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Leaf Phenological Variability in *Fagus sylvatica* L. Seedlings from Contrasting European Provenances Across Two Growing Seasons

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ABSTRACT

Phenological monitoring plays a critical role in understanding how forest ecosystems respond to climate change, particularly in economically and ecologically important forestry species such as European beech (*Fagus sylvatica* L., Fagaceae). This study assessed the variability of leafing phenophases in seedlings from 29 European beech provenances originating from Central and Southeastern Europe, grown under common conditions at a trial site on Mt. Goč, Serbia. Observations were conducted during two consecutive growing seasons (2022 and 2023), both warmer than average, with 2022 being notably drier. Significant variation was observed in the timing and duration of leafing phenophases among provenances, especially in 2022. Between-year comparisons revealed a statistically significant difference only for phenophase III (bud cracking), with shorter durations observed in 2022. In general, our results suggest that local climatic parameters and the genetic background influenced phenological variability, although no consistent eco-geographic pattern emerged. These findings represent early-stage results and should be interpreted as a preliminary step toward understanding adaptive potential in juvenile beech populations. Long-term monitoring across multiple years and developmental stages is essential to determine the stability of phenological traits and their relevance for provenance selection. This study contributes to the broader effort of integrating phenological data into climate-resilient forest management and highlights the importance of sustained multi-year research to support future breeding and conservation strategies.

Keywords: leaf phenology, provenance variation, seedlings, phenological plasticity, spring and autumn phenology, climate adaptation, season variability, common garden experiment

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INTRODUCTION

Phenology refers to the timing of recurring biological events such as budburst, leafing, flowering, and senescence. It serves as a major indicator of how plants respond to environmental variability. In the context of global climate change, phenological traits are particularly valuable for assessing how tree species react to shifts in temperature and precipitation regimes (Post et al. 2018, Jean et al. 2023). In forestry, phenology influences critical processes such as productivity, growth cycles, reproductive success, and vulnerability to abiotic stressors. Therefore, monitoring phenological responses is essential for developing adaptive forest management strategies.

Rising temperatures have already led to observable changes in tree phenology, including earlier leaf-out and extended growing seasons (Post et al. 2018). These shifts can increase exposure to late spring frosts and intensify drought stress due to reduced soil moisture (Dolschak et al. 2019). Phenological traits thus not only reflect climatic trends but also directly affect tree development and fitness (Journé et al. 2021, Jean et al. 2023). For example, the timing of leaf emergence influences photosynthetic efficiency and reproductive potential, and is closely linked to long-term productivity (Journé et al. 2021).

European beech (*Fagus sylvatica* L., Fagaceae) is one of the most widespread and ecologically significant broadleaf species in Europe. Its broad distribution across diverse altitudes and climates makes it an ideal model for studying local adaptation (Stojnić et al. 2022, Garosi et al. 2025). However, beech is highly sensitive to climate change. Rising temperatures and prolonged droughts have negatively impacted its growth, transpiration dynamics, and survival, especially in the southern parts of its range (Bolte et al. 2016, Del Castillo et al. 2022). Beech mortality near range margins has been more strongly associated with climatic variables than with geographic factors, suggesting that genetic variability and local adaptation play a central role in resilience (Bolte et al. 2016, Leuschner 2020).

Previous research has demonstrated that beech provenances differ in their phenological behavior under common environmental conditions, indicating a genetic basis for leafing time variability (Vander Mijnsbrugge et al. 2021). Earlier flushing provenances may be more vulnerable to frost damage, while increased temperature extremes can lead to greater inter-individual variability in phenological timing (Geng et al. 2020). These changes complicate predictions of future performance and highlight the need for provenance-level studies to support reforestation and restoration efforts.

Recent investigations further highlight the role of provenance and phenotypic plasticity in shaping the adaptive potential of *Fagus sylvatica* under climate change. Long-term monitoring across the Western Carpathians revealed a significant advancement of spring phases and an extended growing season, with clear variation across elevation zones (Skvareninová et al. 2024). Similarly, multi-trait evaluations of 85 provenances over 25 years showed pronounced differentiation in growth and stability, underscoring the potential for selecting well-adapted seed sources (Liepe et al. 2024). Controlled common-garden experiments have also demonstrated that leaf phenology responses are both species- and provenance-specific under drought and nutrient treatments, illustrating the complexity of provenance-by-environment interactions (Bačurin et al. 2025a). Together, these findings reinforce the relevance of our study, which focuses on provenance-level variation in leafing phenophases and seeks to clarify how timing and duration respond to contrasting growing seasons.

