



Full Length Research Article

Intraspecific Variability of Radial Increment of Scots Pine (*Pinus sylvestris* L.) in Forest Sites in the East European Forest-Steppe

Sergey Matveev^{1,*}, Daria Litovchenko¹, Marko Gutalj²

¹ Faculty of Forestry, Voronezh State University of Forestry and Technologies named after G.F. Morozov, Voronezh, Russia

² Department of Forestry, Faculty of Agriculture, University of East Sarajevo, Lukavica, Republic of Srpska, Bosnia and Herzegovina

* Corresponding author. E-mail address: lisovod@bk.ru

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ABSTRACT

This article presents results from a study of differentiated responses of the annual radial increment of individual Scots pine (*Pinus sylvestris* L.) trees (dendrophenotypes) to changes in climatic factors at two forest sites: mixed-grass pine forest and purple moor-grass pine forest. For the first time in Scots pine in the East European forest-steppe, intraspecific (intrapopulation) differentiation of trees based on their adaptive potential to changing climatic conditions was established, and principles for identifying dendrogroups based on responses to limiting climatic factors were developed. The identified dendrogroups differ significantly from one another. The relationship between pine radial increment dynamics and climatic factors decreases from the 1st to the 3rd dendrogroup at both studied sites. Correlation analysis between climatic factors and pine radial increment under the two forest-growing conditions showed that the climatic signal is stronger under moderately moist conditions (mixed-grass pine forest). For example, for dendrogroup 1, the correlation coefficient between radial increment and total atmospheric precipitation during May–September was 0.58 in the mixed-grass pine forest and 0.47 in the purple moor-grass pine forest during 1961–1990; during 1991–2020, the corresponding values were 0.27 and 0.22. The study also revealed a strong influence of May–September precipitation on pine radial increment, making it possible to construct regression equations that reflect radial-increment dynamics under changing climatic factors. The dendrogroups identified in this study showed differentiated responses to climatic factors limiting tree growth within populations. These data should support effective forest management in pine forests of the East European forest-steppe.

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1. Introduction

Forests play an important role in maintaining the biological, ecological and energy balance of the earth (Ameray et al. 2021). They are also crucial for human well-being (Mo et al. 2023). Forest ecosystems may soon face severe impacts of global climate change, mainly due to rising temperatures and adverse changes in precipitation patterns (Ranasinghe et al. 2021; Seidl et al. 2017; Vacek et al. 2023). Many studies worldwide have examined the potential impacts of global climate change on forest stand growth and productivity (McDowell et al. 2020; Schaphoff et al.

2016; Seidl et al. 2017). Climate change has already caused many changes in forests, and future changes of this scale may even lead to local extinctions within individual stands and the loss of important functions and services (Allen et al. 2025). Climate influences tree growth differently by species and habitat (Flynn et al. 2025; Klisz et al. 2025). In the southern regions of the forest zone, cambial growth is associated with summer precipitation (Bykov et al. 2023; Camarero et al. 2021). In the temperate latitudinal zone, the relationship between tree growth and individual climatic factors is weaker than at high latitudes; therefore, it is necessary to account for the combined effects of precipitation and temperature on tree growth (Camarero et al. 2021; Kowal et al. 2026; Tishin et al. 2024).

However, species-level studies of forest stand responses to current climate change mask the unique adaptive abilities of individual trees and populations and do not provide opportunities to identify their adaptive potential or select adaptive dendrophenotypes for creating sustainable artificial forest stands.

Rapid climate change has been recorded in several regions of Russia, including the East European forest-steppe. Therefore, studying the condition of forest trees in the face of global warming (Degtyareva 2022), as well as their adaptive potential to changing climate conditions, is a pressing issue.

The dendroclimatic method can effectively address questions about the degree and nature of impacts from natural and anthropogenic factors on forests. Radial increment is a comprehensive indicator that allows us to track changes in tree condition throughout their lifespans and account for the climatic component. When analyzing forest ecosystem dynamics, a reliable assessment of this indicator is essential.

Identifying variability in any biological species is possible only by analyzing the behavior of a large group of individuals interacting within a limited territory under changing environmental conditions. The complexity of this task lies in the fact that the degree of adaptation of any genotype (a separate tree) in plant cenopopulations is not a constant value, but depends on the age of the individual, its relationships with neighbors, the diversity of the soil cover and the rate of change of abiotic environmental factors (Cotto and Day 2023; Dragavtsev 2019; Wulandari et al. 2022). The main problem in population biology is identifying a mechanism that allows different genotypes to optimize their strategies for responding to fluctuations in habitat conditions (Li and He 2026). For such studies, the annual radial increment of coniferous trees is most appropriate, as it is easy to assess and adequately reflects the extent of phenotypic adaptation to environmental conditions. In this regard, dendrochronological analysis across habitats is therefore relevant (Büntgen and Esper 2025; Esper et al. 2025; Katyutin et al. 2017).

Scots pine is ideal for dendrochronological and dendroclimatic studies: it has well-defined annual rings, a weak influence of fruiting on annual growth, and is highly sensitive to climatic factors (Kuznetsova and Solomina 2022; Matveev and Litovchenko 2023; Seftigen et al. 2025).

