

Article

The More the Merrier or the Fewer the Better Fare? Effects of Stand Density on Tree Growth and Climatic Response in a Scots Pine Plantation

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Abstract: In forests, the growth and productivity of individual trees and stands as a whole are regulated by stand density among other factors, because access to vital resources is limited by competition between trees. On 18 experimental plots of Scots pine (*Pinus sylvestris* L.) planted with a density of 500–128,000 trees/ha in the south taiga (Middle Siberia), interactions between stand density, tree- and stand-scale productivity, and tree-ring parameters were investigated. Tree-scale productivity variables, tree-ring width, and latewood width had stable negative allometric relationships with stand density ($R^2 > 0.75$), except for tree height (insignificant for inventory surveys at ages of 20 and 25 years; $R^2 > 0.4$ at the age of 35 years), while positive allometry was registered for stand productivity variables ($R^2 > 0.7$) and the all-time average latewood ratio ($R^2 = 0.5$ with planting density). Tree-ring parameters aside from the age trends correlate ($p < 0.05$) between the plots and demonstrate common responses to moderate moisture deficit. Although, its seasonality apparently depends on the resource base and intensity changes with stand density. February–June precipitation is more important for pine growth in dense stands, July–August conditions affect the latewood ratio stronger in sparse stands, and medium-density stands are more resistant to winter frosts.

Keywords: stand density; productivity; tree-ring width; latewood width; latewood ratio; Scots pine; growth–climate relationship



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1. Introduction

Forest ecosystems play an indispensable role in the mitigation of climate change and in the protection of the environment [1,2]. However, shifts in the phenology and spatial distribution of tree species due to observed climate warming are leading to changes in forest productivity, biodiversity, structure, and, ultimately, the functioning of forest ecosystems as such [3–6]. Therefore, understanding the mechanism of forests' response to climate change is of great importance for sustainable forest management [7].

Tree growth is modulated by a large number of abiotic and biotic factors: from climate, landscape, and catastrophic natural phenomena to interrelations within the biocenosis, the impact of phytophages, etc. [8–14]. At the same time, there is a significant contribution of the individual tree characteristics, including the genotype, phenotype, age, etc., to tree growth and its response to external impacts [15–17].

Due to complex tree–environment interactions, the intensity of competition plays a vital role within a homogeneous habitat limited by common conditions, such as the soil substrate, topography, established biocenosis structure, and so on [18–24]. Access to vital resources can be limited by interactions between trees, mainly competition dependent on stand density; this leads to the gradual differentiation of the stand structure with age [25–27]. With a rapidly changing environment, including a warming climate, competition can intensify dramatically, with effects ranging from increased water stress and altered pest and disease resistance to altered availability of basic nutrients [9,28–31]. As a result, the competition for limited resources can fundamentally determine the ability of individual trees to allocate biomass, particularly, radial growth and its response to abiotic factors including droughts [31–36].

The result of the intra-specific competition for each individual tree depends on the morphophysiological characteristics and individual heredity, as well as on development conditions such as the micro-landscape, an excess or lack of moisture, cover from frost and sun, etc. [37–39]. In this regard, the phytosocial structure of stands is a key factor that significantly regulates the availability of life-sustaining resources such as light, water, and soil nutrients for each tree [35,40,41]. Additionally, competition significantly affects the allometric ratios and the distribution of biomass along the stem, branches, and foliage [42–44]. Social status may be crucial in the process of differentiating the biomass accumulation by parts of a tree [27]. The result of such competitive relationships is clearly visible in the external appearance of woody plants, since in almost any forest (mono- or mixed-species and even- or mixed-aged), we can visually observe the differentiation of trees in terms of growth and development. However, there is no clear answer to the question of whether dominant trees always gain a competitive and survival advantage [45–47].

As stand density changes, tree species vary greatly in their ability to alter their radial growth [48] due to the interaction between competition and environmental conditions (e.g., [32]). Scots pine as a subject for dendroclimatic research is unique in its versatility due to the wide ecological range from extremely xeric sites in semiarid climates to humid wetland habitats [49,50]. The radial growth of this species, as a good indicator of water stress [51], can be successfully used to assess forest management options designed to mitigate climate change in regions with moisture deficiency. In addition, the regulation of stand density will be an option here which assists forest stands in adaptation to the future climate [52].

This study was carried out in unique experimental plantations in the southern taiga of Middle Siberia, where the conifers were planted with a wide gradient of stand density [20,24,53,54]. Evaluation of the contribution of the initial planting density (and its dynamics due to self-thinning) to the dynamics of productivity, tree radial growth, the ratio of earlywood and latewood, and their response to external stresses provides data useful in silviculture. For example, it assists in determining a forest management regime that provides a compromise between the tree growth stability in a changing climate, the stock of organic matter in the forest stand (carbon deposition), and the quality of the developed wood. In practical terms, the results of this experiment are applicable for optimizing the phytosocial structure of artificial plantations and natural forest stands on a fairly large spatial scale due to the investigation of widespread species that are dominant trees in many Siberian forests.

In addition to the relationship between the competition intensity (stand density) and the productivity and growth indicators in the Scots pine stand, the study addressed the question as to how this factor impacts: (i) the reactions of pine growth to climatic variability and (ii) the dynamics of the tree ring width, latewood width, and latewood ratio.

2. Materials and Methods

2.1. Study Area and Experimental Plantation

The study was carried out in Middle Siberia (central part of the Krasnoyarsk Krai), in the subzone of the southern taiga represented by conifer forests with the addition of

broad-leaf species. The landscape of the study area is flat; the climate is continental, with large amplitudes of daily and seasonal temperature fluctuations. This study object is the experimental plantations of conifers planted by the Sukachev Institute of Forest, Siberian Branch of the USSR Academy of Sciences (Krasnoyarsk) in the vicinity of Talovka village ($57^{\circ}12'18''$ N $93^{\circ}08'36''$ E, 240 m a.s.l.) on agricultural lands. These territories were historically covered with pine–larch forests before the Russians settled there, so the soil on the plantation is a loamy alfisol. For the experiment in 1982, two-year-old seedlings of Siberian spruce (*Picea obovata* Ledeb.), Scots pine (*Pinus sylvestris* L.), and Siberian larch (*Larix sibirica* Ledeb.) were planted on the flat plain in a mostly rectangular pattern using 18 planting densities ($DENS_0 = 500\text{--}128,000$ trees/ha; Figure 1a and Table 1). At least 500 individuals were planted for each planting density.

