How the timberline formed: altitudinal changes in stand structure and dynamics around the timberline in central Japan

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INTRODUCTION

Global warming possibly changes vegetation distribution on the global scale (Iverson and Prasad, 1998; Parmesan and Yohe, 2003; Thuiller et al., 2005). In particular, the timberline is one of the most sensitive sites of global warming because treelines are in cold environments (Camarero and Gutiérrez, 2002; Danby and Hik, 2007). Generally, growth rates decrease at higher altitudes because of lower temperatures (Coomes and Allen, 2007; Takahashi, 2010a). The mean trunk diameter growth rate of a sub-alpine species at the upper distribution limit is only a quarter of that at the lower distribution limit (Takahashi et al., 2003, 2005). Undoubtedly tree growth is limited by low temperatures at high altitudes, such as at treelines. Therefore, treelines may move upward in altitude according to increases in temperature. Several studies have reported an upward shift of treelines (Kullman, 2002; Walther et al., 2005; Danby and Hik, 2007; Devi et al., 2008).

However, whether vegetation moves according to an increase in temperature is still uncertain. Latitudinal and altitudinal treelines do not always move by global warming (Holtmeier and Broll, 2007). Upward shifts of treelines are recognized in only half the treelines in the world by meta-analysis (Harsch et al., 2009). The existence of treelines with no evidence of distribution shift suggests that the altitudinal location of treelines is not always determined by thermal conditions alone. Some studies examined long-term vegetation changes at high altitudes by monitoring permanent plots and by comparing new and old photographs or remote sensing data (Juntunen et al., 2002; Camarero and Gutiérrez, 2004; Devi et al., 2008; Zhang et al., 2009). Although the fact of vegetation changing or not can be revealed by these methods, the mechanisms behind changes are unknown. Distribution shift is determined through population dynamics, including growth, recruitment and mortality. Therefore, population dynamics needs to be examined in studies of global warming impacts on vegetation distribution.

In central Japan, vegetation changes with altitude from lowland evergreen broad-leaved forests to montane deciduous broad-leaved forests to sub-alpine coniferous forests to dwarf...
pine scrub. The upper distribution limit of sub-alpine forests is the timberline. Miyajima and Takahashi (2007) investigated altitudinal changes of stand structure from 800 m a.s.l. to the timberline (2500 m a.s.l.) on Mount Norikura in central Japan. Although mechanical damage of conifer trunks and branches was not observed between 800 and 2000 m a.s.l., damaged trees increased from 2200 to 2500 m a.s.l. associated with reduced trunk height. Generally, wind velocity increases with altitude (Araki, 1995; Baker and Weisberg, 1995). Strong winds in winter often causes mechanical damage of trees at high altitudes by snow abrasion due to wind-blown ice crystals; this damage causes winter desiccation (Hadley and Smith, 1983, 1986). Trunks and branches are also often broken by snow pressure (Seki et al., 2002). Thus, not only temperature, but also strong winds and snow are important for timberline formation.

This study examined the mechanisms of timberline formation in central Japan. First, we describe altitudinal changes in tree density and size structure for two dominant sub-alpine tall tree species and a dwarf pine around the timberline. Secondly, we describe altitudinal changes in trunk diameter growth rates of the three species, and mechanical damage and mortality of a dominant tall tree species around the timberline. Even if trees cannot increase their trunk height due to mechanical damage caused by strong wind and snow at high altitudes, they may be able to increase their trunk diameter if the temperature is high enough for growth. Therefore, the following two hypotheses are possible. (1) Growth limitation due to low temperature is not an immediate cause of timberline formation if growth of the trunk diameter of sub-alpine tall tree species does not decrease from the upper part of the sub-alpine forest to the timberline. (2) If strong wind and snow mainly affect tall tree species, larger trees are prone to be damaged and to die at higher altitudes because wind velocity increases with height within a stand (Araki, 1995) and because larger trees tend to die of disturbances (Takahashi, 2010b). The purpose of this study was to examine these two hypotheses.

