



Longevity of tall tree species in temperate forests of the northern Japanese Archipelago

Katsuhiro Osumi & Takashi Masaki

To cite this article: Katsuhiro Osumi & Takashi Masaki (2023) Longevity of tall tree species in temperate forests of the northern Japanese Archipelago, Journal of Forest Research, 28:5, 333-344, DOI: [10.1080/13416979.2023.2207261](https://doi.org/10.1080/13416979.2023.2207261)

To link to this article: <https://doi.org/10.1080/13416979.2023.2207261>



© 2023 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.



[View supplementary material](#)



Published online: 10 May 2023.



[Submit your article to this journal](#)



Article views: 4478



[View related articles](#)



[View Crossmark data](#)



Citing articles: 9 [View citing articles](#)

ORIGINAL ARTICLE

OPEN ACCESS



Longevity of tall tree species in temperate forests of the northern Japanese Archipelago

Katsuhiro Osumi^a and Takashi Masaki^b

^aTohoku Research Center, Forestry & Forest Products Research Institute, Morioka, Japan; ^bForestry & Forest Products Research Institute, Tsukuba, Japan

ABSTRACT

The longevity of tall tree species is an essential variable for understanding the dynamics and structure of forest ecosystems. However, it is difficult to accumulate sufficient observations on the mortality of mature individuals in natural populations to obtain a general longevity index. Therefore, we applied a statistical method based on annual ring-count data for approximately 1,700 large-diameter trees from 42 tree species to estimate an age limit for each species. The estimated attainable age varied widely among species, with the longest-living group (approximately 700 years) that included *Aesculus turbinata*, *Kalopanax septemlobus*, and *Quercus crispula* reaching seven times the lifespan of the shortest-living group that included *Populus suaveolens*, *Betula platyphylla*, and *Cornus controversa*. *Fagus crenata*, the dominant climax species in the region, had moderate longevity. Longevity was not necessarily linked to the regeneration strategy of pioneer species, which are highly shade intolerant during seedling establishment, as many long-lived species also exhibited pioneer-species-like regeneration. Although longevity varied greatly within some genera such as *Betula*, we detected a phylogenetic influence on longevity across a wide range of taxa. A comparison of longevity among common taxa in the northern Japanese Archipelago and North America showed that each taxon had similar longevity in both regions. These findings imply that the longevity of the tree species examined in this study is phylogenetically fixed, and that the longevity of each component species has similar effects on forest dynamics in forest communities in both regions, each of which contains many closely related species and has similar species compositions.

ARTICLE HISTORY

Received 15 January 2023
Accepted 23 April 2023

KEYWORDS

Annual ring data;
phylogenetic influence;
temperate forests in the
northern hemisphere; tree
lifespan; tree longevity

Introduction

Trees are characterized by long, perennial lifespans supported by robust xylem. Lifespan significantly regulates the life cycle of individual trees, as well as population dynamics (Harcombe 1987; Loehle 1988; di Filippo et al. 2015), and has a substantial influence on the niche formation of each tree species (Osumi 2005). Therefore, knowing the lifespan of each tree species greatly improves our understanding of the dynamics of forest communities, which have cycles longer than an observer's lifetime, and the forest structure shaped by these dynamics (Lorimer et al. 2001; Piovesan and Biondi 2021). In particular, the lifespans of natural populations of target tree species can be useful information for forest management. Understanding the relationship between the age of a managed population and the potential lifespan of the species will allow foresters to choose more appropriate management options.

Although longevity is a useful index for understanding forest community dynamics, it remains poorly understood (Lorimer et al. 2001), with records available mainly for exceptionally large, old landmark trees, or old trees studied for empirical data by foresters; much of this information is anecdotal or speculative rather than scientific (Piovesan and Biondi 2021). In recent years, records on the oldest long-

lived individual trees in various regions have been posted online; however, these are usually exceptional records of isolated trees, and are not useful as indicators to explain the dynamics of forest communities and tree populations. To date, only a few North American studies have presented scientific longevity data for various tree species constituting forest communities (Loehle 1988; Brown 1996; Pederson 2013; Hayek 2019; Liu et al. 2019). Except for a few tree species, such as *Fagus sylvatica* (di Filippo et al. 2012; Piovesan et al. 2019), *Picea abies* (Rötheli et al. 2012) and *Pinus montana* (Bigler 2016), no study has conducted statistical analyses of longevity based on large numbers of measurements.

There are two fundamental obstacles to comparing and analysing tree longevity data. The first obstacle is the limited opportunity to observe the death of old individual trees (Lorimer et al. 2001). Because species-rich temperate forests have been subjected to anthropogenic disturbance throughout human history (di Filippo et al. 2015), only small areas of old-growth forest remain. Dead and dying trees frequently have rotting or hollow trunks that make annual rings indistinguishable (Ranius et al. 2009). Thus, it remains difficult to collect sufficient data to analyse longevity in comparison to other life-history events such as regeneration.

The second obstacle is that it is difficult to define the life span of a tree species in the first place, and methods for estimating longevity has not yet been established. Trees grow over many years and are mainly iteroparous.

However, unlike animals and annual or biennial herbs, trees do not appear to have a fixed lifespan. Classically, the whole-tree carbon balance has been thought to break down as the tree ages, followed by a growth decline and death (Loehle 1988). However, it remains unclear whether this is a common process in actual forest communities. For example, two of the tallest and longest-lived tree species worldwide, *Eucalyptus regnans* and *Sequoia sempervirens*, continue to grow as they age, attaining huge sizes over time (Sillett et al. 2010). Some studies have reported that tree growth is size rather than age dependent (Mencuccini et al. 2005; Van and Sillett 2009). Trees are thought to have fewer intrinsic constraints on lifespan because they have developed systems to overcome aging, such as long-lived stem cells and cambium (Connor and Lanner 1990; Thomas 2013), telomere repair to avoid limiting the number of cell divisions (Flanary and Kletetschka 2005), structural plasticity through modularity (Borges 2009; Peñuelas and Munné-Bosch 2010; Thomas 2013; Burian et al. 2016), and dormancy to escape stressful periods (Peñuelas and Munné-Bosch 2010). Tree death in field populations occurs mainly due to extrinsic rather than intrinsic factors, e.g. weather damage, disease, and overthrow following trunk decay (Ranius et al. 2009; Piovesan and Biondi 2021). Thus, tree mortality appears to be a passive phenomenon that depends on the local environment and biota, making it difficult to determine the specific lifespan of each tree species.

Several arguments have been proposed to investigate the longevity of tree species by overcoming such difficulties (e.g. Loehle 1988; di Filippo et al. 2015; Katsuki 2019; Piovesan and Biondi 2021). Some such studies have noted that super-longevity beyond a millennium is almost exclusively limited to gymnosperms (Loehle 1988; Pederson 2013; Farjon 2018; Piovesan and Biondi 2021), and that long-lived individuals tend to be found in mid-latitude environments with low disturbance frequency (di Filippo et al. 2015), harsh environments such as oligotrophic sites (Schulman 1954; Piovesan et al. 2019), arid sites (Bigler and Veblen 2009), and areas with high elevation and low temperature (di Filippo et al. 2012; Bigler 2016). However, although differences in longevity among species in the same environment are an important factor in defining tree species niches and influencing the dynamics and structure of forest communities, few reports have examined differences in longevity among tree species.

The objective of this study was to provide tree-species longevity data to elucidate forest community dynamics and structure. We measured annual ring data from logs of major tall-tree species in temperate forests in the northern Japanese Archipelago, and applied uniform sampling criteria to estimate the longevity of each tree species statistically. Instead of using dead or aged trees, which are often difficult to find, we measured annual rings on approximately 1,700 thick logs from 42 species harvested from natural forests and accumulated in a lumber market to estimate the attainable age of each species. Then, we explored the longevity characteristics of Northern Hemisphere cool-temperate forest tree species, as Northern Hemisphere deciduous broadleaf forests are phylogenetically similar to those of the northern Japanese

Archipelago due to their common Arcto-Tertiary Geoflora origin (Chaney 1947; Axelrod 1983). We compared the longevity of each tree species from the Japanese Archipelago with those of phylogenetically related species in North America to investigate whether longevity is evolutionarily fixed in each lineage.

Materials and methods

Samples

Most logs sampled in this study were harvested in the Tohoku region in north-eastern Honshu Island, and some were sampled on Hokkaido Island (Iwate Federation of Forest Owners' Co-operative Association 1990). The logs were presumed to have been harvested from cool-temperate natural forests consisting mainly of deciduous broadleaf trees with some temperate coniferous trees. Dense forests with closed canopies are well developed in this region. In the Tohoku region and southern Hokkaido, *Fagus crenata* is overwhelmingly predominant, accompanied by *Quercus crispula*, *Acer pictum*, *Aesculus turbinata*, birches such as *Betula grossa* and *Betula maximowicziana*, and conifers such as *Cryptomeria japonica*, *Thuja standishii*, and *Pinus parviflora* (Miyawaki 1987, 1988). In northern central Hokkaido, beeches are absent and northern conifers such as *Abies sachalinensis* and *Picea jezoensis* are mixed with *Q. crispula*, *A. pictum*, and *Betula* spp. (Miyawaki 1988).

