

Non-native drought-resistant species withstand winter cold and spring frost in Central Europe

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ABSTRACT

Assisted migration of drought-resistant species represents an increasingly important strategy in forest management to mitigate the effects of climate change in Central Europe. However, their ecophysiology remains poorly understood, particularly regarding frost tolerance, limiting our ability to predict their establishment potential. Using a forest plantation established in 2012 at 658 m a.s.l. in Switzerland, we assessed winter frost hardiness and the risk of late spring frost in drought-resistant non-native tree species (*Fagus orientalis*, *Tilia tomentosa*, *Abies bornmuelleriana*, and *Cedrus libani*) and compared them with phylogenetically related native species (*Fagus sylvatica*, *Quercus petraea*, *Tilia platyphyllos*, and *Abies alba*). We measured lethal temperature thresholds (LT_{max}) for frost damage in buds and leaves, and evaluated phenological timing in relation to historical frost probability. Contrary to expectations, non-native species exhibited frost hardiness comparable to native species, with no significant differences in LT_{max} values. As our study was conducted during the relatively mild winter of 2024–2025, the estimated frost hardiness may underestimate their full acclimation potential under colder conditions. The lack of consistent differences between native and non-native origins suggests that phenotypic plasticity and seasonal acclimation outweigh genetic differentiation. Frost probability analyses indicated a low risk of lethal frost temperatures during leaf emergence for non-native broadleaved species, while native *F. sylvatica* and *Q. petraea* were more likely to be affected by late frost. Although the two *Tilia* species were first to leaf out, they showed low vulnerability to late frost. Our findings suggest that frost tolerance is currently not a limiting factor for the establishment of the tested drought-resistant non-native species in Central Europe. However, their ability to acclimate to abrupt cold fronts remains unknown and may be critical for predicting susceptibility to sudden frost events. Future management practices should consider increasing phenological diversity through the use of multiple species provenances to enhance species suitability for climate-adaptive forest management.

1. Introduction

The human-aided shift of species from one location to another has long been practiced by foresters to increase timber production or to grow more resistant species compared to the native population (Frischbier et al., 2019; Isaac-Renton et al., 2014; Palik et al., 2022; Schober, 1959), or by conservation biologists to preserve threatened species (Williams and Dumroese, 2013). In recent decades, assisted migration, defined as the translocation of species outside their current range (Vitt et al., 2010), has been increasingly recognized as a potential climate change adaptation strategy, as natural processes such as tree acclimation, genetic adaptation, and species range shifts may not be

sufficient to keep pace with the rapid rate of climate change (Aitken et al., 2008; Vitasse et al., 2021). Given that a mismatch between current local climatic conditions and the climatic optima of local tree species has already emerged, assisted migration can facilitate the expansion of non-native tree species better suited to future local climatic conditions. Despite some intrinsic risks involved (e.g. the introduction of potential invasive species and pathogens, or outbreeding depression following hybridization with native species (Grummer et al., 2022)), this mitigation strategy has been found to be appropriate for certain species and settings (Vitt et al., 2010). Assisted migration typically targets species originating from regions where the current climate resembles the projected future conditions of the target habitat (Aitken et al., 2008; Aitken

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and Bemmels, 2016; Aitken and Whitlock, 2013). Therefore, candidate species from warmer and drought-prone regions represent a valuable opportunity (Güney et al., 2015; Imal et al., 2024; Richter et al., 2012). The effectiveness of assisted migration in counteracting native-species decline depends on in-depth knowledge of candidate species and their ability to withstand climate stressors at the destination site. To ensure ecologically sound and sustainable introductions, a priori evaluations should be carried out within plantation networks and extend beyond survival and growth, incorporating a broader set of ecological, functional, and physiological traits.

Recently, multiple studies have assessed the current and future suitability of native and non-native species in warmer climatic scenarios, including *Fagus sylvatica* (Fang and Lechowicz, 2006) and *Fagus orientalis* (Mellert and Šeho, 2022), *Larix occidentalis* (Rehfeldt and Jaquish, 2010), *Pseudotsuga menziesii* (Isaac-Renton et al., 2014), and other relevant species for forest management (Dyderski et al., 2018). While considerable attention has been given to soil properties, precipitation regimes, drought indices, climatic averages, and growing season parameters, winter temperature extremes and late spring frosts have received only minor attention regarding the adaptability of these species. Minimum winter and spring temperatures, however, have been identified as key environmental factors shaping the distribution range of tree species (Baranger et al., 2024; Kollas et al., 2014; Kreyling et al., 2012; Lenz et al., 2013; Sakai and Weiser, 1973). Therefore, gaining knowledge of species-specific maximum frost resistance during winter is critical to improve species distribution models, particularly for non-native species that may serve as candidates for assisted migration and are often understudied.

In temperate climates, trees overcome winter conditions by entering a state of dormancy, during which metabolic and developmental activities are suspended (Sakai and Weiser, 1973). All tree organs undergo distinct hardening processes to withstand harsh winter temperatures and reduce the risk of damage. Deciduous species drop their leaves, and evergreen species have evolved mechanisms to protect the photosynthetic apparatus against freezing (Demmig-Adams and Adams, 2017; D'Odorico et al., 2020). While roots are also protected by soil and litter (Bigras and Colombo, 2001), and the tree trunk by bark (Sakai, 1960), buds containing the apical meristem and leaf primordia remain the most vulnerable portion of woody plants during winter. Tree buds undergo a series of temperature-driven biochemical and biophysical changes that result in a seasonal evolution in their cold hardiness (Kreyling et al., 2015; North and Kovaleski, 2024; Weiser, 1970). For instance, buds can reach frost tolerance by entering a supercooled state followed by progressive dehydration (Sakai, 1960), allowing species from high latitudes to reach freezing resistance as low as -70°C (Sakai, 1960). However, frost risk is not determined solely by cold hardiness, but also by phenology, which governs the exposure of sensitive tissues to freezing events. During the hardening process in buds, water migrates from the cells to the extracellular spaces between the bud scales, where it freezes, creating an ice barrier (Ishikawa and Sakai, 1982). In other species, intracellular water migrates to the apoplast during controlled dehydration, and freezes extracellularly without causing cellular damage (Bigras and Colombo, 2001). Additionally, the accumulation of cryoprotective substances, such as oligosaccharides and proteins, acts as protective agents for cellular membranes against the effects of ice crystals (Cox and Stushnoff, 2001; Kuprian et al., 2017; Sakai and Larcher, 1987). In *Alnus*, Sakai (1960) observed that, inside the buds, hydrophobic substances are deposited on the leaves' surface to prevent ice nucleation. Anatomical properties and bud architecture also contribute to species-specific cold hardiness by creating an impermeable barrier with scales, or by being impregnated with lipophilic substances (Kuprian et al., 2017; Neuner et al., 2019; Pisek, 1958).

In this context, phenology plays a key role in mediating frost risk, particularly the timing of budburst (Lenz et al., 2013). Some recent studies have pointed out that cold acclimation is tightly linked to dormancy depth and therefore influences budburst timing (Kovaleski,

2022; Kovaleski et al., 2018; North et al., 2024), yet different species lose their cold hardiness at different rates depending on the dormancy depth and their responsiveness to environmental cues (North et al., 2024). This variation in hardiness loss becomes critical as spring approaches. Once a species-specific chilling requirement is met, buds become sensitive to warm temperatures and progressively lose their freezing resistance, reaching the minimum at the time of leaf emergence (North et al., 2024; Sakai, 1960). Cold tolerance during leaf-out is therefore one of the most relevant factors determining the survival of new tissues and has been suggested to determine the elevation and latitudinal limits of broadleaved species (Kollas et al., 2014; Körner et al., 2016). Species-specific variability in phenological timing among coexisting species results from the trade-off between resource acquisition and protection against unfavourable conditions (Caffarra and Donnelly, 2011). Despite being more prone to experiencing late frost, early flushing species have developed greater freezing resistance of emerging leaves and can therefore benefit from greater resource availability such as water and light (Capioli et al., 2025; Fabiani et al., 2022; Meinzer et al., 2001). Because phenology is a highly plastic trait (Vitasse et al., 2010), allowing species to adjust their developmental timing to environmental cues, climate warming is likely to influence species unevenly, thereby amplifying existing interspecific contrasts in spring development (Capioli et al., 2025). In the Northern Hemisphere, climate change is leading to an earlier start of spring phenological events such as blooming or leaf-out (Bertin, 2008; Chamberlain et al., 2021; Piao et al., 2019). However, species phenological responses to warming vary considerably (Vitasse et al., 2009). While for some species, warmer winters can promote an earlier budburst and ultimately expose tree leaves to greater risk of late frost, other species may experience little shift due to insufficient chilling which increases the required heat accumulation to budburst (Cannell and Smith, 1986; Chamberlain et al., 2021; Lange et al., 2016). Therefore, depending on species-specific chilling requirements, an increase in winter temperature could delay or offset the expected advance of leaf-out timing due to spring warming. Species with lower chilling requirements (e.g. *Quercus petraea*) are expected to advance their spring phenology more strongly under warming and thus may be more exposed to late spring frost injury compared to species with higher chilling requirements (e.g. *Fagus sylvatica* and *Tilia platyphyllos*) or those more sensitive to the photoperiod (Kramer and Kozlowski, 1979).

