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RESEARCH

Phenological responses of six native *Quercus* species in Korea under elevated CO_2 and temperature treatment

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Background: Climate change, primarily driven by rising atmospheric CO_2 and temperatures, affects plant phenology, a key indicator of ecosystem response. Phenological shifts in dominant forest species such as oaks can alter carbon assimilation, community dynamics, and forest resilience. However, experimental studies in Korea on multiple native *Quercus* species under climate manipulation are limited.
Results: Using a multi-year greenhouse experiment, we quantified the phenological responses of six native deciduous oak species (*Quercus aliena*, *Quercus serrata*, *Quercus variabilis*, *Quercus acutissima*, *Quercus mongolica*, and *Quercus dentata*) under elevated CO_2 (750–800 ppm) and temperature (+2°C). All species exhibited earlier budburst and leaf unfolding, with an average advancement of 12–20 days. Autumn leaf coloration and abscission were generally delayed, leading to a mean growing season extension of 20.3 days. The responsiveness varied across species; *Q. mongolica*, *Q. serrata*, and *Q. variabilis* were most sensitive, whereas *Q. dentata* showed inconsistent or reversed trends. Regression analysis revealed that accumulated temperature significantly predicted phenological timing in the control group, but correlations weakened or disappeared under treatment conditions, indicating saturation effects.
Conclusions: Elevated CO_2 and temperature extend the growing season in temperate oaks, but species-specific thresholds and saturation responses complicate phenological prediction. These findings emphasize the need for adaptive, non-linear modeling and species-targeted strategies in forest management under climate change.

Keywords: accumulated temperature, climate change, greenhouse, growing season

Introduction

Climate change, driven largely by increasing atmospheric CO_2 concentrations and global temperatures, is profoundly altering the phenological patterns of plants. Phenology, the timing of recurrent biological events, is particularly sensitive to climatic variables, and shifts in spring and autumn phenophases can directly affect carbon balance, species interactions, and ecosystem function (Fu et al. 2015; Piao et al. 2019). In temperate deciduous forests, earlier budburst and delayed leaf senescence have been widely reported, contributing to an overall extension of the growing season (Zohner and Renner 2019). These shifts are often species-specific and mediated by physiological traits such as chilling and heat requirements, photoperiod sensitivity, and internal hormonal regulation (Basler and Körner 2014; Laube et al. 2014).

Recent studies have shown that elevated CO_2 and temperature can accelerate early-season development, yet the magnitude and direction of these changes vary among species (Estiarte and Peñuelas 2015; Gill et al. 2015). Such interspecific variability underscores the need for species-level phenological assessments, particularly for dominant forest taxa like *Quercus*. Despite general expectations that warming advances spring and delays autumn events, not all species follow this pattern. Some exhibit weak or even reversed responses, depending on ontogeny, ecological strategy, or environmental thresholds (Zohner et al. 2023).

In Korea, the genus *Quercus* includes several native deciduous species that dominate temperate forests and play key roles in biodiversity and ecosystem resilience. However, phenological studies in the region have largely relied on long-term field observations or limited case studies using single species or herbaceous plants (Kim et al. 2020; Lee et al. 2009). Experimental evidence from controlled environments remains scarce.

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A few studies have investigated phenological changes in oak species under climate manipulation. For instance, Jeong et al. (2021) conducted a seedling-based greenhouse experiment and reported significant advancement in bud emergence under elevated CO_2 and temperature. Hong et al. (2018) observed extreme phenological shifts in various deciduous trees, including *Quercus*, under artificial warming. However, these studies focused on early developmental stages or short-term responses. The present study differs by applying a long-term (three-year) experimental design to mature saplings and evaluating multiple phenophases from budburst to leaf fall.

In this study, we aim to quantify the phenological responses of six native *Quercus* species in Korea under elevated CO_2 and temperature. By examining interspecific differences in the timing of spring and autumn events, and by analyzing the role of accumulated temperature, we seek to improve our understanding of how dominant tree species may respond to future climate conditions and inform forest management strategies accordingly.

Materials and Methods

Plant materials and experimental period

This study investigated six native deciduous oak species in Korea: *Quercus aliena*, *Quercus serrata*, *Quercus variabilis*, *Quercus acutissima*, *Quercus mongolica*, and *Quercus dentata*. Acorns were collected in October 2008 from natural hillsides in the Gongju region, Chungcheongnam-do, South Korea. Seeds were sown in January 2009, and after germination, seedlings were assigned to two treatment conditions: a control and a climate-change treatment. A total of 36 individuals were used, with three saplings per species per treatment group.

