

A DENDROECOLOGICAL ANALYSIS OF FOREST DYNAMICS FOR OLD-GROWTH *ABIES-TSUGA-QUERCUS* ON THE BOSO PENINSULA, SOUTHEASTERN JAPAN

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ABSTRACT

This study investigated the composition, age- and size-structure, and tree-ring relationships for an old-growth, warm-temperate, mixed-evergreen forest at the University of Tokyo Chiba Forest, Japan. A total of 32 tree species were recorded, which was dominated by *Abies firma* and *Quercus acuta*. *Tsuga sieboldii* dominated the recruitment after 1850, followed by *Abies firma*. After 1920, many individuals of *Castanopsis*, *Cinnamomum*, *Cleyera* and *Quercus* became established. The temporal pattern of conifer recruitment did not correspond to the record of strong wind events. Basal area increment in *Abies firma* and *Castanopsis sieboldii* trees increased throughout their lives, a trend not seen in the ring width index. Mean annual temperature was below the 100-year mean between 1920 and 1940 and 1960–1980, but increased rather abruptly after 1980. Mean annual precipitation decreased after 1960. Tree-ring releases are very common at the study forest, which are indicative of frequent small to moderate-sized disturbances. At least one release was recorded in every decade from 1890 to the present day, which is likely the primary causal factor promoting tree growth and recruitment. Our results suggest that early logging activities coupled with natural disturbances had a great influence on the developmental process and current structure of the study stand and that tree growth is varying in a manner consistent with forest dynamics.

Keywords: Dendrochronology, growth releases, disturbance, human activity, *Abies*, *Castanopsis*, *Quercus*.

INTRODUCTION

Fir-hemlock-oak (*Abies-Tsuga-Quercus*) forests at Honshu, Kyushu, and Shikoku in Japan have attracted interest of ecologists for more than one hundred years because of their unique distribution and structure (Honda 1912; Nakano 1943; Kaji 1975; Suzuki 1979; Sanquetta *et al.* 1994; Okano and Aragami 1999). Fir-hemlock-oak forests consist of *Abies firma* (Sieb. & Zucc.), *Tsuga sieboldii* (Carrière) and *Quercus acuta* (Thunb.) as dominant canopy species, with evergreen and deciduous broad-leaved tree species as co-dominant

subcanopy components. The altitudinal and latitudinal distribution of the fir-hemlock-oak forest indicates that it is located in an ecotone between evergreen broad-leaved forests in the warm-temperate zone and deciduous broad-leaved forests in the cool-temperate zone (Honda 1912; Kira 1949; Miyawaki and Fujiwara 1983; Nozaki and Okutomi 1990).

As vegetation in an ecotone, fir-hemlock-oak forest has transitional characteristics with wide ranges of species composition, geographical distribution, and successional status (Kaji 1975). From a viewpoint of species composition and geographical distribution, fir-hemlock forest can be divided into two sub-groups: one with evergreen broad-leaved trees in the southern half of its geographic

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distribution and one with deciduous broad-leaved trees in the northern half of its geographic distribution (Kaji 1975; Numata 1979). Fir-hemlock forest on the Boso Peninsula, the target forest of the present study, belongs to the former sub-group accompanied by evergreen broad-leaved trees. It is one famous example of the fir-hemlock forest and has been considered a representative forest in this region, first described by Honda (1912) in ecological literature.

Despite the long recognition as an interesting research subject, the ecological characteristics of the fir-hemlock-oak forest in the Boso Peninsula have not been fully clarified. For example, there is a long debate on the successional status: some think that it is a climax forest of this region (Suzuki 1968; Research Section of Tokyo University Forests and Tokyo University Forest in Chiba 1974; Kabaya 1975) and some others think that it is a seral forest toward more late-successional evergreen broad-leaved forests (Honda 1912; Nakano 1943; Kaji 1975; Numata 1979). The extent of the influence of human activities on the establishment and development of this forest is not entirely clear. An early piece of literature (Honda 1912) stated that forest management determined the species composition and structure of this forest whereas later literature emphasized the role of natural disturbances as a structuring factor of this forest (*e.g.* Kabaya 1975; Kabaya *et al.* 1992). However, these arguments were not based on adequate evidence. Analyzing historical records including tree-ring, climate, and wind damage information can provide firm evidence from which we can reconstruct recruitment and developmental processes of the fir-hemlock forest.

The recent human-caused climate change is thought to have significant impacts on forest ecosystems including fir-hemlock-oak forests on the Boso Peninsula. Global warming over the last several decades or more has impacted a wide range of ecosystem and physiological processes (Karnosky 2003; IPCC 2007). Many of these changes are considered to have negative impacts, but some positive effects do exist. One important example can be found in temperate regions where trees are exhibiting a recent increase in growth relative to their historic average (Abrams and Orwig 1995; Jacoby and D'Arrigo 1997; Goldblum and Rigg

2005; Johnson and Abrams 2009). This increase is thought to be caused by longer growing seasons and increases in temperature, atmospheric CO₂, nitrogen and precipitation in some locations (Aber *et al.* 1998; Schwartz *et al.* 2006; McMahan *et al.* 2010). In contrast, some trees in tropical regions have exhibited decreases in growth associated with global warming (Clark *et al.* 2003; Feeley *et al.* 2011). Indeed, Way and Oren (2010) hypothesize that trees growing in warmer temperature environments (*e.g.* tropical trees) will likely decline in growth rate caused by added heat stress, whereas trees in cool-cold environments will have increased growth in response to global warming. Other factors such as increased moisture or drought can also contribute positively or negatively to tree growth (Abrams and Orwig 1995; Orwig and Abrams 1997). Abrams *et al.* (1998) reported that the impact of drought on trees was species and site (topographic variation) related. The interaction of temperature and drought will differentially alter the physiological function of trees in contrasting regions of the world (Voelker *et al.* 2008). In general, relatively few dendrochronological studies have been conducted in Japan and most of Asia compared with other parts of the world (*e.g.* North America and Europe) (Kojo 1987; Abrams *et al.* 1999; Kharal and Fujiwara 2013). Alternatively, a variety of studies have been done on climate change impacts in tree-ring growth in Japan, including the fir-hemlock forest type in the southeast region (D'Arrigo *et al.* 1997; Yasue *et al.* 1996, 1997; Haraguchi *et al.* 1999; Takahashi *et al.* 2003, 2005, 2011, 2012, 2013; Sho *et al.* 2009).

