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Stand and self-thinning dynamics in natural *Abies* stands in northern Hokkaido, Japan

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Running title: Stand dynamics of natural *Abies* stands

(Abstract)

Stand dynamics and self-thinning were analyzed in relation to the dynamics of aboveground biomass in natural *Abies sachalinensis* stands growing on sand dunes in northern Hokkaido, Japan, to examine wave-type regeneration in the stands. Fifty-two plots were established in almost pure *Abies* stands that ranged from saplings to the mature and collapsing growth stages. Aboveground biomass and tree height reached asymptotic levels prior to the collapsing phase, unlike wave-regeneration *Abies* stands in central Japan and North America. Stand density was high in the young growth stages, but the self-thinning rate, density decrease per biomass growth, in the study stands was greater than in wave-regeneration stands in central Japan, as indicated by a large self-thinning exponent (-1.26 by RMA regression). The range of tree height distribution was very narrow, and the stands' vertical structure was typically single-layered. The slenderness ratio of trees was large, except in young stands. In mature and collapsing stands, advanced seedling density increased markedly. These stand and tree characteristics were considered to be correlated with the wave-type regeneration in the study stands, and it is assumed that prevailing winds affect tree mortality.

Keywords: *Abies*; aboveground biomass; stand structure; self-thinning; wave-type regeneration.

INTRODUCTION

Natural *Abies sachalinensis* stands grow on sand dunes in the Wakasakanai district of northern Hokkaido, Japan (45°05'N, 147°39'E). As seen in wave-regeneration stands (Sprugel 1976; Kohyama & Fujia 1981), simultaneous mortality of canopy trees and subsequent replacement by saplings has been observed in mature stands in this district (Sato 1994), and stand regeneration occurs by this process. The rotation period between two successive generations has been estimated 80-90 years (Sato 1994), which is short compared to the ecological longevity (about 200 years) of *Abies sachalinensis* in Hokkaido (Yajima 1982).

Wave-regeneration *Abies* stands have been studied previously to investigate the dynamics of even-aged pure tree populations in terms of size structure, density, and stand growth (Kohyama & Fujita 1981; Sprugel 1984; Sato 1994). These stand characteristics are related to wave-regeneration dynamics; however, the factors that trigger regeneration are also important in considering the mechanism of the dynamics. In wave-regeneration stands in central Japan, bands ("waves") of dead trees develop along contour lines and move upslope (Kimura 1984). This shift is affected by prevailing winds and desiccation (Shimazu 1959; Kai 1974; Oka 1983; Kohyama 1988). Such waves are not apparent in the Wakasakanai district; however, the dead tree zone has shifted inland, suggesting that prevailing winds from the sea affect tree mortality (Sato 1994).

The relationship between self-thinning and biomass dynamics is also significant in understanding the regeneration dynamics of even-aged pure stands, where natural thinning processes follow the schematic trajectory shown in Fig. 1 (Yoda *et al.* 1963; Westoby 1984). Starting from below the self-thinning line, a stand moves upward and then follows the self-thinning line. Subsequently, the stand reaches an asymptotic biomass; stand density then decreases, while the asymptotic biomass is maintained until the stand enters a collapsing phase in which both biomass and density decrease. It can be assumed that stand structure, tree proportions, and the causes of tree mortality change depending on the natural thinning phases (*e.g.*, Kohyama 1988) shown in Fig. 1.

In this study, we examined aboveground biomass, size structure, and self-thinning as characteristics related to wave-type regeneration dynamics (Sato 1994) in natural *Abies* stands, to examine the processes of simultaneous mortality of canopy trees and subsequent replacement by saplings. In addition, advanced seedling density was assessed in some stands. Like wave-regeneration *Abies* stands in central Japan (Kohyama 1984), *Abies* seedlings in the study site became established before a stand collapsed (Sato 1994). We examined the timing of the establishment of advanced seedlings in relation to stand dynamics and light conditions. Based on the results, we also derived several significant factors that influence the wave-type regeneration dynamics in these stands.

STUDY SITE AND METHODS

Study site

The study stands extend along coastal shores in a north-south direction in the Wakasakanai district. Some forests on the sand dunes are parallel to the shoreline, and *Abies* dominates several of these, as described in detail by Sato (1994). We established study plots between the second and the fourth sand dune on the seaside of these stands, where nearly pure stands of *Abies* were well established.

In the study area, wind is strong throughout the year, with a mean monthly wind velocity of $>4 \text{ m}\cdot\text{s}^{-1}$ (not including July). The mean annual temperature and precipitation recorded at a meteorological station in Wakkanai (about 50 km north of the Wakasakanai district) were 6.7 °C and 1022 mm between 1978 and 1997, respectively. Snowfall typically occurs between November and April.

Methods

Stand and tree inventory

We established 52 study plots in *Abies* stands of uniform structure in various growth stages, from sapling to collapsing phases (Table 1). Collapsing stands were defined as those in which mortality of canopy trees was evident, and residual canopy trees were unable to refill the

resulting canopy gaps. Plot areas ranged from 2-800 m², depending on tree (or sapling) size. In each plot, all trees were identified, and the following measurements were taken: diameter at breast height (D), diameter at 1/10 of the tree height (D_{0.1}), tree height (H), and height of the live crown base (H_b). Trees apparently deviating from the canopy layer were excluded.

