Seasonal warming alters spring needle unfolding and lammas shoot development in Pinus densiflora S. & Z. seedlings

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Abstract

Context:

Climate warming is reshaping plant phenology worldwide; however, the specific effects of seasonal and extreme temperature accumulation on seedling development remain poorly understood.

Aims:

We investigated the phenological responses of *Pinus densiflora* Siebold & Zucc. seedlings to seasonal warming in an open-field experiment in South Korea.

Methods:

108 one-year-old seedlings were subjected to four treatments: spring–fall warming (W_{SF}), summer warming (W_S), consistent warming (W), and control (C). We assessed spring needle unfolding and lammas shoot development, including occurrence and needle elongation stages.

Results:

Elevated spring temperatures advanced spring needle unfolding in W_{SF} and W but slowed completion. First lammas shoots commenced development in July, with occurrence rates exceeding 95% across warming treatments by October. Rates were consistently higher in W_S and W than in W_{SF} and C, though W_{SF} also increased occurrence by late autumn. Second lammas shoots emerged only in September, with greater frequency and more advanced stages in W_S and W until November. Cumulative extreme heat (EDD >24–27°C) exerted the greatest influence on both first and second lammas shoot development.

Conclusion

These findings indicate that extreme heat accumulation, rather than elevated mean temperatures alone, is the key determinant of altered phenological patterns in *P. densiflora*.

Key message

Field experiments in South Korea show that warming alters the seedling phenology of Pinus densiflora. Spring needle unfolding was accelerated by spring warming and influenced by elevated daily maximum temperatures. Cumulative high-temperature exposure strongly accelerated lammas shoot development, highlighting extreme heat as a key driver of climate impacts on lammas shoot occurrence and needle unfolding.

1. Introduction

Plant phenology rapidly responds to rising global temperatures and is widely considered a sensitive indicator of climate change (Price and Waser 1998; Stuble et al. 2021). Increased temperatures typically lead to earlier bud break, postponed autumn leaf fall, prolonged growing seasons, and alterations in flowering and reproductive phenology (Malyshev 2020; Montgomery et al. 2020; Stuble et al. 2021). Furthermore, high temperatures can increase the occurrence of lammas shoots, which are abnormal shoot elongations that occur after normal spring shoot growth in fixed-growth conifers (Kushida 2005). These phenological changes can influence subsequent plant growth and exert various impacts on plant development, including tree-shape alterations and a high frost damage risk (Kushida 2005; Jo et al. 2019).

Plant responses to warming are contingent upon their developmental stage. In particular, seedlings exhibit sensitivity to changes in their external environments (Rodgers et al. 2018). In a previous study, it was found that more than 90% of one-year-old *Pinus densiflora* seedlings developed abnormal lammas shoots when subjected to experimentally elevated temperatures (Chang et al. 2018; Jo et al. 2019). However, the incidence was considerably lower in two-year-old seedlings than in one-year-old seedlings (Chang et al. 2018). Similarly, lammas shoot development is notably pronounced during the early seedling development stages and has a substantial impact on mortality, subsequent growth, and tree form (Jansons et al. 2016; Neimane et al. 2015).

In addition to developmental stages, plant phenology is influenced by multiple environmental drivers, including heat accumulation, winter chilling, photoperiod, soil moisture, and carbohydrate availability (Piao et al. 2019). Among these, temperature has consistently been recognized as the most influential factor across species (Fu et al. 2016; Piao et al. 2019; Reed et al. 2019). Thermal conditions are often quantified through indices, namely: growing degree days (GDD), which indicate temperature accumulation above a base threshold; extreme degree days (EDD), which measure heat accumulation beyond a high-temperature threshold; and chilling units (CU), which quantify cold exposure (Bailey and Harrington 2006; Lobell et al. 2011; Lobell et al. 2013; Zhang et al. 2015). The magnitude and direction of these indices vary seasonally and depend on the timing of temperature increases. For instance, warming in late spring and early fall increases GDD with minor influences on EDD and CU, whereas summer warming increases both GDD and EDD without affecting CU. Consistent warming from spring through fall increases both GDD and EDD, with GDD levels being higher than those observed during spring and fall warming (Yin et al. 2019). Owing to the non-uniform nature of temperature increases associated with climate change across different regions and seasons, it is critical to examine the impact of seasonal temperature variations on plant phenology (Guralnick et al. 2024; Yan et al. 2021).

Bud burst, a key phenological event reflecting the transition from winter dormancy to spring growth, is often modeled using GDD and CU (Fu et al. 2014). Numerous studies have reported that the combined effects of heat and chilling are the main drivers of dormancy release, leading to earlier spring phenology under warming conditions (Fu et al. 2014; Montgomery et al. 2020). In addition, high summer temperatures are known to induce lammas shoot development, indicating that cumulative EDD may be crucial in their formation (Jo et al. 2019, 2023). However, most phenological studies of this nature have focused on agricultural systems, while comparable research on forest ecosystems remains limited (Fu et al. 2014; Lobell et al. 2013; Luo et al. 2023).

In this study, we aimed to assess how seasonal warming influences spring needle unfolding and lammas shoot development (i.e., occurrence and needle unfolding stages) in *P. densiflora* Siebold and Zucc. seedlings. To accomplish this, we evaluated spring needle unfolding responses to elevated ambient temperatures at different phenological stages in an open-field experimental site in South Korea, examined lammas shoot occurrence and needle unfolding stages under varying seasonal warming treatments, and compared the effects of three warming regimes (i.e., consistent warming throughout the growing season, summer-only warming, and spring–fall warming) on seedling phenological development. *P. densiflora* was selected as the focal species because of its dominance in afforestation initiatives in East Asia and its documented sensitivity to future warming (Allen et al. 2010; Lee et al. 2021). Drawing on existing empirical evidence (Fu et al. 2014; Jo et al. 2019, 2023; Montgomery et al. 2020), we hypothesized the following conclusions: (1) consistent warming and spring and fall warming would accelerate spring bud burst as well as unfolding phenological stages; (2) consistent and summer warming would increase lammas shoot development, with pronounced effects being observed under consistent warming; and (3) GDD would serve as the most influential environmental driver of spring needle phenology, while EDD would be the primary environmental determinant of lammas shoot development. The findings of this study are anticipated to advance our understanding of how seasonal and extreme temperature accumulations influence conifer seedling phenology and provide a theoretical basis for assessing forest regeneration potential and developing adaptive management strategies under climate change.