In each phytocenosis, several contrasting forms can be distinguished based on various characteristics, including the variability of annual radial increment. Therefore, some researchers have introduced the concept of the “dendrophenotype” of the forest-forming species (Krutovsky 2022; Mendez-Cea et al. 2023). Briefly, a dendrophenotype is the individual response of a tree to biotic and abiotic factors. More broadly, a dendrophenotype is a set of morphological, physiological, anatomical and other external characteristics of an individual tree that manifest as a result of the interaction between a tree's genotype and environmental conditions (Krutovsky 2022). To study the individual response of trees to climatic and other stressful influences (of

different nature, periodicity and intensity), an analysis of the dynamics of the width of annual rings is used for the entire period of tree growth, as well as before, during and after stressful events (Frank et al. 2022; Krutovsky 2022; Sánchez-Pinillos et al. 2019; Zhang et al. 2025). Based on this feature, researchers can identify individual dendrophenotypes, group them into "dendrogroups" with similar radial increment dynamics and responses to climate factors, and study intraspecific (intrapopulation) differentiation in responses to climate parameters. A dendrogroup is a group of trees (dendrophenotypes) of a single species in a population (stand) of a homogeneous area, characterized by similar parameters of dendrophenotypic variability: morphological traits and radial growth responses to biotic and abiotic factors, formed as a result of the interaction between genotype and environment. At the same time, it differs from other groups of trees in the population in one or more of these parameters. Such studies in the East European forest-steppe are being conducted for the first time.

Drought, linked to precipitation and temperature, is the most significant factor limiting tree growth in the East European forest-steppe. Data on these parameters from the nearest weather station (15 km from the study sites), Voronezh Weather Station No. 34123, were used for correlation analyses with the dynamics of radial increment in Scots pine.

The study aimed to identify and analyze the differentiated responses to changes in climatic factors (precipitation amounts and average air temperatures) in the annual radial increment of individual Scots pine (*Pinus sylvestris* L.) specimens (dendrophenotypes). The study was conducted at two forest sites: mixed-grass pine and purple moor-grass pine forests.

The objectives of the research included: (1) selection of radial wood increment samples (wood cores) from individual pine trees in each of the two trial plots, followed by dating and measurement of radial increment; (2) selection of climatic data (monthly precipitation amounts by calendar year and average monthly and annual air temperatures) for the closest weather station (15 km from the research objects): weather station No. 34123 "Voronezh"; (3) statistical analysis of the dynamics of annual radial increment of pine in two trial plots and identification of tree groups (dendrogroups) differing in radial increment dynamics from the average values for the forest stand (intraspecific variability); (4) mathematical analysis of the relationships (correlation, influence strength, regression) between dendrogroups of pine radial increment and various climatic factors; and (5) generalization and discussion of the research results and formulation of conclusions.

2. Materials and Methods

2.1. Study Area and Dendrochronological Sampling

The East European forest-steppe covers a significant area of the Russian Plain and is heterogeneous in terms of physical, geographical and climatic conditions. Periodic drought is the main climatic factor limiting woody plant growth in the forest-steppe.

Scots pine (*Pinus sylvestris* L.) is an economically valuable forest-forming species in the East European forest-steppe of the Russian Plain and is second only to English oak (*Quercus robur* L.) in terms of distribution: 29% of forest lands are occupied by stands dominated by pine (Matveev 2017; Musievsky 2022). Scots pine is highly productive and provides vital ecological, protective, recreational, and other functions, including in the East European forest-steppe.

The East European forest-steppe of the Russian Plain is a highly productive pine forest zone. The study sites are located in the Voronezh region.

When selecting sites for establishing trial plots, the ecosystem and intraspecific diversity of natural tree stands across the most common forest site types in the East European forest-steppe were considered. Climate change negatively affects forest biodiversity, but biodiversity underlies the mechanisms of forest adaptation to these changes.

Trial plot 1 (TP 1) was established in a natural pine stand with an admixture of oak and birch located in quarter 60, section 11 of the Left Bank forestry of the Prigorodnoye forestry of the Voronezh region (50°48'43" N, 40°54'27" E). The relief is flat; the groundwater level is 2–5 m. The forest site is a mixed-grass pine forest growing on moderately moist, moderately fertile sandy soil. The size of the trial plot is 0.25 ha (50 m × 50 m). There are 60 trees. The average age of the stand is 140 years. On this trial plot, samples from 25 trees (2 cores per tree) were collected for dendrochronological analysis using an increment borer. The maximum age based on the wood cores is 145 years.

Trial plot 2 (TP 2) was established in a natural pine stand with an admixture of oak, located in quarter 65, section 5 of the Left Bank forestry of the Prigorodnoye forestry of the Voronezh region (51°21'47" N, 39°32'59" E). The relief is flat; the groundwater level is 1–3 m. The forest site is a purple moor-grass pine forest growing on moist, moderately fertile soil. The size of the trial plot is 0.25 ha (50 m × 50 m). There are 68 trees. The average age of the stand is 130 years. On this trial plot, samples from 24 trees (2 cores per tree) were collected for dendrochronological analysis using an age borer. The maximum age based on the wood cores is 140 years (**Table 1**, **Fig. 1**).

Table 1. Characteristics of pine stands at the research sites

No of trial plots	Area of the trial plot (ha)	Composition of tree species (%)	Age (years)	DBH* (cm)	H* (m)	f*	Volume stock (m ³ ha ⁻¹)	Forest site types
1	0.25	100% Scots pine	140 (1879–2023)	42.2	28.5	0.6	450	Mixed-grass pine forest
2	0.25	100% Scots pine + English oak	130 (1883–2023)	48.5	29.0	0.7	490	Purple moor-grass pine forest

Notes: DBH – average diameter at breast height; H – average height; f – density of tree placement (corresponds to the canopy density).

Trees in forest stands on sample plots for collecting wood cores for dendrochronological analysis were selected from each 4-centimeter thickness step of the forest stand, approximately in proportion to the number of trunks in that step, and were straight-trunked and without external damage from pests or diseases. The mixed-grass pine forest, according to the moisture scale developed by P.S. Pogrebnyak ([Fomin et al. 2023](#)), is less humid than the purple moor-grass pine forest. Global warming is deteriorating growing conditions for trees in the East European forest-steppe, particularly in mixed-grass pine forests ([Matveev et al. 2016](#)).

