



Geographical, Climatological, and Biological Characteristics of Tree Radial Growth Response to Autumn Climate Change

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OPEN ACCESS

Edited by:

Sigrid Netherer, University of Natural Resources and Life Sciences Vienna, Austria

Reviewed by:

Larry Lopez, Yamagata University, Japan Martin De Luis, University of Zaragoza, Spain

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Specialty section:

This article was submitted to Forest Disturbance, a section of the journal Frontiers in Forests and Global Change

Received: 30 March 2021 Accepted: 03 August 2021 Published: 26 August 2021

Citation:

Tei S, Kotani A, Sugimoto A and Shin N (2021) Geographical, Climatological, and Biological Characteristics of Tree Radial Growth Response to Autumn Climate Change. Front. For. Glob. Change 4:687749. doi: 10.3389/ffgc.2021.687749 Terrestrial forest ecosystems are crucial to the global carbon cycle and climate system; however, these ecosystems have experienced significant warming rates in recent decades, whose impact remains uncertain. This study investigated radial tree growth using the tree-ring width index (RWI) for forest ecosystems throughout the Northern Hemisphere to determine tree growth responses to autumn climate change, a season which remains considerably understudied compared to spring and summer, using response function and random forest machine learning methods. Results showed that autumn climate conditions significantly impact the RWI throughout the Northern Hemisphere. Spatial variations in the RWI response were influenced by geography (latitude, longitude, and elevation), climatology, and biology (tree genera); however, geographical and/or climatological characteristics explained more of the response compared to biological characteristics. Higher autumn temperatures tended to negatively impact tree radial growth south of 40° N in regions of western Asia, southern Europe, United State of America and Mexico, which was similar to the summer temperature response found in previous studies, which was attributed to temperature-induced water stress.

Keywords: tree-ring width index, forest ecosystem, Northern Hemisphere, random forest algorithm, climate change, temperature-induced water stress, machine learning, response function

INTRODUCTION

Forest ecosystems play a vital role in the global carbon cycle (Pan et al., 2011) and climate systems (e.g., Bonan, 2008). However, since the early 1970s, forest ecosystems across the Northern Hemisphere have experienced varying warming rates. In particular, the warming rates across northern high-latitude regions are higher than anywhere else on earth, a phenomenon known as Arctic amplification (e.g., Serreze and Barry, 2011). This amplified

warming has a potentially significant impact on forest ecosystems (e.g., Tei et al., 2019a,d; Tei and Sugimoto, 2020).

An important role of forest ecosystems is mitigating the accumulation of atmospheric CO_2 (Fan et al., 1998; Bousquet et al., 2000). However, there is significant uncertainty regarding the magnitude and location of the forest ecosystem CO_2 sink (Goodale et al., 2002; Ciais et al., 2010). Consequently, understanding spatial variations in the forest ecosystem response to climate change over a vast biome or region with significant gradients in geographic, climatological, and biological characteristics are crucial for accurate projections of the terrestrial carbon cycle and global climate.

A dendroecological analysis helps study the forest ecosystem response to a changing environment (e.g., Walker et al., 2015; Tei et al., 2015, 2019b). Tree-ring width indices (RWI) are useful long-term indicators of historical forest productivity due to the frequently observed close relationship of the RWI with forestlevel gross primary production (GPP) and/or net ecosystem exchange (NEE) (e.g., Xu et al., 2017; Tei et al., 2019c). A recent synthetic analysis of RWI data from the International Tree-Ring Data Bank (ITRDB) confirmed the widespread negative sensitivity of radial tree growth to warming in circumboreal forests (Tei et al., 2017a,b), which is particularly prevalent in dry continental regions, such as the interiors of Alaska and Canada, southern Europe, and central-eastern Siberia. These researches have indicated a one-year time lag in the forest ecosystem response to climate change in these regions, which is considered to be an adaptation of the forest ecosystem to a severely waterstressed environment (e.g., Chapin et al., 1990; McDowell et al., 2008; Genet et al., 2010; Wiley and Helliker, 2012).