2. Material and methods

2.1. Study site

This study was conducted in an outdoor nursery at the Korea University Arboretum, Seoul, South Korea (37°35'36.4"N, 127°01'30.6"E). The soil at the site was classified as sandy loam (comprising 56.8% sand, 33.7% silt, and 9.5% clay). It exhibited a pH of 4.98, with total carbon and nitrogen contents of 0.64% and 0.05%, respectively, and a C/N ratio of 13.03 (Jo et al. 2025). In the 2023 study year, the mean annual air temperature was recorded at 13.4°C, with minimum and maximum values of -18.1 and 35.5°C, respectively. Annual precipitation totalled 1,615.5 mm (KMA 2025). These values were higher than the annual temperature (12.6°C) and precipitation (1,263.3 mm) recorded at the study site between 2001 and 2020

On March 25, 2023, 108 one-year-old seedlings were transplanted into each experimental plot measuring 1.5 m² (1.5 m × 1.0 m). All seedlings were sourced from the same nursery (Forest Technology and Management Research Center, National Institute of Forest Science) to minimize the initial variability in growth conditions.

2.2. Experimental design

Four temperature-related treatments were used to assess the effects of seasonal warming on *P. densiflora* seedlings: control (C), consistent (W), summer warming (W_S), and spring and fall warming (W_{SF}). The W treatment increased canopy temperature by 4°C relative to that of ambient conditions from mid-April to mid-October. The W_S treatment limited warming to the summer months (June–August), whereas the W_{SF} treatment applied warming during spring (mid-April–May) and fall (September–mid-October). The warming periods for W_{SF} and W_S were each established at three months to ensure comparable accumulated temperatures, whereas that of the W treatment was extended to six months by combining spring-to-fall periods to achieve higher cumulative temperatures. Each treatment was replicated five times (Fig. 1a).

The canopy temperature was increased using infrared heaters (FTE-1000, Mor Electric Heating Associates Inc., MI, USA), simulating the late 21st-century temperature projections under the SSP3-7.0 scenario (KMA 2017; IPCC 2022). The temperature was controlled using a system comprising data loggers (CR-1000X, Campbell Scientific Inc., UT, USA), a relay module (SDM-CD16AC, Campbell Scientific Inc., UT, USA), and infrared radiometers (SI-111, Campbell Scientific Inc., UT, USA; Fig. 1b).

2.3. Data collection

The phenological responses of seedlings to the warming treatments were assessed by recording the unfolding of both the spring and lammas shoot needles from May to November 2023 for 40 seedlings at the study site (excluding the seedlings at the edges per plot, for a total of 800 seedlings). Monthly assessments were conducted in the middle of each month. Needle unfolding was classified into five phenological stages: “stage 0,” closed bud; “stage 1,” swollen bud; “stage 2,” <1 cm long needles; “stage 3,” 1–3 cm long needles; and “stage 4,” >3 cm long needles (Fig. 2). The final stage attainment rate per plot was determined using the ratio of seedlings achieving stage 4 of needle development to the total number of surviving seedlings among the 40 seedlings per plot. The shoot needle unfolding of both the first and second lammas was recorded using the same criteria. Seedlings exhibiting shoot needle unfolding at stage 1 or higher were classified as exhibiting lammas shoot occurrence. Subsequently, the occurrence rate per plot was calculated as the ratio of seedlings exhibiting lammas shoot occurrence to the total number of surviving seedlings among the 40 seedlings per plot.

Environmental conditions were continuously monitored throughout the experimental period to assess their effects on seedling responses. Canopy temperature, soil temperature, and volumetric water content were recorded in each plot using infrared thermometers (SI-111, Campbell Scientific Inc., UT, USA) at 30-min intervals and combined soil temperature–moisture sensors (CS655, Campbell Scientific Inc., UT, USA). The following indices were derived from these assessments: GDD, maximum limited growing degree days (GDDm), EDD, accumulated daily maximum temperature (AHT), and accumulated daily minimum temperature (ALT). The 30-day mean soil water content preceding each observation (SWC30) was calculated to examine the impact of vapor pressure deficit derived from temperature increases on the phenology of seedlings. We did not include CU in this study because warming from spring to fall did not change the CU values.

The GDD and EDD were calculated using the formulas proposed by Lobell et al. (2011, 2013) and Zhang et al. (2015):

$$\mathrm{GDD} = \sum_{\mathrm{h}=1}^{\mathrm{n}} \mathrm{DD_h} \text{ with } \mathrm{DD_h} = \begin{cases} 0, & \mathrm{T_h} < 5 \\ (\mathrm{T_h} - 5)/24, & 5 \leq \mathrm{T_h} \end{cases} \quad \text{(Eq. 1)}$$

$$\mathrm{GDD_m} = \sum_{h=1}^{n} \mathrm{DD_h} \text{ with } \mathrm{DD_h} = \begin{cases} 0, & \mathrm{T_h} < 5 \\ (\mathrm{T_h} - 5)/24, & 5 \leq \mathrm{T_h} < 30 \\ 25/24, & 30 \leq \mathrm{T_h} \end{cases} \quad \text{(Eq. 2)}$$

$$\mathrm{EDD_{30}} = \sum_{h=1}^{n} \mathrm{DD_h} \text{ with } \mathrm{DD_h} = \begin{cases} 0, & \mathrm{T_h} < 30 \\ (\mathrm{T_h} - 30)/24, & 30 \leq \mathrm{T_h} \end{cases} \quad \text{(Eq. 3)}$$

where Th is the temperature (°C) at a specific hour (h); 1 in h = 1 corresponds to 01:00 am on January 1; and h = n indicates 11:00 pm of the day preceding a phenological assessment.

