

RESEARCH ARTICLE

Zinc addition and mowing alter the timing and duration of reproductive phenology in dominant plants of a meadow steppe

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Abstract

1. Plant phenology, while genetically determined, is highly responsive to environmental drivers such as soil nutrient availability and disturbance. As an essential micronutrient, zinc (Zn) plays a critical role in plant development by regulating key processes including RNA polymerase function, auxin synthesis and antioxidant defence.
2. We investigated how Zn addition and mowing disturbance influence the reproductive phenology of six dominant plants in an Inner Mongolian meadow steppe. Over 3 years, we applied Zn ($0.5 \text{ gm}^{-2} \text{ year}^{-1}$) and simulated foraging via mowing in a factorial experiment.
3. Our results revealed strong, yet species-specific, responses. Zn addition advanced reproductive timing in grasses (e.g. *Leymus chinensis* shortened its flowering by 6 days and prolonged fruiting by 8 days) but delayed all reproductive phases in forbs (e.g. by 4–10 days in *Thalictrum petaloideum* and 16–25 days in *Potentilla bifurca*). The phenology of the late-flowering forb *Serratula centauroides* and the early-flowering sedge *Carex duriuscula* was largely unaffected by Zn addition. Mowing generally delayed or shortened reproductive phases in grasses and forbs but advanced them in *S. centauroides* and *C. duriuscula*. Causal analyses indicated that Zn effects were mediated through changes in superoxide dismutase activity, soluble sugar concentration and chlorophyll content, whereas mowing effects were primarily driven by alterations in soil water content and light conditions. Thus, the interactive effects of Zn and mowing arise from complex interplay between carbon metabolism, antioxidant defence, photosynthesis and water use.
4. *Synthesis.* These species-specific phenological shifts to soil Zn availability and disturbance suggest that changes in these drivers could potentially alter plant community structure by differentially affecting the reproductive success of functional groups.

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KEYWORDS

meadow steppe, mowing, reproductive phenology, Zn addition

1 | INTRODUCTION

Grasslands account for more than 40% of the terrestrial vegetated surface (White et al., 2000) and serve as critical carbon sinks by sequestering nearly one-third of global terrestrial carbon stocks. Despite their pivotal role in the Earth system, grasslands frequently experience stoichiometric constraints and their critical phenophases—such as the timing of floral anthesis, pollination and seed maturation—can be strongly modulated by micronutrient availability through their involvement in enzymatic activation, photosynthetic efficiency and carbon allocation (Fay et al., 2015). In the meadow steppe of northern China, where calcareous soils dominate, zinc (Zn) deficiency is especially widespread, imposing a fundamental limitation on development and reproductive performance in selective plant species and potentially modifying plant community structure and altering ecosystem-level carbon sequestration dynamics (Krasnoshchekov, 2024).

Zn is an essential micronutrient and plays central roles in enzyme activation, antioxidant defence and carbon metabolism (Khan et al., 2004). By regulating these physiological processes, Zn availability directly influences developmental trajectories: deficiency leads to stunted growth, delayed reproduction and reduced seed viability, whereas adequate supply promotes faster growth, advances flowering onset and enhances both biomass production and reproductive success (Jochner et al., 2013; Li, Wang, et al., 2022). Zn is actively involved in chlorophyll biosynthesis, thereby exerting profound effects on photosynthetic efficiency and long-term carbon assimilation (Wang, Yan, et al., 2022). It also contributes to the stabilization of cellular membranes under stress conditions and, as a key component of Cu-Zn SOD, scavenges superoxide radicals while activating the antioxidant defence system to mitigate oxidative stress (Ali et al., 2022). These converging pathways suggest that Zn may function as a pivotal modulator of plant phenology, shaping both the pace of individual life cycles and community-level synchrony. However, compared with the extensively documented effects of macronutrients such as nitrogen (N) and phosphorus (P) on plant flowering and phenology, the role of Zn in regulating phenological dynamics has received far less attention (Biederman et al., 2017; Chen & Ludewig, 2018; Cho et al., 2025; Przedpelska-Wasowicz & Wasowicz, 2013).

Mowing, one of the conventional practices for hay production in northern China, can substantially alter plant phenology in addition to affecting growth and community structure (Baoyin et al., 2015; Liu et al., 2017; Socher et al., 2012). By removing above-ground biomass and forcing plants to reallocate resources to vegetative recovery, mowing often delays reproductive development, particularly the onset and peak of flowering, although the magnitude and direction of this effect may vary among species and depend on mowing timing and intensity (Jantunen et al., 2007; Plos et al., 2024; Reisch & Poschlod, 2011). At the same time, mowing favours functional strategies associated with rapid regrowth, increased specific leaf area and

high tissue turnover (Plos et al., 2024). Beyond these direct effects on plant traits, mowing also reshapes micro-environmental conditions by altering soil temperature, moisture regimes and light penetration, with cascading consequences for nutrient cycling, microbial processes and resource-use efficiency (Piao et al., 2019; Wang, Wei, et al., 2025). Importantly, these changes may further modify plant responses to exogenous nutrient supply, because mowing can influence soil nutrient availability, plant uptake and nutrient use efficiency under micronutrient enrichment (Wingate et al., 2015). Together, these observations suggest that mowing may shift the timing and duration of reproductive phenophases, yet whether and how such effects interact with Zn addition remains poorly understood. Clarifying the joint effects of mowing and micronutrient addition on plant phenology is therefore essential for understanding the resilience and adaptive capacity of grassland ecosystems under global change.

To elucidate the role of Zn availability and mowing in affecting the reproductive phenology of grassland plants, we conducted a three-year field experiment (2022–2024) with treatments of Zn addition and mowing in a meadow steppe. Phenological monitoring was carried out using a fixed-plant observation method across six dominant plant species representing three functional groups (grass, sedge and forb), with detailed records of key reproductive phases including the onset and end of flowering and fruiting. We also measured several physiological traits potentially linked to Zn-mediated shifts in reproductive phenology, including superoxide dismutase activity as an indicator of antioxidant defence, soluble sugar concentration as a proxy for carbon metabolism and resource status, and chlorophyll content as an indicator of photosynthetic capacity and assimilate supply for reproductive transition. In addition, environmental variables—mean annual temperature and precipitation, photosynthetically active radiation and soil water content—were monitored to assess microclimatic and edaphic influences. We hypothesized that: (i) Zn addition favours advanced onset and shorter duration of reproductive phases by enhancing chlorophyll biosynthesis, carbon metabolism and antioxidant defence, thereby accelerating resource acquisition and facilitating the transition from vegetative to reproductive growth; and (ii) the effect of Zn supplement could be offset by mowing, hence attenuating or altering the phenological responses induced by Zn addition.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The experiment was conducted in a meadow steppe at the Erguna Forest-Steppe Ecotone Research Station, Chinese Academy of Sciences (50°16'N, 119°39'E, 530 m a.s.l.), northeastern China. This region has a semiarid temperate continental climate, with a

long-term mean annual precipitation (MAP) of 362 mm and a mean annual temperature (MAT) of -2.4°C . Monthly mean temperature ranges from -28.0°C in January to 19.2°C in July. The study area has a haplic chernozem soil (FAO classification) and the experimental site has been fenced since 2010 to exclude livestock grazing, with mowing conducted in August annually for hay harvest. The vegetation is dominated by perennial herbaceous plants including *Leymus chinensis* Tzvel., *Stipa krylovii* and *Carex duriuscula* C. A. Mey, etc. (Ma et al., 2024).