The purpose of this study was to reconstruct the past forest dynamics using tree census and dendrochronological data to document age- and size-structure of the target fir-hemlock-oak forest. We also compared temporal trends in records of environmental factors (strong wind and wind damage to trees) and tree responses (recruitment and ring growth release). Based on the result, we discuss the roles of natural disturbances, human activities (forest management) and climate in determining the recruitment of trees and stand dynamics. Based on the results, we project the dynamics of the fir-hemlock-oak forest in near future. The results should contribute to understanding the impacts of changing environmental conditions for species and

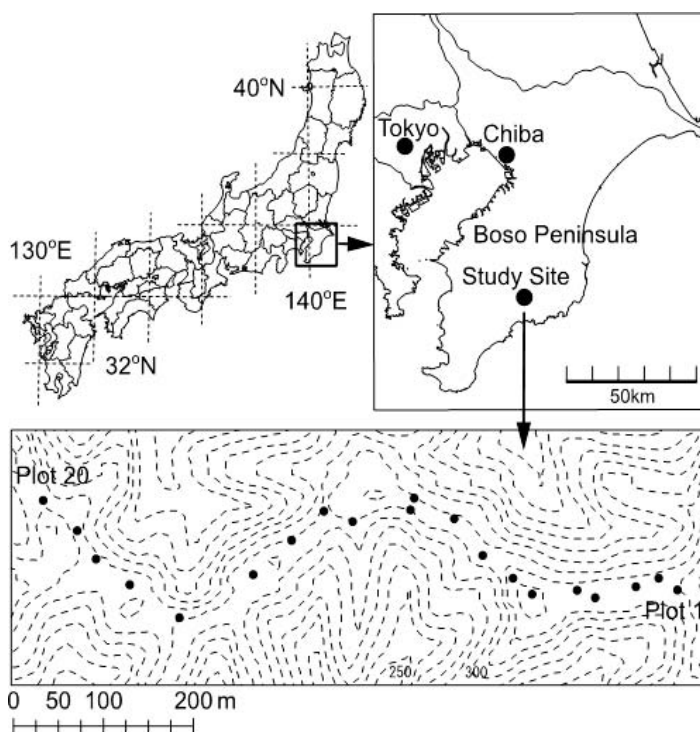


Figure 1. Location of the study site. Points in the lower diagram represent plots. Plots were located sequentially from east (plot 1) to west (plot 20). The interval of contours was 10 m.

a warm-temperate region where such knowledge is lacking.

STUDY AREA DESCRIPTION

The University of Tokyo Chiba Forest (UTCBF) used in this study is located on southern Boso Peninsula, Japan (Figure 1). UTCBF was established in 1894 as the first university forest in Japan (Research Section of Tokyo University Forests and Tokyo University Forest in Chiba 1974). The forest is 2226 ha in area and in the warm-temperate forest zone, and it is covered by various types of forest, which consist of *Cryptomeria*, *Chamaecyparis*, *Abies*, *Tsuga* and evergreen broad-leaved trees.

The forest is a representative example of mature fir-hemlock forest with the following abiotic environmental conditions. The annual mean temperature is 13.9°C, with mean temperature of the coldest month (January) of 3.4°C and mean of the warmest month (August) of 24.9°C. The mean annual pre-

cipitation is 2552 mm (data from 2001 to 2010 at the Fudago Camp observatory, 2.3 km from the study site). The bedrock of this area is Upper Tertiary sedimentary rock (mostly mudstone; Iijima and Ikeya 1976; Economic Planning Agency 1972). The erodible substrate, high precipitation, and high rate of uplift has resulted in a steeply dissected landform (Ozaki and Ohsawa 1995; Sato and Suzuki 2001). The soil is classified as an immature residual soil (Economic Planning Agency 1972).

In forest stands around the study site, there is good correspondence between vegetation types and topography: fir-hemlock stands occur on ridges, stands dominated mostly by evergreen broad-leaved species occur on slopes, and stands dominated mostly by deciduous broad-leaved species occur in valleys (Ozaki and Ohsawa 1995). Deciduous stands in valleys are considered early-successional, but their progression toward more late-successional stands is inhibited by frequent disturbances (*i.e.* landslides; Ozaki and Ohsawa 1995). Our study site was located in a fir-hemlock stand on a ridge.

The known history of this stand can be divided into two periods, *i.e.* before and after 1897 when UTCBF had been expanded to include the study stand. Before 1897, a large part of UTCBF including the study site was managed following the coppice-with-standards method (Honda 1912; Research Section of Tokyo University Forests and Tokyo University Forest in Chiba 1974; Kabaya *et al.* 1992; Smith *et al.* 1997). In this method, conifers in the canopy layer (standards) were reserved for timber production mostly for large-scale construction, whereas evergreen broad-leaved trees under the canopy layer were used for fuel wood and charcoal as short-rotation sprout-coppice. In the early part of the UTCBF period, this stand was still managed by the coppice-with-standards method. There were some records of harvesting including clear cut of broad-leaved trees in 1919. After 1923, however, there were no records of anthropogenic disturbance on the study site over the last 90 years.

METHODS

In July and September 2013, twenty research points (35°10'51"–55"N, 140°9'11"–38"), located at about 35-m intervals on a ridge in the forest interior were selected for dendrochronological and community sampling. The species and diameter were recorded for all trees ≥ 8.0 cm DBH occurring within 0.02-ha circular plots at each point. At each point, one to twelve trees (4.2 trees on average) were cored (one core per tree) at 1.37 m for age determination and radial growth analysis. Across all 20 plots we obtained cores from all the major species over a range of diameter classes. Saplings were counted in a nested circular plot of 9 m² within each of the overstory plots. Saplings were classified as trees ≥ 1.5 m in height but < 8.0 cm in DBH.

A total of 84 cores across six major tree species were collected for age and tree-ring analysis, including crossdating with skeleton plotting and COFECHA. We encountered crossdating problems in some cores because of missing rings ($n = 12$); this existed mainly for *Tsuga sieboldii* and *Quercus acuta*. The cores with less than five missing rings were suitable to describe general age-diameter relations, but were not used for tree-ring releases. The spatial and temporal distribution of recruitment for conifer trees (*Abies firma* and *Tsuga sieboldii*) was

examined. The temporal distribution of recruitment of conifers at the study site and the history of strong wind events was compared to assess whether the coniferous canopy trees regenerated after major disturbances (*e.g.* typhoons). We used a compiled report in UTCBF about tree damage caused by extreme weather events, which mostly consisted of strong wind such as typhoons but also included snow and ice storms (Negisi 1997). This report covered the period from 1900 to 1985. For damage records from 1986 to the present day, we used original records stored in UTCBF (Toyama's personal communication). We also used wind data (maximum wind velocity and direction for days with relatively strong wind; maximum wind velocity > 10 m s⁻¹) recorded at the Katsuura meteorological station (14.5 km from the study site; the Choshi local meteorological observatory 1969, 1987; the Japan Meteorological Agency, <http://www.data.jma.go.jp/gmd/risk/obsdl/top/help1.html>). Both data were used to analyze the relationship of the probability for wind damage with wind velocity and direction. The obtained relationship was used to identify strong wind events that could have caused wind damage. The recognition of strong wind events was necessary because the damage records (Negisi 1997) could be imperfect as they might have put emphasis more on plantations and they included wartime. The following logistic regression was used:

$$\text{logit}(p) = c_0 + c_1 V_{\max} + c_2 \sin \theta + c_3 \cos \theta,$$

where p is the probability of wind damage for a day, V_{\max} is maximum wind velocity for the day, θ is the direction of wind (clockwise angle starting from the north), and c_0 – c_3 are parameters to be determined in the analysis. $\sin \theta$ and $\cos \theta$ represent the effect of wind direction for east-west and north-south components, respectively. $c_2 \sin \theta + c_3 \cos \theta$ can be transformed to $\sqrt{c_2^2 + c_3^2} \sin(\theta + \alpha)$, where $\sqrt{c_2^2 + c_3^2}$ is amplitude and α is a phase shift.