Given the ecological and silvicultural importance of beech, and the increasing stress on its populations under climate change, there is a growing need for improved strategies to achieve forest restoration. This applies to both managed forests and protected areas, where active silvicultural interventions may be necessary to ensure long-term stability and biodiversity conservation (Wagner et al. 2010, Dubravac et al. 2024).

To address these challenges, this study investigates phenological variation among beech provenances under controlled conditions on Mt. Goč, Serbia. The objectives of this study were: (1) to examine whether selected beech provenances from Central and Southeastern Europe differ in the timing and duration of their leafing phenophases within the same growing season; and (2) to determine whether the leafing phenophases of these provenances differ between two successive growing seasons under variable climatic conditions.

MATERIAL AND METHODS

Plant Material

The trial involved 29 European beech provenances selected from their natural distribution areas in Central and Southeastern Europe (Figure 1). Their general characteristics are shown in Table 1. In autumn 2018, approximately 1 kg of visually healthy seeds were collected from each provenance. The collected material was delivered and processed in the laboratory of the Institute of Forestry in Belgrade. After basic cleaning and removal of empty seeds, the material was disinfected in a short H_2O_2 treatment, assessed for quality, and stratified in moist substrate at 3–4°C for 16 weeks. In spring 2019, the seeds were sown in the nursery of the Institute of Forestry in Belgrade, where seedlings were cultivated for two growing seasons under controlled conditions.

The provenance trial was later established in spring 2021 on Mt. Goč (latitude 43.56139° N, longitude 20.80056° E), at 980 m a.s.l., on a northeast-facing slope in the central part of Serbia (Management Unit Gračac, Department 20a, Public Enterprise "Šume Goč" Vrnjačka Banja). The site has temperate continental climate, with a mean annual air temperature of 7.5°C and annual precipitation of 856 mm. Two-year-old seedlings were planted at a spacing of 2 m × 1 m, resulting in a total of 4350 plants across 1 ha (50 seedlings per provenance × 3 replicates (blocks) × 29 provenances). The experimental design was a randomized complete block with three replicates. Each replicate consisted of 50 plants arranged in five rows of 10 planting sites (10 m × 10 m plot). According to von Wühlisch (2004), this plot size is sufficient to maintain trials for up to 60 years.

Figure 1 Geographic origin of 29 European beech (*Fagus sylvatica*) provenances included in the phenological trial at Mt. Goč.

Table 1 Geographic origin and ecological characteristics of 29 provenances of European beech (*Fagus sylvatica* L.) used to establish the trial under common conditions at Mt. Goč, Serbia. Country abbreviations: BG – Bulgaria; SRB – Serbia; MNE – Montenegro; BIH – Bosnia and Herzegovina; HR – Croatia; SI – Slovenia; CZ – Czech Republic; DE – Germany. Climatic characteristics: MAT – mean annual temperature, MAP – annual sum of precipitation (data from https://www.climateengine.org).

N	Provenance ID	Provenance name	Latitude	Longitude	Altitude (m)	MAT (°C)	MAP (mm)
1	BG1	Centralni Balkan	42.86444	24.24941	1100	8	941
2	BG2	Rila	42.26417	23.28333	1280	8	802
3	BIH1	Javor BIH	44.15611	18.94333	1010	8.9	1171
4	BIH2	Lisina	45.02522	17.00861	400	11.4	1110
5	CZ1	Malužin	49.27334	16.66171	360	10.5	571
6	DE1	Harz	51.78503	10.51716	820	7.2	789
7	HR1	Bukovača	45.34747	15.22334	435	11.9	1401
8	HR2	Građevačka Biogora	45.79191	17.12667	185	12.4	899
9	HR3	Južni Papuk	45.50722	17.63802	685	9.7	977
10	HR4	Bublen	45.23139	15.84747	205	12.6	1189
11	MNE1	Borak	42.82738	19.99544	1250	8.6	1100
12	MNE2	Kovač	43.40833	19.11611	960	9.9	1105
13	SI1	Hrastovec	46.35667	15.96667	300	11.4	1066
14	SI2	Osankarica	46.45325	15.38333	1240	6.2	1603
15	SRB1	Mali Jastrebac	43.39092	21.65006	830	9.8	844
16	SRB2	Rudnik	44.10531	20.6136	700	10.3	973
17	SRB3	Povlen	44.16111	19.69861	870	9.6	1144
18	SRB4	Javor SRB	43.44913	20.06806	1350	7.5	1118
19	SRB5	Goč	43.56351	20.75001	920	9.7	1126
20	SRB6	Fruška Gora	45.14194	19.62289	370	11.8	753
21	SRB7	Severni Kučaj	44.12941	21.79868	730	9.7	977
22	SRB8	Veliki Jastrebac	43.36242	21.56092	810	9.9	856
23	SRB9	Južni Kučaj	44.07015	21.75708	700	9.8	996
24	SRB10	Stara Planina	43.38065	22.60313	1260	7.1	1011
25	SRB11	Dubašnica	44.10063	21.88801	900	8.7	849
26	SRB12	Miroč	44.57029	22.37021	450	10.8	576
27	SRB13	Kukavica	42.79124	21.97133	1200	8.3	1011
28	SRB14	Boranja	44.38997	19.28981	650	10.7	1099
29	SRB15	Kačer-Zeleničje	42.82314	22.21206	1180	8.3	971

