Age-Dependent Climate Sensitivity of Korean Pine (*Pinus koraiensis*) in the Southern Sikhote-Alin Mountains

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Abstract

Global climate change is driving profound transformations in forest ecosystems, particularly in monsoon-influenced regions of the Pacific coast of Asia, such as the Sikhote-Alin Mountains. Long-lived conifer species, notably Korean pine (*Pinus koraiensis* Siebold & Zucc.), play a central ecological role in mixed broadleaf–coniferous forests of the region. We examined how the radial growth response of Korean pine to climatic variability changes with tree age and ontogenetic stage, using 191 increment cores from trees ranging from early virginile to old generative stages. We employed two approaches: (i) a stage-based analysis, constructing tree-ring chronologies for each ontogenetic stage; (ii) an individual-tree analysis, applying correlation and regression directly to individual ring-width series. Climate–growth relationships were assessed using monthly temperature, precipitation, and drought indices (PDSI, SPEI). For the stage-based approach, radial growth was positively correlated with the mean August temperature of the previous year (up to $r = 0.61$), minimum November temperature (up to $r = 0.50$), and summer drought indices (up to $r = 0.57$). Age-related trends in climate sensitivity, assessed from regression models under both approaches, were significant for 9 of the 18 monthly climate variables examined. For stage-specific chronologies, simple regressions across six ontogenetic stages described up to 98% of the variance, whereas cambial-age-based relationships were much weaker ($R^2 = 0.03$–0.14). These findings highlight the importance of accounting for ontogenetic structure in dendroclimatic analyses and climate reconstructions. Such insights are critical for understanding long-term forest dynamics and informing climate adaptation strategies in Korean pine-dominated ecosystems.

Keywords: dendroclimatology; climate sensitivity; ontogenetic stage; age effects; *Pinus koraiensis*; tree-ring width; drought indices (PDSI; SPEI); monsoon climate; forest response to climate change

1. Introduction

Global warming is one of the most serious threats to natural ecosystems, increasing the frequency of droughts, floods, and temperature anomalies that strongly affect forest structure and functioning [1,2]. Forests, particularly in northern and temperate latitudes, play a central role in the global carbon cycle but are also highly vulnerable to climate change [3]. Climate-driven alterations in water balance, temperature regimes, and disturbance frequency influence tree growth rates and drive major transformations in forest dynamics [2,4,5]. Models predict that many tree species will be forced to migrate to higher latitudes or elevations, accompanied

by shifts in species composition, productivity, and resilience [6–8]. Anticipating how tree species respond to these changes is essential for conserving biodiversity, sustaining carbon storage, and guiding sustainable forest management.

In dendrochronology, age-related changes in climate response are described as climate signal age effects (CSAE), which may amplify or attenuate the climate signal with age and shift the seasonal timing of sensitivity to temperature or precipitation [9–23]. However, findings remain contradictory: some studies report stronger climate signals in older trees [9–15], others in younger individuals [16,17], while some consider CSAE negligible [18,21,23]. These inconsistencies across regions and species highlight the need for further studies to identify general patterns and mechanisms of age-related climate sensitivity, which are critical for accurate climate reconstructions and forecasting forest ecosystem responses to global change.

The climate of Northeastern Asia is highly heterogeneous due to interactions between continental and maritime air masses and complex topography [24,25]. In recent decades, the region has experienced rising mean annual temperatures, more frequent extreme events, and altered seasonal cycles [26,27]. Projections indicate continued winter warming and shifts in precipitation regimes, with pronounced impacts on forest ecosystems, underscoring the need to assess their responses to climate variability.

Such projected changes highlight the importance of studying dominant species that shape forest structure and function. Korean pine (*Pinus koraiensis* Siebold & Zucc.) is a keystone species of mixed broadleaf–coniferous forests in Northeastern Asia [28]. It is a long-lived and ecologically plastic conifer capable of growing in diverse habitats, from river valleys to mountain slopes [29–32], which makes it especially relevant for assessing age-dependent responses to climate change.

However, the influence of climate change on the growth of Korean pine in the northeastern part of its range—particularly in the Sikhote-Alin Mountains—remains insufficiently studied [33–35]. Previous research indicates that radial growth is sensitive to temperature and moisture, with positive correlations to autumn–winter minimum temperatures [33] and spring–summer precipitation [34]. However, age-related variation in growth response remains poorly understood. In the western part of its range (Northeast China), younger trees are especially vulnerable to rising temperatures and reduced precipitation, which leads to growth declines [35]. Thus, despite growing interest in this species, its age-dependent response to climate remains understudied, underscoring the need for further investigation to forecast the consequences of regional warming for forests where Korean pine is a key component. The aim of this study is to assess how the climate sensitivity of Korean pine varies with age and ontogenetic stage in the Southern Sikhote-Alin, to identify the key climatic drivers of tree growth, and to evaluate the implications of these ontogenetic patterns for forest dynamics under current regional climate change. By testing the ontogenetic-stage approach, we aim not only to advance methodological perspectives in dendroclimatology but also to provide insights relevant for biodiversity conservation, sustainable forest management, and adaptation strategies in East Asian temperate forests.

The remainder of this paper is organized as follows. Section 2 describes the study area, data collection, and analytical methods. Section 3 presents the results of the ontogenetic-stage and cambial-age analyses. Section 4 discusses the implications of our findings in the context of climate sensitivity and forest dynamics. Section 5 summarizes the main conclusions and outlines directions for future research.