While European native-species have been extensively studied, information on non-native species originating from warmer climates remains limited. To assess their potential as candidates for assisted migration, we need to better understand their susceptibility to frost and their timing of leaf-out related to climate. We used a forest plantation established in 2012 in Switzerland at 658 m a.s.l., comprising the non-native species *Fagus orientalis* Lipsky, *Tilia tomentosa* Moench, *Abies bornmuelleriana* Mattf., *Cedrus libani* A. Rich., with *Quercus petraea* (Matt.) Liebl as a reference native species. These species were selected from regions where current climatic conditions resemble the projected future climate of Central Europe, and thus considered potential candidates under warmer and drier scenarios (Schmiedinger et al., 2009). Despite their ecological and economic relevance (Schmiedinger et al., 2009), key traits such as frost resistance and spring phenology remain poorly understood, and potential maladaptation to cold winters and frost at our latitude could undermine their suitability. Combining this field setting with controlled freezing experiments (down to -80°C), we aim to address the following research questions: (i) to what extent can buds and leaves of non-native species originating from drought-prone regions withstand severe frosts compared to phylogenetically related species? and (ii) do drought-resistant non-native species leaf-out earlier and are they therefore more exposed to late spring frosts than native species? Additional sampling of co-occurring native species (*Fagus sylvatica*, *Tilia platyphyllos*, and *Abies alba*) in the forest surrounding the plantation allowed direct comparison.

Here, we hypothesize that (i) native species exhibit greater frost

hardiness compared to the non-native counterparts due to local adaptation to Central European winter conditions, and that (ii) non-native species exhibit earlier phenological timing in response to spring warming, allowing them to take advantage of the favorable growing conditions but potentially exposing them to frost.

2. Materials and methods

2.1. Study site and environmental monitoring

The study site is located in Mutrux (46°52'44" N, 6°44'21" E), on a southeast-facing slope of the Jura mountains, on the northwestern side of Lake Neuchâtel (Switzerland) (Fig. 1). The site lies at an elevation of 658 m a.s.l. on glacier moraine deposits. It is characterized by a long-term mean annual temperature of 9.3°C and annual precipitation ranging from 955 to 1655 mm with an average of 1253 mm per year (1990–2023). The study site consists of a 13-year-old forest plantation comprising five non-native species (*Fagus orientalis* Lipsky, *Tilia tomentosa* Moench, *Cedrus libani* A. Rich., *Abies bornmuelleriana* Mattf., and a native one (*Quercus petraea* (Matt.) Liebl.). The plantation follows a block design with three replicate blocks per species. These species were selected based on climatic variables relevant for future projections in Central Europe, including mean annual temperature, mean minimum temperature in January, and precipitation regimes (Schmiedinger et al., 2009). The studied non-native species originate from regions spanning southeastern Europe, northern Turkey, and the eastern Mediterranean. The distribution range of *F. orientalis* extends from southeastern Balkans to the Caucasus and northern Turkey; *T. tomentosa* occurs from southeastern Europe to western Turkey; *C. libani* is distributed across the eastern Mediterranean mountains; and *A. bornmuelleriana* - often treated as a subspecies of *A. nordmanniana* in some taxonomic frameworks (Litkowiec et al., 2021) - originates from northwestern Anatolia. The origin of the seed material is reported in Table S1. For further details on the selection process, plantation design and survival rates, we refer to Schmiedinger et al. (2009), Frischbier et al. (2019), and Glatthorn et al. (2024). Long-term (1982–2012) mean minimum temperature in January, mean maximum temperature in August, and summer precipitation were obtained for each seed source location using the ERA5-Land

reanalysis dataset (Hersbach et al., 2023), accessed via the Open-Meteo Historical Weather API (Zippenfenig, 2023) at the native 0.1° × 0.1° spatial resolution (Table S1). The studied plantation is surrounded by a mixed mature forest dominated by *F. sylvatica*, with some individuals exceeding 100-years of age.

A new meteorological station was installed in an open area within the plantation on 15 June 2024 (Fig. 1). It records air temperature (T, °C) and relative humidity (RH, %) at 1-minute intervals. Soil water potential (ψ , kPa) is also measured a few meters away from the meteo station at depths of 10 and 40 cm. An older meteorological station, located at ca. 150 m from the new one, has been operating since 2018. It records air temperature (T, °C) and relative humidity (RH, %) at the same temporal resolution. For long-term (period: 1930–2023) daily maximum, minimum and mean temperature we used interpolated climate data provided by MeteoSwiss (Federal Office of Meteorology and Climatology), processed by the Land Change Science Group at the Swiss Federal Research Institute. The long-term average temperature (1930–2023) is 3.2°C during the dormant season (1 October – 31 March) and 14.1°C during the calendar-based growing season (1 April – 30 September). Cumulative precipitation over the same period averaged 553.7 mm during the dormant season and 602.6 mm during the growing season. We used the Mann-Kendall test to assess trends in annual minimum temperatures (McLeod, 2011). To assess the severity of winter conditions experienced by the plantation relative to the long-term climate record, we identified, for each day of the year, the lowest minimum temperature recorded since the establishment of the plantation (2013–2025) and compared it with the corresponding lowest minimum temperature in the historical record (1930–2025). We assessed the growing start, end, and duration of the temperature-based growing season using the vegperiod R package (Nuske, 2022) following the ETCCDI definition (ETCCDI, 2009). With this method, the temperature-based growing season period is defined as the number of days between the first period of at least 6 consecutive days with a daily mean temperature >5°C, and the first period of 6 days with a daily mean temperature <5°C. This method is widely used in climate studies (ETCCDI, 2009). We also calculated, for every year, the last frost date before summer, defined as the last day on which daily minimum temperature fell below 0°C. To detect temporal trends in the start, end,

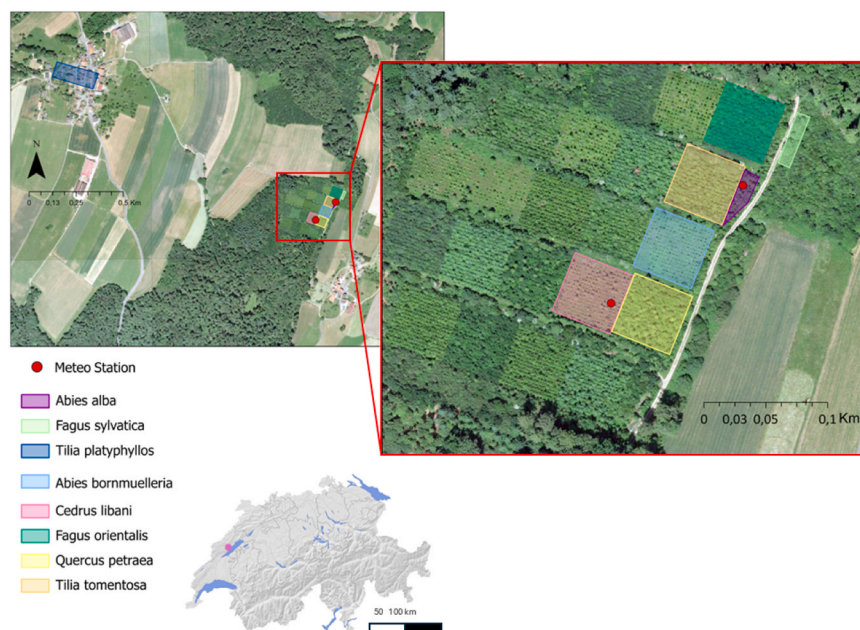


Fig. 1. Experimental design including the overview of the plantation, location of the sampled species, and meteo stations. The four non-native species and *Quercus petraea* belong to the plantation, while the corresponding native species are sampled in the close proximity of the plantation. *Tilia platyphyllos* was sampled in Mutrux village.

duration of the growing season, and late frost occurrence we used Mann-Kendall tests, and the Theil-Sen slope estimator to quantify the rate of change (Vitasse et al., 2025).

2.2. Frost hardness

2.2.1. Buds

We evaluated the freezing tolerance of eight tree species (*F. orientalis*, *F. sylvatica*, *T. tomentosa*, *T. platyphyllos*, *A. bornmuelleriana*, *A. alba*, *C. libani*, and *Q. petraea*) with the relative electrolyte leakage method (REL) in two sampling campaigns in early and mid-winter 2025. The REL method allows the assessment of frost damage in tissues exposed to a range of freezing temperatures by measuring the release of electrolytes resulting from cell membrane damage caused by temperature stress (Flint, 1972). The conductivity of the solution is therefore proportional to the damage caused by frost. We followed the methodology of (Repo and Ryyppö, 2008) with minor modifications detailed below. Since frost resistance is influenced by the temperatures to which the buds were exposed (Lenz et al., 2016), we provide details on the average temperatures during the 2-, 3-, 7-, 14-, and 30-days preceding sampling in Table S2. On January 21st and February 4th, we sampled at least 20 branches from the upper canopy of five individuals for each species with a 7 m-high pole pruner. Trees in the plantation (*F. orientalis*, *T. tomentosa*, *Q. petraea*, *A. bornmuelleriana*, and *C. libani*) were established at a fixed spacing of 2×2 m, ensuring comparable stand density across species. Although tree height varied among species due to differences in growth rates, branches were consistently sampled from the sun-exposed upper canopy to minimize potential effects of canopy structure and light availability on bud development. *F. sylvatica*, *T. platyphyllos*, and *A. alba* were sampled from the surrounding forest (Fig. 1). Although detailed information on the stand characteristics of the surrounding forest is not available, the sampled trees exhibited comparable heights to those in the plantation, suggesting a similar age class. After cutting the sun-exposed upper branches, they were packed into bags and kept at 0–4°C during transport to the WSL laboratory, where they were stored overnight at 4°C. The following morning, we cut the branches into approximately 10 cm-long twigs and placed twigs bearing at least 5 buds in paper bags. We then grouped the bags according to their respective target temperature level, wrapped them in aluminium foil to buffer thermal fluctuations during the freezing test and kept them at 4°C until they were simultaneously placed in seven computer-controlled freezers, each set to a different freezing temperature level (–8, –15, –20, –25, –30, –35, –45°C). A positive control (4°C), and a negative control (–80°C) were included. The samples assigned to the –8, –15, –20, –25, –30, and –35°C treatments were treated by the computer-controlled freezers of the Botanical Institute of the University of Basel. Temperatures were monitored using Pt-100 sensors inserted into the sample packages (see Lenz et al., 2013 for details). Meanwhile, samples for the –45°C treatment were processed at WSL, where temperature was recorded with a datalogger (HOBO TidbiT MX2203 Data Logger; Onset Computer Corp., Cape Cod, MA, USA). Positive and negative controls were processed at WSL. The freezing process began within 12 h after sampling. The samples were cooled at a rate of 5°C h^{–1} and, once the target temperature was reached, they were kept at that temperature for 1 h and 30 min. For further calculations, we used the actual temperature reached by each freezer (see Table S3). Subsequently, they were thawed at the same rate of 5°C h^{–1} until 4°C. After freezing treatment, we selected at least 5 buds per species and treatment, cut them in half longitudinally with a razor blade, and placed them in ca. 7 mL of deionized water. The samples were incubated for 12 h at room temperature (approximately 21°C) on a shaking plate. We quantified the electrical conductivity (that is, electrolyte leakage) by measuring the conductivity of the solution at 22°C (Mettler Toledo Seven Multi S47) and after autoclaving the samples at 121°C for 20 min to simulate total tissue damage. We normalized the raw electrolyte leakage at each temperature into a relative electrolyte leakage (REL):

