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ARTICLE

Contrasting responses of flowering phenology in C_3 and C_4 plants shape grassland community structure under global change

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Abstract

Climate change is known to affect plant phenology. Yet, the sensitivity of flowering phenology in dryland regions to climate change, and the potential implications for community composition, remain largely unexplored. Here, we used an 18-year field experiment to investigate the effects of climate warming and nitrogen addition on flowering phenology of four C_3 plant species and two C_4 plant species, and the cascading effects on the relative abundance of C_3 and C_4 plants in a desert steppe. Across the past 10 years of the experiment (2013–2022), we found that warming had a greater effect on phenological shifts in C_3 than in C_4 plants. Warming significantly advanced the flowering time of C_3 plants by 4.3 ± 0.1 days and of C_4 plants by 2.8 ± 0.1 days, respectively. Warming also reduced the duration of flowering by 1.8 ± 0.1 days for C_3 plants but had no effect on C_4 plants, and decreased the dominance of C_3 plants compared to C_4 plants. Nitrogen addition extended the duration of flowering of C_4 plants by 3.4 ± 0.2 days and increased their relative dominance, while decreasing the dominance of C_3 plants. Structural equation models revealed that these phenological responses were largely driven by soil temperature and soil water availability. Our results demonstrate that the different phenological responses of C_3 and C_4 plants contribute to shifts in dominance between these plant types in temperate dryland ecosystems under global changes.

KEYWORDS
climate warming, nitrogen deposition, plant phenology, soil moisture, soil temperature, species dominance

INTRODUCTION

The Earth is currently experiencing significant environmental changes, including rising air temperatures and increased atmospheric nitrogen (N) deposition (IPCC, 2023). Numerous studies have shown that warming can lead to earlier flowering across temperate regions (Collins et al., 2021; Dorji et al., 2020; Liu et al., 2023; Pérez-Ramos et al., 2020; Piao et al., 2019; Radice et al., 2023; Williams et al., 2021; Yang et al., 2022). Given the timing and duration of plant flowering affect plant survival, reproduction, and community dynamics (Collins et al., 2021; Forrest et al., 2010), it is important to understand how these changes in plant phenology contribute to changes in the structure of ecological communities, such as the relative responses of different plant functional groups to climate change (Collins et al., 2021; Piao et al., 2019; Post et al., 2008). The effects of N deposition on flowering phenology are intricate and can vary among species, plant functional groups, and ecosystems (Xia et al., 2015; Zhou et al., 2023). For instance, in a semi-arid alpine meadow ecosystem on the central Tibetan Plateau, N addition resulted in delayed flowering of grasses, but slightly advanced flowering of forbs (Dorji et al., 2013). These variable phenological responses to warming and increased N availability highlight the need to better understand their linkage to changes in plant community composition and structure in response to global environmental change (Piao et al., 2019).

In arid and semi-arid regions, plant phenological responses to warming and N addition are closely linked to changes in soil temperature and moisture (Dunne et al., 2003; Zhu et al., 2016). For example, warming can enhance soil evaporation, reducing moisture availability for shallow-rooted species (Dorji et al., 2013). Similarly, N addition may increase vegetative growth and evapotranspiration, altering soil moisture dynamics and competitive interactions among plant species (Yang et al., 2023). Furthermore, N addition delays the transition from vegetative growth to the reproductive phase in grasses, boosting productivity (Yang et al., 2023). However, this increase in productivity often leads to greater soil moisture loss through evapotranspiration, which disproportionately affects shallow-rooted plants, such as sedges, which are more sensitive to drought than deep-rooted species (Liu, Fu, et al., 2022). Despite these insights, the mechanisms by which soil conditions act as cues for phenological changes remain poorly understood, particularly in desert steppes. These ecosystems are shaped by the interplay of environmental warming, increased N deposition, and depth-specific changes in soil temperature and moisture. This complexity hinders our ability to predict the ecological consequences of phenological shifts on community structure (Dorji et al., 2013; Nord & Lynch, 2009; Post et al., 2008). For instance, shallow-rooted C_3 plants, which depend on moisture from upper soil layers and typically flower earlier under cooler conditions, may accelerate flowering under warming to avoid drought stress (Munson & Long, 2017). In contrast, deep-rooted C_4 plants, which are better adapted to high temperatures and arid environments, often delay flowering under similar conditions (Curtis & Mcintosh, 1950). These contrasting responses suggest that warming and N deposition could alter the competitive balance between C_3 and C_4 species, reshaping community structure and composition (Munson & Long, 2017). Although some studies have explored the links between phenological changes and community-level consequences, the empirical evidence remains limited, and such relationships are not well understood (Nord & Lynch, 2009; Xia & Wan, 2013).

Phenological changes result in a series of ecological consequences, including plant growth and its temporal dynamics (Cleland et al., 2007; Fitter & Fitter, 2002; Liu et al., 2023). It, however, is often unclear to what extent plant phenology influences community assembly and competition dynamics (Menzel, 2002; Piao et al., 2019; Stone et al., 1998). Differences in flowering times can affect plant density, thereby reducing pollinator competition or interspecific pollen transfer in coexisting species (Wolf et al., 2017). Differential temporal responses of plants and their pollinators to warming can alter the synchrony between plant flowering and pollinator emergence (Forrest, 2015; Rafferty & Ives, 2012; Robbirt et al., 2014), thereby influencing trophic interactions (Harrington et al., 1999; Zohner et al., 2018) and subsequent seed production by plants (Olesen et al., 2008). Additionally, the differential response of flowering phenology to N addition among different plant functional groups (e.g., sedges and forbs) also affects the activity patterns of pollinators, influencing pollination competition and interactions among plants (CaraDonna et al., 2014). Furthermore, N addition alters resource competition among plants by changing the flowering phenology of different species, granting certain species a competitive advantage while reducing the prevalence of others, ultimately decreasing plant community diversity (Yang et al., 2023). Changes in flowering time can enhance the reproductive success of some plants while adversely affecting others, leading to shifts in population dynamics and density, promoting species replacement, and altering community composition (Alexander & Levine, 2019; Wolf et al., 2017). For instance, early-flowering plants may possess advantages over competitors within the population, enabling them to adjust their strategies and adapt to climate change (Fu et al., 2015). Conversely, plants that fail to keep pace with climate change may face disadvantages, but they may also benefit if highly responsive species more frequently encounter climate risks, such as increased late frost damage (Bardgett & Van Der Putten, 2014; Cleland et al., 2012). However, empirical evidence is lacking regarding the mechanisms through which the differential responses of various plant types' phenology to climate change alter the structure of desert grassland plant communities (Cleland et al., 2007; Gordo & Sanz, 2010).