All saplings were cultivated under their respective conditions for approximately 34 months to allow acclimation. Phenological monitoring was conducted from November 2011 to April 2014, using greenhouse-grown saplings that had passed the early seedling stage. These individuals are not mature trees but are more developmentally stable than first-year seedlings, allowing for repeatable multi-year observations.

CO_2 concentration and temperature treatment

Treatment conditions were implemented in a climate-controlled greenhouse to simulate elevated CO_2 and temperature environments. The control group was maintained at ambient outdoor conditions, with CO_2 concentrations of 360–370 ppm. The treatment group was exposed simultaneously to elevated CO_2 levels (750–800 ppm) and a 2°C increase in mean air temperature relative to the control. These conditions reflect projections for the mid-to-late 21st century under the IPCC SRES A1FI and RCP 8.5 scenarios (IPCC 2007), which project CO_2 concentrations reaching ~700–800 ppm by 2100 under fossil fuel-intensive pathways. Because CO_2 and temperature were applied in combination and not in a factorial design, this study evaluates integrated effects rather than their individual contributions. CO_2 enrichment was maintained using two gas cylinders regulated by automatic valves and tubing, connected to a controller. A remote-controlled infrared gas analyzer (LCSEMS-002; Parus Co., Suwon, Korea) monitored atmospheric CO_2 levels at canopy height, maintaining stable concentrations. The air temperature was regulated by automatic vents and heating systems. Air temperature and humidity were continuously monitored using sensors installed at plant height and recorded every 10 minutes (Fig. 1). The pots were arranged in a randomized complete block design within the greenhouse, with periodic rotation to minimize microenvironmental variation. Water was supplied every 3 to 4 days at approximately 9 a.m., with 700 mL per pot based on the carrying water capacity.

Phenological monitoring

For each individual sapling, three representative branches approximately 20 cm in length were selected and labeled at 1 m above ground level. The following phenophases were recorded: (1) budburst, (2) leaf unfolding, (3) onset and completion of autumn leaf coloration, and (4) initiation and completion of leaf fall (Table 1). Budburst was defined as the moment when bud scales visibly separated. Leaf unfolding was recorded when leaves had emerged and fully expanded. Autumn coloration onset and completion were determined when 5% and 95% of leaf surface area, respectively, had turned color. The percentage of colored leaf area was visually estimated by the trained observer, using

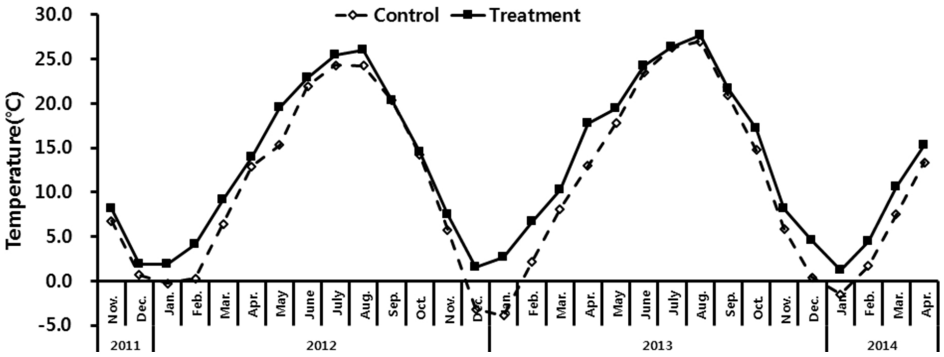

Fig. 1 Monthly fluctuation in temperature of control (dotted line) and treatment (soild line).

Table 1 Criteria for phenological stage classification in *Quercus* species

Phenological event	Criterion
Budding	Time when the scales of the overwintering bud begin to break open
Leaf unfolding	Time when the leaves emerge and acquire full shape (regardless of size)
Autumn coloration start	Time when at least 5% of the leaf area shows visible color change
Autumn coloration end	Time when approximately 95% of the leaf area has changed color
Leaf fall	Time when the first visible leaf abscission is observed

standardized photographic guides and categorical scales following protocols established by the USA national phenology network (USA-NPN 2025). Leaf fall was recorded at its visible initiation and when most leaves had detached.