2. Materials and Methods

2.1. Study Area and Species

The study was conducted in the Southern Sikhote-Alin Mountains, within the Verkhneussuriysky Research Station (Figure 1a) of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences (44°02′ N, 134°12′ E). The Station is located in the basin of the Pravaya Sokolovka River, which has a total area of 4400 ha, a tributary of the Ussuri River. The terrain is characterized by low mountains with rounded peaks; the average slope ranges from 20 to 25°. The minimum and maximum elevations are 450 and 1060 m above sea level, respectively.
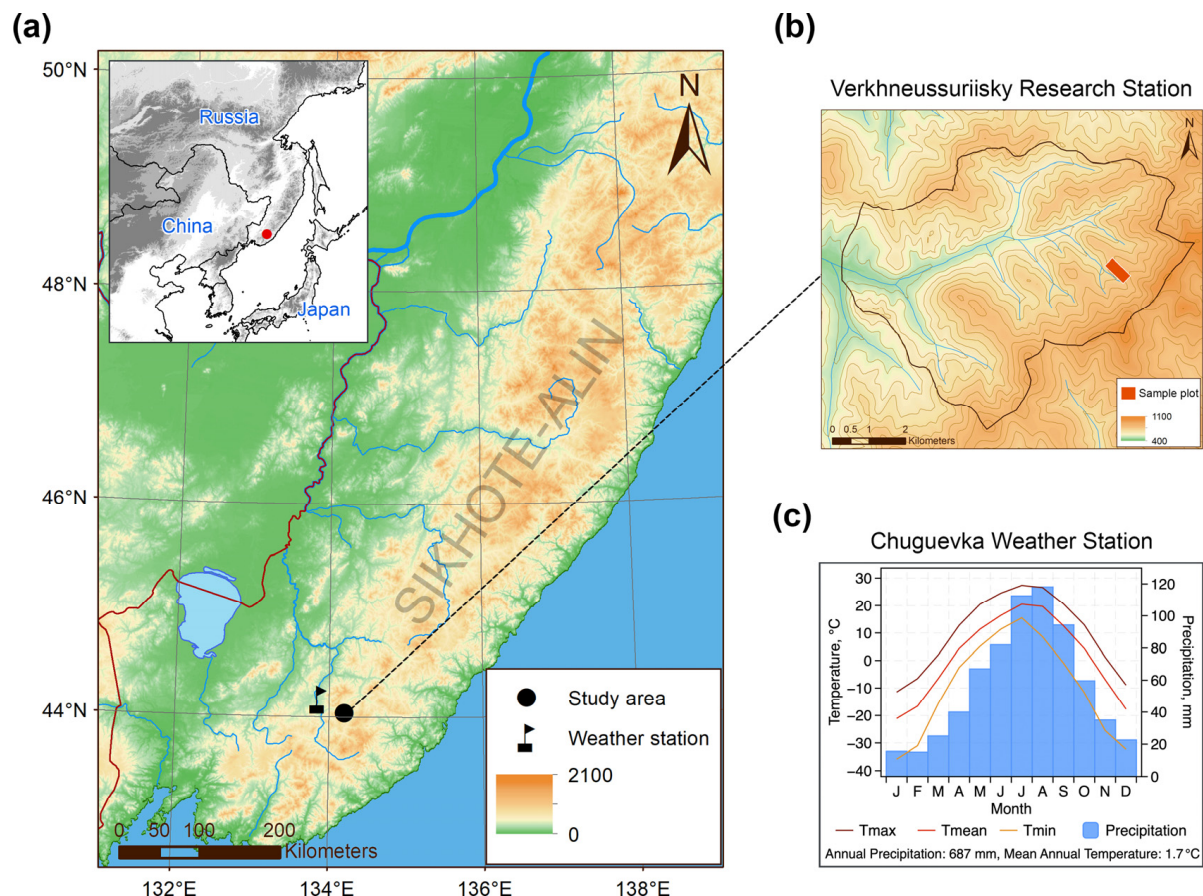
Figure 1. Location of the study area ((**a**) red dot in the inset map), the permanent sample plot (**b**), and the climatogram of the Chuguyevka meteorological station (**c**).

The climate is monsoonal, with an annual precipitation of approximately 830 mm, most of which falls during the summer. The mean annual air temperature is 0.9 °C [36]. Forest vegetation covers more than 99% of the station's territory [37,38], with mixed Korean pine–broadleaf forests (55%) and fir–spruce forests (30%) predominating in area [38]. The topography, climate, and vegetation of the Verkhneussuriysky Station are representative of the mountainous belt of Southern Sikhote-Alin.

Korean pine occurs throughout the station's entire elevational range. Up to elevations of 700–900 m above sea level, it forms a distinct belt of mixed Korean pine–broadleaf forests, and at higher elevations it is present in Korean pine–spruce and spruce–fir stands [28,37].

2.2. Data Collection and Preparation

Field sampling was carried out in 2014–2015 at permanent sample plot 72-2013 (area: 21 ha; Figure 1b). The stand at this site is dominated by *P. koraiensis* and *Tilia amurensis*

Rupr., which together account for approximately 43% of the total cross-sectional area of living trees (Supplementary Table S1). *Picea jezoensis* (Fisch. ex Carrière) W.C. Cheng & L.K. Fu and *Betula costata* Trautv. also represent important components of the stand, with notable contributions to the total basal area. In the subcanopy, *Abies nephrolepis* (Trautv.) Maxim. and *Acer ukurunduense* Trautv. & C.A. Mey. are predominant.

Increment cores of Korean pine were collected from trees of various ages, ranging from saplings to mature trees. For canopy trees, one core per tree was taken at breast height (1.3 m); for small saplings, cores were taken at a height of 50 cm to ensure a sufficient number of rings, as the youngest trees may have fewer than 30 rings at breast height. This minor difference does not affect interannual growth variability, although it may limit comparability of long-term trends. In total, 191 cores were obtained. Coring was performed perpendicular to the slope and/or trunk lean to avoid reaction wood [39]. For each cored tree, measurements of diameter at breast height (DBH), total height, and ontogenetic stage [29,40,41] were recorded.

In the laboratory, the samples were prepared following standard dendrochronological procedures, including drying, surface trimming, and contrast enhancement until individual tracheids became visible under a stereomicroscope [10]. Ring widths were measured using a semi-automated Velmex measuring system (Velmex Inc., Bloomfield, NY, USA) with an accuracy of 0.01 mm.

To assess age-related variation in climate response, we employed two approaches. The first approach consisted of grouping cores from different trees by ontogenetic stage, followed by constructing separate ring-width chronologies for each group. This is because individual trees in forest stands may vary considerably in both growth rate and developmental trajectory. Canopy accession and reproductive onset/termination can differ markedly depending on phytocoenotic conditions.

For example, a pine growing in a canopy gap may quickly reach the upper canopy, whereas a tree growing under closed canopy may experience multiple suppression phases throughout its life [37]. As a result, trees of similar cambial age can differ greatly in size, and tree size has been shown to strongly affect climate sensitivity, e.g., refs. [9,42–44]. Ontogenetic stages thus represent the functional state of a tree, integrating its age, size, and reproductive status. Although this conflation may limit the ability to separate these factors statistically, it reflects the ecological reality that climate sensitivity is mediated by their joint effects.

We classified ontogenetic stages as follows [29,40,41] (Supplementary Figure S1):

- Immature (*im*)—small saplings not exceeding shrub layer height, focusing on nutrient accumulation and root development.
- Virginile (*v*)—medium to large saplings entering a phase of rapid height growth (requires improved light conditions in formerly suppressed trees); in Korean pine [29] subdivided into (a) early (v_1), (b) middle (v_2), and (c) late (v_3) virginile phases; trees in the v_3 phase reach the lower canopy.
- Young generative (g_1)—canopy trees continuing rapid height growth; fruiting begins but is irregular.
- Mature generative (g_2)—canopy trees with slowing vertical growth and increasing radial increment; characterized by peak fruiting.
- Old generative (g_3)—maximum size attained, partial crown dieback, low and irregular fruiting.

