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ORIGINAL ARTICLE

Climate-Growth Response of *Cryptomeria japonica* Cultivars in Southwestern Japan

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Abstract

Understanding how tree growth responds to climate is important for predicting how plantation forests may react to ongoing climate change. In this study, we examined the climate–growth relationships of six *Cryptomeria japonica* cultivars across five common-garden sites in southwestern Japan using dendrochronological methods. We analyzed 48 years of ring width data to evaluate how monthly and annual temperature and precipitation affect radial growth at site and cultivar levels. Static and moving correlation analyses revealed that late winter to early spring temperatures (February–March) positively influenced radial growth at most sites, likely by facilitating cambial reactivation, while high summer precipitation tended to suppress growth at some sites, possibly through reduced solar irradiance. Precipitation effects were variable across sites, with autumn rainfall showing positive effects at lower-elevation sites. At the cultivar level, early-growth type cultivars tended to show positive temperature responses, while late-growth types showed more variable precipitation responses, though the majority of cultivar-level correlations did not reach statistical significance. Multivariate ordination (PCA) and permutational multivariate analysis of variance (PERMANOVA) on correlation-based response profiles indicated that geographic location was a significant driver of climate-growth response patterns ($R^2 = 0.28$, $p = 0.014$), while cultivar type explained a substantial but non-significant proportion of variance ($R^2 = 0.23$, $p = 0.085$). These results suggest that local environmental conditions primarily shape climate sensitivity in *C. japonica*, while genetic provenance provides an additional, non-negligible layer of variation. Our findings underscore the importance of considering both site characteristics and cultivar characteristics in forest management and climate adaptation strategies for *C. japonica* plantations.

Keywords Tree rings · Climate-growth response · Climate sensitivity · Plantation forests · Clonal variation

Extended author information available on the last page of the article

Introduction

Impact of environmental and climatic changes on tree growth depends on a number of factors such as species of tree, region inhabited by the tree, and lifetime of the tree (Carter 1996; Takahashi et al. 2003; Neupane et al. 2023). Temperature and precipitation are major environmental factors that affect tree growth, and in the context of climate change, these manifest as global warming and extreme precipitation variability, respectively (Cedro 2000). Trees as biological organisms, can adjust internal processes in response to such environmental changes through physiological acclimation (Norisada et al. 2005; Mäenpää et al. 2011; Oksanen 2021) and persistence in their current location, or through migration via seed dispersal. Depending on the species' sensitivity and acclimation to environmental changes, external perturbations can lead to reduction of tree growth, and increase in tree vulnerability (Aubin et al. 2016). Species with limited acclimation potential and/or narrow, limited distribution ranges can be the most at risk for extirpation (Thomas et al. 2004; Carter et al. 2021).

Plantation forests, which supply a large share of industrial wood and are often managed for high productivity (Paquette and Messier 2010; Sohngen and Mendelsohn 2001), are therefore particularly exposed to climate-driven changes in growth and vulnerability (Perez-Garcia et al. 2002; Kirilenko and Sedjo 2007; Pawson et al. 2013; Rubilar et al. 2024). For example, warm winters and warm and early springs caused an earlier onset for cambium activity and the formation of wider tree-rings in Sawara cypress (*Chamaecyparis pisifera*) plantations in northwestern and central Poland (Cedro et al. 2021). Long-term impacts of climate change to plantations also include reduction of wood production, resulting in negative impacts on the timber industry (Watt et al. 2019; Nabuurs et al. 2002). Climate change requires an urgent call for a shift in breeding strategy and management of plantations including cultivar selection, pest and disease control, wildfire, etc. (Hirata et al. 2017; Seidl et al. 2020).

In recent decades, attention on management of plantation forests, tree breeding, and silviculture have focused on cultivars which can grow fast or those that produce high-quality timber or other wood products (Pilipović et al. 2020; Alan 2020; Rubilar et al. 2018). Seed source selection for improvement of growth and wood traits has been challenged by the complex interactions between climate and the ecophysiological processes of trees, hence research efforts are needed in tree breeding and silviculture to properly select cultivars that respond to climate change and sustain wood production of plantations (Kirilenko and Sedjo 2007; Mitsuda 2018). It is vital to increase knowledge of the direct and indirect impacts of climate change on plantation forests through cultivar-level in-situ research to understand varying climate-growth responses, as well as forecast changes in physiology and productivity (Tei et al. 2017). Intra-specific variation plays a key role for adapting forests to future climatic conditions (George et al. 2019). Success of clonal tree plantations depends on genotype as well as phenotypic plasticity (Enoki et al. 2020) and physiological functions such as responses of photosynthesis and respiration to warming

may vary with latitude and geographic region (Montgomery et al. 2020, Nishizono et al. 2018).

Physiological responses of trees to climate especially temperature and precipitation are embedded in tree-ring traits, where variations in width and density register drought, excessive rainfall, temperature extremes, and other events (Babst et al. 2019; Jing et al. 2022; Stokes and Smiley 1996). Phenology and seasonal water–light use are key drivers of climate sensitivity and radial growth trends, as shown for Qinghai spruce (*Picea crassifolia*) and Chinese pine (*Pinus tabuliformis*) in the southern Tengger Desert of the Tibetan Plateau (Xue et al. 2023). Dendroclimatic analyses are especially valuable for identifying the climate variables that significantly influence growth and for assessing the relative influence of the different climatic factors (Gauli et al. 2022). Monthly climate variables like average temperature and average precipitation are consistently utilized to investigate the correlation between tree-ring width and climate conditions and to identify temporal, climatological, and eco-physiological processes that affect radial growth (Sun and Liu 2016).

Cryptomeria japonica, commonly known as Japanese cedar or Sugi, is a coniferous tree native to Japan and is widely cultivated in various parts of the world. It is a slender, pyramidal, evergreen conifer species endemic to Japan and is one of the most important forestry species in the country. It accounts for 44% of the plantation area of Japan (Hiraoka et al. 2018) and has been a very valuable tree species because of its excellent attributes (rapid growth, ease of processing, and pleasant color and scent) for use in house beams, rafters, and boards (Ohba 1993). Over 200 clonal cultivars of *C. japonica* exist in Japan, with some tracing back as far as 300 years. These cultivars were traditionally propagated by taking cuttings from multiple individuals displaying similar phenotypes, often sourced from sacred groves found in shrines and temples (Ohba 1993). Significant epigenetic variations exist among genotypes of *C. japonica* which influence traits such as growth rate, wood density, and stress responses (Cai et al. 2023). Hence, productivity of these clonal plantations is shaped by the genotype's capacity to adapt to variations in environmental conditions and disturbance regimes occurring at both edaphic and geographic scales.

The climate sensitivity of *C. japonica* species that thrive in very hot and humid climates such as in southwestern Japan has not been extensively studied, likely due to their minimal growth response to year-to-year climatic variations (Mori et al. 2020). In line with this, investigating variations in growth rings of *C. japonica* growing in common gardens in southwestern Japan in relation to environmental factors such as temperature, precipitation and others, may provide information on the dominant constraint or stimulator (key limiting factor) of the growth of this important plantation species and response variation among cultivars.

This study used dendrochronological methods to examine the relationship between climate variables (temperature and precipitation) and annual ring growth of six cultivars of *C. japonica*. In this present study, we hypothesized that: (1) The relationship between radial growth and climatic factors (e.g., temperature and precipitation) varies among *C. japonica* cultivars; and (2) Varying patterns in response sensitivity to climate are reflected in radial growth differences among cultivars and within sites. Specifically, we aimed to:

1. Determine the long-term inter-site growth response of *C. japonica* across five sites in southwestern Japan
2. Determine the relationship between climate variables (temperature and precipitation) and the growth ring widths of the *C. japonica* cultivars
3. Analyze radial growth variation in response to climate among cultivars and sites

Different clones of the same species can exhibit varying degrees of sensitivity to climate, which can be observed in their ring width responses. In this regard, we expect a cultivar-specific or clone-specific response to climate warming in the climate-growth relationship. A comparison of the climatic responses under various inter-annual and intra-annual growth conditions will help us to understand the mechanisms that control radial growth of *C. japonica* in southwestern Japan.