The micronutrient addition experiment was set up in early August 2013 with a randomized block design with six replicates. Each plot measured $8\text{ m} \times 8\text{ m}$. Four treatments were included: untreated control (CK), Zn addition (Zn), mowing (M) and combined mowing plus Zn addition (MZn). Thus, the experiment comprised 24 plots in total. No Zn was applied in 2013. Beginning in 2014, Zn addition was applied annually in mid-May, and mowing was carried out annually in mid-August. Zn was applied at a rate of $0.5\text{ g Zn m}^{-2}\text{ year}^{-1}$, equivalent to 32 g Zn per $8\text{ m} \times 8\text{ m}$ plot per year, supplied as $142.2\text{ g ZnSO}_4 \cdot 7\text{H}_2\text{O}$ (22.5% elemental Zn). At the time of application, the chemical was dissolved in 10 L of water and evenly sprayed onto each plot, while the zero-Zn plots received the same amount of water without additives. Because this volume corresponded to only about 0.16 mm of precipitation equivalent per $8\text{ m} \times 8\text{ m}$ plot, its effect on plot-level soil moisture was considered negligible. The Zn addition rate was selected as a moderate supplementation treatment based on the background Zn status of the study soil and the aim of testing ecological responses to Zn enrichment under field conditions rather than imposing a toxicity treatment. In our study site, the available Zn concentration was 0.9 mg kg^{-1} in the control plots and 5.6 mg kg^{-1} in the Zn-addition plots. Previous studies have shown that plant responses to Zn fertilization generally occur when soil Zn availability is in the low to moderate range, whereas toxic effects are typically associated with much higher soil or plant Zn concentrations. Therefore, the applied Zn level was intended to represent moderate Zn enrichment under field conditions rather than phytotoxic Zn exposure (Broadley et al., 2007; Lindsay & Norvell, 1978; Martínez Cuesta et al., 2021; Singh, 1986; Takkar & Mann, 1978). To minimize edge effects caused by shading from surrounding vegetation and spill-over of the Zn solution, a 1-m-wide buffer zone was established between adjacent plots and blocks. These buffer zones were mown regularly throughout the experiment, regardless of the mowing treatment applied to the experimental plots.

2.2 | Measurements of plant and environmental variables

Plant reproductive phenology was monitored during the 2022–2024 growing seasons using a fixed-plant, event-based observation approach adapted from PhenObs (Nordt et al., 2021; Sporbett et al., 2022). Observations were conducted at 5-day intervals from

early May, when plants entered the initial growth stage, to late September, when the growing season ended. Although this interval may not capture the exact date of very short-lived phenological transitions in some species, it allowed consistent comparisons of the relative timing and duration of major reproductive phenophases across treatments. Six focal species were selected for phenological monitoring based on their widespread occurrence in the experimental area, representation of the major functional groups, ecological relevance in the local meadow steppe community and feasibility for repeated observations throughout the growing season. These species included two grasses (*L. chinensis* and *S. krylovii*), one sedge (*C. duriuscula*) and three forbs (*Thalictrum petaloideum*, *Serratula centauroides* and *Potentilla bifurca*). Although these species were not selected using a fixed biomass threshold alone, together they accounted for more than 80% of total community biomass in unmown plots and more than 50% in mown plots (Figure 1b,c), indicating that they represented a substantial proportion of the community composition (Chaves & Smith, 2021).

For each species in each plot, eight individuals were permanently tagged and repeatedly monitored throughout each growing season. For each tagged individual, we recorded the dates of four major reproductive phenological events: onset of flowering (FION), end of flowering (FIEnd), onset of fruiting (FrOn) and end of fruiting (FrEnd). FION was defined as the date when the first fully opened flower was observed on an individual, and FIEnd as the date when the last fully opened flower was observed. FrOn was defined as the date when fruits were first observed on an individual, and FrEnd as the date when fruits were no longer present. All observation dates were converted to day of year (DOY) for subsequent analyses. To account for within-species variation in phenological status among individuals, dates were recorded separately for each tagged plant and then averaged across the eight individuals within each plot to obtain plot-level phenological values. Flowering duration and fruiting duration were calculated as the difference between end and onset dates. Because the aim of this study was to compare treatment effects on the timing and duration of major reproductive transitions, we used an event-based approach rather than a traditional ordinal phenological scoring method. Consequently, intermediate stages such as flower bud stage, full bloom and fruit ripening were not quantified in the present study.

To elucidate the underlying mechanisms by which Zn addition and mowing affect the plant reproductive phenology, we collected data on selective environmental factors and physiological variables and tested their effects on the timing of flowering and fruiting. Meteorological data for the period 2022–2024 were obtained from the National Meteorological Information Center of the China Meteorological Administration for the meadow steppe ecotone of Erguna. Monthly mean temperature and precipitation were calculated from the daily records and then averaged to derive mean annual temperature (MAT) and mean annual precipitation (MAP) (Figure 1a). Measurements were also made in 2024 on some of the environmental, physiological and biochemical variables. Photosynthetically active radiation (PAR) measurements were taken