We sampled logs collected for auction at the Morioka Mokuzai-Ryutsuh Center, a timber market in Yahaba, Iwate Prefecture, Japan. Most of the sampled logs were thought to have been harvested from old-growth forests, because there has been very little afforestation in this region except for a few conifers, *C. japonica*, *Thujaopsis dolabrata*, and *Pinus densiflora*, plantations of which were established mainly in the 20th century (Forestry Agency 2021), implying that older individuals sampled in this study (>100 years) had grown naturally.

Old-growth forests in the Tohoku region are located almost exclusively in national forests, and in national and Hokkaido prefectural forests in the Hokkaido region. In 1958, an expansive afforestation program for national forests was launched through aggressive harvesting of old-growth forests and establishment of young, fast-growing coniferous plantations on the cleared sites. This program continued until 1998, when comprehensive national forestry reform led to a shift in management policy from timber supply to sustainable fulfilment of multifunctional roles (Forestry Agency 2013). The data used in this study were collected from 1995 to 1998, immediately before the expansive afforestation program was halted, and therefore represent the last of the period of old-growth forest logging. Previously, each forestry office would harvest its own trees in national forests and sell the timber at associated timber yards. However, beginning in 1992, the Fourth Improvement Program for National Forestry shifted to either stumpage sale or consignment sale of timber to commercial markets (Oura et al. 2003; Ajiki 2010). Against this background, for a short period in the mid-1990s, the Morioka Mokuzai-Ryutsuh Center was among the largest timber markets in Japan for cool-temperate natural forest hardwood timber, handling an annual volume of over 30,000 m³ (Iwate Federation of Forest Owners' Co-operative Association 1990).

Data collection

We recorded the numbers of annual rings on butt logs exhibited for auction at the timber market between June 1995 and March 1998. The sale lists, which were distributed prior to auctions held once or twice per month, showed the tree species, diameter, and length for each tree. Using this information, we sampled five of the largest butt logs per species at every auction. Logs with diameters smaller than the median for each species were excluded from sampling, such that a species for which fewer butt logs were sold may have been represented by fewer than five samples per month, and species with large numbers of entries, such as *F. crenata*, were represented by more than five samples per month. We excluded logs with hollow cores, decay, or annual rings that were unreadable due to roughness or stains on the cut end. The total number of butt logs sampled was 1,684, from 42 species (36 broadleaf, 6 conifer). There were few coniferous logs because this market focused on hardwood sales. Many temperate conifers representative of the Japanese Archipelago such as *Chamaecyparis obtusa*, *Chamaecyparis pisifera*, *Sciadopitys verticillata*, *Abies* spp., and *Tsuga* spp. were not represented, perhaps due to their limited distribution in the Tohoku region.

The size of a sampled butt log was measured as the diameter at breast height (DBH), where breast height (1.3 m) was estimated assuming that the log was cut at a height of 50 cm. The annual rings were counted by selecting one direction to approximate the average radius from the core and drawing a reference line. Because it is time-consuming to count several hundred years of annual rings outdoors, we did not apply the common method of measuring in four directions from the core but rather counted the annual rings in one direction as carefully as possible to minimize errors, in consideration of dense rings that were difficult to distinguish with a hand loupe and the risk of false rings. In this study, we refer to these annual ring counts as tree ages.

Data analyses

Longevity and maximum DBH were analysed under the assumption that age and diameter data were lognormally distributed. Because individual logs collected at the timber market were considered to have exceeded certain age and DBH thresholds, we also assumed that the age and DBH values minus these species-specific thresholds followed a lognormal distribution. The fitted lognormal distribution was shifted to the right by the estimated threshold value (Figures S2 and S3), and values within the top 2.5% of the distribution were used to represent the maximum value. We used the top 2.5% of values (referred to hereafter as the approximate upper limit) because they included information from data other than the actual maximum value, which can vary significantly due to chance.

The approximate upper limit was estimated in the framework of Bayesian statistics as follows. First, we assumed that $E_{1,s}$ is the observed value (age or DBH) of tree s minus a species-specific threshold value, which is drawn from a lognormal distribution with species-specific parameters.

$$E_{1,s} \sim \text{Lognormal}(m_{1,s}, \sigma_{1,s}^2) \quad (1)$$

The species-specific threshold $E_{2,s}$ was assumed to be derived from a uniform distribution with a range from 0 to the minimum of the observed x_s .

$$E_{2,s} \sim \text{Uniform}(0, \text{Minimum}(x_s)) \quad (2)$$

The observed value x_s was then assumed to be derived from a normal distribution with the sum of $E_{1,s}$ and $E_{2,s}$ as the mean.

$$E_s = E_{1,s} + E_{2,s} \quad (3)$$

$$x_s \sim \text{Normal}(E_s, \sigma_s^2) \quad (4)$$

In this model, the two parameters in Eq. (1) were assumed to follow a normal or lognormal distribution with a hyperparameter common to all tree species, stratified by species as follows.

$$m_{1,s} \sim \text{Normal}(\mu_m, \sigma_m^2) \quad (5)$$

$$\sigma_{1,s} \sim \text{Lognormal}(\mu_\sigma, \sigma_\sigma^2) \quad (6)$$

We fitted age or DBH observations to this hierarchical model and estimated the parameters for each species. The Markov chain Monte Carlo (MCMC) method was employed using R ver. 3.6.1 software (R Core Team 2019) with the run.jags (Denwood 2016) in the *runjags* package. To hasten and stabilize the convergence of the calculations, observed values of age (years) and DBH (cm) were divided by 100. The prior distribution of each parameter was assumed to be vague, with a normal distribution, mean of 0, and variance of 100 for distributions that can take both positive and negative values, and a gamma distribution with a shape parameter of 0.01 and scale parameter of 100 for distributions that can take only positive values. The initial values of $E_{2,s}$ were half of the minimum value of x_s . The initial values of parameters that can take both positive and negative values and parameters that can only take positive values were given random numbers generated by Normal(0, 1) and Lognormal(0, 1) respectively. In MCMC, 1,000 adaptations and 5,000 operational tests were followed by 50,000 iterations, sampling every 50 iterations (where the total number of samples was 1,000). We set three chains and obtained a total of 3,000 samplings from the posterior distribution. The chains showed good convergence for all parameters of all species, and the Gelman–Rubin convergence diagnostic was <1.064.

The means of age (years) and DBH (cm) for each species were derived from the MCMC samples of parameters using the following formula.

$$\text{Mean}_s = \left(E_{2,s} + e^{(m_{1,s} + \sigma_{1,s}^2/2)} \right) \times 100 \quad (7)$$

In the expression for the cumulative density function of the lognormal distribution, we determined the value of z_s that most closely approached the value of the cumulative density function $F(z_s)$ of 0.975, $z_{0.975,s}$, by increasing the value of z_s from 0 to 10 in increments of 0.00001.

$$F(z_s) = \frac{1}{2} \text{erfc} \left(-\frac{\ln(z_s) - m_{1,s}}{\sigma_{1,s} \sqrt{2}} \right) \quad (8)$$

This value was then added to the threshold value to be the upper limit of the 95% interval of the distribution of age or DBH, i.e. the sample of approximate upper limit values (defined as U95_s).

$$U95_s = (z_{0.975,s} + E_{2,s}) \times 100 \quad (9)$$

Next, DBH was regressed on age to obtain a benchmark for the average growth after the threshold was exceeded. Letting $a_{0,s}$ and $a_{1,s}$ be the intercept and slope of the regression equation for tree species s , respectively, we performed the following calculations.

$$\mu_{dbh,s} = a_{0,s} + a_{1,s}age \quad (10)$$

$$dbh_s \sim Normal(\mu_{dbh,s}, \sigma_{dbh,s}^2) \quad (11)$$

To avoid outlier effects on the parametric estimation of the regression equation for trees with small sample sizes, both $a_{0,s}$ and $a_{1,s}$ were stratified by tree species and assumed to follow a normal distribution with the same mean and variance as the hyperparameters. We used the method described above for estimation by MCMC, establishing a vague prior distribution and giving initial values. The chains appeared to converge well for all parameters of all species. The Gelman–Rubin convergence diagnostic was <1.004.