Materials and Methods

Research Sites and Materials

Our study was conducted in five experimental forest "common gardens" located in Tano (Kyushu), Shiiba (Kyushu), Kasuya (Kyushu), Takakuma (Kyushu), and Komenono (Shikoku), Japan (Fig. 1). These sites are situated within regions where the potential natural vegetation is characterized by mixed evergreen

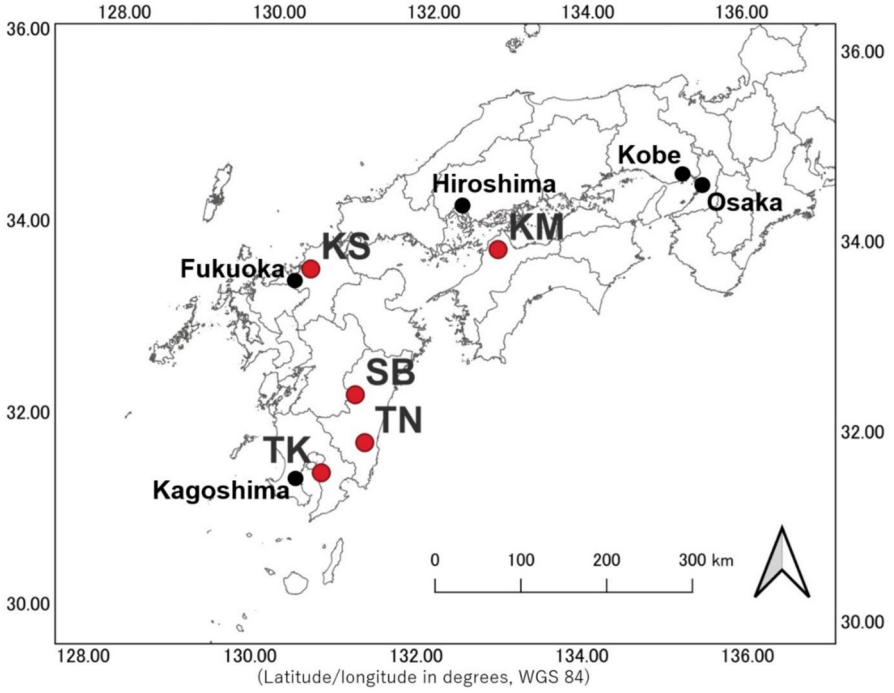


Fig. 1 Locations of the five study sites

broadleaved forests. Each common garden is managed and monitored by the respective host universities (Kyushu, Miyazaki, Kagoshima, and Ehime Universities), and routine plantation management practices (e.g., thinning) have been implemented over time. Clonal trials of *Cryptomeria japonica* were established in these common gardens between 1968 and 1970, with planted material originating from clonal propagation of elite trees (Kinashi 1973).

Six clonal cultivars originating from southwestern Japan—Kumotoshi, Yaichi, Obiaka, Yabukuguri, Measa, and Ayasugi—were planted at each site (Kinashi 1973). Based on tree-ring analyses of stem growth, Miyajima (1989) categorized these cultivars into early-, intermediate-, and late-growth types (Table 1), defined by the age at which periodic annual increment exceeded mean annual increment. These growth-type classifications correspond closely with early post-planting growth performance (1–3 years after planting; Kinashi 1973) and with current cultivar differences in tree size reported in recent assessments (Enoki et al. 2020, 2024). In addition to growth phenotypes, qualitative traits such as stem form, disease resistance, and tolerance to low temperature, shade, and drought have been documented for these cultivars (Miyajima 1989).

Genetic characterization indicates that the cultivars used in this study are not genetically uniform despite clonal propagation. Isozyme analyses showed genetic diversity among the clonal cultivars (Okuizumi 1993), and subsequent studies have identified DNA types (MuPS types) for these materials (Hisaeda et al. 2003). Furthermore, SSR-based assessments suggest that the genetic diversity of clonal cultivars from this region is greater than that of cultivars from other regions of Japan (Matsui et al. 2013), consistent with their long history of selection and propagation.

Site characteristics (site code, planting year, elevation, thinning history, and recorded disturbance events) are summarized in Table 2. Mean annual temperature and precipitation were obtained from the nearest meteorological stations, with Komenono (KM) showing the lowest mean annual temperature, and Tano (TN) and Kasuya (KS) showing the highest mean annual temperature among the five sites (Table 2).

Table 1 *Cryptomeria japonica* cultivar types and names, naming code, and cultivar characteristics (adopted from Miyajima 1989)

Cultivar type	Code	Characteristics
Early-growth type	EG_K	Straight stem; Low resistance against *Oligonychus hondoensis*
Kumotoshi	EG_Y	Straight stem; Small root; Less cold tolerance
Yaichi		
Intermediate-growth type	IG_O	Low wood density; High resistance against *Contarinia inouyei*
Obiaka	IG_Y	Curved stem; Low shade tolerance; Applicable to nutrient-poor sites
Yabukugi		
Late-growth type	LG_M	Less resistance against *Contarinaria inouyei*
Measa	LG_A	Straight stem; High cold and drought tolerance
Ayasugi		

Table 2 Characteristics of the study sites (Ref: Enoki et al. 2020; Japan Meteorological Agency)

Study sites	Tano	Shiiba	Kasuya	Takakuma	Komenono
Site code	TN	SB	KS	TK	KM
Year planted	1968	1970	1968	1970	1969
Average tree girths (cm)	72.93	102.50	96.80	73.04	95.64
Altitude/Elevation (masl)	160	1020	440	315	650
Thinning	1987	1991	None	1994	1978 and 1988
Disturbances	typhoon	typhoon, snow	typhoon, snow	typhoon, snow	typhoon
Average snow depth (cm)	0.10	4	3	4	1.50

Data Collection

Core samples (5 mm diameter) for dendrochronological analyses were taken from 48 trees per site (8 trees per cultivar × six cultivars) using an increment borer (Haglöf Sweden, 5.15 × 200 mm) at breast height (1.3 m) between 2020 and 2022 across the five study sites (TN, SB, KS, TK, and KM). One core sample was taken from each tree yielding 240 core samples in total. All sampled trees were single-stemmed individuals originating from planted clonal stock; no sampled trees showed evidence of coppicing, pollarding, or multi-stem regeneration, and stem form was consistent with standard plantation silviculture.

In the laboratory, the core samples were mounted and dried, and ring boundaries were prepared by sanding with progressively finer sandpaper (100, 120, and 240 grit) to obtain clear annual ring visibility. Annual ring widths were measured from bark toward pith at 0.01 mm resolution using a sliding microscope (NRM-D-3XY, Nippon Optical Works Co. Ltd., Nagano, Japan) with a movable measurement table connected to a counter and RS receiver Lite V4.0 software (AINIX Corp., Tokyo, Japan).

To characterize site climate, annual mean temperature and annual total precipitation were obtained from the nearest meteorological stations (Japan Meteorological Agency; Fig. 2).