Observations were made three times per week during spring and autumn, and weekly during summer. All assessments were performed by the same trained observer to minimize subjective bias.

Calculation of cumulative temperature (thermal accumulation index)

To evaluate thermal accumulation effects, accumulated temperature was calculated by summing daily mean temperatures exceeding a base threshold of 5°C from January 1 until the occurrence of each phenophase. The formula used was:

$$Tn = \Sigma(t_i - 5), \text{ where } t_i > 5°C$$

Where t_i represents the daily mean temperature on day i. Only positive values were included in the summation. This approach represents cumulative thermal input, providing a simple yet effective measure of heat accumulation influencing phenological timing (Lieth 1974). The base temperature of 5°C is commonly used to explain the onset of leaf unfolding in temperate deciduous trees (Basler and Körner 2014; Lieth 1974), and this criterion was also applied in the present study.

Statistical analysis

Differences in phenological traits between control and treatment groups were analyzed using one-way ANOVA with block as a random factor, followed by Fisher's least significant difference test at the 5% significance level (No and Jung 2002). To evaluate the relationship between accumulated temperature and phenophase timing, linear regression analyses were performed using individual plant-year data across three years, with separate models for control and treatment groups. R^2 values were computed to evaluate model fit, and the statistical significance of slope differences between these groups was assessed using the non-parametric Wilcoxon Signed-Rank Test (Hollander et al. 2013). All statistical analyses were conducted using Statistica software (StatSoft 2006). The pots were arranged in a randomized complete block design, and block was included as a factor in the statistical model.

Results

Changes in budburst and leaf unfolding

Under elevated CO_2 and temperature conditions, all six *Quercus* species exhibited significantly earlier timing of both budburst and leaf unfolding compared to the control group, as measured in Julian days (Fig. 2). Budburst occurred an average of 19.0, 19.0, and 16.3 days earlier in *Q. serrata*, *Q. aliena*, and *Q. variabilis*, respectively. *Q. acutissima*, *Q. mongolica*, and *Q. dentata* also showed advancements of 14, 17, and 12 days, respectively.

Leaf unfolding dates were similarly advanced across all species. *Quercus serrata* showed the most pronounced change with an average advancement of 20.3 days. *Quercus mongolica* and *Q. acutissima* followed with 11 and 9 days earlier emergence, while *Q. dentata* advanced by 8.7 days. The observed differences between treatment and control groups were statistically significant for several species ($p < 0.05$).

Changes in autumn coloration and leaf fall timing

Under elevated CO_2 and temperature conditions, most *Quercus* species exhibited delayed timing in both autumn leaf coloration and leaf fall compared to the control group (Figs. 3 and 4). The onset of autumn coloration was significantly postponed in all species except *Q. aliena*. The most prominent delays were observed in *Q. acutissima* (14.3 days), *Q. variabilis* (10.7 days), and *Q. serrata* (4.7 days). In contrast, *Q. dentata* exhibited an earlier onset by 2.3 days, suggesting a divergent response pattern.

The completion of coloration also tended to occur later in the treatment group across most species. *Quercus mongolica* and *Q. acutissima* showed marked delays of 20.3 and 18.3 days, respectively, while *Q. variabilis* and *Q. serrata* were delayed by 8.0 and 3.3 days. No significant difference was observed in *Q. dentata*, and in some individuals, coloration completion occurred slightly earlier than in the control group.

Leaf fall also showed similar trends. *Quercus mongolica* exhibited a 7.7-day delay in the onset of leaf fall and a 17.3-day delay in completion. *Quercus variabilis* and *Q. acutissima* showed delays of 5.3 and 4.0 days (onset), and 16.3 and 6.7 days (completion), respectively. Moderate delays were also observed in *Q. serrata* and *Q. aliena* (3–4 days on average). However, *Q. dentata* displayed earlier onset of leaf fall and no significant difference in completion timing, showing a unique response pattern.