The averages of the MCMC samples for Mean_s, U95_s, and $a_{1,s}$ obtained in the above analysis were used as estimates of each parameter to test the phylogenetic constraints. First, the longest sequences for each species were selected from the rbcL data in the DNA barcode database of Japanese trees (Setsuko et al. 2023), and then aligned using the ClustalW program (Thompson et al. 1994). Only sequences (570 bp) that were aligned throughout the data for all 42 species were used to estimate a mutation model using the PAUP* program (Swofford 2003), and a phylogenetic tree was estimated using the MrBayes software (Ronquist et al. 2012). This phylogenetic tree was used to calculate Pagel's λ using the phylosig function included in the *phytools* package in R (Revell 2012).

We compared the set of approximate upper limit ages for each tree species in this study to an exhaustive list of longevity data for North American tree species. As described above, North America has temperate forests with floras similar to those of the Japanese Archipelago, and the two regions share many tree genera. North America also retains some old-growth forests, such that more longevity data have been collected from old trees (Loehle 1988; Brown 1996; Pederson 2013; Hayek 2019). Unlike the data collected in the present study, these North American tree longevity data have not undergone consistent sampling and statistical procedures. However, we consider them to be reasonable values based on the observations of previous forest-management and ecosystem researchers, rather than a collection of extreme values or anecdotal or speculative information. Comparisons of longevity information for the two regions were made among species of at least the same subgenera or section whenever possible.

Results

Age and DBH of samples

The maximum ages among broadleaf and conifer tree samples were 772 years (*Q. crispula*) and 604 years (*T. standishii*) (Figure S1), respectively. The maximum DBH values for broadleaf and conifer tree samples were 144 cm (*Q. crispula*) and 125 cm (*T. standishii*), respectively. These values were associated with different *Q. crispula* and *T. standishii* individuals.

Age information for all tree species is provided in Table 1. The approximate upper limit age of each species (U95 in “Age distribution parameters”) included *Kalopanax septemlobus*, *A. turbinata*, *T. standishii*, *Q. crispula*, *Taxus cuspidata*, and *Cercidiphyllum japonicum*, which were generally 600 years old or older, to the youngest group, which included *Cornus kousa* subsp. *kousa*, *Fraxinus lanuginosa*, *Hovenia dulcis*, *Juglans mandshurica* var. *sachalinensis*, *Pterocarya rhoifolia*, *Magnolia kobus*, *Cerasus sargentii*, *Alnus japonica*, *Betula platyphylla*, *Cornus controversa*, and *Populus suaveolens*, which were only 100–200 years old. *Fagus crenata*, the most dominant tree in cool-temperate old-growth forests of the Japanese Archipelago, was 401.4 years old at the approximate upper age limit, which was considered a moderate value, in a similar range to *Ulmus laciniata*, *A. pictum*, *B. maximowicziana*, and *Zelkova serrata*. Across all species, the approximate upper limit age was roughly 1.8 times the mean age.

DBH information for each tree species is also shown in Table 1. The approximate upper limit of DBH for each species was approximately 120 cm for the largest group, which included *Q. crispula*, *Ulmus davidiana*, *A. turbinata*, *K. septemlobus*, and *C. japonicum*. The smallest group included *F. lanuginosa*, *A. japonica*, *T. cuspidata*, *B. platyphylla*, *Maackia amurensis*, *C. controversa*, and *C. kousa* subsp. *kousa*, which reached only 50–60 cm. *Fagus crenata* had an approximate upper DBH limit of 102.7 cm, and thus belonged to the large-diameter group, which included *T. standishii*, *Z. serrata*, *Celtis jessoensis*, *C. japonica*, and *P. parviflora*. The approximate upper DBH limit was roughly 1.4 times the mean DBH of all tree species.

The approximate upper age and DBH limits had a positive relationship (regression coefficient, 0.082; $P < 0.001$; $r^2 = 0.49$), indicating that long-lived species tended to have larger diameters (Figure 1). By contrast, a few species had very low DBH values for their age, such as *T. cuspidata*, *Betula schmidtii*, *Ostrya japonica*, and *C. kousa* subsp. *kousa*.

However, the intraspecific relationship between age and DBH for individual trees within each species was less clear than the interspecific relationship between age and DBH. For most species, the regression coefficients for age and DBH per individual were significant ($P < 0.05$) but low (0.023–0.066 cm · year⁻¹), and the slopes of the regression lines were nearly horizontal after the species-specific threshold was exceeded (Figure S1). Among the 42 tree species, *U. davidiana*, *A. turbinata*, and *T. standishii* had relatively large slopes (>0.06). These slopes had no significant relationship to the approximate upper age or DBH limit of each species (Figure 2).

Table 1. Summary of estimates of life span and thickness of tall trees in the northern Japanese Archipelago.

