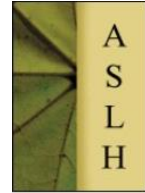




# Variation of Bud Phenology of East European Scots pine Provenances Confirms the Inherited Clinal Pattern of their Adaptation to Climate



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## ARTICLE INFO

## ABSTRACT

**Keywords:**  
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Phenology is a key bioindicator of climate change; however, the genetic and environmental drivers of phenological traits still remain poorly understood. The authors analyzed large-scale patterns of bud burst and bud set (i.e. of vegetation period length) in Eastern European Scots pine provenances to assess the influence of climatic factors and the role of inheritance in phenological adaptation. Phenological traits were correlated with climatic variables and modelled with linear transfer regression analyses using historical data from provenance experiments in Hungary. The results demonstrate that phenological traits of Scots pine populations exhibit a genetically determined clinal variation pattern and strong correlations between bud burst, bud set and temperature-related variables. The findings challenge opinions that emphasize plasticity in spring phenology and photoperiodic control of autumn growth cessation. The hypothesis of rapid plastic adaptation to changing climatic conditions is not supported by our results. The patterns of phenotypic diversity require a critical consideration in adaptive forest management strategies.

## TANULMÁNY INFÓ

## KIVONAT

**Kulcsszavak:**  
rügyfenológia  
növekedési szakasz  
genetikai változatosság  
plaszticitás  
támogatott migráció

**Kelet-európai erdeifenyő származások rügy-fenológiai változatossága megerősíti az éghajlati alkalmazkodás öröklődő klinális mintázatát.** A fenológia a klímaváltozás fontos bioindikátora, de a fenológiai tulajdonságokat meghatározó genetikai és környezeti hatások szerepe kevésbé tisztázott. A szerzők az erdeifenyő rügyfakadásának és rügyképzésének (vagyis vegetációs idejének) nagytérségi mintázatát vizsgálták Kelet-Európa térségében. A cél a klímateretők és a genetikai alkalmazkodás szerepének a feltárása volt. A vizsgálathoz egy magyar származási kísérlet egykori adatait használták fel. A fenológiai adatokat klimatikus változókkal korrelálták és lineáris transzfer egyenletekkel modellezték. Kimutatták az erdeifenyő populációk rügy-fenológiai adatainak genetikailag meghatározott, klinális változatosságát és szoros lineáris korrelációját a hőmérsékleti változókkal. Az eredmények kétségbe vonják azokat a véleményeket, amelyek szerint a fafajok rügyfakadási mintázatát jelentős mértékben a plaszticitás határozza meg, valamint hogy az őszi rügyképzés mintázata a fotoperiódussal van összefüggésben. Ugyancsak vitatható az a hipotézis is, amely szerint változó klímában a populációk plaszticitásuk révén hamar alkalmazkodnak. Az adaptív erdészeti kezelés stratégiájának kialakításában a fenotípusos változatosság figyelembevétele fontos szerepet kell kapjon.

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## 1 INTRODUCTION

Phenology governs the timing of transitions between dormancy and active growth for adaptation to recurring seasonal events. It plays a significant role in determining fitness, may affect competition, growth, carbon sequestration, and the functioning of the ecosystem. Changes in climate are a defining element of future ecological conditions. Climate warming influences tree phenology in boreal and temperate species, affecting their growing season (Morin et al., 2010; Way, 2011; Jing et al., 2021; Langvall – Ottosson Löfvenius, 2021). Phenology was the first widely used bioindicator of climate change. Phenological data are widely used to assess the response of trees and forests to climate change on local and global scales (Skulason et al., 2018; Montgomery et al., 2020; Risk et al., 2021; Camarero – Rubio-Cuadrado, 2025; Wu et al., 2025). The phenological responses of tree populations to climate change are considered insufficiently studied compared to growth (Aspalter et al., 2025).

Provenance tests of forest trees provide valuable information to assess the effect of environment and inheritance on phenotypes. Studies have identified parallel clines in phenology for many tree species, supporting the adaptation of these species to changing growing season conditions at the local level. The transfer to new environmental conditions can be interpreted as a simulation of climatic changes (Mátyás, 1994), allowing for the study of phenological responses (such as bud break, flowering, growth cessation, or dormancy) to assess the risk of damage (Dhar et al., 2015). Although the role of phenology may be critical to forecasting and climate mitigation, links between climate, phenology, and growth are not sufficiently understood. The literature contains conflicting evidence. Common garden studies have been conducted for over 250 years, but there is currently no holistic predictive model of clines between species and phenological events (Zeng – Wolkovich, 2024). Due to the enormous efforts and resources required for field experiments, it is not surprising that common garden studies of forest trees are often limited to traits directly relevant to forestry, such as growth rate, and overlook phenology.

Scots pine (*Pinus sylvestris* L.) is an economically and ecologically dominant tree species in Eastern European forests. Numerous studies have investigated the influence of climatic and weather factors on the growth, development, and survival of the species in this region (Meshkova, 2021; Waszak et al., 2021; Lebedev, 2023; Linkevičius et al., 2024; Lebedev – Dvoychenkov, 2025). Provenance trials indicate that Scots pine populations in the boreal zone exhibit high adaptive potential to climate change, while increased mortality is predicted at the southern edge of their distribution (Nakvasina – Prozherina, 2021; Parfenova et al., 2021; Mátyás et al., 2023; Lebedev – Mátyás, 2025). However, early investigations and tests found low variability and little differentiation in Scots pine phenology (Chmura et al., 2012; Memišević et al., 2023) due to regional approaches and less systematic sampling. The investigations also failed to address the large-scale phenological pattern of the species, especially in Eastern Europe.

This study covers most of the natural range for the species in Eastern Europe, based on a historical survey of bud phenology of provenances. The analysis aims to assess the large-scale phenological trait pattern of the species and the role of climatic factors governing it. The results are expected to contribute to the longer-term future growth and vitality of Scots pine in the region. The following key aspects were investigated: 1) the phenological variability pattern of Scots pine provenances at the study site; 2) the influence of climatic variables on phenological variation; 3) the relationship between climatic transfer distance of provenances and their bud set and bud burst phenology.

## 2 MATERIALS AND METHODS

### 2.1 Study site and tested provenances

The study location in Hungary lies outside the natural distribution of the species. Nevertheless, Scots pine was widely planted in monospecific plantations during the afforestation campaigns after the Second World War. Due to its location beyond the southern, xeric limits of the species, the site is a perfect “tolerance provocation” site for phenology responses.

The test site on brown podzolic soil is located in the Kámon Arboretum, Szombathely, Hungary (47.25°N, 16.61°E). The elevation of the site is 227 m asl. The climate is temperate continental, characterized by warm summers and moderately cold winters. In the climate period relevant for the investigations (1961–1990), the average annual temperature was 9.2°C, with means of -1.9°C in the coldest month and of 19.2°C in the warmest month. Mean annual precipitation was 651 mm, with the highest monthly rainfall occurring during the growing season. Overall, the soil and climate conditions were favorable for the growth of Scots pine.

This study used the results of a phenotypical survey of 31 Scots pine provenances from Eastern Europe, covering a latitudinal gradient from 47.2°N to 62.9°N, a longitudinal gradient from 16.5°E to 58.7°E, and an altitudinal range from 31 to 605 m asl. The seed lots were provided in 1975 by the VNIILM institute (Pushkino, Russia), where they were collected to establish the All-Union Provenance Test Network (Prokazin and Bogachev, 1975; Shutyaev – Giertych, 1997). The provenances originated from Russia (up to the Urals), Ukraine, Belarus, Latvia, Estonia, and Hungary, according to the present boundaries (*Table 1*). The seed lots were intended for parallel provenance tests in Hungary (Mátyás et al., 2023; Lebedev – Mátyás, 2025), and the surplus seeds were used for establishing a short-term phenology test.