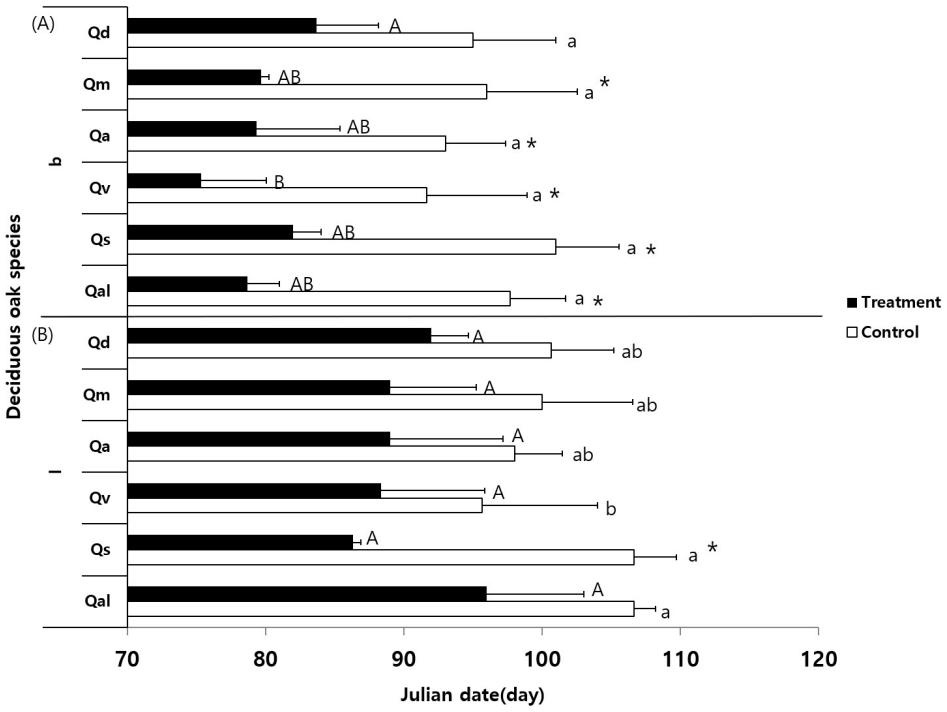

Fig. 2 Comparison of the Julian dates for (A) budburst and (B) leaf unfolding in six *Quercus* species under control (□) and treatment (■) conditions. Bud phenological stages were recorded from 2012 to 2014. Different lowercase and uppercase letters indicate significant differences between phenophases within each species and treatment, based on Fisher's least significant difference tests ($p < 0.05$). Asterisks (*) denote statistically significant differences between control and treatment groups within the same species ($p < 0.05$). Species abbreviations, Qd: *Quercus dentata*; Qm: *Quercus mongolica*; Qa: *Quercus acutissima*; Qv: *Quercus variabilis*; Qs: *Quercus serrata*; Qal: *Quercus aliena*. Phenophase abbreviations, b: budburst; l: leaf unfolding.