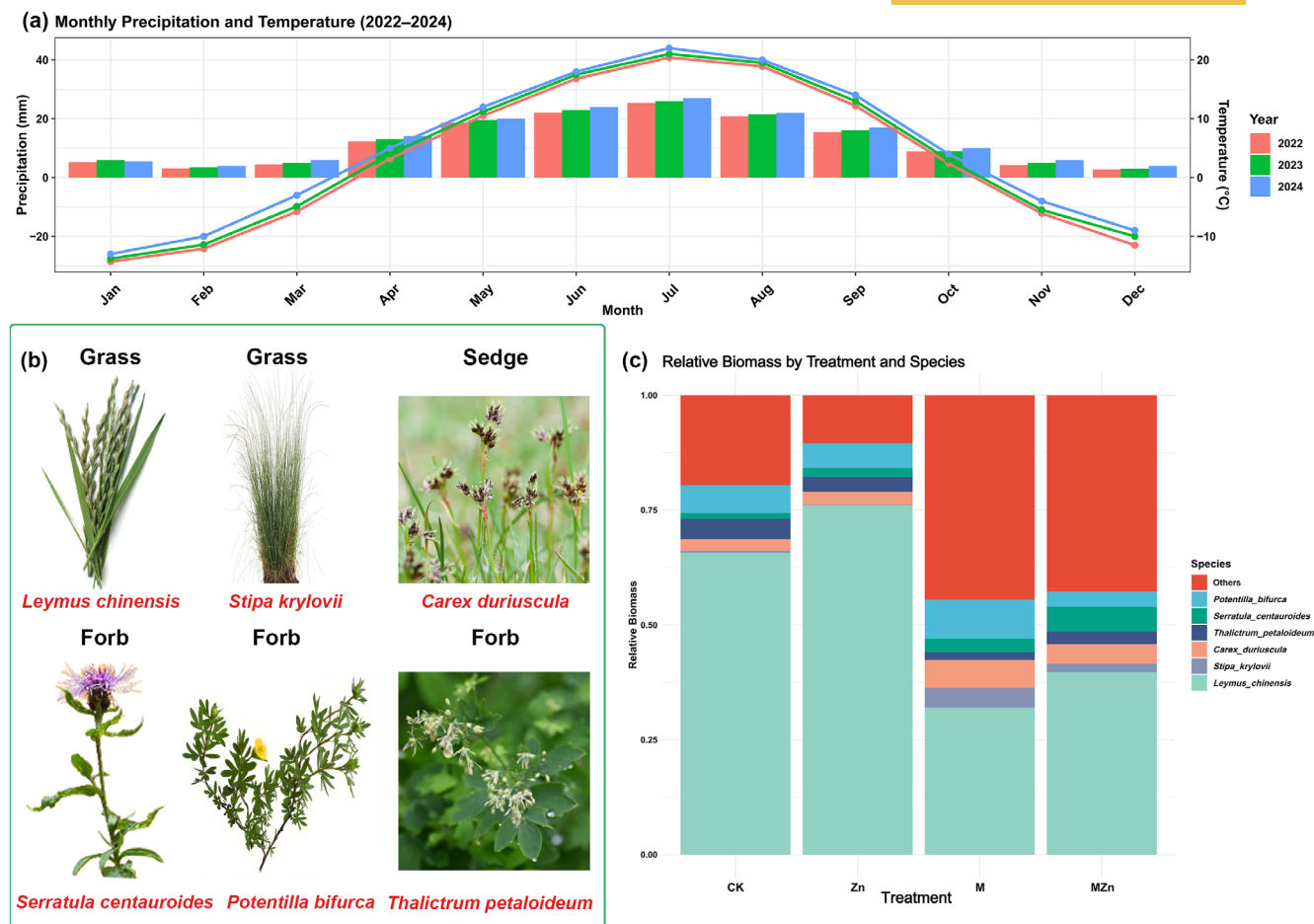


FIGURE 1 Experimental site with climate and vegetation characteristics. (a) Monthly precipitation and mean temperature from 2022 to 2024. (b) The six dominant plants selected for phenological observations. (c) Species-specific relative biomass under different treatments.

in August on clear days (11:00–14:00 local time) using an AccuPAR LP-80 ceptometer (Decagon Devices). Simultaneous readings above the canopy and at ground level in each plot allowed calculation of light penetration (LP) as the ratio of transmitted radiation at the soil surface to incident PAR above the canopy (Wang, Sun, et al., 2022; Zhang et al., 2014).

The soil water content (SWC) in the upper 10 cm of soil was measured in mid-August of each study year by collecting soil core samples from three random locations within each plot. These measurements were used to characterize plot-level soil moisture conditions during the peak growing season. The three subsamples from each plot were thoroughly mixed to form one composite sample on-site and sealed in plastic bags for transportation to the laboratory for subsequent processing and analysis. SWC was determined gravimetrically by oven-drying at 105°C until constant mass (approx. 48 h) following the standard guidelines of the Natural Resources Conservation Service of United States of the America (USDA-NRCS, 2014). All analyses were made in triplicate measurements, and results were expressed as gravimetric water content (% w/w). Measurements of leaf physiological traits, including superoxide dismutase activity (SOD), soluble sugar content (SS) and chlorophyll concentration (Chl), were conducted on fully expanded and healthy leaves collected from five

randomly selected individuals of each species in each plot during the peak growing season (mid-August). After collection, leaf samples were placed in sealed plastic bags, transported to the laboratory in insulated cool boxes, and stored at –80°C prior to biochemical analyses. These physiological traits were used to represent antioxidant defence, carbon/osmotic regulation and photosynthetic capacity, respectively. SOD activity was quantified using the nitroblue tetrazolium photoreduction assay (Li, Cao, et al., 2022), SS was determined by the phenol-sulfuric acid method (Nawaz et al., 2021) and Chl was measured by ethanol extraction followed by spectrophotometric quantification at 652 nm (Lichtenthaler & Wellburn, 1983).

2.3 | Data analysis

The phenological data were analysed using R. The *dplyr* package was used to filter observations corresponding to the four treatments, and differences in phenological timing and duration among dominant plants under different treatments were statistically tested. Three-way ANOVA was conducted to examine the interactive effects among species, Zn addition and mowing. Two-way ANOVA was used to test the interactive effects between species

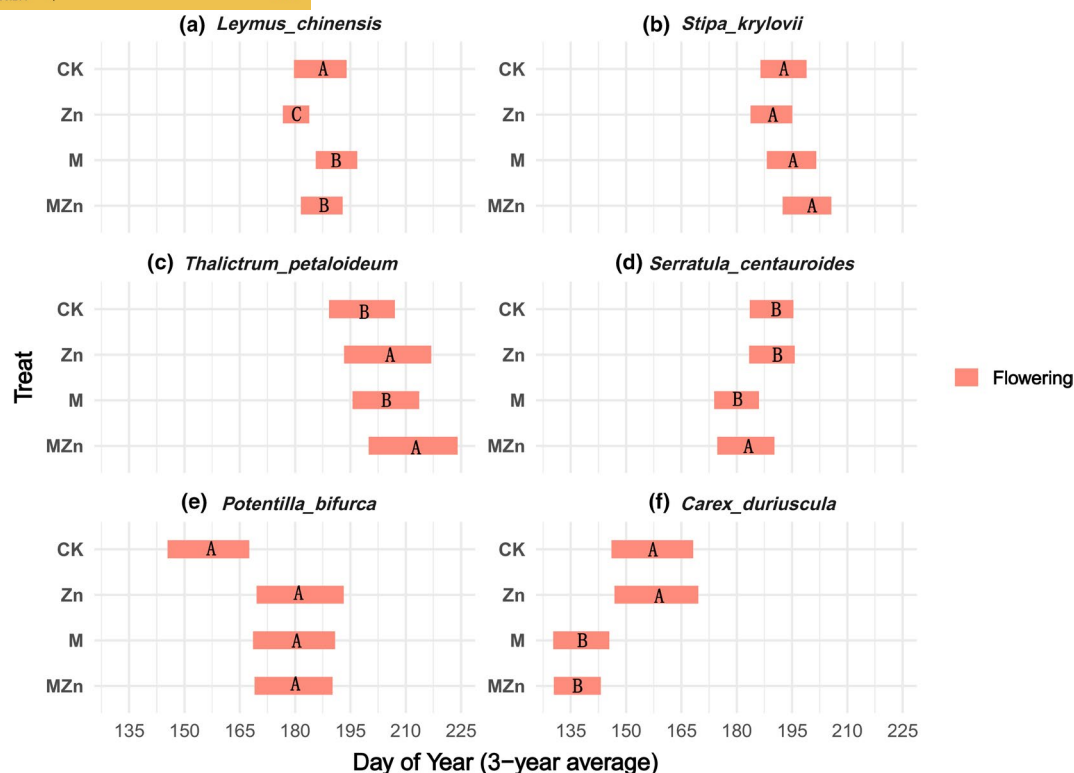


FIGURE 2 Responses of flowering duration in (a) *Leymus chinensis*, (b) *Stipa krylovii*, (c) *Thalictrum petaloideum*, (d) *Serratula centauroides*, (e) *Potentilla bifurca*, and (f) *Carex duriuscula* to Zn addition (Zn), mowing (M), and their combined treatment (MZn) from 2022 to 2024. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

and Zn treatment for mown and unmown plots as well as between Zn addition and mowing treatments by plant species. Duncan's multiple range test was used to determine the level of statistical significance.