To date, broad-scale RWI analysis (e.g., Tei et al., 2017a,b) and satellite remote sensing studies (e.g., Wang et al., 2011; Buermann et al., 2014) have mainly focused on tree radial growth/ecosystem responses to climate change during the spring and/or summer. However, recent studies have reported that climate variables in other seasons can significantly affect tree radial growth and ecosystem activity in the northern high-latitude region (Tei and Sugimoto, 2018). While there have been recent improvements in our understanding of the importance of cold season climate drivers (e.g., Wu et al., 2018), there is still a lack of information regarding the spatial distribution of seasonal climate variables that control temporal variations in RWI. Furthermore, there is a lack of understanding with respect to whether the tree radial growth response to climate change varies by tree genera or species because very few RWI studies have evaluated differences in the climate change response and the genus or species scale (Lloyd and Bunn, 2007).

In this study, we investigate the geographical (latitude, longitude, and/or elevation), climatological and biological (genus and/or species) characteristics of the tree radial growth response to climate change during the autumn over a wide region/biome with significant geographical, climatological and biological gradients. We achieve this by applying statistical response function analysis and the random forest machine learning method to RWI data and autumn climate variables, including temperature, precipitation, and cloud cover, over the past 120 years.

MATERIALS AND METHODS

Tree-Ring Data

We collected raw tree-ring-width chronologies from 2894 ITRDB sites (laccessed during spring-winter 2020) located in the Northern Hemisphere and with a chronology that started before 1950 and ended after 1990. The standard RWI chronology was generated for each site by using R (R Core Team, 2017) and the "dplR" package. We detrended the growth patterns associated with tree age and natural disturbances in the raw time series, derived from the single dominant tree species for each site, using cubic smoothing splines and, subsequently, averaging the standardized ring widths among the samples. Spline fits with a length of 128 years were applied to raw time series. Generally, standardization methods are varied among chronologies/sites; however, in this study, we applied spline fitting to standardize the chronologies across all the sites, which was done because our approach is conservative, and the method is regarded as relatively site-insensitive (Cook, 1985; Cook and Kairiukstis, 1990).

The quality of RWI was assessed using the expressed population signal (EPS). The EPS is a measure of how well a finite sample of tree-ring data represents an infinite population chronology, and an EPS value of 0.85 is considered a threshold of acceptable statistical quality for dendrochronological analysis (Wigley et al., 1984). The EPS values for 2167 of the 2894 sites were higher than 0.85, indicating a high degree of common variability between individual trees. Therefore, for subsequent analysis, we used the RWI for these 2167 sites.

Climate Data

Gridded monthly near-surface average temperature, cloud cover (the fraction of the sky obscured by clouds), and total precipitation datasets from the Climate Research Unit (CRU TS 4.01; 1901–2016; $0.5^{\circ} \times 0.5^{\circ}$; Harris et al., 2014) were used to derive monthly climate records from grids over the RWI sites.

Response Function Analysis

To evaluate the impact of a target climate variable (among temperature, precipitation, and cloud cover) in autumn independently from other seasons, i.e., winter, spring and summer, and other climate variables, we applied response function (RF) analysis for RWI and seasonally averaged climate variables for the 2167 RWI sites over the vast biome/region of the Northern Hemisphere. In this RF analysis, the climate conditions of the current four seasons (from winter to autumn) and previous summer and autumn were used because existing RWI and satellite image studies have shown that the climate conditions of the previous year substantially affected tree radial growth, especially in arid regions (Kagawa et al., 2003, 2006; Tei et al., 2013a; Tei and Sugimoto, 2018). The period when both RWI and climate data were available (1901–2016) was used for the analysis.

