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ORIGINAL ARTICLE

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Comparison of climatic effects on radial growth of evergreen broad-leaved trees at their northern distribution limit and co-dominating deciduous broad-leaved trees and evergreen conifers

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Abstract Using dendrochronological techniques, this study examined whether tree-ring width of two evergreen broad-leaved species (*Cleyera japonica*, *Eurya japonica*) at their inland northern distribution limit in central Japan is more limited by low temperature compared with two co-dominating deciduous broad-leaved species (*Fagus japonica*, *Magnolia hypoleuca*) and two evergreen conifer species (*Chamaecyparis obtusa*, *Abies firma*), whose distribution limits are further north. The two deciduous broad-leaved species and the two evergreen conifers are tall tree species. Evergreen broad-leaved *Cleyera japonica* is a sub-canopy species and *Eurya japonica* is a small tree species. The tree-ring widths of four of the six species (except for *Eurya japonica* and *Magnolia hypoleuca*) correlated positively with the March temperature just before the start of the growth period. For deciduous broad-leaved *Magnolia hypoleuca*, the tree-ring width was correlated positively and negatively with July temperature and precipitation, respectively. However, the other deciduous broad-leaved *Fagus japonica* showed no such relationships. For the evergreen broad-leaved *Cleyera japonica* and evergreen conifers *Chamaecyparis obtusa* and *Abies firma*, tree-ring widths correlated positively with winter temperatures, probably because evergreen species can assimilate during warm winters. The tree-ring width of *Cleyera japonica* also correlated positively with temperatures of many months of the growth period. By contrast, the tree-ring width of the other evergreen broad-leaved *Eurya japonica* showed no positive correlation with the temperature in any month. Most *Eurya japonica* trees were suppressed by tall trees, which might disguise any climate effect. Thus, there were species differences in response to climate for each life form, and the tree-ring width of *Cleyera japonica* at the northern distribution limit was more limited by low temperatures compared with co-dominating species. It is suggested that growth of *Cleyera japonica* is increased by global warming at the latitudinal ecotone.

Keywords Dendrochronology · Ecotone · Global warming · Latitude · Tree-ring width

Introduction

Plant distribution is affected by thermal conditions to a great extent. Therefore, dominant plant species change along a latitudinal gradient. Thermal conditions are hottest at the southern distribution limit and coldest at the northern distribution limit within a distribution range of a certain species in the northern hemisphere. The growth period of plants decreases with latitude. Photosynthesis is often limited by low temperatures in cold conditions, such as those found at high latitudes and altitudes (DeLucia and Smith 1987). It is often reported that tree growth at the northern distribution limits is reduced by low temperatures (Nöjd and Hari 2001; Helama et al. 2002; Wang et al. 2002; Kirdyanov et al. 2003; Hopton and Pederson 2005; Takahashi et al. 2005). Therefore, growth of plant individuals at their northern distribution limits may be more limited by low temperatures than at the southern distribution limit.

Concern exists about the effects of global warming on plant distribution. Based on a 10-year phenological observation of trees, Fujimoto (2008) reported that

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global warming will increase the growth period of plants. Ishigami et al. (2003) also predicted, based on a simulation study, that the vegetation zones of Japan will move to the north because of global warming. Therefore, global warming is presumed to affect plant growth and distribution to a great extent. The latitudinal ecotone consists of species at the northern and southern distribution limits. Latitudinal plant distribution would not move easily to the north under global warming because of competition between species of the northern and southern distribution limits of latitudinal ecotones. Therefore, an investigation into the relationships between plant growth and climatic conditions in a latitudinal ecotone is important to allow examination of plant distribution shifts in the future (Takahashi et al. 2011b).

In Japan, the vegetation changes from evergreen broad-leaved forests to deciduous broad-leaved forests with increasing latitude. The inland northern distribution limits of many evergreen broad-leaved species are in central Japan, forming a latitudinal ecotone in which vegetation changes from evergreen broad-leaved forests to deciduous broad-leaved forests. Various temperate evergreen conifer species are also distributed in central Japan. This study investigated how climatic conditions affect the radial growth of evergreen and deciduous broad-leaved species and evergreen conifers in a latitudinal ecotone.