Chronology Development and Pointer Years Estimation

Tree-ring chronologies were developed following standard dendrochronological procedures (Speer 2010). Crossdating quality control was conducted using COFECHA-style segmented correlation diagnostics (Grissino-Mayer 2001) implemented in R (dplR; Bunn et al. 2022), including segmented correlations against a robust master chronology and interseries correlation statistics (Pearson correlation; prewhitened series; biweight robust mean). Series flagged during segmented checks were re-examined by visual inspection and measurement verification to confirm calendar-year alignment. Because no unresolved dating offsets or measurement errors were detected, all 240 cores were retained for chronology

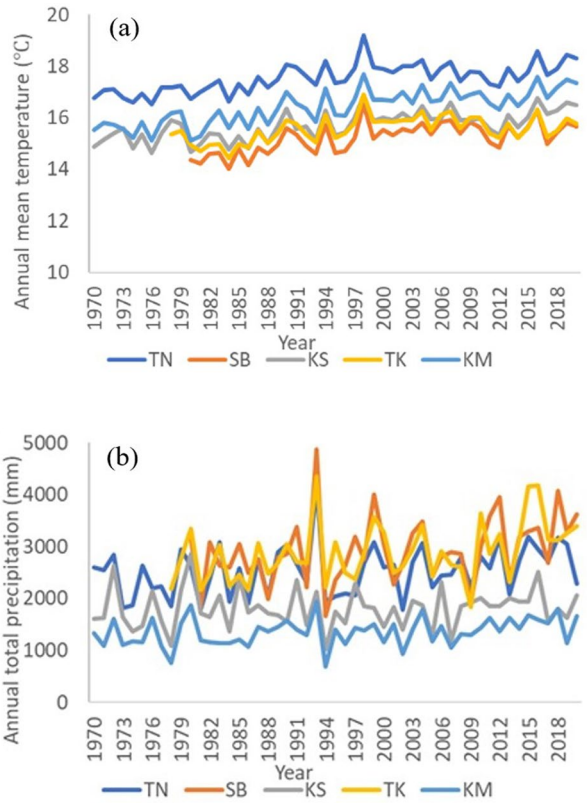


Fig. 2 Climate variables in the study sites, **a**: annual mean temperature, and **b**: annual total precipitation. Site codes are as indicated in Table 1

development. Because some cores did not capture the complete radial record (differences in core length and occasional missing early rings), individual series varied in their start and/or end years; chronology statistics were therefore calculated using the available overlap period.

We computed standard dendrochronological statistics including mean sensitivity (MS), mean series intercorrelation (Rbar), and expressed population signal (EPS). MS reflects year-to-year variability in ring width (0–1), with values ≥ 0.2 generally indicating sufficient variability to reflect climate signals (Speer 2010; He et al. 2019). Rbar, calculated as the mean correlation between individual series and the site master chronology, indicates the strength of the common growth signal. Chronology quality was evaluated using EPS with a threshold of 0.85 (Wigley et al. 1984; Buras 2017).

Individual ring-width series were detrended using a cubic smoothing spline (dplR; Bunn et al. 2022) to remove age- and size-related growth trends and to reduce long-term non-climatic influences (e.g., stand dynamics). Detrended series were combined into site chronologies using Tukey's biweight robust mean to minimize the influence of outliers (Cook and Kairiukstis 1990). We developed standardized (STD) chronologies to preserve low-frequency climatic information

and multi-year growth trends; we used them for climate–growth analyses because they retain common variance across a broad range of frequencies and can be a proxy of cumulative, long-term trends and overall sensitivity. A master regional chronology, fitted with cubic smoothing spline was also developed and cover site chronologies with the following overlap periods: TN/KS (1969–2020), KM (1970–2020), and SB/TK (1973–2020).

Pointer years were identified using the relative growth change (RGC) method (Schweingruber et al. 1990) implemented in pointres (van der Maaten-Theunissen et al. 2015). A year was classified as a pointer year when ≥ 50% of trees exceeded a common threshold (≥ + 25% for positive pointer years; ≤ − 25% for negative pointer years).

Climate-Growth Analysis

The relationships between monthly climate variables and standardized (STD) chronologies were quantified using bootstrapped response and correlation coefficients (Lévesque et al. 2013). We performed both static and moving correlation analyses to detect long-term and medium-term trends, implemented via the treeclim R package (dcc function; v2.07.1, Zang and Biondi 2015). Static bootstrapped correlations were calculated based on the common time period of all chronologies at each site. For moving correlation analysis, we applied a 35-year moving window with a 1-year offset. In both analyses, Pearson's correlation coefficients were calculated for 24 monthly variables, spanning from January of the previous year to December of the current growth year. Significance was assessed at $\alpha < 0.01$ based on 1,000 bootstrap replicates. All visualization of climate responses was performed using the ggplot2 package (Wickham 2016).

To examine yearly climate-growth response patterns per cultivar in each site, we computed Pearson correlation coefficients (r) using annual climatic variables and STD chronologies of each cultivar per site. Annual data covers cumulative, long-term trends and represents total accumulated conditions, which is suitable for assessing overall sensitivity/response (Cook and Kairiukstis 1990; Ravaioli et al. 2019). To compare yearly climate-growth sensitivity across cultivars, we calculated the standard deviation (SD) of climate correlation coefficients of each cultivar in all sites. Cultivars were categorized into three sensitivity levels based on their SD: High (Class H; 1st–2nd highest SD), Moderate (Class M; 3rd–4th), and Low (Class L; 5th–6th).

Finally, we characterized the overall climate-growth response patterns across sites and cultivars using Principal Component Analysis (PCA) via the prcomp function in R (base stats package). To assess broad geographic patterns of climate sensitivity while addressing potential temporal autocorrelation, multivariate analyses (PCA and PERMANOVA) were performed on summarized correlation coefficients (r). By condensing decades of growth dynamics into these singular metrics of sensitivity, the potential bias from year-to-year autocorrelation is integrated within each representative value, ensuring the robustness of the statistical distance between sites**.** The input variables for the PCA were the correlation coefficients between STD chronologies and two climate variables: annual mean temperature and annual total precipitation (r_Temp, r_Precip). Data were centered and scaled prior to

ordination to ensure equal weighting. PCA reduced the correlation-based climate-response profiles to a low-dimensional representation, enabling visualization of similarities among cultivar–site groups in a two-dimensional space (PC1–PC2). To statistically test the relative importance of geographic location (local site) and genetic identity (i.e., cultivar), a Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted using the adonis2 function in the R package vegan (Oksanen et al., 2022). The PERMANOVA was based on a Euclidean distance matrix (vegdist function) computed from the same correlation-based response variables, with significance assessed using 99,999 permutations. We report the proportion of variance explained (R^2) for the factors of site and cultivar.

Results

Dendrochronological Statistics

The STD chronologies revealed site-level variation in interannual growth patterns across the five study sites (Fig. 3) and the quality of the data is sufficient for the analysis (Table 3). The highest expressed population signal (EPS) was observed at KM (0.980), indicating a strong common growth signal among trees,

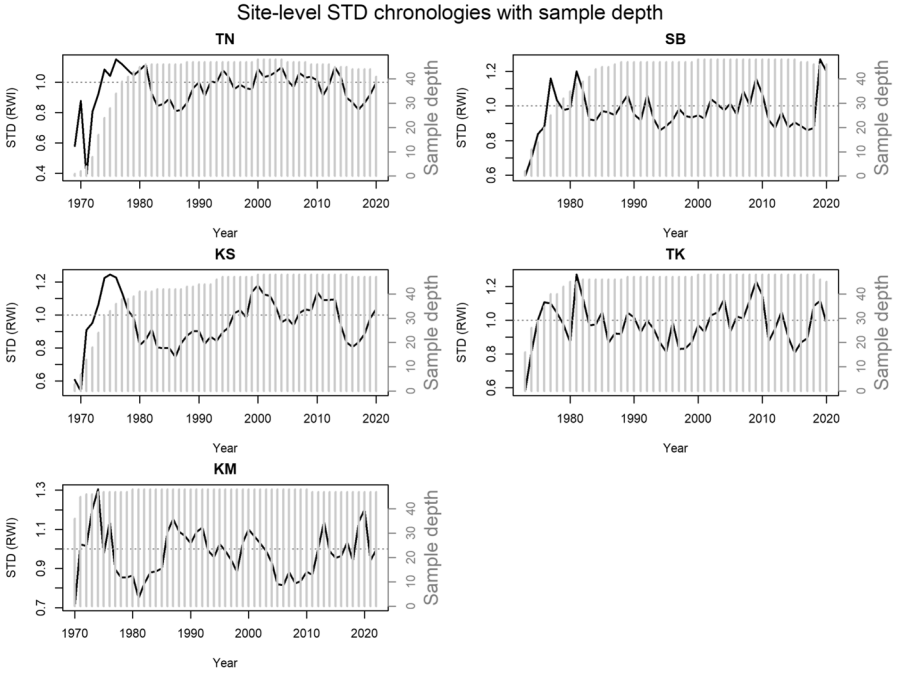


Fig. 3 Standardized (STD) ring width chronology (line) of TN, SB, KS, TK and KM, and their corresponding sample depths (bars). STD chronology represents a standardized tree-ring width series without age-related trends and other non-climatic variations

followed by TK (0.855). These values fulfill the criteria (EPS ≥ 0.85) to show the high replication and dating quality, and other sites also showed the values close to 0.8.