To evaluate the direct and indirect effects of Zn addition (Zn) and mowing (M) on plant physiological traits and phenological events, we constructed structural equation models (SEMs) using the R package lavaan (v0.6–17) (Rosseel, 2012) (Figure 3). Continuous variables were standardized (z-score transformation) to eliminate differences in scale among variables prior to analysis. The hypothesized model specified Zn addition and mowing treatments as exogenous variables influencing two environmental factors (photosynthetically active radiation [PAR] and soil water content [SWC]) and three physiological traits (superoxide dismutase activity [SOD], chlorophyll concentration [Chl] and soluble sugar content [SS]). These traits, together with Zn addition and mowing treatments, were then modelled as predictors of four phenological timing: flowering onset (FION), flowering end (FIEnd), fruiting onset (FrOn) and fruiting end (FrEnd). The a priori conceptual SEM was constructed based on the hypothesized effects of Zn addition and mowing on reproductive phenology through environmental variables (PAR and SWC) and physiological traits (SOD, Chl and SS). The initial hypothesized model is shown in Figure S8, and the ecological rationale for each hypothesized path is summarized in Table S4. The direction of the hypothesized paths from physiological traits to reproductive phenology was specified a priori based on ecological theory

and previous evidence that chlorophyll content, soluble sugar status and antioxidant regulation influence resource acquisition and reproductive transition. In this study, these traits were therefore treated as mechanistic predictors rather than response variables in the SEM. The SEMs were fitted using the lavaan package (v0.6–17) with maximum likelihood (ML) estimation. Model fit was assessed using key fit indices, including the chi-square to degrees of freedom ratio (χ^2/df), comparative fit index (CFI) and root mean square error of approximation (RMSEA). Acceptable model fit was determined based on conventional criteria: $\chi^2/\text{df} < 3$, CFI > 0.90 and RMSEA < 0.08 (Hu & Bentler, 1999). All statistical analyses were conducted in R version 4.4.0 (R Core Team, 2024).

3 | RESULTS

Zn addition and mowing both affected the reproductive phenology in the six dominant grassland plants under investigation, with the effects being strongly species-dependent (Figures 2 and 3; Tables S1–S3). Specifically, Zn addition significantly altered the overall reproductive phenology in *L. chinensis*, *T. petaloideum* and *P. bifurca*, while mowing primarily regulated reproductive timing in *S. krylovii*, *S. centauroides*, and *C. duriuscula*. Notably, a significant interactive effect of Zn addition and mowing on reproductive phenology was observed in *P. bifurca*.

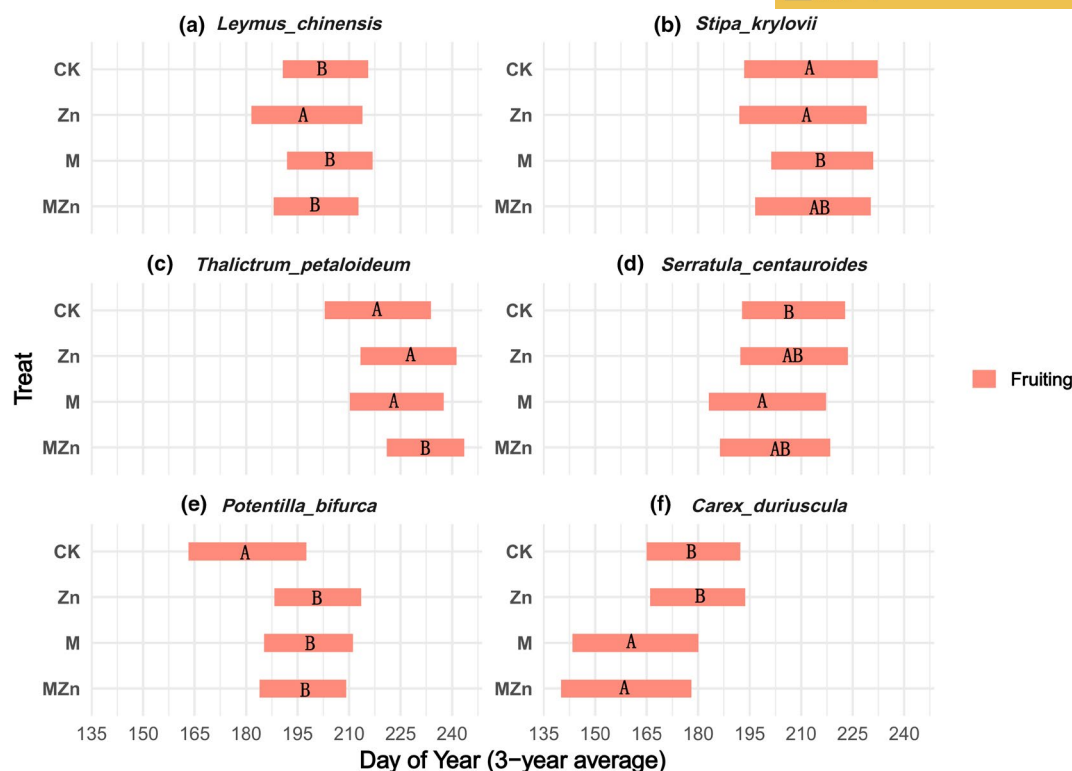


FIGURE 3 Responses of fruiting duration in (a) *Leymus chinensis*, (b) *Stipa krylovii*, (c) *Thalictrum petaloideum*, (d) *Serratula centauroides*, (e) *Potentilla bifurca*, and (f) *Carex duriuscula* to Zn addition (Zn), mowing (M), and their combined treatment (MZn) from 2022 to 2024. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

3.1 | Effects on the timing and duration of flower phenology

Zn addition advanced the FEnd (end of flowering) by 10 days in *L. chinensis* (–10 days) and 4 days in *S. krylovii* ($p < 0.05$; Figure S1c) and shortened the flowering duration by 7 days in *L. chinensis* ($p < 0.05$; Figure 1a). In contrast, the flowering of forbs and sedges was generally delayed by Zn addition. For example, *T. petaloideum* exhibited significant delays in both FION (Onset of flowering; 4 days) and end (10 days; $p < 0.05$; Figures S1a,c), with *P. bifurca* experiencing even more marked delay in those phenophases (24 days in FION and 26 days in FEnd, respectively; $p < 0.05$; Figures S1a,c). Moreover, Zn addition prolonged the flowering duration in *T. petaloideum* by 6 days ($p < 0.05$; Figure 2c). The combination of Zn addition and mowing (MZn) advanced the FEnd by 2 days in *C. duriuscula* ($p < 0.05$; Figure S1d) but delayed that by 10 days in *T. petaloideum* ($p < 0.05$; Figure S1d) compared with the treatment by mowing alone. Under the condition of MZn, the flowering duration was extended by 6 days in *T. petaloideum* and 3 days in *S. centauroides* ($p < 0.05$; Figure 2c,d).