Species	Number of samples	Abbr.	Age distribution parameters (years)					dbh distribution parameters (cm)					Slope of dbh-age regression (cm yr ⁻¹)			
			Threshold		Mean		Maximum observed value	Threshold		Mean		Maximum observed value				
			Mean	SD	Mean	SD		Mean	SD	Mean	SD					
<i>Magnolia obovata</i>	52	Mg.o	31.3	14.2	160.6	7.4	289.6	22.7	26.4	5.3	59.4	1.5	81.4	3.8	0.043	0.002
<i>Magnolia kobus</i>	6	Mg.k	11.6	8.7	82.3	13.7	159.7	34.9	12.8	6.9	52.6	5.1	81.8	10.0	0.045	0.009
<i>Fraxinus mandshurica</i>	44	Fr.m	49.6	23.7	274.4	13.6	489.6	39.4	33.4	5.8	69.2	1.7	93.7	4.5	0.044	0.001
<i>Fraxinus lanuginosa</i>	21	Fr.l	16.0	9.9	95.7	7.6	179.1	21.7	10.9	5.3	42.5	2.3	65.0	5.5	0.043	0.010
<i>Cornus kousa</i> subsp. <i>kousa</i>	9	Crn.k	32.3	18.5	154.6	17.1	280.5	45.8	7.0	4.4	29.6	2.6	44.3	5.5	0.046	0.008
<i>Cornus controversa</i> var. <i>controversa</i>	52	Crn.c	26.0	7.3	65.7	2.6	104.2	8.4	18.4	4.1	35.4	0.9	45.5	2.5	0.046	0.004
<i>Kalopanax septemlobus</i>	69	Kls	37.2	23.8	378.2	16.2	706.1	48.8	43.0	6.4	84.9	1.6	113.8	4.3	0.032	0.003
<i>Cercidiphyllum japonicum</i>	60	Crc.j	62.9	28.3	347.5	14.2	620.4	43.9	48.3	5.8	82.8	1.4	106.1	3.8	0.038	0.000
<i>Tilia japonica</i>	38	Til.j	14.0	10.7	191.0	13.3	398.7	41.9	28.1	6.0	62.1	1.9	87.1	4.9	0.050	0.001
<i>Phellodendron amurense</i> var. <i>amurense</i>	52	Ph.a	34.7	15.9	167.6	7.6	302.4	23.0	27.1	4.9	52.6	1.2	69.1	3.3	0.048	0.000
<i>Aesculus turbinata</i>	64	Aet	33.3	21.7	371.0	17.6	722.1	53.5	30.8	7.2	86.1	2.2	126.0	5.8	0.066	0.000
<i>Acer pictum</i>	51	Ac.p	68.1	21.4	239.7	9.3	399.9	27.2	32.5	5.6	67.4	1.6	90.8	4.1	0.036	0.014
<i>Populus suaveolens</i>	20	Pps	23.7	8.6	63.7	4.2	101.5	13.0	17.2	5.8	44.8	2.1	63.2	5.1	0.038	0.024
<i>Maackia amurensis</i>	32	Mc.a	16.8	10.2	100.2	8.8	185.6	24.9	9.4	4.6	35.6	2.1	52.8	4.8	0.034	0.044
<i>Ulmus laciniata</i>	34	Ull	68.4	24.9	247.9	13.0	433.7	39.1	26.9	6.2	60.0	1.9	82.8	4.9	0.050	0.001
<i>Ulmus davidiana</i> var. <i>japonica</i>	11	Uld	85.9	40.3	290.5	26.2	512.6	76.1	38.3	10.2	87.9	4.7	124.2	10.5	0.060	0.001
<i>Zelkova serrata</i>	40	Zls	62.3	22.4	231.3	10.2	389.9	30.5	23.1	7.3	69.3	2.3	102.7	5.9	0.045	0.005
<i>Celtis jessoensis</i>	6	Clt.j	45.8	27.1	210.9	28.5	388.2	74.1	34.1	9.7	72.2	5.0	99.2	10.2	0.044	0.009
<i>Hovenia dulcis</i>	12	Hvd	24.7	13.1	94.0	8.8	164.0	25.1	15.7	6.5	43.8	2.7	62.4	6.2	0.041	0.017
<i>Padus ssiroi</i>	47	Pds	35.5	15.3	165.8	8.1	298.3	24.7	19.5	5.0	45.1	1.3	61.7	3.4	0.045	0.001
<i>Cerasus sargentii</i> var. <i>sargentii</i>	11	Crs.s	32.6	12.7	79.1	6.5	124.0	19.7	16.3	6.5	45.1	2.9	64.3	6.5	0.043	0.012
<i>Aria alnifolia</i>	8	Ara	79.9	30.4	201.9	18.3	326.7	52.9	19.7	7.1	47.7	3.2	66.2	7.0	0.035	0.030
<i>Betula schmidtii</i>	38	Bes	53.5	29.2	323.8	18.7	613.7	56.1	19.3	5.5	48.9	1.6	68.7	4.1	0.050	0.000
<i>Betula maximowicziana</i>	54	Be.m	24.6	15.5	216.2	11.3	418.7	34.8	24.5	6.9	68.2	1.8	98.1	4.9	0.050	0.000
<i>Betula grossa</i>	50	Beg	57.0	25.8	278.4	14.0	525.5	44.5	27.5	5.9	61.9	1.5	85.0	4.2	0.023	0.042
<i>Betula platyphylla</i> var. <i>japonica</i>	47	Bep	24.8	8.1	71.0	3.2	115.3	9.9	21.3	4.2	40.1	1.0	51.6	2.7	0.039	0.019
<i>Betula ermanii</i>	46	Bee	53.1	21.4	214.1	10.3	386.1	31.9	25.3	6.1	62.0	1.7	86.9	4.5	0.047	0.001
<i>Alnus japonica</i>	11	Al.j	14.5	7.9	76.5	4.3	139.9	13.3	19.8	4.8	42.4	1.2	57.0	3.2	0.046	0.004
<i>Ostrya japonica</i>	49	Os.j	27.1	19.0	289.3	17.2	599.0	57.0	24.1	5.4	54.3	1.4	74.4	3.8	0.027	0.003
<i>Carpinus laxiflora</i>	29	Crp.l	15.6	10.7	141.8	10.2	279.9	30.6	16.3	5.7	47.1	1.9	68.0	4.8	0.032	0.041
<i>Pterocarya rhoifolia</i>	64	Ptr	10.4	6.8	88.3	4.1	167.2	13.2	18.6	4.9	48.4	1.2	68.3	3.3	0.046	0.003
<i>Juglans mandshurica</i> var. <i>sachalinensis</i>	45	Jg.m	27.9	10.1	90.7	4.1	152.5	12.8	22.5	5.3	51.2	1.4	69.6	3.7	0.050	0.001
<i>Fagus crenata</i>	62	Fgc	69.1	20.0	233.1	8.7	401.4	27.0	29.0	5.7	73.0	1.7	102.7	4.6	0.033	0.014
<i>Quercus serrata</i>	26	Qrs	13.2	10.3	215.0	18.0	452.6	55.8	37.0	6.1	66.8	1.9	86.4	4.7	0.040	0.002
<i>Quercus crispula</i> var. <i>crispula</i>	65	Qrc	56.0	28.3	367.9	16.4	690.2	50.0	37.2	6.1	88.7	2.0	124.6	5.4	0.044	0.000
<i>Castanea crenata</i>	54	Cst.c	27.3	15.3	179.4	8.9	344.3	28.0	28.8	6.2	68.0	1.7	94.6	4.5	0.045	0.001
<i>Thuopsis dolabrata</i> var. <i>hondae</i>	53	Tjo.d	75.2	25.6	298.0	11.8	504.5	35.5	33.3	6.1	68.6	1.6	94.8	4.5	0.029	0.042
<i>Thuja standishii</i>	64	Tja.s	78.3	26.1	369.4	13.8	631.4	40.5	32.6	6.4	73.9	1.7	103.6	4.5	0.062	0.000
<i>Cryptomeria japonica</i>	43	Cry.j	78.7	23.9	251.6	11.0	427.4	32.6	33.7	6.3	71.4	1.9	98.3	5.0	0.032	0.024
<i>Taxus cuspidata</i>	32	Txs.c	99.4	33.5	352.3	18.9	614.8	55.9	13.1	5.0	40.2	1.6	58.1	4.1	0.025	0.027
<i>Pinus parviflora</i> var. <i>pentaphylla</i>	56	Pnp	29.0	18.6	314.6	14.4	570.2	41.9	28.4	5.9	67.7	1.6	93.8	4.3	0.039	0.001
<i>Pinus densiflora</i>	42	Pnd	53.8	17.6	172.4	8.1	298.7	24.5	29.5	7.1	71.9	2.1	101.6	5.4	0.047	0.002

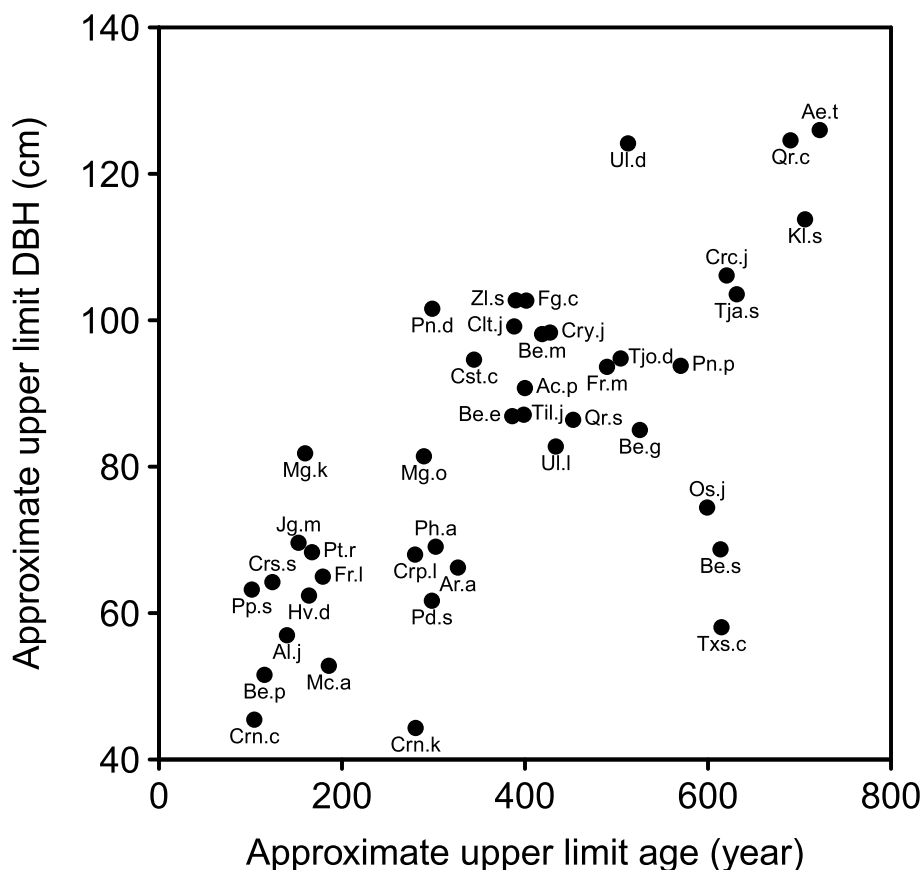


Figure 1. Relationship between approximate upper age and diameter-at-breast-height (DBH) limits.

Relationships among longevity, size, and phylogeny

An estimated phylogenetic tree for the 42 species studied, together with information on the approximate upper age and DBH limits and the slopes of the DBH – age regression (a_1) are shown in Figure 3. The phylogenetic effects on approximate upper age limits were analysed using Pagel's λ (Table 2); significant effects were detected when all tree species were included, when 36 angiosperm tree species were included ("a" in Figure 3), and when 28 Rosales group species from *Tilia japonica* to *Castanea crenata* were included ("b" in Figure 3). By contrast, no phylogenetic effects were detected for the clade consisting of 14 tree species from Betulaceae, Juglandaceae and Fagaceae ("c" in Figure 3), as well as for eight tree species from Betulaceae alone ("d" in Figure 3). Among clades, relatively large approximate upper limit ages were observed for Ulmaceae, Fagaceae, and conifers, whereas smaller approximate upper limit ages were observed for Magnoliaceae, Cornaceae, Rosaceae, and Juglandaceae.

The clade including Tiliaceae to Sapindaceae and the clade consisting of Betulaceae involved species with wide ranges of approximate upper limit ages. Within the systematic range of species tested in this study, approximate upper limit ages for species not included in the cohesive clade varied widely from high (e.g. *K. septemlobus* and *C. japonicum*) to low (e.g. *P. suaveolens* and *M. amurensis*). The approximate upper DBH limit showed the same trend, except that the Magnolia clade showed moderate values. Several clades showed a consistent trend in regression slope values, including low values for the *Ostrya* and *Carpinus* clades, moderate values for the *Fraxinus* and Cornaceae clades, higher values for the Ulmaceae clade, and high values for the

Juglandaceae clade, and variation was observed within each of the *Betula*, Fagaceae, and conifer clades.