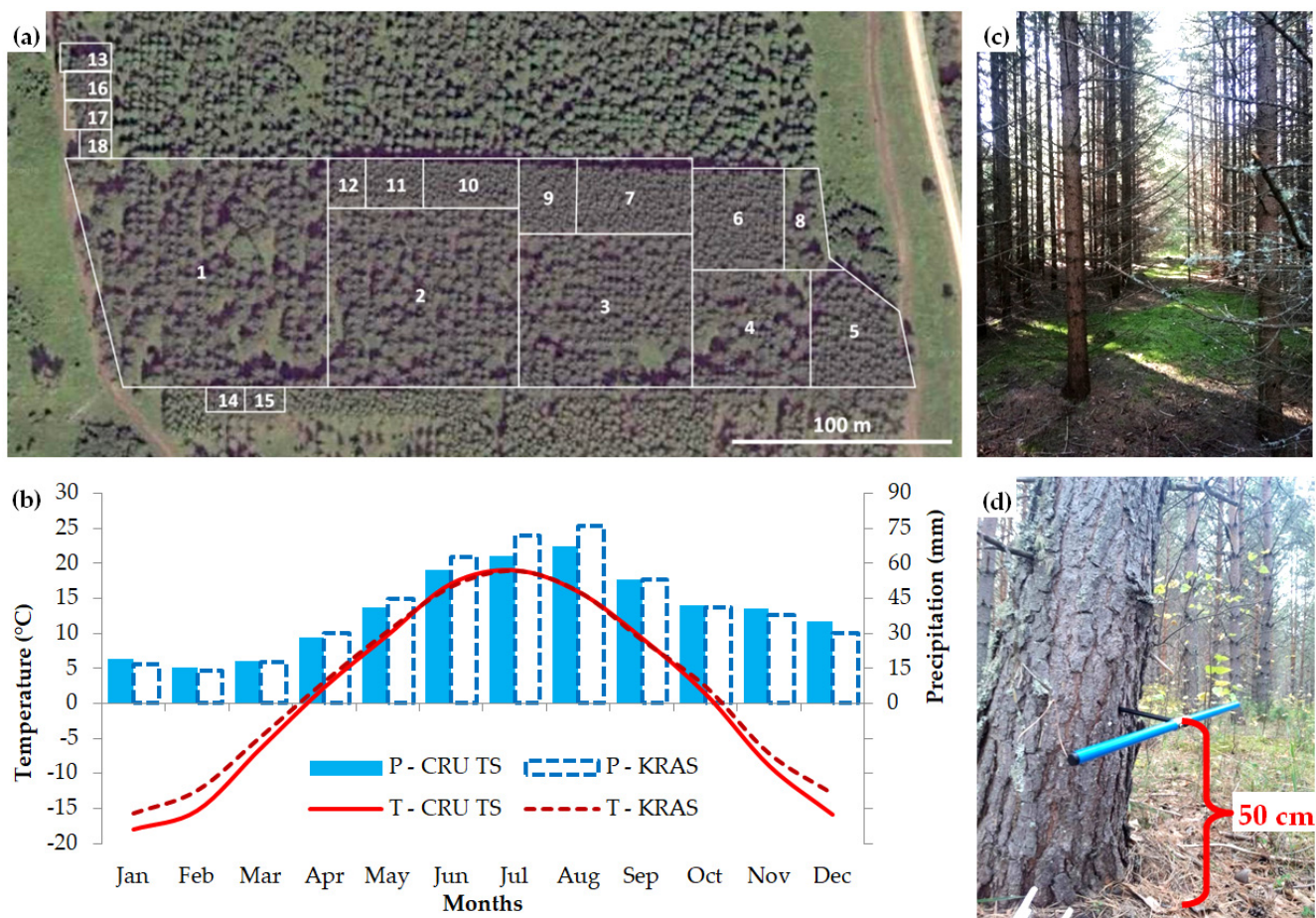


Figure 1. The study area: (a) aerial map of experimental plantation; the plots where the Scots pine was planted are marked and numbered according to Table 1; plot #8 was omitted from the study due to the failure of many seedlings soon after planting; (b) monthly temperature T and precipitation P (1988–2019) from the Krasnoyarsk climatic station (KRAS; dashed lines) and from the CRU TS field (solid lines) for the grid cell corresponding to the plantation’s location; (c) plots of Siberian larch (left) and Scots pine (right) divided by clearing; (d) collecting of a wood sample (core) by an increment borer from a pine tree in the low-density plot.

In this study, a monthly series of mean temperature T and precipitation P from the spatially distributed field CRU TS (https://climexp.knmi.nl/selectfield_obs2.cgi; accessed on 20 January 2023) were used for a geographic grid cell including the plantation location ($57\text{--}57.5^{\circ}$ N $93\text{--}93.5^{\circ}$ E), as well as monthly and daily series of the Krasnoyarsk weather station 120 km south of the study area ($56^{\circ}02'$ N $92^{\circ}45'$ E, 277 m a.s.l.; <http://meteo.ru/data>; accessed on 20 January 2023; Figure 1b). For the period 1988–2020 used for the analysis of the climatic response in the studied plantations, the average annual temperatures are

+0.9 °C in the study area and +2.0 °C in Krasnoyarsk; the average annual precipitation is 480 and 496 mm, respectively. The warmest month is July (+19.0 and +19.1 °C); the coldest month is January (−18.0 and −15.8 °C, respectively). Temperatures exceed +5 °C from May to September on average, during which time about 60% of the annual precipitation falls. The maximum monthly precipitation is observed in August (67 and 76 mm, respectively); the minimum precipitation is observed in February (14–15 mm).

Table 1. Characteristics of the tree-ring width data.

Plot	Raw TRW Measurements				Standard TRW Chronology				
Code	DENS ₀ (Trees/ha)	Trees/ Cores	Period (Years)	Length (Years)	<i>r-bar</i>	<i>SD</i>	<i>sens</i>	<i>r-bar</i>	<i>ar-1</i>
1PS	500	10/20	1987–2020	33	0.68	0.11	0.13	0.41	0.08
2PS	750	10/20	1986–2020	34	0.78	0.10	0.12	0.45	0.01
3PS	1000	10/19	1986–2020	34	0.91	0.10	0.11	0.48	0.07
4PS	1500	9/18	1987–2020	33	0.88	0.09	0.11	0.37	0.03
5PS	2000	10/20	1987–2020	33	0.91	0.11	0.12	0.40	0.13
6PS	3000	10/20	1986–2020	34	0.92	0.11	0.14	0.49	0.01
7PS	4000	11/22	1988–2020	32	0.92	0.12	0.13	0.49	0.06
9PS	8000	10/20	1986–2020	34	0.88	0.15	0.15	0.54	0.17
10PS	10,000	10/19	1983–2020	37	0.83	0.20	0.16	0.47	0.07
11PS	12,000	10/20	1987–2020	33	0.88	0.13	0.15	0.52	0.03
12PS	16,000	10/19	1985–2020	35	0.85	0.17	0.15	0.53	0.31
13PS	24,000	10/20	1985–2020	35	0.84	0.15	0.16	0.42	0.07
14PS	36,000	10/20	1985–2020	35	0.81	0.13	0.16	0.50	−0.02
15PS	48,000	10/20	1986–2020	34	0.78	0.14	0.14	0.45	0.13
16PS	64,000	10/20	1985–2020	35	0.63	0.10	0.12	0.37	−0.04
17PS	96,000	10/20	1984–2020	36	0.71	0.16	0.18	0.33	−0.06
18PS	128,000	10/20	1984–2020	36	0.71	0.14	0.16	0.27	−0.07

DENS₀, initial stand density (planting density); TRW, tree-ring width; *SD*, standard deviation; *sens*, coefficient of sensitivity; *r-bar*, inter-series correlation coefficient; *ar-1*, first-order autocorrelation coefficient.

2.2. Data on Tree Morphometry and Radial Growth

Inventory measurements were carried out in 2000, 2005, and 2015 according to methods generally accepted in Russia [55–58]. For each plot, the stand density (DENS, number of trees per hectare), the diameter at 1.3 m from the soil surface (DBH), and the height (H) of trees were measured. As inventory indicators of tree productivity for each plot, we used root-mean-square DBH values based on measurements for all living trees except the outer rows and arithmetic mean H based on measurements for 25–30 model trees of different sizes. The outer rows were omitted due to differing stand densities on the boundary of the plot (edge effect). The basal area of the trunk was calculated based on the root mean square diameter ($BA = \pi \cdot DBH^2 / 4$). Trunk volume *V* was calculated using the formula $V = BA \cdot H \cdot f$ [59], where $f = Q_{0.5}^2$ is the form factor (ratio of tree trunk volume to the volume of the cylinder with diameter DBH and height H) and $Q_{0.5}$ is the form quotient (ratio of the tree diameter at the half height to DBH). We implemented the average value of the form quotient for the Scots pine species, $Q_{0.5} = 0.67$ [60]. Stand productivity per area unit was estimated in each plot using the total basal area and timber stock, calculated with multiplying the BA and *V* values, respectively, by the stand density DENS.

To collect wood samples (cores) in 2020, ten dominant (the largest and most well developed) trees per plot were selected, also with the exception of the outer rows. The choice of dominant individuals allows one to focus on the growth dynamics of trees that are more likely to survive in the future since both self-thinning and thinning tend to remove depressed trees [61,62].

Cores were collected and processed using standard dendrochronology techniques [63], with two cores per tree. Individual tree ring width (TRW) series were measured on a LINTAB measuring platform using the TSAP program [64] and cross-dated using the COFECHA program [65]. Then, in the ARSTAN program [66], age trends described by a

67% cubic smoothing spline were removed from the original series, using the division of the measured values by the trend values. Based on the raw and indexed series of individual cores, generalized chronologies for the plots were obtained as the bi-weight mean. In the same way as TRW, generalized chronologies of latewood width (LWW) were obtained. The boundary between earlywood and latewood within the ring was determined visually [67]. In addition, for each site, the dynamics of the latewood ratio ($LWR = LWW/TRW$) was calculated based on the generalized raw chronologies of TRW and LWW. For the period 1988–2020, within which this parameter was steadily increasing for all plots, linear trends were calculated and standardization (indexing) of the LWR series was carried out as a division of the actual values by the trend values.