$$REL = \frac{L_t}{L_k} \quad \text{Eq. (1)}$$

where L_t is the conductivity after the freezing treatment and L_k is the conductivity of the same sample after autoclaving. Following Lim et al. (1998) we normalized the REL between 0 and 100 for each individual, based on the minimum and maximum REL values measured. We assessed the lethal temperatures (LT) damaging 20%, 50%, 80% of the samples (LT₂₀, LT₅₀, LT₈₀) using a nonlinear Gompertz model for electrolyte leakage data:

$$y_t = 100 \cdot e^{-be^{-kt}} \quad \text{Eq. (2)}$$

where y_t is the REL at temperature t (freezing temperature), e is Euler's number and b and k are parameters. The Gompertz function has been found to be the best fit for leakage data (Kovaleski and Grossman, 2021; Lenz et al., 2013) and allows to extract more biologically realistic critical values. We also calculated the LT_{max} corresponding to the temperature at which the rate of increase in freezing-induced damage is maximum. The temperature range between LT₂₀ and LT₈₀ provides an estimate of rate of damage, based on the temperature increments used and the species' susceptibility. We calculated LT values for each sampled individual tree separately.

Because frost tolerance can vary relatively fast depending on climate conditions, we exposed half of the material sampled in January to a hardening treatment in order to assess the maximum frost resistance of the buds (Fig. 2). Samples were placed in a freezer at –4.5°C for 3 days under dark conditions. Afterwards, we assessed the frost resistance of buds as described in Section 2.2.1.

2.2.2. Recurrence of lethal temperatures

In order to estimate the return period of species-specific LT_{max}, we used generalized extreme value distributions (GEVs) (Coles, 2001). The annual minimum temperatures were transformed into absolute values and fitted with a GEV frequency distribution by maximum likelihood (Gilleland, 2016). By modeling the tail of the distribution, the GEV provides estimates of the probability of exceeding critical thresholds, thus enabling the risk assessment of rare events beyond long-term records (Kollas et al., 2014). For each species, we calculated the return period in years of its least negative LT_{max} using the fitted GEV distribution. We applied the parametric bootstrap procedure, and the 5th and 95th percentiles of the resulting distributions were used as lower and upper confidence intervals. Following Kollas et al. (2014), return periods longer than 100 years were not considered biologically relevant because the reproductive cycles are generally completed within this time frame.

2.2.3. Leaves

Conifer needles can typically withstand extremely low temperatures without being affected by cold (Angelcheva et al., 2014; Strimbeck and Schaberg, 2009); therefore, we evaluated the lethal temperature (LT) of leaves only in broadleaved species. Although both *Tilia* species are early-flushing species compared to the *Quercus* and *Fagus* species considered in this study, the intraindividual phenological variability within each species plot allowed us to sample all species on 11 April 2025 using the same phenological stage. Using a pole pruner, we sampled the upper canopy to collect buds at phenological stage 3 (i.e. young leaves are unfolding; see Section 2.3.1). Upon return to the lab, for each sampled tree, we distributed the buds in paper bags, grouping them by temperature treatment and one control at 4°C and one negative control at –80°C (Fig. 2). All samples were initially stored overnight at a constant temperature of 4°C. The following morning, we programmed the freezer to progressively reach the target temperatures (–2, –5, –8, –12, and –16 °C) with a constant cooling rate of 5°C h^{–1}. Once the target temperature was reached, it was maintained for 120 min. After this, the corresponding group of samples was removed from the freezer

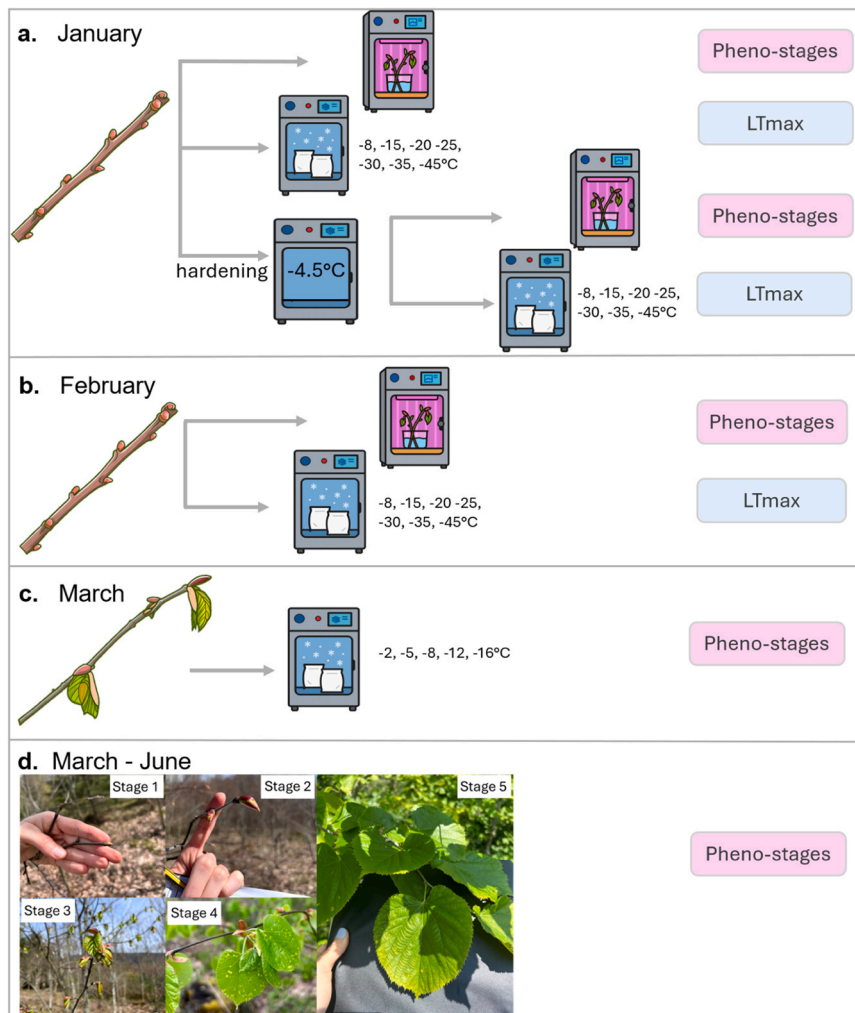


Fig. 2. Schematic of the experimental approach used in the study to assess the lethal temperatures (LT_{max}) and the dormancy depth after sampling in the field, and after an hardening treatment at -4.5°C in January (a), and in February (b). We also assessed the lethal temperatures for broadleaved species in March (c). The phenological monitoring was assessed by placing the twig in growth chambers, while the LT_{max} were assessed by placing the twig in freezers at different temperatures. We also monitored the phenological stages in the field from March to June in 2024 and 2025 (d). The icons of this figure were created with ChatGPT.

and transferred to the 4°C fridge, where they remained for at least two hours before visual assessment of tissue damage. The temperature inside the freezer was continuously monitored using a data logger (HOBO TidbiT MX2203 Data Logger; Onset Computer Corp., Cape Cod, MA, USA) placed among the samples. Discoloration, flaccid, and water-soaked appearance are typical and clear indicators of frost injury (Sakai and Larcher, 1987; Steponkus, 1984): after freezing and thawing, cell content leaks from the cell membranes and oxidizes leading to a change in color associated in some species with a strong odor. Visual assessment of freezing injury has been successfully employed in multiple studies (Lenz et al., 2013; Till, 1956; Vitasse et al., 2014), due to the ease of identifying freezing injury. Frost damage on *Q. petraea* and the two *Fagus* was characterized by a marked darkening of the leaf tissue, whereas in the two *Tilia* the most evident symptom was leaf flaccidity and a transparent appearance (Till, 1956). In all species, frost damage was accompanied by a noticeable odor. For each sample, which included at least two buds producing multiple leaves, we counted the number of living leaves relative to the total number of leaves. We assessed the lethal temperatures (LT) causing the damage to 20%, 50%, 80% of the leaves (LT_{20} , LT_{50} , LT_{80}) using a logistic model as follows:

$$y = \frac{A}{1 + e^{-k(x-x_0)}} \quad \text{Eq. (3)}$$

We selected the logistic model over the Gompertz model based on

lower AIC values and visual inspection of the residual plots. For each day of the year (DOY), we calculated the probability that the air temperature (T_{min}) would fall below the species-specific critical threshold (LT_{50}) using the daily minimum temperature time series from 1930 to 2025. We considered the phenological window from Stage 1–3 for each species, as defined in the following section. For each species, the probabilities were computed as the proportion of years in which T_{min} was below LT_{50} on a given DOY.