MATERIALS AND METHODS

Study site

This study was conducted on the east slope of Mount Norikura (36°06′N, 137°33′E; summit elevation 3026 m a.s.l.) in central Japan in 2004 and 2010. Sub-alpine conifers Abies mariesii Mast., Abies veitchii Lindl. and Tsuga diversifolia (Maxim.) Mast., and deciduous broad-leaved Betula ermanii Cham. were the dominant tall tree species between 1600 and 2500 m a.s.l. (i.e. the timberline) (Miyajima and Takahashi, 2007; Miyajima et al., 2007). Dwarf pine Pinus pumila (Pall.) Regel scrub dominates above the timberline to near the summit. Mean temperatures of the coldest month of January and of the hottest month of August at the timberline (2500 m a.s.l.) were estimated as −12.1 °C and 11.7 °C, respectively, with −0.2 °C annual mean temperature, from temperatures recorded at Nagawa Weather Station (1068 m a.s.l., approx. 12 km in horizontal distance from the summit) using the standard lapse rate of −0.6 °C for each +100 m altitude. Nomenclature followed the Editorial Board of Flora of Nagano Prefecture (1997).
Field methods

Field measurements were made from the upper part of the sub-alpine forest to the timberline in 2004 and 2010 to investigate the mechanism of timberline formation (Fig. 1A). Thirty plots of 10 m × 10 m were randomly established between 2350 and 2500 m in 2004. Trunk diameter at 0.3 m height was measured for *Abies mariesii* and *B. ermanii* taller than 2 m and dwarf pine *P. pumila* taller than 0.3 m. Although the shrub species *Sorbus commixta* Hedland was also found in

![Diagram](image-url)

**Fig. 2.** Altitudinal changes in stand structural parameters of 10 × 10 m plots for *Abies mariesii* around the timberline (about 2500 m a.s.l.): (A) maximum trunk height, (B) maximum DBH, (C) sapling density (0.3 < *H* ≤ 1 m), (D) sapling density (1 < *H* ≤ 2 m), (E) tree density (*H* > 2 m) and (F) total basal area of trees (*H* > 2 m). The Pearson correlation coefficient *R* is shown in each panel with a statistical significance level (*P* < 0.05; **P** < 0.01; ***P** < 0.001).
the plots, this species was not measured because of its high density. Trunk diameter at 0.3 m height was measured again in 2010, and then the absolute diameter growth rate (ADGR) was calculated. The measurement height (0.3 m) for ADGR was determined to equalize among the three species because the stem height of *P. pumila* was short (up to approx. 2.5 m). Dead trees during the census period were also recorded.

Ninety-five plots of 10 × 10 m were established between 2350 and 2600 m in 2010, making a total of 125 plots studied. Geographical position (latitude, longitude and altitude) was recorded for the 125 plots using a global positioning system (Garmin Ltd, Olathe, KS, USA). Although tall tree species were examined in the whole 10 × 10 m area of each plot, *P. pumila* was examined in only a 1 × 10 m area of each of 26 plots established above the timberline because *P. pumila* was densely distributed. Trunk diameter at breast height (DBH) was measured for *A. mariesii* and *B. ermanii* taller than 2 m in all plots and at 0.3 m height for *P. pumila* taller than 0.3 m. The presence of mechanical damage scars of trunks and branches was checked for *A. mariesii*. Mechanical damage was tip dieback, broken stems and canopy anomaly (i.e. a branch lacking within the canopy, flagged trees) (cf. Kajimoto et al., 2002) (Fig. 1B, D). Single trees may be damaged several times. However, it is impossible to count the number of incidents of damage. Therefore, we checked only the presence or absence of damage scars for *A. mariesii*. The presence of mechanical damage scars was not checked for *B. ermanii* because identification of mechanical damage was difficult (Fig. 1C). Trunk height of the tallest *A. mariesii* and *B. ermanii* was measured for each plot. *Abies mariesii* and *Betula ermanii* saplings were counted for two size classes of trunk height (*H*) in each plot: 0.3 < *H* ≤ 1 m and 1 < *H* ≤ 2 m.