Stand age was estimated from the dominant height of the stands, because tree age could not be assessed directly. For this estimation, a standard height growth curve was determined by stem analysis of dead *Abies* trees found just around the study area. We sampled ten dead and previously dominant *Abies* trees, and five trees without wood decay were available for the analysis. A standard height growth curve was determined from the average height growth of the five sampled trees regressed by a Richards function (Richards 1959):

$$y = 12.20(1 + 10.79e^{-0.092x})^{1/(1-1.282)} \quad (r^2=0.999, \text{ Eq. 1})$$

where y and x are dominant height [m] and stand age [years], respectively (Fig. 2). The stand age was determined from the dominant height estimated by this growth curve. The dominant height was defined as the mean height of the ten tallest trees in each plot that contained <50 trees, and as the mean height of the 20 tallest trees in each plot that contained >50 trees. However, the stand age of collapsing stands was not estimated, because the dominant height could not be determined. The oldest stand that had not reached the collapsing phase was estimated to be 77-year-old; we therefore considered all collapsing stands to be >77-year-old.

Estimation of aboveground biomass

Seven dead *Abies* trees (H: 10.3-13.4 m) of complete sets of stem samples out of ten trees for the standard height growth curve and 11 live *Abies* trees (H: 0.6-10.5 m) were sampled at the study site and at the Teshio Experimental Forest of Hokkaido University, respectively, to estimate stem mass. Stem volume was calculated for the sampled trees by ordinary stem analysis, and was converted to stem mass by multiplying by the specific gravity ($0.37 \text{ g}\cdot\text{cm}^{-3}$) of *Abies sachalinensis* wood (Kijima *et al.* 1962). We determined the following allometric equation for stem mass (W_s):

$$W_s = 0.0096(D_{0.1}^2 H)^{1.044} \quad (n=18, r^2=0.999) \quad [\text{kg, cm, m}].$$

To estimate branch and needle mass of individual trees, one medium-sized branch was sampled from each whorl on 30 *Abies* trees that had normal crowns. Branch and needle mass of the medium-sized branches was multiplied by the branch number of a whorl and summed for each trees. Similar estimation methods have been described by Zavitkovski *et al.* (1981) and Hepp & Brister (1982). The mean error of this estimation for 11 trees sampled in the Teshio Experimental Forest was $-0.3 \pm 9.7 \%$ and $+11.2 \pm 11.6 \%$, for branch and needle mass, respectively. The estimation error for needle mass was probably inflated because we sampled trees along a forest road and all of the trees sampled had sunny and shade sides, which probably caused needle density to vary among branches within each tree. Nevertheless, we assumed that this estimation was applicable to the study stands

where the canopy was closed. In the study stands, D , H , H_b , $D_{0.1}$, and D_b (diameter at the live crown base) were also measured for *Abies* trees used to estimate branch and needle mass. The branch (W_b) and needle (W_n) masses of individual trees were estimated by the following equations (Shibuya & Matsuda 1993).

$$W_b = 0.0064 D_{0.1}^{2.903} H^{-0.666} (H - H_b)^{0.361} \quad (n=30, r^2=0.976)$$

$$W_n = 0.0189 D_{0.1}^{2.227} H^{-0.286} (H - H_b)^{0.403} \quad (n=30, r^2=0.989)$$

[kg, cm, m, m]

Seedling density and light conditions

We measured seedling density and, using a light meter (Minolta T-1H), measured the relative light intensity (RLI) 50 cm above ground, or just above the seedlings for those taller than 50 cm. The RLI was measured at 20 points in each of seven plots of various stand ages under the clouded condition. Age of seedling cohort in the seven plots was estimated from their mean height using Eq. 1, because variation in the height was rather small.

RESULTS

Stand condition and vertical structure

Table 1 describes the stand conditions of the study plots. Stands of various growth stages, ranging from initial (*i.e.*, saplings) to mature and collapsing stages, were included, and mean tree height ranged from 0.6-10.6 m. Maximum height was 12-13 m in all plots, and trees

that had reached the maximum height were frequently observed in mature and collapsing stands. Estimated stand age of 47 plots ranged from 26- to 77-year-old. Four plots were estimated to be over 77-year-old. In most plots, *Abies* trees accounted for over 90 % of basal area (Table 1), and *Picea*, *Quercus*, *Acer*, and *Sorbus* occurred concomitantly. In the initial stages, tree density was around 10^5 ha^{-1} , and decreased to 3000-4000 ha^{-1} in the mature stages (>60-year-old).

Figure 3 shows the relationship between $D_{0.1}$ and H in relation to stand age in five plots. Tree height tended to be restricted to a narrow range in comparison to $D_{0.1}$, especially in 56- and 77-year-old stands (Plots 45 and 49; Table 1). Vertical structure was typically single-layered (Fig. 3).

Aboveground biomass

Aboveground biomass (AGB) and needle mass increased rapidly after 20 years of stand age and reached asymptotes of $140 \text{ t}\cdot\text{ha}^{-1}$ and $21 \text{ t}\cdot\text{ha}^{-1}$, respectively, at around 55-year-old (Fig. 4). The AGB and needle mass decreased after 60-year-old of stand age and entered into collapsing phase. The maximum AGB of the study stands was slightly less than that of a wave-regeneration *Abies* stand (about $160 \text{ t}\cdot\text{ha}^{-1}$) in central Japan (Tadaki *et al.* 1977).