3.2 | Effects on the timing and duration of fruit phenology

Zn addition significantly advanced the fruiting in grass species, particularly *L. chinensis*, in which FrOn (Onset of fruiting) occurred

9 days earlier and fruiting duration was extended by 7 days ($p < 0.05$; Figures S2a and 3a). In contrast, it generally delayed fruiting in forbs. For instance, in both *T. petaloideum* and *P. bifurca*, the FrOn was delayed by 10 days and the FrEnd (End of fruiting) by 7 days, respectively ($p < 0.05$; Figure S2a,c). Relative to the M treatment, MZn significantly advanced FrOn by 3 days in *C. duriuscula* and 5 days in *S. krylovii*, respectively, but delayed FrOn by 11 days in *T. petaloideum* ($p < 0.05$; Figure S2b). Under MZn, FrEnd was advanced by 4 days in *L. chinensis* but delayed by 6 days in *T. petaloideum*, accompanied by a 5 day reduction in fruiting duration of *T. petaloideum* ($p < 0.05$; Figures S2d and 3c).

3.3 | Factors influencing reproductive phenological timing

Before SEM analysis, we additionally examined the responses of environmental factors and physiological traits to Zn addition, mowing and their combined treatment, and summarized their relationships with species reproductive phenology in the Supporting Information (Figures S3–S8). Overall, mowing consistently reduced soil water content (SWC) and increased photosynthetically active radiation (PAR), whereas physiological responses differed among species. Correlation analyses further showed that reproductive phenology was associated with environmental factors and physiological traits in a species-specific manner, with some species showing stronger

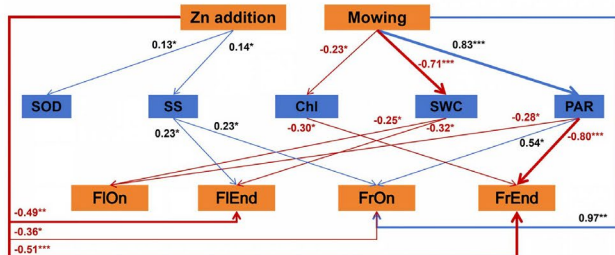
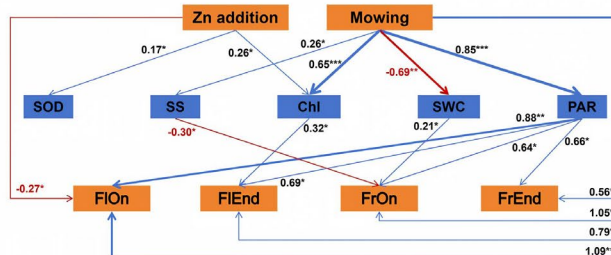
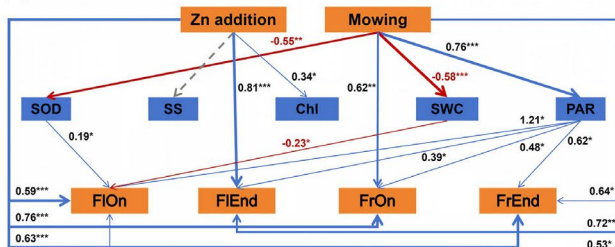
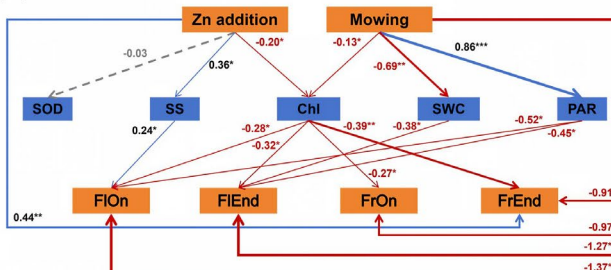
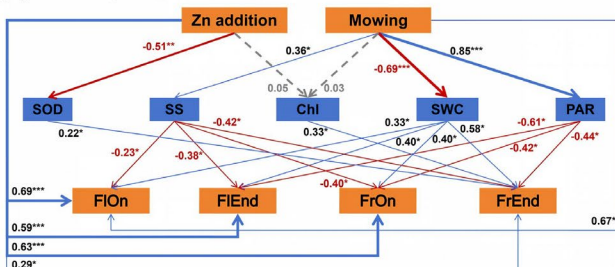
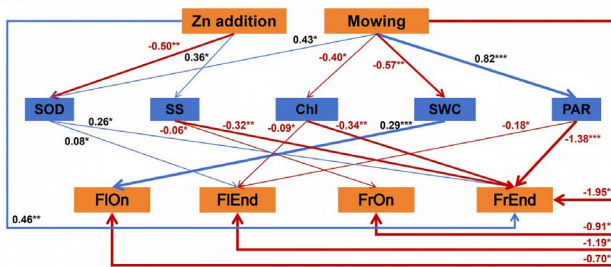
(a) *Leymus chinensis*: $\chi^2/\text{df}=1.44$, $P=0.16$, CFI=0.96, RMSEA=0.04(b) *Stipa krylovii*: $\chi^2/\text{df}=2.78$, $P=0.002$, CFI=0.87, RMSEA=0.03(c) *Thalictrum petaloideum*: $\chi^2/\text{df}=0.75$, $P=0.68$, CFI=1, RMSEA=0(d) *Serratula centauroides*: $\chi^2/\text{df}=2.51$, $P=0.005$, CFI=0.91, RMSEA=0.25(e) *Potentilla bifurca*: $\chi^2/\text{df}=1.82$, $P=0.05$, CFI=0.97, RMSEA=0.18(f) *Carex duriuscula*: $\chi^2/\text{df}=1.44$, $P=0.16$, CFI=0.96, RMSEA=0.04

FIGURE 4 Structural equation models of Zn addition, mowing, superoxide dismutase activity (SOD), soluble sugar content (SS), chlorophyll concentration (Chl), soil water content (SWC), photosynthetically active radiation (PAR) on the reproductive phenology of (a) *Leymus chinensis*, (b) *Stipa krylovii*, (c) *Thalictrum petaloideum*, (d) *Serratula centauroides* (e) *Potentilla bifurca* and (f) *Carex duriuscula*. Blue and red arrows represent significant positive and negative pathways, respectively, and grey dashed arrows indicate non-significant pathways. The arrow width is proportional to the strength of the relationship. The numbers adjacent to the arrows are standardized path coefficients and indicate the effect size of the relationship. The asterisks indicate statistical significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

links to light and water conditions and others to superoxide dismutase activity (SOD), soluble sugar content (SS) or chlorophyll concentration (Chl) levels.

Based on these treatment responses and trait-phenology relationships, structural equation modelling further revealed that Zn addition and mowing influenced reproductive phenology of focal species primarily through indirect pathways involving physiological and environmental factors (Figures 4 and 5). Overall, Zn addition delayed reproductive transitions mainly by altering carbon metabolism and photosynthetic activity, whereas mowing exerted stronger and more complex effects by simultaneously modifying physiological traits and micro-environmental conditions.