Comparison of longevity among associated tree species in the Japanese Archipelago and North America

The regression coefficient for the longevity dataset between the two regions, which contained 21 genera and 25 pairs, was 0.70 ($P < 0.001$; $R = 0.47$; Figure 4). This result indicated that the longevity rankings among species were similar in the two regions. The upper limit ages of tree species in the Japanese Archipelago were on average 1.43 times those of closely related species in North America.

Discussion

Longevity and DBH

The longevity of the studied tree species from temperate forests of the northern Japanese Archipelago varied widely among species (Figure 1). Among broadleaf trees in old-growth forest, *F. crenata*, which was overwhelmingly dominant, and common trees such as *A. pictus*, *T. japonica*, *U. laciniata*, and *Phellodendron amurense*, had a mean age of approximately 200 years and an approximate upper limit age of about 400 years. However, some coexisting trees with high frequency in beech forests tended to live longer, i.e. *Q. crispula*, *A. turbinata*, and *K. septemlobus*, which have a mean age of >350 years and upper limit age of approximately 700 years, which is >1.5 times longer than that of *F. crenata*.

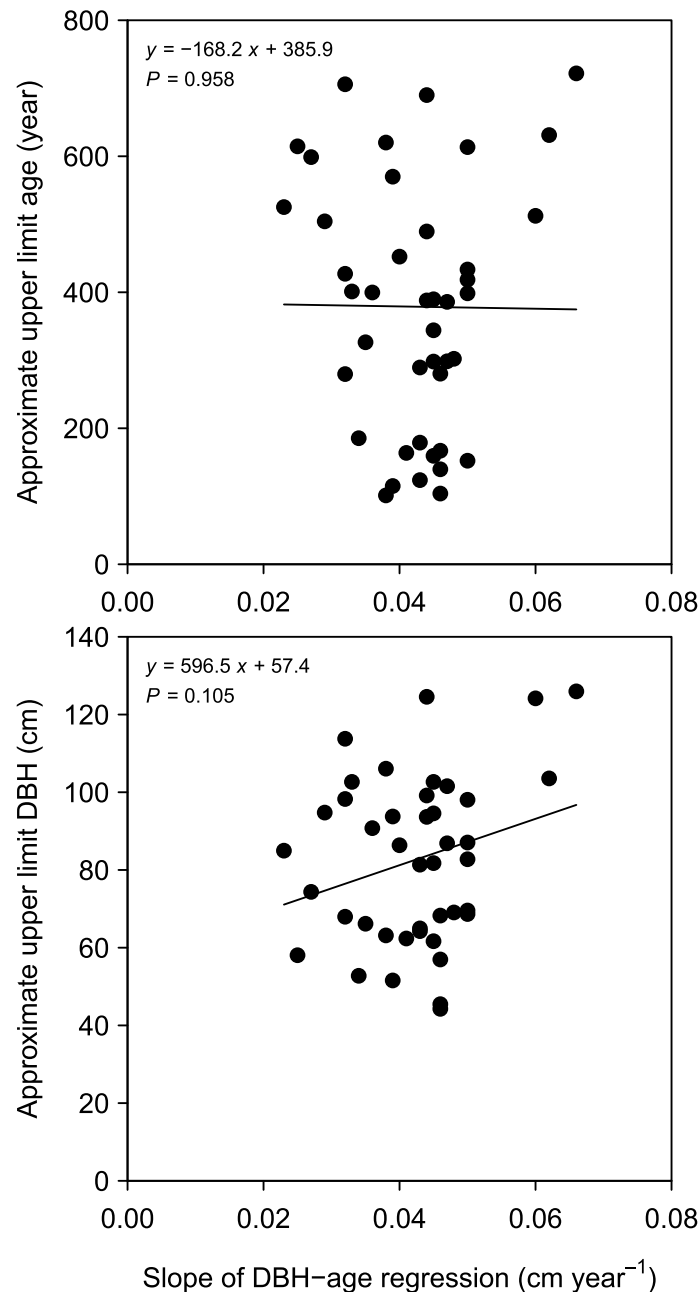


Figure 2. Comparison of slopes of the regression of diameter-at-breast-height (DBH) on age for individual trees of each species, with indices of longevity and thickness for each species.

The longevity of broadleaf trees in old-growth temperate deciduous forests of the Northern Hemisphere has been estimated at approximately 300 years (di Filippo et al. 2015) and seldom exceeds 500 years (Pederson 2013; Hayek 2019). Similar longevity has also been estimated for tropical forests (Martínez-Ramos and Alvarez-Buylla 1998; Worbes and Johannes Junk 1999; Wirth et al. 2009). The ages of the large-diameter hardwoods from the northern Japanese Archipelago examined in this study (Figure 1) were comparable to or longer than those of hardwoods reported elsewhere in the Northern Hemisphere. This finding indicates that our dataset was collected from sufficiently well-aged samples and that the data are likely reliable and representative of the longevity of broadleaf trees in northern Japan.

Typical large, intensive disturbance-dependent species such as *P. suaveolens*, *B. platyphylla*, *A. japonica*, and *P. rhoifolia* had mean longevity values of <100 years and approximate upper limit ages of <200 years. By contrast, some other large and intensive disturbance-dependent tree

species such as *B. schmidtii*, *B. grossa*, *C. japonicum*, and *U. davidiana* were even longer lived than the dominant *F. crenata*. Among these, *C. japonicum* exhibits vigorous and constant sprouting in addition to its high mean stem longevity of 347.5 years and approximate upper limit age of 620.4 years. Because *C. japonicum* replaces aged trunks with young sprouts (Kubo et al. 2005; Osumi 2006), its longevity as a genet is thought to be extremely long for a broadleaf tree species. Almost all *Betula* species are thought to act as pioneer species (Ashburner et al. 2013), but the longevity of the *Betula* species sampled in this study varied from very short for *B. platyphylla* to medium (similar to *F. crenata*) for *Betula ermanii* and *B. maximowicziana*, to the longest among all studied tree species for *B. grossa* and *B. schmidtii*. This finding indicates that pioneer species are not necessarily short-lived (Gutsell and Johnson 2002; Lienard et al. 2015; Piovesan and Biondi 2021).

Among conifers, the shortest longevity was observed in *P. densiflora*, with a mean of 172.4 years and an