The seeds were sown in the spring of 1976 and 1977. In 1978, the seedlings were outplanted in the Kámon Arboretum (Szombathely, Hungary) in a 0.5x1.0 m network, in unreplicated plots of 40 plants (Mátyás, 1981). The registration numbers of provenances correspond to the first publication of Shutyaev and Giertych (1997). The provenance test also contained several additional sources from Central Europe and the Mediterranean (including one provenance from Hungary), which were not part of the VNIILM experiment.

### 2.2 Phenological survey of provenances

The investigation of the phenotypical variation of populations included bud phenology, size, and winter discoloration of needles, juvenile growth, crown form, and needle cast infection tolerance. Adhering to the study’s basic aim, population-level bud burst, and set data were compared to determine the diversity pattern of phenology across East European populations. The plot averages were calculated from data of a minimum of 20 plants per plot.

Surveys to record bud burst were conducted weekly on 6-year-old seedlings in spring 1981. The survey date of April 10, 1981, was selected for analysis due to its best differentiating character among provenances. The average daily air temperature did not reach 15°C until this date, and the daily precipitation did not exceed 5 mm (*Figure 1*). Bud burst phenophases were recorded based on bud elongation. Depending on the development of the top bud of the plants, a score from 1 to 5 was assigned for each plant, where 1 is a closed, undeveloped bud; 5 is a green shoot without covering scales. Due to differences in survival, the first 20 plants of each provenance were scored and averaged.

The presence or absence of developed buds was recorded weekly. Per provenance one hundred nursery-grown seedlings, raised in Nisula containers, were scored. The characteristic date for bud set data was selected for September 6, 1976, on one-year-old seedlings. Bud formation progress was expressed by the percentage of one-year-old seedlings with fully

developed buds at the respective date. *Figure 2* shows the weather conditions for the vegetation season (mean daily temperature and precipitation).

### 2.3 Climate data and analysis

The data on phenology were analyzed decades later because the Scots pine provenance test project was suspended due to economic and political changes in both countries. Moreover, provenance location climatic data obtainable from advanced climate models were still unavailable when the surveys were conducted.

*Table 1. List of Scots pine provenances investigated (MAT – mean annual temperature, MAP – mean annual precipitation)*

No.	Location	Latitude, °N	Longitude, °E	Elevation, m asl	MAT, °C	MAP, mm
4	Plesetsk, Arkhangelsk Oblast	62.9	40.4	108	1.0	661
9	Totma, Vologda Oblast	60.0	43.0	126	2.2	651
15	Pryazha, Republic of Karelia	61.7	33.7	166	1.9	653
19	Lisino, Leningrad Oblast	60.0	30.4	31	4.7	658
22	Strugi Krasnye, Pskov Oblast	57.8	28.4	54	4.6	662
23	Kresttsy, Novgorod Oblast	58.3	32.5	67	4.0	683
24	Elva, Tartu County	58.2	26.5	98	4.9	657
25	Jelgava, Jelgava Municipality	56.5	25.2	79	5.6	667
28	Rasony, Vitsebsk Oblast	56.0	29.3	157	4.9	660
29	Lenino, Homel Oblast	52.2	31.7	154	6.5	613
35	Olevsk, Zhytomyr Oblast	50.4	27.7	226	7.1	623
37	Borisopil, Kyiv Oblast	50.2	32.2	116	8.0	565
38	Svesa, Sumy Oblast	52.0	34.0	163	6.1	673
39	Cherkasi, Cherkasy Oblast	49.6	32.0	96	8.2	566
40	Sloviansk, Donbas Region	48.8	37.6	64	8.4	520
43	Orekhovo-Zuyevo, Moskva Oblast	55.5	39.0	124	4.8	624
44	Kovrov, Vladimir Oblast	56.4	41.3	83	4.7	602
46	Pervomaysk, Nizhny Novgorod Oblast	54.9	43.8	181	4.1	561
48	Kostroma, Kostroma Oblast	58.0	42.0	156	3.6	643
54	Sosnovka, Tambov Oblast	53.2	41.3	137	5.5	556
55	Grafskaya, Voronezh Oblast	51.6	39.5	112	6.6	561
57	Nikolsk, Penza Oblast	53.8	46.0	154	5.0	523
60	Veshenskaya, Rostov Oblast	49.6	41.8	56	7.8	484
62	Kamyshin, Volgograd Oblast	50.2	45.4	154	7.2	422
66a	Kamskie Polyani, Republic of Tatarstan	55.7	51.4	52	4.6	662
67	Votkinsk, Republic of Udmurtia	57.5	54.0	244	2.4	588
69	Dyurtyuli, Republic of Bashkortostan	55.5	54.7	125	4.1	494
70	Duvan, Republic of Bashkortostan	55.7	57.9	312	2.7	516
71	Beloretsk, Republic of Bashkortostan	53.4	57.7	605	1.6	653
72	Zilair, Republic of Bashkortostan	52.4	58.7	360	3.6	366
999	Pornóapáti, Vas County, Hungary	47.2	16.5	273	9.2	633

Climate variables for the provenance sources and the test site have been generated with the ClimateEU v5.00 software package with a spatial resolution of 1 km grid, available at <http://tinyurl.com/ClimateEU>, based on methodology similar to Mahoney et al. (2022) and

Marchi et al. (2020). A total of 17 climate variables were analyzed (Table 2). These variables indicate the annual or seasonal amount of incoming heat, precipitation, and humidity. Data from the climatic period of 1961–1990 were used to characterize the weather conditions at the test site. Data from the “Map of the Sum of Air Temperatures for the Period with a Sustained Temperature Above 10°C” were used to analyze the clinal variability in phenology. The map was developed at the Main Geophysical Observatory of the Chief Administration of the Hydrometeorological Service under the Council of Ministers of the USSR (Institut Geografii AN SSSR, 1964).

The selected databases represent the most precise climate data available for the recent past. Nevertheless, a longer period representing the climate and extremes during the parent generation would have been useful to trace the impact of adaptation and evolution on the inherited responses of the progeny more exactly. Unfortunately, such data does not exist.

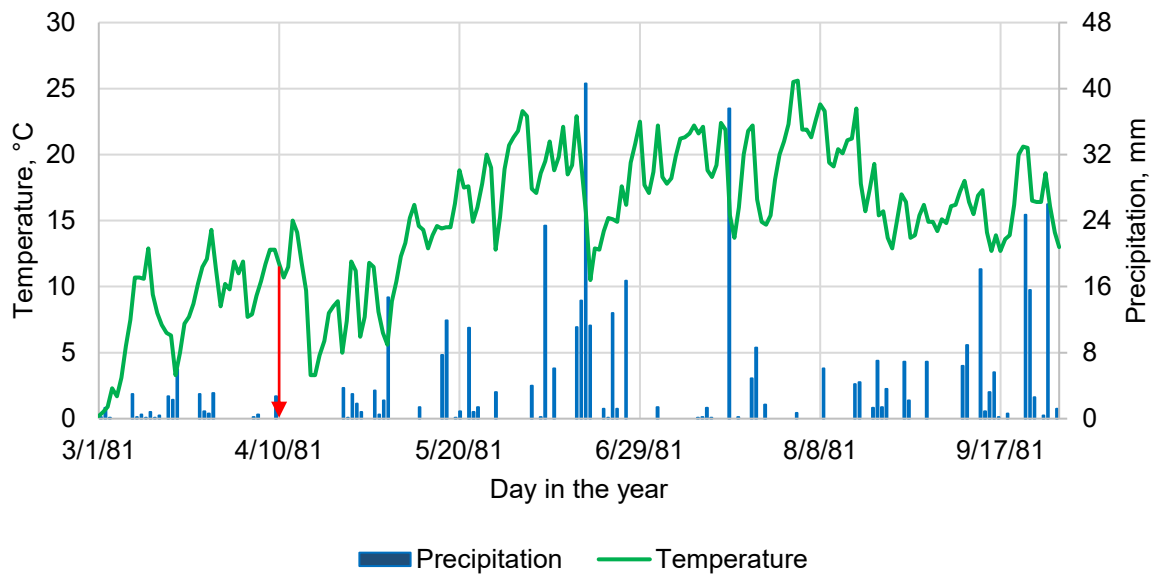


Figure 1. Average air temperature and total precipitation on individual days for the 1981 in Szombathely. The arrow indicates the selected date of assessment of bud burst