Monitoring of Leafing Phenophases

Phenological observations were conducted visually in 2022 and 2023 on fixed dates: 8 April, 15 April, 22 April, 29 April, 6 May, 13 May, 20 May, and 27 May. All seedlings were observed on the same day during each observation date. The two years differed in climatic conditions (Figure 2), primarily in terms of precipitation, with 2022 being significantly drier than 2023 (data from https://www.climateengine.org).

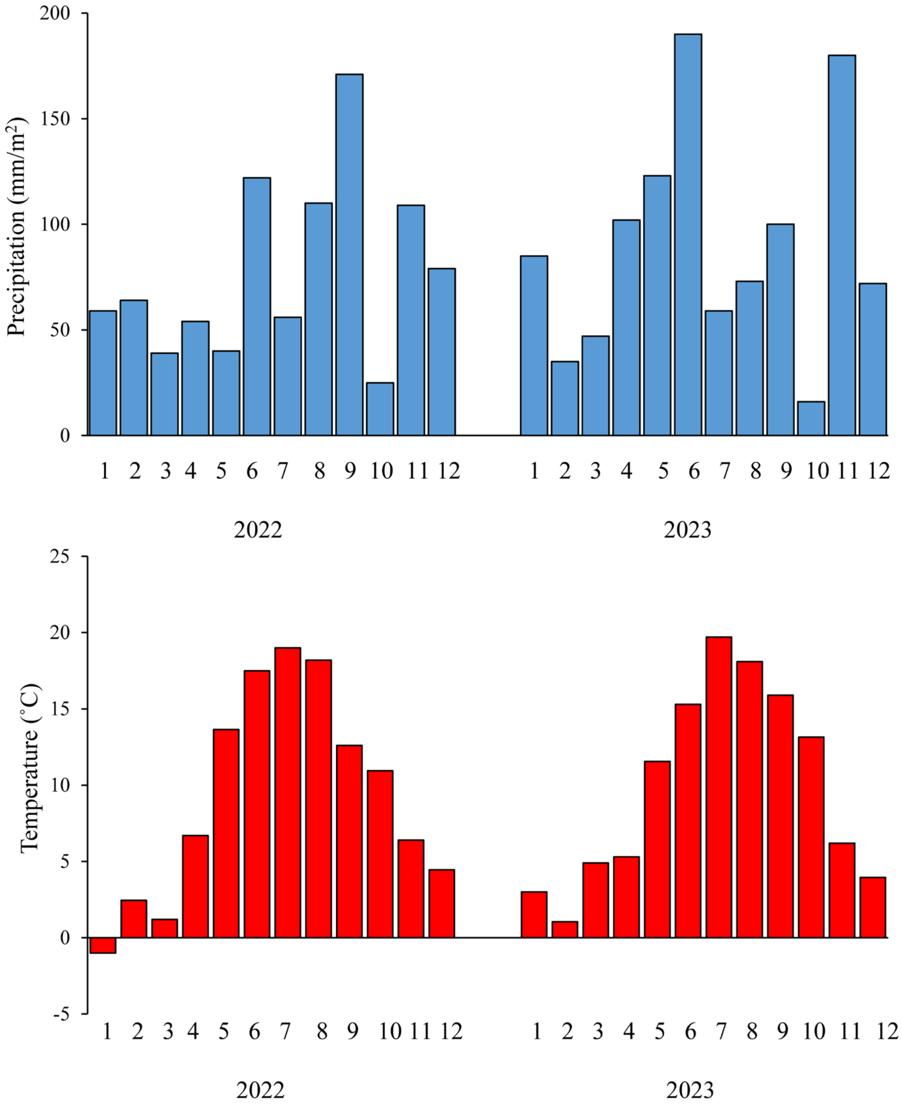

Figure 2 Climatic conditions at the trial site on Mt. Goč: monthly precipitation and temperature in 2022 and 2023.