Zn addition tended to postpone flowering or fruiting in *L. chinensis* and *S. krylovii*, mediated mainly through reduced SS or Chl levels, while delaying reproductive phases in *P. bifurca* and *C. duriuscula* via enhanced SOD. In contrast, mowing generally advanced reproductive events in all species but *S. centauroides* and *C. duriuscula*; the reproductive phenology in these two species was negatively impacted

by mowing through decreased Chl and SWC. Increased PAR due to mowing consistently promoted reproductive progression across species, highlighting the key role of light availability in post-disturbance phenological recovery.

4 | DISCUSSION

4.1 | Zn addition shifts the reproductive phenology

Zn addition altered reproductive phenology in a strongly species-specific manner, with *L. chinensis* showing the clearest advancement in reproductive progression, whereas the other grassland species exhibited delayed or weak responses. These results indicate that Zn addition was an important external factor associated with reproductive phenological change in this study, but its effects were expressed differently among species depending on their physiological regulation and functional strategies. Therefore, Hypothesis 1 was partially supported:

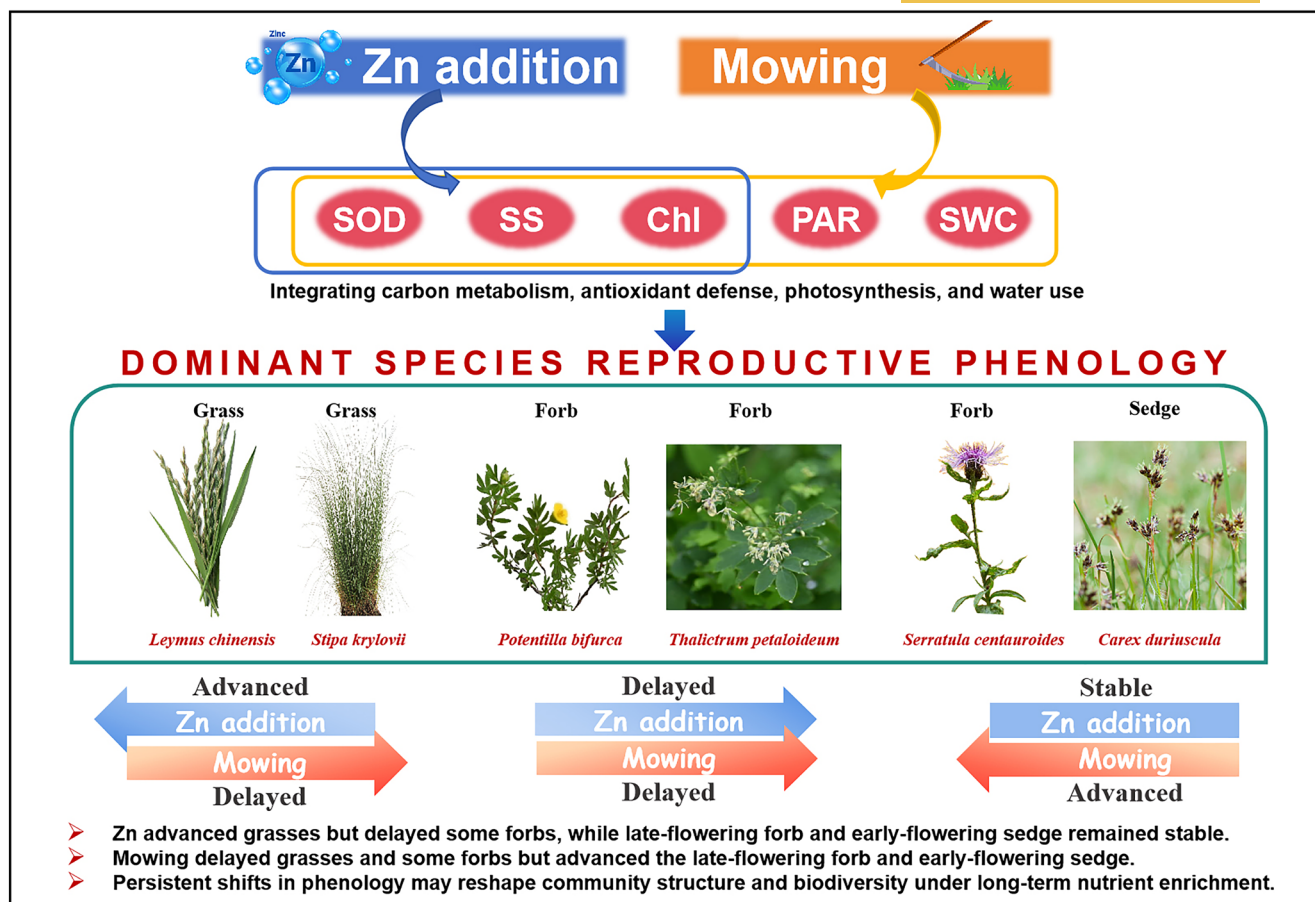


FIGURE 5 Diagram of a conceptual framework illustrating Zn addition and mowing on reproductive phenology in dominant meadow steppe species. Chl, chlorophyll concentration; PAR, photosynthetically active radiation; SOD, superoxide dismutase activity; SS, soluble sugar content; SWC, soil water content.

Zn addition shifted reproductive phenology, but the direction and magnitude of the response were not uniform across species.

Leymus chinensis, a rhizomatous perennial C3 grass with a fibrous root system, exhibited the strongest phenological advancement under Zn addition. Its clonal growth form, fibrous roots and relatively high resource-acquisition capacity may allow it to respond rapidly to changes in soil nutrient availability (Jiang et al., 2021; Li, Wang, et al., 2022). Fibrous roots generally provide a large absorptive surface area for nutrient acquisition, which may facilitate the utilization of increased Zn availability. In our study, Zn addition not only accelerated reproductive progression in *L. chinensis* but was also associated with increased soluble sugar content, suggesting that Zn-related changes in carbon metabolism may be involved in this response. At the same time, the association between higher soluble sugar content and delayed flowering end and fruiting onset suggests that soluble sugars may function not only as metabolic substrates but also as signalling molecules involved in reproductive timing (Blanford et al., 2024; Wahl et al., 2013). Therefore, the phenological response of *L. chinensis* may reflect the coupling between Zn availability, photosynthetic carbon assimilation, soluble sugar accumulation and reproductive allocation. The Zn-induced shortening of flowering duration together with the prolongation of fruiting duration further suggests a potential shift in

reproductive allocation from floral maintenance toward fruit development, a pattern that may contribute to reproductive performance in this dominant grass species (Adamidis et al., 2019; Fang et al., 2024). This overall pattern is consistent with a relatively resource-acquisitive strategy.