Series intercorrelation (Rbar) was highest at KM (0.511) and TK (0.291), while KS had the lowest (0.164), showing the different variations of growth patterns of trees in each site (Table 3). Mean sensitivity (MS), which measures year-to-year variability in tree growth, was highest at KS (0.332) and lowest at TN (0.257), showing that TN exhibited relatively stable growth trends over time while the KS showed more responsiveness to short-term environmental fluctuations (Table 3). Pointer years were estimated to identify years in which the majority of trees showed extraordinary growth responses. There were several site-level extreme growth events from 1970 to 2020 which reflect both regional climatic extremes and local environmental responses. Notably, TN and KS exhibited the most frequent pointer events while SB and TK showed fewer pointer events (Table 3).

Regional Chronology and Pointer Years

Based on the measured tree ring widths (240 individual trees and 5,351 growth rings), a region-wide local chronology (Fig. 4), which we refer to here as regional chronology, was developed. This regional chronology exhibited a mean ring width of 1.004 mm, with a standard deviation of 0.501 mm. Significant inter-annual variability was observed, with wider rings during 1973–1979, and narrower rings during 2010–2016. This chronology result indicated a change in *C. japonica* growth pattern after the year of 1983.

In the context of spatial distribution, estimated pointer years present information on sites with similar growth response patterns to climatic conditions. Based on Table 4, the frequency and direction of pointer years varied markedly among sites. TN exhibited a single positive pointer year (1975) but nine negative years, mainly in the early 1980 s and late 2010s. SB showed one positive year (2019) and two negative years (1994, 2012). KS presented one positive year (1974) but nine negative years distributed across several decades. TK recorded no positive pointer years and three negative years (1986, 1994–1995). KM, compared to the other sites, was characterized exclusively by positive pointer years ($n = 8$; 1989–1992, 2000, 2016, 2018–2019).

Tree Growth-Climate Relationships

Static Correlation Between Tree Ring Width and Climate

Positive and negative static correlations between climate data (temperature and precipitation) in each month and the tree growth were observed (Fig. 5). These direct response positive correlations between temperatures and the tree growth were detected in SB. The temperature in current year February (late winter) and March

Table 3 Summary statistics of *C. japonica* standardized (STD) tree ring chronologies and number of positive (+) and negative (-) pointer years

Sites (elev)	Chronology interval	No. of trees ($n=240$)	No. of cores ($n=240$)	Expressed Population Signal (EPS)	Series inter-correlation (Rbar)	Mean sensitivity (MS)	Total no. of rings measured	Pointer years
TN (160 masl)	1969–2020	48	48	0.834	0.230	0.257	1075	1 (+), 9 (-)
SB (1020 masl)	1973–2020	48	48	0.782	0.195	0.287	1079	1 (+), 2 (-)
KS (440 masl)	1969–2020	48	48	0.834	0.164	0.332	988	1 (+), 9 (-)
TK (315 masl)	1973–2020	48	48	0.855	0.291	0.295	1081	0 (+), 3 (-)
KM (650 masl)	1970–2020	48	48	0.980	0.511	0.282	1128	8 (+), 0 (-)

EPS ranged from 0.782 to 0.980, mostly exceeding 0.85. With 48 cores per site, lower values reflect weaker common forcing, not insufficient sampling. Rbar ≥ 0.3 is considered a common signal sufficient for climate restoration. MS ≥ 0.2 indicates sensitivity to climate

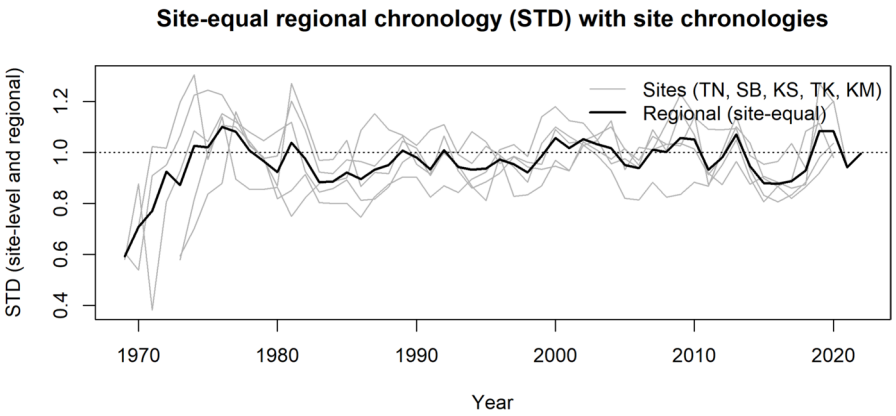


Fig. 4 Regional chronology of *C. japonica* in southwestern Japan. The gray lines represent the standardized (STD) chronologies for each site. The heavy solid line indicates the master regional chronology, fitted cubic smoothing spline. Chronologies cover the following overlap periods: TN/KS (1969–2020), KM (1970–2020), and SB/TK (1973–2020)

Table 4 Calendar years characterized by a strong relative increase or decrease in radial growth. The years and numbers *n* refers to such an occurrence found in 50% of the trees (pointer years)

	TN	SB	KS	TK	KM
Years with increase	1975	2019	1974		1989–1992, 2000, 2016, 2018–2019
n	1	1	1	0	8
Years with decrease	1982–1984, 2017–2018	1994, 2012	1978–1981, 1983–1984, 1986, 2015–2016	1986, 1994–1995	
n	9	2	9	3	0

(early spring) in SB were positively correlated with the growth. Furthermore, the temperature in previous year June (early summer) in SB was positively correlated with growth.

The precipitation in current and previous year November (late autumn) at TN were positively correlated with radial growth. Current year precipitation in June (early summer) in two sites (SB and TK), that in October (middle of autumn) in SB, and that in November (late autumn) in KM are negatively correlated with growth. In addition to these common trends among the sites, as a single site-distinct trend, current and previous year precipitation in March (early spring) in KS are negatively correlated with the tree growth. In TK, the previous year precipitation in June (early summer) is also negatively correlated with the growth.