2.2. Dendrochronological Analysis of Scots Pine Radial Increment

Using the LINTAB-6 software and the TSAP-Win software package developed by Frank Rinn, Heidelberg, Germany ([Rinn 2016](#)), dating and measurement of radial increment of pine trees by calendar year were carried out on cores from the above-mentioned research sites. The values

of the width of annual rings for two cores were averaged for each tree, and the average values of radial wood growth were calculated for each research site. In the analytical package Statistica 13.0 (TIBCO Software Inc. 2022, Palo Alto, CA, USA), statistical parameters of dendrochronological series averaged over the objects of study were calculated: the arithmetic mean of the radial increment, the basic error of the mean, the coefficient of variation, the error of the coefficient of variation, the Student's *t*-criterion, the indicator of the study's accuracy (probable error) (Kiryushin et al. 2024; Shevelina and Nuriev 2022). The signal-to-noise ratio (SNR) (Buras et al. 2025) and the expressed population signal (EPS) (Li and He 2026) were also calculated. In the TSAP-Win software package (professional version) (Rinn 2016), statistical coefficients characterizing the similarity of individual tree-ring-width chronologies with the average chronology for all samples in the studied forest stand were calculated: the synchronicity coefficient (GLK) (Table 2), the synchronicity level (GSL), the correlation coefficient (CC), and the cross-dating index of individual chronologies with the average (CDI) (Rinn 2016; Shiyatov et al. 2000; Tishin et al. 2024).

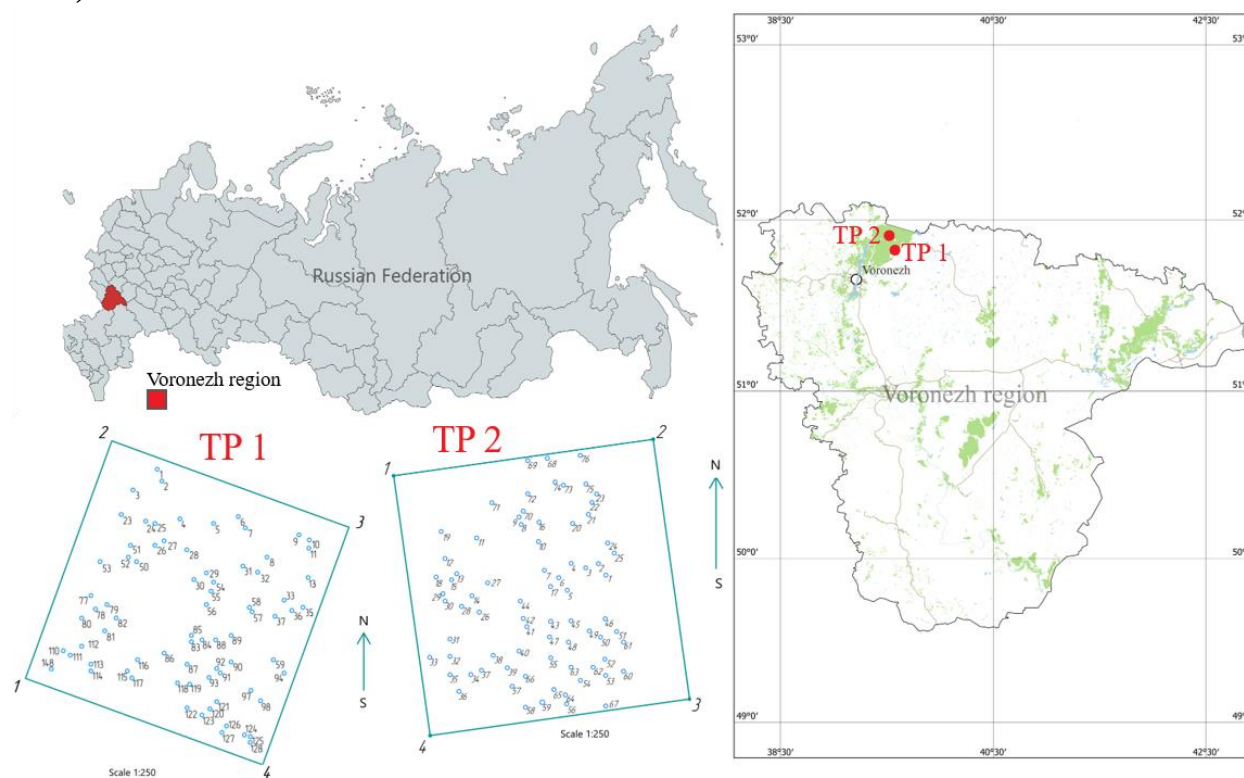


Fig. 1. Location of the study area in the Russian Federation and Voronezh Region, and spatial arrangement of trees in TP 1 and TP 2.

Low synchronicity in changes in radial increment value indicates intensive separation of trees within individual dominance ranks. Differences in trees' responses to environmental changes make it difficult to assess the dependence of radial increment on meteorological factors, so relative indices of radial increment are often used, as they can vary considerably and may be more informative for such assessments (Demakov et al. 2021).

To remove the age trend and compare radial increment dynamics with climatic factors, relative indices were calculated in the TREND program developed in Voronezh, Russia (Mironenko et al. 2023), using a generally accepted method (Shiyatov et al. 2000; Tishin et al.

2024). The age trend was calculated using the sliding smoothing method, followed by polynomial fitting.

Table 2. Synchronicity coefficient scale and synchronicity levels between chronologies (Shiyatov et al. 2000)

Synchronicity coefficient values (%)	Levels of synchronicity between chronologies
45–56	Absent
57–67	Low
68–78	Average
79–89	High
90–100	Very high

2.3. Dendroclimatic Analysis and Radial Increment Modeling

To assess the response of pine tree radial increment to climate factors, monthly precipitation series from Weather Station No. 34123 “Voronezh” (51°42'55" N, 39°12'57" E) were used (Pogoda i Klimat 2025). The WMO climate norm base period is 1961–1990. The WMO proposed updating the climate base norms for operational purposes every 10 years (i.e., the current period is 1991–2020). Nevertheless, the period 1961–1990 remains the baseline for assessing climate change.