Tree cores were dried, mounted, and sanded with incrementally finer sandpaper (60 grit to 1200 grit) to elucidate the rings. The cores were used for skeleton plots and to identify signature years for crossdating (Stokes and Smiley 1968). Each core was measured to the nearest 0.002 mm using the program Measure J2X (VoorTech Consulting, Holderness, NH, U.S.A.) and a Unislide Velmex

tree-ring measuring system (Velmex, Inc., Bloomfield, NY). Once measured, crossdating of the cores was verified using the program COFECHA (Cook *et al.* 1997). Crossdated tree cores of *Abies firma* ($n = 14$) and *Castanopsis sieboldii* ($n = 10$) were used for more sophisticated dendrochronological analyses. Measurements were detrended for tree size impact on ring width (resulting in increasingly narrower rings as trees age) using the program ARSTAN with a negative linear regression or exponential curve (Cook *et al.* 1997). This created ring width index (RWI) values for each core as a percent above or below the expected value for each year, thus removing age and site effects. These were averaged using a biweight robust mean to create the standard chronology for each species. Raw ring widths were also transformed into basal area increments (BAI in mm^2/year) by using the equation $\text{BA}_X - \text{BA}_{X-1}$, where “ BA_X ” is the basal area and “ BA_{X-1} ” is the basal area of the previous year. The BAI may show additional trends not seen in the raw ring width values or ring width index (Johnson and Abrams 2009). We determined the major and moderate tree-ring release dates for representative tree cores of *A. firma* and *C. sieboldii*. These dates are indicative of when small or moderate disturbances impacted individual trees resulting from nearby blowdown or tree mortality. A growth increase of greater than 25% sustained for 10 years was designated a moderate overstory release, whereas an increase of greater than 50% sustained for 10 years was classified as a major overstory release (Abrams *et al.* 1999).

Monthly temperature and precipitation totals were obtained from the Katsuura meteorological station, Japan. The standardized chronology and monthly temperature and precipitation were entered into the program DendroClim2002 (Biondi and Waikul 2004) for correlation and response function analysis. This is a form of principle component regression to determine the effect of climatic variables on tree-ring variance. It uses a bootstrap method to produce 1000 iterations to resample each ring width to create a standard deviation. This threshold is then used to determine significance of correlation. We also conducted a randomization test for the temporal proximity from years with tree-ring release to years with wind damage. First, we calculated a difference (in years) between each year with tree ring release to the nearest year

with wind damage. The differences were averaged to yield the observed mean temporal proximity between years with tree-ring release and years with wind damage. This observed value was compared with a null distribution that was created by randomly scattering the years with tree-ring release in a period from 1906 to 2013 and calculating the mean temporal proximity between years with tree-ring release and years with wind damage. The randomization was repeated 4999 times to create a null distribution. P-value was calculated by dividing the number of randomizations giving mean temporal proximity smaller than the observed mean temporal proximity by 5000.

RESULTS

Species Composition

A total of 32 tree species were recorded in our survey of the study forest, which was dominated by *Abies firma* and *Quercus acuta* (Table 1). These two species had a combined relative importance value of 44%. Other species of moderate importance include *Castanopsis sieboldii*, *Cinnamomum tenuifolium*, *Tsuga sieboldii* and *Prunus jamasakura*. All species had a combined density of 902.7 trees ha^{-1} and basal area of 83.8 $\text{m}^2 \text{ha}^{-1}$.

Size and Age Structure

The diameter distribution for twelve major species can be classified into three categories: conifers, deciduous broad-leaved trees, and evergreen broad-leaved trees (Figure 2). The diameter distribution of conifers included very large trees (DBH > 80 cm), but lacked individuals in the smallest diameter class. The diameter distribution of deciduous broad-leaved species ranged up to intermediate classes, but lacked individuals in the smallest class. The diameter distribution of evergreen broad-leaved species showed reverse-J shapes with the largest number of individuals in the smallest diameter class. One exception was *Litsea lancifolia* for which there were no individuals in the smallest diameter class though the diameter distribution still showed a reverse-J shape.

Age-diameter relations for all cored trees indicate that the forest became established about 1860

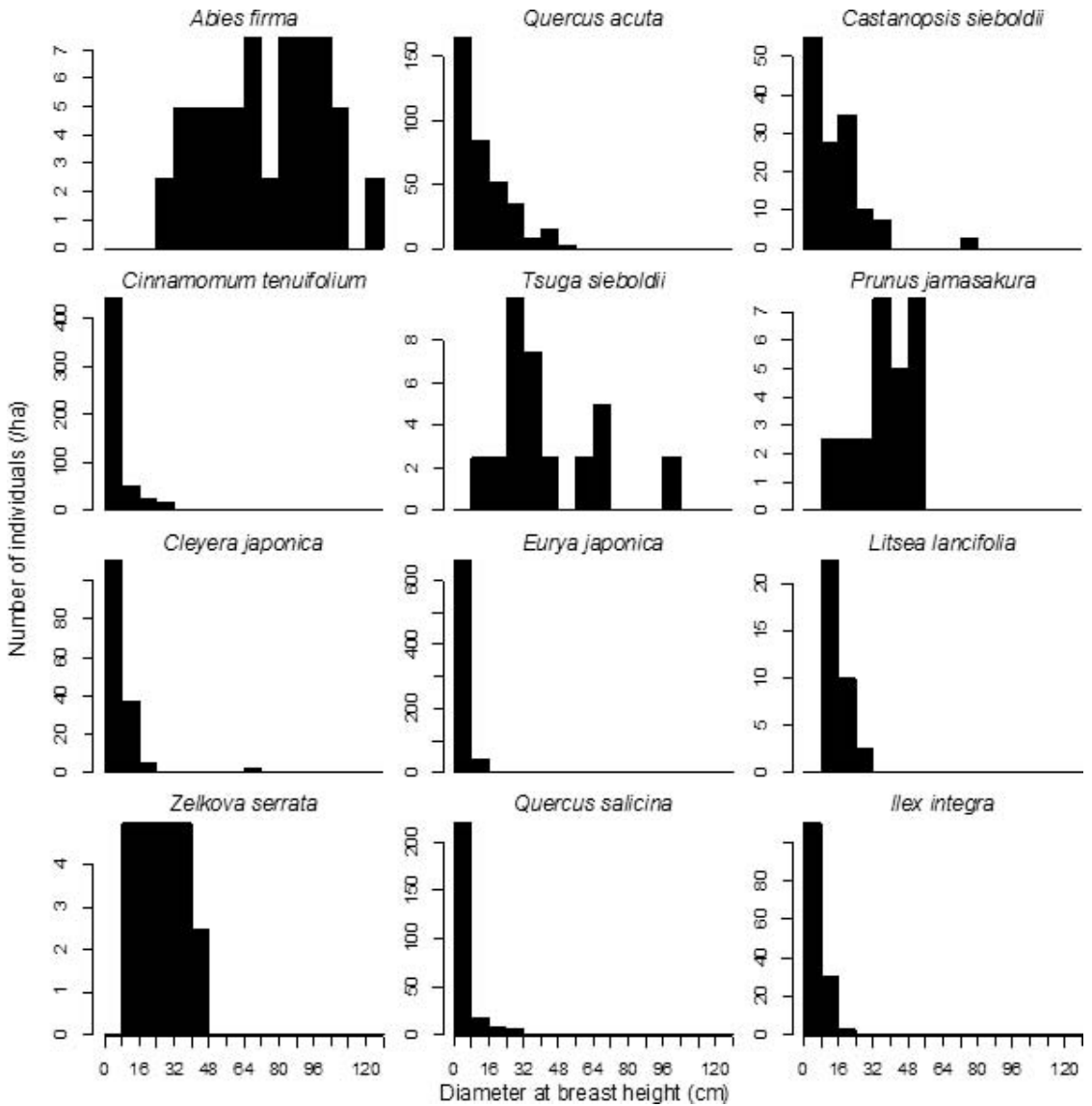


Figure 2. Diameter distribution of major species at the University of Tokyo Chiba Forest study site.

with continuous tree recruitment thereafter, resulting in an uneven age condition (Figure 3). One *Tsuga sieboldii* tree dated to 1810 and was the oldest tree in our survey. *Tsuga sieboldii* dominated the early recruitment in the forest, followed by *Abies firma*. After 1920, many individuals of *Castanopsis*, *Cinnamomum*, *Cleyera* and *Quercus* became established. The recruitment of *Tsuga sieboldii* was relatively evenly distributed during the period from 1861 to 1920 though its spatial distribution was re-

stricted to a range from plot 10 to 20 (Figure 3). The recruitment of *Abies firma* was relatively evenly distributed in the entire research site in a period from 1861 to 1960.