RF represents a result of principal component (PCs) analysis in which climate variables are decorrelated (Fritts, 1976; Cook and Kairiukstis, 1990). In the RF analysis, the multi-collinearity

¹http://www.ncdc.noaa.gov/paleo/treering.html

among seasonal climatic parameters (3 climate variables with six seasons: previous summer and autumn, and current winter, spring, summer, and autumn) was reduced by extracting principal components (PCs). The eigenvectors with relatively low values calculated from the seasonal climate variables are excluded. The relationships between RWI and the PCs of the seasonal climate variables were back-transformed to relationships with the seasonal climate variables, i.e., the coefficient of RF analyses. The RF analysis was applied using R and the "treeclim" package.

With reference to previous studies of plant seasons in boreal/arctic ecosystems (e.g., Morozumi et al., 2020; Nagai et al., 2020), we assumed that the definitions of each season varied depending on the latitude of the RWI site. For sites located between 0 and 60° N, spring was considered to be March, April, and May; summer was June, July, and August; autumn was September, October, and November; and winter was December, January, and February. For sites located between 60 and 67° N, spring was considered to be April and May; summer was June, July, and August; autumn was September and October; and winter was November, December, January, February, and March. For sites located north of 67° N, spring was considered to be May and June; summer was July; autumn was August and September; and winter was October, November, December, January, February, March, and April.

Relationship Between RWI Response to Autumn Climate Change and Latitude/Climate Condition

We used coefficients from the RF analysis for each RWI site to investigate how geographical (latitude, longitude, and elevation), climatological (temperature, precipitation, and cloud cover), and biological (tree genus and species) characteristics impacted the RWI response to autumn climate change. We used the climate conditions throughout the year instead of autumn to consider the typical climate condition of each RWI site. In addition, only those RWI sites with significant RF coefficients for autumn climate variables were included in the analysis. To ensure a sufficient number of sites for each tree genus and species, we further limited our analysis to those RWI sites with tree genera observed at 90 or more sites and species observed at 5 or more sites. We then averaged the RWI site latitude, annual averaged temperature and cloud cover, annual cumulative precipitation, and RF coefficients by tree species and plotted the relationships to identify the most meaningful relationships. The tree genera and species included in our analysis are summarized in **Table 1**.

Random Forest Algorithm

To quantify the relative importance of geographical, climatological, and biological characteristics on the RWI response to each autumn climate variable, we applied the random forest algorithm to the filtered RWI data (refer to section "Relationship Between RWI Response to Autumn Climate Change and Latitude/Climate Condition"). Then, we computed the mean decrease in the Gini importance for each geographical, climatological and biological characteristic after training. The random forest algorithm was applied using R and the "randomForest" package.

Random forest is a supervised learning algorithm, an ensemble of decision trees (Zhao, 2012) commonly trained using the bootstrap aggregation or "bagging" method. The algorithm builds multiple decision trees and merges them to achieve an overall result, generally providing a more accurate and stable prediction. In recent years, the random forest method has also been applied to carbon cycle research in forest ecosystems (e.g., Cai et al., 2020).

A positive attribute of the random forest algorithm is that it is easy to measure the relative importance of each feature (Gini importance). Because the random forest is an ensemble of individual decision trees, Gini importance can be leveraged to calculate the mean decrease in Gini, which is a measure of variable importance for estimating a target variable. This is an effective measure of the importance of a variable in estimating the value of the target variable across all trees that make up

TABLE 1 | Tree genera (tree species) that were observed at more than 90 (5) tree-ring width index (RWI) sites that had a significant response function coefficient for autumn climate variables (temperature, precipitation, and cloud cover).