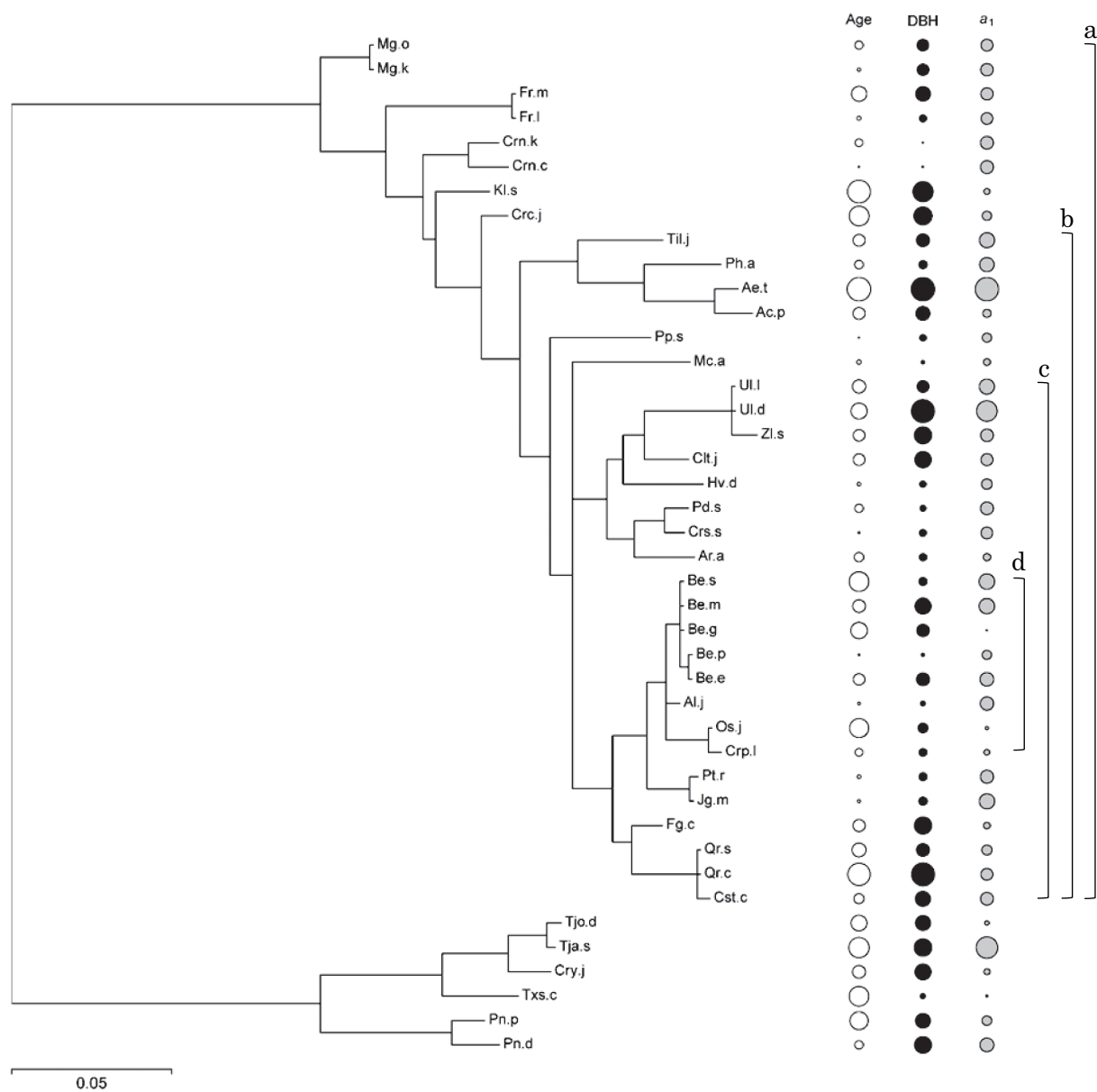


Figure 3. Phylogenetic tree for the 42 species studied, including approximate upper-age (white circles) and diameter-at-breast-height (DBH) (black circles) limits, and the slopes of DBH – age regression (a_1 ; grey circles). Circle sizes indicate the relative magnitudes of values among the species studied. Species name abbreviations are listed in Table 1.

Table 2. Phylogenetic influences on the longevity and thickness of tall trees in the northern Japanese Archipelago.

Clade	U95 of age		U95 of DBH		Slope of dbh-age regression		No. of species
	Pagel's λ	P	Pagel's λ	P	Pagel's λ	P	
All species	0.779	<0.001	0.854	<0.001	0.859	<0.001	42
Angiosperms	0.774	<0.001	0.850	<0.001	0.890	<0.001	36
Rosids	0.801	<0.001	0.845	<0.001	0.891	<0.001	28
Betulaceae, Fagaceae, Juglandaceae	0.000	1.000	0.328	0.201	0.000	1.000	14
Betulaceae	0.000	1.000	0.000	1.000	0.000	1.000	8
Gymnosperm	0.000	1.000	0.000	1.000	0.000	1.000	6

approximate upper limit age of 298.7 years, whereas the longest longevity was observed in *T. standishii* and *T. cuspidata*, with means of approximately 350 years and approximate upper limit ages of >600 years. Conifers are not generally short-lived, and often have comparable longevity to that of non-short-lived broadleaf trees. Outside the northern Japanese Archipelago, many conifer species exceed the longevity of broadleaf trees (Farjon 2018; Piovesan and Biondi 2021). Notably, mid-latitude temperate conifers sometimes live for more than 1,000 years (see

Thuja in Figure 4; Pederson 2013; Farjon 2018; Piovesan and Biondi 2021). A few millennium conifers have also been recorded in the Japanese Archipelago. For instance, *C. japonica*, for which we estimated an upper limit age of 427.4 years, has been reported to exceed 1,000 years of age on the remote island of Yakushima (Suzuki and Tsukahara 1987).

The conifers sampled in this study did not appear to have lived that long, likely due to constraints from past anthropogenic disturbances such as logging. Temperate conifers in

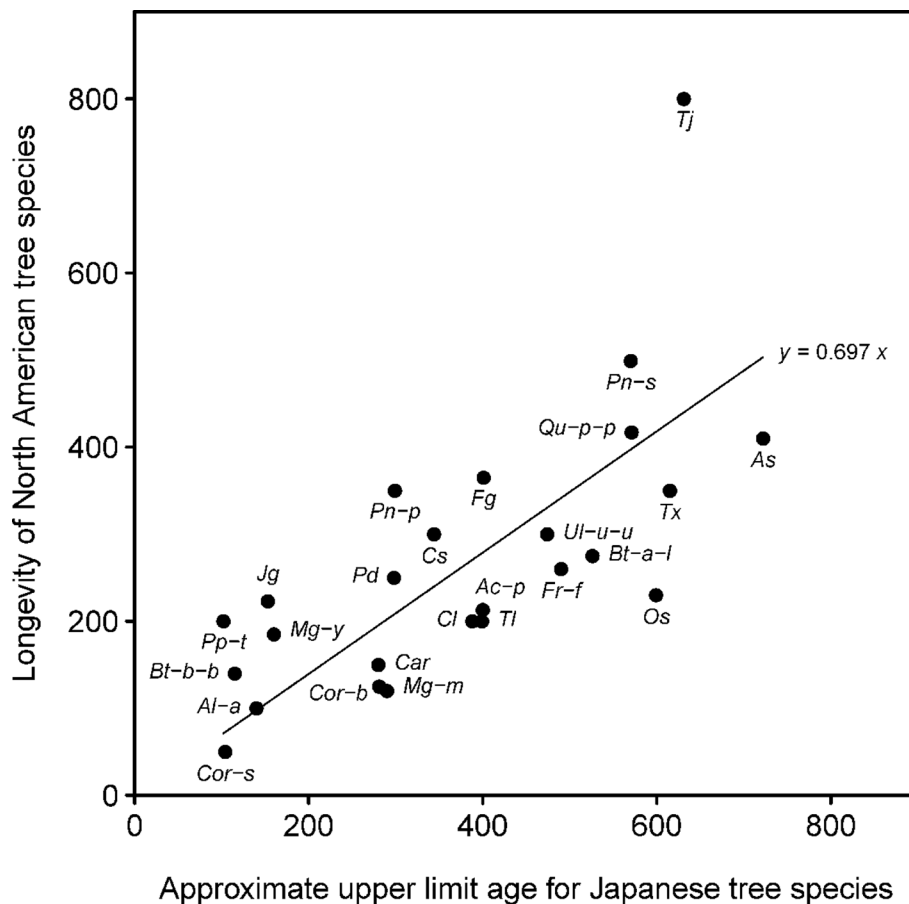


Figure 4. Comparison of longevity between common phylogenetic groups in North America and the northern Japanese Archipelago. Longevity information for North American tree species were retrieved from Loehle (Loehle 1988), Crow (1990), Pederson (Pederson 2013), and Hayek (Hayek 2019). Abbreviations for each taxon (genus-subtaxon) are as follows: Ac-p; *Acer* sect. *Platanioidea*, As; *Aesculus*, Al-a; *Alnus* subgen. *Alnus*, Bt-b-b; *Betula* subgen. *Betula* sect. *Betula*, Bt-a-l; *Betula* subgen. *Aspera* sect. *Lentae*, Car; *Carpinus*, Cs; *Castanea*, Cl; *Celtis*, Cor-b; *Cornus* subgen. *Benthamidia*, Cor-s; *Cornus* subgen. *Swida*, Fg; *Fagus*, Fr-f; *Fraxinus* sect. *Fraxinus*, Jg; *Juglans*, Mg-m; *Magnolia* subgen. *Magnolia*, Mg-y; *Magnolia* subgen. *Yulania*, Os; *Ostrya*, Pd; *Padus*, Pn-s; *Pinus* sect. *Strobus*, Pn-p; *Pinus* sect. *Pinus*, Pp-t; *Populus* sect. *Tacamahaca*, Qu-p-p; *Quercus* subgen. *Prinus* sect. *Prinus*, Tx; *Taxus*, Tj; *Thuja*, Tl; *Tilia*, Ul-u-u; *Ulmus* subgen. *Ulmus*.

Cupressaceae such as *C. japonica*, *C. obtusa*, and *T. dolabrata* var. *hondae* have long been regarded as the finest timbers for use in Japanese Archipelago architecture, and have been repeatedly and selectively, but exhaustively, harvested since around the 3rd century (Totman 1989). Notably, in the 17th century, a construction boom associated with the production of castles and large temples almost completely depleted the prime temperate coniferous old-growth forests of the Japanese Archipelago, exhausting the timber supply (Tokoro 1980).

Therefore, it is likely that most of the temperate coniferous old-growth forests in the Japanese Archipelago represent secondary forests, such that their constituent individuals have not yet reached their potential longevity, although some 300 years have passed since last intensive logging. Species that are typically abundant in managed woodlands, such as *Quercus serrata*, *C. crenata*, and *C. sargentii* (Miyawaki 1987, 1988) may also have had their longevity constrained because these woodlands were repeatedly harvested at short intervals of a few decades until the middle of the 20th century, which presumably suppressed the longevity of these trees.