Temporal Trends in Wind Damages and Strong Wind Events

The probability of wind damage for a day was significantly related to maximum wind velocity and

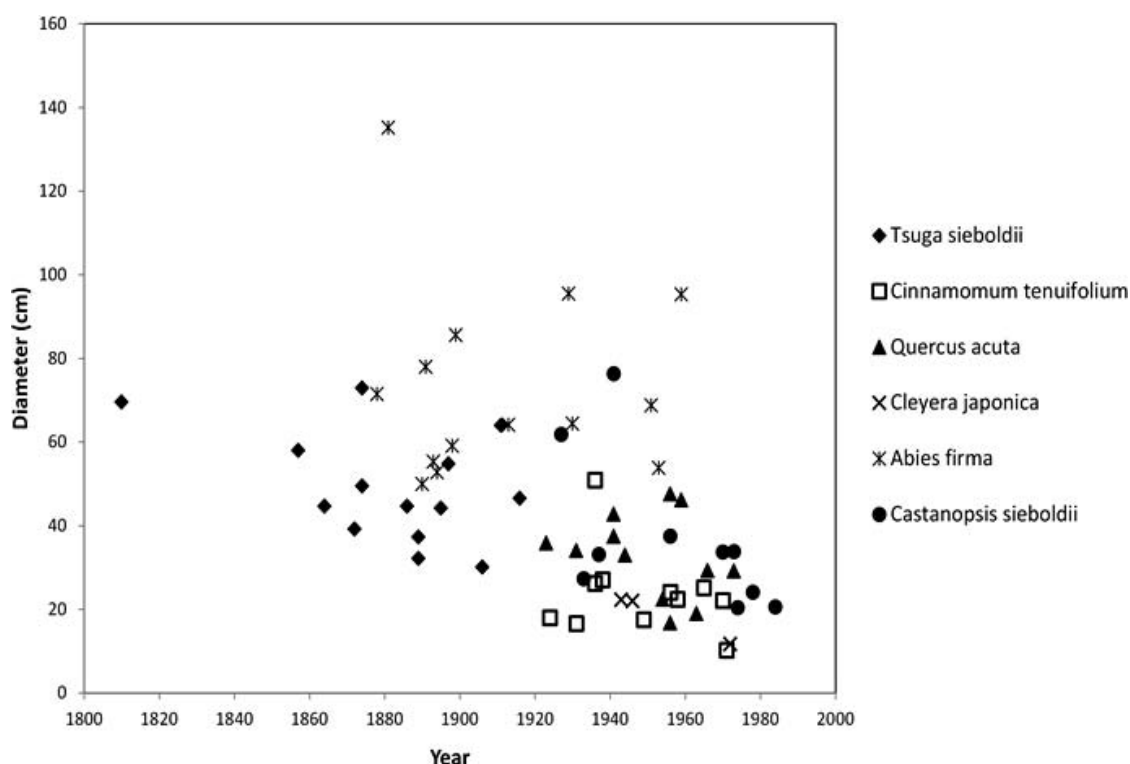


Figure 3. Age-diameter data for each cored tree at the University of Tokyo Chiba Forest study site.

wind direction for the day as mathematically described: $\text{logit}(p) = -8.66 + 0.39 V_{max} + 2.07 \sin\theta + 2.03 \cos\theta$. The adjusted D^2 (an analog of R^2 for generalized linear models; Guisan and Zimmermann 2000) for the above logistic regression was 0.515, and p-values were less than 0.001 for the coefficients for V_{max} and $\cos\theta$ and 0.001 for $\sin\theta$. The second and third terms of the model together indicated that the relationship between the probability of wind damage and wind direction was expressed by a sine curve with the maximum wind-damage probability at 44.4° from the north and the minimum at the angle 224.4° .

We used the meteorological database obtained from the Katsuura station for daily maximum wind velocity and direction for days with relatively strong wind (maximum wind velocity $> 10 \text{ m s}^{-1}$) to calculate the probability that wind caused damage. If the probability was greater than 0.3, we considered that the probability that wind damage occurred in that day was large enough. We counted the number of days with high wind-damage probability in

five intervals with a fixed length (20 years). The temporal trends in the number of days with wind damage records and the number of days with high wind-damage probability closely corresponded (Figure 4). The strong winds occurred more often (10 days in a 20-year period) in the period from 1941 to 1960 but they occurred less frequently (four days in a 20-year period) in other periods. This temporal trend did not match that of conifer recruitment (Figure 3), which had a peak in the period from 1881 to 1900.

Tree-Ring Growth

Raw tree-ring width and RWI oscillated for *Abies firma*, including increases above the means in the 1890s, 1930–1940s and 1970–1980s (Figure 5). A regression line through the raw ring width for *Abies* was horizontal with a slope not significantly different than zero. Average growth rate was about 2.5 mm per year, with peak growth recorded during 1894, 1937 and the 1980s. In contrast, basal area

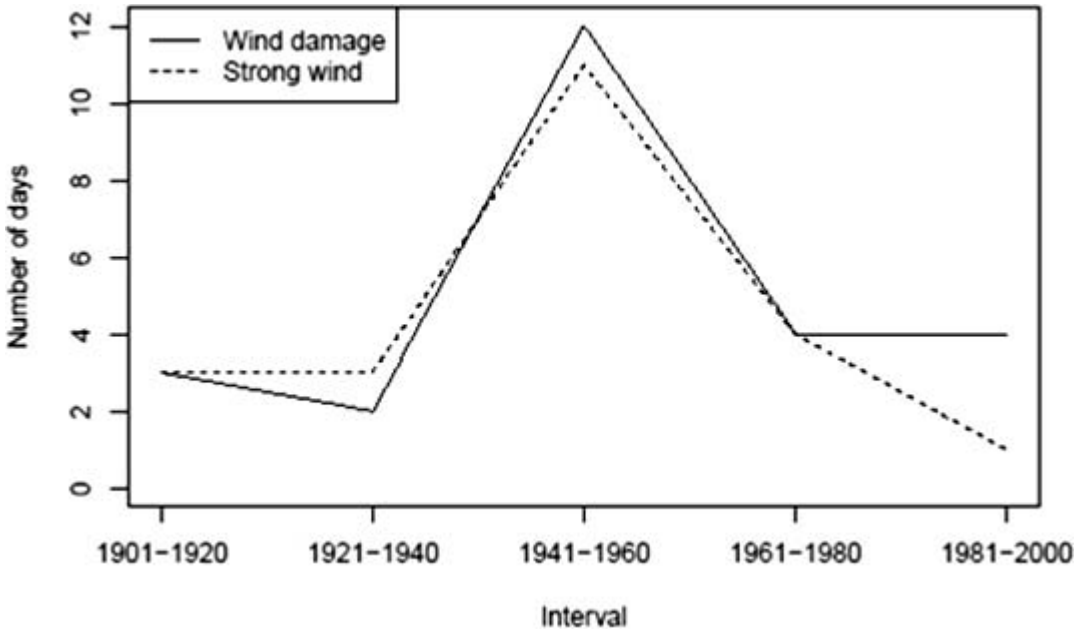


Figure 4. Temporal change in the number of days with wind damage records and the number of days with high wind-damage probability at the University of Tokyo Chiba Forest study site.