The dendrochronological technique is a method with which to analyze how climatic conditions affect the radial growth of trees. Growth–climate relationships at high latitudes (above the cool-temperate zone) and high altitudes (above the subalpine zone) have often been analyzed using dendrochronological techniques (Jacoby et al. 1996; Rolland et al. 1998; Kirdyanov et al. 2003; Hopton and Pederson 2005; Takahashi et al. 2011a) because tree growth is limited to a great extent by low temperatures in these environments. Besides high latitudes and altitudes, many dendrochronological studies have been conducted in seasonal dry forests in the tropics and dry forests in the temperate zone (Fritts 1962; Tessier et al. 1994; Jenkins and Pallardy 1995; LeBlanc and Terrell 2001; Ohashi et al. 2009) because tree growth tends to respond to precipitation in these regions. Thus, growth–climate relationships can be analyzed using the dendrochronological technique.

This study examined the effects of climate on radial growth of evergreen broad-leaved species at their inland northern distribution limit in Japan, and on that of co-dominating deciduous broad-leaved species and evergreen conifers, whose inland distribution limits are further north, by using dendrochronological techniques. Thus, the first objective of this study was to clarify whether growth of evergreen broad-leaved species is more limited by low temperatures at the inland northern distribution limit compared with co-dominating deciduous broad-leaved trees and evergreen conifers. The second objective was to examine whether species-specific responses to climatic conditions are similar for each life form.

Materials and methods

Study site

The study was carried out at 400–500 m above sea level (a.s.l.) in Shizumo Forest Reserve (101.4 ha) on Mount Shizumo (767 m a.s.l., N 35°35′, E 137°34′) in central Japan. The mean annual temperature was estimated as 12.6°C at this study site from temperatures recorded at Nakatsugawa Weather Station (320 m a.s.l., about 13 km from the study area) between 1979 and 2000 using the standard lapse rate of −0.6°C per each +100 m altitude. The mean temperatures in August and January were 24.9 and 0.7°C, respectively. Annual mean precipitation was 1,813 mm between 1979 and 2000 at Nakatsugawa, with most precipitation in summer.

Relationships between plant distribution and climate are often represented by the warmth index (WI) and coldness index (CI) (Kira 1949). WI is calculated as $\Sigma\,(m_t - 5)$, where m_t is monthly mean temperature greater than 5°C. CI is calculated as $-\Sigma\,(5 - m_t)$, where m_t is monthly mean temperature lower than 5°C. Generally, the distribution range of evergreen broad-leaved forests in Japan is WI 85–180°C months and CI > -10°C months. In the case of CI < -10°C months, even if WI is between 85 and 180°C months, deciduous broad-leaved species, such as *Quercus serrata* Thumb. and *Fagus japonica* Maxim., and evergreen conifers, such as *Abies firma* Sieb. et Zucc. and *Tsuga sieboldii* Carrière, dominate without evergreen broad-leaved species (Kira 1949). This suggests that evergreen broad-leaved species cannot distribute at CI < -10°C months because of coldness, even if the thermal conditions during the growth period are high enough for growth (WI 85–180°C months). Evergreen broad-leaved species cannot survive in cold conditions probably because of the low freezing resistance (Sakai 1975). The WI of the study site was 101.4°C months, and the CI was −10.0°C months. Thus, this study site was climatically at the northern distribution limit of warm-temperate evergreen broad-leaved tree species.

A total 519 vascular plant species, including ferns and seed plants, grow in the Shizumo Forest Reserve, and 125 species of these 519 are of warm-temperate origin (Yokouchi et al. 1963). For trees larger than 2 cm in diameter at breast height (DBH), 6 evergreen conifer species, 8 evergreen broad-leaved species and 25 deciduous broad-leaved species grew in a 0.5-ha plot (our unpublished data). The total stand basal area and tree density (DBH > 2 cm) were 32.8 $m^2\ ha^{-1}$ and 1764 ha^{-1}, respectively. Evergreen conifers such as *Abies firma* (7.44 $m^2\ ha^{-1}$) and *Chamaecyparis obtusa* Endl. (7.01 $m^2\ ha^{-1}$) occupied nearly one-half of the stand basal area, but the tree density was low (*Abies firma* 96 ha^{-1}; *Chamaecyparis obtusa* 78 ha^{-1}). By tree density, evergreen broad-leaved *Illicium anisatum* L. (356 ha^{-1}) and *Eurya japonica* Thunb. (228 ha^{-1}) and deciduous broad-leaved *Sapium japonicum* Pax et Hoffim. (162 ha^{-1}) were the dominant species. Many evergreen broad-leaved trees were smaller than 10 cm DBH.