The number of days from the initial observation day (8 April) to the onset of each leafing phenophase was recorded. Leaf development in the studied provenances was monitored across six characteristic phenophases, following Forstreuter (2002), ranging from dormant buds to fully developed leaves:

- I – Dormant bud – brown to dark brown in color
- II – Swollen bud – elongated, swollen, yellowish-green in color, with a membrane not yet pierced by the emerging leaf
- III – Bud cracking – buds begin to open, and the first signs of greenery become visible
- IV – Rolled leaf emergence – a bent, hairy leaf starts to appear
- V – Unrolled pale leaf – fan-shaped, light-colored leaves are visible
- VI – Fully developed leaf – smooth, wide, and fully expanded.

Statistical Methods

Descriptive statistics were obtained using the MEANS procedure in the SAS statistical package (SAS Institute, Inc. 2011). Differences in the duration of leafing phenophases between the two growing seasons (2022 and 2023) were assessed with analysis of variance (ANOVA). To explore geographic and bioclimatic influences, Pearson correlation coefficients (r) were calculated with the CORR procedure, testing the relationships between phenophase durations and eco-geographic variables (elevation, latitude, longitude, mean annual temperature and annual precipitation) of the seed origin sites.

RESULTS

Provenance Comparisons

The timing and duration of leafing phenophases varied substantially among the studied provenances (Figure 3). Overall, variability was greater in 2022 compared to 2023, with larger differences among provenances observed within that season. In contrast, phenophase durations in 2023 were more uniform across provenances, likely reflecting generally shorter leafing periods. Across both seasons, the lowest variability was consistently recorded for phenophase VI, whereas the highest variability was observed for phenophase IV.

Phenophase II was consistently the shortest, whereas phenophases IV–VI contributed the most to the total leafing duration. Provenances SRB1, SRB7, SRB12, and SRB15 showed the shortest durations across nearly all phenophases, indicating rapid leafing progression. In contrast, CZ1, DE1, HR3, SRB2, and SRB3 exhibited the longest durations, especially in phenophases III, V, and VI. Provenances DE1 and SRB2 maintained long phenophase duration over both years, reflecting stable phenology and resilience to interannual climatic variation. Other provenances displayed intermediate or variable durations, with some showing longer phenophases in 2022 (BG1, BG2, HR4, SRB4, SRB6, SRB9) and others in 2023 (BIH1, HR3, CZ1, SL2, SRB3, SRB13).