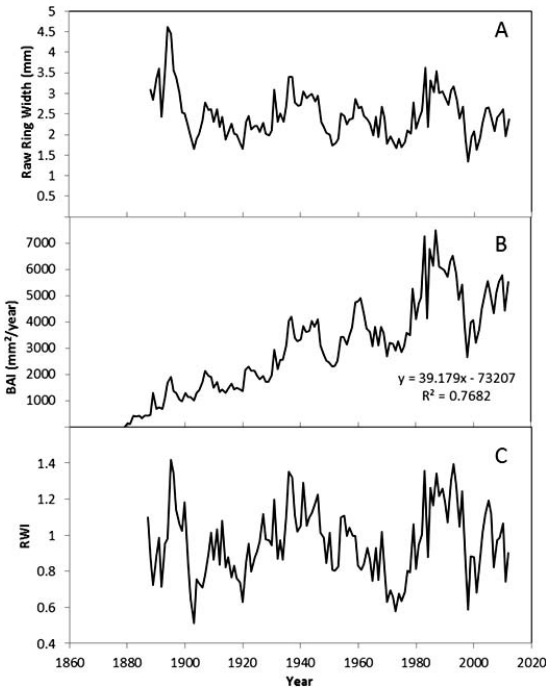


Figure 5. Raw ring widths (A), basal area increment (B), and ring width index (C) for *Abies firma* (n = 14 cores) at the University of Tokyo Chiba Forest study site.

increment exhibited an increasing growth pattern from past to present, although large growth declines occurred at ca. 1950, 1970 and 2000. Tree-ring data for *Castanopsis sieboldii* show similar trends with alternating periods of higher and lower growth in the raw and indexed tree-ring data (Figure 6). Pronounced growth peaks occurred about 1945, 1972 and 1990, which differ somewhat from that in *Abies*. The basal area increment in *Castanopsis* reveals a consistent increase in growth rate as found in *Abies*. A strong-fitting regression line with a positive slope exists for the basal area increment data for both species (Figures 5 and 6). Despite fluctuations in growth at different time periods, both species are showing over-all growth increases over time.

A 100-year climate record from the nearby Katsuura meteorological station, Japan, reveals that average annual temperature was relatively high at ca. 1913, declined to ca. 1945, increased in the 1950s, decreased in the 1960s and 1970s and increased abruptly from the middle 1980s until 2013 (Figure 7). Precipitation averaged 2080 mm per year between 1910 and 1960 and 1940 mm per year thereafter. Basal area increment for *Abies* and

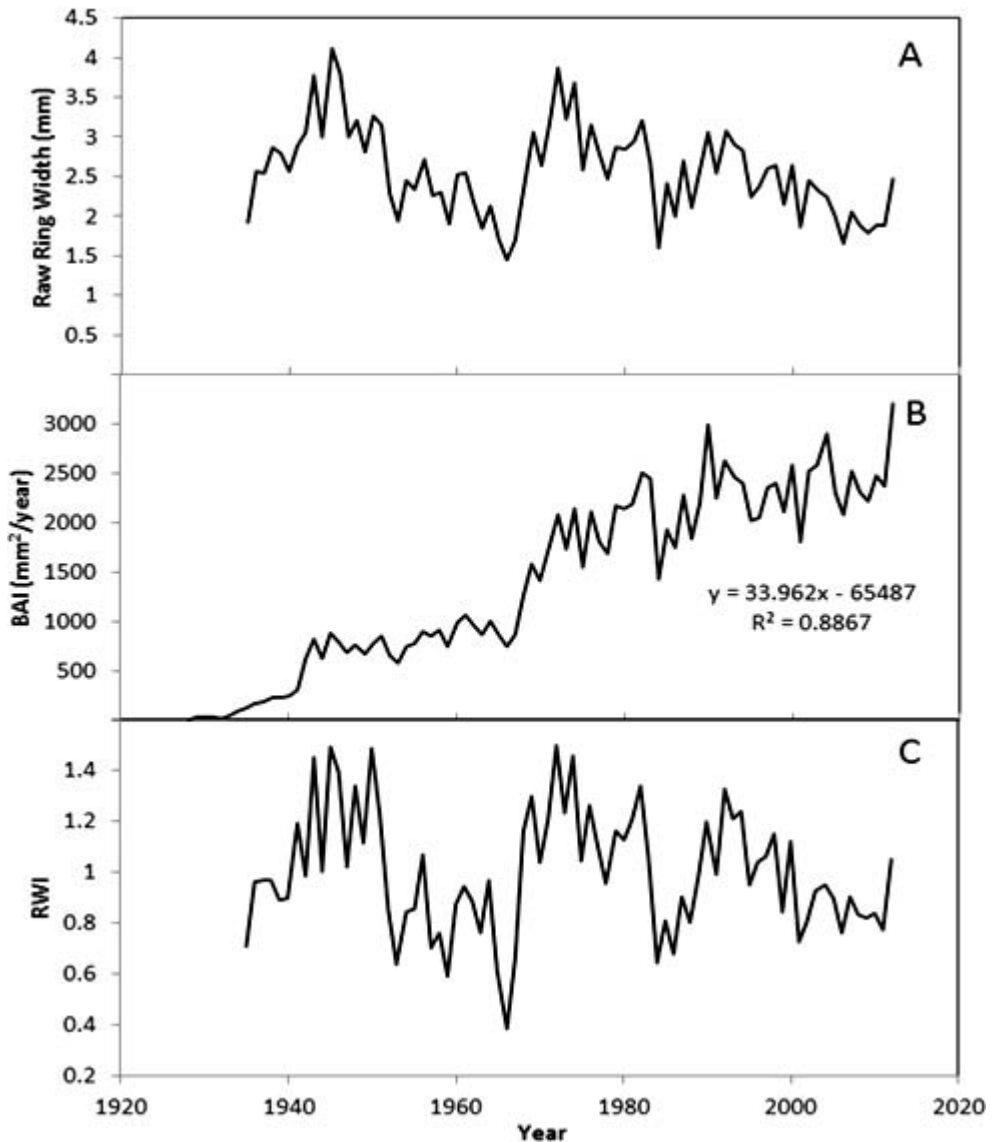


Figure 6. Raw ring widths (A), basal area increments (B), and ring width index (C) for *Castanopsis sieboldii* ($n = 10$ cores) at the University of Tokyo Chiba Forest study site.

Castanopsis was significantly correlated with mean annual temperature ($p = 0.004$ and <0.001 , respectively), but not precipitation. Correlation coefficients derived from response function analysis (using ring width index) for *Castanopsis* were significant for May temperature in the current year ($p < 0.05$). This result was not found for *Abies*. The RWI was not significantly correlated with annual or monthly climate for either species.