Trends in variations in tree size and mass distributions

Relationships between the coefficient of variation (CV) of $D_{0.1}$ and H, and stand age are shown in Fig. 5, excluding plots of stand age

undetermined (Table 1). The CV of H (10-39%) was smaller than that of $D_{0.1}$ (24-49%) in all of the plots. A significant negative correlation was recognized between the CV of H and stand age ($r=-0.557$, $p<0.01$, $n=47$), and was not recognized between the CV of $D_{0.1}$ and stand age ($r=-0.148$, $p>0.05$, $n=47$).

Figure 6 shows trends in CV, skewness, and Gini coefficient of tree mass distribution in the 47 plots. All of the coefficients, CV, skewness, and Gini coefficient, were correlated significantly with stand age, consequently, they decreased with stand age. They were also significantly correlated each other ($r=0.675$ between CV and skewness, $r=0.530$ between skewness and Gini coefficient, and $r=0.960$ between Gini coefficient and CV, $p<0.01$ and $n=47$ in all correlations). Further, the CV and the Gini coefficient of tree mass were positively correlated with the CVs of $D_{0.1}$ and H ($r=0.706$ and 0.860 between CV of mass and $D_{0.1}$ and CV of mass and H, respectively, and $r=0.751$ and 0.856 between Gini coefficient of mass and CV of $D_{0.1}$ and Gini coefficient of mass and CV of H, respectively, $p<0.01$ and $n=47$ in all correlations), whereas the CV of $D_{0.1}$ was not correlated significantly with stand age (Fig. 5). The skewness of tree mass distribution was also positively correlated with the CV of H ($r=0.550$, $p<0.01$, $n=47$), but was not correlated significantly with the CV of $D_{0.1}$ ($r=0.219$, $p>0.05$, $n=47$).

Density dynamics and self-thinning

Figure 7 shows density dynamics averaged in five-year intervals,

including seedling density under the canopy of a previous generation (Table 1). Although seedling density in the study stands ($3\text{-}6 \times 10^5 \text{ ha}^{-1}$) was larger than that in wave-regeneration stands of central Japan (Kohyama & Fujita 1981), rapid mortality occurred in stands aged 30- to 60-year-old. Subsequently, density was 3000-4000 ha^{-1} in the mature stages (60 to 80-year-old) before the collapsing phase. However, density markedly decreased again in the collapsing phase. The decreasing pattern in density of the study stands after 30-year-old was similar to that of the wave-regeneration stands, but mortality was greater in the study stands than in wave-regeneration stands.

The self-thinning line for the study stands was determined by RMA (reduced major axis) regression (Leduc 1987; Osawa & Allen 1993), and did not include stands in initial and collapsing phases (Fig. 8). The self-thinning exponent was -1.26 (95 % confidence interval: $-1.41 < \beta < -1.12$) and was larger than by -1.85 (Manabe 1974), -1.45 (Kohyama & Fujita 1981), and -1.48 (Sato 1994) previously determined for Japanese *Abies* stands.

Seedling density and light conditions

Table 1 shows seedling density and light conditions 50 cm above ground, or just above seedlings, in seven stands. No seedlings were found in Plots 18 and 26 (40- and 43-year-old, respectively). The RLI at 50 cm above ground in these plots was 0.6-0.8 %, and regeneration of seedlings occurred in stands older than 50 years. Seedling density and mean height of the seedlings apparently increased with stand

growth, especially in mature and collapsing stands in which the RLI ranged from 6-29 %.

DISCUSSION

Stand dynamics after regeneration

Seedling density increased markedly in mature and collapsing stands (Table 1). The RLI under the canopy rose in stands older than 60 years, and a sufficient number of seedlings regenerated prior to the collapsing phase. The regeneration of seedlings is related to the stand dynamics of the previous generation and occurs in the later stages of stand growth.

Many dominant trees reached the asymptotic height (Fig. 2) in mature and collapsing stands (Fig. 3), and basal area in those stands was less than the maximum value (55-60 m²·ha⁻¹; Table 1). Therefore, AGB growth is considered to have reached an asymptote at about 140 t·ha⁻¹ after 55-year-old (Fig. 4), which was slightly less than that of a wave-regeneration stand in central Japan (Tadaki *et al.* 1977). However, the needle mass of the study stands was moderate for evergreen coniferous stands and was not considered to be a factor influencing the small asymptote of AGB. The maximum height was limited to around 12-13 m in mature and collapsing stands, which probably resulted in the small asymptote of AGB.

In contrast to our study stands, tree height in wave-regeneration

Abies stands in central Japan (Fig. 3b in Kohyama & Fujita 1981) and AGB in stands in North America (Fig. 3 in Sprugel 1984) did not reach an asymptote prior to the collapsing stage. These stands also differed from the study stands in the magnitude of their canopy gaps. Simultaneous mortality of canopy trees in wave-regeneration stands results in large gaps (waves), as compared to the type of gaps found in the study stands (Sato 1994). Therefore, residual trees in wave-regeneration stands face large gaps and suffer from stress induced by prevailing winds, which causes mechanical attrition of needles and roots (Marchand *et al.* 1986; Kohyama 1988); consequently, subsequent simultaneous mortality of canopy trees probably occurs irrespective of their growth potential.