In contrast, Zn addition delayed reproductive phenology in *T. petaloideum* and *P. bifurca*, indicating that the same Zn treatment can generate contrasting phenological consequences among coexisting species. *T. petaloideum* is a perennial forb with a taproot system (Jiang et al., 2021), whereas *P. bifurca* is a perennial, semi-woody species with partly subterranean stems and a relatively short taproot in temperate grasslands (Flora of China Editorial Committee, 2003; Jiang et al., 2021). Differences in root architecture may influence the spatial range of Zn acquisition and the subsequent allocation of Zn and carbon resources among organs, potentially contributing to divergent physiological and phenological responses. For *P. bifurca*, Zn addition was associated with reduced SOD activity and a delayed end of fruiting in the SEM, suggesting that altered antioxidant regulation may be involved in its delayed reproductive completion. A decline in antioxidant capacity may indicate a more conservative physiological response under Zn exposure, in which resource allocation to reproductive completion is postponed under potential physiological constraint

(Abbas et al., 2025; Yuan et al., 2016). This pattern is consistent with a relatively resource-conservative strategy. By contrast, no significant physiological mediator was identified for *T. petaloideum* in the SEM. Its delayed reproductive phenology and prolonged flowering duration under Zn addition may therefore reflect a different response strategy, potentially involving the adjustment of reproductive timing to maintain pollination opportunity or buffer reproductive risk under altered nutrient conditions (Timerman & Barrett, 2019). However, because Zn uptake, tissue Zn accumulation and below-ground-above-ground Zn allocation were not directly measured, these interpretations should be regarded as trait-based hypotheses rather than direct mechanistic evidence.

Serratula centauroides and *C. duriuscula* showed limited phenological responsiveness to Zn addition. *S. centauroides* is a perennial forb with relatively later seasonal reproduction, which may reduce its exposure to the strongest early-season Zn-related effects. *C. duriuscula*, a perennial sedge with a relatively brief and concentrated reproductive schedule, may have limited phenological plasticity in response to short-term changes in Zn availability (Bernard, 1990). Their relative insensitivity to Zn addition may also reflect lower Zn uptake responsiveness, stronger internal Zn homeostasis or greater phenological canalization that buffers reproductive timing against short-term environmental fluctuations.

4.2 | Mowing modifies the effects of Zn addition on reproductive phenology

In this study, mowing markedly affected plant phenology, as the removal of above-ground biomass reduced photosynthetic capacity and water-use efficiency, forcing most species to prioritize vegetative regrowth and thereby delaying the onset of reproduction. However, the late-flowering species *S. centauroides* flowered early in response to mowing, likely as an 'escape strategy' to mid-season foraging (Doležal et al., 2019) and for avoiding missing the reproductive window. *C. duriuscula*, with its inherently short and concentrated reproductive period, exhibited earlier reproduction to ensure successful pollination and seed set under unstable conditions (Hou et al., 2021; Liu & Li, 2010). These two species rely on wind pollination, making them particularly responsive to the enhanced light penetration and airflow resulting from mowing, which facilitates earlier reproductive initiation (Song et al., 2025; Wang, Bjorkman, et al., 2025).

While mowing exerted a strong influence on the reproductive phenology of grassland plants, it generally weakened the effects of Zn addition, partially supporting Hypothesis 2. Mowing removed a substantial proportion of photosynthetic tissue and thereby increased the need for compensatory vegetative regrowth (Wingate et al., 2015), which may have constrained the extent to which Zn-enhanced physiological functioning could be translated into reproductive development. In addition, mowing can alter near-ground microclimatic and soil moisture conditions (Wang, Wei, et al., 2025), which may further influence plant Zn uptake and utilization. Under such conditions, Zn addition may alleviate trace-element limitation to some extent, but not fully offset

the carbon and resource constraints imposed by biomass removal. This phenomenon is consistent with previous findings showing that mowing counteracted the synergistic effect of Zn addition on *L. chinensis* by biomass removal and reduced soil moisture (Li, Wang, et al., 2022). The interaction between mowing and Zn addition was expressed mainly in fruiting dynamics. In *L. chinensis*, Zn addition under mowing significantly advanced the end of fruiting, whereas in *S. krylovii* it delayed the onset of fruiting; in both species, fruiting duration was shortened. These contrasting responses suggest that the combined treatment compressed the reproductive phase, but the direction of adjustment differed between species. Such species-specific responses may reflect differences in reproductive strategy. *L. chinensis*, a rhizomatous clonal grass, shows a trade-off between clonal and sexual reproduction, and its reproductive mode can shift with resource conditions (Bai et al., 2009). By contrast, different *Stipa* species have been shown to exhibit divergent reproductive strategies under land-use change, which may help explain the contrasting response of *S. krylovii* under mowing and Zn addition (Wang et al., 2019).

Among the forbs, Zn and mowing interactively affected the reproductive phenology mainly in *T. petaloideum*, with significantly delayed reproductive period, extended flowering and shortening of fruiting duration. A prolonged flowering increases pollination opportunities while reallocating limited carbon resources from fruit development to support vegetative growth and flowering success (Cakmak, 2000). Mowing weakened the effect of Zn addition in *P. bifurca* likely because of above-ground biomass loss and altered resource allocation priorities (Li, Wang, et al., 2022; Ye et al., 2024). *S. centauroides* remained largely unresponsive to Zn addition treatment, indicating that the reproductive phenology of late-flowering species is relatively insensitive to micronutrient enrichment (Huang et al., 2018; Sang et al., 2023).

For *C. duriuscula*, the effect of Zn on reproductive phenology was amplified by mowing, with significant advancement in the end of flowering and the onset of fruiting. This can be explained by reduced canopy height and improved light and airflow conditions; both conditions favour Zn-mediated physiological processes (Saleem-Muhammad et al., 2022; Wang et al., 2021). Zn promoted fruit development by increasing soluble sugar content, which serves both as a direct carbon source and an osmotic regulator, maintaining cell expansion and facilitating cell division in developing fruits (Ali et al., 2023; Zhang et al., 2023). As a micronutrient, Zn enhances photosynthetic efficiency, stimulates sugar synthesis and regulates sugar transport to reproductive organs, thereby accelerating fruit maturation (Broadley et al., 2007; Cakmak, 2000). Under mowing-induced carbon limitation, Zn-induced increases in soluble sugars partially compensated for reduced carbon availability, allowing *C. duriuscula* to initiate fruit development earlier while maintaining fruit quality.

Although this study provides new insight into how Zn addition and mowing influence reproductive phenology through physiological and environmental pathways, several limitations should be noted. Our phenological monitoring focused on four major reproductive events and did not quantify intermediate stages such as flower bud formation, full bloom or fruit ripening; moreover, the 5-day observation

interval may have introduced limited uncertainty for short-lived transitions. Thus, our dataset is best suited to detecting treatment effects on major reproductive timing and duration rather than finer-scale dynamics across the full reproductive sequence. Although the SEM suggested potential associations among Zn addition, mowing, leaf physiological traits and reproductive phenology, these relationships should be interpreted as statistical associations and hypothesized pathways rather than direct causal evidence. The measured physiological traits, including chlorophyll concentration, soluble sugar content and SOD activity, mainly reflected leaf photosynthetic capacity, carbon/osmotic regulation, and antioxidant defence, respectively, but did not fully capture the key regulatory processes underlying reproductive development. Moreover, Zn uptake, root-to-shoot translocation, tissue-level Zn accumulation and Zn allocation among organs were not directly measured in this study. Therefore, the proposed links between Zn addition and phenological shifts remain inferential. Future studies integrating measurements of soil available Zn, root Zn uptake, plant tissue Zn concentration, Zn translocation, reproductive hormones, pollen viability and seed setting rate would help more directly clarify the physiological and reproductive mechanisms underlying treatment-induced phenological responses.