2.3. Phenological monitoring

2.3.1. Dormancy depth

To assess the dormancy depth (i.e. time to budburst under forcing conditions), we selected one twig from each tree sampled in January and February, as well as after the hardening treatment, and placed them in a growth chamber at 20°C with a 12-hour light-dark cycle. We monitored phenological development every 4 days for the first two months after sampling and then weekly until end of May. Bud development was assessed following the six-stage categorical scale proposed by Vitasse (2013): stage 0, the bud is dormant with no bud development; stage 1, the bud begins to swell or elongate, and the outermost scale is no longer intact in conifers; stage 2, budburst occurs, with bud scales opening and leaves becoming partially visible; stage 3, leaf-out, leaves are fully

emerged from the bud but still folded, crinkled, or pendant in broad-leaved species, and forming a paintbrush-like structure in conifers; stage 4, at least one leaf is fully unfolded in broadleaves, or shoot elongation has started in conifers (Fig. S3); stage 5, the leaves and needles are fully unfolded.

We calculated the DOY at which at least 50% of the buds on each twig reached stage 1. To compare the budburst timing between sampling dates (i.e., January, January-hardening, February), we calculated, for each individual, the cumulative growing degree days (GDD) required to reach stage 1 from January 1st, thereby integrating field with growth chamber temperatures. We focused on stage 1 because it represents the first signal of phenological activity and was reached by all twigs. Indeed, limited nutrient availability in twigs may prevent progression to later stages across all species (Baumgarten et al., 2021). The GDD for each day was calculated as follows:

$$\text{GDD} = \left(\frac{T_{\max} + T_{\min}}{2} \right) - T_{\text{base}} \quad \text{Eq. (4)}$$

where $T_{\max}$ and $T_{\min}$ are the daily maximum and minimum, respectively, and T_{base} is set to 5°C. GDD is equal to zero when the average daily temperature is below the base temperature.

2.3.2. Phenological development at field conditions

We monitored bud development for five individuals per plot (15 individuals per species in total) for the plantation species (*F. orientalis*, *T. platyphyllos*, *Q. petraea*, *A. bornmuelleriana*, and *C. libani*) in 2024 and 2025, and for five individuals for the native species (*F. sylvatica*, *T. tomentosa*, *A. alba*) in 2025. Observations were conducted weekly to biweekly in spring, from March to June, by the same observer, until the last individual had fully unfolded its leaves (Fig. S3). We followed the same categorical scale as in the previous section. We examined the bulk of the foliage and recorded the proportion of buds that had reached the most advanced stage, considering a stage reached when at least 50% of the canopy had reached that stage. We then calculated DOY at which each phenological stage was reached using linear interpolation, assuming that a stage was reached when 50% of the buds had reached that stage. To assess stages that occurred in between two monitoring dates, we estimated the day of the year (DOY) by linear interpolation (Baumgarten et al., 2021). To describe the seasonal dynamics of bud development, we applied the same non-linear Gompertz model (Eq. 2), as previously described for REL data, with y representing the phenological stage recorded in the field and x representing the day of the year (DOY), separately for each species and year. From the fitted curve, we derived the inflection point, corresponding to the DOY at which the phenological development rate is maximal and the phase duration, as the time span between the early and late phases of development estimated as the difference in DOY between 10% and 90% of the development. To compare the timing of the budburst in the growth chambers with that of the trees in the field, we also calculated the cumulated GDD required to reach Stage 1.

2.4. Data analysis

All statistical analyses were performed with RStudio (RStudio Team 2023) and the figures were created with ggplot2 (Wickham, 2009). To compare species-specific LT values across sampling dates and hardening treatment, we fitted separate Bayesian linear models, and performed pairwise comparisons between sampling campaigns within each species using posterior estimates and 95% credible intervals. We complemented these models with an ANOVA and Tukey's HSD post hoc tests ($p \leq 0.05$) to explore differences in LT between species, separately for buds and leaves. We analyzed variation in LTmax using Bayesian linear mixed models (GLMMs) implemented in the brms package (Bürkner, 2017). The response variable (LT_{max}) was modelled as a function of origin (native vs non-native), genus (*Abies*, *Fagus*, *Tilia*), and their interaction.

This approach allows us to test whether the effect of origin differed within each genus. Species identity was added as a random effect to account for species-level variation within genera, with different individual trees nested within species also included as random effects. *Q. petraea* and *C. libani* were excluded from this analysis because they lack a corresponding species within the same genus, preventing assessment of genus-level effects.

3. Results

3.1. Environmental conditions

The temperature followed a typical seasonal pattern, with minimum temperatures occurring at the beginning of January in both years, progressively increasing throughout spring, and peaking during the summer months (Fig. 3). Average monthly winter temperatures were similar between years in January (2.16 ± 4.6 in 2024 and 2.2 ± 4.1 2025) and March (7.3 ± 3.7 in 2024 and 6.6 ± 4.0 2025), but February was markedly colder in 2025 (6.5 ± 2.5 in 2024 and 2.2 ± 3.1 2025; Table S4). These differences resulted in substantially higher accumulated GDD in 2024 than in 2025, particularly from March onwards (Table S4). Minimum temperatures recorded in 2024 (-8.2°C) and 2025 (-6.1°C) were well above historical extremes, confirming that recent winters have been relatively mild (Fig. 3; $R^2 = 0.074$, $p = 0.008$). Over the long-term record (1930–2023), the lowest minimum temperature was -21.2°C (1956 and 1985), while the highest minimum was -5.6°C (1974), with a long-term average of -11.9°C . Since plantation establishment, winter minimum temperatures have remained consistently above this long-term average, except in 2013 (-13.2°C). Daily minimum temperatures since plantation establishment were generally higher than historical values until late February (Fig. 3, S1), indicating a general increase in the minimum temperature in the past decade. This pattern is supported by a significant upward trend in minimum temperatures (Mann-Kendall test, $p\text{-value} = 0.001$), corresponding to an increase of 0.37°C per decade. However, from March onward, differences between recent and historical temperatures diminished (Fig. 3, S1), with occasional negative values, indicating that cold events can still occur during the late winter-early spring transition. Over the last 95 years, the growing season duration increased significantly (Mann-Kendall $\tau = 0.27$, $p < 0.0001$), with an estimated increase of 3.6 days per decade (Fig. S2). This trend was driven by both an earlier start (Mann-Kendall $\tau = -0.19$, $p < 0.05$) and a later end (Mann-Kendall $\tau = 0.2$, $p < 0.05$) of the growing season (Fig. S2). The late frost events also advanced over time (Mann-Kendall $\tau = -0.14$, $p < 0.04$), with the last frost date occurring 1.09 days earlier every decade.

3.2. Frost hardness

3.2.1. Buds

The average LT_{max} across all samples (January, February and hardening treatment) was $-21.2 \pm 4.0^\circ\text{C}$ for *A. alba* and $-24.7 \pm 4.3^\circ\text{C}$ for *A. bornmuelleriana*, $-17.6 \pm 1.2^\circ\text{C}$ for *F. sylvatica* and $-18.3 \pm 2.0^\circ\text{C}$ for *F. orientalis*, $-27.9 \pm 7.2^\circ\text{C}$ for *T. platyphyllos* and $-28.1 \pm 6.4^\circ\text{C}$ for *T. tomentosa*, $-17.4 \pm 2.0^\circ\text{C}$ for *Q. petraea*, and $-17.1 \pm 1.2^\circ\text{C}$ for *C. libani* (Fabiani et al., 2026)(Table S6). The highest LT_{max} value (-16.5°C) was recorded for *Q. petraea* in February, while the lowest (-32.7°C) was observed in *T. platyphyllos* in January before hardening treatment (Table 1). LT_{max} was consistently less negative than LT₅₀ for all species (Table S6). Contrary to expectations, the hardening treatment did not result in consistent changes in LT_{max} across all species (Fig. S4). Significant effects of hardening or sampling time were detected only for *A. alba* and *T. platyphyllos* (Fig. S4). In *A. alba*, buds were significantly more frost hardy in January and after the hardening treatment compared to February under field conditions. In *T. platyphyllos*, the hardening treatment in January enhanced the frost resistance compared