Statistical analysis

Correlations between altitude and stand structure parameters (density, maximum trunk height and diameter, and total basal area) of the 125 plots were examined by using Pearson product–moment correlation coefficients to investigate how stand structure changes with altitude. Of these variables, the maximum trunk height and DBH in plots are indicators of maximum attainable size at the plot altitude. Although it is hard to consider that size structure at each plot is stable, data of 125 plots are enough to show the general trend of altitudinal changes of tree size.

A generalized linear model with Gaussian distribution was used to analyse the effects of altitude and tree size on ADGR (cm year−1) of the three species in the 30 plots established in 2004. The model including explanatory variables tree size and altitude is:

\[
\text{ADGR} = a_0 + a_1 \ln D_{0.3} + a_2 \text{Altitude} 
\]

where \(\ln\) is the natural logarithm, \(D_{0.3}\) is the trunk diameter (cm) at 0.3 m height in 2004, and coefficients \(a_0, a_1\), and \(a_2\) are constants.

Mortality was examined for *A. mariesii* during 6 years (2004–2010) in the 30 plots. Mortality could not be analysed for *B. ermanii* and *P. pumila* because of an insufficient number of trees in the plots for mortality calculation. Mortality is a discrete event. A datum can have only have value 0 (live) or 1 (dead). Therefore, we analysed the probability of mortality by using a generalized linear model with binomial distribution (i.e. logistic regression). This study examined the effects of altitude and tree size (\(D_{0.3}\)) on tree mortality. Combining these effects, the hypothesized mortality model (*M*, 6 years−1) is:

\[
M = \frac{1}{1 + \exp\left[-(b_0 + b_1 \text{Altitude} + b_2 D_{0.3})\right]} 
\]

where coefficients \(b_0, b_1\) and \(b_2\) are constants. Mortality ranges between 0 and 1.

A model of mechanical damage of trunks and branches was constructed for *A. mariesii*. The presence of damage scars is a discrete event, like mortality. A datum can have only value 0 (absence) or 1 (presence). Therefore, we analysed the damage ratio by using a generalized linear model with binomial distribution:

\[
\text{DR} = \frac{1}{1 + \exp\left[-(c_0 + c_1 \text{Altitude} + c_2 \text{DBH})\right]} 
\]

where DR is the damage ratio (the probability of the presence of damage scars), and coefficients \(c_0, c_1\) and \(c_2\) are constants. The damage ratio ranges between 0 and 1.

A stepwise function was used to choose explanatory variables, based on Akaike information criteria (AIC), for models of growth, mortality and damage ratio. A model with the lowest value of AIC is essentially the best model. However, any model is substantially the same as the best model if the difference in AIC value of the model of interest from the best model is < 2 (Burnham and Anderson, 2002). Model determination and calculation of the AIC values were done by using free statistical software R 2.9.0 (R Development Core Team, 2009).

RESULTS

Alitudinal changes in stand structure

Maximum trunk height and DBH of *A. mariesii* in plots decreased with altitude (*P* < 0.001, Fig. 2A, B). Although the densities of *A. mariesii* for height classes 0.3 < *H* ≤ 1 m,
1 < H ≤ 2 m and H > 2 m and the total basal area were variable, they showed negative correlations with altitude (P < 0.001, Fig. 2C–F). Densities of A. mariesii for height classes 0.3 < H ≤ 1 m and 1 < H ≤ 2 m positively correlated with density and total basal area of conspecific trees taller than 2 m (P < 0.001, Table 1).

Although the maximum DBH of B. ermanii did not decrease with altitude (Fig. 3B), the maximum trunk height decreased
with altitude ($P < 0.001$, Fig. 3A). The total basal area of *B. ermanii* was negatively correlated with altitude ($P < 0.05$, Fig. 3F) due to the absence of *B. ermanii* above 2510 m a.s.l. rather than a gradual decrease in total basal area with altitude. The densities of *B. ermanii* for height classes $0.3 < H \leq 1$ m, $1 < H \leq 2$ m and $H > 2$ m showed no altitudinal trends (Fig. 3C–E). The densities of *B. ermanii*, except for some plots, in height classes $0.3 < H \leq 1$ m and $1 < H \leq 2$ m were less than the density of *B. ermanii* taller than 2 m. In particular, no sapling ($0.3 < H \leq 1$ m) was found, except for two plots with one sapling (Fig. 3C). Although the density of *B. ermanii* saplings ($1 < H \leq 2$ m) positively correlated with the density of *B. ermanii* taller than 2 m ($P < 0.05$, Table 1), the correlation coefficient ($R = 0.227$) was considerably lower than for *A. mariesii* (at least, $R > 0.68$). The three other cases for *B. ermanii* showed no significant correlation (Table 1).