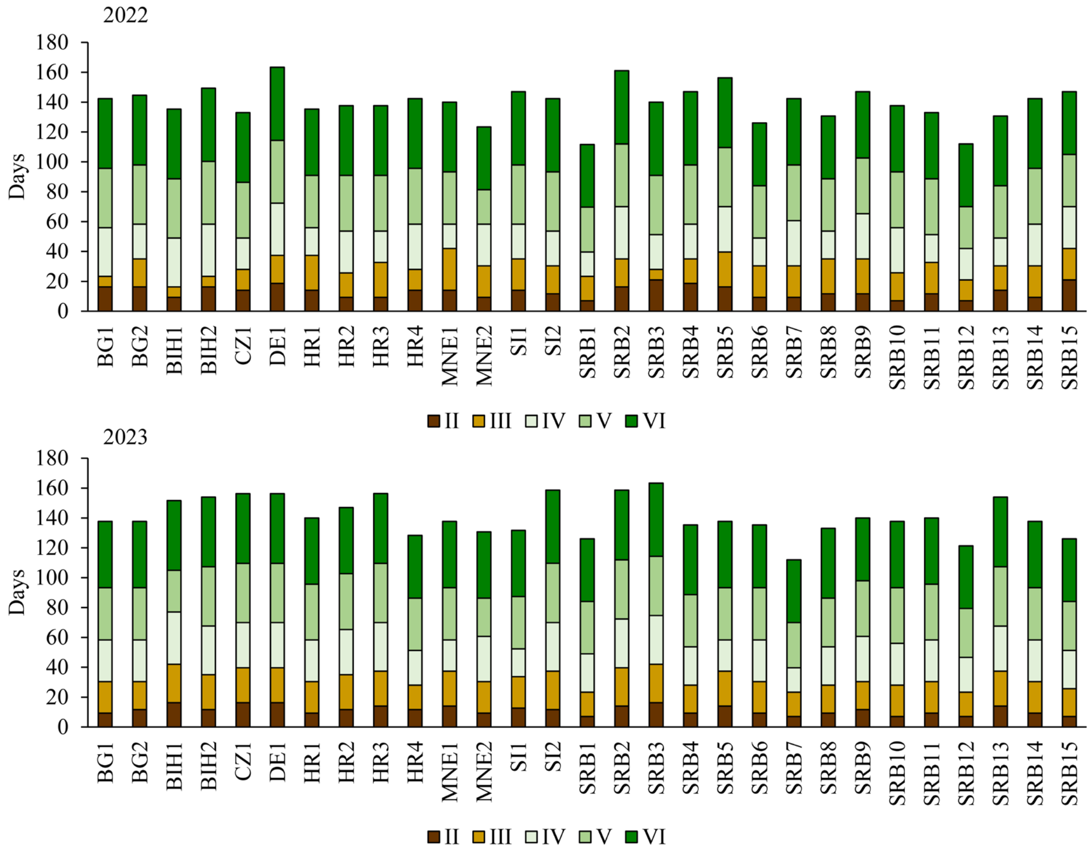

Figure 3 Duration of leafing phenophases (days) in 29 European beech (*Fagus sylvatica*) provenances during two successive growing seasons, 2022 and 2023.

Interannual Variations

Seasonal comparisons revealed the following average durations: phenophase II 13.0 days (2022) vs. 11.3 days (2023); phenophase III 17.9 days (2022) vs. 21.2 days (2023); phenophase IV 25.5 days (2022) vs. 27.7 days (2023); phenophase V 36.9 days (2022) vs. 35.7 days (2023); phenophase VI 45.9 days (2022) vs. 44.8 days (2023). ANOVA results indicated a statistically significant difference between years only for phenophase III ($p < 0.05$).

Correlation Analysis

The analysis revealed no statistically significant correlation between phenophase durations and elevation of the seed collection sites or with mean annual temperature and annual precipitation ($p > 0.05$). Latitude showed weak but statistically significant positive correlations with phenophases II, V, and VI, while longitude exhibited weak but statistically significant negative correlations with the same phenophases ($p < 0.05$). In all cases, correlation coefficients were below 0.4, confirming that geographic gradients exert only a minor influence on the timing and duration of leafing phenophases.

DISCUSSION

The onset and duration of growth and reproductive phenophases in European beech are shaped by the interplay between genetic variation and ecological factors, particularly temperature, photoperiod, and moisture availability (Varela and Valdiviesso 2011, Thiel et al. 2014, Skvareninová et al. 2024). In this study considerable variability was observed among provenances; however, no consistent geographic pattern emerged. Environmental variables of the seed origin sites (elevation, mean annual temperature, and annual precipitation) did not significantly explain phenophase durations. This aligns with findings by Vogel (2022), who emphasized that short-term climatic conditions immediately preceding phenological events, such as temperature in the previous 2–3 months and precipitation in the previous 1–2 months, are stronger drivers than mean climatic parameters of the origin sites. These results are contrast to some extent with those of Robson et al. (2013), who reported that phenological traits in beech are segregated according to the location and elevation of provenance origin, particularly at the species' southern range margin.

Interannual differences between 2022 and 2023 further underscore the strong impact of short-term climatic variability on phenological development. In 2023, warmer spring temperatures combined with higher precipitation accelerated leaf emergence and shortened the duration of early phenophases. Previous research on *Fagus sylvatica* confirms that early leaf-out under limited soil water availability reduces hydraulic conductivity and constrains photosynthetic performance, supporting the assumption that early-leafing provenances are more vulnerable to dry conditions (Gebauer et al. 2020). By contrast, cooler conditions in early 2023 prolonged the duration of early phenophases, especially of phenophase III, and led to more synchronized responses among provenances. Statistical analyses confirmed that phenophase III was significantly affected by year-to-year climatic variation. These findings are consistent with broader European studies (Raffard et al. 2022), which demonstrate that even modest shifts in spring temperature can disrupt leafing synchrony and alter phenophase length.