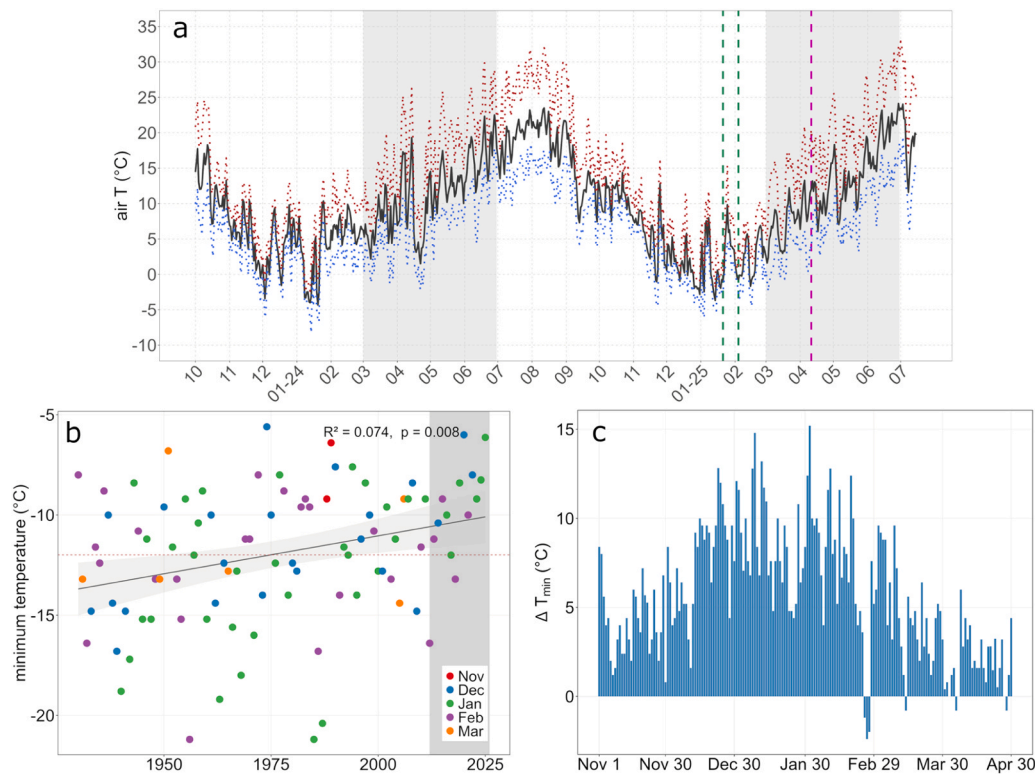


Fig. 3. Minimum, maximum, and average air temperatures (°C) recorded at the meteo station located within the plantation (subfigure a) from October 2024 to July 2025. The x-axis represents calendar dates (day-month). Grey shaded areas indicate the phenological monitoring periods (1 March - 30 June), green vertical lines show the dates of bud sampling for cold hardiness assessment and magenta lines indicate leaf sampling (a). In subfigure b, annual absolute minimum temperatures recorded between 1930 and 2025 are shown colored based on the month (Nov-Mar). The x-axis represents the year of observation. The horizontal dotted line indicates the long-term average of annual absolute minimum temperatures over the period 1930–2025. In subfigure c, bars represent the difference (Fig. S1) between the lowest daily minimum temperature recorded since the establishment of the plantation (2013–2025) and the corresponding minimum in the full historical record (1930–2025). The x-axis shows calendar dates (day-month). Positive values indicate that recent minimum temperatures are warmer than the historical minimum for that day.

Table 1

Lethal temperature values (LT_{max}) of buds with standard errors (SE). Return period with confidence interval [CI upper and lower].

$LT_{max} \pm SD$	January	Jan - hardening	February	Return time [CI]
<i>Fagus sylvatica</i>	-17.2 ± 1.2	-18.1 ± 0.9	-17.6 ± 1.6	22 [13–38]
<i>Fagus orientalis</i>	-18.8 ± 2.3	-18.3 ± 2.3	-18.3 ± 1.4	33 [16–59]
<i>Quercus petraea</i>	-17.7 ± 1.3	-17.1 ± 1.0	-16.5 ± 1.0	18 [11–30]
<i>Tilia tomentosa</i>	-28.7 ± 5.8	-24.8 ± 6.0	-30.2 ± 7.1	> 100
<i>Tilia platyphyllos</i>	-32.7 ± 8.0	-22.7 ± 3.6	-28.6 ± 6.7	> 100
<i>Abies alba</i>	-23.8 ± 2.0	-22.7 ± 2.8	-17.1 ± 3.6	> 100
<i>Abies bornmuelleriana</i>	-22.9 ± 4.8	-25.8 ± 2.8	-25.3 ± 5.3	> 100
<i>Cedrus libani</i>	-21.8 ± 1.4	-21.9 ± 2.6	-19.7 ± 2.3	> 100

to both January and February field conditions. The Bayesian GLMM indicated substantial variation among species (SD = 4.5, 95% CrI: 0.17–15.34) and among individuals within species (SD = 1.9, 95% CrI: 0.25–5.28). However, fixed-effect estimates for origin, genus and their interaction were uncertain, indicating no consistent effect of origin on LT_{max} (Table 2).

Based on LT_{max} values, *T. platyphyllos*, *T. tomentosa*, *A. alba*,

Table 2

Posterior estimates from the Bayesian GLMM assessing the effects of origin (native vs non-native), genus (based on the two species analyzed for each of *Abies*, *Fagus*, and *Tilia*), and their interaction on (LT_{max}). Factors were coded using sum-to-zero contrasts (contr.sum), so the intercept represents the grand mean, and each coefficient represents a deviation from that mean. Because of the sum-to-zero constraint, only $k - 1$ coefficients are shown for each factor (the omitted level is the negative sum of the others). Estimates are shown as posterior means with 95% credible intervals; effects are considered supported when the 95% CI does not include zero.

Parameter	Estimate	SE	CI Lower	CI Upper
Intercept (grand mean)	-22.37	1.82	-26.07	-18.19
Origin (deviation; level = non-native)	0.50	2.56	-5.22	6.12
Genus (deviation; level = <i>Abies</i>)	-0.64	3.75	-8.85	6.77
Genus (deviation; level = <i>Fagus</i>)	4.89	3.62	-2.50	12.74
Genus (deviation; level = <i>Tilia</i>)	-4.25	3.47	-11.42	3.32
Origin $\times$ Genus: (deviation; non-native $\times$ <i>Abies</i>)	0.87	3.71	-7.18	7.79
Origin $\times$ Genus: (deviation; non-native $\times$ <i>Fagus</i>)	0.06	3.52	-6.66	7.83
Origin $\times$ Genus: (deviation; non-native $\times$ <i>Tilia</i>)	-0.93	3.70	-8.64	6.31

A. bornmuelleriana, and *C. libani* showed return periods of lethal temperatures exceeding 100 years, indicating a negligible risk of experiencing critical temperature events (Table 1). In contrast, *Q. petraea* showed the shortest return period (18 years), followed by *F. sylvatica*, and *F. orientalis* (33 years; Table 1).

3.2.2. Leaves

We found a significant effect of species on frost hardiness (ANOVA, $F = 6.6$, $p = 0.001$), but non-native broadleaved species were not more frost-sensitive than the native phylogenetically related species (hereafter counterparts). *Q. petraea* showed the highest LT_{50} ($-4.6^{\circ}C$; Table 3, S5), indicating high susceptibility to frost. No significant differences were detected among the two *Fagus* and *Tilia* species (Fig. S5). The two *Fagus* and *T. platyphyllos* showed similar leaf freezing resistance, whereas *T. tomentosa* displayed the highest resistance (-8.9 ± 1.5 ; Table 3). Based on long-term temperature series (1930–2025), probability analysis revealed species-specific differences in frost risk during the leaf development (Fig. 6). *F. orientalis*, *T. platyphyllos*, and *T. tomentosa* showed low frost risk, with a minimal probability of reaching their LT_{50} thresholds during stages 1–3 (Fig. 6). In contrast, *F. sylvatica* and *Q. petraea* showed higher susceptibility, with *Q. petraea* exhibiting the highest and most recurrent frost risk among species (Fig. 6).

3.3. Winter and spring phenological development

3.3.1. Dormancy depth in the growth chamber

All species required higher GDD under growth chamber conditions than in the field to initiate dormancy release (Fig. S6), with some species requiring substantially greater thermal accumulation (e.g., *A. bornmuelleriana* and *C. libani*) than others (e.g., *F. orientalis* and *T. platyphyllos*). Twigs also showed greater variability in GDD requirements compared to the field observations, as indicated by the broader scatter around the reference line (Fig. S6), suggesting that controlled conditions may not fully capture natural phenological dynamics. Sampling time effects on GDD requirements varied among species and showed no consistent pattern. In *T. tomentosa*, January field-sampled twigs exhibited the highest GDD requirements, likely indicating incomplete chilling fulfillment, whereas *T. platyphyllos* showed more uniform responses. Similarly, *F. sylvatica* displayed relatively consistent GDD requirements, while *F. orientalis* showed delayed budburst following hardening. In *Q. petraea*, February-sampled twigs required lower cumulated GDD than January samples. In contrast, *C. libani* showed relatively uniform responses in January, whereas the hardening treatment resulted in high intra-individual variability. We observed high mortality in twigs of both *A. bornmuelleriana* and *A. alba* in the growth chamber, likely due to a progressive desiccation caused by the presence of old leaves that kept transpiring (Fig. S6).