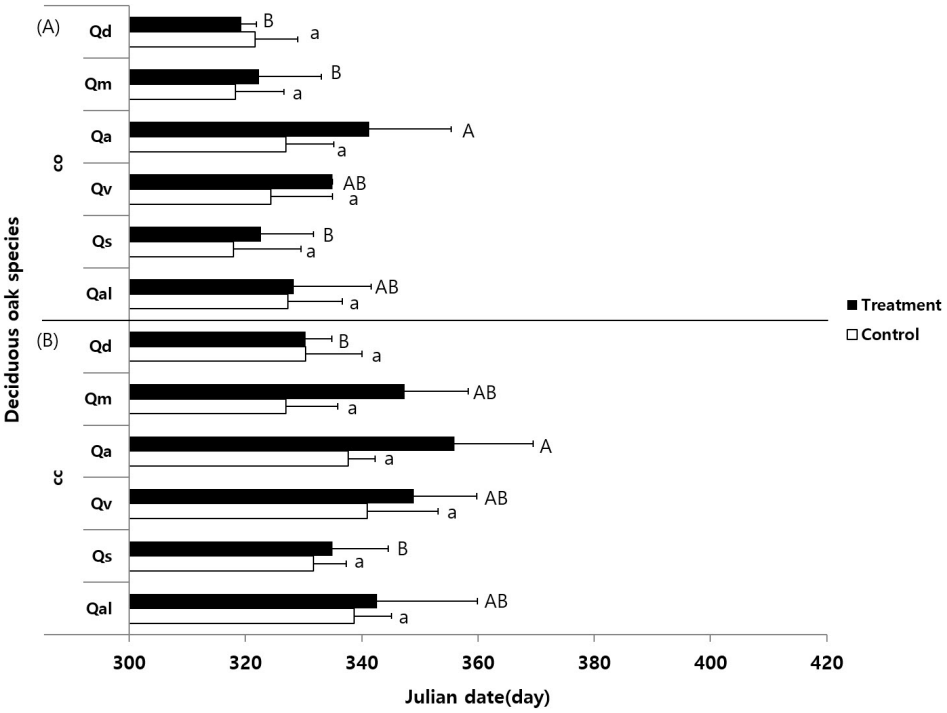

Fig. 3 Comparison of the Julian dates for (A) onset and (B) completion of autumn leaf coloration in six *Quercus* species under control (□) and treatment (■) conditions. Bud phenological stages were recorded from 2012 to 2014. Different lowercase and uppercase letters indicate significant differences between phenophases within each species and treatment, based on Fisher's least significant difference tests ($p < 0.05$). Species abbreviations, Qd: *Quercus dentata*; Qm: *Quercus mongolica*; Qa: *Quercus acutissima*; Qv: *Quercus variabilis*; Qs: *Quercus serrata*; Qal: *Quercus aliena*. Phenophase abbreviations, co: onset of autumn leaf coloration; cc: completion of autumn leaf coloration.

Changes in growing season duration

In all six *Quercus* species, elevated CO_2 and temperature conditions led to earlier leaf unfolding and delayed leaf fall, resulting in an overall extension of the growing season. The average extension across all species was 20.3 days (±7.4 SD), with *Q. mongolica* (28.3 days), *Q. serrata* (25.7 days), and *Q. variabilis* (24.3 days) showing the most pronounced lengthening (Figs. 3 and 4). In contrast, *Q. dentata* and *Q. aliena* exhibited smaller increases of 9.7 and 15.0 days, respectively (Figs. 3 and 4).

Relationship between accumulated temperature and phenology

Linear regression analysis between accumulated temperature (≥ 5°C from January 1) and phenological events revealed significant positive correlations in the control group. Budburst showed $R^2 = 0.248$ ($p = 0.036$), and leaf unfolding showed $R^2 = 0.327$ ($p = 0.013$), indicating temperature accumulation was closely linked to early season phenophase timing (Fig. 5).