For the raw and standardized series of TRW, the inter-series correlation coefficients ($r\text{-bar}$) were calculated to estimate the common external signal. The variability of local standardized TRW chronologies was assessed by the standard deviation (SD), sensitivity coefficient ($sens = |TRW_t - TRW_{t-1}| / mean(TRW_t, TRW_{t-1})$), and first-order autocorrelation coefficient (ar_{-1}). Due to the sampling of two cores per tree, all TRW chronologies were found to have an expressed population signal (EPS) above 0.85 [68].

2.3. Statistical Analysis

Relationships among variables describing the growth of individual trees and total forest stand were assessed using simple linear regression models, where both variables or one of them were usually transformed into a logarithmic scale by a natural logarithmic function. In the first case, the linear function in log–log scale $\ln(y) = a \cdot \ln(x) + b$ (where y is the dependent variable, x is the independent variable, and a and b are the numerical coefficients) corresponds to the simple allometric power function $y = b' \cdot x^a$, where $b' = \exp(b)$. In the second case, the linear function for log-scale dependent variable $\ln(y) = a \cdot x + b$ corresponds to the exponential function $y = b' \cdot \exp(a \cdot x)$. For each relationship, we tested both functions and used the one better fitting the actual data. Fitting of numerical coefficients with the least squares method and calculation of the determination coefficient R^2 were performed in the linear forms of the regression models.

Dendroclimatic analysis was carried out by calculating Pearson's pairwise correlation coefficients between generalized indexed chronologies of TRW, LWW, and LWR and climatic series for the period 1988–2020 (common period of all of the time series). Correlations were calculated for the period from August of the year prior to tree ring formation (previous year) to August of the year of tree ring formation (current year). Comparison of monthly climate data series showed that over the period of dendroclimatic analysis, the correlations between the CRU TS series for the study area and the Krasnoyarsk station series for the same months were 0.89–0.98 (0.96 on average) for temperatures and 0.42–0.91 (0.75 on average) for precipitation. Such spatial synchronicity confirms the suitability for using dendroclimatic analysis not only for the local monthly CRU TS 4.04 series, but also, with some caution, for the daily data from the remote Krasnoyarsk station. In the latter case, to assess the detailed response of tree-ring parameters to climatic factors, a moving series with a window of 21 days and a step of 1 day (for example, 1–21 May, 2–22 May, etc.) were calculated on the basis of daily data and used in the dendroclimatic analysis.

The significance level p of all relationships was estimated with a two-tailed t -test.

3. Results

3.1. Dynamics of Pine Stand Density, Productivity, and Radial Growth Parameters

When establishing experimental stands, planting densities in the range of 500–128,000 trees per hectare were selected with approximately uniform steps on a logarithmic scale (Figure 2). Negative trends in the stand density with age in the absence of logging describe the process of self-thinning, i.e., die-off of the most oppressed trees. Regression models of the stand density versus age, using a negative exponential function $DENS = DENS_0 \cdot \exp[-a(A - A_0)]$ (where $A_0 = 2$ years is the absolute age of seedlings when planted), describe 80 to 99% of its variation (Table A1). In this function, the numerical coefficient a

(regulating the tree mortality rate) slightly decreases with planting density at first, reaches a minimum in plots with planting densities of 3000–8000 trees/ha, and then significantly increases depending on the logarithm of $DENS_0$. This relationship can be described as a linear ($R^2 = 0.566$, $p < 0.05$) or quadratic regression ($R^2 = 0.922$, $p < 0.05$). Indeed, at the time of the last inventory (2015), the actual mortality was 43%–61% of trees in stands with $DENS_0 = 500$ –2000 trees/ha, 33%–49% in stands with $DENS_0 = 3000$ –10,000 trees/ha, and then there was a gradual increase in mortality from 48% to 91% in the densest stands. As a result, the range of stand density decreased to 228–11,750 trees/ha by the age of 35 years.

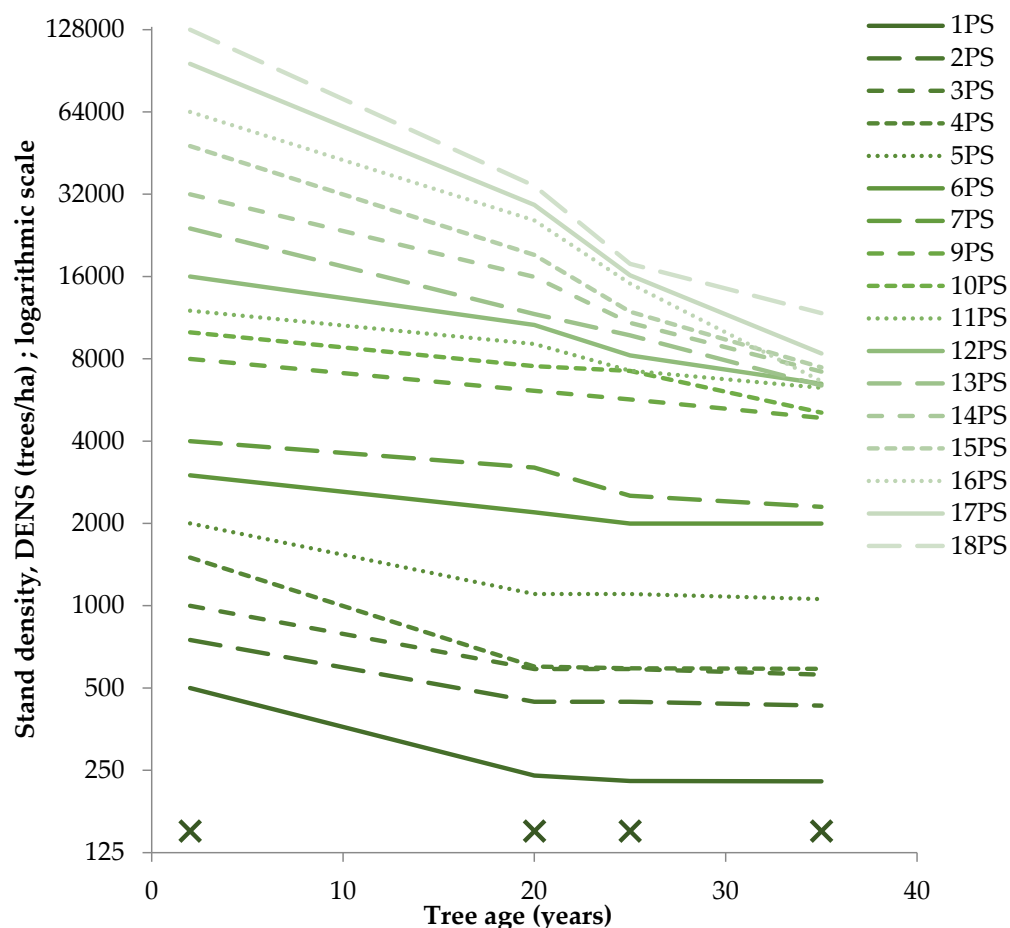


Figure 2. Dynamics of stand density DENS versus the absolute age of the trees in each experimental plot. The planting of 2-year-old seedlings in 1982 and inventories in 2000, 2005, and 2015 are marked with crosses.

The average tree diameter during each inventory significantly ($p < 0.05$) negatively depended on both the planting density and stand density at the moment of inventory (Table 2), and the dependence is closest to linear for the logarithmic scales of both variables. The fitness of the relationship is consistently high, but with age, an increase in the slope of the linear function was observed for functions of contemporary density DENS, both due to the accumulation of differences between the plots in diameter and due to a decrease in the range of the stand density. At the same time, the negative dependence of tree height on stand density became statistically significant ($p < 0.05$) only at the last inventory.

For derivative indicators of tree productivity, average basal area, and trunk volume, the dependence on stand density indicators is negative and consistently high, as it is for DBH, but the slope angle changes little with tree age in functions of both $DENS_0$ and DENS. All indicators of growth and productivity of individual trees, except for height, depend to a greater extent on the stand density at the same moment than on the planting density. On the other hand, their dependences on planting density have slopes more stable with age.

Table 2. Dependences of tree diameter, height, and derivative productivity indicators on stand density variables in experimental plots for various tree ages.