Quantitative characteristics of the relationship between the relative indices of radial increment of pine and limiting climatic factors (sums of atmospheric precipitation for the calendar year, for the hydrological year (October–September), for the period of active vegetation of woody plants (May–September), and air temperatures (May–September) (Matveev 2017) were determined using Pearson's linear correlation in the Microsoft Excel 2020 (Microsoft 2020) software package (Shevelina and Nuriev 2022).

In accordance with the Chaddock scale (Kiryushin et al. 2024), the relationship is considered weak from 0 to 30%, moderate from 31 to 50%, significant from 51 to 70%, high (close) from 71 to 90%, and very high (very close) from 91% and above. The influence strength of climatic factors on wood radial increment was estimated in Statistica 13.0 (TIBCO Software Inc. 2022).

The reliability of the results on the influence strength of limiting factors was verified using the Fisher criterion. If the actual value of the F -criterion is higher than the tabular value ($F_f > F_{st}$), the statistical significance of the equation as a whole is recognized.

Multiple linear regression analysis used precipitation and air temperature as independent variables to model the dependent variable (relative index), and model significance was assessed using Fisher's F -criterion. The equation of multiple linear regression is:

$$Y = b_0 + b_1 \cdot X_1 + b_2 \cdot X_2 \quad (1)$$

where Y - is the dependent variable, b_0 - is the free term (intercept), b_1 , b_2 - are the regression coefficients, X_1 - is the independent variable 1 (atmospheric precipitation), X_2 - is the independent variable 2 (air temperature).

The goodness of fit of the regression equation was assessed using the coefficient of determination R^2 . The closer R^2 is to 1, the better the regression fits the empirical data and the greater the proportion of variation the model explains. The research methodology consisted of the following sequential stages (Fig. 2).

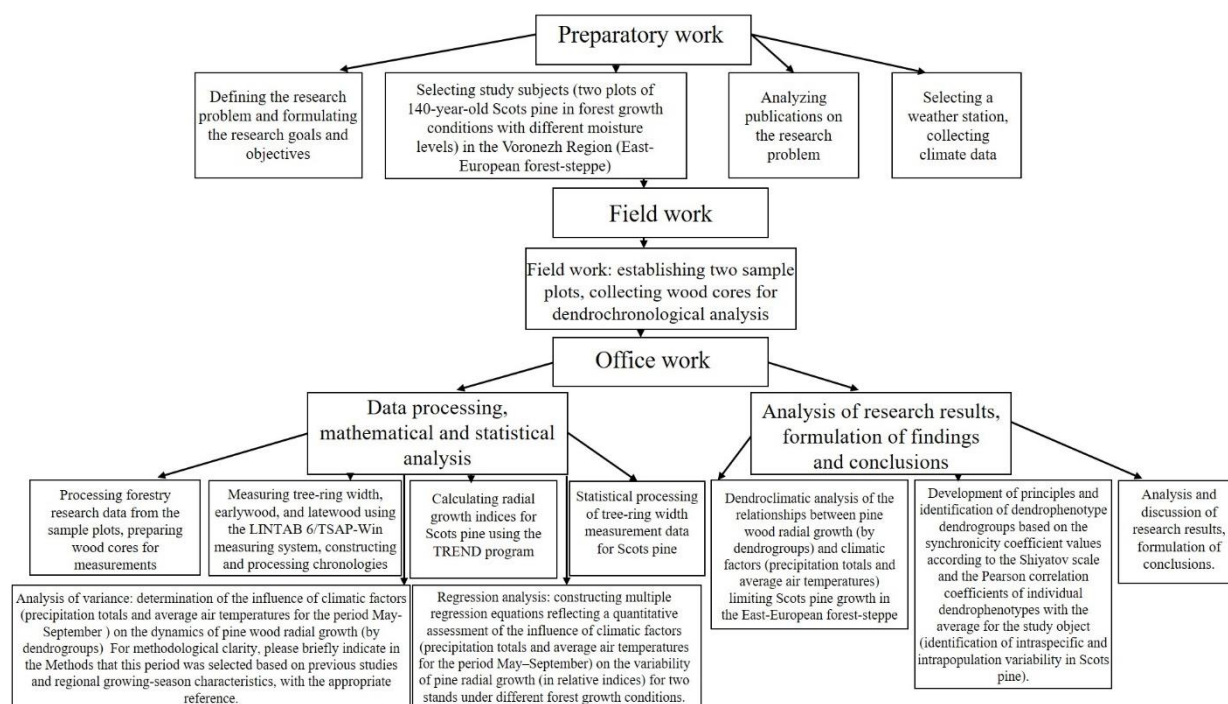


Fig. 2. Block diagram of the research plan.

3. Results and Discussion

3.1. Radial Increment Variability and Dendrogroup Identification

Scots pine radial increment characteristics were statistically analyzed at the research sites. The results of the statistical analysis of the averaged chronologies of Scots pine radial increment, based on total annual ring width, are presented in **Table 3**.

Table 3. Statistical characteristics of the average radial increment of Scots pine at two research sites

Forest site types	$M \pm m_m$ (mm)	$CV \pm M_{cv}$ (%)	$t_{st(r)}$	SNR	EPS	P_M (%)
Mixed-grass pine forest (trial plot 1)	1.6 ± 0.03	45.6 ± 0.01	7.2	80	0.99	6.3
Purple moor-grass pine forest (trial plot 2)	2.1 ± 0.005	49.2 ± 0.04	5.6	85	0.98	5.9

Notes: M – arithmetic mean of radial increment; m_m – basic error of the mean; CV – coefficient of variation; M_{cv} – error of the coefficient of variation; $t_{st(r)}$ – Student's criterion; PM – indicator of the study's accuracy (probable error)

The calculated signal-to-noise ratios (SNRs) for the two research objects are 80 and 85, indicating a strong common signal in both generalized chronologies, which may reflect the sensitivity of the studied trees to climatic conditions. The calculated expressed population signal (EPS) values of the studied generalized tree-ring chronologies were 0.99 and 0.98, respectively; i.e., in accordance with the adopted threshold value (0.85), the chronologies can be considered sufficiently representative (the annual ring width for each year reliably reflects the radial increment of the population).