Here, we present the 10-year findings from a long-term field manipulation experiment conducted in a temperate desert steppe in northern China. Long-term experiments are uniquely suited to capturing both average trends and the temporal dynamics of plant phenological responses to global change factors (Wadgymar et al., 2018). This study provides valuable insights into these dynamics, particularly the year-to-year variations in the phenology of C_3 and C_4 plants, offering a rare opportunity to investigate how these responses unfold over an extended timescale. Our study site is located in the interior of the Asian continent, where notably high rates of climate change have been observed (Zhang et al., 2011). We examined the responses of plant phenology to climate warming and N deposition, and tested the potential implications of these phenological changes on species composition. Our experiment aimed to address two main research questions. First, how do climate warming and N deposition affect the flowering phenology of plants in a desert steppe? Second, how do the differential responses of plant phenology to changes in temperature and N availability contribute to shifts in plant community composition, particularly the relative abundance of C_3 and C_4 plants in the community? We hypothesized that changes in the flowering phenology of C_3 and C_4 species in response to warming and N addition are driven by their distinct sensitivities to soil temperature and moisture across different soil layers (Curtis & Mcintosh, 1950; Wand et al., 1999). In desert steppe ecosystems, soil temperature and moisture are key abiotic factors that directly regulate plant phenology and community dynamics (Li et al., 2013). Soil moisture often serves as the primary limiting factor for plant growth in arid environments (Liu, Fu, et al., 2022), while soil temperature strongly influences metabolic processes such as germination, flowering timing, and seed production (Liu et al., 2024). Previous research (e.g., Bai et al., 2022) has shown that these two variables are critical mediators of plant responses to warming and N addition, justifying their selection as the focal mechanisms in this study. Although other factors, such as the higher N-use efficiency and photosynthetic capacity of C_4 plants or biotic interactions like N-fixing legumes, may also influence shifts in C_3 and C_4 dominance (Lee, 2011), we focused on soil temperature and moisture as the primary drivers of these changes. By addressing these questions, our study provides unique insights into the dynamics of plant phenology and community composition in response to global change in the temperate desert steppe ecosystem.

MATERIALS AND METHODS

Study site

The study was performed in a desert grassland located in Inner Mongolia, China (41°46′43.6″ N, 111°53′41.7″ E; 1456 m above sea level). The climate is a typical mid-temperate continental monsoon climate with a dry and windy spring, hot summer and cold winter. The average annual precipitation (2004–2022) is about 232 mm (Appendix S1: Figure S1), of which about 85% occurs during the growing season from May to September. The average annual temperature during the study period was 3.8°C (Appendix S1: Figure S1) and the annual temperature during the growing season was 16.4°C (2004–2022), with a mean diurnal temperature difference of 13–14°C. The soil (0–10 cm depth) has a soil bulk density of 1.3 g cm^{-3}, a total N of 1.7 g kg^{-1}, a total carbon of 16.9 g kg^{-1} and pH of 8.0. Plant communities at the study site are dominated by two perennial grasses, *Stipa breviflora* Griseb. and *Cleistogenes songorica* (Roshev.) Ohwi, and one perennial semi-shrub, *Artemisia frigida* Willd. Other common species included *Kochia prostrata* (Linn.) Schrad, *Convolvulus ammannii* Desr. in Lam and *Allium tenuissimum* L. More details on growth forms, late or early flowering patterns, pollination and seed dispersal methods of six studied plants were provided in Appendix S1: Table S1.

Experimental design

The experiment was established in May 2006 using a split-plot design, with warming as the whole-plot factor and N as the subplot factor. The area of each main plot was 3 m × 4 m, and a buffer distance of 3 m was set between adjacent main plots. The four treatments included the control, warming, N addition, and the combination of warming and N addition, each of which had six replicates (Appendix S1: Figure S2). Starting from May 2006, each warming plot was continuously heated using a 165 cm × 15 cm MSR-2420 infrared radiator (Kalgo Electronics, Bethlehem, PA). The infrared radiator was installed 2.25 m above the ground of the heating cell, and the output power was set to 2000 W. The radiator led to an average warming of +1.4°C during the growing season (May–September) and of +1.2°C during the non-growing season (October–April) at a height of

0–2 cm above the surface (Ren et al., 2021; Wu et al., 2020). In each of the control plots, a simulant radiator of the same size was hung at the same height to simulate the shading effect of the radiator. Once a year, around the third week of June, N was added in the form of NH_4NO_3 at the rate of $10\ g\ N\ m^{-2}\ year^{-1}$ before rainfall.

Measurements of plant flowering phenology

We selected six dominant and common plant species for phenological observation, including three perennial C_3 grasses (*S. breviflora*, *C. ammannii*, and *A. tenuissimum*), one perennial C_3 subshrub (*A. frigida*), one C_4 grass (*C. songorica*), and one perennial C_4 subshrub (*K. prostrata*). Five individuals per plant species were randomly chosen and numbered in each plot, and their reproductive phenology was observed and recorded using the measured scoring method. We continuously recorded plant phenology from 2013 to 2022. Here, the phenological observation of a species started once the first flower buds were discovered. The observation frequency was once every 3–5 days. For non-grasses and grasses, a 6-point system (Dunne et al., 2003) and a 4-point system (Price & Waser, 1998) were used to record scores, respectively. For grasses, the phenological phases observed were 0 = spikelet in the boot, 1 = spikelet out of the boot, 2 = exserted anthers and styles, 3 = developing seed, 4 = all seed dropped (Price & Waser, 1998). For non-grass plants, plant phenology can be divided into seven stages: 0, not flowering; 1, flower buds appear; 2, flowering; 3, flower senescence; 4, the fruit begins to develop; 5, the fruit begins to disperse; 6, the fruit falls off completely. For each species within each plot, the start dates of phenophases and the duration of phenoperiods were recorded for five randomly selected individual plants. The average phenophase start date and phenoperiod for these individuals were calculated to represent the phenological characteristics of the species within the plot. These plot-level averages were then used in subsequent analyses to assess the effects of treatments at the population level. Each phenological event was recorded, and subsequently, the observation time was transformed into an integer value that represents the sequential date within the year, with January 1 being designated as the first day of the year and recorded as 1 (Julian Day). The actual phenological sequences of plants were then used to fit Richard's equation in 1STOPT software (Sherry et al., 2007). The first flowering date and flowering duration of each phenological period were calculated based on the optimal simulation curve according to the Richards equation (Price & Waser, 1998).

$$Y = \frac{K}{1 + a^{-bX}} m,$$

where K is the maximum growth, that is, the maximum value in the phenology score; a is the start-up parameter of the date when observation of the evaluated species began; b is the reproductive phenological rate during the observed period; and m is the curve shape variation parameter. All phenological scores were well described by the Richards equation ($R^2 > 0.99$).

Four parameters can be determined by equation fitting and substituted into the conversion formula as follows:

$$X = -\frac{1}{b} \ln \left[\frac{m\sqrt{\frac{K}{Y}} - 1}{a} \right],$$

where Y is the phenological value and X is the corresponding phenological date. A phenological value of 1 represents the emergence of flowering buds. A phenological value of 2 represents the flowering date. A phenological value of 3 represents the finishing of the duration of the flowering period. The duration of flowering of each plant was defined as the period from the emergence of flowering buds until the end of the duration of the flowering period.

Measurements of plant dominance and soil characteristics

Species' dominance was quantified as the mean of relative density, relative coverage and relative height of plants (Curtis & Mcintosh, 1950; Koerner et al., 2018; Lindsey, 1956; Meng et al., 2023). The relative density, coverage and height is determined by dividing the density of the species by the total density of all species and multiplying by 100. Specifically, plant density, which was indicated by the total number of individuals of each species, was measured within a permanent quadrat of 1 m × 1 m in each subplot in the middle of the annual growing season (August). In the same quadrat, plant cover was determined by placing a 1 m × 1 m metal frame with 100 equally distributed grids (10 × 10 cell grid) above the canopy and counting the junctions of the grids whose vertical projections overlapped with plants. Plant height within a subplot was calculated as the mean values of at least five random measurements of species' natural height. Soil temperature and moisture (0–10 cm) were monitored by water content

TABLE 1 Effects of warming (W), Nitrogen (N) addition, and their interactions on plant dominance, flowering time, and duration of flowering in C_3 and C_4 plants, based on linear mixed-effects models.