ID	Genera	Species						
		For temperature	For precipitation	For cloud cover				
QU	Quercus	Quercus spp., Quercus douglasii, Quercus macrocarpa	Quercus stellate, Quercus macrocarpa, Quercus douglasii	Quercus stellate				
ΡI	Pinus	Pinus balfouriana, Pinus flexilis, Pinus edulis, Pinus ponderosa, Pinus sylvestris, Pinus cembra, Pinus banksiana, Pinus nigra, Pinus strobus	Pinus flexilis, Pinus edulis, Pinus ponderosa, Pinus sylvestris, Pinus albicaulis, Pinus nigra, Pinus banksiana, Pinus pinea	Pinus edulis, Pinus ponderosa, Pinus sylvestris, Pinus albicaulis				
JU	Juniperus	Juniperus przewalskii	Juniperus occidentalis, Juniperus przewalskii	Juniperus virginiana				
PC	Picea	Picea abies, Picea glauca, Picea mariana, Picea engelmannii	Picea abies, Picea glauca, Picea engelmannii, Picea mariana, Picea schrenkiana	Picea abies, Picea glauca, Picea engelmannii				
AB	Abies	Abies lasiocarpa	Abies lasiocarpa	Abies alba, Abies lasiocarpa				
TS	Tsuga	Tsuga mertensiana	Tsuga mertensiana,	Tsuga mertensiana				
LA	Larix	Larix decidua	Larix siberica, Larix gmelinii	Larix Iyallii, Larix siberica, Larix gmelinii, Larix decidua				
PS	Pseudotsuga	Pseudotsuga menziesii	Pseudotsuga menziesii	Pseudotsuga menziesii				

the forest. A higher mean decrease in Gini indicates remarkable variable importance.

Geographical, climatological, and biological characteristics were used as explanatory variables to ensure the reliability of the random forest models. Climatological characteristics included annual averaged temperature and cloud cover and annual cumulative precipitation. A total dataset for each climate variable was randomly divided into two datasets, comprising 80 and 20% of the total number of RWI sites. The former was prepared for random forest model training, while the latter was used for model verification. Finally, we confirmed that the RF coefficient for each climate variable in the autumn season, estimated from each random forest model using geographical, climatological and biological characteristics, showed significant correlation with the coefficients in the verification dataset (temperature: r = 0.77, *p* < 0.01; precipitation: *r* = 0.49, *p* < 0.01; cloud cover: *r* = 0.73, p < 0.01), demonstrating the reliability of our model. Finally, we built an additional similar random forest model for the widely distributed Pinus genus and confirmed the reliability of each random forest model (temperature: r = 0.72, p < 0.01; precipitation: *r* = 0.40, *p* < 0.01; cloud cover: *r* = 0.63, *p* < 0.01).

RESULTS

Reginal Characteristics of the RWI Response to Autumn Climate Change

Figures 1A-C shows the significant RF coefficients for each autumn climate variable (temperature, precipitation, and cloud cover). We found that positive (negative) coefficients for autumn temperature were dominant over higher (lower) latitude regions (Figure 1A). The negative RF coefficients were distributed mainly in the United States of America and are mainly derived from the autumn temperature in the previous year (Figures 2A, 3A). Interestingly, almost no significant RF coefficients with autumn temperature were observed at sites north of latitude 50° N for the Siberian and Asian regions (Figure 1A). The opposite spatial pattern of the RF coefficients with temperature was observed for cloud cover (Figure 1C). Positive RF coefficients were distributed mainly in the United States of America (Figure 1C), and were mainly derived from autumn cloud cover in the previous year (Figures 2C, 3C). The RF coefficients for autumn precipitation were positive over a broader geographic region than temperature and cloud cover (Figure 1B), derived mainly from autumn precipitation in the previous year (Figures 2B, 3B).

Table 2, based on the results from Figure 1, summarizes the percentage of sites showing positive or negative coefficients for each climate variable by region. Positive RWI responses to autumn temperature were more dominant in Europe (except for southern Europe), eastern Asia, and Canada, whereas negative responses were more dominant in western Asia, southern Europe, the United States of America, and Mexico. A positive RWI response to autumn precipitation was predominant in all regions. The RWI responses to cloud coverage were more regional, with RWI sites showing predominantly negative responses in Europe. These negative responses might be related to moist environments from moist westerly air in the European region.