GDD and EDD were expressed as cumulative sums from January 1, 2023, until the day preceding each observation. EDD was computed using 10 distinct reference temperatures, ranging from 24 to 33°C (Appendix Table 1). The AHT and ALT levels were calculated as cumulative values over the treatment period (from April 15 to October 15).

Data analysis

The uneven distribution of phenological stages across treatments resulted in the unreliable convergence of the cumulative link mixed model (CLMM). As an alternative, phenological stages were treated as continuous observations, enabling the application of a linear mixed-effects modeling approach to assess treatment and month effects, while accounting for random variability in soil conditions and microtopography across plots. We modeled the final stage attainment rates in spring and the shoot occurrences of the first and second lammas using beta regression mixed models, whereas phenological stages were modeled using linear mixed-effects models (LMMs). Beta regression mixed models and LMMs were fitted using the glmmTMB and nlme packages, respectively (McGillycuddy et al. 2025; Pinheiro and Bates 2000). The response variables in these models included occurrence rates and needle unfolding stages. The months of observation and treatment were considered fixed factors and modeled as categorical variables. The final stage attainment rates in spring and the shoot occurrences of the first and second lammas were calculated at the plot level; however, the model did not converge, likely because of the limited number of observations per plot. Consequently, the random term was excluded from the beta regression mixed model, and the model was refitted with fixed effects only. For the LMMs, Plot ID and seedling ID (plot ID/seedling ID) were included as random factors to account for potential effects of pseudo-replication within plots and unknow homogeneity between plots.

An analysis of variance (ANOVA) was performed to test the significance of the complete models, fixed effects, and their interactions. Pairwise comparisons were performed using emmeans package in R (Lenth et al. 2018). Because strong interaction effects between month and treatment were detected in the preliminary analyses, separate models were subsequently fitted for each month.

Partial least squares (PLS) regression was applied to assess the relative importance of environmental variables (i.e., GDD, GDDm, EDD30, AHT, ALT, and SWC30) in explaining variations in phenological responses. PLS was employed because of the high collinearity among the environmental variables. To account for the random effects of the plots in the PLS regressions, we first fitted an LMM for each response variable with no fixed factor and plot ID as a random term. The residuals from these models were extracted and utilized as response variables in the PLS regressions (Noulèkoun et al. 2021, 2023). PLS regression was performed using Pls and plsVarSel packages only for the months in which treatments significantly affected phenological stages (Linland et al. 2020; Mevik and Wehrens 2007). Variable Importance in Projection (VIP) scores were derived from the PLS model, with variables exhibiting VIP values > 1 considered influential (Mahieu et al. 2023). The regression coefficients (β) from the PLS model were estimated to determine the direction of the effects of environmental factors. PLS regressions were conducted both on the combined data of all treatments and individually for each treatment because we assumed that the effects of environmental variables might differ between the treatments (Appendix Table 2–4).

Preliminary analysis revealed that EDD was the major environmental factor influencing lammas shoot development. Consequently, we conducted additional PLS regressions to determine the reference temperature of EDD that most accurately described the lammas shoot phenological stages. Given the high multicollinearity among the various EDD variables (Appendix Table 1), separate PLS regressions were independently performed for each variable. These individual PLS regressions were compared based on three goodness-of-fit statistics: the coefficient of determination (R2), Akaike information criterion (AIC), and β. The optimal EDD reference temperature was identified based on the highest R2, lowest AIC and highest β values. All statistical procedures were conducted in R version 4.2.2 (R Core Team 2022), with model significance assessed at $p < 0.05$.

3. Results

3.1. Environmental data response to warming treatments

During the spring and fall treatment periods, canopy temperatures in the W and W_{SF} plots were on average 3.8°C higher than those in the C and W_S plots. Similarly, during the summer treatment period, canopy temperatures in the W and W_S plots exceeded those of the C and W_{SF} plots by 3.8°C (Fig. 3a). Changes in soil temperature were smaller than those in canopy temperature. Soil temperatures were approximately 3.5°C higher in W and W_{SF} than those in C and W_S during spring and fall. Similarly, Soil temperatures were higher in W and W_S than those in C and W_{SF} during summer (Fig. 3b). These warming patterns were clearly reflected in the seasonal temperature trends.

Soil volumetric water content ($m^3\ m^{-3}$) also differed across treatments. During spring and fall, W_S exhibited the highest soil moisture content (0.064), followed by C (0.056), W_{SF} (0.054), and W (0.052). In contrast, during summer, W_{SF} had the highest value (0.078), followed by C (0.065), W (0.067), and W_S (0.066) (Fig. 3c).

3.2. Responses of spring needle unfolding to warming treatments

Spring needle unfolding reached its final stage (stage 4) by June, and all seedlings completed needle unfolding by July (Fig. 4a). The results of the beta regression analysis indicated a significant interaction effect between the month of assessment and treatment (Table 1). Subsequent analysis of the monthly treatment effects showed that seedlings in W_S reached the final stage faster than those in W in June (Appendix Table 5; Fig. 4a).

The LMM results revealed a significant interaction between month and treatment (Table 2). Compared with the final needle stage attainment, when separately analyzed by month, May showed significant differences, with higher needle unfolding stages observed in the W (1.90 ± 0.03) and W_{SF} (1.85 ± 0.03) plots than those in the W_S plot (1.60 ± 0.04; Fig. 4b). However, these differences disappeared by June when all seedlings reached the final stage.