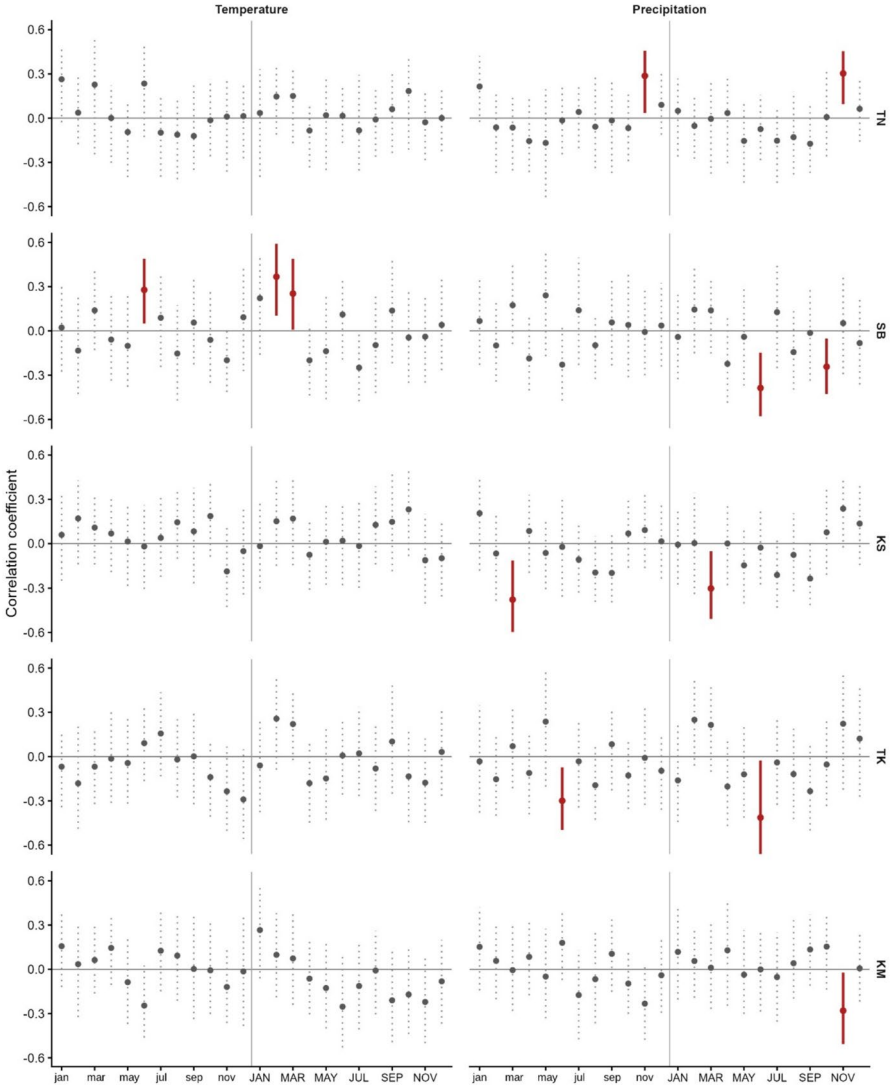


Fig. 5 Static correlations between ring chronologies and climate (temperature and precipitation) among sites in previous growing season and current growing season. Months in capital letters correspond to the present growing season while months in lower-case letters refer to the previous growing season. Error bars represent 95% confidence interval.

Moving Correlation of Ring Width and Climate

The 35-year moving correlation analysis revealed varying regional cumulative growth and dynamic responses to temperature and precipitation (Fig. 6a, 6b). Temperatures in current year late winter to early spring (February or March) were

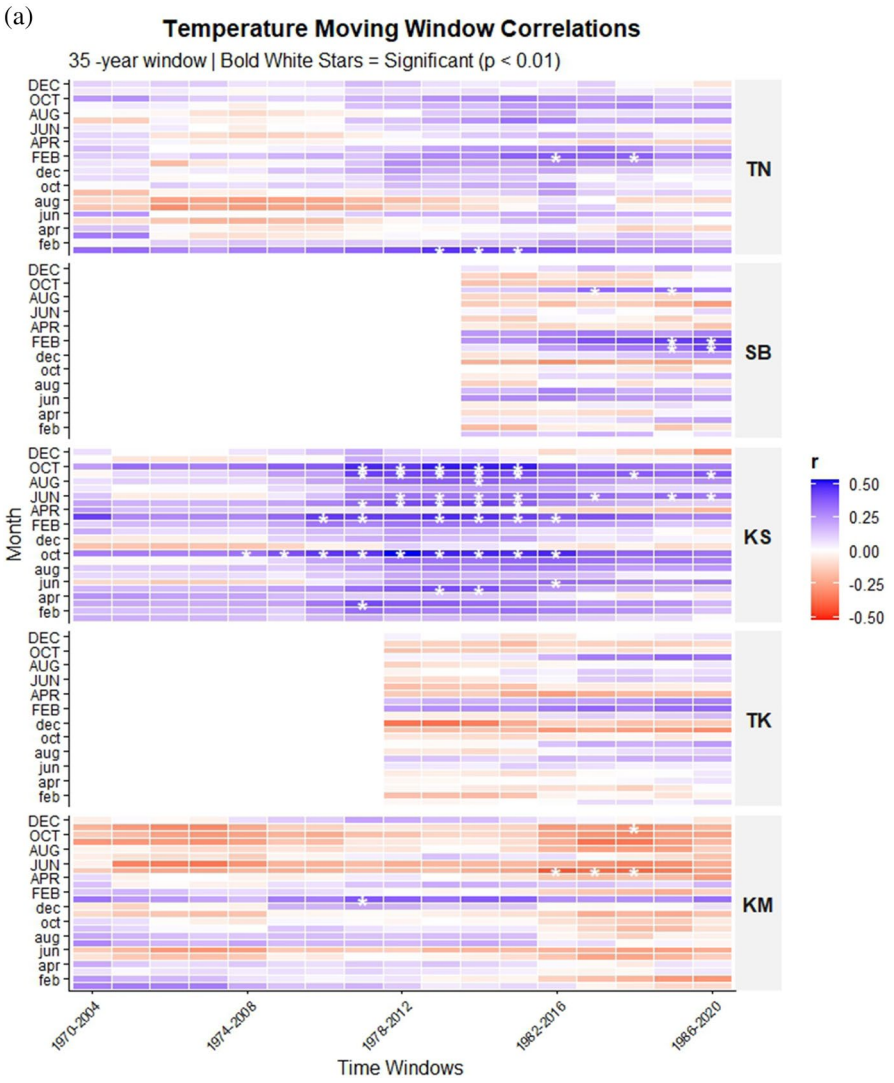


Fig. 6 **a** Moving correlation of TN, SB, KS, TK and KM sites. Asterisks indicate significant ($p < 0.01$) correlations between the tree growth and temperature in the bootstrapped 35-year period. Months indicated in capital letters correspond to present growing season while months non-capitalized refer to previous growing season

positively correlated with radial growth in TN, SB, and KS sites (Fig. 6a) in more than one moving window. Temperatures in early to mid-autumn (September or October) were positively correlated with radial growth in SB and KS sites (Fig. 6a) in more than one moving window. Temperatures in previous year early summer (June) are positively correlated with radial growth in KS. For KS specifically, we observed positive correlations with temperature throughout pre-growing and current

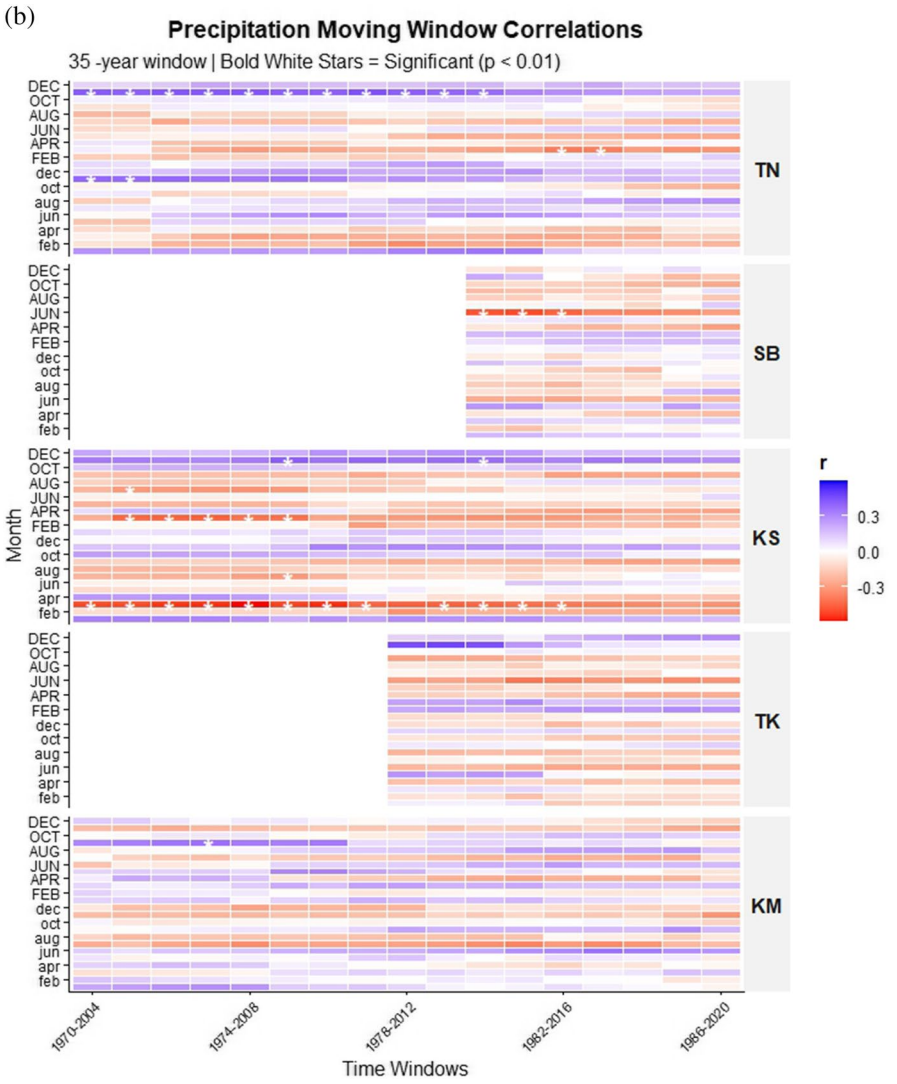


Fig. 6 (continued)

growing seasons. On the other hand, the negative correlations between current and previous year temperature in each month and tree growth were also observed. These negative correlations were detected in KM. Current growing season temperatures in late spring (May) and late autumn (November) were negatively correlated with the growth in KM.

