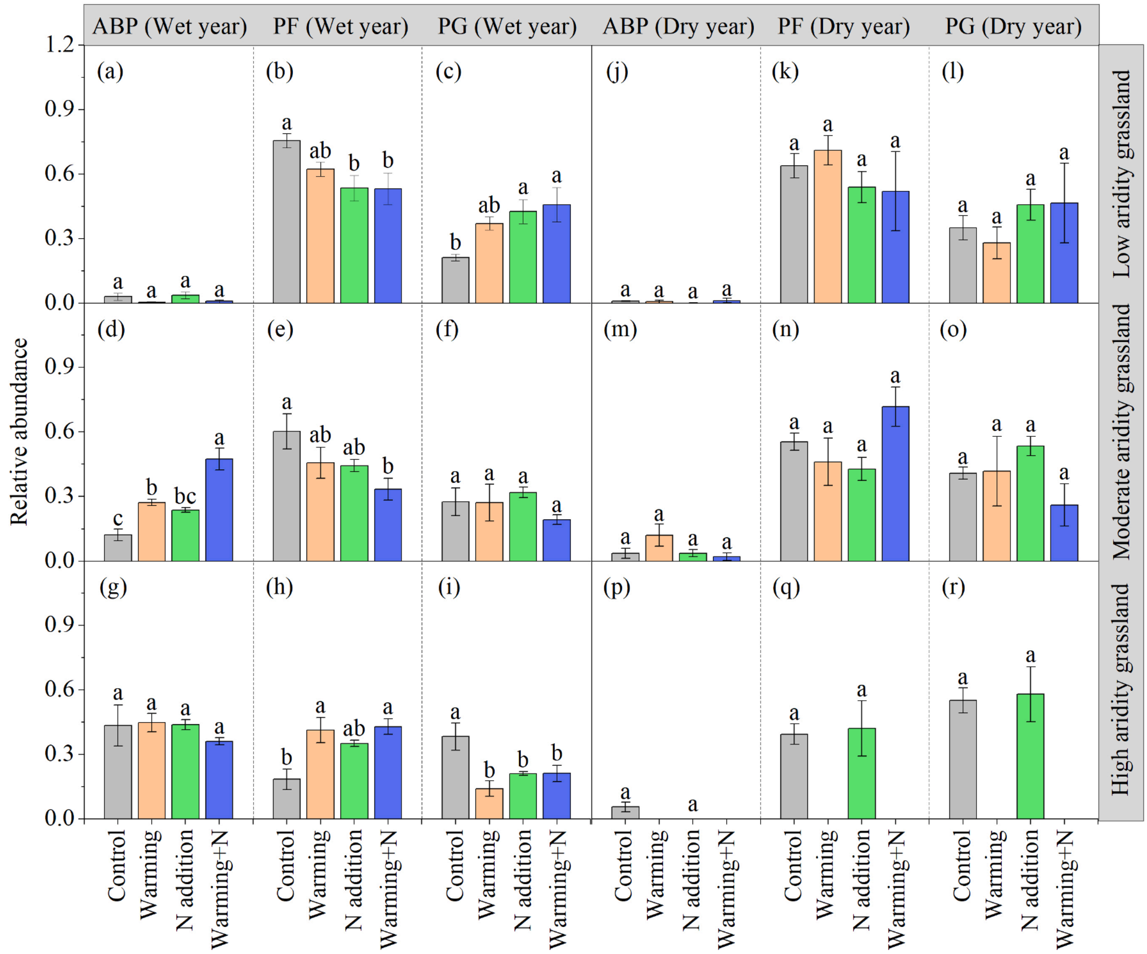

Fig. 5. Effects of warming, N addition, and warming plus N addition on the relative abundance of annual and biennial plants (ABP), perennial forbs (PF), and perennial grasses (PG) in low- (a–c, j–l), moderate- (d–f, m–o), and high- (g–i, p–r) aridity grasslands in a wet year (2018) and a dry year (2019). Values represent mean ± S.E. Different lowercase letters indicate significant differences among treatments ($P < 0.05$).

consistent with this hypothesis, as warming-induced reduction in soil moisture reduced species richness in the low-aridity grassland in the dry year and in the moderate-aridity grassland in the wet year, thereby delay SOS. This may be because species richness is related to species compensation, and niche differentiation among species can enhance the extension of community phenology (Rheault et al., 2015). Therefore, warming-induced reduction in species richness may reduce species compensation in the early growth stage and thereby delay SOS. However, warming-induced reduction in species richness did not change SOS in the low-aridity grassland in the wet year. Neither did it affect the moderate-aridity grassland in the dry year. Similarly, changes in species richness caused by N addition alone did not alter SOS in all three grasslands. This may be because functional groups compensate for temporal changes in community growth caused by reduced species richness (Bai et al., 2004).