Sampling and measurements

We investigated six tree species: evergreen broad-leaved *Cleyera japonica* Thunb. and *Eurya japonica*, deciduous broad-leaved *Fagus japonica* and *Magnolia hypoleuca* Sieb. et Zucc. and evergreen conifers *Chamaecyparis obtusa* and *Abies firma*. *Magnolia hypoleuca* is a mid-shade-tolerant species, whereas the other five species are shade-tolerant species. The two deciduous broad-leaved species and the two evergreen conifers are tall tree species. Evergreen broad-leaved *Cleyera japonica* is a subcanopy species and *Eurya japonica* is a small tree species in the study site.

The latitudinal distribution ranges of the six species were determined according to Horikawa (1972, 1976). Although the northern distribution limits of evergreen broad-leaved *Cleyera japonica* (latitudinal distribution range: N 22°30′–37°0′) and *Eurya japonica* (N 22°30′–39°36′) were in the north of this study site (N 35°35′), these two species were present only along the coast in the north of the study site. Therefore, this study site is the inland northern distribution limit. The latitudinal distribution ranges of the other species are as follows: evergreen conifers *Chamaecyparis obtuse* N 30°12′–37°6′, *Abies firma* N 30°12′–39°18′, deciduous broad-leaved *Fagus japonica* N 31°54′–40°36′, *Magnolia hypoleuca* N 31°36′–45°30′.

In 2007, at least 20 trees were cored at 1.3 m trunk height for each species, with two cores from each tree. The DBH was measured for each sampled tree. All cores were dried, mounted, sanded, and then the tree-ring widths were measured at a precision of 0.01 mm under a microscope by using a measurement stage (TA Tree-Ring System, Velmex, Bloomfield, NY).

Chronology development

All cores were cross-dated visually by matching characteristic wide and narrow rings that were synchronous in trees within a species. Visual cross-dating was verified statistically using the COFECHA program (Holmes 1983, 1994), which tests each individual series against a master dating series (mean of all series) from correlation coefficients. Several cores for each species that had low correlations with other trees were eliminated from further analyses.

All raw ring-width series were standardized by fitting smoothing splines (Cook and Peters 1981) with a 50% frequency–response cutoff of 32 years using the ARSTAN program (Cook 1985; Holmes 1994). A standardized series usually shows autocorrelation that negates the assumption of the independence that is necessary for most statistical analyses (Fritts 1976; Monserud 1986). To remove the effects of autocorrelation, we transformed each standardized series to a residual series through pooled autoregressive modeling by using the ARSTAN program (Cook 1985). The residual chronology of tree-ring width for each species was calculated by averaging the individual series in each year. We used at least five cores to make the tree-ring width chronologies in each year.

Six statistics were calculated for the residual tree-ring width chronologies: (1) mean correlation among trees represents the chronology signal strength; (2) mean sensitivity and (3) standard deviation are measures of interannual variation; (4) first-order autocorrelation is a measure of the influence of the previous year's growth on the current-year's growth; (5) signal-to-noise ratio expresses the strength of the observed common signal among trees; (6) expressed population signals (EPS) quantifies the degree to which a particular sample chronology represents the hypothetically perfect chronology, which may in turn be regarded as potential climatic signals; a threshold of 0.85 is suggested empirically as an acceptable statistical quality (Wigley et al. 1984).

Principal component analysis (PCA) was performed to assess the similarity of tree-ring width chronologies among the six species, and was based on the correlation matrix of the six residual tree-ring width chronologies for the common interval (1910–2006) among the six species.

Responses to climatic conditions

The relationships of residual tree-ring width chronologies with monthly climatic data were analyzed using a bootstrapped correlation function for the common interval (1910–2006) among the six species using the program DENDROCLIM2002 (Biondi and Waikul 2004). DENDROCLIM2002 uses 1,000 bootstrapped samples to compute correlation coefficients, and to test their significance at the 0.05 level. The recording period of the meteorological data at Nakatsugawa—the nearest weather station from the study site—was comparatively short (from 1979). However, long-term records (from 1898) were available at Iida (516 m a.s.l., about 25 km from the study site). Thus, we used climatic data at Iida for the bootstrapped correlation function.