We determined the major and moderate tree-ring release dates for representative tree cores of *Abies firma* and *Castanopsis sieboldii* (Figures 8, 9). Across the ten individual chronologies, tree-ring releases are common at the study forest. At least one release was recorded in every decade from 1890 to the present day. The observed mean temporal proximity between years with major tree-ring release and years with wind damage was 1.42 years.

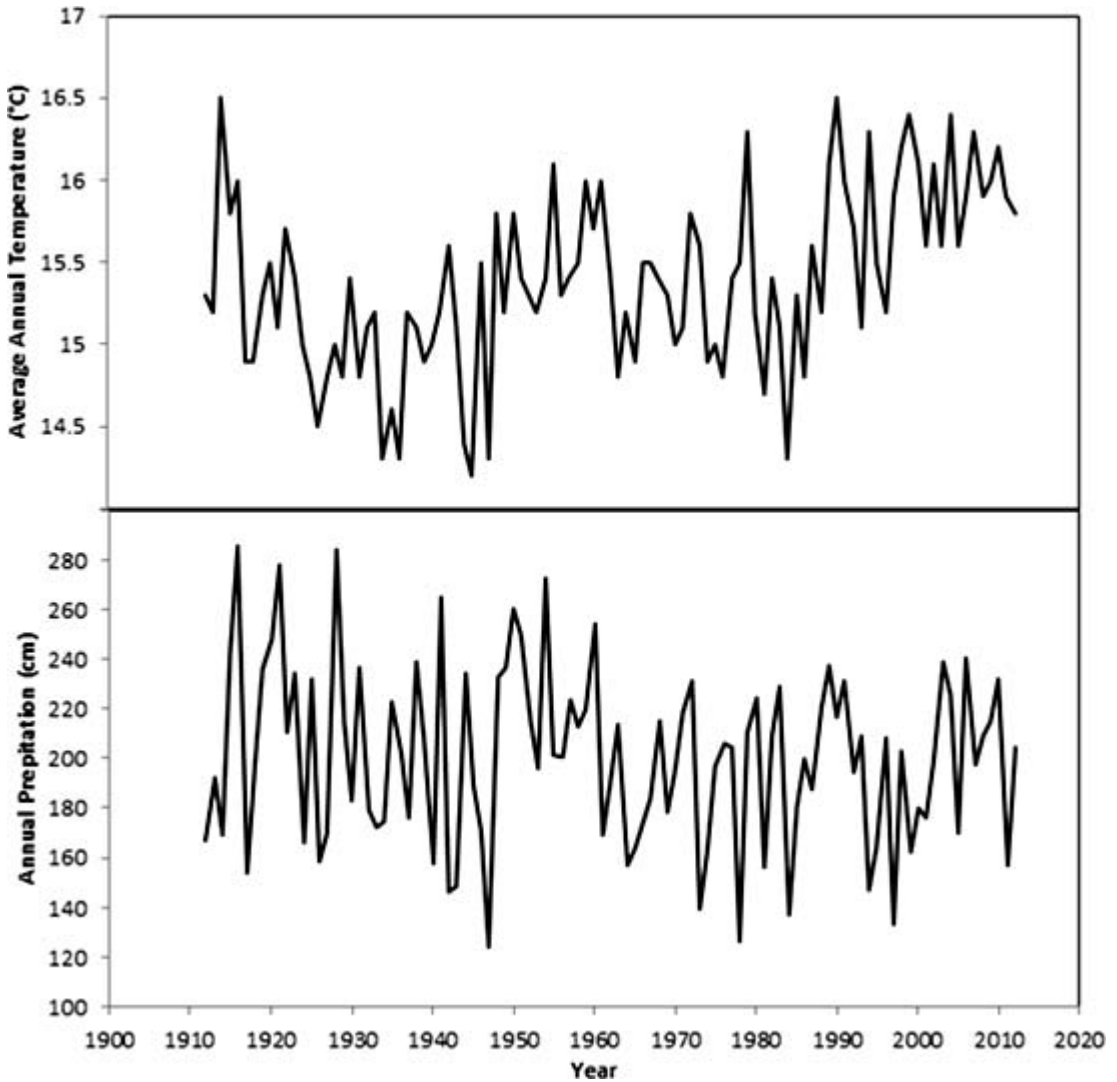


Figure 7. Annual temperature and precipitation totals (1910–2013) obtained from the Katsuura meteorological station, Japan.

This value was statistically smaller than the temporal proximity calculated for randomly scattered release years ($p = 0.012$) indicating that occurrence of major tree-ring releases tended to coincide with wind damage events.

DISCUSSION

The species composition and size-structure of the study forest stand was typical of fir-hemlock forest in the warm-temperate zone; the large to-

tal basal area ($83.8 \text{ m}^2 \text{ ha}^{-1}$) was comparable to the values in previous papers (Suzuki 1979; Kabaya *et al.* 1992; Ozaki and Ohsawa 1995; Okano and Aragami 1999). Two coniferous species (*Abies firma* and *Tsuga sieboldii*) dominated the canopy layer, and evergreen and deciduous broad-leaved trees co-dominated the sub-canopy layer (Table 1, Figure 2). The diameter distributions of the major species (Figure 2) indicated differences in shade-tolerance among three species groups (conifers, deciduous broad-leaved trees, and evergreen broad-leaved trees). Evergreen broad-leaved trees are more