We observed that warming enhanced perennial grasses in the low-aridity grassland in the wet year. *L. chinensis* is the dominant perennial grass species in this region because it has high growth rates and strong competition for nutrients and light (Ding et al., 2021). Perennial grasses grow early and occupy a favorable ecological niche for competition and growth; thus, increasing the relative abundance of perennial grasses could advance SOS. In moderate- and high-aridity grasslands, the warming-induced increase in the relative abundance of annual and biennial plants and perennial forbs delayed SOS. This may be because soil moisture was low (< 9%) in the early growing season in moderate- and high-aridity grasslands (Fig. S5) and resulted in nil or negative effects of warming on the growth of early growing perennial grasses. Annual and biennial plants (mostly C_4 plants such as *S. viridis, S. collina*, and *C. glaucum*) and perennial forbs (*T. terrestris*) are likely more tolerant of warming-induced reductions in soil moisture, and they generally begin growing later in the season (Morgan et al., 2011). Thus, SOS was delayed by the warming-induced increase in annual and biennial plants in the moderate-aridity grassland and perennial forbs in the high-aridity grassland. N-induced changes in functional group composition did not alter SOS in three types of grasslands. This may be because the compensatory effects of different functional groups may vary with the availability of soil water. Our study indicated that biotic factors had complex effects on SOS in grasslands.

4.4. Warming and N addition effects on SOS, species richness and functional group composition among sites

In general, our results showed that the effects of warming and N addition on SOS varied among three grasslands via species richness and functional group composition. In low-aridity grassland, with low temperature and high soil water, warming likely increased the SOS interannual variability due to differences of soil water availability or aridity (Montgomery et al., 2020; Wang et al., 2019). Possible reasons may be that temperature and/or water are the main limiting factors in this region (Fu et al., 2021; Prevey et al., 2017). However, in moderate- and high-aridity grasslands with high temperature and low soil water, warming delayed the SOS due to warming-induced soil water stress and aridity (Yu et al., 2010). We infer that water is the dominant factor in this region (Tao et al., 2020). Conversely, the effects of N addition on