Current and previous year precipitation in each month were also correlated with tree growth. Radial growth of *C. japonica* cultivars had positive correlation with precipitation in current year early or late autumn (September or November) in TN, KS, and KM sites, in one or more than one moving window. TN showed

positive correlations in previous year late autumn (November) (Fig. 6b). Negative correlations between current and previous year precipitation in each month and growth were also observed. Common trends in all sites were not detected. Current year precipitation during early spring (March) is negatively correlated with the growth in two sites (TN and KS). In addition, precipitation in early summer or middle of summer (June or July) are also negatively correlated with the growth in two sites (SB and KS). For the previous year precipitation, negative correlation with precipitation in early spring (March) were observed in KS. KS had more than one month (in current year and previous year, respectively) when negative correlations were observed between precipitation and radial growth.

Cultivar Variation Based on Annual Climatic Variables and Ring Width Across Sites

In terms of climate-growth response patterns alone, early-growth types (EG_K and EG_Y) responded similarly to climatic factors in TN, SB, and KS (Fig. 7). Both cultivars had positive correlation with temperature and negative correlations with precipitation in those three sites. Although only correlation between growth of EG_K and temperature was statistically significant in SB, the two early-growth types showed similar responses to temperature and precipitation.

Intermediate-growth types (IG_O and IG_Y) showed similar patterns of correlation in KS. Both cultivars have relatively strong negative correlations with precipitation and positive correlation with temperature. The correlations observed in KS are not statistically significant. However, the negative correlations between precipitations and growth of the two intermediate-growth type cultivars are relatively strong compared with those of other cultivars. The result shows the existence of similarity in climate response patterns among the intermediate-growth type cultivars in KS.

For late-growth types (LG_M and LG_A), they showed similar patterns of correlations with precipitation in TK. Both of the late-growth types have relatively strong negative correlations with precipitation in TK.

Each cultivar's climatic response variations among sites (Fig. 8) are summarized in Table 5, indicating common characteristics in each growth type. For temperature, the early growth type showed high and low variations and all correlations except the one in KM were positive. For precipitation, early-growth type showed moderate variations with both positive and negative correlations. On the other hand, the intermediate-growth type showed low variations, and the late-growth type showed high variations. As for the individual cultivars, Yaichi (EG_Y) showed lowest variations for temperature, and Obiaka (IG_O) showed lowest variations for precipitation. In particular, all correlations of Obiaka (IG_O) for precipitation were negative. Yabukuguri (IG_Y) showed lowest variations for temperature, and Measa (LG_M) showed highest variations for precipitation (Table 5).

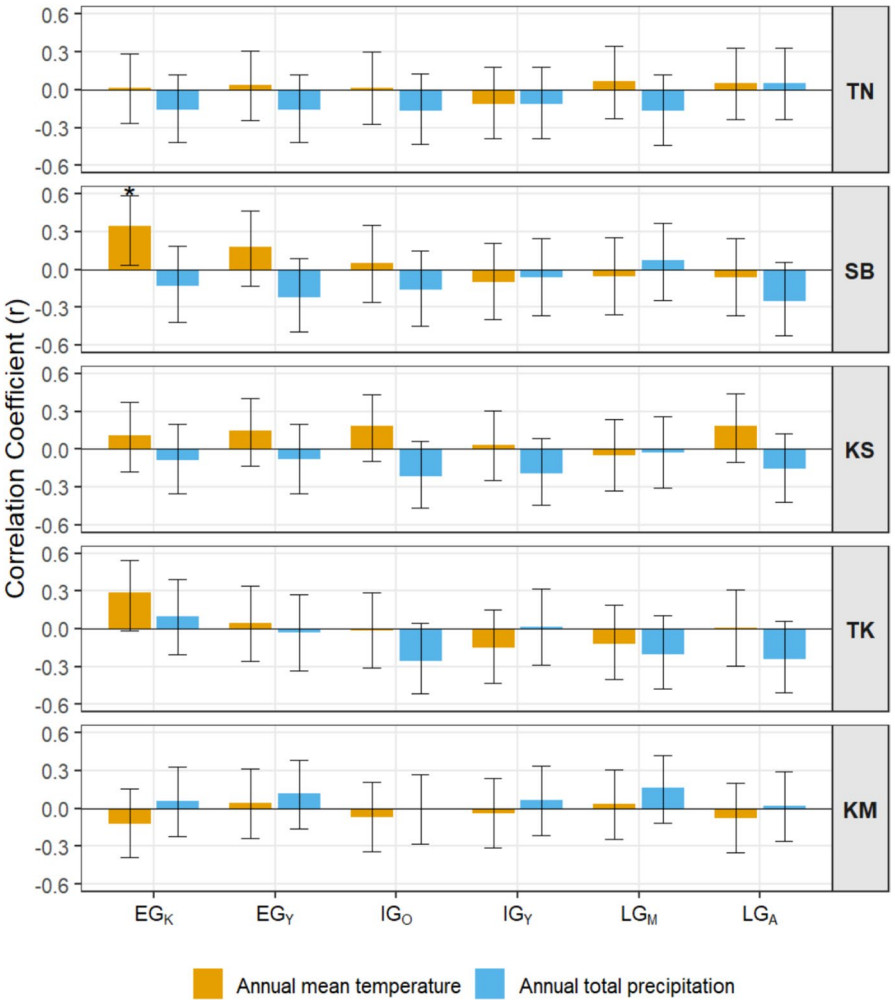


Fig. 7 Correlation between STD chronology of all cultivars and mean annual climatic variables at each site with 95% confidence intervals. Significant correlations are marked with asterisks (*) ($p < 0.05$)

Climate-Growth Relationships Across Sites and Cultivars

Multivariate ordination revealed differences in climate-growth relationships across site and the cultivars. Because the PCA was based on two correlation variables, the first two principal components (PC1 and PC2) together accounted for all of the variance in the climate–growth response matrix, with PC1 and PC2 explaining 56.6% and 43.4%, respectively. The PCA biplot (Fig. 9) showed a clear geographic structure especially in TN, KM, and SB, where samples from the same site tended to cluster together regardless of cultivar. PERMANOVA further confirmed that Site was a significant driver of climate response patterns,

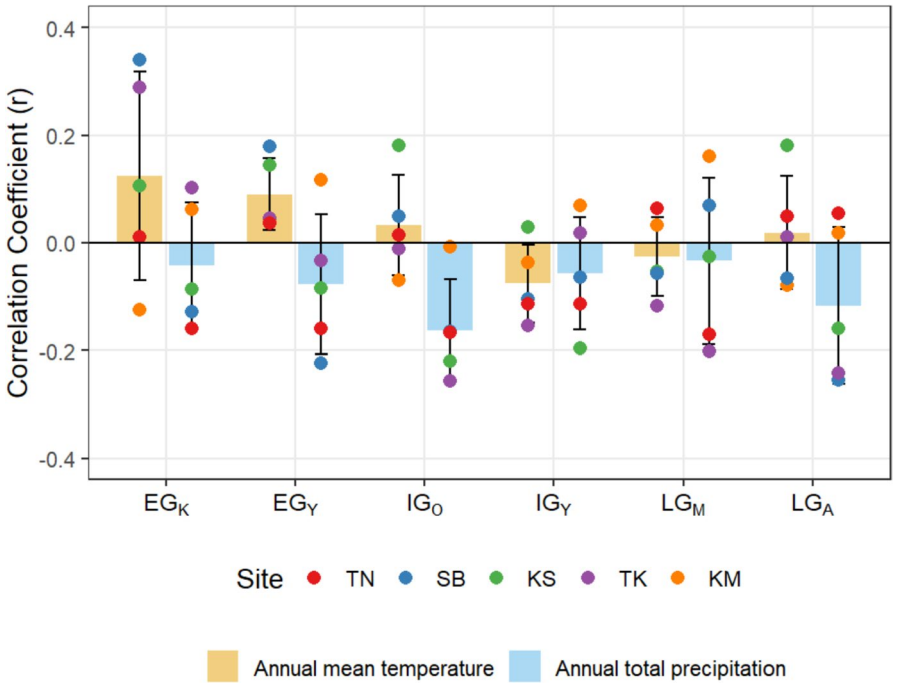


Fig. 8 Mean correlation coefficient between mean annual temperature/mean annual precipitation and standardized (STD) chronologies. Thin error bars represent standard deviations in correlation coefficients