3.3. Responses of lammas shoot development to treatments

The shoot occurrence rates of the first and second lammas were influenced by seasonal warming treatments, as indicated by the significant interaction between month and treatment (Tables 1 and S2). The first lammas shoot occurrence commenced in June and peaked in July, with the highest rates in W (81.1 ± 2.4%), followed by W_S (64.4 ± 6.2%), C (42.8 ± 5.6%), and W_{SF} (34.4 ± 9.9%). The occurrence rates remained higher in the W and W_S plots than those in the C and W_{SF} plots until September. W_{SF} exhibited a sharp increase in October, reaching 97.5 ± 1.1% by November, thereby attaining occurrence rate comparable to that of W and W_S. Although occurrence remained lowest in C throughout the season, it still reached 90.7 ± 2.1% at the end of the assessment period (Fig. 4c). Similarly, the LMM results also indicated that the responses of the shoot unfolding stages of the first lammas to treatments varied based on the month of assessment (Table 1). When analyzed by month, seedlings in the W (1.37 ± 0.07) and W_S (1.02 ± 0.07) plots were at more advanced stages than those in the C (0.67 ± 0.07) and W_{SF} (0.49 ± 0.06) plots at the start of July, and this trend persisted through November (Fig. 4d). Advancements in phenological stage in response to the treatments were most pronounced in July, August, and September, with only minor changes thereafter (Appendix Table 5). By November, the final assessment showed mean stages of 3.94 ± 0.03 in W, 3.81 ± 0.04 in W_S, 2.74 ± 0.13 in C, and 2.53 ± 0.12 in W_{SF} (Fig. 4d) in that order.

The second lammas shoot occurrence rates increased significantly in W and W_S from September, with the highest occurrence rate observed in W. Specifically, they reached 43.2 ± 6.8%, 29.0 ± 3.3%, 4.4 ± 2.1%, and 3.7 ± 2.3% in W, W_S, C, and W_{SF}, respectively, in November (Fig. 4e; Appendix Table 5). The second lammas shoot unfolding stages exhibited a similar response to the occurrence. The second lammas shoot developed from September to November, with the most advanced stages observed in W, followed by W_S (Fig. 4f). The second lammas shoot needle unfolding stage was limited to stage 1 until November and recorded as 0.96 ± 0.11 (W), 0.57 ± 0.08 (W_S), 0.07 ± 0.03 (C), and 0.07 ± 0.03 (W_{SF}) in mean stage. Most second lammas shoots did not advance to the needle elongation stage, with only four seedlings in W reaching stage 4 (Appendix Fig. 1).

3.4. Effects of environmental variables on phenological parameters

For spring needle unfolding, AHT (VIP = 1.257, β = 0.032) was the most influential factor driving phenological advancement in May. EDD also exhibited a positive effect, whereas ALT had a negative effect (Table 2). For the shoot development of the first and second lammas, EDD consistently displayed the highest variable importance (VIP > 1.1) and positive β values in every month, indicating its dominant role in promoting lammas formation (Table 3). The extreme degree value of EDD that best describes the lammas shoot stages varied from 24 to 27°C (Appendix Table 1).

GDD, GDDm, AHT, and ALT also had positive and negative effects on the shoot occurrence stages of the first-lammas. GDD had a positive influence on lammas shoot unfolding stages until September but turned negative in October. The effect of GDDm was weaker than that of GDD, indicating a positive influence in July, a negative influence in August and September, and no significant effect from October onward. The AHT generally exhibited a negative effect, with a single positive effect observed in September. However, the regression coefficient remained low (β = 0.003). ALT consistently showed negative values and exerted a notable influence from August to November (Table 3). The results of the complementary analyses conducted separately for each treatment confirmed these patterns (Tables S3–S5).

4. Discussion

4.1. Spring and consistent warming alter spring needle unfolding

In this study, warming treatments were initiated in mid-April, and significant differences in needle unfolding were observed one month later. Consistent with our hypothesis, we observed more needle unfolding stages in the W and W_{SF} plots than those in the other treatment plots. This indicates that elevated spring and fall temperatures, along with consistent warming, advance spring needle phenology (Fu et al. 2014; Montgomery et al. 2020). However, this treatment effect disappeared by June, a lower final spring needle attainment rate in W than that in W_S.

Some coniferous species demonstrate fixed growth, which means that all stem primordia in the current year originate from the buds of the previous year. These buds open in spring, leading to shoot elongation, which occurs only during this period (Hover et al. 2017). Consequently, the environmental conditions in the preceding year are typically considered as having a greater influence on seedling growth. Nevertheless, even with identical conditions from the previous year, differences in environmental factors during the following year can lead to distinct outcomes, such as earlier needle unfolding, as demonstrated in this study and corroborated by previous research (Chang et al. 2018). Considering that bud burst in *P. densiflora* typically occurs in early April (Chang et al. 2018), the significant treatment effects observed in May and June indicate that warming can influence needle development through pre- and post-budburst temperature changes.

In addition, the lower final spring needle attainment in June for W, despite the higher needle unfolding stages in May, indicated that rapid needle unfolding initiation did not necessarily lead to rapid completion. This may be because although high temperatures accelerate needle unfolding, early leaf development creates a mismatch between temperature conditions and other phenological control factors, such as chilling requirements and photoperiod (Körner and Basler 2010; Pletsers et al. 2015). Furthermore, accelerated spring development increases nutrient demand during periods when carbon supply is limited, potentially delaying the completion of needle elongation (Fahad et al. 2017; Jo et al. 2025; Saini et al. 2022).

We anticipated that GDD would be the main driver influencing changes in spring leaf phenology. However, contrary to our hypothesis, GDD did not significantly affect spring leaf phenology. Instead, AHT was identified as the most influential environmental factor affecting spring phenology, with EDD and ALT exhibiting additional positive and negative effects, respectively. The discrepancy between our hypothesis and the findings may arise because the AHT reflects only the daily maximum temperature, whereas GDD accounts for the temperature accumulation throughout the day. For instance, low night-time temperatures or relatively high midday peaks can result in AHT values exceeding GDD. Although the association between ALT and the spring needle unfolding stages was weak, its negative effect indicated that lower minimum temperatures (i.e., colder nights) could accelerate spring phenological development.

Our findings suggest that needle unfolding is primarily influenced by maximum daily temperature, reinforcing concerns expressed by various authors regarding the suitability of GDD as a key index for assessing spring phenology (Fu et al. 2016; Bigler and Vitasse 2019). Given its pronounced effects on spring needle phenological stages and alignment with EDD dynamics in spring (Appendix Fig. 2c, d), AHT emerges as a key driver influencing spring phenological responses in *P. densiflora*.

