

A 370-year dendroecological history of an old-growth *Abies*–*Acer*–*Quercus* forest in Hokkaido, northern Japan

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Abstract: Dendroecological techniques were used to study the dynamics and species recruitment patterns, spanning nearly four centuries, for a mesic, montane, old-growth forest in Hokkaido, northern Japan. The forest is dominated by *Abies sachalinensis* (Masters), *Acer palmatum* (Thunb.), *Quercus mongolica* var. *grosseserrata* (Rehd.), and *Cercidiphyllum japonicum* (Sieb.). From 1620 to 1750 and 1820 to 1840, *Q. mongolica* exhibited continuous recruitment into the overstory. A lack of recruitment for all tree species from 1750 to 1820 followed a 1739 volcanic eruption 200 km from the study area. Release events for individual trees occurred almost every decade of the stand history, indicating that frequent small-scale disturbances coupled with infrequent large-scale disturbances, impact tree growth and species recruitment. From 1870 to 1950, canopy recruitment of *Abies* and *Acer* dominated the forest, while recruitment of *Quercus* ceased. These later successional species appeared to be replacing *Quercus*, suggesting that the syndrome of declining oak dominance is an increasingly global phenomenon. However, successional patterns in the forest are difficult to predict because intensive deer browsing has recently prevented canopy recruitment of all tree species and the possibility of future large-scale disturbances, such as fire and volcanic eruption.

Résumé : Des techniques dendroécologiques ont été utilisées pour étudier la dynamique et les patrons de recrutement des espèces, sur près de quatre siècles, d'une vieille forêt montagnarde mésique de l'île de Hokkaido, dans le nord du Japon. La forêt est dominée par l'*Abies sachalinensis* (Masters), l'*Acer palmatum* (Thunb.), le *Quercus mongolica* var. *grosseserrata* (Rehd.) et le *Cercidiphyllum japonicum* (Sieb.). De 1620 à 1750 et de 1820 à 1840, le *Q. mongolica* a montré un recrutement continu dans l'étage dominant. Le manque de recrutement de toutes les espèces entre 1750 et 1820 a suivi une éruption volcanique qui s'est produite en 1739, à 200 km de l'aire étudiée. Le dégagement des arbres individuels s'est produit presque à chaque décennie de l'histoire du peuplement, indiquant que de fréquentes perturbations à petite échelle, combinées à des perturbations peu fréquentes à grande échelle, avaient un impact sur la croissance des arbres et le recrutement des espèces. De 1870 à 1950, le recrutement dans la canopée d'*Abies* et d'*Acer* a dominé la forêt, tandis que celui du *Quercus* a cessé. Ces dernières espèces successionales semblaient être en train de remplacer le *Quercus*, suggérant que le syndrome du déclin de la dominance du chêne est un phénomène de plus en plus global. Toutefois, les patrons de succession forestière sont difficiles à prédire à cause du broutage du cerf, qui a récemment empêché le recrutement dans la canopée de toutes les espèces arborescentes, et à cause de la possibilité que surviennent dans le futur des perturbations à grande échelle, telles que les feux et les éruptions volcaniques.

[Traduit par la Rédaction]

Introduction

Over the past decade, dendroecological techniques have become an important tool in the study of stand dynamics and ecological history (Fritts 1976; Fritts and Swetnam 1989). From tree-ring chronologies, researchers have been able to reconstruct the historical development of forests in terms of species recruitment patterns, periodicity and intensity of disturbances, the impacts of yearly climatic variation and ex-

treme weather phenomena, and populations and successional dynamics (Canham 1985; Foster 1988; Frelich and Graumlich 1994; Abrams and Orwig 1995; Abrams et al. 1995). Coupling tree-ring chronologies, age structure, and land-use history has proven to be a particularly robust approach for understanding long-term variation in forest dynamics and history (Foster 1988; Abrams and Orwig 1995; Abrams et al. 1997).

Stand dynamics is an important subject of ecological research in Japan, and these studies have provided a substantial data base of information on the regeneration ecology and population structure of forests, particularly in relation to canopy gaps (Nakashizuka 1984; Yamamoto 1989; Kubota 1995; Namikawa 1996). However, there have been very few dendroecological studies conducted in Japan, despite the fact that most trees produce distinct annual rings. A few recent papers have reported on the age structure of trees in old-growth forests and the effects of climatic factors on radial