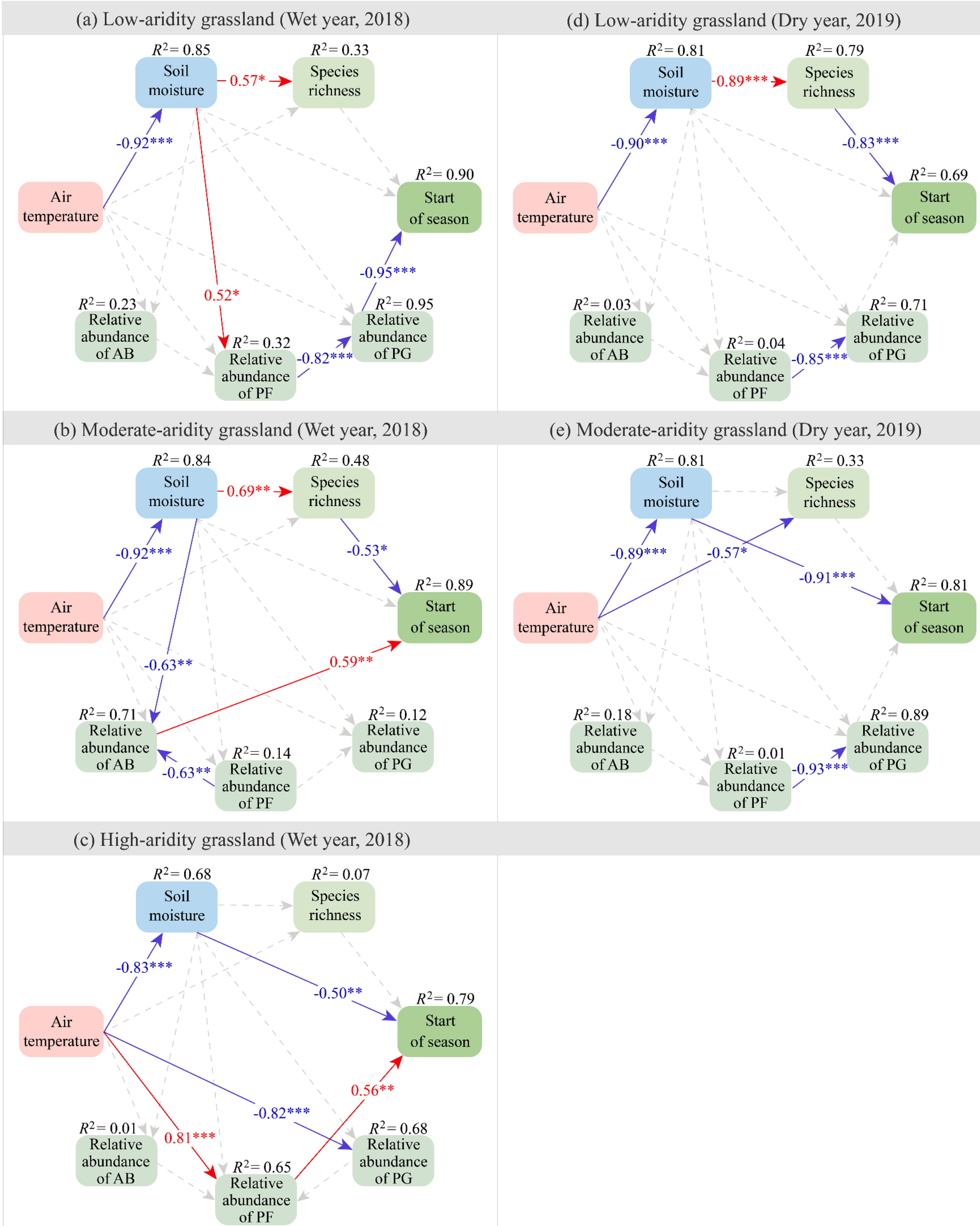

Fig. 6. Final structural equation model (SEM) for the effects of mean spring air temperature, mean spring soil moisture, species richness, and relative abundance of annual and biennial plants (ABP), perennial forbs (PF), and perennial grasses (PG) on the start of season under warming and warming plus N addition in low- (a, d), moderate- (b, e), and high- (c) aridity grasslands in a wet year (2018) and a dry year (2019). All plausible pathways based on theoretical and empirical predictions were considered. Numbers on the arrows are standardized path coefficients indicating the effect size of the relationship. Red and blue solid arrows represent positive and negative significant relationships between two variables, respectively. Light black dotted arrows indicate a non-significant relationship between two variables. Goodness-of-fit statistics of all SEMs refer to composite reliability (CR) = 1, average variance extracted (AVE) = 1, and heterotrait-monotrait ratio of correlations (HTMT) < 0.85. CR > 0.8 indicates good internal consistency and reliability. AVE > 0.5 and HTMT < 0.85 indicate good fit and discriminant validity, respectively. * P < 0.05, ** P < 0.01, *** P < 0.001.

SOS were marginal and much less than warming effects for three grasslands, because N was not a key driver for SOS when compared to temperature and water in arid and semiarid grasslands (Xu et al., 2021).

The effects of warming and N addition on plant species had obvious differences among the three grassland types (Fig. 4). Consistent with previous studies, species richness was reduced by short-term warming and N addition in the grasslands with high precipitation and species richness (Klein et al., 2004; Ma et al., 2020a). One potential mechanism may be that light limitation caused by increasing plant productivity and litter under warming and N addition reduces species richness (Borer et al., 2014; Ma et al., 2021). Furthermore, warming-induced heat stress in aboveground plant tissue and N-induced soil acidification also may be important mechanisms (Chen et al., 2013; Klein et al., 2004). In contrast, slight changes in species richness after these warming and N addition treatments in high-aridity/low precipitation grassland may contribute to higher plant tolerance, and low sensitivity to soil water stress and N enrichment (Morgan et al., 2011; Wang et al., 2017; Wu et al., 2020). Our results indicated that warming and N addition-induced changes in biotic factors were not the main drivers for SOS in these specific sites. However, whether the differences in SOS among sites resulted from the treatment-induced changes in biotic factors were not detected in our study. Further research is needed to investigate these potential mechanisms (Wolf et al., 2017).

5. Conclusions

We investigated how climate warming and N enrichment affected spring vegetation phenology in three types of grasslands in Inner Mongolia, China, and whether abiotic and biotic factors modulated these effects. Our results indicated that the magnitude and direction of SOS response to warming depended on soil moisture. N deposition slightly advanced SOS in grasslands with high soil moisture, but slightly delayed SOS in grasslands with low soil moisture. Warming and N addition affected SOS independently in semiarid grasslands. Our results indicated that soil water, rather than soil N, had a crucial role in modulating the response of SOS to climate warming in semiarid grasslands.

Declaration of Competing Interest

We declare that we have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109039.

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