Trees can respond to the same changes in external conditions in ambiguous ways; conversely, different impacts can manifest identically. The annual increment of Scots pine varies significantly: apical shoot increment ranges from 1 to 90 cm, and annual ring width from 0.05 to

15 mm, indicating high responsiveness to environmental changes and significant ecological plasticity (Demakov et al. 2021).

Based on calculated individual dendrophenotype variability according to the Shiyatov scale (Shiyatov et al. 2000) and the correlation coefficients of individual samples with the stand average, dendrogroups were identified that differed in growth dynamics relative to the average stand chronology. Samples were assigned to one or another dendrogroup based on the values of the correlation coefficients of each sample with the average chronology according to the following criteria: 1st dendrogroup $0.71 \leq r \leq 1.0$; 2nd dendrogroup $0.31 \leq r \leq 0.70$; 3rd dendrogroup $0.0 \leq r \leq 0.30$. The identified dendrogroups differ significantly in increment dynamics at the Student's *t*-criterion significance level ($p \leq 0.01$; Table 4).

Table 4. Values of synchronicity coefficients (GLK, %), correlation coefficients (CC, %), synchronicity level (GSL, *), and cross-dating indices (CDI, %) of the average radial increment chronologies of Scots pine by combined dendrogroups in the studied forest site types

Dendrogroups by increment dynamics	Average width of annual ring (mm)	GLK (%)	GSL	CC (%)	CDI (%)
Trial plot 1 (mixed-grass pine forest)					
Similarity of increment dynamics for all trees in a stand with average chronology	1.6	74	Average	82	63
1st dendrogroup: similar to the average increment dynamics (high synchronicity)	1.9 ^a	82 ^a	High	89 ^a	71 ^a
2nd dendrogroup: different from the average increment dynamics (average synchronicity)	1.5 ^b	68 ^b	Average	77 ^b	62 ^b
3rd dendrogroup: significantly different from average increment dynamics (low synchronicity)	1.3 ^c	60 ^c	Low	60 ^c	45 ^c
Trial plot 2 (purple moor-grass pine forest)					
Similarity of increment dynamics for all trees in a stand with average chronology	2.1	77	Average	81	67
1st dendrogroup: similar to the average increment dynamics (high synchronicity)	2.6 ^a	84 ^a	High	86 ^a	77 ^a
2nd dendrogroup: different from the average increment dynamics (average synchronicity)	1.9 ^b	73 ^b	Average	76 ^b	62 ^b
3rd dendrogroup: significantly different from average increment dynamics (low synchronicity)	1.6 ^c	46 ^c	Absent	52 ^c	31 ^c

Notes: Statistically significant differences between dendrogroups in each sample area ($p \leq 0.01$) are indicated by superscript letters (a – 1st dendrogroup, b – 2nd dendrogroup, c – 3rd dendrogroup). Differences between the 1st and 2nd dendrogroups (a and b) were significant at $p = 0.007$; between the 2nd and 3rd dendrogroups at $p = 0.003$; and between the 1st and 3rd dendrogroups at $p = 0.008$.

Trial plot 1, mixed-grass pine forest: – 1st dendrogroup: similar to the average increment dynamics for the entire stand (the most numerous group, 15 trees/60%: Nos. 23, 24, 25, 26, 27, 50, 52, 51, 53, 5, 32, 58, 89, 85, 78); – 2nd dendrogroup: different from the average increment dynamics (6 trees/24%: Nos. 28, 54, 79, 77, 81, 86); – 3rd dendrogroup: significantly different from the average increment dynamics (4 trees/16%: Nos. 1, 2, 55, 88).

Trial plot 2, purple moor-grass pine forest: – 1st dendrogroup: similar to the average increment dynamics for the entire stand (also the most numerous group, 13 trees/54%: Nos. 1–5, 9, 11, 14–16, 21, 23, 25); – 2nd dendrogroup: different from the average increment dynamics (4

trees/17%: Nos. 7, 8, 13, 24); – 3rd dendrogroup: significantly different from the average increment dynamics (7 trees/29%: Nos. 6, 10, 12, 17, 18, 19, 22).

The average tree-ring width is higher in the purple moor-grass pine forest (**Table 4**), as the growing conditions are more favorable for Scots pine. Under more favorable growing conditions, annual ring width increases (Soldatov et al. 2014; Timerbulatov 2024). In both studied stands, the average tree-ring width decreases from dendrogroup 1 to dendrogroup 3.

In the quantitative distribution of trees across dendrogroups, the differences between forest types are not very large. However, in both forest types, with slightly greater differentiation at the humid site, the traditional response to climatic factors predominated (60% and 54% for plots 1 and 2, respectively), while some trees showed a different (24% and 17%) or sharply different response (16% and 29%).

The traditional response reflects decreased growth in the year of drought and a slow recovery over 1–3 years or longer after drought. In the purple moor-grass pine forest, which is more humid, the similarity in dendrophenotype growth dynamics is slightly greater than in the mixed-grass pine forest (77% versus 74%), including in dendrogroups 1 and 2. The slightly lower overall similarity in dendrophenotype growth dynamics in the mixed-grass pine forest suggests that this forest type may be somewhat more susceptible to warming stress. In dendrogroup 3, synchronicity with the average is lower in TP 2 (46%) than in TP 1 (60%; **Table 4**). Thus, under humid conditions, seven trees show a sharply different response to climate, which may partly reflect genetic differences among trees and may become more apparent under global warming.

In general, the statistical parameters of similarity of individual chronologies with the average (GLK, CC, CDI) for the two studied stands are high, especially CC (82% and 81% at TP 1 and TP 2, respectively; **Table 4**).