			Flowering time		Duration of flowering		Plant dominance	
			C_3 plants	C_4 plants	C_3 plants	C_4 plants	C_3 plants	C_4 plants
Effect	**df1**	**df2**	***F*-ratio**	***F*-ratio**	***F*-ratio**	***F*-ratio**	***F*-ratio**	***F*-ratio**
W	1	15	9.64*	4.31*	7.72*	2.62	28.92**	11.49*
N	1	15	0.14	0.13	0.11	7.09*	10.64*	20.48**
W × N	1	15	3.35*	0.16	5.21*	1.42	11.32*	15.79*

Note: df1 and df2 denote the numerator and denominator df, respectively.
$^{**}p < 0.01$; $^{*}p < 0.05$.

and temperature sensors (ECH2O-TE/TM, Decagon Devices, Inc.) throughout the study period, and data were logged every 2 h.

Data analyses

We used linear mixed-effect models to analyze the effects of warming and N addition on plant dominance, flowering phenology, and soil characteristics. Warming was treated as the main-plot effect and N addition as the subplot effect, distinguishing the hierarchical structure of the split-plot design. The six blocks were treated as random factors to account for variability between blocks. We treated "year" as a random effect to estimate variance components across years and control for interannual differences, assuming year-to-year variation as a source of random fluctuation (Table 1). Second, to capture temporal trends and assess interactions between year and treatment effects, we treated "year" as a repeated-measures factor in a separate analysis (Appendix S1: Table S2). In this study, we employed the "Ljung-Box" test to assess whether the collected time series data exhibit significant autocorrelation (Ljung & Box, 1980). The primary objective of the test was to determine whether autocorrelation at various lags is significant. We used the "Box. test()" function in R software, setting the lag to 12 months, to perform the "Ljung-Box" test (Appendix S1: Figure S3). To ensure temporal autocorrelation was properly addressed, we assessed residuals for autocorrelation using an autocorrelation function (ACF) plot (Appendix S1: Figure S3). Residuals were extracted from the primary linear mixed-effect model, and the ACF plot, generated using the "acf()" function in R, displayed the autocorrelation coefficient (*y*-axis) at various lags (*x*-axis). However, no significant temporal autocorrelation was observed in the residuals (Appendix S1: Figure S3), confirming that the model adequately accounted for temporal dependency. To compare the phenological responses of C_3 and C_4 groups, we calculated species averages. The phenological equation was fitted using 1stOpt (First Optimization software, 7D-Soft High Technology Inc.).

To contextualize our experimental findings within regional patterns, we conducted a systematic synthesis of published studies assessing the effects of warming on flowering phenology in northern China's grasslands. We included data from studies that met the following criteria: (1) experimental warming with clearly defined control and treatment groups, (2) measurements of flowering time and duration, and (3) adequate reporting of data, including mean values, sample sizes, and SDs. We extracted mean values for both control and warmed treatments from 18 qualifying studies (153 phenological records). To minimize methodological variability, we: (1) excluded studies using non-standard warming methods (e.g., open-top chambers that alter light conditions), (2) standardized the definitions of phenophases (flowering onset = first observed open flower; flowering duration = number of days between the first and last flower), and (3) stratified the data by grassland type (meadow grasslands: $n = 17$ plots; arid and semi-arid grasslands: $n = 13$ plots; alpine grasslands: $n = 28$ plots). We compared group means using one-way ANOVA in R (version 4.2.2). The analysis included sixteen C_3 plant species (*S. breviflora* Griseb., *Leymus chinensis* (Trin.) Tzvelev, *A. frigida* Willd., *Potentilla bifurca* L., *Caragana microphylla* Lam., *Poa pratensis* L., *Agropyron cristatum* (L.) Gaertn., *Astragalus galactites* Pall., *Heteropappus altaicus* (Willd.) Novopokr., *Stipa krylovii* Roshev., *Allium tenuissimum* L., *Convolvulus ammannii* Desr., *Veronica eriogyne* (Bunge) Juz., *Poa poophagorum* Bor., *Anaphalis flavescens* Hand.-Mazz., *Artemisia scoparia* Waldst. & Kit.) and five C_4 plant species (*Cleistogenes squarrosa* (Trin.) Keng, *Kochia prostrata* (L.) Schrad., *Cleistogenes songorica* (Roshev.) Ohwi, *Chenopodium glaucum* L., *Elymus nutans* Griseb.).

Structural equation modeling (SEM) was used to evaluate the direct and indirect effects of temperature and N addition on species dominance. SEM analyses were conducted using the lavaan package in R (Rosseel, 2012).

Given consistent phenological and dominance responses to warming and N addition across years, but significant variation among species, we analyzed the differential responses of individual species to these treatments. Year was treated as a repeated measure, and an initial full SEM was constructed, incorporating all theoretically plausible pathways based on the previous knowledge and ecological relationships. The initial SEM framework incorporated all theoretically plausible pathways derived from existing literature (Appendix S1: Figure S4). Pathways were evaluated for statistical significance using the maximum likelihood estimation (MLE) method, and non-significant pathways were sequentially removed to simplify the model while retaining biologically meaningful and statistically robust relationships. In this study, we applied Convergent Cross Mapping (CCM) to explore the potential causal relationships between flowering phenology and plant dominance (Runge, 2023). Specifically, the data were processed using the rEDM package in R, and different library sizes (LibSize, ranging from 10 to 480) were used to examine the trend of prediction correlation (ρ values) as library size increased. To ensure the robustness of the results, the "ccm()" function was used to determine the optimal embedding dimension ($E = 3$), and 100 random samples were drawn to minimize the noise effect on the ρ values. Flowering phenology and plant dominance were set as the library and target columns, respectively, to test the causal relationship between the two variables. The "ccm means()" function was used to compute the mean ρ values for each library size, allowing for the visualization of trends. If the ρ values stabilized and maintained high values as the library size increased, it indicated a significant potential causal relationship between the variables. Additionally, causal direction was further confirmed by comparing relationships in different directions. This method not only provided a tool for causal relationship detection but also ensured the robustness of the findings through repeated sampling and random permutation.

RESULTS

Effects of warming and N addition on environmental factors

Experimental warming increased soil temperature by 1.0°C ± 0.1°C at 0–10 cm depth ($F_{1,9} = 16.63$, $p = 0.002$), 1.2°C ± 0.2°C at 10–20 cm depth ($F_{1,9} = 9.11$, $p = 0.01$) and 1.4°C ± 0.1°C at 20–30 cm depth ($F_{1,9} = 33.56$, $p = 0.0003$; Appendix S1: Table S3; Figure 1). Nitrogen addition had no effect on the soil temperature at depths of 0–10 cm, 10–20 cm, and 20–30 cm. Combined warming and N addition led to an increase of soil temperature by 1.0°C ± 0.2°C at 0–10 cm depth ($F_{1,9} = 11.13$, $p < 0.05$), 0.9°C ± 0.2°C at 10–20 cm depth ($F_{1,9} = 12.03$, $p < 0.05$), and 1.2°C ± 0.1°C at 20–30 cm depth ($F_{1,9} = 18.67$, $p < 0.05$; Appendix S1: Table S3; Figure 1).