The collected cores encompassed the developmental span from the early virginile phase to the old generative stage. Accordingly, the cores were divided into six groups based on ontogenetic stage and phase, with 28 to 41 cores in each group.

The second approach examined how individual trees of different cambial ages respond to climate variability, similar to previous studies (e.g., refs. [9,17,22]). We sought to compare the outcomes of both approaches and to assess whether ontogenetic grouping offers a more biologically meaningful perspective on climate–growth relationships.

2.3. Development of Tree-Ring Chronologies

Ring-width series for each ontogenetic stage were cross-dated with TSAP V3.5 software [45] by visually matching individual series to a group mean. Dating quality and the detection of missing rings were verified with COFECHA [46]. Subsequent processing was performed in the dplR package [47] under R v.4.2.1 (R Core Team, Vienna, Austria) [48].

To minimize growth variability caused by age trends and stand dynamics—and thus maximize the climatic signal—each series was standardized with a 40-year cubic spline. This detrending method was chosen because forest-grown trees often experience several release events associated with canopy gaps over their lifetimes [30]; simple negative-exponential curves cannot fully remove such pulses. In addition, even in the youngest trees, the majority of ring series contained substantially more than 40 rings, ensuring that subsequent detrending with a 40-year spline preserved interannual variability while removing only long-term biological growth trends. Chronologies were then constructed using the bi-weighted robust mean of individual indices [49].

To characterize both the raw series sets and the resulting chronologies, and to assess their quality, we calculated the following statistics: MS—mean sensitivity; $RBAR_{eff}$—weighted average inter-series correlation accounting for within- and between-tree correlations; EPS—expressed population signal; SNR—signal-to-noise ratio; first-order autocorrelation (AR1); mean and standard deviation (Mean, SD); skewness and kurtosis [10,50–52].

2.4. Climate Data

Meteorological data were obtained from the Chuguevka weather station (44°09′05″ N, 133°52′10″ E; 260 m a.s.l.), located about 30 km west of the study area (Figure 1c). The variables used were as follows: monthly precipitation totals (available 1936–2019); monthly mean, maximum, and minimum air temperatures (available 1959–2019). To evaluate the influence of wet and dry years on Korean pine growth, we also used the Palmer Drought Severity Index (PDSI [53]) and the Standardized Precipitation–Evapotranspiration Index (SPEI [54]). PDSI data (0.5° grid) were downloaded from https://crudata.uea.ac.uk/cru/data/drought/ (accessed on 10 June 2024); SPEI data (0.5° grid) from http://sac.csic.es/spei/database.html (accessed on 10 June 2024). For both indices, we extracted the 0.5° cell closest to the study site. Such data provide a reliable representation of regional interannual variability, which is essential for our analysis.

2.5. Climate–Growth Relationships

The influence of climate on radial growth was analyzed with the treeclim package [55] in R v.4.2.1. Pearson correlation coefficients—along with bootstrapped confidence intervals—were calculated between ring-width indices and monthly climate variables from June of the year preceding growth to September of the current year [50]. Climate variables examined were as follows: monthly mean, maximum, and minimum temperatures; monthly precipitation; drought indices PDSI and SPEI. These analyses provided the basis for assessing climate sensitivity across ontogenetic stages and cambial ages.

2.6. Age- and Ontogeny-Dependent Climate Sensitivity

To assess how the influence of specific climate parameters (i.e., correlation coefficients) on the radial growth of Korean pine changes with age, we conducted a regression analysis. For chronologies constructed for trees at different ontogenetic stages, the independent

variable was the median age of trees within each group (v_1, v_2, v_3, g_1, g_2, g_3). The choice of the median was due to its robustness to outliers and skewed age distributions within the sample, which is particularly important when certain age classes dominate the population. In groups containing both very young and very old trees, the arithmetic mean may be biased toward extreme values, thereby misrepresenting the group's central tendency. In such cases, the median age better reflects the central tendency of the distribution.

At the stage of selecting independent variables for the regression analysis, we initially considered three potential predictors: median tree age, height, and diameter. Pearson correlation analysis revealed strong correlations among these variables ($r > 0.96$), indicating that including all three would introduce multicollinearity; therefore, only median age was retained for subsequent analysis.

To preliminarily assess the statistical significance of differences in median tree ages among ontogenetic stages, we used nonparametric statistical methods that do not require the assumption of normality. For an overall comparison across all groups, we applied the Kruskal–Wallis test [56], a nonparametric alternative to ANOVA, which tests for statistically significant differences in the ranked age distributions among groups. The test statistic and corresponding *p*-value were used to evaluate the null hypothesis of equal medians across groups. For pairwise comparisons between individual groups, we used the Mann–Whitney U test [57], with *p*-values adjusted using the Bonferroni correction [58] to control for Type I errors in multiple comparisons. All analyses used a significance level of $\alpha = 0.05$, and differences were considered statistically significant if the adjusted *p*-value was less than 0.05.

To determine the best-fitting model for the dependence of correlation coefficients on median age, we tested two types of models: a linear regression and a second-degree polynomial regression. The models were evaluated using the coefficient of determination (R^2) and the Akaike Information Criterion (AIC; [59]). The model that provided the best fit based on these metrics was selected.

For individual ring-width series, the independent variable was the tree's cambial age. In this case, only a linear model was tested to describe the dependence of correlation coefficients on cambial age.

For both chronologies and individual series, model significance was assessed using the *F*-test for overall regression significance. A model was considered statistically significant if the *p*-value for the *F*-statistic was below 0.05. Regression analyses were performed using Python v.3.12.2 (Python Software Foundation, Wilmington, DE, USA) with the libraries scipy [60], statsmodels [61], and matplotlib [62].

3. Results

3.1. Ontogenetic Stages and Cambial Age of Trees

The ranges of cambial age for trees at different ontogenetic stages (Figure 2) provide insight into how rap idly trees can reach a given ontogenetic state, as well as the maximum age they may attain within that stage. These age ranges gradually increase and reach their maximum in the old generative stage. Interestingly, trees can reach this stage, characterized by maximum size, by the age of 182 years, which is close to the upper age limit observed in the v_2 stage. The growth patterns visible in the cores suggest that these trees most likely established in canopy gaps and did not experience suppression during their lifespan.