The approximate growth period of plants at this study site was determined based on phenological data of the Japan Meteorological Agency. Cherry trees (*Prunus × yedoensis* Matsumurae) bloom from early April at Iida, and most of leaves of deciduous broad-leaved *Acer palmatum* Thunb. and *Ginkgo biloba* L. change to red or yellow by early November. It is considered that radial growth ceases before leaf coloring. Therefore, the growth period was estimated as April to October. The bootstrapped correlation function was calculated using monthly climatic data from April of the previous year to October of the current year (total 19 months), because growth of many tree species is affected not only by the climatic conditions of the current year, but also by the climatic conditions of the previous year (cf. Fritts 1962; Takahashi 2003; Takahashi et al. 2003). Monthly climatic data (mean temperature and sum of precipitation) during the common interval (1910–2006) among the six species were used for the analyses.

Results

Tree-ring width chronologies

Evergreen conifers *Abies firma* and *Chamaecyparis obtusa* had a large DBH, and the chronology length was longer than for evergreen broad-leaved and deciduous broad-leaved species (Fig. 1; Table 1). Although the DBH of the evergreen broad-leaved *Cleyera japonica* and *Eurya japonica* was smaller than that of the four other species, the chronology length of the evergreen broad-leaved species was similar to that of the deciduous broad-leaved species because of the narrow tree-ring width of the two evergreen broad-leaved species. The mean sensitivities and standard deviations did not differ greatly among the six species. The EPS of evergreen broad-leaved *Eurya japonica* and the deciduous broad-leaved *Fagus japonica* and *Magnolia hypoleuca* were lower than 0.85 (Table 1). The mean correlation between trees and the signal-to-noise ratio were also lower in the three species (EPS < 0.85) than in the three other species (EPS > 0.85). Especially, *Eurya japonica* showed the lowest values of mean correlation, signal-to-noise ratio and EPS among the six species.

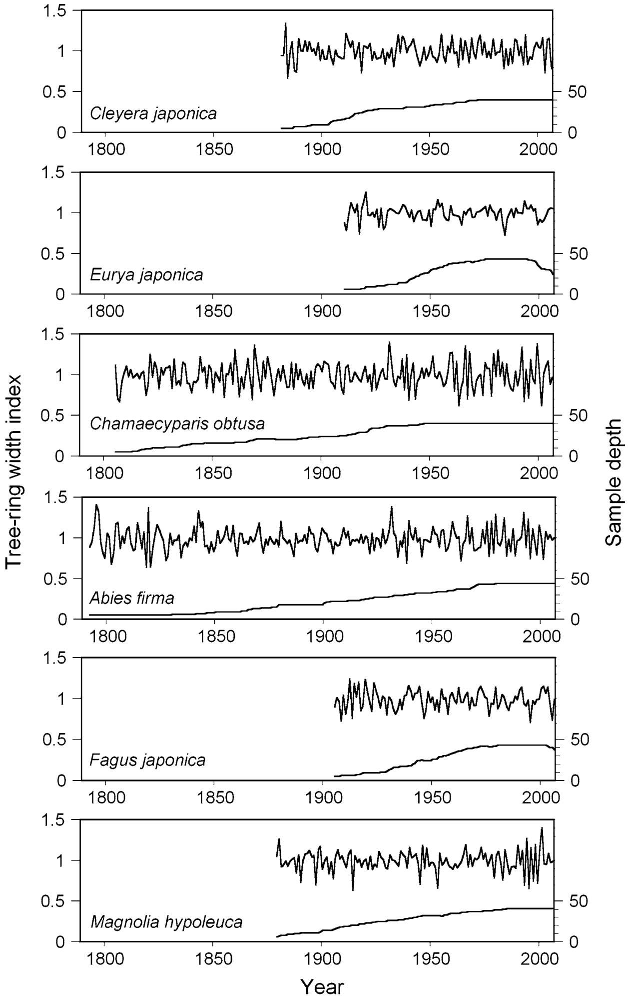

Fig. 1 Residual tree-ring width chronologies and sample depths of evergreen broad-leaved species (*Cleyera japonica*, *Eurya japonica*), evergreen conifer species (*Chamaecyparis obtusa*, *Abies firma*) and deciduous broad-leaved species (*Fagus japonica*, *Magnolia hypoleuca*)

Principal component analysis showed that tree-ring width chronology was similar between the two evergreen conifers because the two points in Fig. 2 were on similar coordinates. However, similarity was low between the two evergreen broad-leaved species and between the two deciduous broad-leaved species. Although tree-ring width chronology was correlated positively between the two evergreen conifers (Pearson product–moment correlation coefficient $R = 0.687$, $P < 0.001$, $n = 97$), tree-ring width chronologies showed no significant correlation between the two evergreen broad-leaved species ($R = -0.041$) and between the two deciduous broad-leaved species ($R = -0.104$).