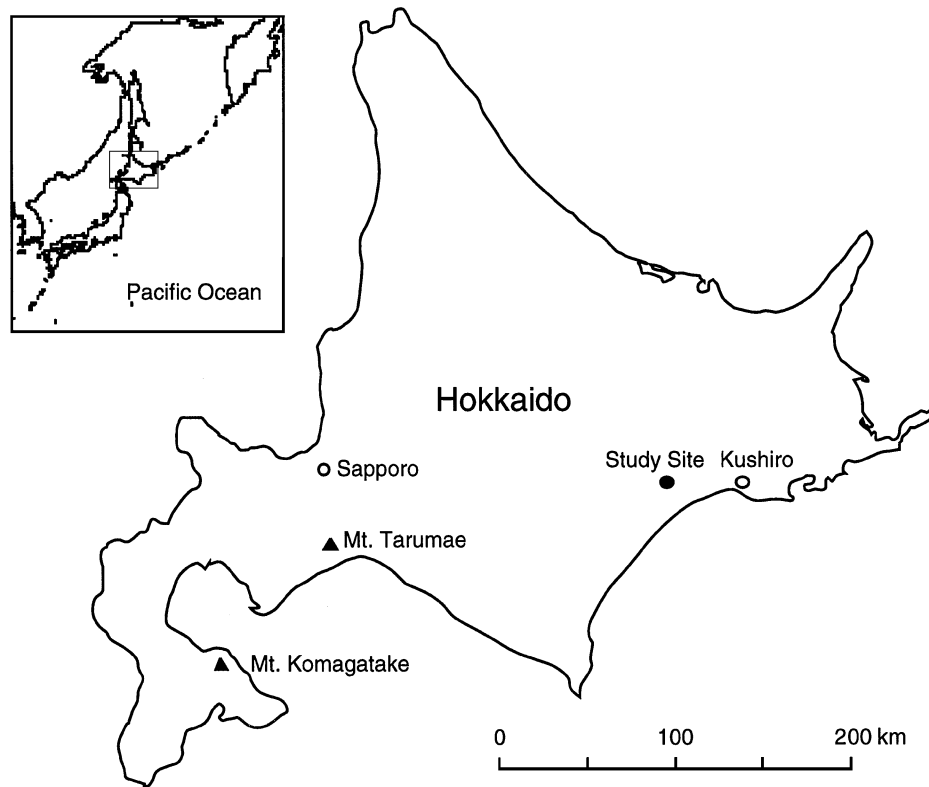
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Fig. 1. The main islands of Japan (insert) with Hokkaido (in square) and an enlargement of the island of Hokkaido showing principal localities for this study.



growth, including paleoclimatic reconstruction (Yasue et al. 1996; Hiura et al. 1996; Sano 1997; D'Arrigo et al. 1997). Japan has one of the highest concentrations of active volcanoes of any country. Research outside of Asia indicates that tree-ring growth may be suppressed for several years following a volcanic eruption, yet little is known about the long-term dendroecological impacts of ash deposition on intact forests (Egler 1967; Yamaguchi 1983; LaMarche and Hirschboeck 1984; Segura et al. 1995; Briffa et al. 1998). In addition, the forests of Japan are impacted by windstorms and deer browsing of varying intensity (Nakashizuka 1984; Yokoyama et al. 1996). We believe that the study of long-term tree ring records from Japanese forests will represent a major new source of dendroecological data contributing to the understanding of forest dynamics on a global scale, including the impacts of volcanic activity.

Quercus species dominate in many forest types throughout Japan, although the ecological requirements for this genus are poorly understood (Miyawaki 1988). In the United States, the dominance of *Quercus* on upland sites is a result, at least in part, of periodic burning of these forests by low-intensity surface fire caused by human activity or lightning strikes (Abrams 1992). In the absence of periodic fire during the 20th century, most oak forests in the eastern United States are showing definitive signs that they will be replaced by later successional species (Abrams 1992; Lorimer et al. 1994). In contrast, *Quercus* species in Japan are often considered to be late successional and an important component of climax forests (Koike 1988; Ishikawa and Ito 1989). Nonetheless, the dominance of *Quercus serrata* (Thunb.) in old-growth and second-growth, mixed-deciduous forests in

central and western Japan is the result of fire (Masaki et al. 1992; Sano and Ohtsuka 1998).

In this study, we report on the dendroecology of an old-growth *Abies-Acer-Quercus* forest in eastern Hokkaido, northern Japan. The forest is located approximately 200 km from an active volcano, Mount Tarumae, which last experienced a violent eruption in 1739 and covered the region with a thick ash deposit (Fig. 1; Tokui 1989). Thus, the forest represents a rare opportunity to study forest dynamics spanning nearly four centuries, and the potential impacts of volcanic activity. The objectives of this study were to (i) quantify the composition and structure of this old-growth forest; (ii) report on the long-term patterns of species recruitment and radial growth variation; (iii) investigate the impacts of small- and large-scale disturbances (including the 1739 Mount Tarumae eruption), on the long-term dendroecological features of the forest; and (iv) gain an understanding of the ecological history and successional status of *Quercus* in an old-growth forest in northern Japan.