Biological Characteristics of the RWI Response to Autumn Climate Change

Table 3, which is also based on the results from **Figure 1**, summarizes the percentage of RWI sites showing positive or negative regression coefficients by tree genus. Positive RWI responses to autumn temperature and precipitation were more dominant for most tree genera; however, negative responses to autumn temperature and precipitation were more common for *Pinus* and *Pseudotsuga*, and *Juniperusa* and *Tsuga*, respectively. Conversely, negative RWI responses to the autumn cloud cover were more dominant for most tree genera; however, positive responses were more common for *Pinus*, *Tsuga*, and *Pseudotsuga*.

Variations in RWI Response to Autumn Climate Change With Latitude

We observed clear relationships between the latitude of the RWI site and the RF coefficients of each climate variable during autumn (**Figure 4**). Except for the *Juniperus* genus, negative RF coefficients for autumn temperature were dominant for the sites lower than 40° N, mainly consisting of Pinus trees (**Figure 4A**). Autumn precipitation showed a positive RF coefficient, but the variability varied widely, especially around 50° N (**Figure 4B**). In addition, the positive RF coefficients tended to be stable at the south of latitude 40° N. Unlike the response to autumn temperature and precipitation, the RWI response to autumn cloud cover in relation to the RWI site latitude was unclear but tended to show a positive RF coefficient for the sites at the south of 40° N (**Figure 4C**).

Pinus trees covered a wide range of latitudes and showed positive and negative relationships between speciesbased averaged site latitude and the RF coefficients for autumn temperature, and precipitation and cloud cover, respectively. Nevertheless, this relationship was less clear for other tree genera.

Variations in RWI Response to Autumn Climate Change With the Climatic Condition

We also observed relationships between RF coefficients of RWI with autumn climate variables and the annual average or sum of the climate variables (**Figures 5A–C**). The negative RF coefficients for autumn temperature were dominant for the sites with annually averaged temperatures exceeding 5 °C, especially for *Pinus* trees (**Figure 5A**). Autumn precipitation tends to show a positive RF coefficient with RWI and shows a negative relationship with annual cumulative precipitation (**Figure 5B**). Unlike the response to autumn temperature and precipitation, the RWI response to autumn cloud cover in relation to the annual averaged cloud cover is unclear but tends to show a positive RF coefficient for the sites with annual averaged cloud cover lower than 55% (**Figure 5C**).







TABLE 2 Percentage of RWI sites with significant positive or negative response function coefficients for each autumn climate variable (temperature, precipitation, and cloud cover) summarized by region.

	Temperature			Precipitation			Cloud Cover		
	Positive (%)	Negative (%)	N.S. (%)	Positive (%)	Negative (%)	N.S. (%)	Positive (%)	Negative (%)	N.S. (%)
Eastern Asia	10.3	2.8	86.9	18.6	16.8	64.6	6.5	6.5	87.0
Western Asia	6.2	15.6	78.2	9.3	4.6	86.1	0.0	0.0	100.0
Southcentral Asia	8.9	5.6	85.5	6.7	5.6	87.7	5.6	8.9	85.5
Eastern Europe	5.7	3.8	90.5	16.5	0.6	82.9	7.0	7.6	85.4
Western Europe	12.6	2.1	85.3	21.3	3.9	74.8	3.0	8.7	88.3
Northern Europe	12.3	3.7	84.0	4.9	0.0	95.1	0.0	6.1	93.9
Southern Europe	11.7	17.6	70.7	17.6	2.9	79.5	11.7	0.0	88.3
Canada	35.9	2.7	61.4	21.6	2.7	75.7	3.9	8.5	87.6
United States of America	9.4	13.1	77.5	33.7	4.8	61.5	15.3	6.0	78.7
Mexico	4.2	5.5	90.3	31.9	4.1	64.0	5.5	6.9	87.6

Blue (red) shading indicates regions where more sites showed positive (negative) responses.