Table 5 Cultivar-specific climatic response variation among sites. Mean r = mean Pearson correlation coefficient between standardized (STD) chronologies and annual climate variable across sites; SD = standard deviation of site-level correlations; n = number of sites. Classification: H = high variation (1st–2nd highest SD), M = moderate (3rd–4th), L = low (5th–6th). Sign qualifiers: (+) all correlations positive, (-) all negative, (±) mixed signs

	EG$_K$	EG$_Y$	IG$_O$	IG$_Y$	LG$_M$	LG$_A$
n (sites)	5	5	5	5	5	5
Temperature						
Mean r	0.124	0.090	0.033	−0.076	−0.026	0.019
SD	0.193	0.067	0.094	0.072	0.074	0.105
Class	H (±)	L (+)	M (±)	L (-)	M (±)	H (±)
Precipitation						
Mean r	−0.042	−0.077	−0.163	−0.057	−0.033	−0.117
SD	0.117	0.130	0.095	0.105	0.154	0.145
Class	M (±)	M (±)	L (-)	L (±)	H (±)	H (±)

explaining 27.7% of the total variance ($R^2 = 0.28$, $p = 0.014$) (Table 6). This indicates that geographic location accounted for a substantial proportion of the variation in responses to annual temperature and precipitation. Although

Table 6 Result of PERMANOVA for climate-growth response at sites and cultivars

Factor	Df	Sum of Squares	R^2	F value	*p* value
Site	4	0.23996	0.2766	2.78	0.014
Cultivar	5	0.19629	0.2262	1.82	0.085
Residual	20	0.43139	0.4972		
Total	29	0.86763	1		

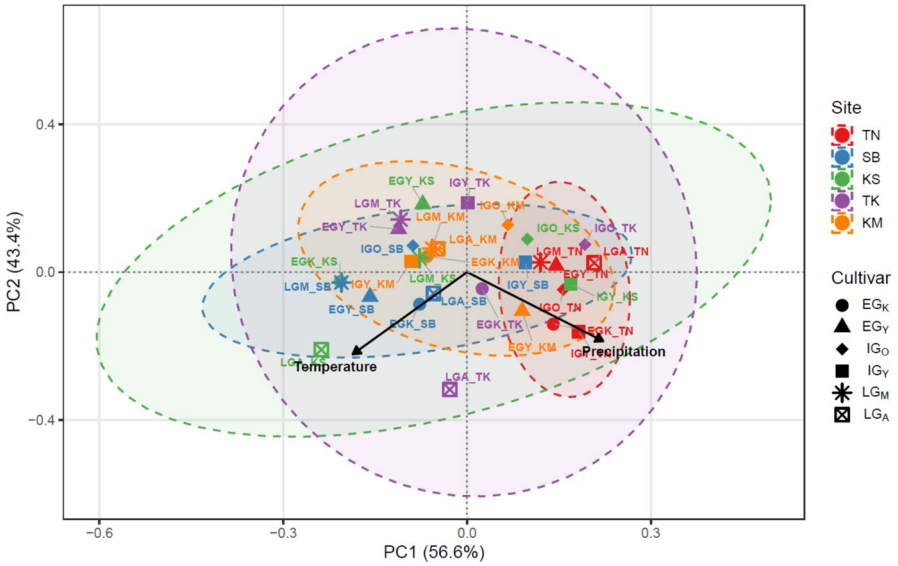


Fig. 9 Principal component analysis (PCA) of cultivar- and site-specific climate response of tree ring width. Each point represents one cultivar × site combination ($n = 30$), plotted according to the Pearson correlation coefficients between standardized (STD) chronologies and two climate variables: annual mean temperature and annual total precipitation. Arrows indicate the direction and relative magnitude of each climate variable in PCA space. Point colors indicate site and point shapes indicate cultivar. Shaded ellipses represent 95% confidence regions for each site. PC1 and PC2 explained 56.6% and 43.4% of the total variance, respectively

cultivar factor did not reach the conventional significance threshold ($R^2 = 0.23$, $p = 0.085$) (Table 6), it still explained 22.6% of the variance.

Discussion

Site-Specific Response to Temperature

Across all sites, warmer early spring temperatures positively influenced radial growth (Fig. 6), underscoring the importance of favorable thermal conditions for physiological processes such as budburst, cambial reactivation, and early xylem

differentiation (Begum et al. 2010a, 2018). Likewise, early autumn temperatures contributed positively to growth, likely reflecting a seasonal shift from shoot elongation to latewood formation. In a high-elevation site such as SB, the positive influence of temperature extended into late winter (Fig. 5), suggests that milder winter conditions—through mechanisms like earlier snowmelt, reduced frost damage, and maintenance of metabolic activity—can support growth resumption in spring (Zhang et al. 2019; Dusenge et al. 2019; Fry and Phillips 1976; Harvey et al. 2020; Janecka et al. 2020). Warmer winters have also been shown to facilitate earlier cambial activity and extend the growing season in conifers (Rossi et al. 2008; Pavão et al. 2024). They support non-structural carbon (NSC) accumulation during dormancy (Hiejima et al. 2025), which enhances cold hardiness and provides critical carbon reserves for early-season growth (Hoch et al. 2003; Tixier et al. 2019; Morin et al. 2007). These findings align with previous studies of *C. japonica*, which show positive growth responses to mild winters and early spring warming (Oribe and Kubo 1997; Begum et al. 2010a).

The positive correlations with early summer temperature were found in a higher elevation site (Fig. 6; KS), where warmth may enhance cell enlargement and hydraulic conductivity, especially if accompanied by sufficient water availability (Pandey 2021). An early warm summer (Fig. 6) characterized by KS would be advantageous for radial growth due to snowmelt and recharge of soil water storage. However, at the low-elevation TN, these positive correlations were absent. This suggests a site-specific response where heat stress may outweigh temperature-related benefits under lower elevation and potentially drier conditions (Sanui et al. 2009). On the other hand, soil water availability from precipitation and snowmelt water may provide adequate soil moisture which can buffer against extreme heat, promoting better growth conditions, as may be the case of KS.

Negative correlations with late spring and autumn temperatures—particularly at KM (Fig. 6)—indicate that heat during the growing season can impair radial growth especially in less precipitation condition like KM. This is likely due to heat-induced increases in evapotranspiration, leading to soil moisture deficits and physiological water stress (Qaderi et al. 2019). These findings are consistent with prior studies on *C. japonica* that report reductions in photosynthetic capacity and carbon assimilation under high-temperature conditions and increased water stress (Jung et al. 2022; Song et al. 2021; Pavão et al. 2024).

Interestingly, TN showed a temporal increase in positive growth response to growing-season temperatures (Fig. 6), potentially reflecting acclimation by cultivars at this low-elevation, warmer site. Acclimation of radial growth to temperature among cultivars can differ depending on their capacity to follow shifts in their optimal conditions (i.e., conditions of maximal growth and minimal stress) or to persist under sub-optimal conditions i.e., conditions of reduced growth due to increased stress (Keddy 2017; Cocozza et al. 2021). In TN, suggestive negative growth responses to high temperatures in May and August have decreased in the last 10 years (Fig. 6), which may be related to physiological acclimation of *C. japonica* trees as they matured.