Warming did not alter soil moisture at any depth (Appendix S1: Table S3; Figure 1). Nitrogen addition significantly increased soil moisture by 4.2% at 10–20 cm depth ($F_{1,9} = 5.74$, $p = 0.02$) and 2.3% at the 20–30 cm depth ($F_{1,9} = 5.78$, $p = 0.03$; Appendix S1: Table S3; Figure 1), but did not affect soil moisture at 0–10 cm depth. Combined warming and N addition significantly enhanced soil moisture by 6.1% at 10–20 cm depth ($F_{1,9} = 9.85$, $p = 0.03$) and 3.2% at 20–30 cm depth ($F_{1,9} = 7.85$, $p = 0.04$; Appendix S1: Table S3; Figure 1).

Effects of warming and N addition on plant flowering phenology and community dynamics

Warming advanced the flowering time of C_3 plants by 4.3 ± 0.1 days ($F_{1,15} = 9.64$, $p = 0.01$) and of C_4 plants by 2.8 ± 0.1 days, respectively ($F_{1,15} = 4.31$, $p = 0.04$; Table 1; Figure 2). In five of the six species monitored, we observed earlier flowering times under warming conditions. Specifically, we observed advances of 5.6 ± 0.1 days for *S. breviflora* ($F_{1,15} = 7.01$, $p = 0.02$), 4.5 ± 0.2 days for *A. frigida* ($F_{1,15} = 8.82$, $p = 0.01$), 3.3 ± 0.1 days for *Co. ammannii* ($F_{1,15} = 5.22$, $p = 0.03$), 3.7 ± 0.1 days for *A. tenuissimum* ($F_{1,15} = 4.34$, $p = 0.04$) and 3.6 days for *C. songorica* ($F_{1,15} = 4.53$, $p = 0.04$) (Appendix S1: Table S4, Figure S5). Warming had no effect on the flowering time of *K. prostrata*. In contrast, while N addition advanced the flowering time of *S. breviflora* by 5.6 ± 0.1 days ($F_{1,15} = 4.42$, $p = 0.04$; Appendix S1: Table S4, Figure S5), it did not alter that of other studied species.

Warming reduced the duration of flowering of C_3 plants by 1.8 ± 0.1 days ($F_{1,15} = 7.72$, $p = 0.03$), whereas N addition extended the duration of flowering of C_4 plants by 3.4 ± 0.2 days ($F_{1,15} = 7.09$, $p = 0.04$; Table 1; Figure 2). Warming significantly shortened the duration of flowering by 3.0 ± 0.6 days for *S. breviflora* ($F_{1,15} = 6.86$, $p = 0.03$), 2.3 ± 0.2 days for *C. ammannii* ($F_{1,15} = 6.73$, $p = 0.03$), and 2.1 ± 0.1 days for *A. tenuissimum* ($F_{1,15} = 7.42$, $p = 0.02$); (Appendix S1: Table S4, Figure S6). However, it had no impact on that of other studied species. Nitrogen addition prolonged the duration of flowering by 3.9 ± 1.0 days for *C. songorica* ($F_{1,15} = 6.24$, $p = 0.03$) and 3.0 ± 0.3 days for *K. prostrata* ($F_{1,15} = 6.38$, $p = 0.04$) (Appendix S1: Table S4, Figure S6), but did not influence the duration of flowering of other studied species. To assess the broader applicability of our results, we compared them with data

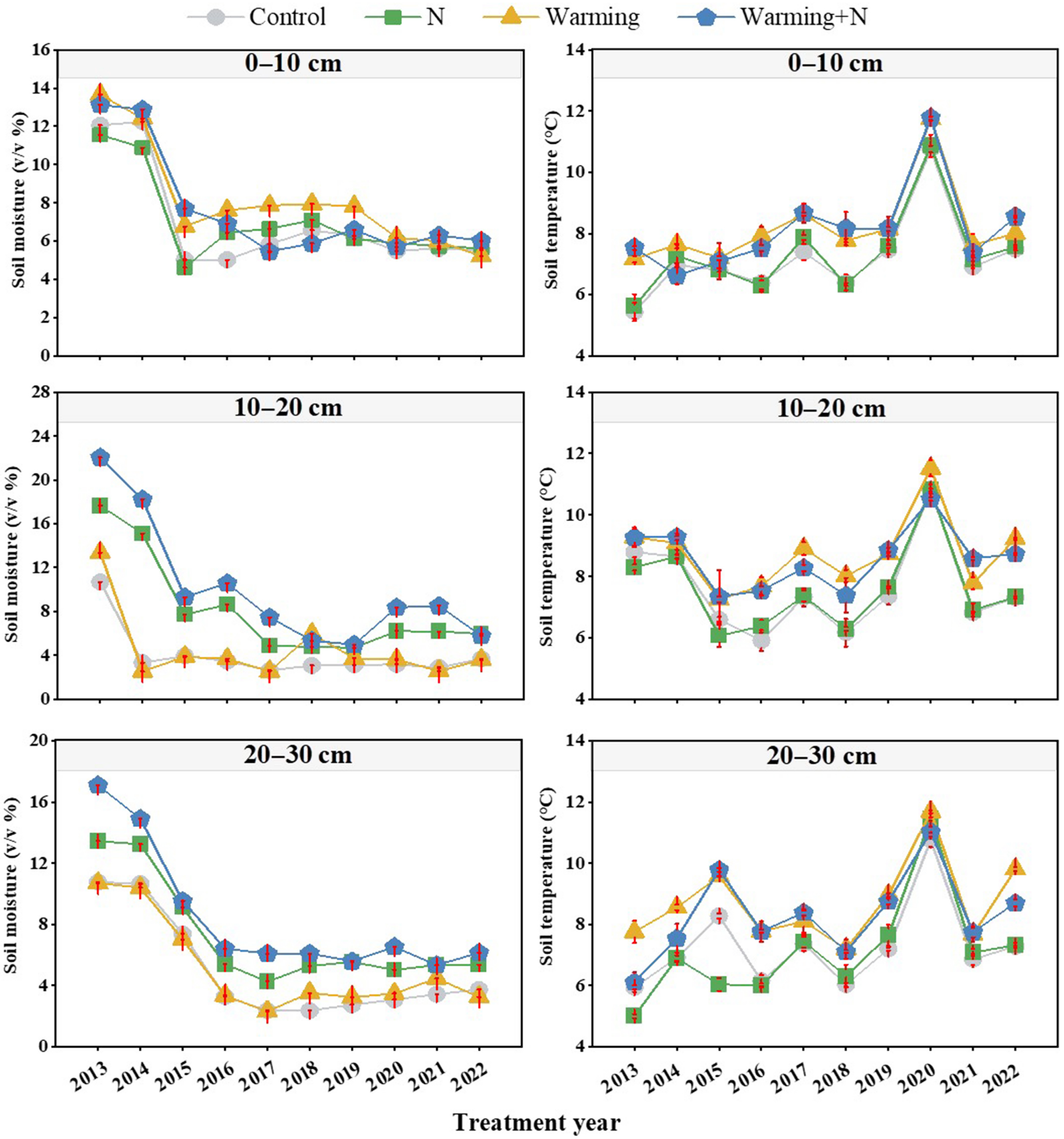

FIGURE 1 Responses of soil moisture (0–30 cm) and soil temperature to warming and N addition from 2013 to 2022 in a desert steppe. Different letters indicate significant differences between treatments. Error bars show one SE of the mean.

from various grassland types across northern China, including meadow, arid, semi-arid, and alpine grasslands (Figure 3). In these ecosystems, warming consistently advanced flowering time in both C_3 and C_4 plants (Figure 3). Additionally, warming shortened the flowering duration of C_3 plants in arid, semi-arid, and alpine grasslands, but had no effect on the flowering duration of C_4 plants (Figure 3). These consistent patterns across different grassland ecosystems reinforce the robustness of our conclusions.