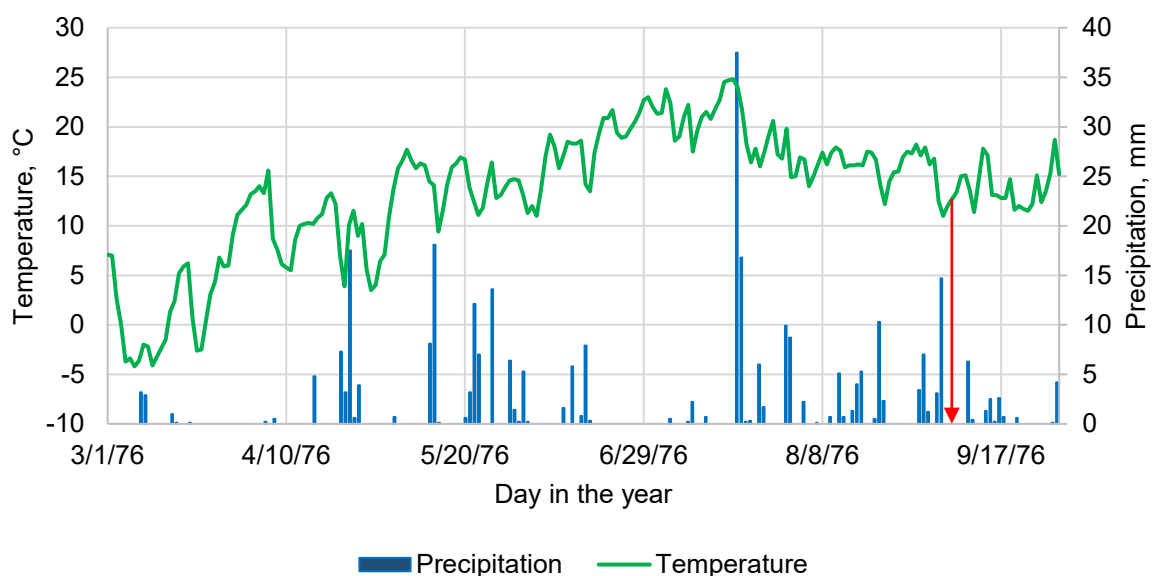


Figure 2. Average air temperature and total precipitation on individual days for the 1976 in Szombathely. The arrow indicates the selected date of assessment of bud set

Climate variables were used in their original and transformed form. To assess the phenological response of provenances to transfer to new conditions, the climate transfer distance was calculated as (Mátyás 1994):

$$\Delta X = X_s - X_p \quad (1)$$

Where:

$\Delta X$ :	climate transfer distance for climate variable $X$
$X_s$ :	climate variable $X$ for test site
$X_p$ :	climate variable $X$ for provenance.

Thus, local populations have a  $\Delta X = 0$ , and positive values of  $\Delta X$  characterize the transfer of populations from colder or drier climates to warmer or wetter ones. Since most of the provenances were transferred from north to south, their temperature transfer distance is greater than 0, i.e., indicating warming.

Phenological response of provenances was related to their climate transfer distance, providing individual transfer functions for each climate variable. In this study, we used a linear regression, i.e., phenological variable =  $f(\Delta X)$ , where  $f$  is a linear function.

Table 2. Analyzed climate variables (ClimateEU v5.00)

Code	Definition	Units
<i>MAT</i>	Mean annual temperature	°C
<i>MWMT</i>	Mean warmest month temperature	°C
<i>MCMT</i>	Mean coldest month temperature	°C
<i>MAP</i>	Mean annual precipitation	mm
<i>MSP</i>	Mean summer (May to September) precipitation	mm
<i>AHM</i>	Annual heat-moisture index	-
<i>SHM</i>	Summer heat-moisture index	-
<i>DD_above_5</i>	Degree-days above 5°C	°C
<i>FFP</i>	Frost-free period	-
<i>Prec_wt</i>	Winter precipitation	mm
<i>Prec_sp</i>	Spring precipitation	mm
<i>Prec_sm</i>	Summer precipitation	mm
<i>Prec_at</i>	Autumn precipitation	mm
<i>Tave_wt</i>	Winter mean temperature	°C
<i>Tave_sp</i>	Spring mean temperature	°C
<i>Tave_sm</i>	Summer mean temperature	°C
<i>Tave_at</i>	Autumn mean temperature	°C

## 2.4 Data analysis

All statistical analyses were conducted using R software, version 4.0.3 (R Core Team, Vienna, Austria). We calculated Pearson correlation coefficients to investigate the relationships between phenological traits (bud break and bud set) and selected climatic variables at the provenance origins. Additionally, we visualized and analyzed the effect of climatic gradients on phenotypic diversity among populations. Spatial data were processed and analyzed in QGIS 3.16, utilizing standard toolkits for vector and raster data manipulation.

### 3 RESULTS AND DISCUSSION

#### 3.1 Spatial and temporal pattern of phenological diversity

Bud burst and bud set values display high inter-provenance variability (Table 3). At the test site in Hungary, bud burst varied from 2.4 (provenance No. 62) to 5.0 (provenance No. 15). Bud set varied from 10 % (provenance No. 60) to 100% (provenances No. 9 and 15). These two phenological traits display a significant positive correlation ( $r = 0.719$ ,  $p < 0.001$ ), indicating strong genetic links.

Table 3. Bud burst and bud set values of Scots pine provenances in the Hungarian test