TABLE 3 | Percentage of RWI sites with significant positive or negative response function coefficients for each autumn climate variable (temperature, precipitation, and cloud cover) summarized by tree genera.

	Temperature			Precipitation			Cloud Cover		
	Positive (%)	Negative (%)	N.S. (%)	Positive (%)	Negative (%)	N.S. (%)	Positive (%)	Negative (%)	N.S. (%)
Quercus	9.8	5.1	85.1	15.7	3.5	80.8	4.3	5.9	89.8
Pinus	12.8	14.6	72.6	33.9	2.6	63.5	11.4	4.4	84.2
Juniperus	11.7	7.4	80.9	15.9	18.0	66.1	6.3	9.5	84.2
Picea	23.0	4.3	72.7	17.7	3.7	78.6	1.5	8.7	89.8
Abies	26.4	1.7	71.9	23.0	12.8	64.2	5.9	9.4	84.7
Tsuga	25.0	3.3	71.7	5.8	10.0	84.2	15.0	5.8	79.2
Larix	8.4	3.6	88.0	11.4	1.2	87.4	7.2	9.6	83.2
Pseudotsuga	2.8	11.3	85.9	52.3	0.9	46.8	25.0	3.3	71.7

Blue (red) shading indicates regions where more sites showed positive (negative) responses.

Importance of Geographical, Climatological, and Biological Characteristics on RWI Response to Autumn Climate Change

The reliability of the random forest model differed for each autumn climate variable, with temperature having the highest reliability (r = 0.77, p < 0.01), followed by cloud cover (r = 0.73, p < 0.01) and precipitation (r = 0.49, p < 0.01). Conversely, the importance (i.e., the mean decrease in the Gini coefficient) of each explanatory variable was relatively similar for all climate variables (**Table 4**), with geographical (latitude, longitude, and elevation) or climatological (annual averaged temperature/cloud cover, and annual cumulative precipitation) characteristics having the highest importance, and followed by biological characteristics (tree genus). In other words, latitude and annual cumulative precipitation have the highest explanatory power for the RWI response to autumn temperature/cloud cover and precipitation, respectively, whereas the genus has the lowest explanatory power for all climate variables.

When the random forest analysis was limited to the *Pinus* genera with a broad latitudinal distribution, the tree species significantly impacted the model, especially concerning the RWI response to autumn temperature (**Table 5**). We could not develop such random forest model for other tree genera due to the small number of tree species included in the model.

DISCUSSION

Negative Impacts of Autumn Temperature on RWI in Lower Latitude Regions Across the Northern Hemisphere

The RWI response to autumn climate change showed evident regional characteristics (**Figure 1** and **Table 2**), and the response changed significantly with latitude (**Figure 4**) and climate condition (**Figure 5**). Negative responses of RWI to autumn temperature were dominant south of 40° N (western Asia,



southern Europe, United State of America and Mexico; **Table 2**), where *Pinus* was the dominant genus (**Figure 4A**). There are several possible attributions for this negative response, including direct temperature stress (D'Arrigo et al., 2004), temperature-induced drought stress (Barber et al., 2000), temperature-induced respiratory carbon losses (Piao et al., 2008; Liu et al., 2018), and changes in the timing of autumn leaf senescence (Jeong et al., 2011). Previous studies also stated that the previous autumn-current spring climate affects tree physiology through changes in the timing of spring-snow melting

and/or nitrogen availability in the following summer (e.g., Kirdyanov et al., 2003; Sidorova et al., 2009).

However, considering the dominant positive response of the RWI to autumn precipitation across lower latitude sites (Figures 1B, 4B), temperature-induced drought stress seems to be the most reasonable cause of the negative RWI response to autumn temperature. The observed inverse pattern of RF coefficient for RWI with autumn temperature and cloud coverage (Figures 1A,C) may also support this hypothesis. If there are many cloudy days, evapotranspiration of water from the soil surface might be suppressed. However, it should be noted that this interpretation is for sites with relatively warm environments (Figure 5A) mainly distributed south of 40° N latitude, not the entire Northern Hemisphere high latitudes.