Height distribution was typically single-layered in study stands (Fig 3). This suggests that suppressed trees are thinned rapidly, and intensive competition for light occurs during the self-thinning process. The mean ratio of crown length to tree height was 23-31 % in all but one of the stands in Fig. 3, which is less than in wave-regeneration stands in central Japan (Kohyama 1988). Such-shaped trees are vulnerable to wind-sway. Also, gap restoration was generally difficult in mature stands, as indicated by increases in RLI in mature and collapsing stands (Table 1). A thinning experiment by Marchand *et al.* (1986) indicated that canopy openings by gaps result in abundant needle loss of trees in dense *Abies* stands, followed by simultaneous mortality of canopy trees. Similar processes of needle loss and tree mortality indicated by Marchand *et al.* (1986) may occur in the mature

and collapsing stands in this study.

In self-thinning plant populations that experience strong competition, the skewness in plant mass distribution generally decreases with plant growth (Mohler *et al.* 1978; Hara 1988). Skewness in tree mass distribution in the study stands clearly decreased with stand age (Fig. 6). This tendency of decreasing skewness in the self-thinning phase is probably a general trend in even-aged pure plant populations. The CV and the Gini coefficient of tree mass in the study stands also decreased with stand age (Fig. 6). In wave-regeneration stands in central Japan, the CV of tree mass decreased with stand age (Kohyama & Fujita 1981). Although, in a case of tree plantations including stands of various tree densities, the decreasing trend in Gini coefficient of tree volume was not obvious (Brand & Magnussen 1988), the Gini coefficient may decrease with tree growth in stands under strong competition such as the study stands in this study and wave-regeneration *Abies* stands in central Japan, taking a strong positive correlation between the CV and the Gini coefficient of tree mass into consideration. Relationships between variations in tree sizes and variation in tree mass were complicated (*cf.* Figs. 5 and 6). For example, the CV of tree mass was correlated negatively but the CV of $D_{0.1}$ was not correlated significantly with stand age, whereas a positive correlation was recognized between them. Both the variations in $D_{0.1}$ and H may affect the variation in tree mass distribution, however, the variation in H seems more close to the variation in tree mass distribution in stands

under strong competition such as the study stands.

The mortality rate by self-thinning was greater in the study stands than in wave-regeneration stands in central Japan (Fig. 7). Before the collapsing phase, tree height reached approximately 12-13 m and 10 m in the study stands and wave-regeneration stands, respectively, and this difference in height related to the difference in density before the collapsing phase. The self-thinning exponent (-1.26) was large for *Abies* stands, which suggests that a larger relative decrease in density is necessary for a given relative growth of mean tree mass. Moreover, this indicates that the relative increase in crown size, as compared to the tree mass of surviving trees in the study stands, is larger than in the wave-regeneration stands, because the canopy completely closed during the self-thinning phase of the study stands. Competition belowground may also influence the large self-thinning exponent in the study stands.

Significant factors contributing to stand collapse

From the characteristics of the stand dynamics and tree growth, we derived significant factors that affected the collapse of the study stands. Prevailing winds are assumed to significantly influence the wave-regeneration phenomenon in central Japan (Shimazu 1959; Kai 1974; Oka 1983; Kohyama 1988). The spatial patterns of wave-regeneration also appeared in a grid-model, in which the prevailing winds were also assumed to affect tree mortality (Sato &

Iwasa 1993). Thus, wind may be a direct factor that causes stand collapse in wave-regeneration *Abies* stands, because it results in tree sway and needle mortality by mechanical attrition (Marchand *et al.* 1986) and desiccation (Berg & Chapin 1994) after gap formation. In the Wakasakanai district, the prevailing onshore winds are strong, especially in winter (unpublished data), and the dead tree zone has shifted inland (Sato 1994). We therefore assume that wind affects tree mortality in the study stands by the same process as in wave-regeneration stands.

Furthermore, it is important that height growth reaches an asymptote at the mature stages, in which AGB also reaches the asymptote in the study stands (*cf.* Figs. 2 and 4). Vigorous increases in crown width are not expected in trees that have reached the asymptotic height (Zeide 1991). Accordingly, gap restoration is generally difficult in the mature stands investigated in this study, and the influence of the prevailing wind, resulting in forced needle mortality, would easily extend to surrounding residual trees. Furthermore, the residual trees are subject to the influence of wind because of their high slenderness ratio, the ratio of tree height to stem diameter, and narrow leaf layer (Fig. 3). The surrounding trees will die, gaps will become enlarged, and eventually many canopy trees will die within a short period. However, the influence of prevailing winds on tree mortality in the study stands has not yet been verified. We need to examine the survival of needles and branches of trees surrounding a gap. If our concept of wave-type regeneration is accurate, it is

expected that the simultaneous mortality of a cohort is dependent on the simultaneous mortality of the previous cohort.

In conclusion, although some characteristics of the study stands were similar to other examples of wave-regeneration dynamics (Kohyama 1988), the regeneration pattern was closely related to stand and tree growth characteristics; AGB and tree height reached an asymptote before the collapsing phase, and high stand density caused a high slenderness ratio and narrow leaf layer. Advanced regeneration of *Abies* seedlings was important in maintaining the dominance of *Abies* in the study stands.

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Figure legends

Fig. 1. Schematic density and biomass dynamics of an even-aged pure plant population. Lines with arrows indicate a schematic trajectory of the population.

Fig. 2. Standard height growth curve for dominant trees. Regression curve: $y = 12.20(1 + 10.79e^{-0.092x})^{1/(1-1.282)}$ ($r^2 = 0.999$).

Fig. 3. Relationships between $D_{0.1}$ and H . $D_{0.1}$: stem diameter at 1/10 of the tree height, H : tree height.