Age (Years)	Function of Planting Density $DENS_0$ (Trees/ha)			Function of Contemporary Stand Density $DENS$ (Trees/ha)		
	Equation	R	R^2	Equation	R	R^2
Tree diameter at the breast height, DBH (cm)						
20	$\ln(DBH) = -0.246 \cdot \ln(DENS_0) + 4.377$	0.981	0.962	$\ln(DBH) = -0.268 \cdot \ln(DENS) + 4.404$	0.982	0.965
25	$\ln(DBH) = -0.248 \cdot \ln(DENS_0) + 4.597$	0.981	0.962	$\ln(DBH) = -0.306 \cdot \ln(DENS) + 4.858$	0.988	0.976
35	$\ln(DBH) = -0.221 \cdot \ln(DENS_0) + 4.688$	0.954	0.910	$\ln(DBH) = -0.325 \cdot \ln(DENS) + 5.262$	0.987	0.974
Tree height, H (m)						
20	$\ln(H) = -0.010 \cdot \ln(DENS_0) + 2.153$	0.306	0.094	$\ln(H) = -0.010 \cdot \ln(DENS) + 2.148$	0.285	0.081
25	$\ln(H) = -0.007 \cdot \ln(DENS_0) + 2.486$	0.247	0.061	$\ln(H) = -0.008 \cdot \ln(DENS) + 2.489$	0.232	0.054
35	$\ln(H) = -0.030 \cdot \ln(DENS_0) + 2.966$	0.737	0.543	$\ln(H) = -0.036 \cdot \ln(DENS) + 2.987$	0.637	0.406
Tree trunk volume, V (m ³)						
20	$\ln(V) = -0.501 \cdot \ln(DENS_0) + 0.655$	0.972	0.944	$\ln(V) = -0.545 \cdot \ln(DENS) + 0.702$	0.972	0.945
25	$\ln(V) = -0.503 \cdot \ln(DENS_0) + 1.428$	0.976	0.952	$\ln(V) = -0.620 \cdot \ln(DENS) + 1.953$	0.982	0.964
35	$\ln(V) = -0.472 \cdot \ln(DENS_0) + 2.090$	0.956	0.914	$\ln(V) = -0.687 \cdot \ln(DENS) + 3.258$	0.979	0.958
Tree basal area, BA (m ²)						
20	$\ln(BA) = -0.491 \cdot \ln(DENS_0) - 0.697$	0.981	0.961	$\ln(BA) = -0.535 \cdot \ln(DENS) - 0.645$	0.982	0.965
25	$\ln(BA) = -0.496 \cdot \ln(DENS_0) - 0.257$	0.981	0.962	$\ln(BA) = -0.612 \cdot \ln(DENS) + 0.265$	0.988	0.976
35	$\ln(BA) = -0.443 \cdot \ln(DENS_0) - 0.076$	0.954	0.910	$\ln(BA) = -0.650 \cdot \ln(DENS) + 1.073$	0.987	0.974
Total wood volume, i.e., timber stock, ΣV (m ³ /ha)						
20	$\ln(\Sigma V) = 0.404 \cdot \ln(DENS_0) + 0.874$	0.927	0.859	$\ln(\Sigma V) = 0.455 \cdot \ln(DENS) + 0.702$	0.960	0.923
25	$\ln(\Sigma V) = 0.287 \cdot \ln(DENS_0) + 2.463$	0.883	0.780	$\ln(\Sigma V) = 0.380 \cdot \ln(DENS) + 1.953$	0.953	0.909
35	$\ln(\Sigma V) = 0.193 \cdot \ln(DENS_0) + 3.998$	0.794	0.631	$\ln(\Sigma V) = 0.313 \cdot \ln(DENS) + 3.258$	0.909	0.827
Total basal area, ΣBA (m ² /ha)						
20	$\ln(\Sigma BA) = 0.413 \cdot \ln(DENS_0) - 0.478$	0.945	0.892	$\ln(\Sigma BA) = 0.465 \cdot \ln(DENS) - 0.645$	0.977	0.954
25	$\ln(\Sigma BA) = 0.294 \cdot \ln(DENS_0) + 0.778$	0.902	0.813	$\ln(\Sigma BA) = 0.388 \cdot \ln(DENS) + 0.265$	0.970	0.941
35	$\ln(\Sigma BA) = 0.222 \cdot \ln(DENS_0) + 1.833$	0.864	0.747	$\ln(\Sigma BA) = 0.350 \cdot \ln(DENS) + 1.073$	0.957	0.917

R is the correlation between the actual values and the model; significant correlations ($p < 0.05$) are in bold; R^2 is the determination coefficient.

Stand productivity indicators (total basal area and timber stock per area unit), on the contrary, are positively related to both density variables. The fitness of these relationships is consistently high for all considered tree ages ($R^2 > 0.9$ for most of functions). On the contrary, a decrease in the slope of the function was observed with age, more pronounced for planting density.

The long-term mean value of the tree ring width was strongly negatively correlated with the planting density on a log–log scale (Table 3). Comparing the data of further inventories, its dependence on the stand density gradually decreased with age, although the slope increased. It is also noticeable in the graphs of the raw TRW values (Figure 3a) that the maximum radial increment gradually shifts from 1995 in the 1PS–5PS plots to 1987 in the 17PS–18PS plots. Until the occurrence of this maximum, the tree-ring width dynamics is similar in all plots. The synchronous nature of age trends within each plot is confirmed by the very high inter-series correlations of the raw TRW series (0.63–0.92) compared to the ones of the standardized series (0.27–0.54). At the same time, the standardized TRW chronologies (Figure 3b) show a high similarity of interannual growth variation between all plots. For the common period 1988–2020, the correlations between the standardized chronologies are all significant (0.36–0.96, $p < 0.05$) (Figure 4). The highest correlations were observed between chronologies from plots of similar densities, but even correlations between chronologies of the most and the least dense stands became significant after standardization. The variability of standard TRW chronologies is low, both in general ($SD = 0.09$ – 0.20) and year-to-year ($sens = 0.12$ – 0.18).

Table 3. Dependencies of tree-ring parameters (average values since respective inventories) on stand density in experimental plots for various tree ages.

Age (Years)	Function of Stand Density DENS (Trees/ha)		
	Equation	R	R ²
Tree-ring width, TRW (mm)			
2	$\ln(\text{TRW}) = -0.222 \cdot \ln(\text{DENS}_0) + 2.911$	0.961	0.923
20	$\ln(\text{TRW}) = -0.278 \cdot \ln(\text{DENS}) + 2.918$	0.947	0.897
25	$\ln(\text{TRW}) = -0.295 \cdot \ln(\text{DENS}) + 2.881$	0.925	0.856
35	$\ln(\text{TRW}) = -0.333 \cdot \ln(\text{DENS}) + 2.934$	0.883	0.780
Latewood width, LWW (mm)			
2	$\ln(\text{LWW}) = -0.198 \cdot \ln(\text{DENS}_0) + 1.233$	0.946	0.894
20	$\ln(\text{LWW}) = -0.237 \cdot \ln(\text{DENS}) + 1.339$	0.935	0.874
25	$\ln(\text{LWW}) = -0.255 \cdot \ln(\text{DENS}) + 1.388$	0.916	0.838
35	$\ln(\text{LWW}) = -0.321 \cdot \ln(\text{DENS}) + 1.712$	0.867	0.751
Latewood ratio, LWR (dimensionless)			
2	$\ln(\text{LWR}) = 0.031 \cdot \ln(\text{DENS}_0) - 1.642$	0.708	0.502
20	$\ln(\text{LWR}) = 0.038 \cdot \ln(\text{DENS}) - 1.522$	0.735	0.540
25	$\ln(\text{LWR}) = 0.034 \cdot \ln(\text{DENS}) - 1.434$	0.632	0.399
35	$\ln(\text{LWR}) = 0.012 \cdot \ln(\text{DENS}) - 1.215$	0.209	0.044

R is the correlation between the actual values and the model; significant correlations ($p < 0.05$) are in bold; R² is the determination coefficient.