4.2. Lammas shoot development is promoted during summer under consistent warming

The first lammas shoot occurrence ultimately exceeded 90% across all treatments, and even the second lammas shoot occurrence was observed. This is consistent with previous findings indicating that younger seedlings demonstrate a high frequency of lammas shoot formation (Chang et al. 2018). Significant lammas shoot emergence commenced in July, with higher stages observed in W and W_S; however, no significant differences were established between the two treatments. This finding aligns with that of previous reports indicating that high summer temperatures promote lammas shoot development (Byun et al. 2013; Kushida 2005; Lee et al. 2007; Jo et al. 2019, 2023).

A higher occurrence of the first lammas shoots was signalled by the onset of the fall warming treatment observed in W and W_S from July, despite the earlier spring phenological progression observed in W_{SF}. This suggests that the timing of achieving the final spring needle stage may not strongly influence lammas shoot incidence. Moreover, no increase in lammas shoot occurrence was noted until fall treatment initiation, indicating that spring warming had a minor effect on lammas shoot occurrence in *P. densiflora* seedlings. Lammas shoot occurrence in W_{SF} increased following the onset of the fall warming treatment and, by the end of the season, the overall incidence was comparable among all warming treatments (Fig. 4c). This finding suggests that both high summer temperatures and elevated fall temperatures can advance lammas shoot development in *P. densiflora* within South Korea. The latter is corroborated by the high mean and maximum daily temperatures (22.8 and 27.2°C, respectively) in September, which signal the onset of the fall warming treatment, relative to those in June (22.6 and 27.5°C, respectively) (KMA 2025).

Although lammas shoot occurrence peaked in W, W_{SF}, and W_S in November at similar rates, these shoots exhibited more advanced developmental stages in W and W_S. This may be attributed to the higher EDD in W and W_S than that in W_{SF} (Appendix Fig. 2c). Moreover, GDD, AHT, and ALT levels were similar in W_S and W_{SF}, indicating that changes in EDD are likely the main drivers of advanced lammas shoot development in W_S. Consequently, PLS regression analysis revealed that EDD was the most influential environmental factor in lammas shoot development. EDD represents the cumulative temperature above a defined high threshold, with the most significant relationship between EDD and lammas shoot development stages observed at a reference temperature range of 24–27°C (Appendix Table 1). Excessive temperatures can accelerate developmental transitions in plants, thereby altering their phenology (Badeck et al. 2004; Jo et al. 2019; Lizaso et al. 2018). The accelerated transitions observed in this study appear to have substantially triggered abnormal shoot growth.

The shoot development stages of the first lammas were influenced by GDD, GDDm, AHT, and ALT (Table 3). Both GDD and GDDm demonstrated positive and negative effects, respectively, with GDD exhibiting a stronger positive association. This difference likely arises because GDDm excludes temperatures above 30°C, thereby failing to capture the effects of extreme heat on plant development. Because lammas shoot formation is known to be strongly affected by high temperatures, GDD, which is not limited by an upper temperature threshold, better explains the shoot stage progression of lammas than GDDm. In contrast, AHT and ALT generally displayed negative associations with lammas shoot developmental stages. The modest influence of ALT, which is consistent with the observed pattern during spring needle unfolding, suggests that lower minimum temperatures can similarly accelerate lammas shoot needle unfolding. However, the negative effect of AHT was more pronounced in identical treatment comparisons (Appendix Table 3), indicating that in the C and W treatments, those with or without consistent warming, exposure to extreme daily maximum temperatures (heat stress) can inhibit lammas shoot development (Sanwong et al. 2023). Overall, cumulative high temperatures advance lammas shoot stage progression; however, excessively high daily maximum temperatures may suppress lammas shoot needle development under similar thermal conditions.

The shoot development of the second lammas, which involved an additional bud burst following the extension of the first lammas shoot, was higher under the W and W_S treatments. A greater proportion of shoot development was observed in W; however, both the W and W_S treatments were grouped together in the post hoc analysis (Fig. 4e). Their incidence increased in September, with seedlings in W_S displaying a high frequency of second lammas shoots even after conclusion of the summer warming period. The occurrence rate of second lammas shoots in W_{SF} remained low and comparable to that in C, indicating that elevated summer temperatures exerted a stronger influence on their formation (Jo et al. 2019, 2023).

Most of the second lammas shoots failed to reach the final leaf-unfolding stage. However, seedlings in the W and W_S treatments reached more advanced needle unfolding stages than those in the C and W_{SF} treatments, with W demonstrating significantly greater progression than W_S in October (Fig. 4f). This

suggests that greater heat accumulation is required for needle elongation in the second lammas shoots. In the PLS analysis, EDD emerged as the main driver of the second lammas shoot development, exhibiting a higher optimal base temperature than that of the first lammas shoot development (Appendix Table 1). Therefore, stronger thermal conditions may be required for second lammas shoot initiation. The observed low frequency of the second lammas shoots observed in the W_{SF} treatment likely resulted from its reduced EDD accumulation (Appendix Fig. 2c). In addition, second lammas shoot occurrence may have been limited by the delayed developmental completion of the first lammas shoots in the W_{SF} treatment. Other environmental variables showed patterns similar to those observed for the second lammas shoot occurrence, implying comparable underlying mechanisms (Table 3).

The second lammas shoots experienced insufficient time for needle elongation because of their late occurrence, leading to undeveloped needles by the end of the growing season (Appendix Fig. 1). Consequently, less advanced phenological stages were observed for seedlings in the W_{SF} and C treatments than those in the W and W_S treatments. Although to a lesser extent than in W and W_S, approximately half of the first lammas shoots in C and W_{SF} did not reach stage 4 by November (Appendix Fig. 1). Similarly, in W and W_S, approximately half of the seedlings failed to reach stage 4 for the second lammas shoots. Underdeveloped lammas shoots are susceptible to frost damage and unlikely to mature into normal seedlings. Therefore, multiyear observations are required to assess the long-term consequences of these abnormal growth patterns (Kollas et al. 2014; Zohner et al. 2020).