Site description

Hokkaido is the northernmost of the four main islands of Japan (Fig. 1). The cool temperate climate of the region supports sub-boreal forests dominated by *Quercus*, *Ulmus*, *Fraxinus*, *Tilia*, *Acer*, *Carpinus*, *Alnus*, *Picea*, and *Abies* (Miyawaki 1988). The native Ainu people maintained a hunting and gathering culture until the late 1800s, after which significant settlement by Japanese from the southern islands took place (Hokkaido 1970). Logging of forests in Hokkaido began with Japanese settlement. Nonetheless, the natural vegetation of Hokkaido is generally much less disturbed compared with that in mainland Japan, North America, or Europe. One major

compositional and structural difference between the forests of Hokkaido and the northern forests of Europe or America is the presence of dwarf bamboo species, *Sasa kurilensis* (Rupr.), *Sasa senanensis* (Rehd.), and *Sasa nipponica* (Makino et Shibata), which form a dense undergrowth in many Japanese forests and may have a profound impact on tree regeneration and recruitment (Miyawaki 1988).

This study was conducted at an old-growth forest in the Siranuka Hills in eastern Hokkaido, northern Japan (Fig. 1). The location of the study site is 43°20'N and 143°47'E and about 20 km inland from the coast of the Pacific Ocean. The site is composed of two topographic units, a flat terrace at the bottom and an upper south-facing sideslope inclined 30° at maximum. The elevation of the site ranges from 230 to 260 m above sea level. Mean annual temperature is 5.7°C, and mean annual precipitation is 1043 mm. Maximum snow depth ranges from 20 to 142 cm and averages 62 cm (Masuda 1983). The depth to bedrock of Tertiary mudstone is 70–80 cm throughout the study site. The humic layer has a crumbly and (or) blocky soil structure and is thicker at the terrace compared with the sideslope. The subsurface soil texture is clay-loam. The volcanic ash layer in the upper soil profile has a silty texture and a depth of 15 cm at the terrace and 10–12 cm at the sideslope. Most of the layer is dark in color because of perforated humus. The ash layer contains two different tephra, Ko-c2 and Ta-a, which originated from the eruptions of Mt. Komagadake in 1694 and Mount Tarumae in 1739, respectively (Tokui 1989). Evidence of early logging at the study site in the form of an occasional cut stump still exist. There is no record of cutting in this forest after the middle of the 20th century according to the local forestry office responsible for its management.

Methods

During September 1996, the species and diameter were recorded for all trees ≥ 8.0 cm DBH (diameter at breast height, 1.37 m) within a permanent plot on each topographic unit: terrace and sideslope. The areas of the permanent plots are 0.25 ha for the terrace and 0.315 ha for the sideslope. A total of 450 trees were measured at the two plots. For each tree species, a relative importance value was calculated as an average of the relative density and dominance (basal area) based on the summed data of both plots.

In August 1997, twenty fixed-area plots, located at 20-m intervals along transects through the forest interior, were used for dendroecological sampling. The species, diameter, and crown class were recorded for all trees ≥ 8.0 cm DBH occurring within 0.02-ha circular plots at each point. Tree crowns were classified into four categories (dominant, codominant, intermediate, and overtopped) based on the amount and direction of intercepted light (Smith 1986). At each point, two to four trees 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 and seedlings were counted in nested circular plots of 9 and 5 m², respectively, within each of the overstory plots. Saplings were classified as trees ≥ 1.5 m in height but < 8.0 cm in DBH, and seedlings were < 1.5 m in height. The cover of *Sasa* bamboo was estimated into cover classes in each of the 5-m² seedling plots.

Radial growth analysis

All increment cores ($n = 67$) from the study area were dried, mounted, and sanded (Phipps 1985). A number of cores ($n = 35$) contained rotten sections or were badly broken (particularly the *Abies sachalinensis*). For these cores, we counted ages, but these are considered minimum, non-cross-dated ages. The remaining cores ($n = 32$) were skeleton plotted and cross-dated to help identify missing or false rings and provide a solid chronology for the cores (Stokes and Smiley 1996). For cores where the pith had been

missed, we overlaid a transparency with concentric circles to determine how many years needed to be added for an accurate age at DBH. This correction involved only about 20% of the cores, and in those the age only needed to be adjusted by 1–3 years.