In the treatment group, the correlation between accumu-

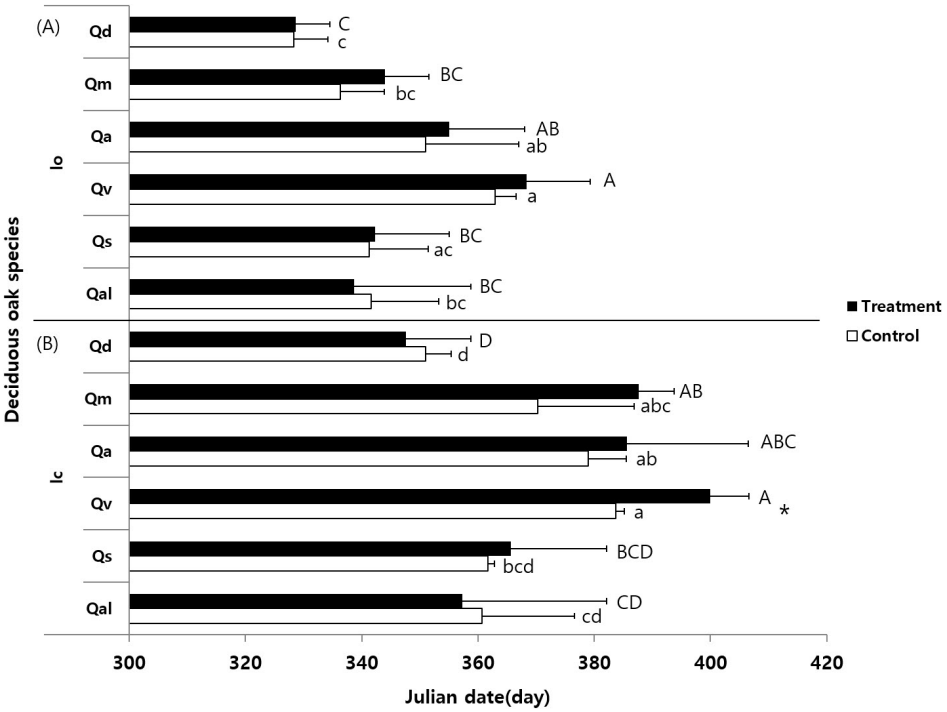

Fig. 4 Comparison of the Julian dates for (A) onset and (B) completion of leaf fall in six *Quercus* species under control (□) and treatment (■) conditions. Bud phenological stages were recorded from 2012 to 2014. Different lowercase and uppercase letters indicate significant differences between phenophases within each species and treatment, based on Fisher's least significant difference tests ($p < 0.05$). Asterisks (*) denote statistically significant differences between control and treatment groups within the same species ($p < 0.05$). Species abbreviations, Qd: *Quercus dentata*; Qm: *Quercus mongolica*; Qa: *Quercus acutissima*; Qv: *Quercus variabilis*; Qs: *Quercus serrata*; Qal: *Quercus aliena*. Phenophase abbreviations, lo: onset of leaf fall; lc: completion of leaf fall.

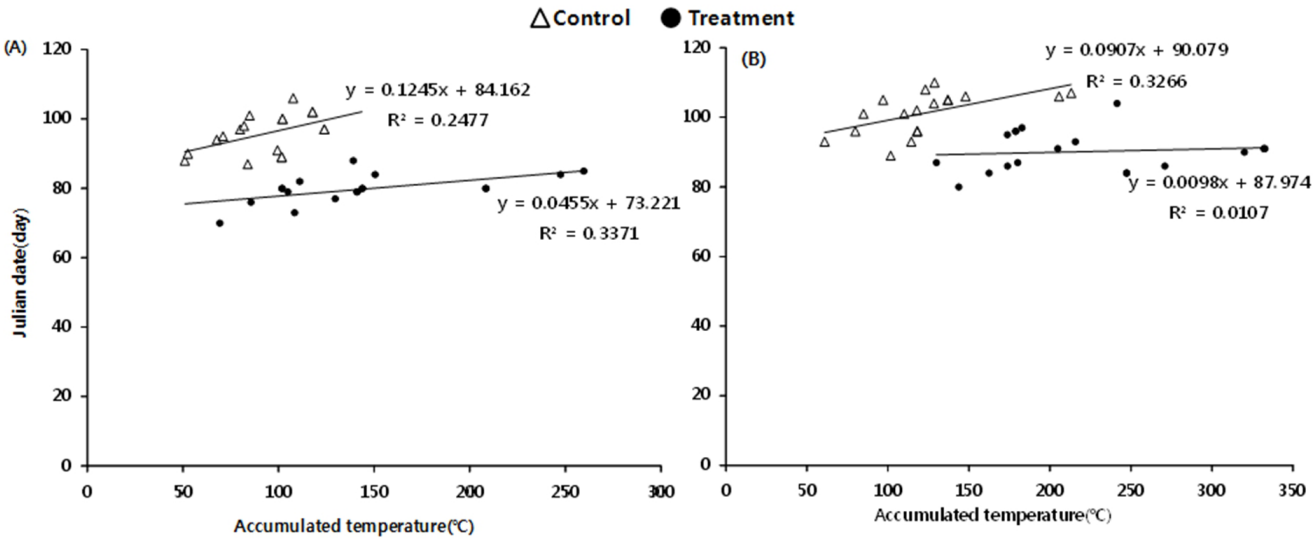

Fig. 5 Linear regression model of Budding (A) and leaf unfolding (B) in control and treatment (increased CO_2 concentration - increased air temperature) from 2012 to 2014.

lated temperature and leaf unfolding was not significant ($R^2 = 0.011$, $p = 0.683$). Budburst retained a significant correlation ($R^2 = 0.337$, $p = 0.011$), suggesting a partial sensitivity remained under elevated CO_2 and temperature conditions (Fig. 5).

Discussion

Changes in budburst and leaf unfolding timing

The advancement of budburst and leaf unfolding observed in this study suggests that elevated CO_2 and temperature directly influence early-season physiological responses in temperate deciduous oaks. High temperatures promote dormancy release through changes in endogenous hormones—particularly by increasing gibberellin activity and decreasing abscisic acid levels—thereby accelerating growth initiation (Matsumoto et al. 2003). Elevated CO_2 concentrations further enhance early growth by increasing photosynthetic capacity and early biomass accumulation (Wang et al. 2008).