It is also noteworthy that the age range for young generative trees is wider than that for mature generative trees. During fieldwork, we repeatedly encountered g_1 trees that had reached the canopy layer but, for various reasons, later ended up in unfavorable conditions and nearly ceased growing. As a result, they exhibit characteristics typical of g_1 trees—such as size and reproductive behavior—despite having a cambial age closer to that of g_2 trees.
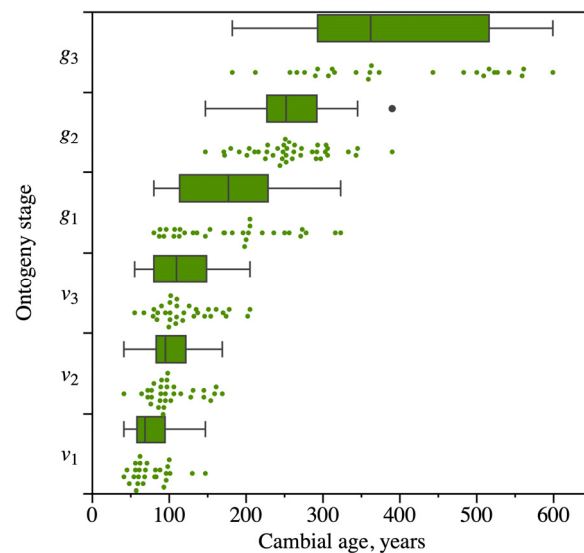
Figure 2. Cambial age ranges of Korean pine trees across different ontogenetic stages (from v_1 to g_3). Boxplots show median, interquartile range, and outliers.

The median cambial ages were as follows: 68.5 years for v_1, 95 years for v_2, 107 years for v_3, 177 years for g_1, 252 years for g_2, and 362 years for g_3. Results of the Kruskal–Wallis test used to evaluate differences in median ages across the six ontogenetic stages showed that these differences were statistically significant ($H = 141.04$, $p < 0.001$), indicating heterogeneity in the age structure of the trees. Pairwise comparisons using the Mann–Whitney test with Bonferroni correction confirmed significant differences ($p < 0.05$ after correction), thereby supporting the significance of the differences in median ages across the ontogenetic stages (Supplementary Table S2). These median ages were subsequently used as the predictor in the stage-level regressions (Section 3.4).

3.2. Characteristics of Tree-Ring Chronologies

Following cross-dating of the selected cores, tree-ring chronologies were developed for each of the six ontogenetic stages. Characteristics of the raw series and the detrended series are presented in Table 1, while the properties of the resulting chronologies are summarized in Table 2.

Table 1. Characteristics of the raw and detrended tree-ring series. $N_{t/c}$—number of trees and cores; RW—mean ring width; Corr.—mean inter-series correlation; MS—mean sensitivity; EPS—expressed population signal; SNR—signal-to-noise ratio; $RBAR_{eff}$—effective inter-series correlation (within and between trees).

Stage	Raw Series						Detrended Series		
	$N_{t/c}$	Time Span	N. Years	RW	Corr.	MS	EPS	SNR	$RBAR_{eff}$
v_1	28/28	1914–2015	102	0.587	0.53	0.43	0.92	11.8	0.298
v_2	32/32	1846–2015	170	0.889	0.52	0.35	0.92	11.9	0.307
v_3	26/32	1845–2015	171	1.308	0.50	0.32	0.92	11.9	0.314
g_1	24/32	1740–2014	275	1.119	0.48	0.30	0.91	9.7	0.298
g_2	41/41	1709–2014	306	1.277	0.52	0.28	0.95	20.4	0.332
g_3	26/38	1451–2014	564	1.086	0.52	0.24	0.93	12.9	0.341

The total length of the chronologies ranged from 101 years (v_1) to 564 years (g_3), and the segment length starting from the point at which the EPS value exceeds 0.85 ranged from 68 to 429 years. For virginile and young generative trees, this effectively reduces the usable chronology length by nearly half (Figure 3). Inter-series correlation values varied between 0.50 and 0.53, while the mean sensitivity of the detrended series ranged from 0.24 to 0.43.

Table 2. Summary statistics of the standardized tree-ring chronologies across different ontogenetic stages. MS—mean sensitivity; Mean—mean index value; SD—standard deviation; Skew—skewness; Kurtosis—excess kurtosis; AR1—first-order autocorrelation.

Stage	MS	Mean	SD	Skew	Kurtosis	AR1
v_1	0.26	1.008	0.31	0.49	0.19	0.445
v_2	0.20	0.998	0.23	0.06	0.34	0.367
v_3	0.16	1.001	0.19	0.10	−0.04	0.315
g_1	0.17	1.003	0.18	0.34	0.59	0.229
g_2	0.17	1.003	0.18	0.13	0.24	0.256
g_3	0.16	1.000	0.17	0.24	0.07	0.269
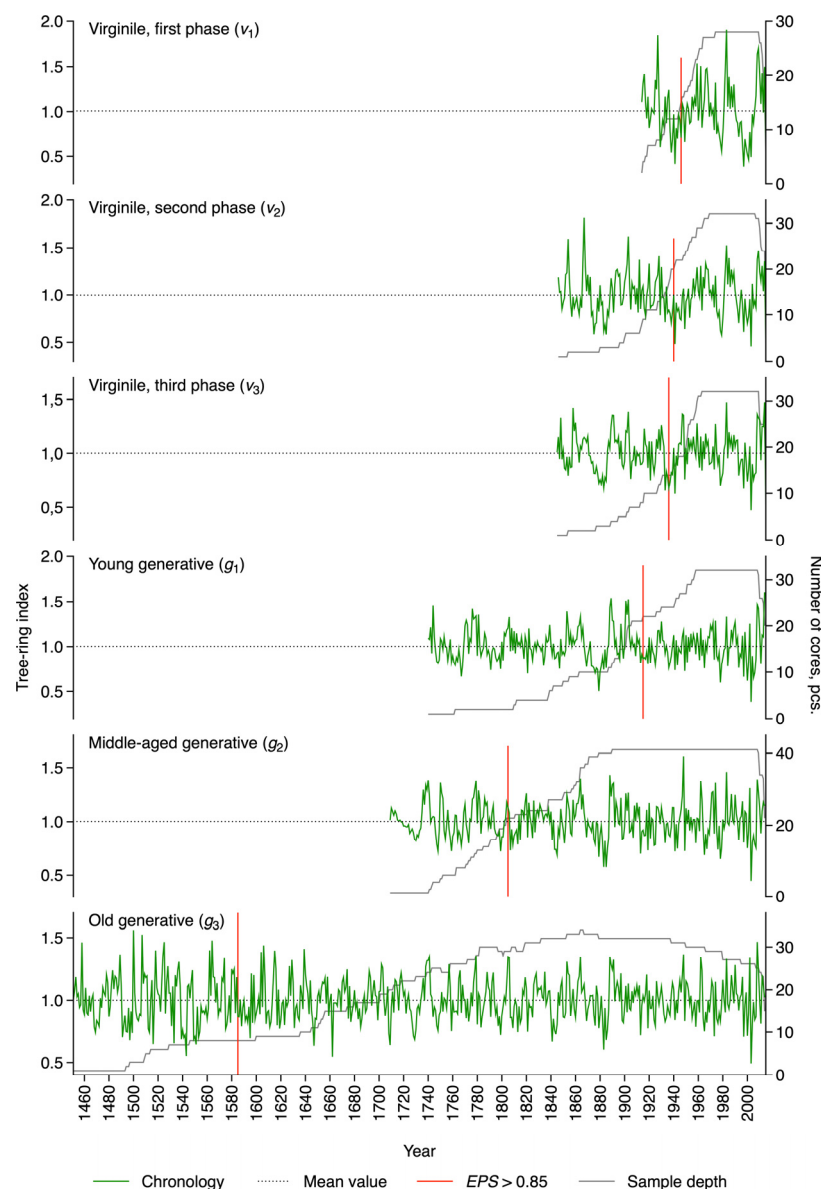
Figure 3. Tree-ring chronologies of Korean pine across six ontogenetic stages. Chronologies are shown with mean growth curves, sample depth (gray lines), and threshold of EPS > 0.85 (vertical red lines).