These 32 cross-dated cores were then scanned with a tree-ring measuring device and the annual growth increments were measured to the nearest 0.01 mm (Regents Instruments Inc., Quebec, Canada). We identified canopy accession dates for each of the 32 cross-dated series. We defined the canopy accession date as the release event during which an overtopped tree in the understory grew into the intermediate canopy position in the overstory as determined by Lorimer and Frelich (1989). The early radial growth pattern of each series was classified into one of three categories: open grown (or large gap origin), release after suppression, or ambiguous growth. The missed pith in some cores did not significantly change our interpretation of assigning trees as gap origin or understory origin. Eight series were classified as open grown because of their high, initial growth rates. Nineteen series were classified as released from suppression because they exhibited a major or moderate understory release following an initial period of suppressed radial growth. The five remaining series had ambiguous growth patterns with no obvious accession date. Our field data indicated that these five trees had not yet reached the overstory. We determined the major and moderate understory release dates for the portion of the chronologies before the accession date for all 32 series. Understory release dates were determined according to Lorimer and Frelich's (1989) definition of a major release as being greater than 100% average growth increase lasting at least 15 years and a moderate release as a greater than 50% average growth rate lasting at least 10 years. We calculated the major and moderate overstory release dates for the portion of the chronologies after the accession date only for series that had reached the overstory (i.e., the eight open-grown and 19 released from suppression series). We used a modified version of Nowacki and Abrams' (1997) method for determining overstory releases. A growth increase of greater than 25% sustained for 10 years was identified as a moderate overstory release while an increase of greater than 50% sustained for 10 years was classified as a major overstory release.

Results and discussion

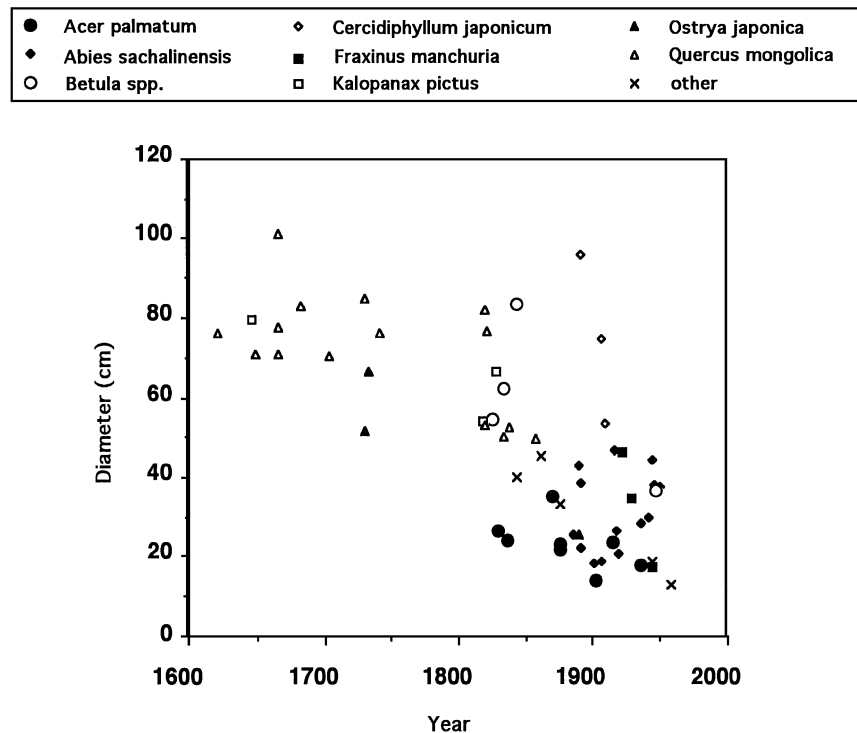
The forest is dominated by *Abies sachalinensis*, *Acer palmatum*, *Quercus mongolica* var. *grosseserrata*, and *Cercidiphyllum japonicum* (Table 1). The relatively high importance value for *Q. mongolica* is due to the large size of most individuals (e.g., 50–100 cm DBH; Fig. 2), despite having low tree density. In contrast, *Abies sachalinensis* had the highest tree density of any species, and most trees of this species are between 8 and 30 cm DBH. We found a greater abundance of *Abies sachalinensis* on the terrace compared with the sideslope portion of the forest. Most trees of *Acer palmatum* are in the 10- to 20-cm DBH class (Fig. 2). Regeneration of all tree species was very sparse within the stand, with only 10 seedlings and 15 saplings, mainly *Acer palmatum* and *Abies sachalinensis*, counted in all 20 plots (data not shown). *Sasa* bamboo in the understory plots averaged 17.8% cover.

Quercus mongolica exhibited fairly continuous recruitment between 1620 and 1750, including three individuals established in 1664–1668 and two individuals in 1740–1750 in this uneven-aged stand (Fig. 2). We recorded no episodes of tree recruitment for any species between 1750 and 1820, following the 1739 volcanic eruption of Mount Tarumae, located 200 km west of the study site. A volcanic ash layer 10–15 cm thick in the surface soil at the study site originated

Table 1. Density, dominance, and importance values for tree species in an old-growth forest in eastern Hokkaido, Japan, surveyed in 1997.