A clear distinction was observed between early- and late-leafing provenances, with important implications for adaptive strategies. Provenances such as CZ1, DE1, SRB2, and SRB3 consistently exhibited late leafing, particularly in phenophase III (green leaf emergence), thereby reducing exposure to low temperatures during sensitive developmental stages (Menzel et al. 2015, Flynn and Wolkovich 2018, Malyshev et al. 2022). In contrast, early-leafing provenances such as SRB12, MNE2, and SRB1 were more vulnerable to frost due to earlier bud break and underdeveloped foliage. On fertile and moisture-rich sites, however, early-leafing provenances may enhance productivity through increased leaf area index, carbon assimilation, and biomass accumulation (Myneni et al. 1997, Meier and Leuschner 2008, Scartazza et al. 2016, Tumpa et al. 2022). Late-leafing provenances, by contrast, provide greater resistance to abiotic stress and phenological stability under less favorable environments (Aertsen et al. 2014). In conclusion, selecting provenances requires the balancing of growth and stress tolerance, with careful attention to habitat suitability for successful reforestation (Gömöry and Paule 2011, Memišević Hodžić and Ballian 2021b, Vukmirović et al. 2024, Vidaković et al. 2025).

Genetic studies in European beech have demonstrated substantial intrapopulation variability and a genetic basis for phenological differences (Kraj and Sztorc 2009, Meger et al. 2021), including early and late leafing. At the same time, research on phenotypic plasticity shows that local growing conditions, particularly temperature and precipitation in the months preceding phenophases, often exert a stronger influence than the climatic parameters of the seed origin (Unterholzner et al. 2024). Similar results from common-garden trials in Southeastern Europe confirm that provenance differences reflect both inherited genetic variation and the modifying effects of local environments (Bogunović et al. 2020). Our findings, which reveal variability without a consistent geographic pattern, can therefore be interpreted through this combined effect of genetic inheritance and local environmental conditions.

In addition to European beech, several economically important members of the Fagaceae family, such as sweet chestnut (*Castanea sativa* Mill.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and pedunculate oak (*Q. robur* L.), exhibit substantial variation in morphological and functional traits depending on local growth conditions (Brushi et al. 2003; Denéchère et al. 2021; Popović et al. 2021, 2024; Tumpa et al. 2021; Sever et al. 2022; Memišević Hodžić et al. 2024). These studies indicate that both morphological traits (e.g., leaf size, specific leaf area) and functional traits (e.g., photosynthetic capacity, water-use efficiency) are strongly influenced by environmental gradients such as temperature, soil moisture, and light availability. This broader evidence emphasizes the importance of considering multiple Fagaceae species when investigating adaptive strategies and managing forest resources.

Building on these findings, further research should expand beyond spring phenology to include autumnal phases, particularly leaf senescence, which plays a crucial role in determining the total length of the growing season and the ecological performance of different provenances. A more complete phenological profile would enhance our understanding of adaptive strategies and inform provenance selection under changing climatic conditions. Recent advances in remote sensing technologies, such as UAVs and satellite imagery, offer scalable and precise tools for real-time monitoring of phenophases, facilitating the integration of phenological data into reforestation planning and long-term forest management (Ciocîrlan et al. 2022, Wang et al. 2024). Incorporating a diverse set of provenances – ranging from early to late leafing types – into restoration programs increases the likelihood of successful adaptation across heterogeneous environments and provides a valuable framework for further molecular and genetic studies. The identification and selection of phenologically resilient provenances, particularly those demonstrating local adaptation and tolerance to climatic stressors, should be prioritized as a central strategy in forest conservation and improvement under ongoing climate change (Ivanković et al. 2011; Čehulić et al. 2019, 2023; Antonucci et al. 2021; Sperlich et al. 2024).

CONCLUSION

This study provides the first assessment of leafing phenology in the juvenile phase of 29 European beech provenances from Southeastern and Central Europe. The results reveal significant variability in the timing and duration of leafing phenophases, reflecting both genetic differentiation and climatic responsiveness. These traits offer practical value for adaptive forest management since early leafing may reduce disease risk, while late leafing may enhance frost avoidance and phenological stability.

The observed patterns suggest that phenologically resilient provenances can be strategically selected to improve the health and productivity of beech ecosystems under changing environmental conditions. Continued monitoring of the same provenances at later developmental stages will enable deeper insights into ontogenetic variability and long-term adaptation potential.

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