Jeong et al. (2021) reported that *Q. variabilis*, *Q. mongolica*, and *Q. serrata* exhibited advances in leaf emergence of 36, 29, and 23 days, respectively, when grown under greenhouse conditions, which is consistent with the 20-day average advancement observed in our study. However, a key

distinction lies in the fact that our saplings were monitored for over three years under the same treatment conditions, providing a more stable and long-term dataset compared to short-term experiments on seedlings.

Nevertheless, interpretation of greenhouse experiments must be made with caution due to differences from natural ecosystems, including altered light regimes, soil moisture, and wind exposure. Despite these limitations, species-specific differences in response were clearly evident. Such variability may reflect differences in physiological tolerance to warming, temperature thresholds for dormancy release, and photoperiod sensitivity among species (Basler and Körner 2014).

These results underscore the importance of incorporating physiological mechanisms—such as hormonal control and species-specific thermal sensitivity—when predicting phenological shifts under future climate scenarios.

Changes in autumn coloration and leaf fall timing

Delayed timing of both autumn leaf coloration and leaf fall under elevated CO_2 and temperature was one of the most notable findings of this study. On average, the onset and completion of both phases were delayed by 10–20 days across most species in the treatment group. *Quercus mongolica*, *Q. acutissima*, and *Q. variabilis* showed statistically significant delays (Figs. 3 and 4), indicating increased leaf longevity under warming conditions.

These responses are likely driven by physiological mechanisms such as delayed chlorophyll degradation, suppression of senescence-related enzymes, and improved water-use efficiency under elevated CO_2 (Estiarte and Peñuelas 2015; Gill et al. 2015). The extended retention of functional leaves may contribute to increased photosynthetic capacity and short-term gains in gross primary productivity. However, photosynthesis in late autumn is more sensitive to light availability than temperature. As a result, the net carbon balance may be limited, or even negative, if increased respiration offsets photosynthetic gains (Doughty et al. 2015).

Beyond carbon dynamics, phenological shifts in the late growing season can influence broader ecosystem functions. Delayed senescence may alter water cycling, nutrient return through leaf litter, soil organic matter inputs, and even forest community dynamics. These ecological effects emphasize that changes in phenology are not merely seasonal markers but are functionally tied to ecosystem processes.

In this study, species-specific differences were also observed. For example, *Q. dentata* showed an atypical pattern of earlier coloration and leaf fall under elevated conditions, in contrast to the delayed responses of other species. Such deviations may be attributed to intrinsic physiological differences, such as higher sensitivity to photoperiod cues, lower water retention capacity in leaf tissues, or species-specific leaf anatomical traits (Schaberg et al. 2000).

While greenhouse experiments are valuable for isolating climate variables, caution must be taken when extrapolating these findings to natural ecosystems. Controlled environments differ from field conditions in terms of wind exposure, light quality, and soil structure. Nonetheless, the consistency of multi-year trends observed in this study supports the relevance of these results for climate adaptation modeling.

Overall, the clear variation among species in their late season phenological responses underscores the importance of incorporating species-specific sensitivities and physiological mechanisms when predicting forest ecosystem responses to climate change.

Changes in growing season duration

In all six *Quercus* species, the combination of earlier leaf unfolding and delayed leaf fall resulted in an extended growing season under elevated CO_2 and temperature conditions. On average, the growing season length increased by 20.3 days (±7.4 SD). Among the species, *Q. mongolica* showed the greatest extension (28.3 days), followed by *Q. serrata* (25.7 days), *Q. variabilis* (24.3 days), *Q. acutissima* (21.0 days), *Q. aliena* (15.0 days), and *Q. dentata* (9.7 days), indicating a clear interspecific variation in response.

An extended growing season suggests a longer period for photosynthesis, which may lead to greater potential for carbon sequestration. However, in late autumn, photosynthetic rates tend to decline sharply due to reduced light availability, while respiration remains elevated under warmer conditions. This can limit the net gain in carbon storage and, in some cases, even reverse the carbon balance (Doughty et al. 2015).

In addition to carbon cycling, the extended growing period can impact multiple ecosystem functions. It may prolong water uptake, extend root activity, and lengthen the interaction period with soil microbiota, potentially altering soil carbon dynamics and nutrient cycling. These physiological and ecological linkages emphasize that phenological shifts must be interpreted in an ecosystem-wide context.