Species	Density (no./ha)	Dominance (m ² ·ha ⁻¹)	Relative density	Relative dominance	Relative importance
<i>Abies sachalinensis</i>	341.6	15.0	35.7	29.3	32.5
<i>Acer palmatum</i>	157.5	5.8	16.5	11.4	13.9
<i>Quercus mongolica</i>	24.8	10.2	2.6	19.9	11.2
<i>Cercidiphyllum japonicum</i>	40.7	5.2	4.3	10.2	7.2
<i>Syringa reticulata</i>	77.9	1.1	8.1	2.2	5.2
<i>Carpinus cordata</i>	72.6	1.0	7.6	1.9	4.7
<i>Kalopanax pictus</i>	21.2	3.6	2.2	7.1	4.7
<i>Acer mono</i>	24.8	2.7	2.6	5.3	3.9
<i>Tilia japonica</i>	31.9	1.1	3.3	2.2	2.8
<i>Ostrya japonica</i>	23.0	1.3	2.4	2.5	2.5
Others ^a	141.6	4.1	14.8	8.0	11.4
Total	957.5	51.2			

^a*Magnolia obovata* (Thunb.), *Acer japonicum* (Thunb.), *Fraxinus lanuginosa* (Koidz.), *Styrax obassia* (Sieb. et Zucc.), *Magnolia kobus* (Sarg.), *Sorbus alnifolia* (C. Koch), *Alnus hirsuta* (Trucz.), *Sorbus comixta* (Hedl.), *Betula maximowicziana*, *Phellodendron amurense* (Rupr.), *Betula ermanii*, *Fraxinus mandshurica*, *Prunus sargentii* (Rehder), *Cornus controversa* (Hemsley), and *Prunus ssiori* (Fr. Schm.).

Fig. 2. Age–diameter (at 1.37 m) relationships for all cored trees in the old-growth forest study sites in eastern Hokkaido, Japan.

mainly from the Mount Tarumae eruption (Tokui 1989). Five additional *Q. mongolica* trees recruited between 1820 and 1840, after which recruitment of this species ceased (barring one individual in 1860). Following 1820, many individuals of *Acer palmatum*, *Abies sachalinensis*, *Betula ermanii* (Cham.), *Betula maximowicziana* (Regel), and *C. japonicum* recruited into the tree-size classes. *Acer palmatum* and *Abies sachalinensis* recruited continuously into the overstory from 1825 or 1890 to 1950, respectively.

The period following the 1739 volcanic eruption of Mount Tarumae was remarkable at our study site because of the ab-

sence of tree recruitment. Previous studies suggest that volcanic ash may not be responsible for long-term inhibition of tree regeneration, especially in conifer species (Griggs 1918; Antos and Zobel 1986; Caruso et al. 1990; Zobel and Antos 1997). Based on our recent observations at the study sites, we believe that changes in browsing pressure by Sika deer (*Cervus nippon yesoensis*) and (or) sasa bamboo dynamics may have impacted tree recruitment following the Mount Tarumae eruption. High density of deer population may impact seedling recruitment in both negative and positive ways. Negative effects are low growth rate and high mortality of

tree seedlings and saplings caused by browsing (Takatsuki 1994). In fact, very sparse regeneration of tree species in natural stands in this region, including our study site, is due to intensive deer browsing during recent decades (K. Terazawa, unpublished data). On the other hand, a positive effect of high density of deer population on seedling recruitment may be the reduction of sasa bamboo (Kaji and Yajima 1987). Therefore, possible explanations for the absence of tree recruitment from 1750 to 1820 and the restart of seedling recruitment after 1820 include (i) the population density of Sika deer in this region may have increased drastically in the middle of the 1700s, (ii) the increased population of Sika deer may have prevented the recruitment of tree species into tree-size class and sasa bamboo on the forest floor may have declined because of browsing; and (iii) high mortality of the deer population may have occurred around the 1800s allowing the seedling bank to recruit into tree-size classes. A possible cause of high mortality of deer population in the northern Japan is heavy snowfall and subsequent reduction of food availability (Takatsuki et al. 1994). Evidence of massive death of Sika deer caused by very heavy snowfall in this region during the late 1700s and early 1800s and starvation of the native Ainu people who hunted them was reported by several explorers (Inukai 1952; Hokkaido 1970); this coincides with the re-initiation of recruitment at the study site. Moreover, mass death of sasa bamboo populations following synchronized flowering may also allow for a pulse of tree recruitment, which is otherwise inhibited by sasa bamboo competition (Takatsuki et al. 1994; Hiura et al. 1996).