Responses to climate

The tree-ring width chronologies of four of the six species (i.e., excluding *Eurya japonica* and *Magnolia hypoleuca*) showed positive correlations with the March temperature of the current year (Fig. 3). March is just before the start of the growth period. By contrast, *Magnolia hypoleuca* showed a negative correlation with the March temperature of the current year.

For evergreen broad-leaved *Cleyera japonica* and the two evergreen conifers and the deciduous broad-leaved *Fagus japonica*, the tree-ring widths correlated positively with the temperature of (at least) 1 month in winter between December and February (Fig. 3). This tendency was more conspicuous for evergreen broad-leaved *Cleyera japonica* than for the other species because *Cleyera japonica* showed significant correlations in all three winter months between December and February. The tree-ring width of *Cleyera japonica* also correlated positively with the temperature of more months during the growth period of the current year compared with the two evergreen conifers. By contrast, the tree-ring width of evergreen broad-leaved *Eurya japonica* did not correlate with the temperature in any month. Thus, the responses to climate evidently differed between the two evergreen broad-leaved species.

Four of the six species (i.e., except *Abies firma* and *Fagus japonica*) showed a positive correlation with precipitation of (at least) 1 month during the growth period of the previous year (Fig. 4). Of these four species, the tree-ring widths of *Cleyera japonica* and *Chamaecyparis*

Table 1 Basic statistics of residual tree-ring width chronologies of the six species examined in this study

	Evergreen broad-leaved trees		Evergreen conifers		Deciduous broad-leaved trees	
	Cleyera japonica	*Eurya japonica*	*Chamaecyparis obtusa*	*Abies firma*	*Fagus japonica*	*Magnolia hypoleuca*
Number of cores	40	43	40	44	43	41
Range of DBH (cm)	13–35	9–19	27–113	28–118	22–72	30–79
Range of chronology (years)	126	97	202	215	102	128
Mean tree-ring width (mm ± SD)	1.24 ± 0.68	0.72 ± 0.40	1.06 ± 0.67	1.36 ± 1.17	2.17 ± 1.55	1.99 ± 1.45
Residual chronology						
Mean correlation between trees	0.301	0.058	0.302	0.263	0.141	0.167
Mean sensitivity	0.180	0.159	0.218	0.182	0.139	0.190
Standard deviation	0.157	0.156	0.197	0.168	0.118	0.178
First-order autocorrelation	−0.283	−0.045	−0.104	−0.043	0.024	−0.054
Signal-to-noise ratio	12.046	2.235	8.642	7.487	5.601	4.614
Expressed population signal	0.923	0.691	0.896	0.852	0.849	0.822

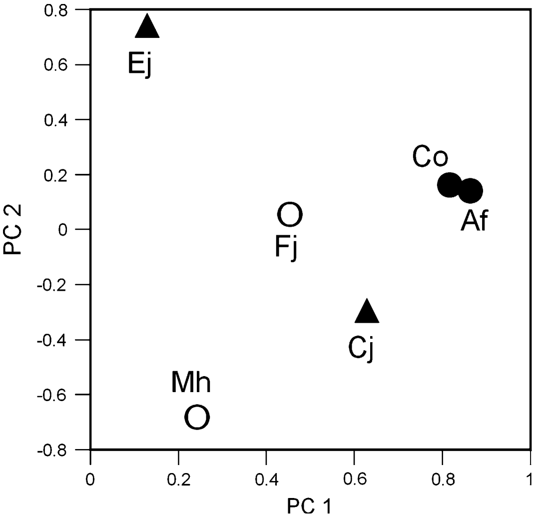

Fig. 2 Scatter diagram of principal components 1 and 2 for residual tree-ring width chronologies. *Solid triangles*, *solid and open circles* represent evergreen broad-leaved species [*Cleyera japonica* (Cj) and *Eurya japonica* (Ej)], evergreen conifer species [*Chamaecyparis obtuse* (Co) and *Abies firma* (Af)] and deciduous broad-leaved species [*Fagus japonica* (Fj) and *Magnolia hypoleuca* (Mh)], respectively

obtusa correlated negatively with temperatures during these months (Fig. 3). For example, the tree-ring width of *Chamaecyparis obtusa* correlated positively with the July precipitation of the previous year, and negatively with the temperature of the month.