Many tree species in the northern Japanese Archipelago have approximate upper DBH limits of >1 m (Figure 1). These trees are sufficiently thick as mature individuals, given that in old-growth forests dominated by *F. crenata* in a typical cool-temperate forest of the Japanese Archipelago, the minimum threshold diameter of canopy

trees is approximately 30 cm (e.g. Nakashizuka and Numata 1982; Hiruma and Hukusima 2001). The approximate upper DBH limits varied widely among species, indicating that there is a species-specific upper limit to the size of mature individuals, just as there is for longevity. As Farjon (2018) noted for conifers, larger trunk diameters may be an evolutionary response to overcome decay and achieve high longevity, because the primary mortality factor for tall tree species in stable environments is trunk decomposition. Although, long-lived tree species such as *A. turbinata* and *Q. crispula* are generally large in size, some tree species such as *B. schmidtii* and *T. cuspidata* remain small despite their high longevity. These trees may have different life-history strategies from most tree species; for example, mature trees retain a degree of shade tolerance to live as sub-canopy trees, or they grow slowly, mitigating severe vegetative competition by selecting sites within forest canopy that are less closed. Many tree species showed a positive relationship between individual diameter and longevity within a species, but the slopes of the regression lines were nearly flat (Figure S1), implying that longevity is not clearly associated with larger diameter at the individual level.

Phylogenetic influence on tree longevity

Significant relationships between upper limit age and phylogeny were detected among the entire dataset of 42 tree

species examined in this study, as well as for the large clade Rosaceae (Figure 3). Longevity relationships among phylogenies were also similar between the Japanese Archipelago and North America, implying that longevity is to some extent a fixed property in phylogeny (Figure 4). For example, the longevity of birch species varies widely within the genus, and phylogenetic effects appear limited. However, when the genus was subdivided into subgenera, species of subgenus *Betula* were found to be extremely short-lived in the northern Japanese Archipelago (*B. platyphylla*) as well as in North America (*Betula papyrifera* and *Betula populifolia*) (Loehle 1988), whereas species of subgenera *Aspera* (*B. grossa* and *B. schmidtii* in the Japanese Archipelago and *Betula alleghaniensis* and *Betula lenta* in North America) and *Acuminatae* (*B. maximowicziana*) were more than twice as long-lived as species of subgenus *Betula*, implying phylogenetic effects within the genus *Betula*.

Deciduous broadleaf trees such as the genera *Fagus*, *Quercus*, *Acer*, *Ulmus*, *Betula*, and *Juglans*, which are common to cool-temperate forests in the Japanese Archipelago and North America, are widely distributed in the Northern Hemisphere despite geographic fragmentation. These taxa are considered remnants of ancient flora that once flourished at high latitudes during the Tertiary (Arcto-Tertiary Geoflora concept; Chaney 1947; Axelrod 1983). Later, Wolfe (1997) revised the concept into the Boreotropical hypothesis, in which pan-Northern Hemisphere flora emerged in several locations in the mid-latitudes of the Northern Hemisphere during the Eocene. The commonality of tree floras in remote regions of the Northern Hemisphere, including the northern Japanese Archipelago and North America, is the result of this long geo-historical process.

The isolation of closely related phylogenetic groups between the Japanese Archipelago and North America would have continued over a long geo-historical period. For tree species to expand their distribution and continuity between the two regions, it would have been necessary to bypass either the Bering or North Atlantic land bridge. However, these land bridges are under the influence of subarctic climates, even today during an interglacial warm period, and it is estimated that during the more than 2 million years since the Quaternary, global temperatures were almost never higher than they are today (Petit et al. 1999; Lisiecki and Raymo 2005). At present, the only taxa among the studied tree species that are distributed across these land bridges under subarctic climates are section *Asperae* (genus *Betula*), section *Takamahaca* (genus *Populus*), and subgenus *Alnus* (genus *Alnus*), whereas the other taxa are distributed at lower latitudes, with northern limits below this region. Thus, it is likely that these land bridges did not function for tree species whose present distribution remains at lower latitudes, at least since the Quaternary, when glacial cooling became pronounced. Thus, isolation between phylogenetically closely related species between North America and the northern Japanese Archipelago is estimated to have persisted for approximately the last 2 million years.

Despite this presumed long-term geographic isolation, the longevity of each phylogenetic group and the ordinal relationships among them were similar between the two regions, implying that the potential longevity exhibited by each phylogenetic

group may have been inherited over a long period. Given this supposition, it is reasonable to expect that the combination of diverse longevity values for component phylogenetic groups has continued to have similar effects on the dynamics of both temperate forest regions originating from the Arcto-Tertiary Geoflora, which are now isolated in East Asia and North America.

How diverse is the lifespan of tree species? Is that diversity species-specific or plastic? The answers to these questions are important to understanding the niches of tree species whose life forms are characterized by perennality, as well as the dynamics of forest communities. In addition to the cool-temperate East Asian temperate forest examined in this study, it will be both necessary and interesting to clarify longevity diversity in other biomes with different phylogenetic group compositions in a future study.

Acknowledgements

The authors are grateful to Iwate Federation of Forest Owners' Cooperative Association for providing us with the opportunity to collect data on the timbers and the relevant information, to Dr. S. Sakurai for advising us of the possibility of obtaining tree longevity information from logs in lumberyards, to Dr. S. Setsuko for the support relating to phylogenetic analyses, and to Mr. K. Takahashi and Mrs. M. Osumi for assistance in collecting data at the lumberyard.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the JSPS KAKENHI under Grants 21H04946

ORCID

Katsuhiro Osumi  <http://orcid.org/0000-0002-6911-9881>
Takashi Masaki  <http://orcid.org/0000-0001-8616-6068>

Geolocation information

Northern part of Honshu Island and Southern part of Hokkaido Island of Japan

References

- Ajiki K. 2010. Changes of national forest management after the 1980's and regional characteristics. Bulletin of the Faculty of Humanities, Law and Economics, Mie University. 27:1–21.
- Ashburner K, McAllister HA, Hague J, Brown A, Williams P 2013. The genus *betula*: a taxonomic revision of birches (botanical magazine monograph). London.
- Axelrod DI. 1983. Biogeography of oaks in the Arcto-Tertiary Province. Annals of the Missouri Botanical Garden. 70(4):629–657. doi:10.2307/2398982.
- Bigler C. 2016. Trade-offs between growth rate, tree size and lifespan of mountain pine (*Pinus montana*) in the Swiss National Park. Plos One. 11(3):e0150402. doi:10.1371/journal.pone.0150402.
- Bigler C, Veblen TT. 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos. 118(8):1130–1138. doi:10.1111/j.1600-0706.2009.17592.x.