The dominance of C_3 plants decreased by 4.1% ± 0.3% ($F_{1,15} = 28.92$, $p < 0.01$) under warming and 6.0% ± 0.06% ($F_{1,15} = 10.63$, $p = 0.01$) under N addition, respectively (Table 1; Figure 2). Combined warming and N addition

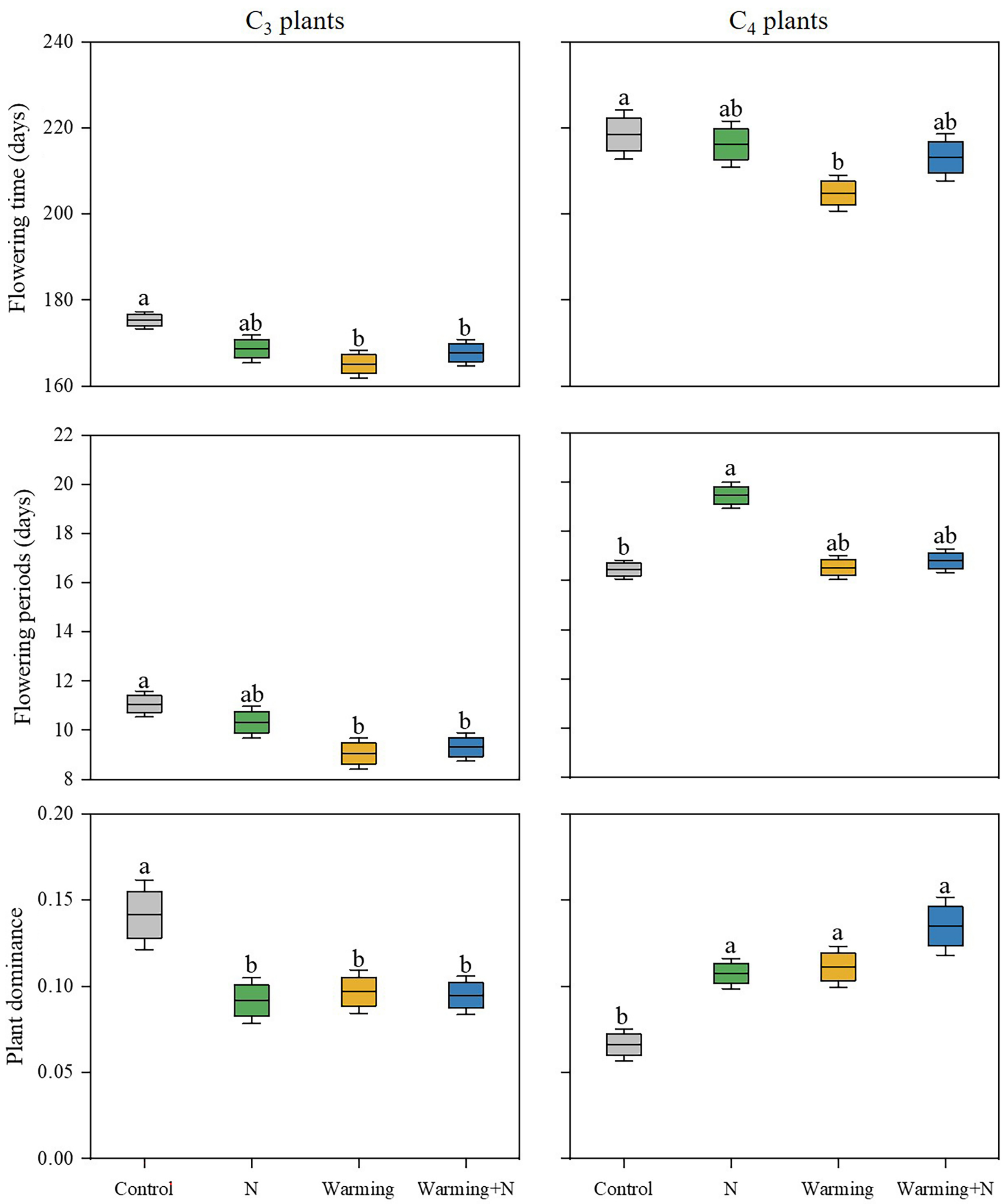

FIGURE 2 Responses of flowering time, duration of flowering, and plant dominance of C$_3$ plants (*Stipa breviflora*, *Convolvulus ammannii*, *Allium tenuissimum*, and *Artemisia frigida*) and C$_4$ plants (*Cleistogenes songorica* and *Kochia prostrata*) to warming and N addition from 2013 to 2022 in a desert steppe. Different letters indicate significant differences between treatments.