The tree-ring width of deciduous broad-leaved *Magnolia hypoleuca* correlated positively with the July temperature of the current year, and negatively with the precipitation of the same month (Figs. 3, 4). By contrast, the tree-ring width of deciduous broad-leaved *Fagus japonica* showed no such correlations. Thus, the responses to climatic conditions between the two deciduous broad-leaved species differed.

Discussion

Low EPS

EPS were lower than 0.85 (an empirical threshold value as an acceptable statistical quality) for the three species (*Eurya japonica* [0.691], *Fagus japonica* [0.849] and *Magnolia hypoleuca* [0.822]) among the six species. The temperate zone in Japan is characterized as mild climatic conditions with moderate temperature and humid conditions. If climatic conditions are extremely severe (e.g., low temperature, drought, etc.), many trees respond synchronously to climatic conditions, which leads to high EPS and mean correlation among trees. Therefore, the low EPS of the three species can be, at least partly, ascribed to the mild climatic conditions in the study site.

Responses to temperature

Four of the six species (i.e., with the exception of *Eurya japonica* and *Magnolia hypoleuca*) correlated positively with the March temperature of the current year (just before the start of the growth period). It is often reported that tree-ring widths correlate positively with temperatures at the start of the growth period (Lara et al. 2001; Peterson and Peterson 2001; Wilson and Hopfmueller 2001; Kirdyanov et al. 2003; Hopton and Pederson 2005). In the region of this present study, cherry trees usually bloom from early April, and the blooming day is earlier when March temperature is warmer (Hamada 2008). Therefore, a high March temperature is suggested to hasten the start of the growth period, and so increases tree-ring widths by prolonging the growth period.

High winter temperature increased tree-ring widths of evergreen broad-leaved *Cleyera japonica* and the two evergreen conifers. Although the tree ring-widths of the

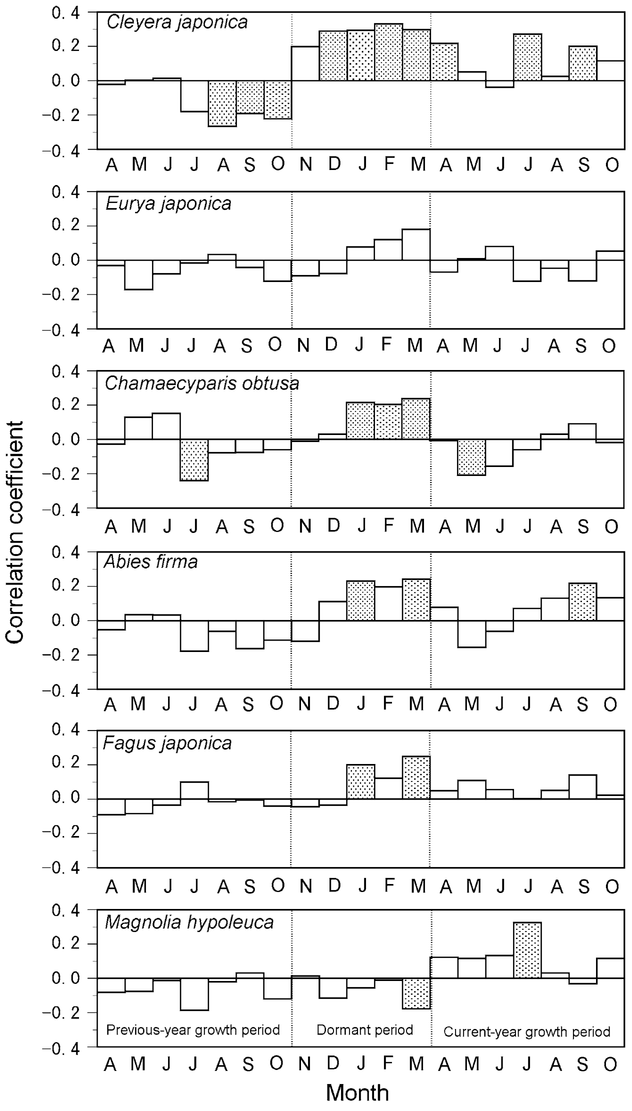

Fig. 3 Correlation coefficients between residual tree-ring width chronologies and monthly mean temperature for evergreen broad-leaved species (*Cleyera japonica*, *Eurya japonica*), evergreen conifer species (*Chamaecyparis obtusa*, *Abies firma*) and deciduous broad-leaved species (*Fagus japonica*, *Magnolia hypoleuca*). *Open* and *shaded bars* indicate non-significant and significant correlations ($P < 0.05$), respectively