3.3.2. Under field conditions

Bud break varied among species, occurring between late March and mid-May. *T. tomentosa* (DOY 81 ± 8 and 83 ± 4 in 2024 and 2025) and *C. libani* (DOY 85 ± 15 and 88 ± 7 in 2024 and 2025) were the earliest among broadleaves and conifers, respectively (Table 4). Both *Abies* showed the latest budburst (DOY 125 ± 9 and 125 ± 6 in *A. bornmuelleriana* and *A. alba*, respectively; Table 4). Conifers generally showed higher intra-individual variability in bud development than broadleaves in both years (Table 4), resulting in a longer phenological

development period (time between 10% and 90% bud development; see Section 2.3.2, Fig. S7). Comparison between 2024 and 2025 did not reveal consistent interannual patterns for the plantation species (*F. orientalis*, *Q. petraea*, *T. platyphyllos*, *A. bornmuelleriana*, and *C. libani*). While *F. orientalis*, *Q. petraea*, and *A. bornmuelleriana* showed earlier budburst in 2025, *T. tomentosa* and *C. libani* reached stage 1 earlier in 2024 (Table 4). Overall, non-native species showed an earlier onset of phenological development compared to native species (Fig. S7), including an earlier occurrence of the maximum growth rate (inflection point of the fitted curve; Fig. S7, Fig. 5). Stage 3 - the stage we sampled in spring 2025 to assess the frost resistance of young leaves (see Section 2.2.3) - was also reached earlier in the non-native species than in native counterparts (Table 4).

4. Discussion

4.1. Non-native species withstand European cold winter

Frost hardiness, like other phenotypic traits, is influenced by both genetic factors and environmental conditions (Hofmann et al., 2015). In our study, we found that drought-resistant non-native species are not currently threatened by current Central European winter temperatures (Table 1, Fig. 4). The absence of significant differences in frost resistance between native and non-native species (Table 2) suggests that frost tolerance is primarily driven by phenotypic plasticity and seasonal cold acclimation rather than genetic differentiation. This interpretation is consistent with previous studies showing that short-term plastic responses to local climate often exceed inter-population differences in freezing resistance (Flint, 1972; Lenz et al., 2016; Li et al., 2003).

When comparing LT_{max} values among native broadleaved species, we observed a different ranking from previous literature. In our study, *T. platyphyllos* was the most frost hardy ($-29.2^{\circ}C$), followed by *F. sylvatica* ($-17.4^{\circ}C$) and *Q. petraea* ($-17.4^{\circ}C$, Table 1), whereas earlier work (Till, 1956) reported *F. sylvatica* as the most frost resistant ($-29^{\circ}C$), followed by *Q. petraea* ($-24^{\circ}C$) and *T. platyphyllos* ($-25^{\circ}C$). These discrepancies likely reflect differences in acclimation conditions and methodology. Within the genus *Fagus*, *F. orientalis* showed frost hardiness comparable to *F. sylvatica*, despite occupying warmer and drier habitats. This similarity may partly reflect the origin of the seed material used in this study (Table S1; Schmiedinger et al., 2009), where populations exhibit strong genetic similarity to *F. sylvatica* (Kurz et al., 2023) and experience relatively low winter temperatures (Table S1). This supports previous literature carried out between twenty provenances of *F. sylvatica* highlighting that frost hardiness does not always directly reflect the climate of origin (Hofmann et al., 2015). A similar pattern was observed in *Tilia*. Overall, the genus *Tilia* showed the highest frost hardiness among the broadleaved species. Despite contrasting ecological niches, *T. platyphyllos* (occurring in mesophilous central European forests up to 1800 m a.s.l.) and *T. tomentosa* (occurring in thermophilous forests (Radoglou et al., 2009)) showed similar LT values under the same environmental conditions. This suggests that winter minimum temperature is not the primary factor limiting the distribution of this genus, with soil properties and resource availability likely playing a stronger role (Radoglou et al., 2009). Previous studies have also reported very low LT values for *Tilia* species (Kreyling et al., 2015; Larter et al., 2025). Likewise, in Till (1956), *T. cordata* displayed very negative LT_{max} , surpassed only by *Alnus glutinosa* and *Betula pendula*. During the cutting of the buds of the two *Tilia*, we observed the excretion of a jelly substance that gave the solution a jelly consistency. A similar excretion has been documented in the buds of *Alnus*, *Betula* and *Populus*, and is presumed to enhance freezing resistance by protecting developing tissues (Neuner et al., 2019).

Differences between our LT estimates and previous studies carried out on the same species (Kreyling et al., 2015; Larter et al., 2025; Till, 1956) are likely explained by variation in cold acclimation conditions, as frost hardiness is a dynamic trait influenced by past short-term

Table 3
Lethal temperature values (LT) at 80%, 50% and 20% damage of leaf material (stage 3) with standard deviation (SD).

Species	$LT_{80} \pm SD$	$LT_{50} \pm SD$	$LT_{20} \pm SD$
<i>Fagus sylvatica</i>	-6.3 ± 1.1^{ab}	-5.9 ± 0.9^{ab}	-5.4 ± 0.9^{ab}
<i>Fagus orientalis</i>	-8.1 ± 1.4^{bc}	-7.1 ± 0.9^{abc}	-6.4 ± 3.2^{ab}
<i>Quercus petraea</i>	-4.8 ± 1.7^a	-4.6 ± 1.6^a	-4.4 ± 1.6^a
<i>Tilia tomentosa</i>	-9.2 ± 1.5^c	-8.9 ± 1.5^c	-8.6 ± 1.5^b
<i>Tilia platyphyllos</i>	-7.7 ± 0.2^{bc}	-7.4 ± 0.2^{bc}	-7.1 ± 0.1^{ab}

Superscript letters indicate significant differences among species for each lethal temperature (LT) (Tukey HSD, $p < 0.05$).

Table 4

Day of the year (DOY) when the different phenological stages were reached in 2024 and 2025. (Stage 1 = bud swelling, Stage 2 = budburst, Stage 3 = leaf-out, Stage 4 = laves fully visible). For 2024, phenological observations were limited to species in the plantation.

Species	Stage 1		Stage 2		Stage 3		Stage 4	
	2024	2025	2024	2025	2024	2025	2024	2025
<i>Fagus sylvatica</i>	-	97 ± 4	-	109 ± 1	-	119 ± 1	-	129 ± 0.2
<i>Fagus orientalis</i>	99 ± 2	93 ± 3	101 ± 2	103 ± 3	104 ± 2	115 ± 2	112 ± 5	127 ± 1
<i>Quercus petraea</i>	97 ± 2	93 ± 1	101 ± 2	102 ± 2	108 ± 5	115 ± 2	121 ± 5	127 ± 0.5
<i>Tilia tomentosa</i>	81 ± 8	83 ± 4	96 ± 2	94 ± 2	100 ± 1	101 ± 3	111 ± 7	122 ± 2
<i>Tilia platyphyllos</i>	-	90 ± 4	-	96 ± 4	-	105 ± 7	-	122 ± 4
<i>Abies alba</i>	-	126 ± 6	-	136 ± 5	-	145 ± 4	-	156 ± 1
<i>Abies bornmuelleriana</i>	130 ± 7	125 ± 9	137 ± 7	133 ± 7	143 ± 6	140 ± 7	150 ± 5	151 ± 6
<i>Cedrus libani</i>	85 ± 15	88 ± 7	98 ± 4	101 ± 7	111 ± 8	119 ± 9	136 ± 8	139 ± 7

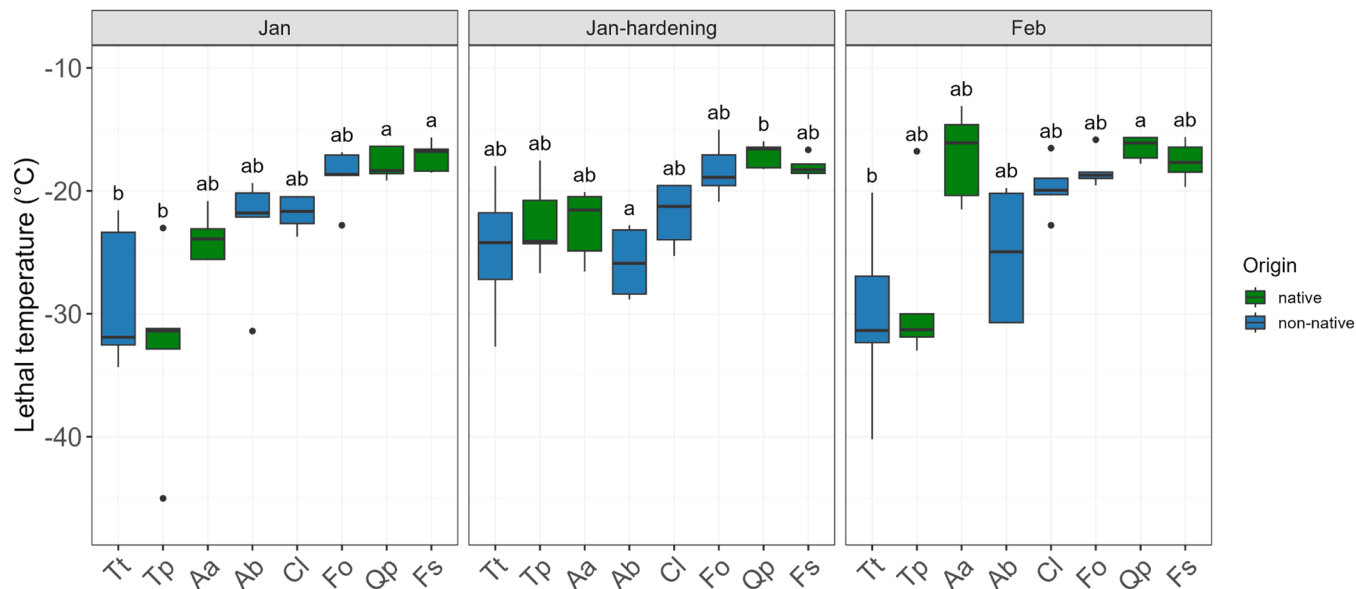


Fig. 4. Species-specific freezing resistance (LT_{max} , °C) of buds assessed on the buds in January and February and after a hardening treatment in January. Within each treatment, differences among species are tested with the Kruskal-Wallis test. Different letters above boxes indicate significantly different groups according to post-hoc Dunn's test ($p < 0.05$). Green boxplot represent native species (Qp= *Quercus petraea*, Fs= *Fagus sylvatica*, Aa= *Abies alba*, Tp= *Tilia platyphyllos*) and blue boxplot non-native species (Cl= *Cedrus libani*, Ab= *Abies bornmuelleriana*, Fo= *Fagus orientalis*, Tt= *Tilia tomentosa*).