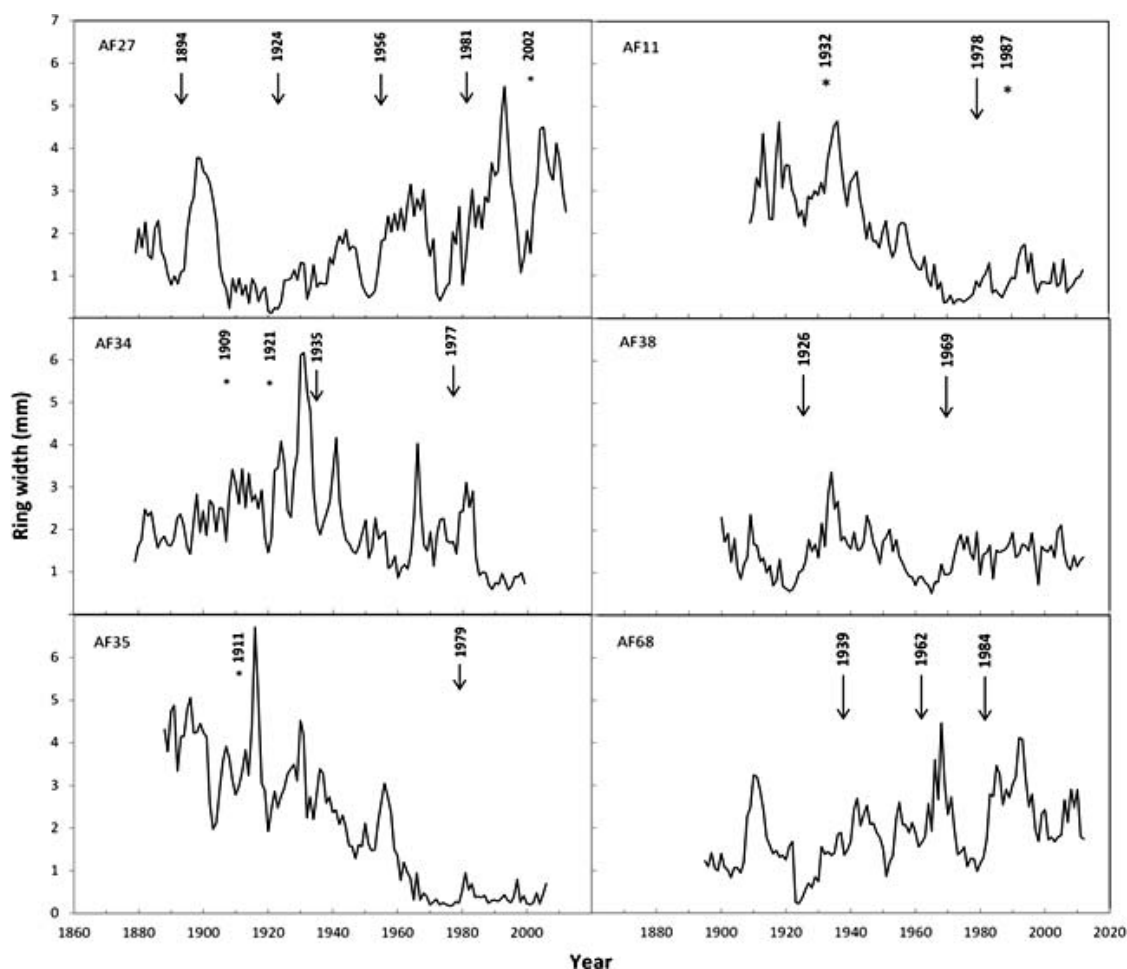


Figure 8. Raw ring widths for individual trees of *Abies firma* (AF) at the University of Tokyo Chiba Forest study site. The arrows indicate years at the start of a major release, whereas the asterisk indicates years of a moderate tree-ring release.

shade-tolerant with many small individuals surviving under the canopy, whereas conifers and deciduous broad-leaved trees are less shade-tolerant. Their seedlings and saplings cannot survive under shaded conditions created by thick foliage of evergreen broad-leaved trees. This difference, also recognized by many researchers (Honda 1927; Kaji 1975; Suzuki 1979; Ozaki and Ohsawa 1995), should be one of the bases for the reconstruction of past forest dynamics and future prediction.

Tree Recruitment Patterns

Considering the temporal patterns of conifer recruitment (Figure 3) together with the low shade-

tolerance of the conifers, we can infer that the canopy was generally sparse and the forest floor was not very dark from 1861 to 1960. The temporal patterns of conifer recruitment did not correspond to those for wind damage and strong wind events, which had a clear peak in a period from 1940–1960 (Figure 4). It indicated that natural disturbance (*i.e.* strong wind) was not a major factor causing conifer recruitment in the study site. Instead, the temporal pattern of conifer recruitment can be readily understood from the history of human activities (forest management).

Before the study site became a part of UTCBF in 1897, the majority of fir-hemlock forest in this region including the study site was managed by

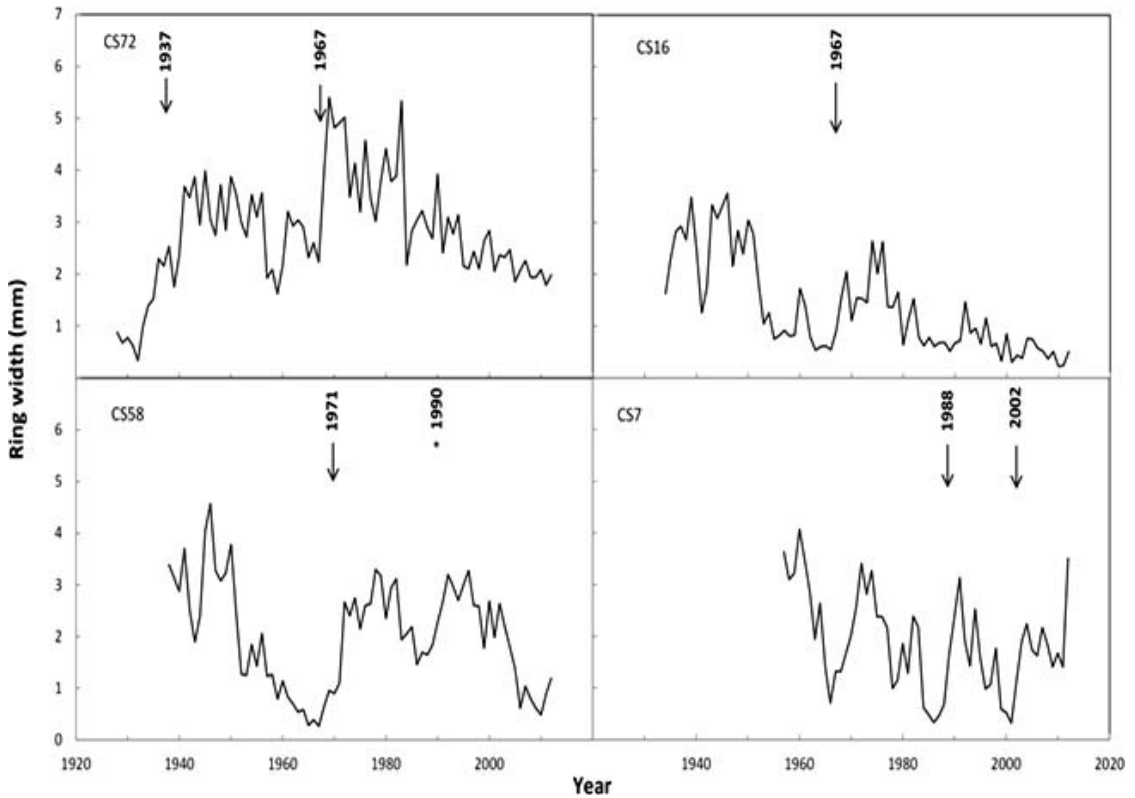


Figure 9. Raw ring widths for individual trees of *Castanopsis sieboldii* (CS) at the University of Tokyo Chiba Forest study site. The arrows indicate years at the start of a major release, whereas the asterisk indicates years of a moderate tree-ring release.

the coppice-with-standards method. Under this method, evergreen broad-leaved trees under the canopy layer were cut frequently (once in 20–30 years; Honda 1927). Therefore, there were good opportunities for less shade-tolerant conifers to regenerate (Smith *et al.* 1997). Some conifer trees (standards) were reserved for timber production to form a sparse canopy layer (Honda 1927; Research Section of Tokyo University Forests and Tokyo University Forest in Chiba 1974). Therefore, several old conifers remained in the present day. Even after the study site was included in the UTCBF, the study site was managed by coppice-with-standards method for about 20 years. This may be why we presently had many conifers that had regenerated from 1881 to 1990. Our finding that recruitment of broad-leaved trees suddenly started around 1920, and not beforehand, matched the record that the last clear-cut was conducted for broad-leaved trees in 1919. The recruitment of conifers started to

decrease after 1900 and no recruitment was observed after 1961. The decrease in conifer recruitment may be caused by the lack of available light on forest floor because of the growth of established trees (especially broad-leaved).

The above reconstruction of recruitment processes in the study site corresponded well to the early ecological descriptions of the fir-hemlock forest in this region (Honda 1912; Honda 1927), which stated that forest management (coppice-with-standards method) was a primary factor in determining the forest structure before the establishment of the UTCBF. Sanquetta *et al.* (1994) described similar developmental processes in a younger secondary fir-hemlock forest in Shikoku. However, as forests grew rapidly from the intensively managed status, and people's memory of the management faded away, less attention has been paid to the human impacts on the forests. Ecological publications on the fir-hemlock forest from 1950 concentrated

Table 1. Density, dominance, and importance values for tree species in an old-growth forest in southern Boso Peninsula, Japan, surveyed in 2013.