5. Conclusion

This study demonstrated that seasonal warming patterns differentially influenced spring and lammas shoot phenology in *P. densiflora* seedlings. Spring needle unfolding was primarily driven by AHT rather than traditional GDD. Although spring and year-round warming expedited early developmental stages, they did not necessarily accelerate completion. In contrast, lammas shoot development was predominantly controlled by cumulative high temperatures (EDD > 24–27°C), with summer and growing-period warming promoting both the second lammas shoot occurrence and advancement. While elevated fall temperatures also advanced the first lamma shoot occurrence, they produced less developed shoots. The high frequency of underdeveloped lammas shoots, particularly the first lammas shoots under spring-fall warming and second lammas shoots that failed to reach the final needle unfolding stage by the end of the season, raises concerns regarding frost vulnerability and long-term seedling survival under warming scenarios. These findings highlight that extreme temperature accumulation, rather than mean temperature increases in isolation, may be a critical factor driving abnormal phenological responses in *P. densiflora*. Future studies should incorporate multiyear observations to assess whether warming-induced phenological shifts lead to reduced seedling establishment and forest regeneration success in the context of climate change.

Declarations

Funding Declaration

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Author Contribution

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Data Availability

Additional data are available from the corresponding author upon reasonable request.

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Tables

Table 1 Significance statistics from beta regression mixed models assessing the effects of month of assessment and warming treatment on spring needle final stage attainment and occurrence rates of first and second lammas shoots in *Pinus densiflora* seedlings. F-values and associated p-values were derived from Type II ANOVA applied to each beta regression model.

Explanatory variables	Phenological parameters					
	Spring needle final stage attainment rate		1st lammas shoot occurrence rate		2nd lammas shoot unfolding stage	
	F value	p-value	F value	p-value	F value	p-value
Month	2930.80	**<0.001**	833.10	**<0.001**	235.64	**<0.001**
Treat	11.66	**0.009**	119.59	**<0.001**	150.01	**<0.001**
Month*Treat	55.98	**<0.001**	81.04	**<0.001**	98.46	**<0.001**

Month: month of assessment; Treat: treatment; σ2: variance. The significant p-values are highlighted in bold.

Table 2 Significance statistics from the linear mixed-effects models (LMMs) assessing the effects of month of assessment and warming treatments on phenological stages of *Pinus densiflora* seedlings. F-values and associated p-values were derived from Type III ANOVA applied to each LMM.

Explanatory variables	Phenological parameters					
	Spring needle unfolding stages		1st lammas shoot unfolding stages		2nd lammas shoot unfolding stages	
	F value	p-value	F value	p-value	F value	p-value
Month	8277.61	**<0.001**	3052.5	1.000	146.49	1.000
Treat	0.34	0.800	18.22	**<0.001**	26.49	0.394
Month*Treat	13.94	**<0.001**	49.92	**<0.001**	41.25	**<0.001**
$\sigma^2_{PlantID}$	0.00		0.29		0.03	
σ^2_{PlotID}	0.00		0.05		0.00	
σ^2_{Rsd}	0.07		0.46		0.13	

Month: month of assessment; Treat: treatment; σ2: variance. The significant p-values are highlighted in bold.

Table 3 Partial least squares (PLS) regression results assessing the relative importance of environmental variables on spring and lammas shoot unfolding stages in *Pinus densiflora* seedlings.

	Spring needle stage		1st lammas shoot stage											2nd lam
Parameter	May		Jul		Aug		Sep		Oct		Nov			Sep
	VIP	β	VIP	β	VIP	β	VIP	β	VIP	β	VIP	β	VIP	β
GDD	0.989	-0.009	**1.113**	**0.021**	**1.095**	**0.008**	**1.084**	**0.004**	**1.045**	**-0.005**	**1.040**	**-0.006**	**1.081**	**0.027**
GDD_m	0.964	-0.011	**1.076**	**0.007**	**1.066**	**-0.005**	**1.049**	**-0.012**	0.959	-0.021	0.950	-0.026	**1.065**	**0.033**
EDD_{30}	**1.182**	**0.017**	**1.235**	**0.089**	**1.181**	**0.068**	**1.188**	**0.063**	**1.373**	**1.149**	**1.360**	**0.083**	**1.113**	**0.007**
AHT	**1.257**	**0.032**	**1.044**	**-0.030**	**1.074**	**-0.013**	**1.090**	**0.003**	**1.070**	**-0.002**	**1.069**	**-0.005**	**1.044**	**-0.034**
ALT	**1.036**	**-0.005**	0.986	-0.059	**1.054**	**-0.024**	**1.032**	**-0.029**	**1.009**	**-0.010**	**1.003**	**-0.012**	**1.050**	**-0.007**
SWC_{30}	0.205	-0.003	0.123	0.001	0.063	-0.001	0.240	-0.003	0.002	-0.001	0.134	0.004	0.513	-0.016

GDD: growing degree days; GDDm: maximum-limited growing degree days; EDD30: extreme degree days at a reference temperature of 30° C; AHT: accumulated daily maximum temperature; ALT: accumulated daily minimum temperature; SWC30: 30-day mean soil water content preceding each observation; VIP: Variable importance in projection; β: regression coefficient. Variables with variable importance in projection (VIP) > 1 are highlighted in bold along with their regression coefficient (β).