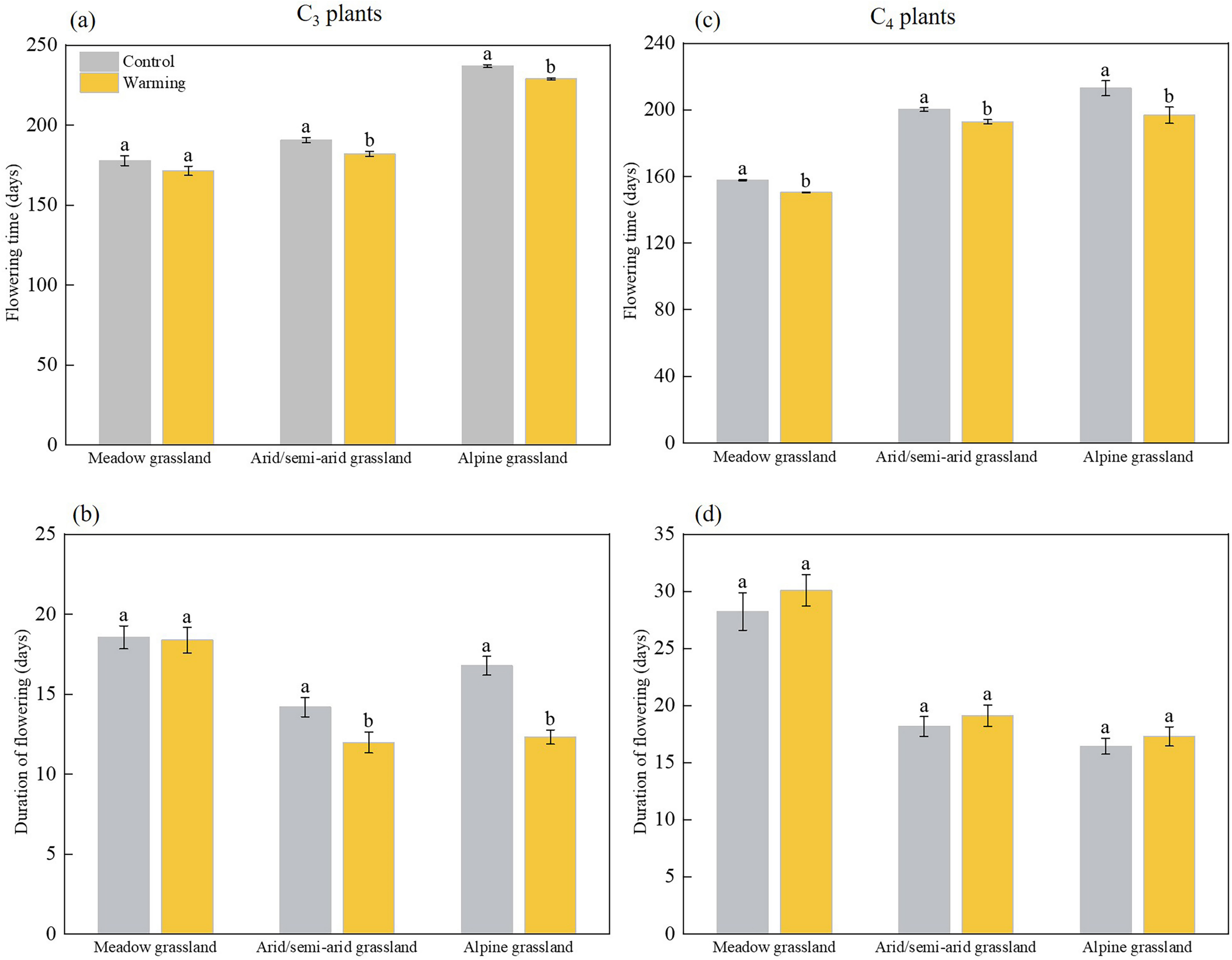

FIGURE 3 Effects of warming on flowering time and duration in meadow, arid, semi-arid and alpine grasslands. This comparison shows the effects of warming (orange bars) and control (gray bars) treatments on flowering time and duration. Bar plots represent mean values (±SE) for each treatment.

led to a decrease of 6.0% ± 0.01% ($F_{1,15} = 11.33$, $p = 0.004$) in C_3 plants (Table 1; Figure 2). On the contrary, the dominance of C_4 plants, *C. songorica* and *K. prostrata*, increased by 5.0% ± 0.4% ($F_{1,15} = 11.50$, $p = 0.003$) under warming and 4.1% ± 0.01% ($F_{1,15} = 20.48$, $p < 0.01$) under N addition, respectively (Table 1; Appendix S1: Figure S7). Combined warming and N addition led to an increase of 7.0% ± 0.5% ($F_{1,15} = 15.79$, $p = 0.002$) in C_4 plants (Table 1; Figure 2).

Pathways through which warming and N addition influenced species dominance

The analyses suggested that soil temperature and moisture at different soil depths played key roles in determining the flowering phenology of all the studied species (Figure 4). For C_3 plants (*S. breviflora*, *A. tenuissimum*, and *C. ammannii*), the duration of flowering decreased with increasing soil temperature, causing declines in plant dominance. In contrast, for C_4 plants (*C. songorica* and *K. prostrata*), flowering phenology was largely driven by soil moisture. Nitrogen addition prolonged the duration of flowering by increasing soil moisture, consequently leading to an increase in the dominance of C_4 plants (Figure 4). Additionally, N addition not only affected soil moisture and temperature but also directly stimulated plant growth, further contributing to the observed shifts in flowering phenology (Appendix S1: Figure S4). Causal Community Modeling analysis revealed that flowering duration exerted a stronger influence on plant dominance than vice versa, as evidenced by a more pronounced convergence of ρ values as library size increased, particularly in pathways where phenology influenced dominance (Figure 5).

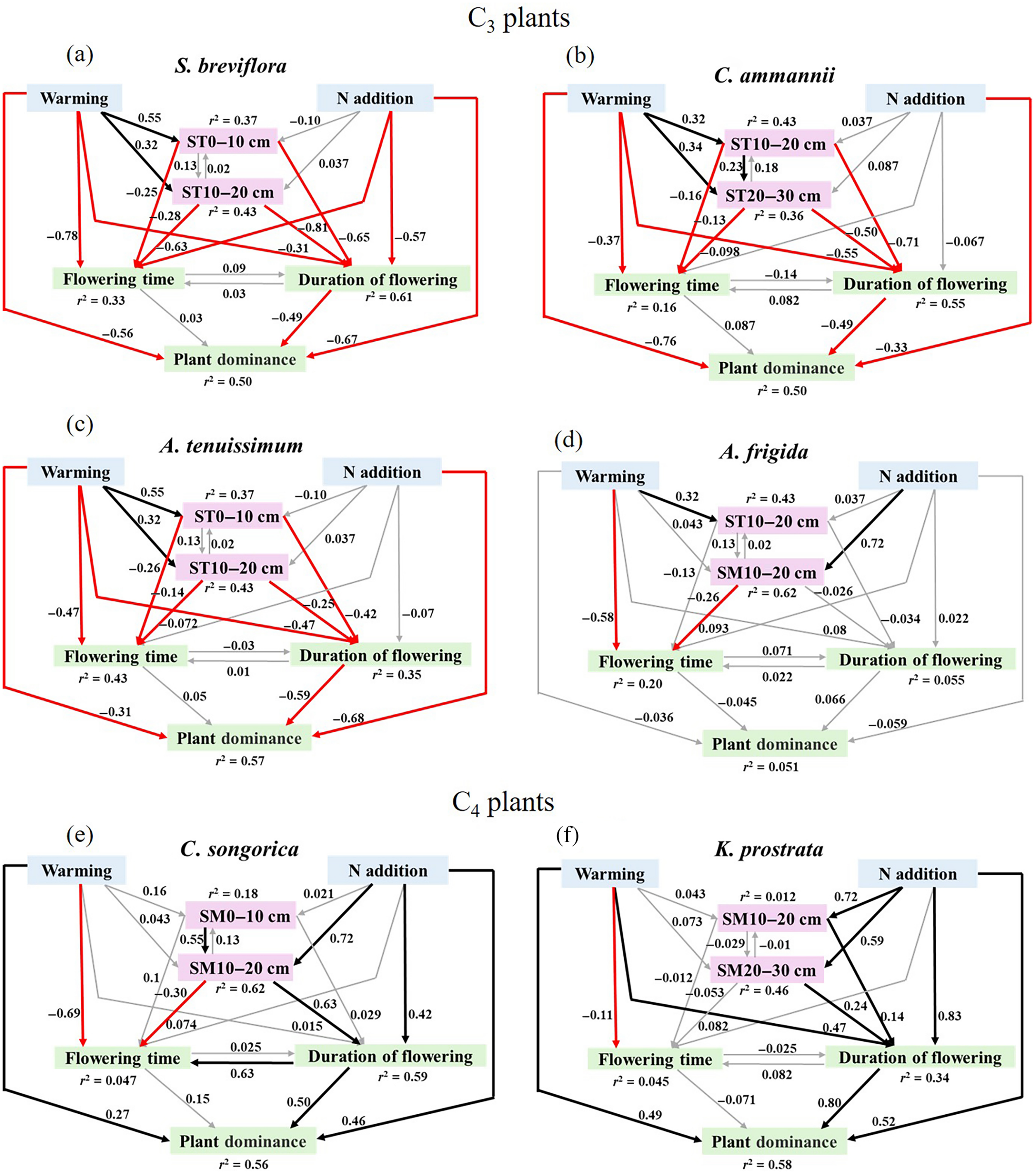

FIGURE 4 Structural equation model analysis showing the pathways through which warming and N addition affect flowering phenology and plant dominance. Model fitting results for each species: Sb: RMSEA = 0.02, CFI = 0.971, χ^2 = 28.167, df = 22, p = 0.170; Ca: RMSEA = 0.058, CFI = 0.951, χ^2 = 36.757, df = 22, p = 0.025; At: RMSEA = 0.062, CFI = 0.933, χ^2 = 31.639, df = 22, p = 0.02; Af: RMSEA = 0.03, CFI = 0.99, χ^2 = 27.678, df = 22, p = 0.08; Cs: RMSEA = 0.03, CFI = 0.97, χ^2 = 32.022, df = 22, p = 0.08; Kp: RMSEA = 0.03, CFI = 0.97, χ^2 = 31.709, df = 22, p = 0.082. The proportion of variation explained is represented by R^2. Solid black lines indicate significant positive pathways with $p < 0.05$, solid red lines indicate significant negative pathways, and gray lines indicate non-significant pathways. CFI, Comparative Fit Index; RMSEA, root mean square error of approximation.