Annual radial growth in the oldest *Q. mongolica* and *Kalopanax pictus* (Nakai) trees indicates a high degree of variation in their early growth (Fig. 3). One *Q. mongolica* persisted as an overtopped, understory tree for 70 years before it had a canopy accession release in 1736 (Fig. 3b). In contrast, another *Quercus* tree experienced canopy accession very early in its life and had declining growth afterwards, suggesting this tree is of gap origin (Fig. 3c; Lorimer and Frelich 1989; Abrams et al. 1995). The tree in Fig. 3d had a canopy accession release 32 years after recruitment and declining growth with increasing age. Most trees shown here had their canopy accession release 10–35 years after reaching the sapling stage (a height of 1.37 m). Trees in Figs. 3e and 3a already in the overstory had their first major release in 1747 and 1755, respectively, following the 1739 volcanic eruption. The tree in Fig. 3e exhibited increasing growth with age. Trees in Figs. 3b and 3f had their canopy accession release very near the eruption date. Very few trees exhibited releases in the same years, suggesting the frequent occurrence of small-scale disturbances with only localized impacts in the forest (Fig. 3). Major or moderate releases typically occurred every 20–50 years throughout the life of each tree. One or more releases in radial growth occurred in most decades from 1650 to the present (Fig. 4). In general, about 25–35% of the sample trees exhibited release in a decade. The large number of major releases in the 1970s reflects, in part, the increased sample size.

The 1739 volcanic eruption may have been responsible for some of these tree-ring releases and canopy recruitment events. Following a brief period of growth suppression, the ash deposit may have been responsible for stimulated tree

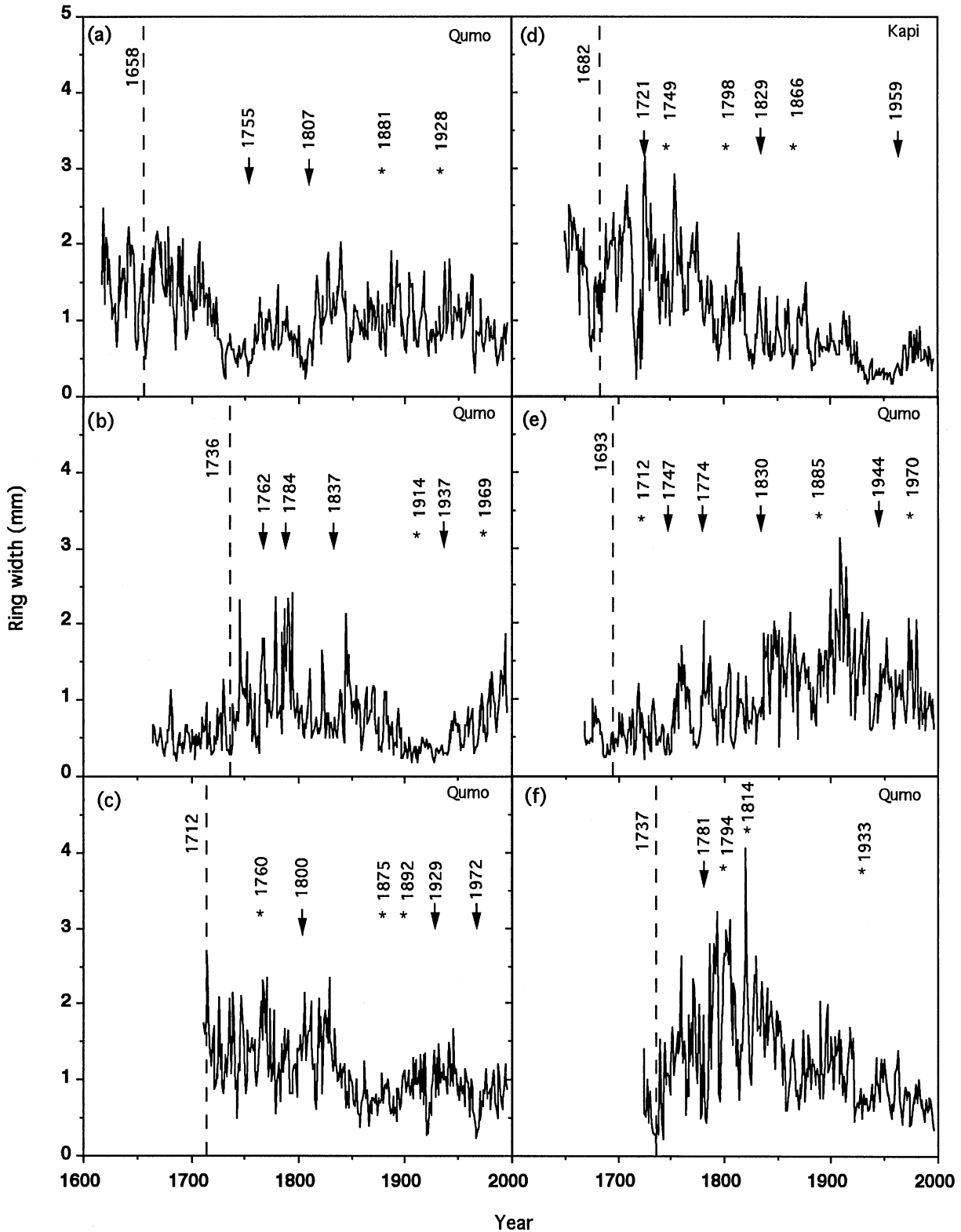
growth in the following decades because of the fertilizing and mulching effects of volcanic ash or the lower competition from partial stand mortality (Egler 1967; Mahler and Fosberg 1983; Mizota et al. 1992; Velasquez-Pereira et al. 1996; Segura et al. 1995). Depressed growth for several years following a volcanic eruption has been attributed to atmospheric cooling from airborne particles and volcanic sulfate aerosols and the ash covering of tree foliage, both of which can result in lowered seasonal rates of photosynthesis (Egler 1967; Seymour et al. 1983; LaMarche and Hirschboeck 1984; Hinckley et al. 1984; Scuderi 1990; Segura et al. 1994, 1995; Briffa et al. 1998).