No.	Location	Latitude, Longitude,		Bud burst on 10/04/1981	Bud set on 06/09/1976
		°N	°E		
4	Plesetsk, Arkhangelsk Oblast	62.9	40.4	4.6	95
9	Totma, Vologda Oblast	60.0	43.0	4.4	100
15	Pryazha, Republic of Karelia	61.7	33.7	5.0	100
19	Lisino, Leningrad Oblast	60.0	30.4	3.8	70
22	Strugi Krasnye, Pskov Oblast	57.8	28.4	3.0	70
23	Kresttsy, Novgorod Oblast	58.3	32.5	3.7	80
24	Elva, Tartu County	58.2	26.5	3.6	50
25	Jelgava, Jelgava Municipality	56.5	25.2	3.0	70
28	Rasony, Vitsebsk Oblast	56.0	29.3	3.1	70
29	Lenino, Homel Oblast	52.2	31.7	3.0	30
35	Olevsk, Zhytomyr Oblast	50.4	27.7	3.1	35
37	Borispil, Kyiv Oblast	50.2	32.2	2.6	50
38	Svesa, Sumy Oblast	52.0	34.0	2.9	50
39	Cherkasi, Cherkasy Oblast	49.6	32.0	2.9	40
40	Slovyansk, Donbas Region	48.8	37.6	2.7	40
43	Orehovo-Zuyevo, Moskva Oblast	55.5	39.0	4.0	60
44	Kovrov, Vladimir Oblast	56.4	41.3	4.0	50
46	Pervomaysk, Nizhny Novgorod Oblast	54.9	43.8	3.9	65
48	Kostroma, Kostroma Oblast	58.0	42.0	3.5	90
54	Sosnovka, Tambov Oblast	53.2	41.3	3.3	70
55	Grafskaya, Voronezh Oblast	51.6	39.5	2.7	60
57	Nikolsk, Penza Oblast	53.8	46.0	3.8	80
60	Veshenskaya, Rostov Oblast	49.6	41.8	2.5	10
62	Kamyshin, Volgograd Oblast	50.2	45.4	2.4	65
66a	Kamskie Polyani, Republic of Tatarstan	55.7	51.4	4.0	70
67	Votkinsk, Republic of Udmurtia	57.5	54.0	4.2	95
69	Dyurtyuli, Republic of Bashkortostan	55.5	54.7	3.9	90
70	Duvan, Republic of Bashkortostan	55.7	57.9	3.5	90
71	Beloretsk, Republic of Bashkortostan	53.4	57.7	4.5	80
72	Zilair, Republic of Bashkortostan	52.4	58.7	3.9	70
999	Pornóapáti, Vas County, Hungary	47.2	16.5	2.5	20

The direction and gradient of the clearly clinal pattern of bud burst across Eastern Europe display the expected configuration. As described in earlier studies, northern populations were the earliest at the test location, while southern ones were the last to break bud, consistent with their thermal conditions at origin (Chmura et al., 2012; Memišević et al., 2023). Consequently,

the isophase lines describing the budburst pattern are not aligned with latitude everywhere. For example, they are adapted to a milder climate along the Baltic coast. Both bud burst and set follow their winter temperature variables, such as January temperature. This anomalous zone forms a triangle in the southwest of the East European Plain and is truncated approximately at 60° N latitude (Figure 3). A similar anomaly appears in both traits in the southeast towards the steppe region, where isophase lines run parallel to July isotherms, i.e., to summer temperature sums. Beyond these anomalies, the phenotypic isophase lines run approximately parallel to latitudes, a pattern that also holds for the Siberian part of the range. (See the following subchapters for correlation data of phenology with climate factors.) Thus, contrary to numerous findings by other sources, the present study found the growth cessation pattern (bud set) among provenances to be similar to that of spring bud burst in East Europe (Figure 3) (Mátyás 1981).

The temporal process of bud setting was investigated in autumn 1982 and 1983. The progression from the appearance of the first buds to complete growth cessation within a population may last 30 to 40 days. Bud formation timing and bud burst depend on local weather conditions, showing 20 to 30 days of variation between years; however, the ranking of the provenances remains consistent.

Temperature conditions primarily determine the active growth phase. Latitude (photoperiod) plays no decisive role. The differences between provenances observed at a specific location are dominated by genetic adaptation; the role of plasticity (as proposed by some sources – see subchapter 3.4) could not be identified in this analysis (Mátyás 1987).

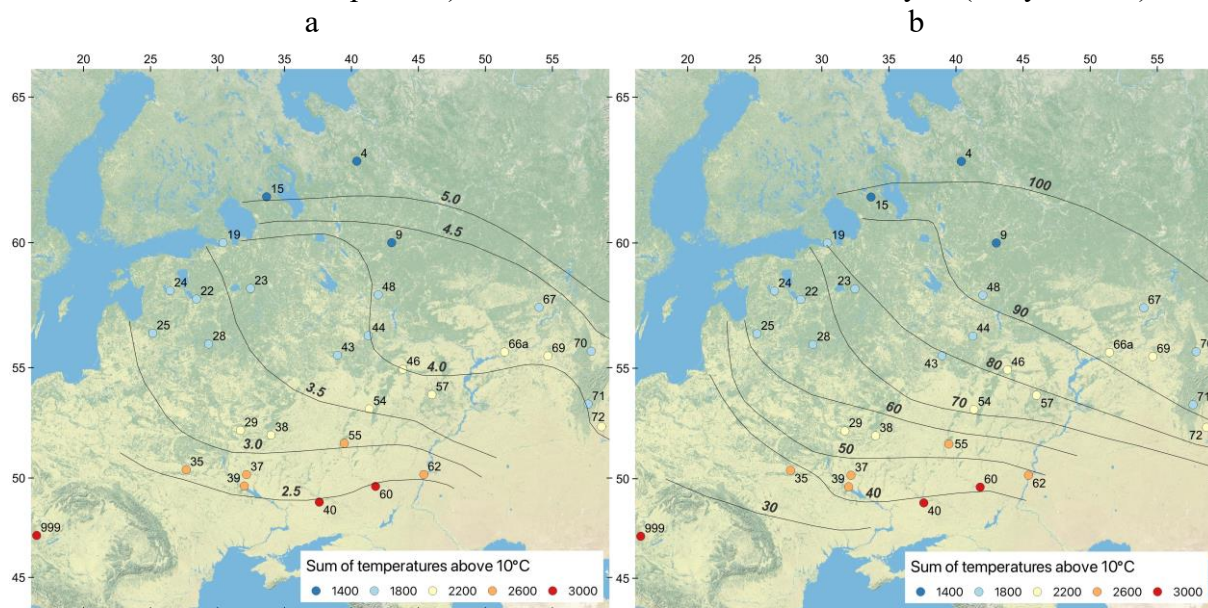


Figure 3. Clinal variation (black lines and bold italic numbers) in bud burst (a) and bud set (b) among Scots pine provenances, and annual temperature sum above 10°C at their origin. Provenance (dots) numbers explained in Table 1.

### 3.2 Correlation of climatic factors and phenology

We calculated Pearson correlation coefficients between climatic and phenological variables to account for ecological drivers of population differentiation. The dataset allowed us to examine trait-climate correlations across a wide range of climatic conditions in Eastern Europe. Both phenological variables showed significant negative correlations with all temperature-related variables (primarily *MAT*, *Tave\_at*, *Tave\_sp*, and *FFP*) and the heat-moisture index. To a lesser

extent, phenological variables also correlated with precipitation, though only *Prec\_at* exhibited a significant positive correlation.

Scots pine bud phenology was most significantly influenced by mean annual temperature of the seed source (*MAT*,  $r < -0.88$ ,  $p < 0.001$ ). Although this climate variable is commonly used in climate change projections, it does not account for seasonal variations or periodic extreme conditions. Spring and autumn temperatures play a crucial role in the initiation and cessation of Scots pine growth (Metslaid et al., 2018; Li et al., 2021). As expected, phenological traits also showed highly significant correlations with mean spring (*Tave\_sp*,  $r < -0.87$ ,  $p < 0.001$ ) and autumn (*Tave\_at*,  $r < -0.87$ ,  $p < 0.001$ ) temperatures. The length of the frost-free period (*FFP*) significantly affected the phenology of the provenances as well (Figure 4). In spite of strong correlations between temperature and precipitation variables, rainfall alone shows mostly low significance with bud phenology. The low correlation with precipitation is understandable, due to sufficient rainfall in the majority of regions of Scots pine's distribution in East Europe – the few sampled provenances adapted to the drought-exposed South have negligible effect on the correlations.

It is, however, unexpected that bud burst and set are highly correlated, indicating strong genetic links between the two traits and/or similar climatic cues. The comparison of correlations of all climate variables with bud burst and bud set (Figure 4) indicates also that Scots pine phenology displays strong links both with the same spring and autumn climate variables, which is a unique finding, contradicting the recent literature (see subchapter 3.4).