DISCUSSION

Our study explored the long-term effects of warming and N addition on plant flowering phenology and community structure in a temperate desert steppe, uncovering significant changes in flowering patterns and species dominance over a 10 year period. Specifically, we found that warming advanced flowering by an average of 4.3 days in

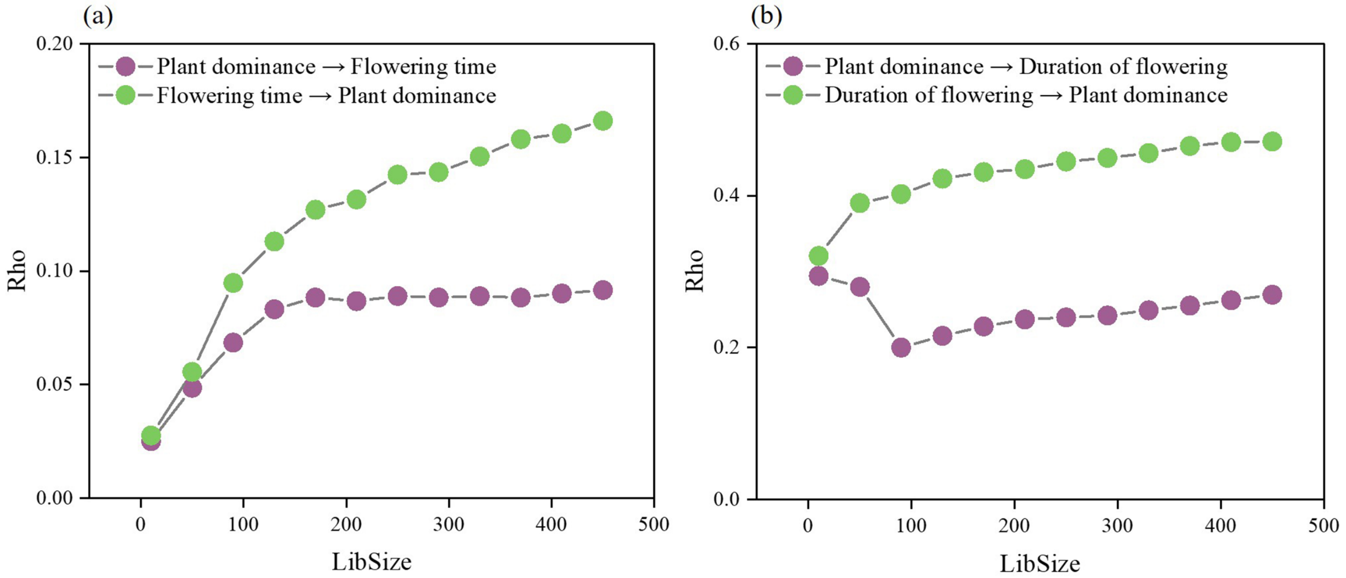

FIGURE 5 Convergent Cross Mapping (CCM) analysis illustrating the trends of cross-mapping correlation coefficients (Rho) as library size increases. CCM tests causal relationships between time-series variables by assessing whether the historical states of one variable can predict those of another. Convergence of ρ values with increasing library size indicates the strength and direction of the causal relationship. (a) Bidirectional relationship between flowering time and plant dominance. (b) Relationship between flowering duration and plant dominance. The green and purple points represent ρ values for the two interacting variables, showing distinct convergence trends and highlighting the asymmetry and strength of causal influences.

C_3 plants and 2.8 days in C_4 plants. Warming also shortened the flowering duration and reduced the dominance of C_3 species while increasing the dominance of C_4 species. Nitrogen addition further amplified these effects, extending the flowering duration and enhancing the dominance of C_4 plants. Additionally, our results indicate that phenological responses to warming are influenced by interannual climate variability. For instance, years with higher precipitation were associated with longer flowering periods, whereas drier years saw shorter flowering periods (Appendix S1: Figure S8). These findings highlight the dynamic nature of phenological responses, modulated by annual fluctuations in precipitation, a key driver in arid and semi-arid ecosystems. Comparative analyses across grassland types revealed that meadow grassland ecosystems had earlier flowering initiation and longer flowering durations for both C_3 and C_4 plants compared to arid and semi-arid steppes (Figure 3). Our findings also align with studies from other regions, such as semi-arid Australia, where C_3 grasses flower in cooler seasons (winter and spring), and C_4 grasses flower in warmer seasons (summer and autumn) (Williams et al., 2007). This supports the notion that climate change, characterized by rising temperatures and increased drought frequency, may shift plant communities toward C_4 dominance (Peñuelas & Filella, 2001; Williams et al., 2007). Further analyses show that C_4 plants, such as *K. prostrata* and *C. songorica*, exhibited significant increases in relative abundance under warming and N addition (Appendix S1: Figure S9). This suggests that C_4 plants are likely to become key species in future ecosystems shaped by climate change. Such increases in C_4 dominance signal potential shifts in ecosystem composition, with implications for biodiversity, resource allocation, and ecosystem function. Overall, our study suggests that shifts in flowering phenology induced by warming may be key factors influencing changes in plant community composition. These changes occur through altered species dominance, with important implications for understanding and predicting the impacts of global climate change on temperate desert steppe ecosystems.

A key question remains: what are the underlying causes of the observed variation in the effects of warming on the phenophases of C_3 and C_4 plants, particularly their flowering time and flowering duration, over the 10 years of this experiment? Our results revealed that warming significantly advanced the flowering time of the studied plants. This may be attributed to warmer temperatures speeding up development and thus leading to earlier flowering (Forrest, 2015; Zhang et al., 2007), whereby an increase in temperature could induce a shift from vegetative to reproductive growth of plants (Liu et al., 2021; Zhang et al., 2003). We also found that warming shortened the flowering duration of C_3 plants but had no effect on the flowering duration of C_4 plants. Such different responses are likely attributable to the greater temperature sensitivity of C_3 plants (Post et al., 2008; Sherry et al., 2007;

Zhang et al., 2007). This is probably because most C_3 plants flower in spring or early summer, when hormone levels and biochemical reactions are more active within C_3 plants than in C_4 plants, which flower later in autumn as temperatures gradually decline (Wolkovich et al., 2012; Xia et al., 2015). Several mechanisms can potentially explain the observed changes in the shortened flowering duration with warming. First, warming may alter plant physiology through the mediation of plant enzyme and hormone activity, which in turn influences plant phenology (Crimmins et al., 2010; Fanin et al., 2022; Weih & Karlsson, 2001). Second, warming can alter flowering phenology by affecting leaf water loss (Weih & Karlsson, 2001). Increased temperature can accelerate vegetative growth by affecting the rate of leaf water loss and reduce the period of flowering phenology (Pallas et al., 1967; Sadok et al., 2021). Finally, warming can alter plant traits related to resource acquisition, which in turn can impact flowering phenology. For example, warming-induced soil surface water loss has been shown to limit the growth and development of shallow-rooted plants and shorten their duration of flowering (Wang et al., 2021).