Compared to previous studies such as Jeong et al. (2021) and Hong et al. (2018), the present experiment provides more reliable evidence of long-term trends. This is due to its use of standardized conditions, multi-year monitoring, and repeated treatment application over three consecutive years. The use of well-established saplings rather than seedlings further increases the ecological relevance of the findings.

Overall, variation in growing season extension appears to be closely tied to species-specific physiological tolerance and structural traits. These results offer a valuable foundation for developing predictive growth models that incorporate differential species responses under future climate scenarios.

Relationship between accumulated temperature and phenology

This study examined the relationship between accumulated temperature (i.e., the sum of daily mean temperatures above 5°C starting from January 1) and key phenological events such as budburst and leaf unfolding in both control and treatment conditions.

In the control group, both budburst and leaf unfolding showed statistically significant positive correlations with accumulated temperature, with R^2 values of 0.248 (p = 0.036) and 0.327 (p = 0.013), respectively (Fig. 5). These findings indicate that under ambient conditions, the cumulative thermal input plays a key role in initiating early-season phenological responses.

However, in the treatment group—subjected to elevated CO_2 and temperature—phenological sensitivity to accumulated temperature diverged. Budburst still maintained a significant relationship (R^2 = 0.337, p = 0.011), suggesting that this earlier developmental phase remains thermally responsive (Fig. 5). In contrast, leaf unfolding exhibited almost no correlation with accumulated temperature (R^2 = 0.011, p = 0.683), indicating that once a certain thermal threshold is surpassed, further temperature accumulation ceases to influence the timing of this event (Fig. 5).

This result supports the concept of temperature saturation or threshold response, wherein phenological events occur abruptly once a minimum thermal requirement is met, regardless of additional temperature accumulation (Basler and Körner 2014). Similar patterns were observed in previous studies by Jeong et al. (2021) and Hong et al. (2018), where rapid phenological shifts occurred after reaching certain accumulated temperature levels.

Moreover, the weakened correlation under elevated climate conditions underscores the limitations of traditional linear degree-day models in predicting plant responses under climate change. As warming continues, these models may lose predictive power. Recent research has emphasized the need for more complex approaches—such as non-linear or machine learning models—that incorporate photoperiod sensitivity, soil moisture, and internal carbon reserves (Czernecki et al. 2018).

In conclusion, future predictive models of phenology should integrate species-specific thermal thresholds and multiple environmental interactions. Long-term experimental data, like those used in this study, are critical to building robust forecasting tools for phenological changes under accelerating climate change.

Conclusions

This study demonstrated that elevated CO_2 and temperature conditions significantly altered the phenological responses of six native *Quercus* species in Korea. All species showed earlier budburst and leaf unfolding, while most exhibited delayed autumn coloration and leaf fall, resulting in an overall extension of the growing season by an average of 20.3 days. However, the magnitude and direction of these responses varied among species, reflecting distinct physiological thresholds and ecological strategies. Notably, *Q. mongolica*, *Q. serrata*, and *Q. variabilis* were highly responsive to climate treatment, whereas *Q. dentata* exhibited weaker or opposite patterns.

Our findings suggest that early season phenophases remain thermally sensitive even under climate change, but later events become increasingly decoupled from accumulated temperature, indicating a saturation or threshold response. These results challenge the validity of traditional linear models for predicting phenology under future warming and highlight the need for species-specific, non-linear approaches that incorporate multiple environmental cues.

While greenhouse experiments provide valuable insights, caution is warranted when extrapolating to natural ecosystems due to inherent differences in abiotic conditions. Nonetheless, the consistent multi-year patterns observed here suggest that dominant forest species like *Quercus* may experience marked shifts in growth timing and duration under future climate scenarios. These phenological changes could have far-reaching implications for forest carbon dynamics, nutrient cycling, and species interactions.

Long-term experimental data from multiple species, as presented in this study, are essential to improve phenology-based forecasting models and to inform climate-resilient forest management strategies in temperate regions.

Abbreviations

Not applicable.

Acknowledgements

Not applicable.

Authors' contributions

JML collected, analyzed, and visualized the data, wrote the original draft, and reviewed the finished version. EJK, YBP planned the article, collected, and analyzed the data and wrote the original draft. JWP, JHP collected, and created the manuscript and reviewed the finished version. YHY planned and supervised the article, conceived the paper, conducted experiments, collected, and analyzed data, visualized the data, and reviewed the completed version and received research funding.

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Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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