The decrease in annual ring width from the 1st to the 3rd dendrogroups indicates that climate responses differ from the traditional response (predominant in the stand) in depressed trees (smaller in diameter and height).

It can be hypothesized that differentiated responses to limiting climatic factors during stand development lead to a change in "leaders," i.e., the transition of trees from growth leaders to laggards and vice versa. In mature stands, under severe climatic stress (e.g., severe drought), differentiated responses may allow trees in dendrogroups 2 and 3, thanks to their weak or absent stress response, to maintain their stability and contribute to the survival of the population as a whole.

Permata et al. (2023) studied the growth dynamics of forest stands in permanent measurement plots after selective logging and in control plots, and grouped the data into five diameter classes at 10-cm intervals. The data were analyzed by constructing a stand structure model and calculating growth and mortality rates. Growth values varied with increasing diameter class in both treated and untreated forests.

That is, in this study, the method for identifying groups of trees in a tree stand (diameter classes) was applied to compare growth and mortality rates, thereby contributing to the evaluation of the outcomes of forestry measures.

3.2. Radial Increment Responses to Climatic Factors

A graphical analysis of growth index dynamics in the three dendrogroups allowed us to assess variability in fluctuation amplitudes and growth extremes across different forest growth

conditions. **Fig. 3** shows the growth index dynamics for all dendrogroups across both sites. Dendrogroups 1 and 2 have the highest relative index values, reaching 250% in some years. All dendrogroups showed significant minimums in the early 1890s and after 2010.

Between 1980 and 2010, radial increment increased significantly in the mixed-grass pine forest, and between 1980 and 1990 in the purple moor-grass pine forest. Since 2010, radial increment has decreased in the mixed-grass pine forest, and since 1990 in the purple moor-grass pine forest. Moreover, the decrease in radial increment in the mixed-grass pine forest is more abrupt and significant, while in the purple moor-grass pine forest the decline is gradual.

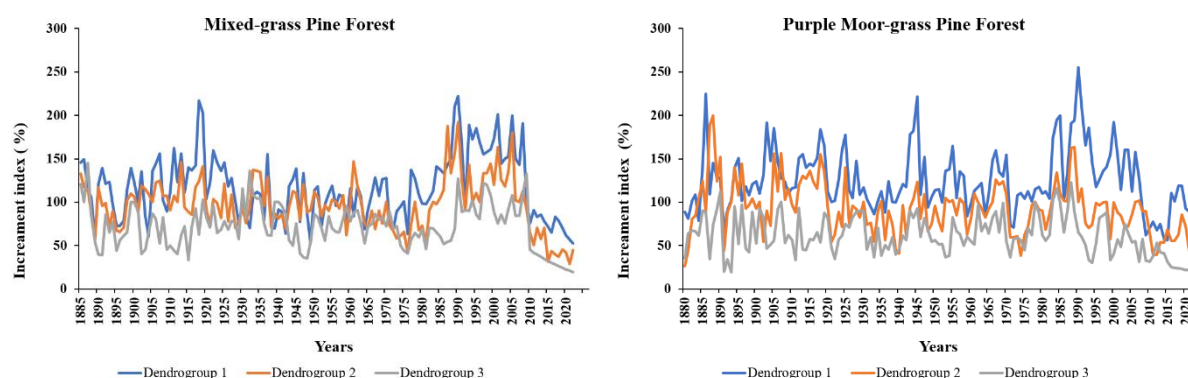


Fig. 3. Dynamics of increment indices in different forest site types: mixed-grass pine forest (left) and purple moor-grass pine forest (right).

[Demakov \(2023\)](#) argues that, along with age, genotypic features contribute to variability in trees' annual increment and, in some populations, account for up to 42.7% of the total variance. This variability was also evident in the correlation analysis, which showed asynchronous growth among trees that respond differently to environmental fluctuations. Our research identified dendrogroups within the studied stands that show statistically significant differences in radial growth dynamics. Variability in annual tree growth likely stems largely from genotypic differences.

According to many studies ([Matveev and Timashchuk 2019](#); [Matveev et al. 2022](#); [Yang et al. 2026](#)), atmospheric precipitation and temperatures during the active growing season (May–September) strongly influence radial increment in coniferous tree species, with regional characteristics considered.

A mathematical analysis was conducted to assess the relationships between the identified dendrogroups of Scots pine radial increment and climatic factors based on observations from the Voronezh meteorological station for the entire growth period (1883–2023). The selected climatic variables included precipitation amounts (as a limiting factor for tree growth in the forest-steppe) for the calendar year, the hydrological year, and the period May–September, as well as average air temperatures for May–September. The relationship between Scots pine radial increment and precipitation was also analyzed for two climatic periods: 1961–1990 and 1991–2020.

Our analysis of Scots pine radial increment across dendrogroups in response to precipitation fluctuations revealed significant differences in how the climatic signal was expressed. **Table 5** presents the correlation coefficients between Scots pine radial increment indices and climatic factors in forest plots with different moisture conditions over various periods. As shown in the table, most values are low (< 0.3) on the Chaddock scale ([Kiryushin et al. 2024](#)), except for precipitation totals during May–September, particularly in 1961–1990.