Chronologies for ontogenetic stages that are closer to each other showed stronger mutual correlation (Figure 4). Thus, the correlation between "successive" ontogenetic stages (v_1 and v_2, v_2 and v_3, etc.) ranged from 0.87 to 0.92. The lowest correlation was observed between trees at the early virginile phase and those in the old generative stage (0.51).
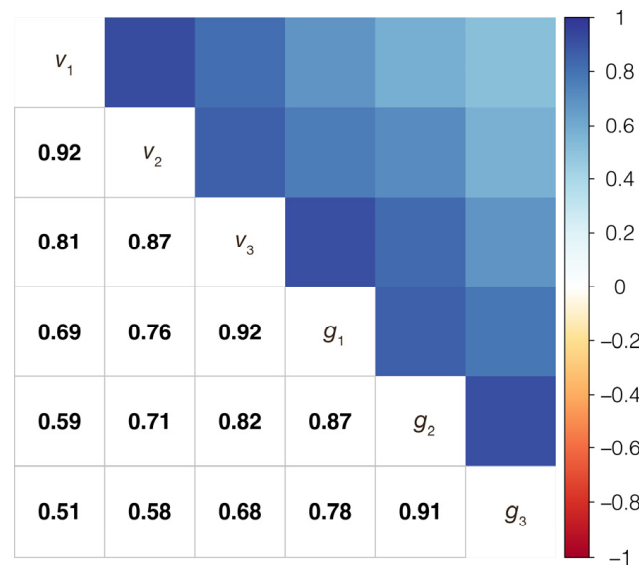
Figure 4. Cross-correlations among tree-ring chronologies of Korean pine for different ontogenetic stages based on Pearson correlation coefficients.

3.3. Climate Response at Different oOntogenetic Stages

Analysis of the response of Korean pine radial growth to climatic variations revealed which climate parameters and their monthly values exert the greatest influence (Figure 5). Overall, the radial growth of Korean pine is most strongly determined by temperature and drought/wetness conditions, as reflected by the PDSI and SPEI indices. Significant correlations with monthly precipitation were rare, and only in the case of January of the current year were significant negative correlations observed in three of the six ontogenetic stages. It is also noteworthy that among the temperature variables, the mean monthly temperature had the greatest importance. Significant correlations with temperature were predominantly positive, indicating that increases in mean, maximum, and minimum temperatures generally promote the growth of Korean pine. The only exception was a negative effect of maximum temperatures in June and July on the radial growth of mature generative trees. Significant correlations with PDSI and SPEI indices were also positive, suggesting that a decrease in drought intensity and an increase in moisture availability during the summer–autumn period positively affect the growth of Korean pine.

When analyzing individual months, we found that trees at all ontogenetic stages were affected by the mean temperature of the previous August (with a maximum correlation of 0.61 for v_1 trees) and by the minimum temperature of the previous November (maximum correlation of 0.50 for v_3 trees). Additionally, drought/wetness indices had a strong effect, with PDSI values from July to September of the current year (maximum correlation of 0.54 for v_3 trees in September) and SPEI values in July of the current year (maximum correlation of 0.57 for mature generative trees) showing significant relationships with growth. Trees in four to five ontogenetic stages were also influenced by the mean temperature in June and October of the previous year and April of the current year; the maximum temperature in April of the current year; the minimum temperature in August and December of the previous year; and the PDSI value for June of the current year. Trees at three ontogenetic stages were influenced by the mean September temperature of the current year, the maximum August and October temperatures of the previous year, the maximum April temperature of the current year, January precipitation, and the June SPEI of the current year.

Based on these results, the following climate variables were selected for regression analysis as having the strongest influence on Korean pine radial growth across ontogeny (i.e., those showing significant correlations with at least three of the six ontogenetic stages):

(a) mean temperatures: June, August, October (current year), and April and September (previous year); (b) maximum temperatures: August and October (current year), and April (previous year); (c) minimum temperatures: August, November, and December (previous year); (d) precipitation: January (current year) only; (e) PDSI: June to September (current year); (f) SPEI: June and July (current year). These climate variables were used in the regression analysis for both the chronologies and individual tree-ring series.

Figure 5. Correlation between Korean pine radial growth and monthly climate variables across six ontogenetic stages (v_1 to g_3). Color represents the strength and direction of the correlation (green—positive, red—negative), while the orientation of ellipses reflects the slope of the relationship: ellipses tilted upward indicate positive correlations, those tilted downward indicate negative ones. Both indicators are shown intentionally to provide complementary visual cues for easier interpretation. Asterisks denote statistically significant correlations ($p < 0.05$).

3.4. Ontogenetic Change in Climate Response

Regression analysis was performed for each dependent variable—that is, for each correlation coefficient between radial growth and a given climate parameter—to identify the

best-fit model on the basis of the Akaike Information Criterion (AIC) and the coefficient of determination (R^2). In most cases, second-degree polynomial models provided a better fit to the data, whereas linear models generally yielded higher AIC values and lower explanatory power. The model coefficients and the results of their statistical tests are presented in Supplementary Table S3. Graphical inspection (Supplementary Figure S2) confirms that the selected models adequately describe the data. Given the small number of stage groups (n = 6), these fits are treated as descriptive summaries. To minimize overfitting, model complexity was constrained to simple forms (linear or quadratic); higher-order polynomials were not considered.