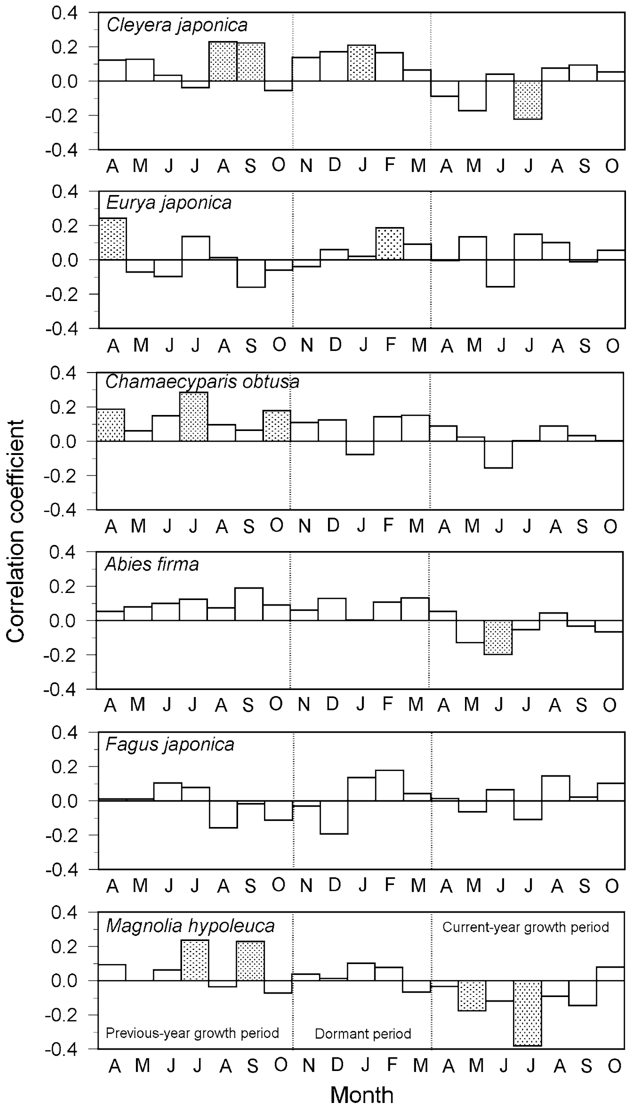

Fig. 4 Correlation coefficients between residual tree-ring width chronologies and monthly sum of precipitation for evergreen broad-leaved species (*Cleyera japonica*, *Eurya japonica*), evergreen conifer species (*Chamaecyparis obtusa*, *Abies firma*) and deciduous broad-leaved species (*Fagus japonica*, *Magnolia hypoleuca*). *Open* and *shaded bars* indicate non-significant and significant correlations ($P < 0.05$), respectively

two conifers correlated positively only with January temperature, which is the lowest temperature in a year, the tree-ring width of *Cleyera japonica* correlated positively with temperatures during the long period from November to April. Although maximum photosynthetic rates of evergreen species decrease in winter, photosynthetic ability is still maintained (Miyazawa and Kikuzawa 2005). Therefore, the three evergreen species can assimilate in warm days in the winter, which increases the tree-ring width of the next growth period.

We also found a positive correlation between January temperature and tree-ring width of the deciduous broad-leaved *Fagus japonica*. However, we cannot determine if this relation is ecophysiologically meaningful or not because deciduous species cannot assimilate in winter.