- Borges RM. 2009. Phenotypic plasticity and longevity in plants and animals: cause and effect? *J Biosci.* 34(4):605–611. doi:10.1007/s12038-009-0078-3.
- Brown PM. 1996. OLDLIST: a database of maximum tree ages [Internet]. [accessed 2023 Jan 12]. <http://www.rmtrr.org/oldlist.htm>
- Burian A, Barbier de Reuille P, Kuhlemeier C. 2016. Patterns of stem cell divisions contribute to plant longevity. *Current Biology.* 26(11):1385–1394. doi:10.1016/j.cub.2016.03.067.
- Chaney RW. 1947. Tertiary centers and migration routes. *Ecol Monogr.* 17(2):139–148. doi:10.2307/1943260.
- Connor KF, Lanner RM. 1990. Effects of tree age on secondary xylem and phloem anatomy in stems of Great Basin bristlecone pine (*Pinus longaeva*). *Am J Bot.* 77(8):1070–1077. doi:10.1002/j.1537-2197.1990.tb13602.x.
- Denwood MJ. 2016. Runjags: an R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *J Stat Softw.* 71(9). doi:10.18637/jss.v071.i09.
- di Filippo A, Biondi F, Maugeri M, Schirone B, Piovesan G. 2012. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. *Glob Chang Biol.* 18(3):960–972. doi:10.1111/j.1365-2486.2011.02617.x.
- di Filippo A, Pederson N, Baliva M, Brunetti M, Dinella A, Kitamura K, Knapp HD, Schirone B, Piovesan G. 2015. The longevity of broadleaf deciduous trees in Northern Hemisphere temperate forests: insights from tree-ring series. *Frontiers in Ecology and Evolution.* 3:1–15. doi:10.3389/fevo.2015.00046.
- Farjon A. 2018. A natural history of conifers. Portland: Timber Press.
- Flanary BE, Kletetschka G. 2005. Analysis of telomere length and telomerase activity in tree species of various life-spans, and with age in the bristlecone pine *Pinus longaeva*. *Biogerontology.* 6(2):101–111. doi:10.1007/s10522-005-3484-4.
- Forestry Agency. 2013. Annual report on forest and forestry in Japan fiscal year 2013. Tokyo.
- Forestry Agency. 2021. Forest and Forestry Statistics [internet]. [accessed 2023 Jan 12]. <https://www.rinya.maff.go.jp/j/kouhou/toukei/index.html>
- Gutsell SL, Johnson EA. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. *J Ecol.* 90(1):153–166. doi:10.1046/j.0022-0477.2001.00646.x.
- Harcombe PA. 1987. Tree life tables. *Bioscience.* 37(8):557–568. doi:10.2307/1310666.
- Hayek JC. 2019. Maximum tree age and longevity [internet]. [accessed 2023 Jan 12]. <https://extension.illinois.edu/forestry/resources>
- Hiruma A, Hukushima T. 2001. Differences in forest structure and regeneration of beech (*Fagus crenata*) forest between at surface and slope surface in N.E., Nagano Prefecture, Japan. *Vegetation Science.* 18:23–29.
- Iwate Federation of Forest Owners' Co-operative Association. 1990. 50 years of Iwate federation of forest owners' co-operative association. Morioka.
- Katsuki T. 2019. The life-span in trees and shrubs. *Tree and Forest Health.* 23:239–247.
- Kubo M, Sakio H, Shimano K, Ohno K. 2005. Age structure and dynamics of *Cercidiphyllum japonicum* sprouts based on growth ring analysis. *For Ecol Manage.* 213(1–3):253–260. doi:10.1016/j.foreco.2005.03.045.
- Lienard J, Florescu I, Strigul N. 2015. An appraisal of the classic forest succession paradigm with the shade tolerance index. *Plos One.* 10(2):e0117138. doi:10.1371/journal.pone.0117138.
- Lisiecki LE, Raymo ME. 2005. Correction to “A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. *Paleoceanography.* 20(2):A2007. doi:10.1029/2005PA001164.
- Liu J, Yang B, Lindenmayer DB. 2019. The oldest trees in China and where to find them. *Front Ecol Environ.* 2019. doi:10.1002/fee.2046.
- Loehle C. 1988. Tree life history strategies: the role of defenses. *Can J for Res.* 18(2):209–222. doi:10.1139/x88-032.
- Lorimer CG, Dahir SE, Nordheim EV. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *J Ecol.* 89(6):960–971. doi:10.1111/j.1365-2745.2001.00619.x.
- Martínez-Ramos M, Alvarez-Buylla ER. 1998. How old are tropical rain forest trees? *Trends Plant Sci.* 3(10):400–405. doi:10.1016/S1360-1385(98)01313-2.
- Mencuccini M, Martínez-Vilalta J, Vanderklein D, Hamid HA, Korakaki E, Lee S, Michiels B. 2005. Size-mediated ageing reduces vigour in trees. *Ecol Lett.* 8(11):1183–1190. doi:10.1111/j.1461-0248.2005.00819.x.
- Miyawaki A. 1987. Vegetation of Japan. Vol. 8. Tokyo: Shibundo.
- Miyawaki A. 1988. Vegetation of Japan. Vol. 9. Tokyo: Shibundo.
- Nakashizuka T, Numata M. 1982. Regeneration process of climax beech forests. I. Structure of a beech forest with the undergrowth of *Sasa*. *Japanese Journal of Ecology.* 32:57–67.
- Osumi K. 2005. Reciprocal distribution of two congeneric trees, *Betula platyphylla* var. *japonica* and *Betula maximowicziana*, in a landscape dominated by anthropogenic disturbances in north-eastern Japan. *J Biogeogr.* 32(12):2057–2068. doi:10.1111/j.1365-2699.2005.01368.x.
- Osumi K. 2006. The life history of *Cercidiphyllum japonicum*; paradox in which disturbance-dependent species constitute a climax stage forest. In: In: Masaki T, Tanaaka H, Shibata M, editors. The society for the study of species biology. Tokyo: Bun Ichi Sogo Shuppan; pp. 159–177.
- Oura Y, Sato A, Noguchi T. 2003. Development of national forest contractors under the “watershed management system”: a case study on the Kiso Valley watershed. *Journal of Financial Economics.* 49:11–18.
- Pederson N. 2013. Eastern OLDLIST a database of maximum tree ages for eastern North America [Internet]. [accessed 2023 Jan 12]. <http://www.ldeo.columbia.edu/~adk/oldlisteast/>
- Peñuelas J, Munné-Bosch S. 2010. Potentially immortal? *New Phytol.* 187(3):564–567. doi:10.1111/j.1469-8137.2010.03360.x.
- Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola J-M, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature.* 399(6735):429–436. doi:10.1038/20859.
- Piovesan G, Biondi F. 2021. On tree longevity. *New Phytol.* 231(4):1318–1337. doi:10.1111/nph.17148.
- Piovesan G, Biondi F, Baliva M, de Vivo G, Marchianò V, Schettino A, di Filippo A. 2019. Lessons from the wild: slow but increasing long-term growth allows for maximum longevity in European beech. *Ecology.* 100(9). doi:10.1002/ecy.2737.
- Ranius T, Niklasson M, Berg N. 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). *For Ecol Manage.* 257(1):303–310. doi:10.1016/j.foreco.2008.09.007.
- R Core Team. 2019. R: a language and environment for statistical computing [Internet]. [accessed 2023 Jan 12]. <https://www.R-project.org/>
- Revell LJ. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol.* 3(2):217–223. doi:10.1111/j.2041-210X.2011.00169.x.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model Space. *Syst Biol.* 61(3):539–542. doi:10.1093/sysbio/sys029.
- Rötheli E, Heiri C, Bigler C. 2012. Effects of growth rates, tree morphology and site conditions on longevity of Norway spruce in the northern Swiss Alps. *Eur J for Res.* 131(4):1117–1125. doi:10.1007/s10342-011-0583-4.
- Schulman E. 1954. Longevity under adversity in conifers. *Science.* 119(3091):396–399. doi:10.1126/science.119.3091.396 <https://doi.org/10.1126/science.119.3091.396>
- Setsuko S, Yoshimura K, Ueno S, Worth JRP, Ujino-Ihara T, Katsuki T, Noshiro S, Fujii T, Arai T, Yoshimaru H. 2023. A DNA barcode reference library for the native woody seed plants of Japan. *Molecular Ecology Resources.* 23:855–871. doi:10.1111/1755-0998.13748.
- Sillett SC, van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM. 2010. Increasing wood production through old age in tall trees. *For Ecol Manage.* 259(5):976–994. doi:10.1016/j.foreco.2009.12.003.
- Suzuki E, Tsukahara J. 1987. Age structure and regeneration of old growth *Cryptomeria japonica* forests on Yakushima Island. *The Botanical Magazine Tokyo.* 100(3):223–241. doi:10.1007/BF02492832.

- Swofford DL. 2003. PAUP*. Phylogenetic analysis using parsimony (* and other methods). Version 4. Sunderland: Sinauer Associates.
- Thomas H. 2013. Senescence, ageing and death of the whole plant. *New Phytol.* 197(3):696–711. doi:[10.1111/nph.12047](https://doi.org/10.1111/nph.12047).
- Thompson JD, Higgins DG, Gibson TJ. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Res.* 22(22):4673–4680. doi:[10.1093/nar/22.22.4673](https://doi.org/10.1093/nar/22.22.4673).
- Tokoro M. 1980. History of forestry in Tokugawa Japan. Tokyo: Yoshikawa Koubunkan.
- Totman CD. 1989. The green archipelago: forestry in preindustrial Japan. Berkeley: University of California Press.
- Van PR, Sillett SC. 2008. Crown development of coastal *Pseudotsuga menziesii*, including a conceptual model for tall conifers. *Ecol Monogr.* 78(2):283–311. doi:[10.1890/07-0158.1](https://doi.org/10.1890/07-0158.1).
- Wirth C, Messier C, Bergeron Y, Frank D, Fankhänel A. 2009. Old-GrowthForest Definitions: a Pragmatic View. In Wirth C, Gleixner G, Heimann H, editors. *Old-Growth Forests*. Berlin: Springer; p. 11–33. doi:[10.1007/978-3-540-92706-8_2](https://doi.org/10.1007/978-3-540-92706-8_2).
- Wolfe JA. 1997. Relations of environmental change to angiosperm evolution during the late cretaceous and tertiary. In Iwatsuki K, Raven PH, editors. *Evolution and diversification of land plants*. Tokyo: Springer Japan; p. 269–290.
- Worbes M, Johannes Junk W. 1999. How old are tropical trees? the persistence of a myth. *Iawa J.* 20(3):255–260. doi:[10.1163/22941932-90000689](https://doi.org/10.1163/22941932-90000689).