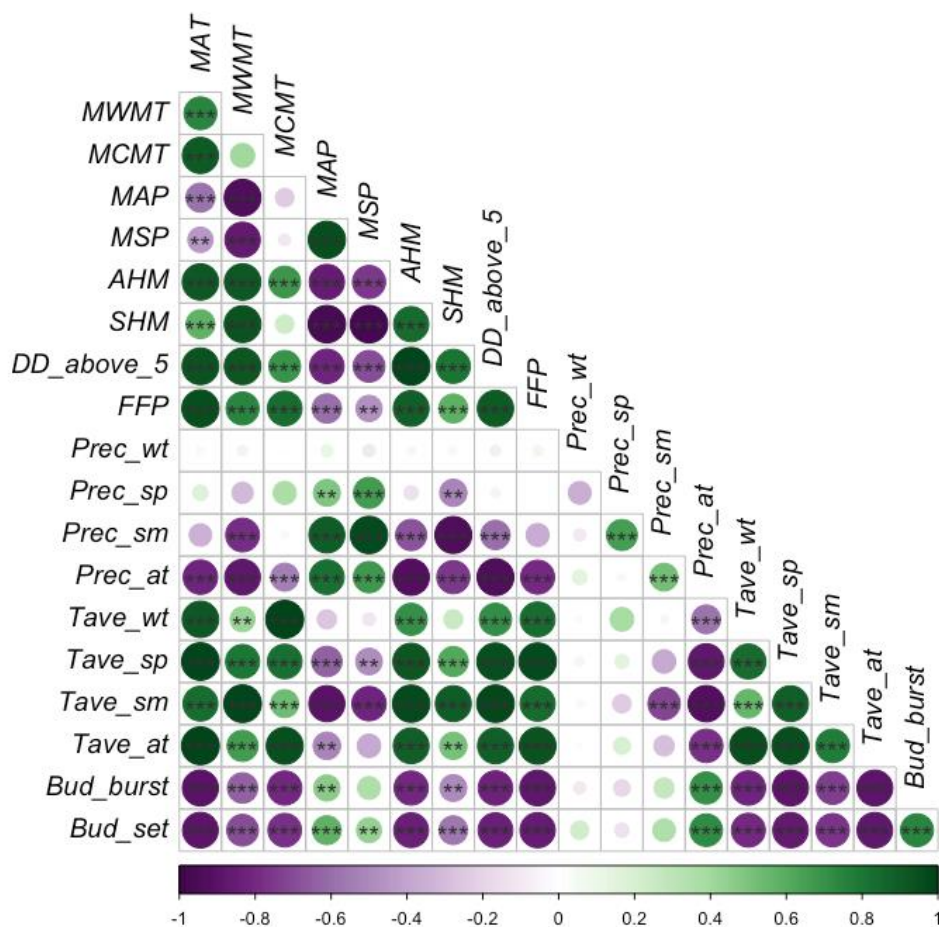


Figure 4. Correlation of climate and phenological traits of provenances. The significance level (\* 0.05, \*\* 0.01, \*\*\* 0.001) between  $-1.0$  and  $1.0$  is indicated by the size of symbols and their sign by color (positive: green, negative: purple)

### 3.3 Phenological pattern of provenance adaptation to climate

For the four thermal climate variables (*MAT*, *Tave\_at*, *Tave\_sp*, and *FFP*), which showed the most significant correlation with bud phenology, we calculated the climate transfer distances and estimated linear transfer equations for the climate variables to survey the within-species adaptive pattern across the cline of changing climatic conditions. For both phenological traits (bud burst and bud set), all linear equations were statistically significant ( $p < 0.001$ ) and explained more than 70% of the between-population variance ( $R^2 > 0.7$ ). This indicates strong genetic differentiation among populations according to their geographical origin, which supports their clinal character (*Figures 5 and 6*). The correlations of both phenological traits with climate found for Scots pine are similarly significant and warrant attention.

East European Scots pine provenances exhibit genetic differentiation across ecological and vegetation zones, which is reflected in the pattern of morphological and physiological trait variation. Our results, deduced from continental-scale data, support and extend the findings of Chmura et al. (2012), Ballian et al. (2019), Galdina et al. (2023), and others on the pattern of phenological variation in Scots pine. In Eastern Europe, where the topography and climate conditions across the range of Scots pine are uniform, respectively constantly changing, the pattern of phenotypic variation has a clinal character and shows high similarity to the growth traits measured in the same experiment (Shutyaev – Giertych, 1997; Mátyás et al., 2023; Lebedev – Mátyás, 2025).

### 3.4 Genetic differentiation and phenological adaptation of provenances

Common garden studies in many species have established similar clines in phenology; in general, the shorter the growing season, the earlier the cessation of growth (bud set). However, the evidence for genetic background in tree spring phenology is inconsistent. While spring phenology is more plastic (Aitken – Bemmels, 2016) and seems to be more strongly determined by temperature (Flynn – Wolkovich, 2018), the review by Zeng and Wolkovich (2024) of numerous species also concludes that there is no evidence of genetic (provenance) effects on spring phenology. This stands in sharp contrast to the significant clines with latitude and mean annual temperature found in autumn phenology. Research has linked these autumn clines to photoperiodic effects (Savolainen et al., 2007; Alberto et al., 2013). Zeng and Wolkovich (2024), along with other studies, suggest that a weaker and more varied plastic response is the cause of differentiation in spring phenology, while clines in autumn phenology appear stronger and more consistent across species.

Directional selection by environmental factors results in intraspecific patterns of adaptive traits, although the determinant cues may change. Therefore, the results of phenology and growth investigations may be dependent on the intensity and range of sampling. Consequently, regional studies may result in conclusions of regional validity.

It is unquestioned that thermal factors dominate in determining the active growth period. According to the general interpretation, autumn events create strong clines to avoid tissue loss from early frost at the end of the season. The high uncertainty of spring phenology found in many studies is explained by the higher unpredictability of frost risk, which triggers plastic (i.e., faster, and less genetically determined) adaptive responses to spring events. The hypothesis of Chamberlain and Wolkovich (2021) is that in the future, warming winters and late spring frosts will especially press tree species to change phenology and growth dynamics with the support of plasticity. However, the high significance of the linear regressions of both bud burst and bud set vs. thermal variables (*Figures 5 and 6*) leaves little space for plasticity; the populations follow the genetic imprint from their origin, at least at an early age. The hypothesis of fast

phenological adaptation to changing climatic conditions through plasticity cannot be supported by our results.

An example of changing determinant climatic factors in changing environments is the abrupt change in the phenotypic pattern of Scots pine populations north of latitude 60° N (e.g., around Saint Petersburg) in our study. The switching from a thermally controlled to a latitudinal pattern further north is thought to be caused by lower heat sums, which increases the regulatory role of photoperiod (Mátyás, 1981). The opinion that autumn phenology clines are determined by photoperiod (Savolainen et al., 2007) has most probably its origin in the fact that the authors investigated boreal populations in northern Scandinavia.