Table 5. Correlation coefficients between relative indices of radial increment of the Scots pine and climatic factors in forest site types with different moisture conditions

Dendrogroups by increment dynamics	Climatic factors					
	P_{year} (1883–2023)	$P_{\text{May-September}}$ (1883–2023)	$P_{\text{hydrological year}}$ (1883–2023)	$T_{\text{May-September}}$ (1883–2023)	$P_{\text{May-September for the period of the climatic norm}}$	
					1961–1990	1991–2020
Trial plot 1 (mixed-grass pine forest)						
1st dendrogroup: high synchronicity	0.19	0.29	0.24	0.14	0.58	0.27
2nd dendrogroup: average synchronicity	0.17	0.26	0.21	0.11	0.52	0.23
3rd dendrogroup: low synchronicity- asynchronous	0.16	0.21	0.19	0.07	0.40	0.19
Trial plot 2 (purple moor-grass pine forest)						
1st dendrogroup: high synchronicity	0.13	0.20	0.18	0.10	0.47	0.22
2nd dendrogroup: average synchronicity	0.12	0.16	0.15	0.07	0.41	0.19
3rd dendrogroup: low synchronicity- asynchronous	0.09	0.15	0.11	0.05	0.30	0.17

Notes: P_{year} – precipitation amount of the calendar year, mm; $P_{\text{May-September}}$ – precipitation amount of the period May–September, mm; $P_{\text{hydrological year}}$ – precipitation amount of the hydrological year, mm; $T_{\text{May-September}}$ – average air temperatures of the period May–September, °C.

A significant correlation between the radial increment of Scots pine and precipitation during May–September is observed in dendrogroups 1 and 2 in the mixed-grass pine forest, and a moderate correlation is observed in dendrogroup 3 in the mixed-grass pine forest and in dendrogroups 1 and 2 in the purple moor-grass pine forest. However, over the last 30 years (1991–2020), the correlation is weak at both sites. In the mixed-grass pine forest, the correlation coefficient between these variables is generally higher than in the purple moor-grass pine forest, and it decreases from the 1st to the 3rd dendrogroup at both study sites.

The significantly higher correlation coefficients between precipitation and radial increment for 1961–1990, and the decrease in these coefficients for 1991–2020, result from a combination of factors. In particular, temperature is increasingly important due to global warming, while precipitation as a limiting factor for tree growth is somewhat decreasing. Increasing climate instability and deteriorating forest conditions may explain a more differentiated response among different dendrophenotypes (adaptive response), and the correlation with dendrogroups is correspondingly reduced. Based on these data, precipitation during May–September was used in the regression analysis. In the mixed-grass pine forest, the strength of the influence of precipitation on the radial increment of pine is generally higher than in the purple moor-grass pine forest, and on both study sites it decreases from the 1st to the 3rd dendrogroup, as does the influence of air temperature (**Table 6**). Correlation analysis and the strength of climatic influence on radial increment across the two forest site types showed that the climatic signal is stronger under moderately moist conditions.

Table 6. Values of the influence strength of atmospheric precipitation and air temperatures on the radial increment of Scots pine for the selected dendrogroups in forest site types with different moisture conditions for the period from 1883 to 2023

Dendrogroups by increment dynamics	Climatic factors			
	P _{year}	P _{May–September}	T _{May–September}	P _{hydrological year}
Trial plot 1 (mixed-grass pine forest)				
1st dendrogroup: high synchronicity	0.33	0.69	0.25	0.55
2nd dendrogroup: average synchronicity	0.31	0.55	0.23	0.52
3rd dendrogroup: low synchronicity-asynchronous	0.30	0.52	0.18	0.45
Trial plot 2 (purple moor-grass pine forest)				
1st dendrogroup: high synchronicity	0.25	0.60	0.16	0.38
2nd dendrogroup: average synchronicity	0.24	0.51	0.13	0.30
3rd dendrogroup: low synchronicity-asynchronous	0.20	0.46	0.10	0.23

Analysis of the temporal dynamics of the relationship between the temperature/precipitation signal and radial increment during the growing season in the European North-East (Kutyavin and Manova 2022) showed a relatively unstable relationship between these indicators. In pine forests, a tendency towards a decrease in the climatic response of tree increment is observed. This pattern may reflect trees' adaptation to rising temperatures and, consequently, a reduced response to improving climatic conditions (Esper et al. 2024; Knorre et al. 2025). In the East European forest-steppe, where the limiting factor (drought) is strongly expressed and intensifying due to global warming, the climate signal is more pronounced in drier forest conditions (in the mixed-grass pine forest) than in moister conditions (in the purple moor-grass pine forest). Even with a small influence of air temperature directly on the increment dynamics, when the temperature changes, the evaporation conditions change significantly; that is, air temperatures change the impact of the limiting factor - the amount of precipitation.

3.3. Modeling Scots Pine Radial Increment

The authors of a review assessing forest biomass in Southeast Asia (Latifa et al. 2025), like many others, note the need to develop models characterizing ecosystem diversity. Based on the present study, multiple linear regression models of pine radial increment were constructed using growth-limiting climatic factors. The identified high values of the influence strength of atmospheric precipitation on the dynamics of the radial increment of pine during the warm period of the year (May–September), taking into account the variability of the average air temperatures for the same period, make it possible to construct an equation of multiple linear regression (1) for calculating the radial increment of pine (in relative indices) according to the named climatic factors for certain forest growth conditions:

Mixed-grass pine forest (trial plot 1) (Fig. 4A):

$$I(\%) = 107.2179 + 0.092 \cdot P_{5-9} - 0.09637 \cdot T_{5-9} \quad (2)$$

$$r = 0.91; R^2 = 0.825; F = 45 > F_{st}(3.06)$$

Purple moor-grass pine forest (trial plot 2) (Fig. 4B):