Although the maximum trunk diameter of *P. pumila* did not correlate with altitude, the density markedly increased at $>2465$ m a.s.l. ($P < 0.001$, Fig. 4). Tall tree species *A. mariesii* and *B. ermanii* taller than 2 m showed a negative correlation with *P. pumila* for density and total basal area (Fig. 5).

**Altitudinal changes in ADGR of the three species**

Variables of $D_{0.3}$ and altitude were selected in a stepwise regression for ADGR of *A. mariesii* (Table 2). The ADGR of *A. mariesii* was greater for trees of greater trunk diameter and at higher altitudes within the examined range of altitude.
Altitudinal changes in mechanical damage and mortality of A. mariesii

The variables of DBH and altitude were selected in a stepwise regression for the ratio of mechanical damage scars of A. mariesii (Table 2). A. mariesii suffered mechanical damage more at higher altitudes and for trees of greater trunk diameter (Fig. 7). Although the damage ratio was 0.35 for trees with DBH 20 cm at 2350 m a.s.l., the damage ratio increased up to 0.8 at 2500 m a.s.l. (Fig. 7). The damage ratio was only 0.12 for trees with DBH 5 cm at 2500 m a.s.l. However, the damage ratio increased up to 0.95 for trees with DBH 40 cm at the same altitude.

The full model of mortality of A. mariesii was substantially the same as the best model because the difference in AIC between the best model and full model was <2. The ADGR of A. mariesii was greater for trees of greater trunk diameter (Fig. 8). Mortality was about four times greater at 2500 m a.s.l. than at 2350 m a.s.l. irrespective of DBH; nevertheless, the altitudinal difference was only 150 m. The mortality of trees with DBH 40 cm was 1.8 times greater than the mortality of trees with DBH 5 cm at 2500 m a.s.l.

DISCUSSION

Altitudinal changes in density and growth of tall tree species

We expected that the ADGR of tall tree species A. mariesii and B. ermanii would decrease from the upper part of the sub-alpine forest to the timberline if insufficient temperature for growth is the immediate cause of timberline formation. However, the ADGR of B. ermanii was constant irrespective of altitude, and the ADGR of A. mariesii was greater at higher altitudes. The intensity of tree competition would decrease with altitude on Mount Norikura because of lower density and shorter stand height at higher altitudes (Miyajima and Takahashi, 2007), which probably increased the ADGR of A. mariesii at higher altitudes. Therefore, growth limitation due to low temperature may not be an immediate cause of timberline formation.

As we expected, the maximum trunk height of A. mariesii and B. ermanii decreased with altitude because of greater mechanical damage and mortality of larger trees at higher altitude, at least for A. mariesii. Thus, even if trunk diameter growth of tall tree species is not limited by low temperature around the timberline, tall tree species cannot increase their trunk height. Although the maximum trunk diameter of A. mariesii also decreased with altitude, this is not true for B. ermanii. Trunks and branches of conifers are often broken in snowy environments (Kajimoto et al., 2002), because of less plasticity of trunk shape (vertical straight form) compared with broad-leaved tree species, such as B. ermanii. High wood density is also another important factor for the solid trunk of B. ermanii. Therefore, the trunk diameter of B. ermanii may be able to continue to grow even around the timberline.