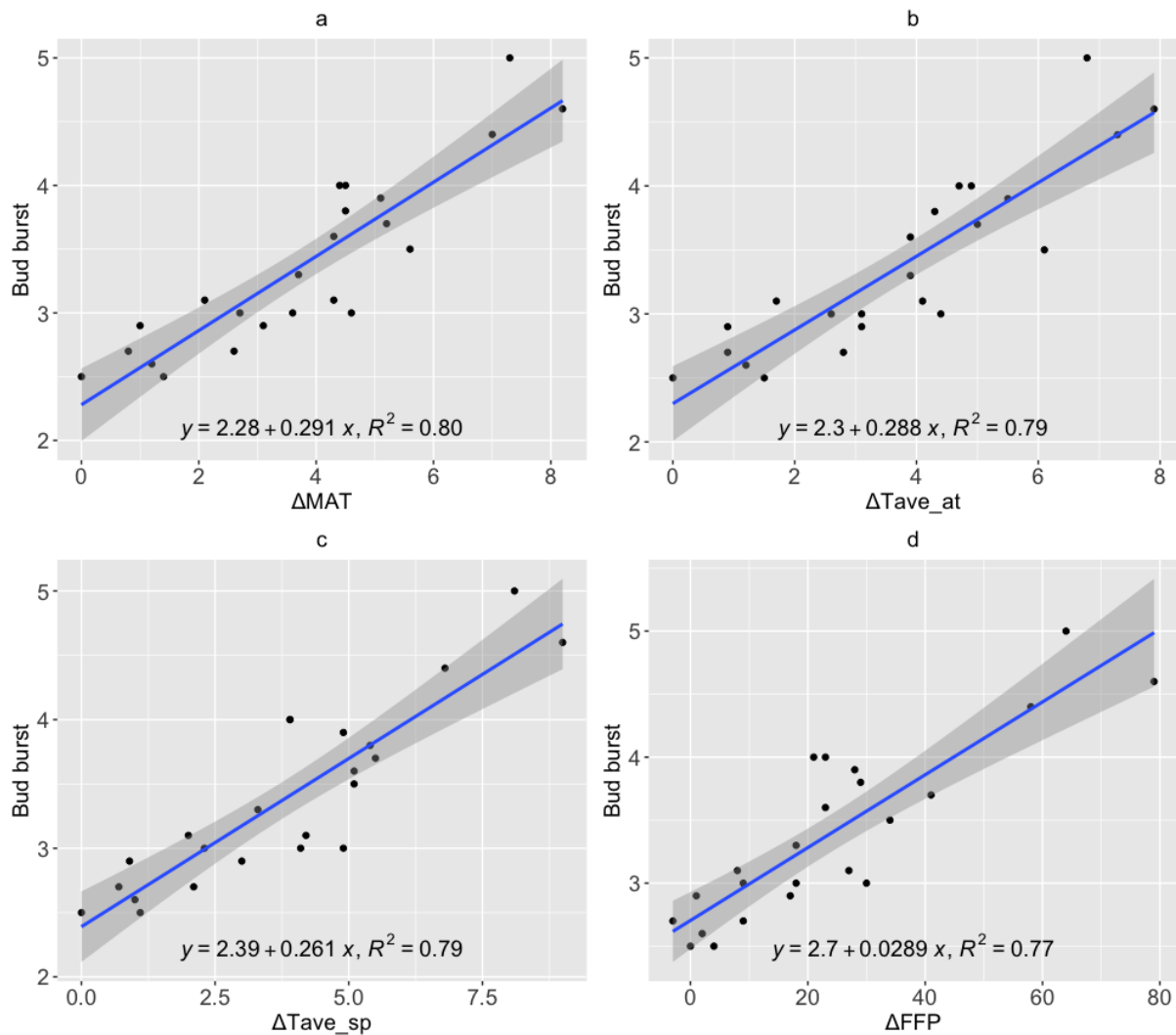


Figure 5. Linear regression between provenance bud burst value and climate transfer distance of: a) mean annual temperature, b) autumn mean temperature, c) spring mean temperature, d) frost-free period

However, our study on Scots pine shows that data for both bud burst and bud set confirm clear, genetically determined clinal variation across the eco-climatic range in Eastern Europe, and their determination and response appear similar. In this respect, the results presented on Scots pine differ from those of certain other studies, irrespective of species. One reason for this contradiction might be the limited range and non-representative sampling of populations in many studies. Distinguishing between genetic and plastic (“non-genetic”) causes for the within-species phenotypic pattern was impossible in this study, because proving the effect of plasticity

requires multiple test sites. It is most probable that there are no universally applicable laws for tree species with different distributional ranges. The climatic conditions at the test sites may also contribute to contradicting results. Climates with late springs and fast progress of heat sum may accelerate phenological phases and diminish differentiation. The fact that the majority of the rare investigations of Scots pine phenology had been conducted in the boreal zone is thought-provoking in this respect.

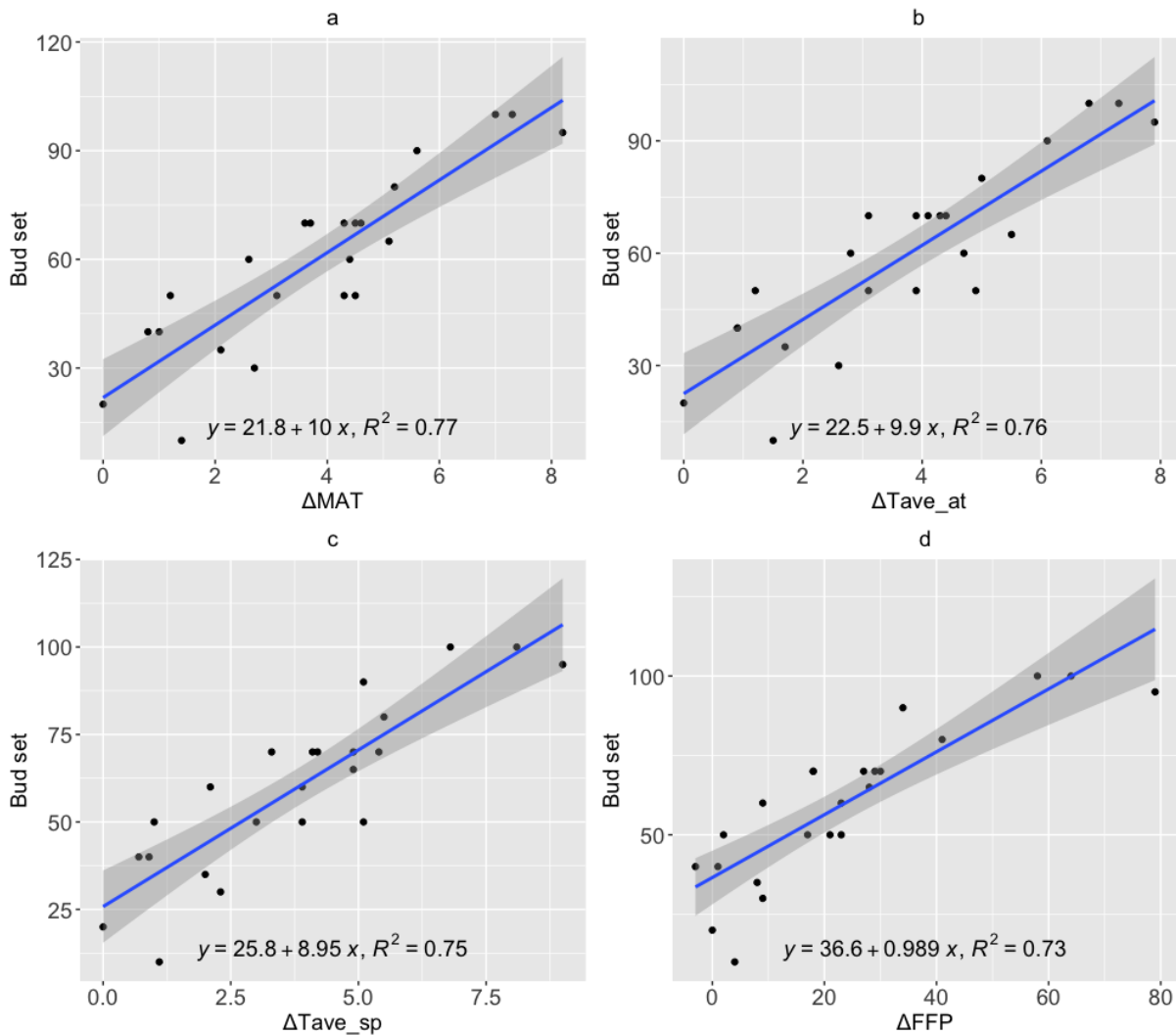


Figure 6. Linear regression between provenance bud set value and climate transfer distance of: a) mean annual temperature, b) autumn mean temperature, c) spring mean temperature, d) frost-free period

#### 4 CONCLUSIONS

This research provides valuable insights for forecasting forest responses to climate change, emphasizing the need to integrate both adaptive genetic characteristics and phenotypic plasticity into models that project the future carbon balance and dynamics of plant communities.