Fig. 4. Aboveground biomass (AGB) and needle biomass.

Fig. 5. Coefficient of variation (CV) for $D_{0.1}$ (white dots) and H (black dots) in plots excluding 5 plots of stand age undetermined (Plots 37, 46, 50, 51 and 52).

Fig. 6. Coefficient of variation (CV), skewness, and Gini coefficient of tree mass. Stands are the same as in Fig. 5.

Fig. 7. Average density in five-year intervals (black dots). White dots depict the density of wave-regeneration stands in central Japan (Kohyama & Fijita 1981).

Fig. 8. Self-thinning line. The regression line is: $\log(\text{mean biomass}) = 6.00 - 1.26 \log(\text{density})$; ($r^2 = 0.971$, by RMA regression). Stands in the initial and collapsing stages were excluded from the analysis.

Table 1 Stand description and density of advanced seedlings

Plot No.	Stand age (years)	Plot area (m ²)	DBH ³⁾ (cm)	H ³⁾ (m)	Density (ha ⁻¹)	Basal area (m ² ·ha ⁻¹)	BA ratio ⁴⁾ (%)	RLI ⁶⁾ (%)	Seedling density ⁷⁾ (m ⁻²)	Mean height ⁸⁾ (cm)
1	26	2	–	0.6	160000	–	97 ⁵⁾	–		
2	28	3	–	1.2	80000	3.3	100 ⁵⁾	0.6		
3	30	4	1.2	1.5	77333	7.0	97	0.8		
4	31	9	–	1.6	88889	6.8	98 ⁵⁾	1.1		
5	31	5	1.2	1.7	135556	14.8	100	0.4		
6	32	8	1.6	2.1	78750	19.7	100	1.1		
7	33	7	–	2.0	122857	25.2	100 ⁵⁾	0.6		
8	34	5	2.2	2.4	82222	37.2	100	0.6		
9	34	12	2.3	2.4	65000	32.4	97	0.9		
10	35	6	3.1	2.8	45000	35.9	98	0.4		
11	36	6	3.1	3.2	43333	36.6	93	1.4		
12	38	12	2.7	3.4	67500	45.1	98	0.6		
13	39	28	3.3	3.6	41071	37.6	100	0.5		
14	39	24	4.3	4.2	31667	49.8	100	0.8		
15	39	32	4.2	4.3	36825	55.2	99	1.0		
16	40	30	3.8	4.1	38000	47.8	96	1.0		
17	40	40	4.7	4.6	30500	55.5	100	0.5		
18	40	20	3.9	3.9	26000	37.1	97	0.6	0	–
19	41	40	5.2	4.8	22750	52.4	90	0.6		
20	41	32	4.5	4.5	32188	57.3	95	0.7		
21	42	32	5.3	5.0	22188	52.8	96	0.8		
22	42	42	4.4	4.5	30714	53.4	96	0.6		
23	42	49	4.6	5.0	32927	59.3	99	0.9		
24	43	40	6.6	5.3	13750	52.9	99	1.3		
25	43	42	5.2	5.0	18571	43.9	89	0.5		
26	43	40	5.8	5.4	17750	53.0	98	0.8	0	–
27	44	49	4.8	5.1	27347	56.9	96	0.6		
28	45	75	4.8	5.4	27467	54.6	99	0.8		
29	45	45	7.0	6.0	9111	37.7	93	5.7		
30	46	50	6.4	6.0	14200	50.7	94	5.2		
31	46	75	6.4	6.1	12400	46.2	90	1.3		
32	47	72	5.2	5.7	15417	37.7	92	0.9		
33	47	90	8.8	6.9	7000	45.8	83	4.1		
34	48	50	7.6	6.4	8800	45.5	99	1.0		
35	48	45	7.9	6.4	9556	51.5	88	2.6		
36	49	60	9.1	7.2	5833	42.5	94	4.0		
37	77< ¹⁾	72	9.9	7.6	2797	24.7	94	46.6		
38	50	90	8.3	7.5	6222	37.9	83	1.9		
39	51	90	10.0	7.4	4889	42.2	95	3.6	4	3.3
40	52	96	10.3	7.7	4167	38.3	89	8.0		
41	52	169	7.8	7.2	6982	40.2	92	2.0		
42	52	80	7.6	7.6	8875	47.6	96	1.4		
43	52	50	8.0	7.2	8200	48.6	99	2.0		
44	56	120	13.0	8.7	3083	47.3	96	2.7	5.9	26
45	56	100	10.9	8.7	4900	49.5	87	2.0		
46	77< ¹⁾	112	12.0	8.5	3214	41.2	92	21.8		
47	60	144	11.9	9.2	4167	52.3	89	12.7		
48	66	150	12.1	8.6	3200	39.0	88	4.2		
49	77	180	12.2	10.6	3444	42.6	80	6.5	26	40
50	77< ¹⁾	800	21.5	9.7	600	23.8	80	34.0		
51	77< ¹⁾	140	13.1	10.3	1429	21.8	92	29.0	41	78
52	Undetermined ²⁾	300	11.7	10.4	3300	51.5	93	5.9	57	34

¹⁾ Stands in collapsing phase.

²⁾ Stand age was not determined because the dominant height was larger than an asymptotic height of the standard height growth curve.

³⁾ Mean value.

⁴⁾ Basal area ratio of *Abies sachalinensis* trees.

⁵⁾ Ratio of the number of trees of *Abies sachalinensis*.