Species	Density (no. ha ⁻¹)	Dominance (m ² ha ⁻¹)	Relative Density	Relative Dominance	Relative Importance
<i>Abies firma</i>	62.2	38.9	6.9	46.4	26.6
<i>Quercus acuta</i>	201.4	10.5	22.3	12.6	17.4
<i>Castanopsis sieboldii</i>	82.1	4.8	9.1	5.8	7.4
<i>Cinnamomum tenuifolium</i>	94.5	3.6	10.5	4.3	7.4
<i>Tsuga sieboldii</i>	34.8	8.0	3.9	9.5	6.7
<i>Prunus jamasakura</i>	27.4	4.1	3.0	4.9	4.0
<i>Cleyera japonica</i>	44.8	1.6	5.0	2.0	3.5
<i>Eurya japonica</i>	39.8	0.4	4.4	0.5	2.5
<i>Litsea lancifolia</i>	34.8	0.9	3.9	1.1	2.5
<i>Zelkova serrata</i>	22.4	1.8	2.5	2.2	2.3
<i>Quercus salicina</i>	29.8	0.9	3.3	1.1	2.2
<i>Ilex integra</i>	32.3	0.5	3.6	0.6	2.1
Others ^a	196.5	7.6	21.8	9.0	15.4
Total	902.7	83.8			

^a*Camellia japonica* L., *Quercus glauca* Thunb., *Acer pictum* subsp. *mono* (Maxim.) H. Ohashi, *Acer palmatum* Thunb., *Carpinus tshonoskii* Maxim., *Machilus thunbergii* Sieb. et Zucc., *Styrax japonica* Sieb. et Zucc., *Swida controversa* (Hemsl. ex Prain) Soják, *Dendropanax trifidus* Makino, *Carpinus laxiflora* (Sieb. et Zucc.) Blume, *Litsea acuminata* (Teschner) Kosterm., *Ilex macropoda* Miq., *Benthamedia japonica* H. Hara, *Sapium japonicum* Pax et K. Hoffm., *Illicium anisatum* L., *Torreya nucifera* (L.) Sieb. et Zucc., *Albizia julibrissin* Durazz., *Diospyros japonica* Sieb. et Zucc., *Acer amoenum* Carr., *Idesia polycarpa* Maxim., *Neolitsea sericea* (Blume) Koizumi.

mainly on ecological characteristics of component species, abiotic environmental factors, and natural disturbance regime (Research Section of Tokyo University Forests and Tokyo University Forest in Chiba 1974; Kaji 1975; Kabaya 1975; Numata 1979; Miyawaki and Fujiwara 1983; Ozaki and Ohsawa 1995). However, human impacts on various types of ecosystems have been reviewed recently (e.g. Tsujino 2011; Ogura 2012). Generally, human impacts on ecosystems were much greater than previously thought. The results of this study also showed that human impact (forest management) was a primary factor in determining the developmental processes in the past and the species composition and structure in the present day for the fir-hemlock forest in southern Boso Peninsula.

Tree-Ring Growth

Johnson and Abrams (2009) reported that annual basal area increment is a more robust measure of tree growth than is the ring-width index (RWI). The calculation of RWI involves fitting a regression line through a plot of raw ring width by year. The regression represents the expected growth increment for each year taking into account tree size

impacts on ring width (ring width tends to decline as tree size increases). The RWI for each year is calculated as the relative distance (%) above or below the regression line. One problem with using RWI is that it typically masks long-term growth trends compared with other metrics. Annual basal area increment increases during life of many tree species, as reported in this study and for many temperate tree species in the eastern US (Johnson and Abrams 2009). This reflects the amount of radial wood being produced each year and is independent of the tree getting larger with age. This trend is masked using RWI which presents annual growth variation across a horizontal regression line. Basal area increment is not impacted by tree size. In this study, the raw ring width for *Abies* and *Castanopsis* was fairly consistent during the life of the tree. The slope of a regression line through these data was not significantly different than zero. Thus tree rings produced later in the life of these trees, although similar in width to those produced earlier, actually represented a large production of wood (distributed over a large tree area) and a larger basal area increment. Hence, growth increases in the basal area data were masked in the RWI data.

The long-term increases in basal area increment for both *Abies* and *Castanopsis* may be caused

by a combination of frequent small to medium-sized disturbances (tree fall gaps) and generally warmer climate condition from the early 1900s to the present day. The climate correlation existed despite relatively cool temperatures between 1960 and 1980. The growth trends reported here are also indicative of a forest aggrading in biomass accumulation (Oliver and Larson 1990). This is somewhat unusual for an uneven age forest that is *ca.* 150 years old, as in the case of our study forest, but consistent with growth trends reported for eight major tree species in old-growth forests of the eastern US (Johnson and Abrams 2009). These authors attributed growth increases to a combination of global change phenomenon, including climate and land-use history. The increasing basal area growth at the Chiba forest is even more remarkable considering the decline in average precipitation after the first half of the 20th Century. The results of this study suggest that some, but not all, tree species in warm-temperate forests in southeastern Japan are suitable for dendrochronology and that their growth varies in a manner consistent with forest dynamics and recent warming. Takahashi and Okuhara (2012) examined the effects of climate on radial growth in an evergreen broad-leaved forest at their inland northern distribution limit in Japan, and found that radial growth of *Abies firma* was generally positively correlated with temperature in winter and during the growth period but not with precipitation. They also found that responses to climate were species-specific.

The very common tree-ring releases (at least one release in every decade from 1890 to the present day) at the study forest are indicative of small or moderate disturbances. A high frequency of tree-ring release was also reported for an old-growth forest in northern Japan (Abrams *et al.* 1999). Although records of wind damages and strong wind events did not correspond to the timing of recruitment of conifers, they showed some correspondence to tree-ring growth releases. Frequent small- to moderate-scale disturbances, often caused by strong wind, promoted tree-ring growth. The study forest would be particularly prone to individual tree blowdown because it is a ridge-top site on a steep slope containing a relatively thin soil and exposed to high winds near the ocean. It seems likely that the increasing basal area of trees in the forest is related

to frequent small- to moderate-scale disturbances to promote growth in residual trees.

Future Projection

Disturbance factors will likely continue to maintain growth of the dominant conifers and broad-leaved trees in regions that receive adequate precipitation. Therefore, the fir-hemlock forest in the Boso Peninsula will not decline in this respect. However, we cannot expect new recruitment of conifers under the current regime of natural disturbances as the forest continues to age. As large coniferous trees in the canopy layer die, the dominance of shade-tolerant evergreen broad-leaved trees will increase (Honda 1912; Kaji 1975). The dominance of *Abies firma* may rapidly decrease as big individuals of the species are exposed to strong wind, and as their ages are approaching the relatively short lifespan of this species in the region (*ca.* 200 years; Honda 1927; Research Section of Tokyo University Forests and Tokyo University Forest in Chiba 1974). The recent rapid increase in deer population in this area may also impact the future dynamics of the fir-hemlock forest because deer browsing can greatly inhibit tree recruitment (Kabaya 1988; Suzuki *et al.* 2008). However, Suzuki (2013) concluded that limited light resulting from excessive shading was a primary factor that prevented the establishment of ground-layer vegetation in the Boso Peninsula, and the negative effects of herbivory on species richness seemed to be much smaller than that of limited light.

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