Figures

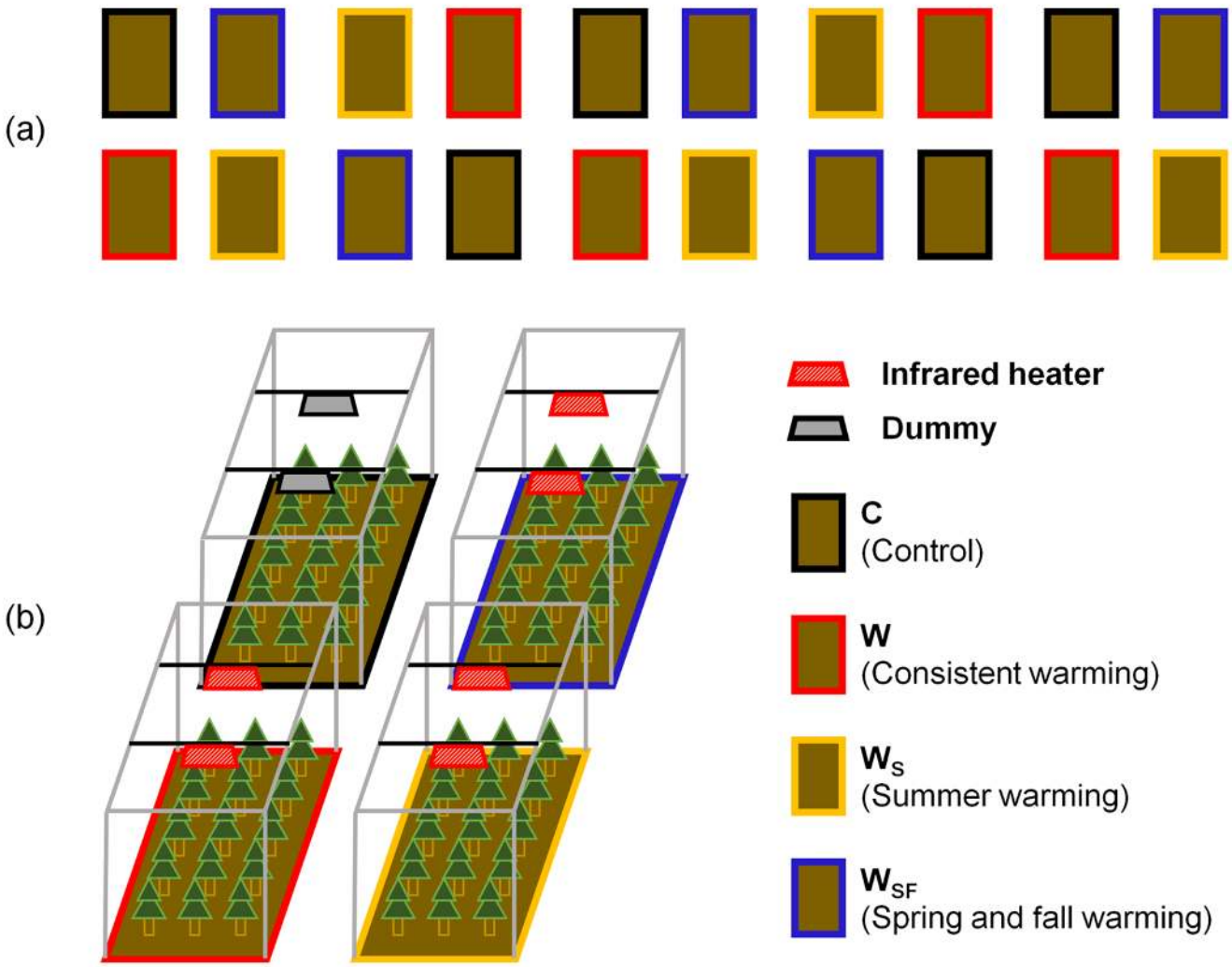

Figure 1

Experimental design schematic: (a) overview of study site layout; (b) sensor and data logger connections within each treatment plot.

Figure 2

Needle unfolding stages in Pinus densiflora seedlings. Stage 0: closed bud; stage 1: swollen bud; stage 2: < 1 cm long needles; stage 3: 1–3 cm long needles; stage 4: >3 cm long needles.