⁶⁾ Relative light intensity at 50 cm above ground or just above saplings.

⁷⁾ Density of advanced seedlings. Advanced seedling density was measured in 6 plots.

⁸⁾ Mean height of seedlings.

Table 2 Density of advanced *Abies* seedlings

	Plot 18	Plot 26	Plot 39	Plot 44	Plot 49	Plot 52	Plot 51
Stand age (yrs)	40	43	51	56	77	– ²⁾	77<
Tree density (ha ⁻¹)	26000	18500	4889	3083	3444	3300	1429
Seedling density (m ⁻²)	0	0	4	5.9	26	57	41
Mean height of seedlings	–	–	3.3	26	40	34	78
RLI ¹⁾ (%)	0.6	0.8	3.6	2.7	6.5	5.9	29.0

¹⁾ Relative light intensity at 50 cm above ground or just above seedlings.

²⁾ Stand age is undetermined. See in Table 1.

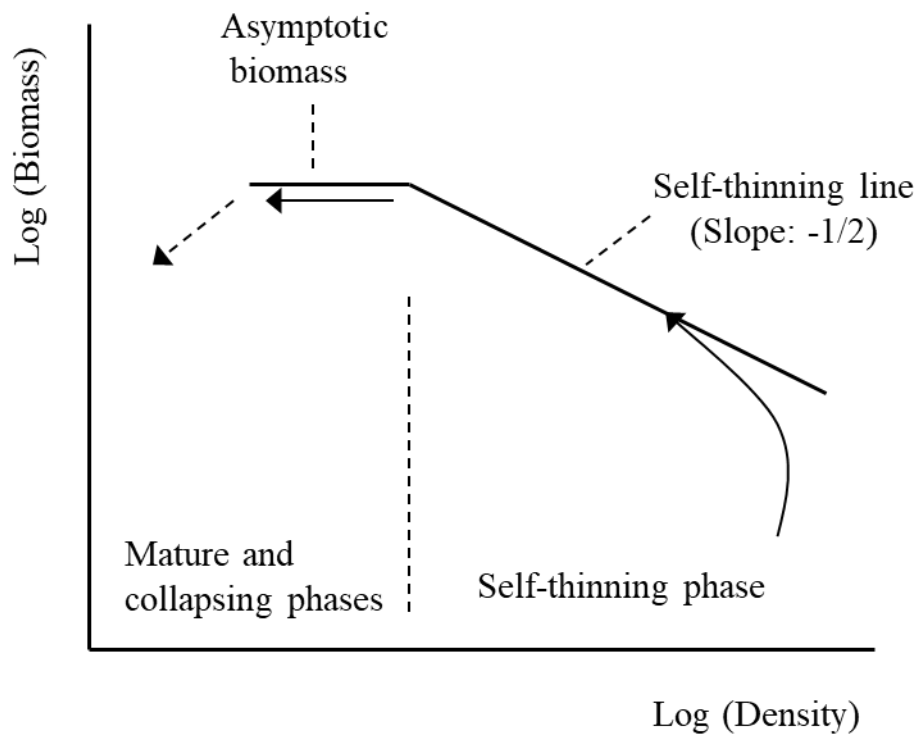