Of the 18 models considered, 9 proved to be statistically significant ($p < 0.05$; Figure 6a). This indicates that in half of the cases no significant age-related change in the correlation coefficient was detected—for mean June and October temperatures of the previous year, minimum August and November temperatures of the previous year, PDSI for all examined months, and SPEI for July of the current year. One reason may be the limited statistical power resulting from the small sample size. Accordingly, the influence of these climate variables—and of the drought indices they represent—remains approximately constant across ontogenetic stages. Also, the reported coefficients of determination should be interpreted with caution and viewed as descriptive effect summaries rather than strict inferential metrics. Where regression equations were significant, the proportion of explained variance ranged from 0.72 to 0.98, indicating pronounced changes in the importance of certain climatic factors for tree growth, particularly spring–summer temperature and winter–spring precipitation.
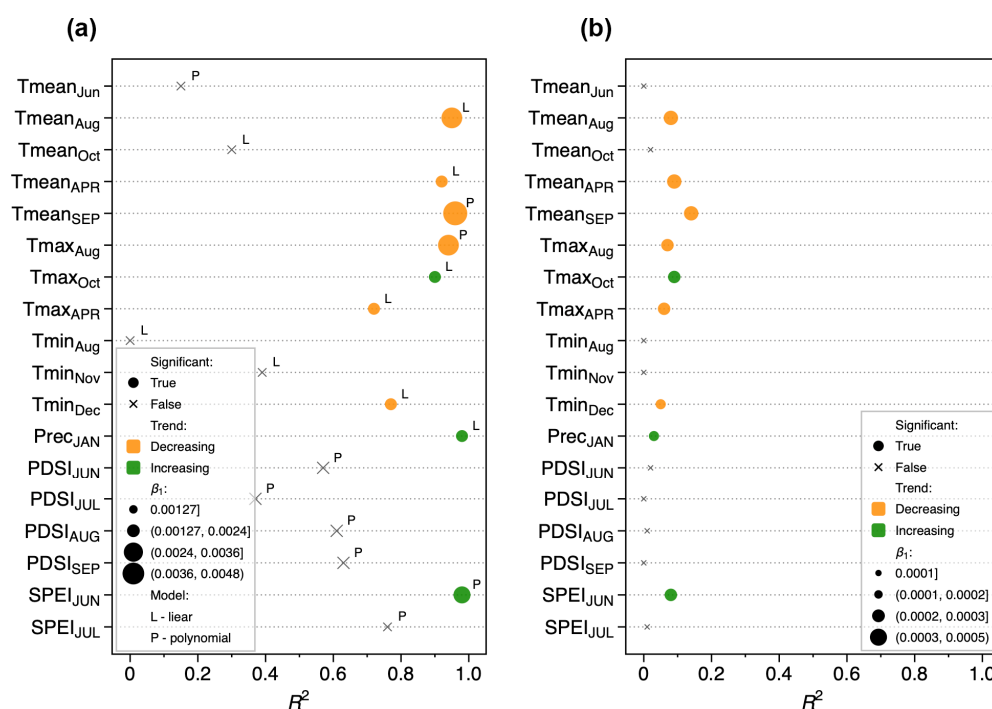
Figure 6. Regression analysis of age-related changes in the correlation between Korean pine radial growth and climatic parameters: (**a**) best-fitting models describing climate response across ontogenetic stages, with median age as the independent variable (model type: linear—L, or second-order polynomial—P). (**b**) regression models based on cambial age (only linear models). Circle size indicates the magnitude of the regression coefficient (β_1); color represents trend direction (green—increasing, orange—decreasing). Filled circles indicate statistically significant models ($p < 0.05$); crosses mark non-significant results. The x-axis shows the coefficient of determination (R^2).

Significant increasing trends were detected only in three cases. As trees progress through ontogenetic stages, (i) the positive correlation with maximum October temperature of the previous year strengthens, and (ii) the negative influence of current-year January precipitation diminishes. For SPEI, correlation values increase up to the mature generative stage and then decline slightly. In the remaining six cases, the trends were negative, both linear and nonlinear, meaning that the influence of mean, maximum, and minimum temperatures (except the maximum temperature of the previous October) weakens as trees advance through successive ontogenetic stages.

3.5. Climate Response and Cambial Age

For each dependent variable (correlation coefficient between radial growth and a given climate parameter), a linear model was fitted using cambial age as the independent variable (Supplementary Figure S3) and its significance was tested. Model coefficients and test statistics are listed in Supplementary Table S4.

When the results based on individual series (cambial age) are compared with those based on ontogenetic stages, several points emerge (Figure 6b). First, the direction of trends coincided across both frameworks, providing convergent evidence that the stage-level patterns are not artifacts of the chosen model form. Increases or decreases in climate sensitivity that were significant in the stage-based analysis are likewise significant when cambial age is used. However, the proportion of explained variance for individual-tree models ranges only from 3% to 14%, that is, four- to eight-fold lower than in the chronology-based models. Moreover, the absolute values of the slope parameter (β_1) show that changes in climate response with increasing cambial age proceed roughly an order of magnitude more slowly than the changes observed across ontogenetic stages.

4. Discussion

4.1. Influence of Climatic Parameters on the Growth of Korean Pine

Our results indicate that Korean pine growth is primarily limited by temperature and water availability. Elevated summer and autumn temperatures of the previous growing season, as well as warmer spring and autumn conditions of the current year, generally enhanced radial increment, consistent with patterns reported for other conifers at high elevations in cold and moist habitats [63–70]. These effects reflect both extended photosynthetic activity and improved carbohydrate storage, while warm early winters may reduce frost damage to living tissues [71–73]. At the same time, excessively high mid-summer temperatures can depress growth by increasing evaporative demand and soil drying, particularly during earlywood formation when water requirements are greatest [72,74–81].

Moisture availability is equally critical. In southern Sikhote-Alin, growth is limited by early-summer precipitation during the transition from the dry winter to the humid summer monsoon [34], with large mature trees showing especially strong sensitivity to water supply because of their extensive crowns and high transpiration demand [9,19,23,43,79,80]. Heavy reproductive effort in generative stages may further increase vulnerability to drought [9,19,23,43,79]. These mechanisms explain the positive correlations we observed with precipitation and drought indices (PDSI, SPEI), which underscore the moisture dependence of Korean pine both within and beyond its natural range [34,35,72,78,82–87]. Differences between PDSI and SPEI reflect their integration over long-term versus short-term moisture anomalies, respectively.

The importance of soil moisture availability is corroborated by dendrometer data from young generative trees and concurrent measurements of volumetric soil water content ($m^3 \, m^{-3}$). From August 2019 to August 2021, peaks in rapid stem expansion coincided with increases in soil-water storage in the upper 50 cm (Supplementary Figure S4).