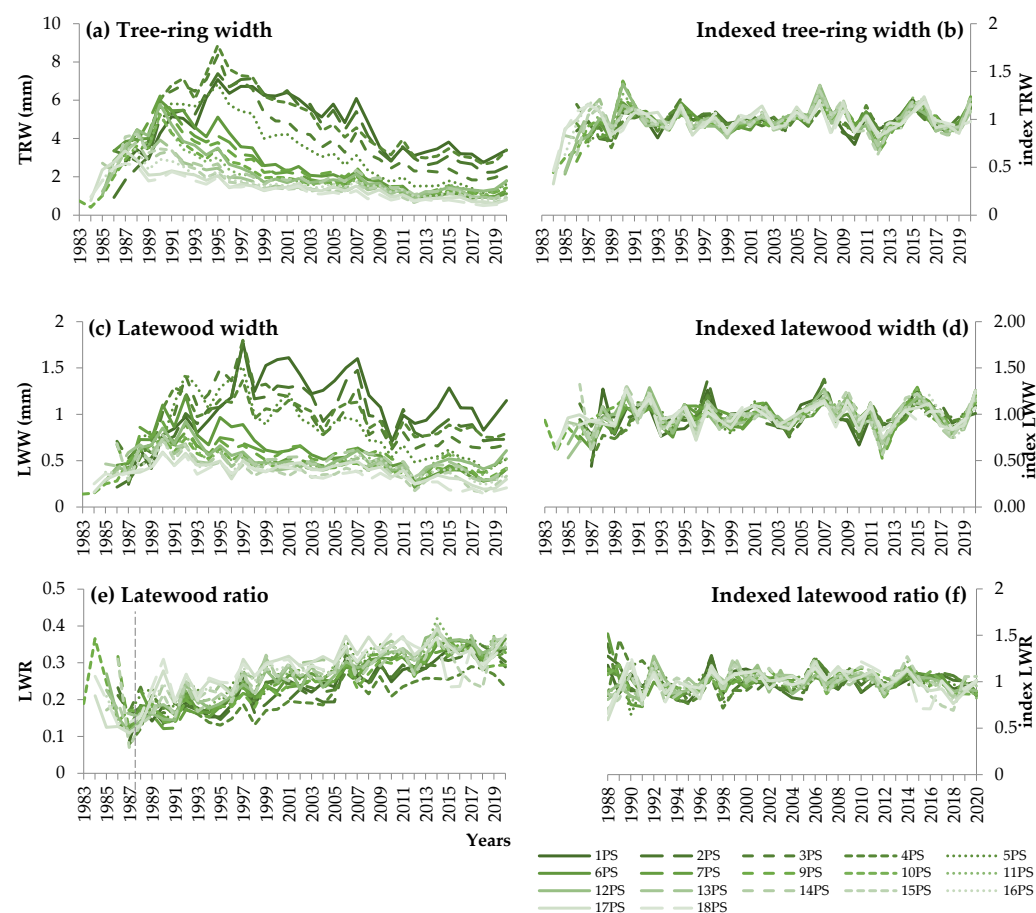


Figure 3. Dynamics of tree-ring parameters of pine at the experimental plots: raw (a) and standard (b) chronologies of tree-ring width TRW; raw (c) and standard (d) chronologies of latewood width LWW; latewood ratio LWR, i.e., the ratio of LWW to TRW based on their raw chronologies (e) and its index after elimination of linear trend calculated for the period 1988–2020 (f).

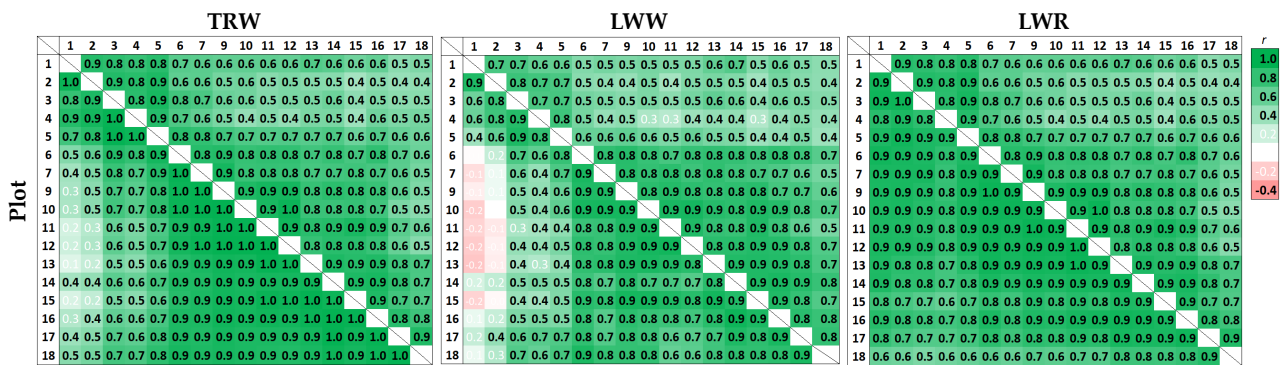


Figure 4. Between-plot correlations of raw (below diagonal) and indexed (above diagonal) chronologies (1988–2020): tree-ring width (TRW), latewood width (LWW), and latewood ratio (LWR). The color gradient marks the correlation values (legend). Black values are significant at $p < 0.05$.

Latewood width LWW also has a significant ($p < 0.05$) negative allometric dependence on planting density (Table 3) and, to a lesser extent, on the contemporary values of the stand density. Its raw series and standard chronologies (Figure 3c,d) are slightly less synchronous with each other compared to TRW (raw: $r = -0.22-0.95$, $p < 0.05$ for 82% of correlations; standard: $r = 0.28-0.95$, 98%; Figure 4). Nevertheless, there is a common pattern in the correlations of the TRW and LWW chronologies: the presence of two groups, 1PS–5PS and 6PS–18PS, where within-group correlations are higher than between-group ones (for both raw and standard chronologies). The latewood ratio in the ring LWR (Figure 3e), in contrast, increases with the planting density. The dependence of the latewood ratio in subsequent rings on the stand density is the maximum for the age of 20 years and then weakens, losing significance by the age of 35 years (Table 3). For the raw LWR series over 1988–2020, the correlations between the plots are the most stable in comparison to other tree-ring parameters under consideration, being in the range $r = 0.52-0.97$. After removing long-term trends (Figure 3f), the correlations decrease to $r = 0.36-0.96$ but still remain significant at $p < 0.05$.

Note that the raw LWW and TRW values are closely positively related to each other for all plots: $r = 0.67-0.95$ (Table 4). The negative relationship between LWR and TRW is somewhat less pronounced but stably significant; the correlations range from -0.48 to -0.93 . The width and proportion of latewood also correlate negatively in most stands (from -0.80 to 0.31), but this relationship is not always significant. After standardization of the LWW and TRW chronologies, the relationship between them somewhat weakens: $r = 0.46-0.86$. The LWW and LWR indices, in contrast to their raw values, are positively related to each other ($r = 0.14-0.71$), while the correlations between the TRW and LWR indexed chronologies range from -0.43 to 0.08 and are mostly not significant. Along the stand density gradient, the correlations between the raw tree-ring parameter series and between the TRW and LWW indices increase from 1PS to 5PS–17PS, are stable up to 13PS–14PS, and then weaken again in the densest stands. Calculating the above relationships for the full sample from all plots together, all of them are significant at the $p < 0.05$ level except for the correlation between the LWW and LWR indices.

3.2. Climatic Response of Tree-Ring Parameters at Different Planting Densities

Due to the short period of dendroclimatic analysis, the threshold of significance at level $p < 0.05$ is about $|r| = 0.34$; thus, most of the correlations between the tree-ring chronologies and monthly or seasonal climatic variables are not significant (Figure 5). However, if a significant reaction of the tree rings to climatic factors is observed in some of the plots, insignificant correlations of the same sign to the same factors in other plots are probably associated with similar but weaker reactions.

Table 4. Between-parameter correlations: within-plot (for generalized chronologies) and in total.

Plot	Sample Depth	Correlations between Two Parameters					
		Raw Chronologies			Indexed Chronologies		
		TRW LWW	LWW LWR	TRW LWR	TRW LWW	LWW LWR	TRW LWR
1PS	20	0.67	0.31	−0.48	0.67	0.71	0.08
2PS	20	0.72	−0.04	−0.69	0.55	0.57	−0.32
3PS	19	0.87	−0.41	−0.78	0.70	0.55	−0.13
4PS	18	0.76	−0.30	−0.82	0.68	0.14	−0.41
5PS	20	0.87	−0.54	−0.86	0.62	0.44	−0.36
6PS	20	0.95	−0.76	−0.89	0.84	0.52	0.10
7PS	22	0.90	−0.80	−0.93	0.86	0.20	−0.23
9PS	20	0.86	−0.59	−0.87	0.84	0.45	−0.01
10PS	19	0.93	−0.74	−0.89	0.75	0.21	−0.35
11PS	20	0.80	−0.47	−0.86	0.78	0.39	−0.16
12PS	19	0.84	−0.54	−0.86	0.77	0.36	−0.22
13PS	20	0.87	−0.63	−0.89	0.80	0.28	−0.21
14PS	20	0.78	−0.39	−0.85	0.80	0.38	−0.18
15PS	20	0.84	−0.39	−0.76	0.67	0.56	−0.09
16PS	20	0.72	−0.30	−0.83	0.71	0.52	−0.11
17PS	20	0.72	−0.25	−0.81	0.67	0.48	−0.12
18PS	20	0.84	−0.28	−0.71	0.46	0.40	−0.43
Total	337	0.89	−0.38	−0.71	0.72	0.42	−0.19

Bold values are significant at $p < 0.05$.