The influence of climate on tree growth at the study site can not be overlooked. Radial growth of *Quercus dentata* (Thunb.) in northeastern Hokkaido increased sharply between 1750 and 1760, followed by below average growth until 1785, a period that includes the 1783 “year without a summer” (Yasue et al. 1996; D’Arrigo et al. 1997). Growth of *Fraxinus mandshurica* (Maxim.) in northern Hokkaido was relatively high from 1749 to 1765, but this was followed by decreasing growth until 1782 (Yasue et al. 1996). These studies indicate that significant growth increases around 1750 occurred in several different tree ring chronologies in northern Japan, which was attributed to warmer climate. Therefore, we believe that the post-1739 growth changes at our study site may be a result of both volcanic (nutrient input, mulching effects, and tree mortality) and climatic impacts.

After 1860, tree recruitment became dominated by *Abies sachalinensis* and *Acer palmatum*, coupled with *F. mandshurica* and *C. japonicum*, while that of *Q. mongolica* ceased. All of these species can live over 250 years, except for *Abies sachalinensis* (Ishikawa and Ito 1989; Hiura et al. 1996; Sano 1997). Despite being relatively short lived, *Abies sachalinensis* is an important component of later successional forests in Hokkaido by being a gap opportunist species (Ishikawa and Ito 1989). The general pattern of oak replacement by later successional species has been reported in several dendroecology studies of old-growth forests in the eastern United States in which oak species recruited consistently from the early 1600s to about 1900, after which oak recruitment stopped (Mikan et al. 1994; Abrams et al. 1995, 1997; Cho and Boerner 1995). The lack of recent oak recruitment in forests of the eastern United States has been attributed, at least in part, to the suppression of fire and large increases in deer browsing pressure after 1900 (Abrams 1992, 1998). These factors have led to an increase in later successional tree species, such as *Acer rubrum* L., *Acer saccharum* Marsh., and *Fagus grandifolia* Ehrh., which out-compete the less shade-tolerant oak species (Lorimer et al. 1994; Abrams 1996, 1998). Given the current management of these United States forests, a major loss of oak dominance is predicted during the 21st century (Abrams 1992).

It appears that the replacement of oak dominance by later successional species is also taking place in the Hokkaido old-growth forest. However, there are several complicating factors that make it difficult to ascertain the exact successional status of this forest. First, the ecological requirements for oak regeneration in northern Japan are not well understood. Scientific opinion ranges from oak being shade tolerant, late successional to it being disturbance dependent and