It should be noted that our analysis was limited to monthly temperature, precipitation, and drought indices (PDSI, SPEI). Other potentially influential drivers—such as soil moisture dynamics, extreme weather events, and large-scale atmospheric circulation patterns—were not included. These factors may interact with the variables analyzed here and could further modulate tree growth. However, our focus was to assess how widely used climatic indicators of temperature and water balance vary in their effects across ontogenetic stages. Future studies incorporating soil moisture records, high-resolution meteorological data, and circulation indices could provide a more comprehensive view of climate–growth interactions in Korean pine.

We also note that the meteorological data were obtained from the nearest long-term station (~30 km away) and the drought indices from 0.5° gridded products. While such data sources are standard in dendroclimatic research, they inevitably introduce some spatial mismatch with the complex topography of the site, particularly for winter precipitation and snowpack. Our interpretation therefore prioritizes robust, biologically consistent tendencies over precise absolute values.

4.2. Changes in Climate Response During the Growth and Development of Trees

Regression analysis showed that the correlation between radial growth of Korean pine and certain climatic variables—such as the mean temperature in August of the previous year, January precipitation of the current year, and July SPEI—changes significantly throughout ontogeny. In contrast, for some parameters, such as PDSI from June to September of the current year, no significant ontogenetic change was detected. These differences are likely attributable both to the nature of the climatic variables themselves and to the physiological processes they affect.

For example, the Palmer Drought Severity Index (PDSI) reflects long-term cumulative changes in soil moisture balance [53], incorporating both past precipitation and evapotranspiration. It defines the general "background" level of soil wetness, which is equally important for trees of all ages and developmental stages. As a result, the dependence of growth on this index remains relatively stable. In contrast, the Standardized Precipitation–Evapotranspiration Index (SPEI) for individual months (e.g., July) captures short-term deviations in water balance [54], which may affect trees differently depending on their age.

When comparing shifts in climate sensitivity at the individual (i.e., tree-level series) and population levels (i.e., chronologies for trees at different ontogenetic stages), all trends between cambial age/ontogenetic stage and the correlation of radial growth with specific climatic parameters remain consistent. However, these relationships are much weaker at the individual level. This may be explained by individual variability in tree responses to climate, as well as by factors such as microtopography, microsite conditions, and local competition. These factors can mask or weaken the overall climate signal, which becomes more detectable in averaged chronologies where individual variation is smoothed out. At the same time, it should be emphasized that stage-level regressions were based on six median-age points, which limits statistical power. To minimize the risk of overfitting, model complexity was constrained to simple forms (linear or quadratic), and higher-order polynomials were not considered. The very high R^2 values therefore reflect descriptive fit to aggregated data rather than strict inferential strength. Accordingly, we interpret these results as tendencies that are consistent with physiological and ecological expectations, rather than as precise effect-size estimates.

Our results demonstrate that the positive influence of temperature on growth generally decreases with tree age. One explanation for this pattern may lie in the reduced physiological capacity of older trees to capitalize on favorable thermal conditions. Young trees tend to exhibit faster growth rates and more flexible physiological processes; they are

capable of initiating cambial activity earlier and extending the growing season under warm conditions [22]. As a result, they accumulate more wood in warm years than in cold ones, and their growth directly reflects improved environmental conditions [22].

In contrast, adult (mature generative) trees may reach physiological limits: by the time favorable conditions arise, their growth may be constrained by accumulated structural and hydraulic limitations [9,22]. Furthermore, older trees have more developed nutrient reserves, allowing them to buffer against temperature fluctuations, whereas virginile trees are under constant stress due to limited light access and competition [29,37], making them particularly sensitive. Consequently, warm autumns in the preceding year stimulate growth more strongly in virginile trees than in generative ones.

An opposite trend was observed for the maximum temperature in October of the previous year: its positive effect on growth increases with age. Warm conditions during late autumn likely prolong photosynthetic activity. It is well known that end-of-season conditions can influence next-year growth, as a portion of carbohydrates assimilated in the fall is stored and then used for early wood formation in the following season [88,89]. This reserve-based growth is more prominent in generative trees, which accumulate more resources and rely more on internal stores at the beginning of the growing season—before the foliage is fully developed. Generative trees also have deep root systems [29], enabling them to extract water later into the fall, and thick bark and trunks that help retain heat and protect the cambium from early frosts. These features allow them to maintain metabolic activity into October under favorable conditions, while virginile trees typically cease growth much earlier.

The age-related decline in temperature sensitivity (except for late-autumn warmth) revealed in our study is rather atypical compared to many other works. In most cases, the opposite pattern is observed: climate sensitivity tends to increase with age (e.g., ref. [9,90]. A global meta-analysis confirmed that trees with larger diameters generally show stronger growth responses to climate variability [90], especially in dry environments and at range margins. For instance, in *Pinus cembra* and other species in arid mountain environments, older trees demonstrate tighter correlations with precipitation and temperature [9,43]. This is believed to result from increased hydraulic constraints and a greater proportion of non-conductive tissue in older trees, which makes them more susceptible to climate stress [9].

Nevertheless, cases of declining climate sensitivity with age have also been documented. For example, Szeicz and MacDonald (1994) [11], studying *Picea glauca* in the subarctic, found that summer-temperature sensitivity weakens with age. Similar results were obtained in temperate, moist climates, where younger trees were more climate-sensitive than older ones [22,79,91]. These findings underscore that with increasing age, climate sensitivity may either rise or decline depending on environmental context and species biology.

As noted above, a thick snowpack that melts slowly can delay soil warming in spring and thus postpone cambial reactivation. Virginile trees are especially vulnerable to this effect. Their fine roots are concentrated in the upper soil layers [29], which freeze more deeply and thaw more slowly under snow cover. In contrast, generative trees may have roots deeper than the frost line, and their taller crowns shed snow earlier. In addition, virginile trees typically grow under the canopy of older trees in mixed stands, where snowmelt is delayed due to shading, which limits their ability to respond to favorable spring conditions [34]. These factors explain the negative correlation between snow abundance and radial growth in virginile trees: prolonged snow cover shortens the effective growing season and delays cambial activity [82,83]. Moreover, heavy snow can exert mechanical

pressure on branches, causing damage or deformation that impairs growth even after winter ends.

In the virginile stage, Korean pine shows relatively low growth sensitivity to moisture availability. Virginile trees typically grow in shaded understory conditions [30], where low light and competition reduce transpiration and photosynthesis, thereby weakening the link between growth and drought [86]. As trees transition to mature generative stage, they develop larger crowns and root systems [29], which increases transpiration and strengthens dependence on summer water balance [92,93]. These trees are no longer limited by light or space, but are highly sensitive to water deficit, particularly in July, when evapotranspiration peaks. Drought sensitivity at this stage may also be amplified by heavy cone production, which peaks during mature generative stage [29]. This interpretation is consistent with global evidence showing that fecundity often declines in large trees despite continued biomass accumulation [94]. Such patterns reflect increased reproductive allocation costs and physiological constraints, supporting the view that ontogenetic stage integrates functional changes that mediate climate sensitivity.