The climatic response of pine TRW is similar for all plots, but its intensity and seasonality depend on the planting density (Figure 5). In August of the previous year, the temperature slightly negatively affects the growth of the pine plantations (significant at $p < 0.05$ only at 3PS). The positive response of the tree-ring width to the temperature of the cold season for all plots includes the period from January to April (for the temperature averaged over these months, $r = 0.24$ – 0.49) and is less pronounced in plots with middle and high planting densities (insignificant at 9PS–11PS, 13PS, 15PS, and 18PS). In low-density plantations, the period of positive reaction also includes May (up to 0.51 for January–May temperatures at the plot 2PS), and it includes December in denser stands (7PS–16PS). In June, the sign of the reaction of pine growth to temperature changes to negative but not significant. Furthermore, in July–August, a positive, mostly insignificant reaction is observed again.

Precipitation contributes to an increase in pine growth closer to the end of the cold season (the only significant responses are observed at six of the denser plots in February). In April, precipitation tends to slow down the subsequent radial growth (significant only at 10PS), but its effect is again positive in May–June ($r = 0.11$ – 0.56 , significant at 7PS–18PS for two-month sum). The overall response of TRW to precipitation is more pronounced for denser stands.

For the standard LWW, a slightly negative response to temperature is observed from August to October of the previous year ($r = -0.14$ – -0.46 , significant at 1PS, 2PS, and 13PS). Then, the positive reaction to temperature lasts from January to May ($r = 0.16$ – 0.49 , significant at 10 plots of various densities). In June, the LWW reacts slightly negatively to temperature in stands of high and especially medium density (significant at 7PS and 10PS–11PS), stronger than TRW reacts. The response to winter precipitation is weakly positive for the period from December to March $r = 0.19$ – 0.41 (significant at 1PS, 3PS, 4PS, 13PS, and 17PS) but negative in April for all stands except for the sparsest ones 1PS–5PS (significant at 6PS and 15PS). From May or June to August, the influence of precipitation is again positive; it is more pronounced and begins earlier for the plots of medium and high density 6PS–17PS ($r = 0.31$ – 0.59 , significant at 7PS–9PS and 11PS–17PS).

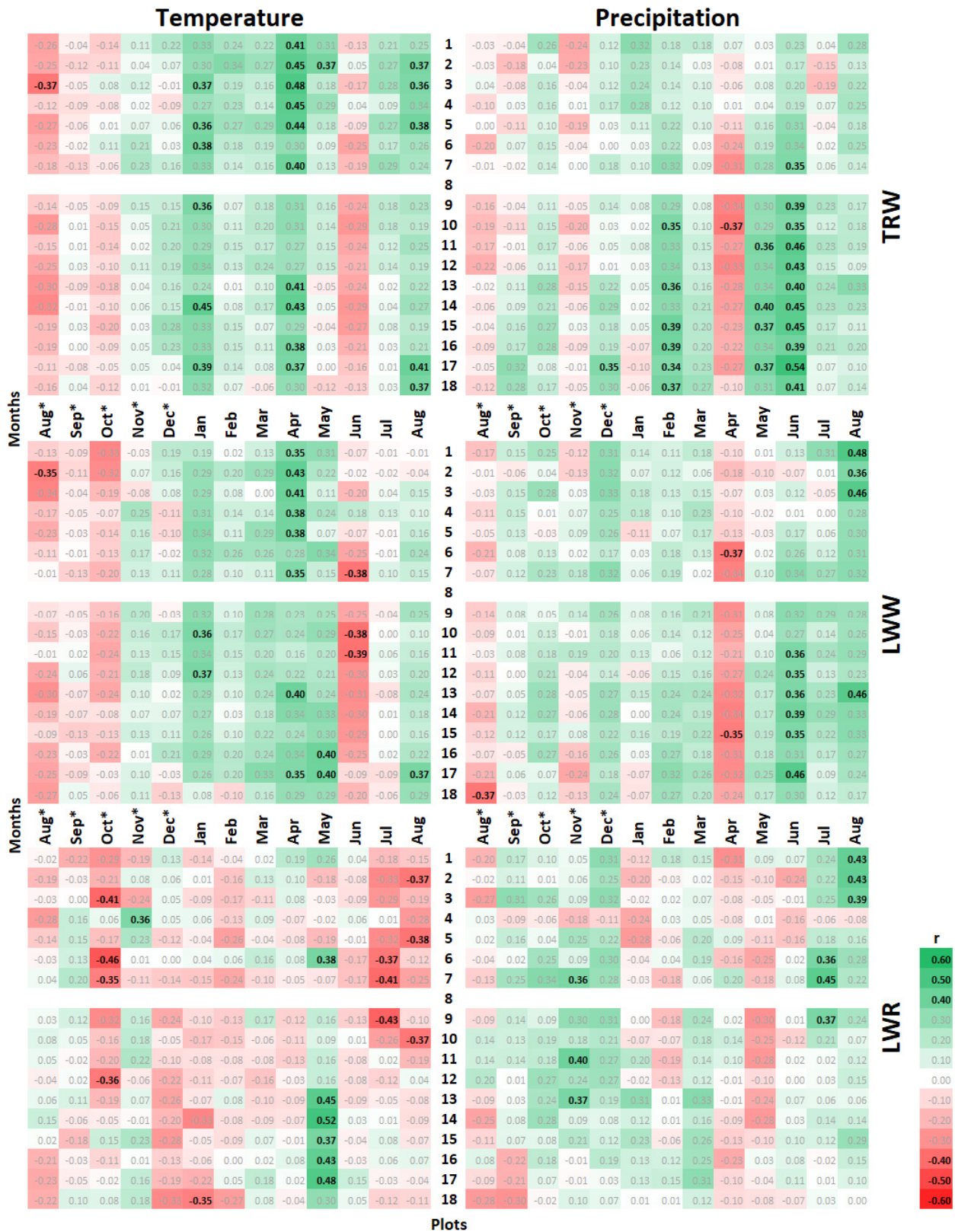


Figure 5. Correlations of tree-ring width (TRW), latewood width (LWW), and latewood ratio (LWR) indexed chronologies with monthly temperature and precipitation from the CRU TS 4.04 grid series (previous August–current August, 1988–2020). Asterisks mark the months of the previous year. The color gradient marks the correlation values (see legend); significant correlations ($p < 0.05$) are marked with black bold font.

For the LWR, the climatic response is less stable and differs sharply from the above parameters of pine tree rings. A positive response to temperature is observed for dense stands (13PS–17PS) in May ($r = 0.37$ – 0.52), while for the sparser stands (1PS–12PS), the latewood ratio is weakly negatively related to the temperatures of the previous October (up to -0.46 , significant at four plots), and the current July–August (up to -0.54 , significant at 2PS–3PS and 5PS–9PS). The response to precipitation is also positive only for sparser stands from September or October to December of the previous year (up to 0.52 , significant at 3PS, 6PS–9PS, and 11PS–13PS) and in July to August of the current year (up to 0.46 , significant at 1PS–3PS and 6PS–9PS). There are no pronounced shifts in the timing of the climatic response for this wood parameter.

An obvious disadvantage of the analysis performed above is the low temporal resolution being accurate to a calendar month, which makes it difficult to identify the smaller-scale differences in the seasonality of the climatic signal. Therefore, the response was detailed on the basis of the moving climatic series of the Krasnoyarsk station (Figure A1). Note that the short duration of the considered climatic series here means that each correlation registers only a small part on the total climatic signal registered in the integral tree-ring parameters. Thus, insignificant but consistent dendroclimatic correlations during some intra-seasonal interval can be transformed into one significant response to climatic factor generalized over this interval by the sum or average.