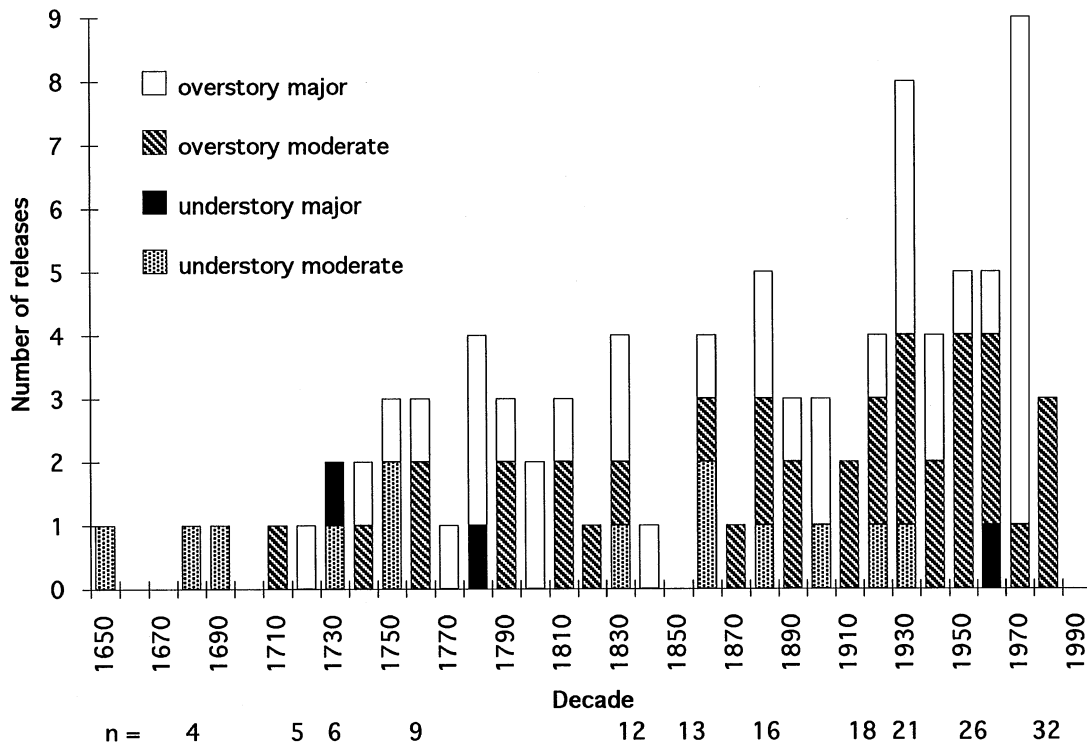
Fig. 3. Radial growth chronologies for five selected *Quercus mongolica* (Qumo) and an individual *Kalopanax pictus* (Kapi) in the old-growth forest. The broken line indicates the canopy accession date; asterisks are moderate release dates, and arrows are major release dates (criteria from Lorimer and Frelich 1989; Nowacki and Abrams 1997).



needing large canopy gaps or fire for successful recruitment (Koike 1988; Ishikawa and Ito 1989; Masaki et al. 1992; Yamamoto 1996; Sano and Ohtsuka 1998). Prior to 1840 in

this study, *Q. mongolica* demonstrated the dual ability to persist for long periods in a suppressed condition in the understory followed by canopy recruitment as well as for

Fig. 4. Decadal distribution of major and moderate overstory (over) and major and moderate understory (under) releases in 32 cores of the major species in the old-growth forest. (criteria from Lorimer and Frelich 1989; Nowacki and Abrams 1997).



gap capture early in its life. Recently, however, *Q. mongolica* has not recruited in the forest and intensive deer browsing has resulted in a scarcity of all forest floor vegetation, including sasa bamboo and tree species. Indeed, there has been almost no overstory recruitment in the forest since 1950, supporting the idea that intensive herbivory can cause large gaps in the age structure of the forest. Similarly, a lack of tree recruitment during the last 50 years because of intensive deer browsing was also reported for an old-growth white pine (*Pinus strobus* L.) – eastern hemlock (*Tsuga canadensis* (L.) Carr.) forest in the eastern United States (Abrams and Orwig 1996). If the present intensity of deer browsing on tree regeneration does not lessen in the future we anticipate very little opportunity for canopy recruitment for any species. Even *Abies sachalinensis*, considered a low preference browse species, will be eaten when Sika deer population densities are high (K. Terazawa, unpublished data).

In our study area, the pattern of oak recruitment follows the United States old-growth examples fairly closely in that oak regenerated consistently from the early 1600s until the 1860s, excluding the years from 1750 to 1820; Japanese settlement of the region started in the late 1800s. We found evidence of past fires in the forest in the form of soil charcoal and charring on logs and stumps (personal observation). It is possible that *Q. mongolica* dominated tree recruitment prior to the 1739 volcanic eruption due to periodic fire coupled with gap capture following small-scale disturbances (cf. Masaki et al. 1992; Abrams 1996; Sano and Ohtsuka 1998). Additional *Q. mongolica* recruitment occurred soon after the exclusionary years of 1750–1820 but ceased with the large increases in *Acer* and *Abies* after 1860. Evidence of fire was

also reported for an old-growth *Q. mongolica* – *Pinus koraiensis* (Sieb et Zucc.) forest in northeastern China (Barnes et al. 1992). These authors found a scarcity of oak and pine in the forest understory and suggested that in the absence of fire or severe windstorm successional trends would favor more shade tolerant *Tilia* and *Acer* species. This general conclusion seems applicable to our Hokkaido study area in that we predict that the stand will contain less *Q. mongolica* and much more *Acer* and *Abies*, barring the future impacts of deer browsing and large-scale disturbance, e.g., fire and volcanic eruptions. Therefore, the syndrome of declining oak dominance from fire exclusion and animal browsing may be an increasingly global phenomenon.

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