Responses to precipitation

The tree-ring width of four of the six species (i.e., excluding *Abies firma* and *Fagus japonica*) correlated positively with precipitation of (at least) 1 month during the previous-year growth period, suggesting that water stress in the previous year reduces tree-ring widths. Although *Eurya japonica* showed a positive correlation only with April precipitation, the other species correlated with summer months. Interannual variation in the monthly sum of precipitation is large. The minimum monthly sum of precipitation at Iida was about half of the average of the summer months (July–September) during 1910–2006. Reduction of soil moisture due to less precipitation decreases maximum photosynthetic rates of plants in summer (Panek and Goldstein 2001). For example, Takahashi et al. (2004) showed that the photosynthetic rate of *Betula ermanii* in northern Japan was decreased by about 30% after 10 days from the last precipitation. Thus, even if rainfall does not occur during the short term, photosynthetic production decreases to some extent. Although radial growth continues by the end of the growth period, growth rates decrease from May or June in central Japan (Yamashita et al. 2006). Photosynthetic production after the active period (late spring and early summer) of radial growth is stored in plants, and is used for the next-year growth (Wong et al. 2003). Therefore, tree-ring widths of these species may be reduced by water stress of a previous year with extremely low summer precipitation.

Interspecific differences between two species for each life form

Although the two conifers showed similar growth–climate relationships, interspecific differences were found between the two deciduous broad-leaved species and between the two evergreen broad-leaved species. The tree-ring width of deciduous broad-leaved *Magnolia hypoleuca* showed a positive correlation with the July temperature of the current year and a negative correlation with precipitation of the same month. The negative correlation with precipitation does not mean that high precipitation reduced the growth of *Magnolia hypoleuca*. It is suggested that high precipitation reduces insolation and temperature, which in turn reduces the growth of *Magnolia hypoleuca*. On the contrary, the growth–climate relationships of *Magnolia hypoleuca* were not recognized in the other deciduous broad-leaved *Fagus japonica*. Therefore, *Magnolia hypoleuca* (mid-successional species) seems to need more light in summer for growth compared with *Fagus japonica* (late successional species).

Evergreen broad-leaved *Cleyera japonica* showed a more positive correlation with temperatures in both the growth and dormant periods compared with the other evergreen broad-leaved *Eurya japonica*. This can probably be ascribed to differences in the maximum attainable size between the two species. The maximum tree size is greater for *Cleyera japonica* (subcanopy tree species) than for *Eurya japonica* (small tree species). The difference in maximum size further influences the responses to climatic conditions for the following three reasons. First, most *Eurya japonica* trees were suppressed by tall trees, which might disguise any climatic effect if one exists. The lowest EPS value of *Eurya japonica* among the six species is probably due to the suppressed conditions. Second, *Cleyera japonica* may be damaged by low temperatures in winter. Embolism is prone to occur in evergreen broad-leaved tree species with large diameter of vessels at the northern distribution limit through freezing and thawing of water in vessels (Taneda and Tateno 2005). The risk of embolism may be greater for larger trees because vessel diameter is greater in these trees (cf. Noshiro and Baas 2000). Thus, high winter temperatures may increase growth of *Cleyera japonica* by avoiding the risk of embolism. Third, maintenance costs differ between the two species. More photosynthate is required for the maintenance of larger trees. Eight evergreen broad-leaved tree species (DBH > 2 cm) were observed at our plot (0.5 ha) at this study site (unpublished data). These species were small tree species or subcanopy tree species, and canopy tree species was not observed. Evergreen broad-leaved tree species possibly cannot grow to a large size near the northern distribution limit because of embolism in the dormant period and insufficient temperature in the growth period. The tree-ring width of larger trees responds more to climatic conditions (Carrer and Urbinati 2004). Therefore, embolism and the greater maintenance cost of *Cleyera japonica* (subcanopy tree species) compared to *Eurya japonica* (small tree species) possibly resulted in the high sensitivity of tree-ring width of *Cleyera japonica* to climatic conditions.

Conclusion

Evergreen and deciduous broad-leaved species showed no specific growth–climate relationships, but the two evergreen conifer species showed similar responses to climatic conditions. Of the six species, the tree-ring width of *Cleyera japonica* showed many positive correlations with temperature. Therefore, at the latitudinal vegetation ecotone, global warming will have a greater effect on tree-ring width of *Cleyera japonica* than the other five species. However, this study analyzed only two species for each life form, and the results of this study are not sufficient to show general responses of the three life forms to climatic conditions. Therefore, it is necessary to analyze many species for each life form at latitudinal ecotones to clarify general responses of radial growth to climatic conditions.

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