5 | CONCLUSIONS

In a three-year field experiment (2022–2024) in the Inner Mongolian meadow steppe, we investigated how Zn addition ($0.5 \text{ g Zn m}^{-2} \text{ year}^{-1}$) and mowing, individually and jointly, affected the reproductive phenology in six dominant plants representing grasses, forbs, and sedges. Zn addition promoted earlier reproductive timing in grasses, notably *L. chinensis*, with a markedly shortened flowering period (6 days) and prolonged fruiting (8 days), while mostly delaying reproductive timing in forbs (*T. petaloideum* [4–10 days] and *P. bifurca* [16–25 days]). Both *S. centauroides*, a late-flowering forb species, and *C. duriuscula*, an early-flowering sedge species, had limited responses to Zn addition in their reproductive phenology. Mowing, in contrast, imposed strong constraints, generally delaying reproduction by reducing photosynthetic capacity but advancing phenology in late- or early-flowering species through improved light and airflow conditions. SEM analyses suggested that Zn-related phenological shifts were mainly associated with variation in superoxide dismutase activity, soluble sugar content and chlorophyll concentration, whereas mowing effects were more closely linked to changes in soil water content and light availability. Overall, our findings demonstrate that species-specific physiological and environmental responses drive highly plastic phenological patterns, promoting functional differentiation and temporal complementarity within the meadow steppe plant communities.

AUTHOR CONTRIBUTIONS

Qihua Li analysed the data and wrote the original draft of the manuscript. Lixin Yu, Xiaotian Fan, Jiaqiang Wang, Bin Wang maintained the experiments and collected soil and plant samples. Ying Zhang, Yuxue Zhang, Ruzhen Wang and Osbert Jianxin Sun edited the

manuscript. Yong Jiang designed the research, edited the manuscript and provided funding. Heyong Liu advised and assisted with the research design, data interpretation and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors state that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0p2ngf2hb> (Li et al., 2026).

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SUPPORTING INFORMATION

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

Figure S1. Responses of timing of flowering phenology in grasses (*Leymus chinensis* [Ley] and *Stipa krylovii* [Sti]), forbs (*Thalictrum petaloideum* [Tha], *Serratula centauroides* [Ser], *Potentilla bifurca* [Pot]) and sedges (*Carex duriuscula* [Car]) to Zn addition (Zn), mowing (M) and their combined treatment (MZn) were evaluated from 2022 to 2024. T-test results for comparisons between Zn addition and control treatments were indicated by ns non-significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Abbreviations are provided in Table S1.

Figure S2. Responses of timing of fruiting phenology in grasses (*Leymus chinensis* [Ley] and *Stipa krylovii* [Sti]), forbs (*Thalictrum petaloideum* [Tha], *Serratula centauroides* [Ser], *Potentilla bifurca* [Pot]) and sedges (*Carex duriuscula* [Car]) to Zn addition (Zn), mowing (M) and their combined treatment (MZn) were evaluated from 2022 to 2024. T-test results for

comparisons between Zn addition and control treatments were indicated by ns non-significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure S3. Responses of soil water content (a) and photosynthetically active radiation (b) under control (CK), Zn addition (Zn), mowing (M) and their combined treatment (MZn). Different letters indicate significant differences among treatments ($p < 0.05$).

Figure S4. Responses of superoxide dismutase activity (SOD) in grasses (*Leymus chinensis* [Ley] and *Stipa krylovii* [Sti]), forbs (*Thalictrum petaloideum* [Tha], *Serratula centauroides* [Ser], *Potentilla bifurca* [Pot]) and sedges (*Carex duriuscula* [Car]) to control (CK), Zn addition (Zn), mowing (M) and their combined treatment (MZn). Different letters indicate significant differences among treatments ($p < 0.05$).

Figure S5. Responses of chlorophyll concentration (Chl) in grasses (*Leymus chinensis* [Ley] and *Stipa krylovii* [Sti]), forbs (*Thalictrum petaloideum* [Tha], *Serratula centauroides* [Ser], *Potentilla bifurca* [Pot]) and sedges (*Carex duriuscula* [Car]) to control (CK), Zn addition (Zn), mowing (M) and their combined treatment (MZn). Different letters indicate significant differences among treatments ($p < 0.05$).

Figure S6. Responses of soluble sugar content (SS) in grasses (*Leymus chinensis* [Ley] and *Stipa krylovii* [Sti]), forbs (*Thalictrum petaloideum* [Tha], *Serratula centauroides* [Ser], *Potentilla bifurca* [Pot]) and sedges (*Carex duriuscula* [Car]) to control (CK), Zn addition (Zn), mowing (M) and their combined treatment (MZn). Different letters indicate significant differences among treatments ($p < 0.05$).

Figure S7. Species-specific spearman correlations between environmental and physiological variables and flowering and fruiting phenology in grasses (*Leymus chinensis* and *Stipa krylovii*), forbs (*Thalictrum petaloideum*, *Serratula centauroides*, *Potentilla bifurca*) and sedges (*Carex duriuscula*).

Figure S8. A priori conceptual structural equation model illustrating the hypothesized pathways by which Zn addition and mowing influence reproductive phenology through environmental and physiological variables. Zn addition and mowing were specified as exogenous variables. Photosynthetically active radiation (PAR) and soil water content (SWC) were included as environmental variables, whereas superoxide dismutase activity (SOD), chlorophyll concentration (Chl)

and soluble sugar content (SS) were included as physiological variables. Flowering onset (FION), flowering end (FIEnd), fruiting onset (FrOn) and fruiting end (FrEnd) were included as reproductive phenological response variables. This figure represents the initial hypothesized SEM before model fitting and path refinement; therefore, not all paths shown here were necessarily retained in the final fitted models for each species.

Table S1. Two-way ANOVA of Zn addition (Zn) and mowing (M), on the timing and duration of six dominant plants reproductive phenology from 2022 to 2024. Three-way ANOVA results were indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. FION, onset of flowering; FIEnd, end of flowering; FrOn, onset of fruiting; FrEnd, end of fruiting.

Table S2. Three-way ANOVA of Zn addition (Zn), mowing (M) and species (S) on the timing and duration of reproductive phenology from 2022 to 2024. Three-way ANOVA results were indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. FION, onset of flowering; FIEnd, end of flowering; FrOn, onset of fruiting; FrEnd, end of fruiting.

Table S3. Two-way ANOVA of Zn addition (Zn) and species (S) on the timing and duration of reproductive phenology under non-mowing and mowing conditions from 2022 to 2024. Three-way ANOVA results were indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. FION, onset of flowering; FIEnd, end of flowering; FrOn, onset of fruiting; FrEnd, end of fruiting.

Table S4. Ecological rationale and literature basis for the hypothesized paths included in the a priori structural equation model.

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