environmental conditions (Baranger et al., 2024; Lenz et al., 2016; Sakai and Weiser, 1973). For example, Kreyling et al. (2015) reported lower LT values for *Q. petraea*, *F. sylvatica*, and *F. orientalis* ($LT_{50} = -32.8$, -31.2 , -31.9 °C) compared to our estimates. However, in their study the trees were exposed to daily minimum temperatures as low as -20 °C for multiple days prior to sampling, which likely enhanced their cold acclimation. In contrast, the conditions at our study site were considerably milder, with an average minimum temperature of only -3.0 °C during the week preceding our January sampling campaign (Table S2). Similarly, our hardening treatment may have induced only partial acclimation, preventing individuals from reaching their maximum frost hardiness. Therefore, differences in frost hardiness across studies may originate from differences in bud acclimation status at the time of sampling (Lenz et al., 2013), methodological approaches, experimental protocol (Gömöry et al., 2010; Lenz et al., 2013; Palacio et al., 2015) and the statistical model chosen to fit the electrolyte leakage data (Kovaleski and Grossman, 2021). In addition, intraspecific variation in frost tolerance and phenology exists across populations and provenances (Hofmann et al., 2015; Jensen and Deans, 2004; Montwé et al., 2018), which should be considered when extrapolating results beyond the specific provenance context of this study.

The comparable frost hardiness of *A. bornmuelleriana* (mean $LT_{max} = -24.7$ °C) and *A. alba* (mean $LT_{max} = -21.2$ °C, Table S6) may reflect similar ecological adaptations. Although *A. bornmuelleriana* originates from the Mediterranean region around the Black Sea, it occurs at high

elevations (from 900 to 2000 m a.s.l.; (Alizoti et al., 2011; Liu, 1971), where the combination of limited precipitation regimes and cold winter temperatures make this species both drought and frost resistant (Frischbier et al., 2019). The seed source used in this study originates from 1400 m a.s.l (Schmiedinger et al., 2009) (Table S1), supporting its observed high frost tolerance. To our knowledge, this is the first study to assess bud frost resistance of this species, demonstrating that this species has sufficient cold hardiness to withstand winter conditions in Switzerland, at least in the lowland. In contrast, *A. alba* has been more extensively studied (Kreyling et al., 2015; Strimbeck and Schaberg, 2009) due to its economic and ecological importance in European forests. Similarly, *C. libani* originates from drought-prone environments across a wide altitudinal range (from 800 up to 2400 m asl; (Imal et al., 2024)), where temperature can reach -31 °C (Messinger et al., 2015). Consistent with previous findings (Imal et al., 2024; Kreyling et al., 2015; Messinger et al., 2015), our results confirm that this species can tolerate frost events down to -21.8 °C under mild acclimation conditions (Table 1), which is well below the mean minimum temperature registered at the site origin of the seed material (Table S1). Evergreen species often experience drought and freezing simultaneously (Medeiros and Pockman, 2011), particularly during sunny winter days when frozen soil prevents water uptake while transpiration continues (Medeiros and Pockman, 2011). Both stressors share common physiological outcomes at the cellular and molecular level (Beck et al., 2007), by inducing progressive cellular dehydration which results in negative water tension

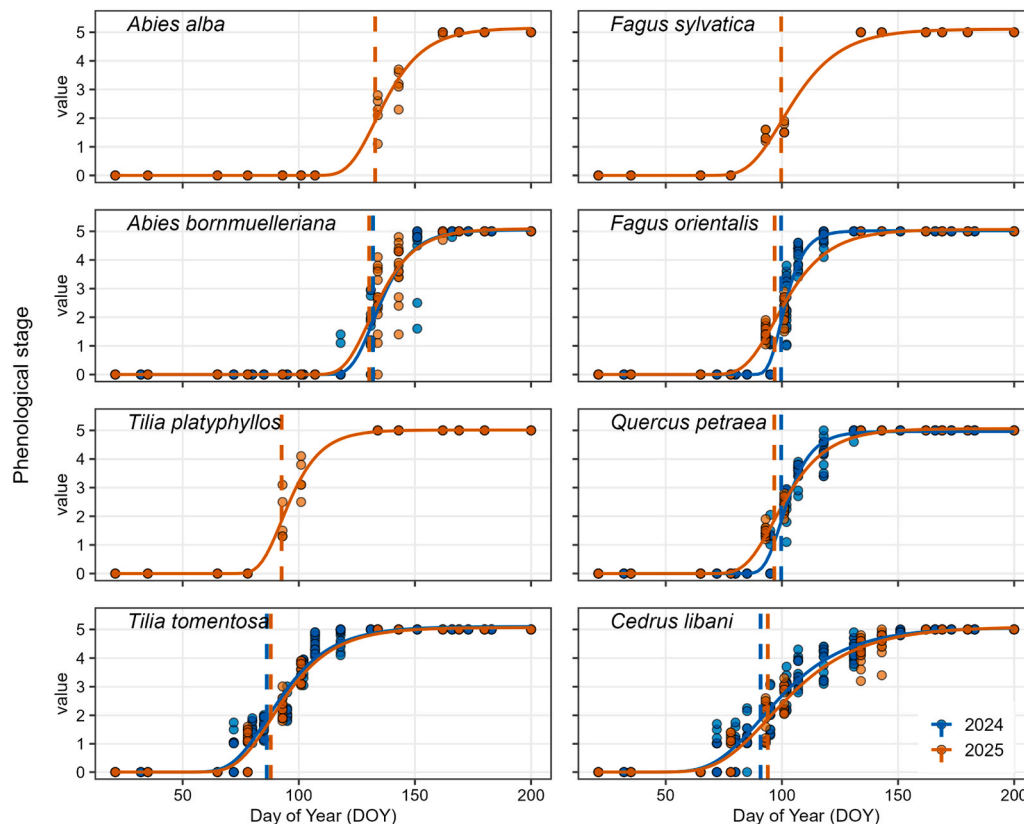


Fig. 5. Bud development progress from closed buds (stage 0) to unfolded leaves (stage 5) based on field observation in spring 2024 and 2025. Points represent the observations for each year, and lines represent the fitted Gompertz curve. Dotted vertical lines indicate the inflection point of the Gompertz curve for each species and year, in blue 2024 data and in orange 2025 data.

and accumulation of cellular solutes. This overlap may explain why drought-resistant species also exhibit frost tolerance comparable to that of native species. However, this relationship is not universal, as a recent meta-analysis found no consistent correlation between drought and frost resistance (Larter et al., 2025).

Since the establishment of the plantation, minimum winter temperatures have remained above species-specific LT_{max} thresholds (Fig. 3, Table 1), suggesting limited current risk of frost. However, historical records (1930–2025) indicate that critical temperature thresholds can occasionally be reached, particularly during late winter or early spring (Fig. 3), when cold hardiness declines. Frost risk therefore remains species-specific and depends on both climatic variability and acclimation dynamics (Till, 1956). Return period analyses further suggest that broadleaved species may be more frequently exposed to critical temperatures (Fig. 4), with *Q. petraea*, *F. sylvatica* and *F. orientalis* having the shortest return period. Future studies should complement the assessment of late-spring frost resistance with analyses of autumn and winter transition periods to improve our understanding of how species track - or potentially mismatch - local climatic regimes, and to better inform assisted migration and forest management strategies.

4.2. Genus determines the onset of budbreak more than species origin

Modelling studies investigating budburst timing under different climate scenarios have reported contrasting species-specific responses, including advances, delays, or no change (Lange et al., 2016; Smekal et al., 2025). While temperatures are increasing, photoperiod remains constant, which can limit the effects of warming on phenological advancement (Meng et al., 2021). The decoupling amplifies interspecific differences, as some species respond primarily to temperature, whereas others, such as *F. sylvatica*, are also strongly influenced by day length

(Basler and Körner, 2014; Vitasse and Basler, 2013). Early budburst and leaf-out increase exposure to late spring frost (Sakai and Larcher, 1987), and frost susceptible species therefore tend to leaf out later (Vitasse, Lenz, Hoch, et al., 2014). In our study, the earliest broadleaved species to leaf-out were *Tilia* (Table 4), which also showed the lowest LT_{50} values (-8.9 and -7.4, respectively; Table 3), consistent with previous literature (Vitasse, Lenz, Hoch, et al., 2014). However, late flushing does not necessarily guarantee protection against frost, as risk depends on the timing of frost events relative to sensitive developmental stages. At a second study site in eastern Bavaria (Germany), we observed frost damage in *C. libani* and *A. bornmuelleriana*, representing the earliest and latest flushing species, respectively (Table 4, Fig. S7). The damage was associated with late frost events occurring in May (Fig. S8). In contrast, no damage was observed in other species, as their phenological development had already ended and mature leaves are more frost resistant than emerging ones. These observations indicate that phenological timing alone does not guarantee frost avoidance. In particular, although *C. libani* flushes early, its slow and intra-individually variable development prolongs the period during which sensitive tissues are exposed, increasing vulnerability to late frost. Similarly, late-flushing species such as *A. bornmuelleriana* can also be affected if frost events coincide with their extended developmental phase (Fig. S7). A similar observation has been made by Kreyling et al. (2012), who found that earlier budburst in *F. sylvatica* did not lead to an increase in frost damage as leaves increase frost tolerance very rapidly after leaf-out. Consistent with Kurz et al. (2023), we found that *F. orientalis* flushed slightly earlier than *F. sylvatica* (Table 4, Fig. S7), and its leaves were more frost tolerant than those of the corresponding native species (Table 3). While no consistent differences were observed within genera, *Q. petraea* exhibited lower leaf frost hardiness compared to other broadleaved species (Fig. S5). Despite this, probability analyses indicate that *Q. petraea* can

tolerate occasional frost events during leaf development (Fig. 6), even near its LT_{50} . This tolerance may be explained by the species' bud architecture: approximately 40% of buds in *Q. petraea* remain quiescent (Harmer, 1992), providing a reservoir of dormant buds for resprouting quickly after frost or herbivory. These quiescent buds are usually referred to as secondary (Baumgarten et al., 2023; Heuret, 2003), and produce leaves that have been found to be more frost hardy than those from apical buds in *Q. petraea* (Liepe, 1993).