Fig. 1

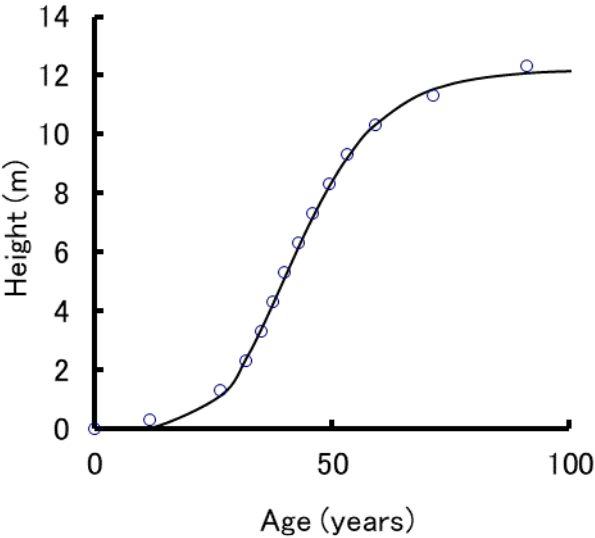


Fig. 2

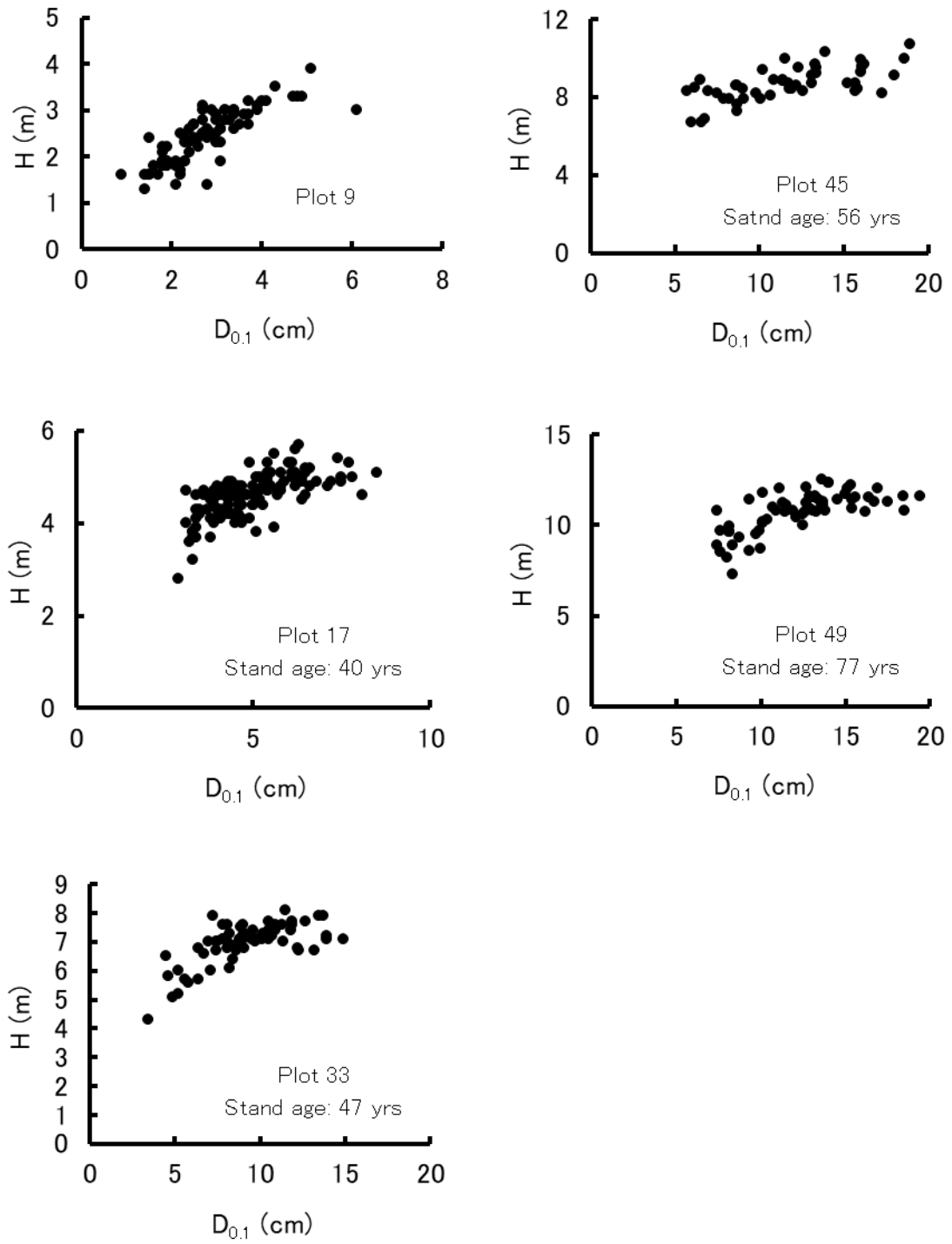


Fig. 3

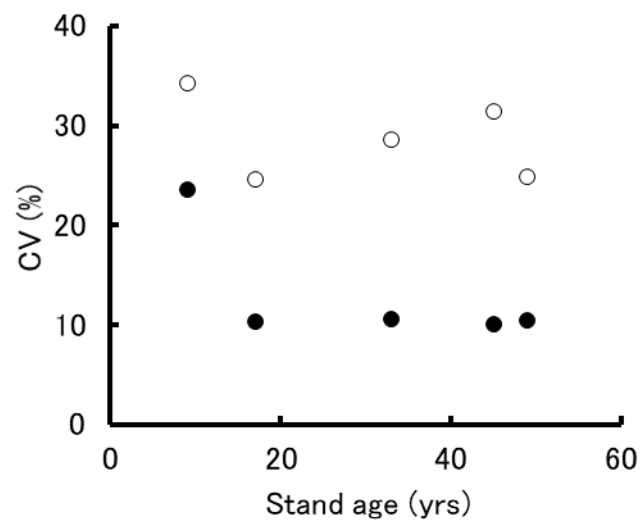


Fig. 4

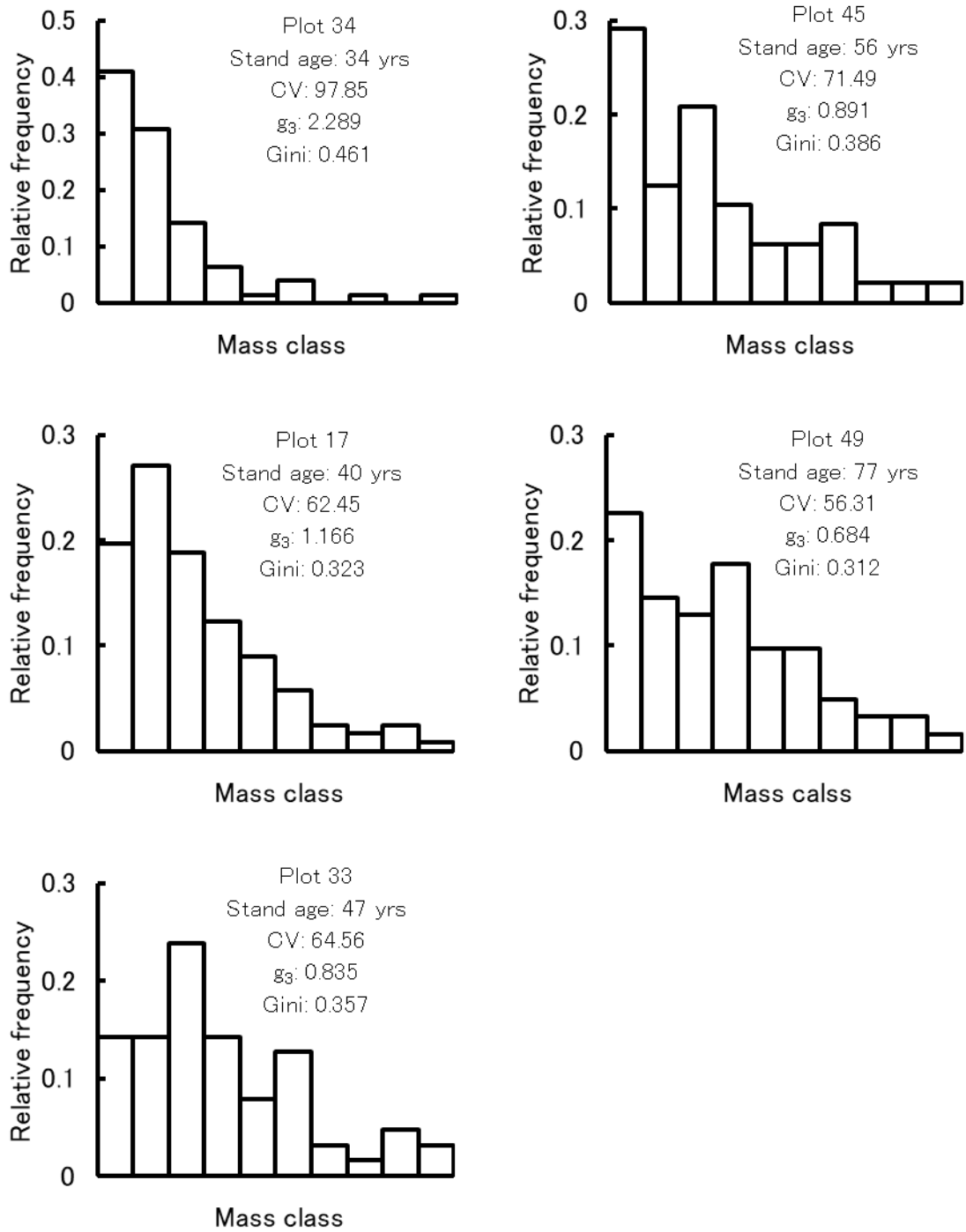


Fig. 5

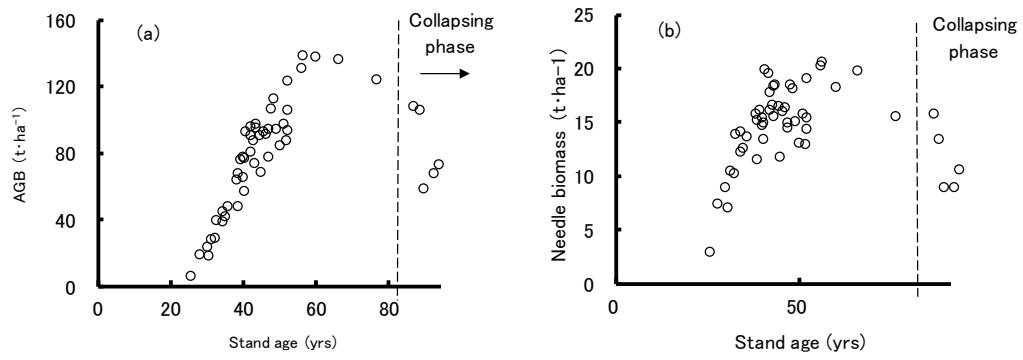


Fig. 6

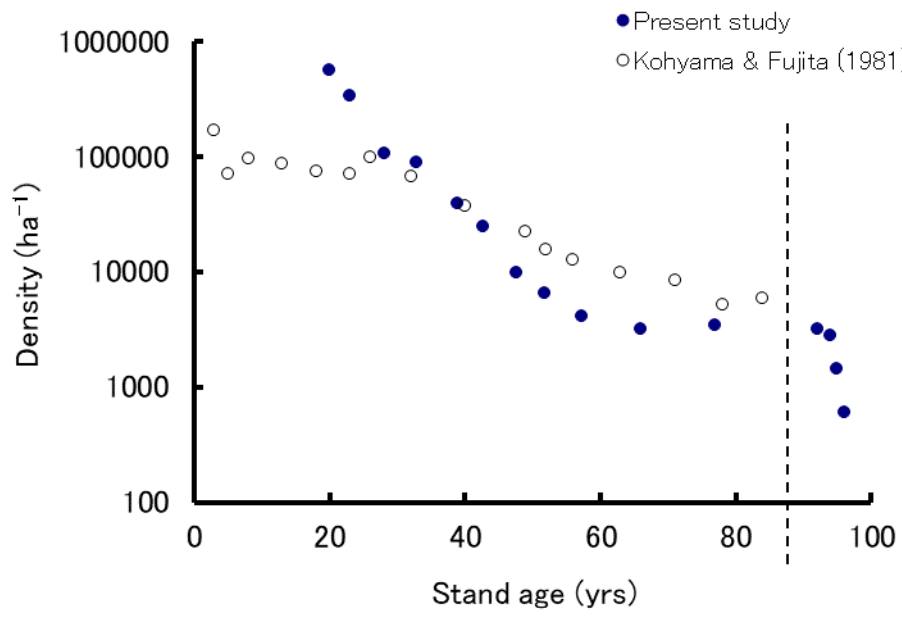


Fig. 7