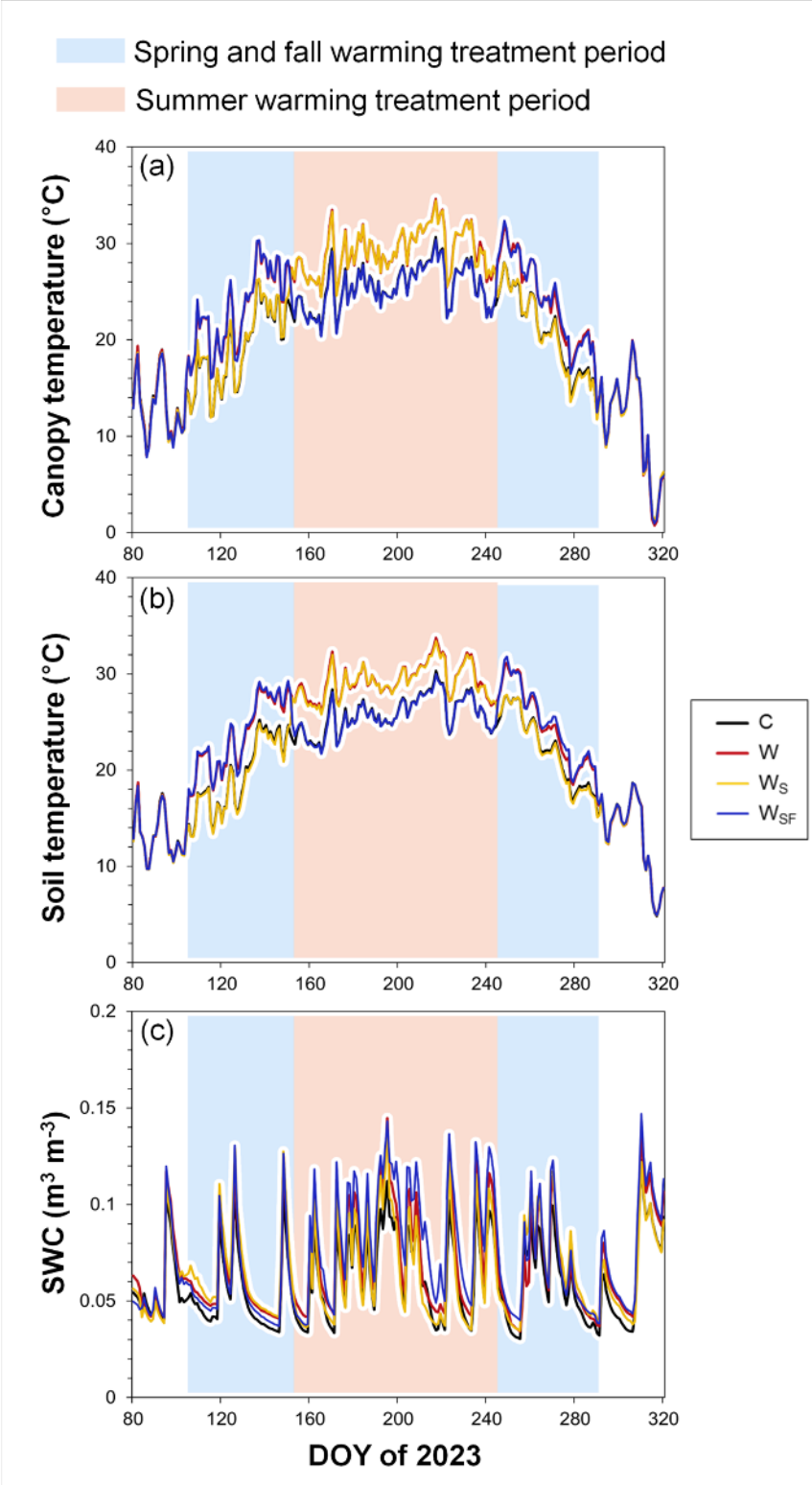

Figure 3

Seasonal trends in (a) canopy temperature, (b) soil temperature, and (c) volumetric soil water content (SWC) over the study period. SWC: soil volumetric water content; DOY: day of year; C: control; W: consistent warming; W_S: summer warming; W_{SF}: spring and fall warming.

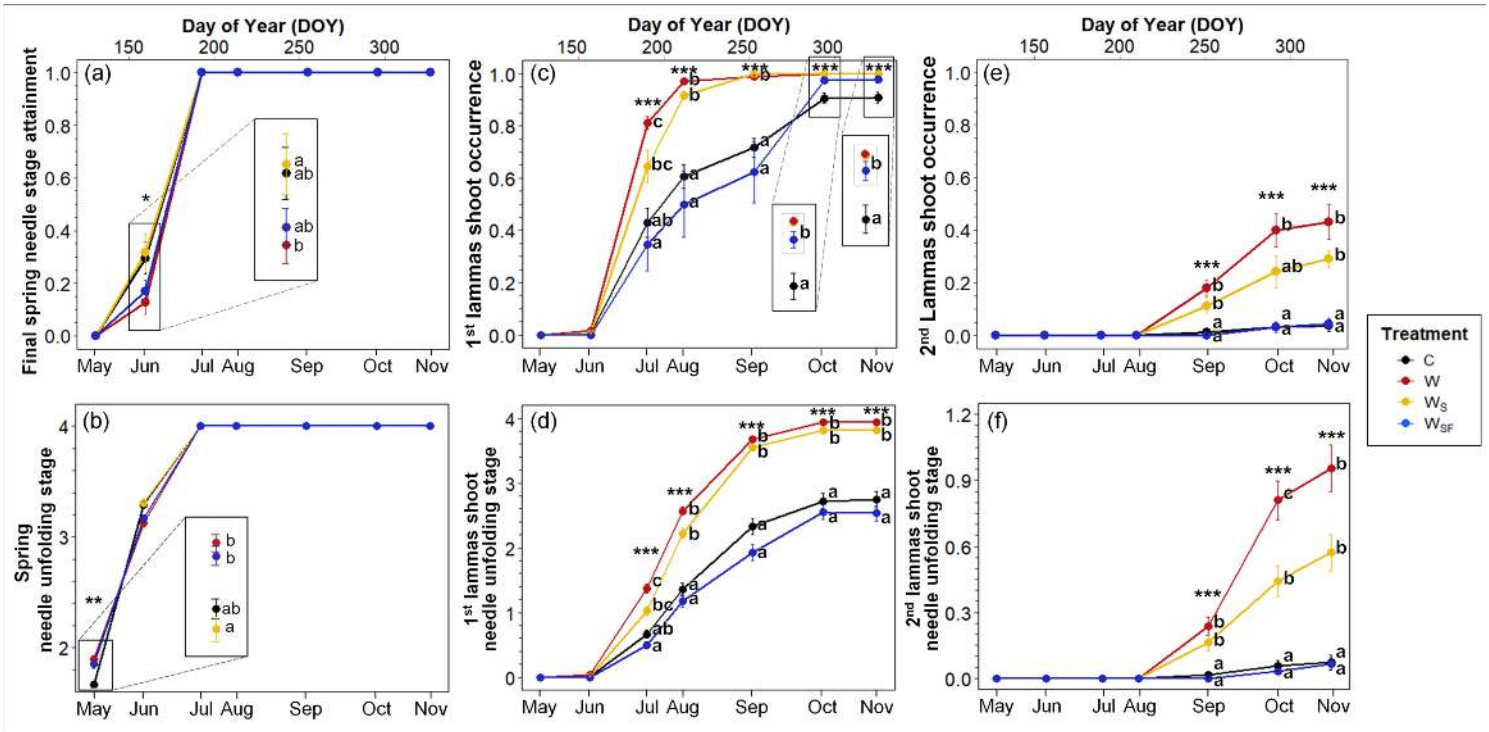

Figure 4

Seasonal trends in (a) final spring phenological stage attainment rate, (b) spring needle unfolding stage, (c) first lammas shoot occurrence rate, (d) first lammas shoot needle unfolding stage, (e) second lammas shoot occurrence rate, and (f) second lammas shoot needle unfolding stage over the study period. Dots indicate mean values, while bars represent standard errors. Insets highlight significant differences not readily visible in the main panels. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Supplementary Files

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