For this type of analysis, it becomes noticeable that the positive effect of temperature on pine growth begins in early November, reaches significant values (in some plots) in the first half of January, and ends around 20 May, regardless of the planting density. Only the intensity of the response differs between the plots. On the other hand, a weak negative reaction to the June temperature lasts longer by about 10 days in denser stands. For the positive effect of winter precipitation, the planting density affects only the intensity of the response. In May, the positive reaction to precipitation is not only stronger but also begins earlier for high-density plantations; the difference in the start date of the response reaches two weeks. The end of this response is less abrupt, fading away by about the 10th of August.

For the latewood width, the beginning of the negative effect of the temperatures in the August of the previous season depends on the planting density (occurring earlier in denser stands; the difference reaches 2 weeks), but the end of this response in the last days of October is synchronous for all plots. For the negative impact of June temperatures, a non-linear dependence of intensity on planting density is observed, but the beginning and end of the response are stable. In response to precipitation, a dependence on planting density is observed for the transition from a negative response in April to a positive response in May. This transition shifts up to two weeks earlier in dense stands. The intensity of the positive response to precipitation in the second half of July and early August also increases with the density.

4. Discussion

The conditions of the ongoing long-term experiment, such as the homogeneity of the local soil and the landscape conditions and the even-age structure of forest stands within the plantation, made it possible to simplify the interpretation of the results of this study. The exclusion of species-specific and habitat differences and the synchronicity of ontogenetic development allowed us to focus on the variation in growth and productivity of Scots pine due to the planting density gradient.

4.1. Stand Density Dynamics and Tree and Stand Productivity

The density of the even-aged forest stands at the early ages (before reproduction) changes only due to the death of trees. Therefore, for the experimental plots in this study, in the absence of logging, the dynamics of the stand density describes only the process of natural mortality, i.e., self-thinning. During the first years after planting, seedlings practically do not compete with each other even in the densest plots. This means that

mortality during this period is independent of planting density. However, over forty years, the gradual closure of crowns and root systems as trees increase in size is leading to the emergence and gradual increase of competition for limited resources [69–72], primarily sunlight and water. The nonlinear increase in size with age causes the observed negative exponent in the dynamics of stand density. Competition stratifies the population according to social roles, leading to growth inhibition and the subsequent death of some individuals under environmental stresses [73–75]. A higher stand density reduces the living space and resources available to each individual tree, which increases the intensity of competition. In addition, the “race for height” (an allocation of a larger share of resources for growth in height) in dense stands leads to the formation of vertically elongated trees with thin trunks and underdeveloped crowns [35,69,76–79]. As a result, depressed trees in such areas, in addition to climatically determined stresses, also become more vulnerable to mechanical loads of wind and snow. On the contrary, the beneficial effect of stand density on the growth of young trees has been previously recorded within the range from tens to several thousand trees per hectare [80–82]. Since the mentioned observations were made under conditions of moisture deficiency of various severities, it could be possible that lower moisture losses in the soil during shading of its surface contribute to the growth and survival of trees, slowing down self-thinning. These phenomena can explain the observed non-linear dependence of the mortality rate on the planting density. It is worth noting that the presence of an “optimal” range of planting density, which ensures the maximum survival of Scots pine seedlings, may be of interest for forest management in the conditions of the region.

Allometric relationships of the morphometric variables of individual plants among themselves and with the density of their growth can be described by power functions [83,84], which are linearized by a logarithmic transformation of variables. It is also known that specific quantitative ratios depend on habitat conditions and plant species, and their long-term dynamics can be disturbed by uneven self-thinning [85–87]. It is logical that the size, shape, and allometric ratios of different parts of a tree also change with age, as well as their relationship with stand density [71,87,88]. This includes the dynamics of the influence of density variables on growth and productivity observed in this study. In this study, well-known patterns are observed. With the increasing density of the forest stand, (1) the total productivity indicators (the sum of productivity variable values per area unit) also increase, but (2) the size and radial growth of individual trees decrease (for example [89,90]). However, the particular numerical terms of these relationships change with age.

Tree height is less dependent on stand density than other growth indicators, as shown in previous studies [25,80,91–93]. Indeed, the race for height due to competition for light compensates to some extent for the lesser availability of resources in dense stands. However, the cumulative impact of resource constraints has resulted in 40%–50% of the average stand height variability at the time of the last inventory being explained by density variables. For the remaining indicators, the effect of planting density or stand density during further inventories follows allometric functions more closely and from an early age. It should be noted that, unlike the indicators of individual trees, the indicators of the total productivity of the forest stand are regulated to a greater extent by the contemporary density of the forest stand than by the initial one, i.e., having a higher potential for regulation by partial logging. This can be explained by the fact that the morphometric tree structure, e.g., the proportions of trunk diameter with tree height or crown size, becomes less flexible with age [94,95] (cf. lesser reaction of radial growth to thinning for old trees in [29]). At the same time, the utilization of resources (light and water) by the forest stand as a total constantly tends to the maximum, retreating from it for a short time only after the massive die-off of trees during catastrophic events (strong winds, droughts, or snowfall) or cutting down.

Based on the TRW maximum and its subsequent suppression, an analysis of the dynamics of radial growth made it possible to identify the moment when significant intra-specific competition appeared in the forest stands. Interestingly, the latewood ratio in the ring starts to increase at approximately the same moment. It is possible that the beginning of the race for height causes an increase in the requirements for the mechanical strength

of the trunk wood, which is provided, among other things, by a greater proportion of latewood. This is indicated by the reasoning of Zeide [33] about the limitation of tree morphology (the dependence of crown size on tree diameter and height) in terms of the mechanical load on the trunk. For conifers, in particular *Pinus* species, a pith-to-bark increase in wood density is typical [96–98], which may also be associated with an increase in the proportion of denser latewood [98] and is driven by a combination of mechanical strength, hydraulic efficiency, and safety requirements [97,99].

An increase in correlations after standardization between the chronologies of pine radial growth between stands of different density indicates that competition in the forest stand affects the long-term dynamics of growth much more than its inter-annual variability. Nevertheless, the experimental stands are clearly divided by density into two groups, the differences in the growth dynamics between which, as shown below, are due to shifts in the intensity and seasonality of the response to climatic factors.

The very close relationships between measurements of latewood width and the total tree-ring width show that cell production in latewood is largely “pre-programmed”, presumably through the state of the tree at the beginning of the growing season. Both positive correlations between the standardized chronologies of these tree-ring parameters [67,100] and their similar climatic response [101] have already been noted not only for conifers but also for deciduous trees [102]. The very close relationships observed in this study both before and after standardization of chronologies show that their common component includes both the impact of external factors, including climatic variables (significant relationships between the standard chronologies), and common long-term trends (high correlations between the raw series). To confirm this hypothesis and to analyze the stability of these ratios over the course of time, further studies are required using data from mature forest stands. The counter-intuitive negative relationship between the LWW and LWR are obviously associated with opposite long-term trends—a decrease in the latewood growth clearly connected to a decrease with age in the total radial growth within the considered time interval—while the latewood ratio in the ring increases steadily with the exception of the very first rings. However, it should be noted that the almost completely insignificant relationships between the indexed chronologies of the LWR and TRW demonstrate the independence of the external signal in these variables, i.e., the fundamentally different effect of climatic fluctuations on the quantity (radial growth, i.e., TRW) and quality (density and mechanical strength, positively related to LWR) of developing wood.

4.2. Climatic Response of Pine Radial Growth Parameters and its Dependence on the Stand Density

An analysis of the influence of climatic dynamics on the tree-ring width, latewood width, and ratio of Scots pine in artificial plantations in the southern taiga zone showed the presence of similar patterns for all planting densities, due to the common natural and climatic conditions of the study area and the ecophysiological characteristics of the species.

For TRW, there is a positive response to winter–spring temperatures, which has been previously recorded in other areas within the southern and middle taiga zones [103–106] from Germany to Central Siberia. On the contrary, in the mountain taiga of Southern Siberia and Mongolia, despite the similar seasonal dynamics of temperature and precipitation, such a response does not occur in pine (for example [107,108]). We assume that the positive correlations with the temperatures in the cold season may be associated with damage to the root system during severe frosts due to the freezing of soil saturated with moisture after late autumn precipitation in the plains [109], in contrast to soil quickly losing moisture and being frozen while dry on the mountain slopes.

During the growing season, the limitation of pine growth by the moisture deficit can be observed, expressed as a negative relationship with temperatures and a positive one with precipitation [110–113]. The intensity of this response is low, which corresponds to the location of the plantation within the inner part of the species distribution range and, consequently, a relatively weak moisture deficit compared to forest-steppe stands

and band forests located on the southern semiarid borders of the Scots pine distribution range [106–108,114–116].