In old generative trees, growth sensitivity to moisture decreases. Several factors may explain this. First, their deep root systems allow them to access water from more stable soil horizons, buffering short-term drought effects [92]. Second, reproductive effort declines in late generative stages [29]. Third, age-related reductions in cambial activity and increases in non-conductive wood further limit growth [14,95]. As a result, even under favorable conditions, old trees accumulate less wood and exhibit lower correlation with SPEI. Plantation studies of Korean pine have shown that growth sensitivity to precipitation increases until middle age, then decreases [93]. Similar trends are documented in other conifer species across various climatic zones [86].

4.3. Potential Impact of Climate Change on the Growth of Korean Pine at Different Ontogenetic Stages

In recent decades, the region has experienced steady warming, as indicated by both meteorological observations and dendrochronological studies, with the most pronounced increases occurring in autumn and winter temperatures [27,33,96]. For example, records from the nearest long-term station (Chuguevka) show that mean annual temperature increased by about 0.40 °C per decade. The warming was driven mainly by minimum temperatures, which rose by 0.61 °C per decade, compared to 0.21 °C per decade for maximum temperatures. Over the same period, total annual precipitation showed a weak, statistically insignificant increase of about 5 mm per decade. In addition to these mean trends, summers have also become warmer—though less dramatically—but there has been a notable increase in the frequency of extreme heat events. In particular, the frequency of heatwaves has steadily increased since the mid-20th century [97], and the warming trend is expected to continue in the near future [27].

Changes in precipitation are more ambiguous, though certain important trends can be identified. On the one hand, observational data from the second half of the 20th century indicate a decline in annual precipitation in some parts of Northeast Asia [96]. On the other hand, increased typhoon activity has brought significant rainfall during July–September [98]. The frequency and intensity of heavy precipitation events have increased since 1950 [81]. Thus, summer precipitation shows an overall upward trend, which raises the risk of flooding. While winter precipitation remains relatively low, it has also increased modestly due to more frequent thaws and enhanced cyclonic activity during warm winters [99]. Additionally, there are signs of regional climate aridification at lower elevations and, conversely, increased humidity at higher elevations [100]. Overall, the general trend is toward increased moisture input, especially during the warm season, although this trend is unevenly distributed across the landscape.

The observed warming theoretically increases evapotranspiration, but the concurrent increase in precipitation may offset these losses. According to reports, soil moisture availability across much of high-latitude Asia has increased, and the risk of prolonged droughts has declined. In terms of climate indices, this translates to higher PDSI and SPEI values, indicating relatively moist rather than drought-prone conditions [99].

These climatic shifts are highly relevant to the growth and ontogenetic development of Korean pine. The rise in temperature, particularly in mean monthly values, is likely to positively affect growth, especially in virginile trees. Increases in October maximum temperatures may benefit generative trees by extending the growing season. However, warming may also produce adverse effects. The most serious concern is the negative impact of high maximum temperatures in June and July on the growth of mature generative trees. First, as temperatures rise, this negative correlation is expected to strengthen. Second, maximum temperatures will likely have an increasing impact on both young and old generative trees. This may lead not only to reduced radial growth but also to diminished reproductive intensity.

Decreasing drought severity will also positively affect the growth of Korean pine, particularly in mature generative trees. However, continued increases in winter precipitation are expected to have a negative effect on the growth of virginile trees—and this effect may become even more pronounced.

Thus, although ongoing warming and increased precipitation in the Southern Sikhote-Alin might seem to favor Korean pine growth—through extended frost-free periods and reduced water stress—a more nuanced view reveals contrasting impacts across ontogenetic stages. Rising temperatures will likely benefit virginile trees but may suppress the growth and reproduction of generative trees. In parallel, increased winter precipitation is expected to negatively affect the growth of virginile trees.

In terms of the altitudinal range occupied by Korean pine, where it forms mixed Korean pine–broadleaf forests in the Southern Sikhote-Alin, climate warming and increased moisture may shift the upper boundary of this range upslope. The lower boundary may remain relatively stable; however, not all habitats at these lower elevations will remain suitable for generative Korean pine trees. This is particularly true on south- and southwest-facing slopes, which receive higher solar radiation [101] and thus warm up more intensely. Such processes, if confirmed across multiple sites, could contribute to habitat fragmentation under future climate change. Korean pine may persist in narrow river valleys and ravines in the lower parts of mountain ranges, where temperature inversions [102] help mitigate the effects of increasing summer maximum temperatures.

These projections should be viewed in a regional context, since our climatic drivers were derived from a station ~30 km away and 0.5° gridded indices. Local departures related to topography, soils, and stand structure are possible, and multi-site comparisons will be essential to generalize these findings.

5. Conclusions

This study demonstrated that the influence of climatic parameters on the radial growth of Korean pine varies significantly with tree age and ontogenetic stage. A comparison of two approaches to analyzing climate response dynamics—based on individual tree-ring series with cambial age versus grouping trees by ontogenetic stages—revealed the clear advantage of the latter. Stratifying by ontogenetic stages enabled the identification of more consistent and interpretable relationships between climatic variables and radial growth, with regression models explaining several times more variance.

The analysis showed that temperature conditions and moisture availability, as reflected by PDSI and SPEI indices, have the strongest influence on Korean pine growth. However,

various climatic parameters were significant at different ontogenetic stages. For instance, virginile trees responded more strongly to the mean summer temperatures of the previous year, whereas generative trees were more sensitive to current-year summer maximum temperatures and SPEI. Moreover, some climatic parameters (e.g., PDSI) exert a relatively stable influence regardless of tree age, while sensitivity to others (e.g., August temperature or January precipitation) either increases or decreases with ontogenetic developmental stage.

These findings have important applied implications for predicting the consequences of climate change. Under continued global warming and increasing aridification, the response of Korean pine will depend not only on the nature of climatic shifts but also on the age structure of populations. Rising summer temperatures and declining water availability may have opposing effects on trees of different ontogenetic stages, leading to more complex dynamics within forest communities. This is especially critical for species such as Korean pine, which plays a key role in the formation of stable forest ecosystems.

Therefore, modeling forest responses to climate change requires consideration of stand age structure. The results underscore the importance of further investigating age-dependent climate responses of tree species in dendroclimatic studies. Although our findings demonstrate the promise of the ontogenetic-stage approach in dendroclimatology, they should be interpreted as a case study of a single species in one region (Southern Sikhote-Alin) and should not be generalized to the entire range of Korean pine without additional evidence. Further research across other species and climatic regions will be essential to evaluate the broader applicability of this framework.

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

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

CSAE   Climate signal age effects

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