$$I(\%) = 116.7285 + 0.0162 \cdot P_{5-9} - 0.09285 \cdot T_{5-9} \quad (3)$$

$$r = 0.89; R^2 = 0.789; F = 50 > F_{st}(3.06)$$

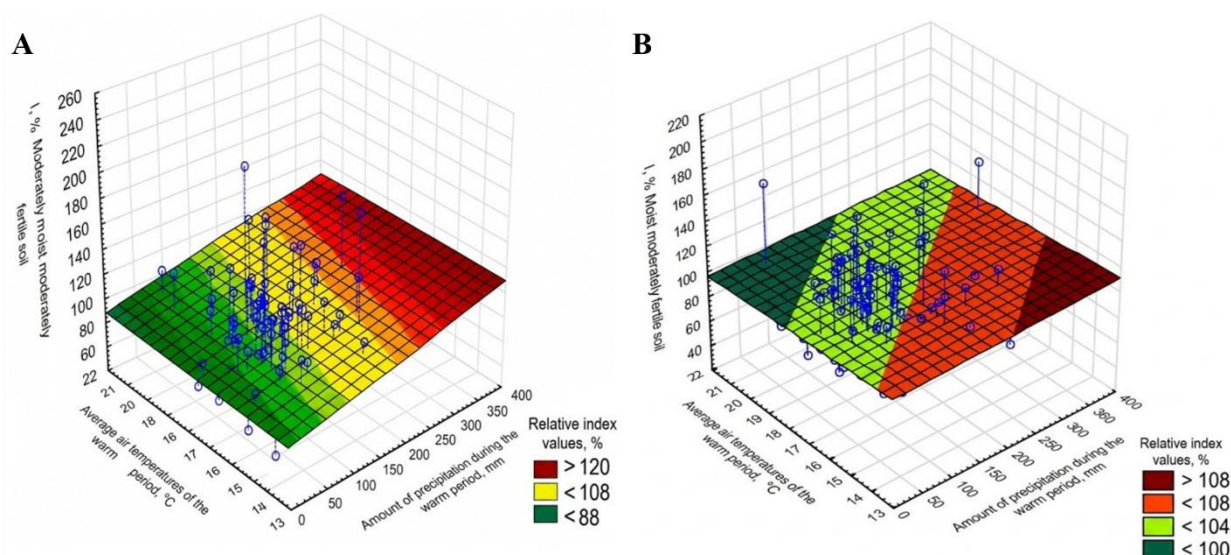


Fig. 4. Model of dependence of growth indices on precipitation amounts and average air temperatures for the period May–September from 1883 to 2023 by forest site types: A) mixed-grass pine forest; B) purple moor-grass pine forest.

An assessment of the statistical accuracy of the parameters of the obtained multiple regression equations, conducted using the Student's *t*-test, confirmed the high reliability of the extracted climate signals. Low standard errors (S_b) relative to the regression coefficients themselves indicate high mathematical accuracy of the approximation. The calculated 95% confidence intervals for all coefficients are narrow and do not include zero, indicating statistical significance. In the mixed-grass pine forest (trial plot 1), the 95% confidence interval for the coefficient of variable P_{5-9} is from 0.019 to 0.165, and that for variable T_{5-9} is from -0.167 to -0.026 . In the purple moor-grass pine forest (trial plot 2), the corresponding intervals are P_{5-9} : 0.001 to 0.031 and T_{5-9} : -0.159 to -0.026 .

While correlation coefficients show the strength and form of the relationship between the dynamics of radial wood growth and the dynamics of climate factors, the regression coefficients in the statistical model reflect the quantitative influence of climatic factors on the variability of radial increment. The Fisher criterion confirms the statistical significance of the regression equations.

Based on the statistical model obtained, the dependence of growth indicators on precipitation and average air temperature during May–September from 1883 to 2023 was graphically modeled for each forest site type (**Fig. 4**). A statistically significant increase in radial increment with increasing precipitation in the corresponding forest site types was observed.

The sharper transitions in color groups, reflecting the ranges of relative indices on the surface of the graphic model under wet conditions, indicate strong separation of trees within individual dominance ranks in the purple moor-grass pine forest. In contrast, the greater surface slope and smooth gradations of relative index ranges reflect the higher climatic response in the mixed-grass pine forest compared to the purple moor-grass pine forest.

The regression model presented in the work of [Nikiforchin et al. \(2020\)](#), compiled based on the results of multiple regression analysis using one tree as an example, also showed that the greatest contribution (57%) to the description of changes in tree growth is made by the total amount of precipitation per year. The average annual temperature accounted for 43% of the influence.

Individual tree growth depends on size, population- and individual-level characteristics, climate, stand density and anthropogenic and biogenic impacts on soil and ground conditions (Evans et al. 2016).

Climate warming promotes phytomass accumulation and carbon sequestration in forested areas with sufficient moisture, but threatens ecosystems on poor soils with insufficient moisture by suppressing tree growth and compromising stability (Malysheva et al. 2021). To maintain the sustainability and environmental functions of Scots pine forests in the East European forest-steppe, it is necessary to develop differentiated models of tree stand growth and development under a changing climate.

4. Conclusions

For the first time, intraspecific (intrapopulation) differentiation of trees based on their adaptive potential to changing climatic conditions has been established for Scots pine growing in the Eastern European forest-steppe. Principles for identifying dendrogroups based on their response to limiting climatic factors have also been developed. The climate signal is stronger in mixed-grass pine forest (moderately humid conditions) than in purple moor-grass pine forest (humid conditions), suggesting greater sensitivity to climate change under the less humid conditions examined in this study. The identified dendrogroups demonstrated differentiated responses of individual dendrophenotypes to climatic factors limiting tree growth within populations. The presence of differentiated responses indicates the need for a differentiated approach to constructing models of growth and development of forest stands in each population, taking into account the presence of dendrogroups, to improve forest management and maintain the stability of pine forests in changing climatic conditions, as well as for the selection of promising dendrophenotypes with high adaptive potential for artificial reforestation.

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Author Contributions

S.M.: Conceptualization, Supervision, Data Collection, Data Processing and Analysis, Interpretation, Visualization, Literature Search, Writing – Original Draft Preparation, Writing – Review and Editing, Funding Acquisition; D.L.: Conceptualization, Data Collection, Data Processing and Analysis, Interpretation, Visualization, Literature Search, Writing – Original Draft Preparation, Funding Acquisition; M.G.: Interpretation, Writing – Original Draft Preparation.

Conflict of Interest

The authors declare no conflict of interest.

Declaration of Generative AI and AI-Assisted Technologies in the Manuscript Preparation

During the preparation of this work, the authors used ChatGPT (OpenAI) to improve language clarity and academic writing quality. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the content of the publication.

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