The effects of N addition on flowering phenology could be due to several factors. First, our results indicate that N addition significantly affected the flowering time of only one species, *S. breviflora*, which belongs to the early-flowering group and is more sensitive to environmental changes than late-flowering species (Li et al., 2016). Second, SEM revealed a direct effect of N addition on flowering phenology (Figure 4), likely due to enhanced physiological processes such as nutrient uptake, photosynthesis, and accelerated growth (Xia & Wan, 2013). These changes were most pronounced in C_4 plants, which exhibited longer flowering durations and increased dominance in the community. In addition, N addition prolonged the duration of flowering of C_4 plants but did not affect that of C_3 plants. SEM showed that the N effect on flowering phenology was mediated by soil water availability. High N supply has been shown to affect soil porosity and soil structure by increasing litter content, promoting the retention and migration of soil water and nutrients, and thereby enhancing soil water availability (Prevéy & Seastedt, 2014; Richardson et al., 2018). In parallel, N addition also resulted in increased N uptake by plant roots. This suggests that, from a resource allocation perspective, more resources will be allocated to reproductive growth, leading to an extension of the time needed for the development of reproductive organs and consequent increases in the duration of flowering (Tilman & Wedin, 1991; Xia & Wan, 2013). The interactive effects of warming and N addition can also influence the timing of key phenological events. Nitrogen addition enhances nutrient availability, which accelerates plant growth and may lead to earlier phenological events (Xia & Wan, 2013). Similarly, warming accelerates metabolic processes, resulting in an earlier onset and progression of phenological events (Crimmins et al., 2010). When combined, N and warming may further accelerate nutrient accumulation, thereby altering the timing and duration of phenological events (Yang et al., 2020).

Several potential factors were likely to explain the relationship between plant phenology and community structure, including variations in reproductive allocation, clonal growth strategies, and differences between wind- and insect-pollinated plants. First, our analysis of reproductive traits, such as the number of spikelets per reproductive branch and the number of reproductive branches per plant, showed that these traits are strong predictors of plant dominance across years. Significant positive linear relationships were observed between spikelet number per branch and dominance, as well as between reproductive branch number per plant and dominance during the same periods (Appendix S1: Figure S10). However, current-year dominance was not significantly correlated with current-year reproductive traits (e.g., spikelet number per branch, reproductive branch number per plant) (Appendix S1: Figure S11). This temporal decoupling suggests that reproductive phenology structurally influences community competition dynamics, rather than dominance shaping reproductive development within the same growing season. Overall, these findings highlight the importance of phenological and reproductive traits in determining plant dominance, providing valuable insights into the mechanisms driving community dynamics under global environmental changes (Dorji et al., 2013). Second, differences in reproductive output and recruitment with changes in phenology can influence community structure. Increases in the duration of flowering and decreases in the vegetative period of C_4 plants induced by N addition may promote reproductive success and expand their population size (Chen et al., 2020; Rafferty et al., 2015; Richardson et al., 2018). Third, clonal growth, particularly for grass species, may be enhanced due to increased soil water and N availability that occurred with increased temperature and N supply (Pottier & Evette, 2010; Zheng & Ma, 2018). Finally, differences in plant pollination modes can affect flowering phenology and reproductive strategies, leading to shifts in plant community structure (Chen et al., 2020; Ottaviani et al., 2020). Wind-pollinated plants prioritize dispersal and reproductive efficiency, while insect- and animal-pollinated plants enhance reproductive success by attracting pollinators (Rafferty & Ives, 2012). However, warmer temperatures can alter the timing of flowering, potentially leading to mismatches between plants and their pollinators, thus affecting reproductive success (Forrest, 2015; Rafferty et al., 2020).

Additionally, N addition can influence plant growth and competitive interactions, potentially favoring species that can more effectively utilize the additional N (Clark & Tilman, 2008). As a result, this tradeoff can potentially change the size of plant populations and the dominance of certain species (Obeso, 2002).

Current models of plant phenological responses to global change have primarily focused on shifts in ecosystem functioning, but often neglect possible effects on plant community structure (Liu, Wang, et al., 2022; Wang et al., 2020; Wolf et al., 2017). We found that changes in flowering duration induced by warming have a significant impact on plant dominance, suggesting that the dominance of C_4 plants increased with increasing flowering duration and the dominance of C_3 plants decreased with decreasing duration of flowering. Our results emphasize the importance of flowering phenology in mediating community dynamics under global change. A caveat of note is that our study focused on the effects of warming and N addition, and future research should explore the impacts of other global change factors. For example, previous studies have reported the influences of CO_2 enrichment on C_3 and C_4 plant biomass, community structure, and belowground processes (Reich et al., 2018). Therefore, future studies should consider the relationship between plant phenology and community dominance under elevated CO_2 to gain a more comprehensive picture of the ecological consequences of global change in plant-based ecosystems. Also note that our study only focused on exploring the role of flowering phenology in mediating grassland community structure in response to global change. However, it is crucial to investigate how important this pathway is compared to other pathways, such as altered plant physiology and clonal growth (Parmesan & Yohe, 2003; Roller & Schmidt, 2015). While our SEM focused on soil temperature and moisture as the primary mechanistic variables, we acknowledge that other environmental factors, such as light availability and nutrient cycling, may also influence plant dominance and phenology (Nord & Lynch, 2009). Future studies that incorporate these additional factors could provide a more comprehensive understanding of the underlying mechanisms driving plant community dynamics (Cleland et al., 2006). Nevertheless, our findings suggest that soil temperature and moisture are among the most critical drivers of the observed responses in our study grassland. A caveat arises from the observational nature of our phenology-dominance correlations. Although our cross-mapping and time-lagged models suggest that phenology is a key predictor of community dynamics, future experimental manipulations (e.g., phenological mismatching through translocations) are necessary to confirm causality and disentangle these relationships from potential confounding factors, such as legacy effects in soil microbial communities (Revillini et al., 2016).

Our results indicate that plant flowering phenology plays an important role in modulating the responses of plant communities to global environmental change. To our knowledge, this study is the first to identify the role of soil temperature and water availability in regulating the duration of flowering, and in turn, species dominance in the face of global change. Our results provide novel insights for understanding the effects of climate change on plant phenology and plant species composition in a climatically sensitive ecosystem and underscore the need to assess how climate change will impact plant flowering phenological periods.

AUTHOR CONTRIBUTIONS

Guodong Han and Haiyan Ren designed and maintained the long-term manipulative experiment. Guodong Han, Haiyan Ren, Lu Bai, Yi Zhu, and Jinglei Tang conducted the research (field sampling and laboratory analysis). Lu Bai performed the data analyses. Lu Bai, Haiyan Ren, Lin Jiang, Thomas W. Crowther, Constantin M. Zohner, and Kailiang Yu conceived this study and wrote the manuscript. All authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Bai, 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.28942472.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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