Similar patterns of the RWI response to autumn temperature (Figures 1-5A) have been reported with respect to vegetation activity responses to summer climate change across southern boreal forests and continental dry climate regions (e.g., Nikolaev et al., 2009; Silva et al., 2009; Dulamsuren et al., 2010; Andreu-Hayles et al., 2011; Tei et al., 2014, 2017b). These response patterns were also attributed to temperature-induced drought stress caused by a reduction in the stomatal conductance of plants under limited soil moisture availability (Barber et al., 2000). Compared to summer, moisture stress could be more severe in the late summer and autumn, especially in dry regions. More water is usually available for vegetation in spring due to the infiltration of snowmelt water, which then gradually decreases from spring to summer and autumn (Sugimoto et al., 2003). Consequently, the impact of soil moisture on stomatal conductance is low during the spring and then increases in late summer and autumn (Tei et al., 2013b). The authors reported that the signal of the severe water stress in the late growing season had been recorded in the latewood ring δ^{13} C chronologies of larch trees in eastern Siberia. In addition, latewood ring δ^{18} O for pine trees in southwestern China reportedly correlates with autumn precipitation (Fu et al., 2017).

It is also should be mentioned that the significant negative (positive) RF coefficients of the RWI with autumn temperature (precipitation and cloud cover) tend to be calculated from the climate variables of the previous year (**Figure 2**). Previous dendroecological studies (e.g., Tei et al., 2017b; Tei and Sugimoto, 2018) has indicated such a one-year time lag in the response of the forest ecosystem to climate change in continental climate regions over circumboreal forests, which is regarded as the adaptation of the forest ecosystem to the severely water-stressed environment (e.g., Chapin et al., 1990; McDowell et al., 2008; Genet et al., 2010; Wiley and Helliker, 2012).

Juniperus trees were common south of 40° N; however, they showed an opposite response pattern to *Pinus*; that is, positive and negative responses to autumn temperature and precipitation, respectively (**Figures 4A,B**), likely because *Juniperus* tend to grow at higher elevations (2000–4500 m a.s.l.) compared to other tree genera. Due to the lower temperatures at higher altitudes (**Figure 5A**), tree growth is considered to be limited by temperature. Positive vegetation response to warming in cool environments has been frequently reported in RWI (Tei et al., 2017a,b) and normalized difference vegetation index studies (e.g.,





TABLE 4 | Mean Gini coefficient decrease for geographical (latitude, longitude, and elevation), climatological (annual averaged temperature and cloud cover, and annual cumulative precipitation), and biological (tree genus) characteristics in random forest models explaining response function coefficients of the RWI with autumn climate variables.

	Mean Decrease Gini					
	For temperature	For precipitation	For cloud cover			
Latitude	2.70	0.98	1.43			
Longitude	1.90	1.45	1.13			
Elevation	1.29	1.43	0.89			
Annual averaged temperature	1.96	1.07	0.92			
Annual cumulative precipitation	1.18	1.73	0.74			
Annual averaged cloud cover	2.16	1.15	1.03			
Tree genera	0.58	0.87	0.64			

TABLE 5 | Mean Gini coefficient decrease for geographical (latitude, longitude, and elevation), climatological (annual averaged temperature and cloud cover, and annual cumulative precipitation), and biological (tree species) characteristics in random forest models limited to the Pinus tree genus explaining the response function coefficients of the RWI with autumn climate variables.

	Mean decrease Gini					
	For temperature	For precipitation	For cloud cover			
Latitude	0.70	0.11	0.26			
Longitude	0.26	0.14	0.13			
Elevation	0.35	0.11	0.08			
Annual averaged temperature	0.66	0.13	0.06			
Annual cumulative precipitation	0.25	0.07	0.16			
Annual averaged cloud cover	0.59	0.11	0.19			
Tree species	0.64	0.11	0.15			

Buermann et al., 2014; Wu et al., 2015). Furthermore, northward and upward shifts of tree lines under warming conditions in forest ecosystems have also been reported (Shiyatov et al., 2005, Devi et al., 2008).