Length of the growing season can be affected when warmer winters and earlier spring onset promote earlier cambial activation and longer periods of photosynthesis

(Öquist and Huner 2003). This may reduce frost hardiness (Riikonen et al. 2023) and may increase the risk of winter embolism (Cox and Malcolm 1997). Trees can adjust their growth patterns, and an extended radial growth and an earlier cambial reactivation may indicate trait plasticity, as shown in Gricar et al. (2014), with *Picea abies* in Slovenia and Czech Republic conferring phenological differences due to extrinsic and intrinsic factors. In regions with lowest precipitation, *P. abies* tended to shorten growth duration. In *C. japonica*, the gradual increase in tree radial growth as influenced by an increase in annual average temperature was a trend in SB (Fig. 7a).

Site-Specific Response to Precipitation

Early or late autumn precipitation positively affected growth in TN, KS, and KM sites (Fig. 6). Static correlation analysis supported the importance of autumn precipitation, particularly in TN (Fig. 5). These timings align with prior studies emphasizing the role of cool-season rainfall in promoting soil moisture recharge and cambial activity in *C. japonica* (Hirano et al. 2020; Komatsu et al. 2007). Positive correlations with previous year precipitation in TN —especially in late autumn—suggest that water availability before the growing season contributes to radial growth. This reflects indirect effects of increased soil moisture reserves and carbohydrate accumulation supporting the subsequent year's growth.

Although there was no common trend across all sites regarding the negative impact of rainfall on growth (Fig. 6), high summer precipitation in SB and KS may have reduced solar irradiance and photosynthetic efficiency, leading to growth suppression (Jung et al. 2022). Radial growth in KS is probably influenced by the seasonality of precipitation, in such a way that leaf flushing and radial increment rate may be having a synchronous response to water availability in dry sites (Mendivelso et al. 2016). Negative correlations between growth and early summer temperature suggest that increased evaporative demand during this season can offset the benefits of precipitation, reducing net water availability (Zhang et al. 2024; Li et al. 2024). The negative correlation results (Fig. 5) are also in line with earlier findings in *C. japonica* plantations in South Korea where abnormally high summer precipitation suggested interruption of photosynthesis by reducing sunshine duration and evaporation (Jung et al. 2022). In our study, precipitation in June in SB coincided with the negative growth response (Fig. 6). Such growth suppression may also suggest complex dynamics aside from reduced light availability, which includes leaching or acid precipitation effects (Sekiguchi et al. 1986; Takahashi et al. 1986) and interference to radial growth due to recurrent flushing or shoot growth (Jung et al. 2022).

Light availability may have contributed to radial growth among sites and cultivars; however, because light interception was not quantified in our study due to data limitation, such effects cannot be explicitly separated from temperature- and precipitation-driven mechanisms. Over the multi-decadal lifespan of the sampled trees, changes in stand structure due to growth of neighboring vegetation, natural disturbances, and silvicultural practices may have altered light interception among individuals and sites. In this study, the common-garden design and within-site comparisons among clonal cultivars mitigate site-related variability. Cultivar-specific

responses to temperature and precipitation should be interpreted as reflecting combined responses to such climatic variables and site conditions.

Cultivar-Specific Response to Annual Temperature and Precipitation Across Sites

Analysis of annual climate-growth correlations indicated early-growth type cultivars tended to show positive responses to temperature across sites. Conversely, late-growth types showed more variable responses to precipitation. Intermediate-growth type showed negative correlation with temperature or precipitation. When examining annual climate-growth correlations (Fig. 7), the majority of relationships did not reach statistical significance ($p < 0.05$). Consequently, the observed climate-growth relationship should be viewed as qualitative trends rather than definitive genetic traits.

As an example of cultivar-specific response to climate at individual sites, early-growth types (EG_K, EG_Y) showed relatively strong positive correlations with temperature and suggestive negative correlations with precipitation at SB. On the other hand, EG_Y and LG_M showed suggestive positive correlations with precipitation at KM. These findings align with studies showing positive effects of temperature on intra-annual growth processes of *C. japonica* (Begum et al. 2010b; Rahman et al. 2020), as well as mixed effects of precipitation depending on site water balance (Shigenaga et al. 2005; Matsumoto et al. 2006). Precipitation can become a key mitigating factor to buffer against heat stress—as observed in drought-sensitive species such as *Pinus sylvestris* (Bozkurt et al. 2021). This was apparent at cultivars in the driest site KM (Fig. 7), but is not significant, highlighting the complexity and nonlinearity of tree responses to climate (Vaganov et al. 2006).

The result of PERMANOVA indicate local adaptation of the cultivar populations to the climatic conditions of their region of origin is the primary determinant of climate-growth interactions, however it also indicated that the inherent genetic characteristics of cultivars may provide an additional layer of variation in their plasticity. Considering these results for cultivar and site-specific response to climate, both cultivar and site need to be examined further to identify their interaction.

Cultivar-Level Variation as Clonal Plastic Response to Environmental Changes

Topographic factors also influence growth of the clonal cultivars of *C. japonica* tree height decreases from lower to upper slope (Enoki et al. 2020). The early-growth types have greater phenotypic plasticity and are able to exploit favorable conditions to realize greater height growth especially at lower-slope positions. In our study, we found that the two early-growth types, EG_K and EG_Y, showed distinct positive growth to temperature (Fig. 8). Phenotypic plasticity in response to temporal changes in climate may also be manifested in morphological (leaf mass per leaf area, shoot mass per area) and physiological traits (leaf nitrogen content, nitrogen-resorption efficiency) (Vallicrosa et al. 2024; Zhang et al. 2024), contributing to differences in growth rate among the cultivars in this study.

Silvicultural intervention such as thinning and site-specific forest management strategies (e.g., selecting species and clones suited to future climates, adjustment of rotation length based on site productivity and genotype) may increase forest resilience during drought and drought-induced water stress leading to growth releases. In our results, IG_Y exhibited relatively consistent climate-growth response patterns across sites, as indicated by the low variation (Class L) in its annual temperature and precipitation correlations (Fig. 8, Table 5). While these correlations were generally weak and often non-significant, the stability of this pattern across diverse environments is noteworthy. These findings complement a previous study by Enoki et al. (2024), which observed the highest growth-release in IG_Y following site management, suggesting that this cultivar may possess high acclimation potential and the ability to recover growth effectively from disturbances.

Conclusion

Overall, this study demonstrated clear site-specific variation in the growth–climate relationships among *C. japonica* cultivars across five sites in southwestern Japan. Our results reinforce the potential of *C. japonica* as a model for studying long-term relationship between tree growth and climate, and underscores the importance of site-specific strategies in forest management and the need for trait-based selection to sustain plantation forestry in an uncertain future.

This study also provides new insights into the climate sensitivity of *C. japonica* cultivars grown across diverse environments in southwestern Japan. Remarkably, cultivars categorized by growth timing (early-, intermediate-, late-growth types) often showed consistent climate responses within groups, particularly at sites with clear seasonal climate signals. Late-growth cultivars in drier regions benefited from precipitation, suggesting potential advantages under shifting rainfall regimes. The observed cultivar–climate interactions underscore the importance of genetic variation in shaping growth responses and resilience to climate change.

These findings have practical implications for forestry management and climate adaptation strategies. Selection and deployment of climate-resilient cultivars tailored to local environmental conditions could improve productivity and reduce vulnerability under future warming and hydrological shifts. We acknowledge that our findings include uncertainties arising from site management differences or limited sampled trees. Studies including a wider range of sites and cultivars would elucidate climate effects on radial growth among sites and cultivars of *C. japonica*. Furthermore, research is needed to evaluate long-term growth plasticity, physiological mechanisms underlying climate responses, and the role of cambium, root, and hydraulic traits in influencing radial growth and mediating drought resilience across cultivars of *C. japonica*.

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Author Contributions HRI conceived the study. HRI, CU, WAA, TE, MT and SU conducted the field work and collected the samples. CU prepared and measured the samples. CU wrote the first version of the manuscript. HRI, WAA, TE, MT and SU provided edits to the manuscript.

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Data Availability The data underlying this article will be shared on reasonable request to the corresponding author.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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