The climatic signal in latewood ratio chronologies, if looked at closely, more or less corresponds to those parts of the LWW response in that are independent of the TRW. For example, a positive reaction to precipitation in July–August and to the temperature in May, negative to the temperature of the previous October is common for the LWW and LWR but is not reflected in the TRW. This is to be expected given the lack of statistically significant relationships or weak relationships between the TRW and LWR indexed chronologies. However, this regularity means that the latewood ratio, apparently, reflects not so much the influence of current climatic fluctuations on cambial activity directly during the formation of earlywood and latewood, but rather a climate-dependent trigger for the transition to differentiation of cells into the latewood-type tracheids (small and thick-walled) during the subsequent stages of xylogenesis. However, the dynamics of the switch in the sign of the LWR climatic response within the growth season indicates that in May, cool and humid conditions contribute to an increase in the earlywood ratio in the ring and in July–August they drive an increase in the latewood ratio. The fact that according to the more detailed 21-day dendroclimatic analysis, the effect of temperature and precipitation on the latewood ratio appears decoupled in June, may be due to the year-to-year instability of the transition to latewood within this month (see other examples of variation in the phenology of xylogenesis in [117–121]).

The revealed differences in the climatic response between stands of different densities can be related directly to the degree of competition, as well as to the size of the trees and the living space they occupy. E.g., a decrease in competition and a corresponding increase in the resources available to an individual tree occurs after the artificial thinning of forest stands. Dendroclimatic studies show that this changes both the overall climate response and vulnerability to adverse events, including droughts [36,48,122–125]. In less dense forest stands, the soil contains more nutrients and available moisture in general [16,126] and even more so per individual trees, which can regulate their response to droughts [127]. On the other hand, differences in sensitivity to climate fluctuations have been recorded within one stand, associated with such morphometric characteristics of individual trees such as crown class, DBH, and root depth [46,61,62,128], which are obviously also modulated by the density of the forest stand [35]. It should be noted that the components of the water and the thermal balance of the habitat also depend on the stand density through components such as the interception of precipitation by tree crowns, the soil moisture losses through transpiration and evaporation from the soil surface, and the micro-scale regulation of surface and air temperature by the ratio of shaded and sunlit surfaces [129–131]. The complex nature of all the listed factors and interactions ensures uncertainty in the direction of change in the climatic response depending on the planting density and the degree of competition. On the one hand, there is evidence of the “complacency” of growth, i.e., a weakened climatic response, for the most dominant, large, or fast-growing trees in the stand [106,132,133]. On the other hand, extreme degrees of competition, i.e., restrictions on living space and resource availability, can make it impossible for a tree to take full advantage of favorable conditions and increase growth, thus also reducing tree growth variability and climatic signals [46,134–136]. As our previous study showed, the dependence of the climatic response on the degree of competition can even be nonlinear within the same habitat [137].

We can suggest that in the study area, the competition of pine trees for water increases with the stand density, which leads to an increase in their response to summer precipitation. As for the uneven effect of winter frosts on growth, among the possible contributing factors are different depths of fine roots damaged by frost, different degrees of growth stability after these injuries, and the presence of dense grass cover in sparser plantations additionally isolating the soil in winter [138]. In addition, a greater degree of intercept of the snow cover by canopies is possible in denser stands [139,140]. This was indirectly confirmed by the

shift to earlier dates of the climatic response in April–May, possibly associated with an earlier end of snowmelt and the thaw of soil [141,142].

Temporal shifts in the climatic response, which are more pronounced for parameters of latewood, obviously indicate an increase in the duration of cambial activity and a shift in the timing of the transition to formation of latewood toward later periods in sparse stands. Previously, a similar hypothesis was put forward for a change in the climatic response of trees in a thinned Scots pine stand, which was presumably associated with an extension of the period of latewood cell division due to more favorable moisture conditions in the second half of the growing season with less competition [126]. Finally, the stable end dates for the climatic response during the previous autumn in all of the plots clearly indicate that air temperature regulates the transition from nutrient storage (active photosynthesis in evergreen pine needles) to dormancy regardless of stand density.

5. Conclusions

An analysis of tree growth in Scots pine plantations of different planting densities with the natural dynamics of tree stand self-thinning demonstrated that the expected opposite gradients, depending on the stand density, are observed for the productivity indicators of individual trees and the total stand (per unit area). The productivity shifts from the maximum on the tree scale and the minimum on the stand scale in the sparsest plots toward the opposite pattern in the densest plots. As for the radial growth, the tree-ring width and latewood width direction depend negatively on stand the density, but the latewood ratio in the ring increases with the stand density. For most of the considered timeframe, the first two tree-ring variables have negative age trends, while the latewood ratio increases; thus, we can assume that the similar influence of age dynamics and stand density on tree-ring development is based on the intensity of competition. All of the observed dependencies are well described by allometric power functions (i.e., linear relationships in a log–log scale).

The contribution of planting density to the climate response is more ambiguous. In the seasonality of the response and, accordingly, the phenology of xylogenesis, there is a direct dependence of the duration of active growth on the available resource base, whereas the intensity of the influence of climatic fluctuations on the production and quality of wood is ambiguous, and for some seasons, it even nonlinearly depends on the planting density. The amount of precipitation in February–June is more important for pine growth in dense stands, the conditions in July–August have a stronger effect on the latewood ratio in sparse stands, and trees from medium-density stands show the greatest resistance to winter frosts.

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Data Availability Statement: The data presented in this study are available from the corresponding author upon reasonable request.

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Appendix A

Table A1. Dependences of stand density DENS on absolute tree age A.

Plot	Stand Density DENS (Trees/ha) at Ages A (Years) *				Function ** $DENS = DENS_0 \cdot \exp[-a(A - A_0)]$		
	$A_0 = 2$	20	25	35	a ***	R	R^2
1PS	500	239	228	228	-0.0274	0.911	0.830
2PS	750	445	445	431	-0.0190	0.915	0.837
3PS	1000	567	567	560	-0.0196	0.924	0.854
4PS	1500	599	590	588	-0.0330	0.899	0.808
5PS	2000	1103	1103	1057	-0.0218	0.919	0.844
6PS	3000	2196	1997	1997	-0.0136	0.947	0.897
7PS	4000	3198	2523	2300	-0.0157	0.968	0.938
9PS	8000	6108	5683	4867	-0.0139	0.999	0.999
10PS	10,000	7524	7227	5085	-0.0166	0.968	0.937
11PS	12,000	9070	7236	6268	-0.0182	0.983	0.966
12PS	16,000	10,639	8236	6487	-0.0250	0.991	0.983
13PS	24,000	11,668	9742	6388	-0.0370	0.999	0.999
14PS	36,000	15,951	10,826	7181	-0.0414	0.994	0.988
15PS	48,000	19,207	11,890	7449	-0.0525	0.995	0.990
16PS	64,000	25,662	15,062	6627	-0.0594	0.987	0.974
17PS	96,000	29,243	16,115	8367	-0.0682	0.996	0.992
18PS	128,000	34,336	17,795	11,750	-0.0706	0.990	0.980

R is the correlation between the actual values and the model; significant correlations ($p < 0.05$) are in bold; R^2 is the determination coefficient. * Planting density $DENS_0$ was measured at the tree age of $A_0 = 2$ years because plantation was established with 2-year-old seedlings. ** Dependence of stand density DENS on the absolute tree age A was initially described as a log-linear function in relative units ($DENS/DENS_0$) because within the plot, $DENS_0$ can be considered as constant. Taking into account that $DENS = DENS_0$ at the age A_0 in all plots, it can be written as $\ln(DENS/DENS_0) = a(A - A_0)$. Then, the equation was transformed to the exponential form to use DENS as the dependent variable. *** Numerical term a in the equation $DENS = f(A)$ changes with the planting density. Its dependence can be described with function $a = -0.00433 \cdot \ln(DENS_0) + 0.0697 \cdot \ln(DENS_0) - 0.297$, which explains $R^2 = 0.922$ of the actual variance in a .



Figure A1. Correlations of the indexed chronologies of tree-ring width (TRW), latewood width (LWW), and latewood ratio (LWR) with the 21-day temperature and precipitation from Krasnoyarsk station, 1988–2019. The color gradient marks the correlation values (see legend); black marks show significant correlations ($p < 0.05$); asterisks “*” mark months of the previous year.

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