In conclusion, our study demonstrates that phenological traits in Scots pine populations across Eastern Europe exhibit a clear, genetically determined clinal variation pattern. The strong correlations between bud burst, bud set, and geographic-climatic variables underscore that

phenological variability is a complex process influenced not only by local climate but also by the intrinsic genetic factors and adaptive history of populations.

In the trial, situated beyond the xeric distribution limit of the species, all transferred provenances responded with bud break and set controlled by their inherited traits. Direct damages caused by phenological maladaptation were observed only at extreme transfer distances, such as with the early flushing Murmansk provenance, which became extirpated in the trial (most probably due to spring frost damage). Other damages due to maladaptation, such as pest infestation or drought mortality, were not observed during the limited period of the investigation. The long-term consequences of unadapted phenology at sites with a rapidly changing climate are difficult to predict. However, the successive shift of climate zones in Hungary during the first decades of the 2000s already led to significant tree mortality in commercial stands of Scots pine under analog site conditions.

These findings are pivotal in the context of the anticipated global temperature rise. While previous research suggests that warming springs will be tracked more closely by trees than warming autumns, our results highlight that the pattern of phenotypic response is not uniform in tree species and certainly not valid in Scots pine. Responses are fundamentally filtered by species-specific genetic adaptation. The hypothesis of fast plastic adaptation to changing climatic conditions, as proposed by Chamberlain and Wolkovich (2021), cannot be supported by our results. The observed patterns of phenotypic diversity require a critical consideration in forest management strategies, particularly when planning the transfer (assisted migration) of propagation material to ensure resilience in future climates.

Although our findings do not allow for broad generalizations across other tree species, they provide an essential foundation for assessing the impact of genetic variation in Scots pine and for predicting the responses of southern lineages to extreme “northern” conditions. Phenology will play a key role in determining how species shift their distribution areas and how they participate in the carbon sequestration of future ecosystems. Therefore, refining predictions requires new, provenance-level phenological data.

Future studies are necessary to refine our understanding of phenological responses to environmental change by establishing experiments outside the natural ranges of the species and conducting detailed assessments of phenology in relation to growth and stress tolerance. The need for such research is underscored by the challenge of forecasted serious climate change impacts. Both the adaptive genetic characteristics of populations and phenotypic plasticity must be considered when projecting how climate change will alter dynamic forces shaping forest ecosystems.

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## REFERENCES

- Aitken, S.N., Bemmels, J.B., 2016. Time to get moving: assisted gene flow of forest trees. *Evol Appl* 9, 271–290. <https://doi.org/10.1111/eva.12293>.
- Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R., Savolainen, O. (2013). Potential for evolutionary responses to climate change – evidence from tree populations. *Glob Change Biol* 19, 1645-1661. <https://doi.org/10.1111/gcb.12181>.
- Aspalter, S., Ciceu, A., Landivar Albis, C.M., Chakraborty, D., Schueler, S. (2025). Provenance Variation in Functional Traits of European Forest Trees: Meta-Analysis Reveals Effects of Taxa and Age Despite Critical Research Gaps. *Ecology and Evolution* 15(8), e71834. <https://doi.org/10.1002/ece3.71834>.

- Ballian, D., Lizdo, E., Bogunić, F., 2019. Analiza diferenciranosti rasta i fenologije provenijencija običnog bora (*Pinus sylvestris* L.) u pokusu provenijencija kod Kupresa (Bosna i Hercegovina) [Analysis of differences of growth and phenology of provenances of Scots pine (*Pinus sylvestris* L.) in provenance experiment at Kupres (Bosnia and Herzegovina): In Croatian]. Šumarski List 143(1-2), 25–34. <https://doi.org/10.31298/sl.143.1-2.3>.
- Camarero, J.J., Rubio-Cuadrado, A., 2025. Leaf phenology and tree growth are uncoupled in three deciduous tree species. *Trees, Forests and People* 19, 100761. <https://doi.org/10.1016/j.tfp.2024.100761>.
- Chamberlain, C.J., Wolkovich, E.M., 2021. Late spring freezes coupled with warming winters alter temperate tree phenology and growth. *New Phytol* 231, 987–995. <https://doi.org/10.1111/nph.17416>.
- Chmura, D.J., Rożkowski, R., Chałupka, W., 2012. Growth and phenology variation in progeny of Scots pine seed orchards and commercial seed stands. *Eur J Forest Res* 131, 1229–1243. <https://doi.org/10.1007/s10342-012-0594-9>.
- Dhar, A., Balliet, N., Hawkins, C.D.B., Carlson, M.R., Berger, V.G., Mahoney, R., 2015. Bud flush phenology and nursery carryover effect of paper birch provenances. *iForest* 8, 809–817. <https://doi.org/10.3832/ifor1367-008>.
- Institut geografii AN SSSR [Institute of Geography of the USSR Academy of Sciences], 1964. Fiziko-geograficheskij atlas mira [Physical and Geographical Atlas of the World]. Izdanie AN SSSR i Glavnogo upravleniya geodezii i kartografii GGK SSSR [Published by the USSR Academy of Sciences and the Main Directorate of Geodesy and Cartography of the USSR: in Russian], Moscow 298 p.
- Flynn, D.F.B., Wolkovich, E.M., 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytol* 219, 1353–1362. <https://doi.org/10.1111/nph.15232>.
- Galdina, T.E., Chernodubov, A.I., Mikhailova, M.I., 2023. Vnutrividovoe raznoobrazie *Pinus sylvestris* L. v geograficheskix kul'turax Central'noj lesostepi [Intraspecific Diversity of *Pinus sylvestris* L. in Provenance Trials of the Central Russian Forest-Steppe Area: In Russian]. *Lesnoy Zhurnal* [Russian Forestry Journal], 3 3, 84–98. <https://doi.org/10.37482/0536-1036-2023-3-84-98>.
- Jing, T., Rongzhou, M., Qing-Lai, D., 2021. Earlier and more variable spring phenology projected for eastern Canadian boreal and temperate forests with climate warming. *Trees, Forests and People* 6, 100127. <https://doi.org/10.1016/j.tfp.2021.100127>.
- Langvall, O., Ottosson Löfvenius, M., 2021. Long-term standardized forest phenology in Sweden: a climate change indicator. *Int J Biometeorol* 65, 381–391. <https://doi.org/10.1007/s00484-019-01817-8>.
- Lebedev, A.V., 2023. Changes in the growth of Scots pine (*Pinus sylvestris* L.) stands in an urban environment in European Russia since 1862. *J For Res* 34, 1279–1287. <https://doi.org/10.1007/s11676-022-01569-z>.
- Lebedev, A., Mátyás, C., 2025. Effect of climate change on height growth and carbon storage of Eastern European Scots pine populations. *Eur J Forest Res* 144, 1597–1611. <https://doi.org/10.1007/s10342-025-01828-8>.
- Lebedev, A.V., Dvoychenkov, K.I., 2025. Optimal'noe i kriticheskoe rasstoyanie ispol'zovaniya semyan geograficheskix kul'tur sosny obyknovenoj v zonu hvojno-shirokolistvennyh lesov [Optimal and critical climatic seed transfer distance of Scots pine in the coniferous-broadleaf forests zone: In Russian]. *Lesovedenie* 3, 388–408. <https://doi.org/10.31857/S0024114825030082>.
- Li, J., Song, F., Jin, Y., Yun, R., Chen, Z., Lyu, Z., Zhao, Y., Cui, D., 2021. Critical temperatures controlling the phenology and radial growth of *Pinus sylvestris* var. *Mongolica* on the southern margin of a cold temperate coniferous forest. *Ecological Indicators* 126, 107674. <https://doi.org/10.1016/j.ecolind.2021.107674>.
- Linkevičius, E., Šidlauskas, G., Kliučius, A., Armoška, E., Mikalajunas, M., Sidabriene, D., Andriuškevičiute, P., Augustaitis, A., 2024. The growth dynamics of East European Scots pine (*Pinus sylvestris* L.) populations - a Lithuanian field trial. *iForest* 17, 59–68. <https://doi.org/10.3832/ifor4359-016>.
- Mahoney, C.R., Wang, T., Hamann, A., Cannon, A.J., 2022. A CMIP6 ensemble for downscaled monthly climate normals over North America. *International Journal of Climatology* 42, 5871–5891. <https://doi.org/10.31223/X5CK6Z>.
- Marchi, M., Castellanos-Acuna, D., Hamann, A., Wang, T., Ray, D., Menzel, A., 2020. ClimateEU, scale-free climate normals, historical time series, and future projections for Europe. *Scientific Data* 7, 428. <https://doi.org/10.1038/s41597-020-00763-0>.
- Mátyás, C., 1981. Kelet-európai erdeifenyő-származások fenológiai változékonysága [Phenological variability of Eastern European pine provenances: In Hungarian]. *Erdészeti Kutatások* 74, 71–80.
- Mátyás, C., 1987. Adaptációs folyamatok erdei fák populációiban [Adaptation processes in forest tree populations.] *Dr. Acad. Sci. thesis (manuscript, in Hungarian.)* 198 p. <http://tananyag.uni-sopron.hu/61/>
- Mátyás, C., 1994. Modeling climate change effects with provenance test data. *Tree Physiol* 14(7-9), 797–804. <https://doi.org/10.1093/treephys/14.7-8-9.797>.
- Mátyás, C., Balázs, P., Nagy, L., 2023. Climatic Stress Test of Scots Pine Provenances in Northeastern Europe Reveals High Phenotypic Plasticity and Quasi-Linear Response to Warming. *Forests* 14, 1950. <https://doi.org/10.3390/f14101950>.