A smaller number of B. ermanii saplings (0.3 H ≤ 1 m and 1 < H ≤ 2 m) than that of conspecific trees (H > 2 m) indicates that regeneration of B. ermanii is discontinuous around the timberline. Betula ermanii is a shade-intolerant species (Koike, 1988), so B. ermanii seedlings cannot establish in forest understory conditions. Therefore, B. ermanii needs disturbances for their regeneration. In contrast, sapling density (0.3 H ≤ 1 m and 1 < H ≤ 2 m) of A. mariesii positively correlated with the density of conspecific trees (H > 2 m), unlike B. ermanii. The positive correlations between sapling and tree densities in A. mariesii probably relates to their seed size and shade tolerance. Seeds of A. mariesii can germinate and survive in snowy environments (Kajimoto et al., 2002), because of less plasticity of trunk shape (vertical straight form) compared with broad-leaved tree species, such as B. ermanii. High wood density is another important factor for the solid trunk of B. ermanii. Therefore, the trunk diameter of B. ermanii may be able to continue to grow even around the timberline.

Also, shade-tolerant A. mariesii can germinate and survive in

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<td>(a) Growth model</td>
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† P<0.1; *P<0.05; **P<0.01; ***P<0.001.

Variables of best models were selected by stepwise function.
forest understorey conditions (Kohyama, 1984). Seedling emergence of *A. mariesii* is proportional to the seed rain (Mori et al., 2004). Seed production is proportional to tree size (Messaoud et al., 2007). In this study site, seed production of *A. mariesii* at the stand level is thought to decrease with altitude because of a decrease of tree density and tree size due to an increase in mortality. Therefore, regeneration of *A. mariesii* may further decrease around the timberline by negative feedback of reduced seed production, which leads to difficulty in *A. mariesii* invading *P. pumila* scrub above the timberline.

**Dominance of dwarf pine above the timberline**

Shade-intolerant *P. pumila* cannot grow in forest understorey conditions below the timberline (Takahashi, 2003). In short, *P. pumila* is a competitively inferior species to tall tree species. Therefore, the lower distribution limit of
P. pumila may be determined by interspecific competition with tall tree species.

The suitable warmth index [WI, \( \Sigma (m_i - 5) \)] for A. mariesii is between 15 and 50 °C months, where \( m_i \) is the mean monthly temperature above 5 °C (Tanaka et al., 2009). WI = 15 °C corresponds to 2800 m a.s.l. (the upper distribution limit of P. pumila) on Mount Norikura, suggesting that A. mariesii can potentially distribute up to 2800 m a.s.l. However, A. mariesii hardly grows and survives above the current timberline (2500 m a.s.l.) because of mechanical damage to trunks and branches by strong wind and snow abrasion. In contrast, P. pumila is hardly damaged by strong wind and snow abrasion (Maruta et al., 1996), because P. pumila is completely covered with snow in winter. Snow protection allows P. pumila to survive even in wind-exposed environments above the timberline. Therefore, P. pumila may be able to dominate only at high altitude where tall tree species (A. mariesii and B. ermanii) cannot survive.

Conclusions

The findings of this study lead to the conclusions (1) that growth limitation due to low temperature is not an immediate cause of timberline formation because trunk diameter growth of tall tree species did not decrease even at the timberline; and (2) that larger trees of tall tree species are prone to die from mechanical damage due to strong wind and snow at higher altitude. Models that predict a distribution shift of plant species due to global warming have been made based on relationships between current distribution area and the environmental conditions, such as temperature and precipitation, i.e. niche-based models (Iverson and Prasad, 1998; Pearson et al., 2002; Thuiller, 2003). Niche-based models assume that the distribution area of plant species tracks suitable climatic conditions because macro-scale vegetation distribution is well explained by such climatic conditions (Yin and Kira, 1975; Fang and Yoda, 1989). However, this study suggested that the upper distribution limits of tall tree species (i.e. the timberline) are greatly affected by strong wind and snow, not by temperature alone. Upward shift of vegetation due to global warming may be less likely in wind-exposed sites than in wind-sheltered sites (Kullman and Öberg, 2009; Kullman, 2010). Holtmeier and Broll (2010a, b) also suggested paying great attention to varying wind effects on a potentially climatically driven upward shift of treeline position at the landscape scale. Therefore, we need caution in considering that the altitudinal location of the timberline will always move upward in proportion to the increase in temperature due to global warming.

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LITERATURE CITED