Under current conditions, only the native *Q. petraea* and *F. sylvatica* showed a non-negligible probability of late frost damage (Fig. 6). Kollas et al. (2014) already highlighted late frost sensitivity in *F. sylvatica*, *Q. petraea* and even *T. platyphyllos* up until May. However, their approach may have been particularly conservative, as they used LT estimates from Till (1956), which were less negative than the ones we measured at our study site. Consistent with broader observations across mid and high latitudes (Menzel et al., 2006), the onset of the climate-based growing season at our study site has advanced by approximately 3.6 days per decade over the past century (Fig. S2). This trend could become problematic if our species were to advance their phenological development at the same pace, thereby increasing their exposure risk to late spring frosts (Sakai and Larcher, 1987), especially if last frost events do not shift at the same pace. However, the phenology of late successional species is more often constrained by photoperiod than temperature (Caffarra and Donnelly, 2011; Körner and Basler, 2010), potentially limiting further advances. Predicting species-specific responses remains challenging, as the molecular and physiological mechanisms underlying dormancy release and bud break are not yet fully understood (Kovaleski, 2022). At our site, the low probability of air

temperature reaching lethal thresholds during leaf development in non-native species (Fig. 6) suggests that late spring frosts currently pose a low risk for these species. Given that spring frost is a key determinant of species distribution (Kollas et al., 2014; Körner et al., 2016), this finding supports their potential suitability under current conditions and potentially in regions of Central Europe with similar climatic regimes. The same non-native species are also being evaluated in other experimental sites in Germany (Frischbier et al., 2019; Glatthorn et al., 2024), where climatic regimes differ and late spring frosts may occur more frequently or reach critical temperature thresholds. This highlights the importance of long-term, multi-site monitoring to better assess frost vulnerability under changing climate conditions.

When evaluating dormancy release in growth chambers, high mortality in twigs of conifers limited our ability to interpret the results (Fig. S6). Nevertheless, across all species, twigs in growth chambers required higher cumulative GDD to reach budburst compared to trees in the field. This reflects the complex interaction of environmental drivers (Caffarra and Donnelly, 2011; Körner and Basler, 2010) as well as nutrient availability (Capioli et al., 2025). The higher GDD requirement in controlled conditions may also indicate incomplete chilling fulfilment (Baumgarten et al., 2021; North and Kovaleski, 2024). This was particularly evident in *T. tomentosa*, where twigs sampled in January required greater GDD to flush than those exposed to hardening or collected in February. The lack of natural temperature fluctuation, known to modulate dormancy release in the field (Kronenberg et al., 2021; Polgar and Primack, 2011) likely contributed to this pattern. Finally, limited carbohydrate reserves in excised twigs may constrain bud development, particularly in conifers such as *Abies*, where needle

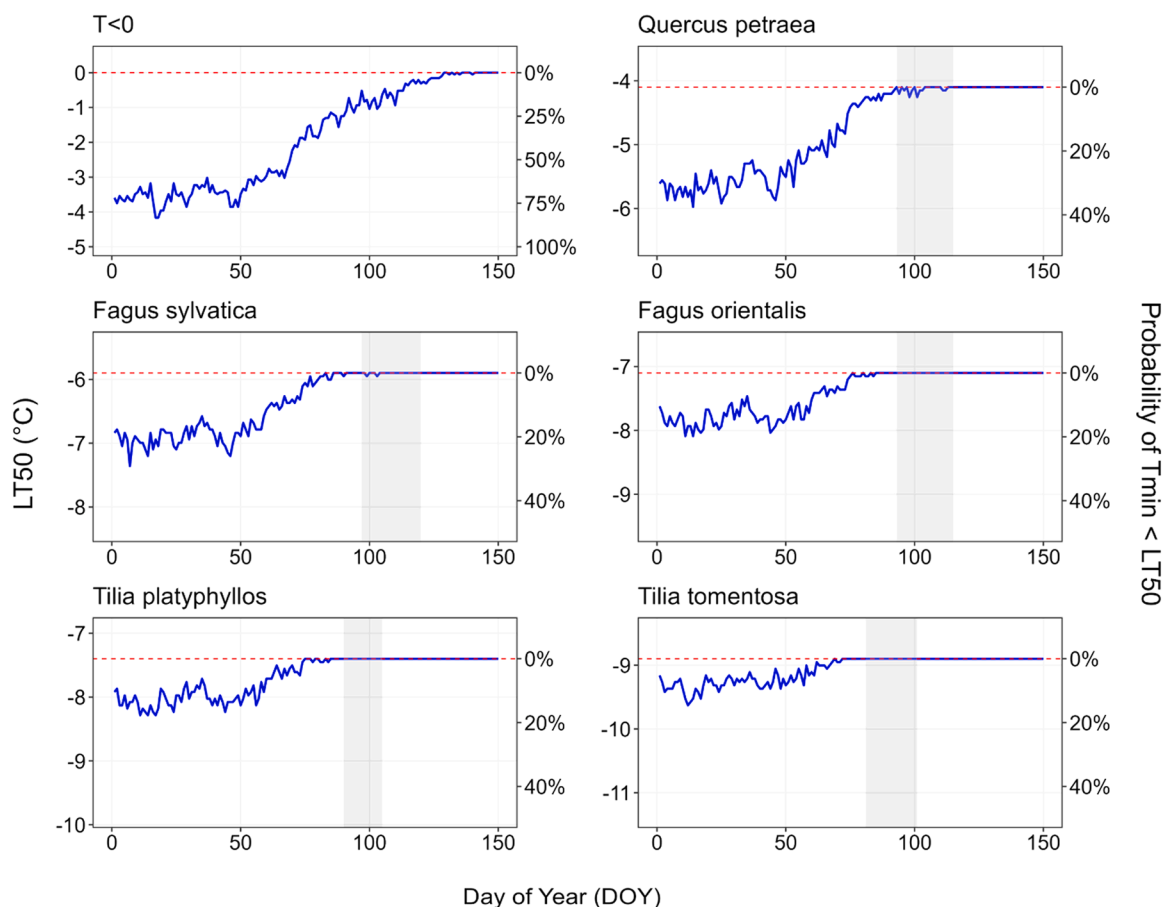


Fig. 6. Probability of minimum environmental temperature (T_{min} , °C) falling below the species-specific critical threshold (LT_{50}) of leaves. Red dashed lines indicate LT_{50} values for each species, while shaded grey areas represent the relevant phenological period (Stage 1–3) based on 2024 and 2025 field observations. Probabilities were calculated using daily temperature data from 1930 to 2025, and the secondary y-axis shows the corresponding probability in percentage. In the first plot is displayed the probability of the minimum daily temperature being lower than 0.

growth and shoot elongation require substantial energy reserves for tissue development (Heide, 1993).

5. Conclusion

Our study provides new insights into the frost tolerance of drought-resistant and previously understudied non-native tree species in Central Europe. Contrary to our initial hypothesis, non-native species exhibited frost hardness comparable to their phylogenetically related species, with no significant differences in lethal temperature values. This suggests that frost tolerance is primarily driven by phenotypic plasticity and seasonal cold acclimation rather than genetic differentiation linked to geographic origin. Phenological timing was relatively similar between native and non-native species; however, long-term observations are needed to confirm these patterns. We also show that non-native species have a low probability of experiencing lethal frost temperatures during leaf development at the study site. Our findings suggest that winter temperatures and late spring frosts are currently not limiting factors for drought-resistant non-native species (*Fagus orientalis*, *Tilia tomentosa*, *Abies bornmuelleriana*, and *Cedrus libani*) in Central Europe, supporting their potential role in climate-adaptive forest management strategies. However, to guarantee the success of these plantations, management practices should consider increasing phenological diversity through the use of multiple species provenances and establishing long-term monitoring to better capture site-specific frost risk.

CRediT authorship contribution statement

D'Odorico Petra: Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Yann Vitasse:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Ginevra Fabiani:** Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI in the manuscript preparation process

ChatGPT (OpenAI; model version 4) was used for the preparation of Fig. 2: we uploaded photographs of buds and growth chamber to ChatGPT, and prompted the tool to convert them into simplified schematic icons.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123788](https://doi.org/10.1016/j.foreco.2026.123788).

Data availability

The data used in this manuscript are made available on EnviDat at

the following doi: [10.16904/envi.dat.752](https://doi.org/10.16904/envi.dat.752)

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