There is a growing body of evidence to suggest that the response of tree radial growth to summer temperature tends to be positive in higher latitude regions such as the Arctic, whereas it tends to be negative in lower latitude regions such as southern boreal forests and continental dry climate regions (Tei et al., 2017b; Tei and Sugimoto, 2020). In the current study, we investigated the spatial distribution of tree radial growth responses to autumn climate change and obtained results corresponding with those of the summer.

Less Substantial Impact of Tree Genera on RWI Response to Autumn Climate Change

It is unclear whether the RWI response to climate change varies by tree genus or species. Lloyd and Bunn (2007) reported

on different tree radial growth responses to climate change (considering all seasons, but not revealing the impact of each season) by tree species over a circum-boreal forest (>55° N). They found that *Picea (Picea abies, Picea* glauca, *Picea mariana,* and *Picea obovata*) and *Pinus banksiana* tended to show inverse responses to temperature, whereas *Larix (Larix gmelinii* and *Larix siberica), Pinus (Pinus sylvestris* and *Pinus sitchensis),* and *Tsuga mertensiana* tended to show a positive response. However, our study focused on the autumn climate and a target region covering the entire Northern Hemisphere and did not show the same tree species characteristics. Instead, we showed predominantly negative responses to autumn temperature from several species of *Pinus* trees below 40° N (**Figure 4A**).

These results indicate that tree radial growth responses to climate change may differ with the season, and the impact of the genus is less critical compared to other geographic and climatological factors, although we did show that some characteristics of the RWI response to autumn climate change were due to genera differences (**Table 3**). This interpretation is strongly supported by the low importance of genera in the random forest models (**Table 4**).

We observed a more sensitive response to autumn temperature and precipitation with latitude and climate conditions for *Pinus* than other genera (Figures 4A,B, 5A,B). Furthermore, when the random forest model was applied to *Pinus* only, the importance of tree species was improved, especially for temperature (Table 5). We could not develop such an individual random forest model for other tree genera due to the small number of tree species included in the model. In our study, *Pinus* covered a wider latitude range compared to other tree genera (Figure 4); therefore, more observation points for other tree genera are needed to determine whether the higher importance of tree species is a natural characteristic of the *Pinus* genus, or it could be applied to the other genera.

The distribution of RWI sites is biased toward Europe and North America. Therefore, it is likely that our findings will have some regional bias. Further efforts to fill the gaps in RWI data, such as in central and western Canada and Siberia, are required. Notwithstanding, this study contributes to our understanding of the RWI-based tree radial growth response to autumn climate change, which has received less research interest compared to the spring and summer seasons.

CONCLUSION

We investigated the RWI for forest ecosystems in a vast biome/region of the Northern Hemisphere and observed spatial variations in the tree radial growth response to autumn climate change with respect to geographical, climatological, and biological gradients. Our results showed that warmer autumn temperatures tended to negatively affect tree radial growth south of 40° N in regions such as western Asia, southern Europe, United State of America and Mexico, which was attributed to temperature-induced water stress in line with the findings of previous studies that focused on the summer season. Furthermore, it was clear that geographical and climatological characteristics had a more significant impact on the RWI response compared to biological characteristics. Further efforts to fill spatial gaps in the RWI data, for example, in central and western Canada and Siberia, are required to better understand the tree radial growth response to climate change, resulting in more accurate future projections of forest dynamics and global climate change.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

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AUTHOR CONTRIBUTIONS

ST, AK, and NS designed the study. ST and AS collected and analyzed the data. ST, AK, AS, and NS wrote the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This study was supported partly by the Grant for Joint Research Program of the Japan Arctic Research Network Center and KAKENHI (Grant Nos. 20K19950).

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