- Memišević Hodžić, M., Mioč, T., Ballian, D., 2023. Phenological Variability of *Pinus sylvestris* L. Provenances in the International Provenance Test in Kupres, Bosnia and Herzegovina. *South-east Eur For* 14(2), 1–7. <https://doi.org/10.15177/see-for.23-12>.
- Meshkova, V., 2021. The Lessons of Scots Pine Forest Decline in Ukraine. *Environ. Sci. Proc.* 3, 28. <https://doi.org/10.3390/IECF2020-07990>.
- Metslaid, S., Hordo, M., Korjus, H., Kiviste, A., Kangur, A., 2018. Spatio-temporal variability in Scots pine radial growth responses to annual climate fluctuations in hemiboreal forests of Estonia. *Agricultural and Forest Meteorology* 252, 283–295. <https://doi.org/10.1016/j.agrformet.2018.01.018>.
- Montgomery, R.A., Rice, K.E., Stefanski, A., Rich, R.L., Reich, P.B., 2020. Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and geographic range. *Proc. Natl. Acad. Sci. U.S.A.* 117(19), 10397–10405. <https://doi.org/10.1073/pnas.1917508117>.
- Morin, X., Roy, J., Sonié, L., Chuine, I., 2010. Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist* 186, 900–910. <https://doi.org/10.1111/j.1469-8137.2010.03252.x>.
- Nakvasina, E.N., Prozherina, N.A., 2021. Scots pine (*Pinus sylvestris* L.) reaction to climate change in the provenance tests in the north of the Russian plain. *Folia Forestalia Polonica* 63(2), 138–149. <https://doi.org/10.2478/ffp-2021-0015>.
- Parfenova, E.I., Kuzmina, N.A., Kuzmin, S.R., Tchebakova, N.M., 2021. Climate Warming Impacts on Distributions of Scots Pine (*Pinus sylvestris* L.) Seed Zones and Seed Mass across Russia in the 21st Century. *Forests* 12, 1097. <https://doi.org/10.3390/f12081097>.
- Prokazin, E.P., Bogachev, A.V., 1975. Nasledstvennaya adaptaciya sosny obyknovnoj k klimaticeskim faktoram i vozmozhnost' ee ocenki i prognozirovaniya [Hereditary adaptation of Scots pine to climatic factors and the possibility of its assessment and prediction: In Russian]. In: *Genetika, selekciya, semenovodstvo i introdukciya lesnyh porod* [Genetics, selection, seed production and introduction of forest species], Moscow 131–146.
- Risk, C., McKenney, D.W., Pedlar, J., Lu, P., 2021. A compilation of North American tree provenance trials and relevant historical climate data for seven species. *Sci Data* 8, 29. <https://doi.org/10.1038/s41597-021-00820-2>.
- Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene Flow and Local Adaptation in Trees. *Annual Review of Ecology, Evolution, and Systematics* 38, 595–619. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095646>.
- Shutyaev, A.M., Giertych, M., (1997) Height Growth Variation in a Comprehensive Eurasian Provenance Experiment of Scots Pine (*Pinus sylvestris* L.). *Silvae Genetica* 46. 332–349.
- Skulason, B., Hansen, O.K., Nielsen, U.B., 2018. Provenance Variation in Phenology and Frost Tolerance in Subalpine Fir (*Abies lasiocarpa*) Planted in Denmark and Iceland. *Forests* 9, 17. <https://doi.org/10.3390/f9010017>.
- Way, D.A., 2011. Tree phenology responses to warming: spring forward, fall back? *Tree Physiology* 31(5), 469–471. <https://doi.org/10.1093/treephys/tpr044>.
- Waszak, N., Robertson, I., Puchałka, R., Przybylak, R., Pospieszynska, A., Koprowski, M., 2021. Investigating the Climate-Growth Response of Scots Pine (*Pinus sylvestris* L.) in Northern Poland. *Atmosphere* 12, 1690. <https://doi.org/10.3390/atmos12121690>.
- Wu, Z., Zohner, C.M., Zhou, Y., Crowther, T.W., Wang, H., Wang, Y., Peñuelas, J., Gong, Y., Zhang, J., Zou, Y., Van den Hoogen, J., Fu, Y.H., 2025. Tree species composition governs urban phenological responses to warming. *Nat Commun* 16, 3696. <https://doi.org/10.1038/s41467-025-58927-8>.
- Zeng, Z.A., Wolkovich, E.M., 2024. Weak evidence of provenance effects in spring phenology across Europe and North America. *New Phytol* 242: 1957–1964. <https://doi.org/10.1111/nph.19674>.