

Altitudinal variation in lifetime growth trajectory and reproductive schedule of a sub-alpine conifer, *Abies mariesii*

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ABSTRACT

To determine whether forest trees are differentiated in terms of reproductive schedules among populations under different environmental conditions within a species, we studied three populations of Japanese subalpine snow-fir, *Abies mariesii*, located at different altitudes (1000, 1250 and 1400 m) on Mt. Hakkoda in northern Japan. We examined life-history schedules, including lifetime growth trajectories, reproductive maturation timing and size-dependent resource allocation to reproduction. With increasing altitude, the asymptotic maximum size of trees decreased and trees approached their maximum size at younger ages: a substantial reduction in tree growth occurred earlier and life span tended to become shorter with increasing altitude. We found that trees advance their reproductive schedules at higher sites in relation to both maturation timing (size, age and whole-tree growth rate at typical reproductive onset) and resource allocation (reproductive biomass and reproductive effort), coinciding with a general prediction of life-history theory. The rate of growth in height, which was increasing, tended to decrease at around the height at which most trees produced cones, and this height was much less with increased altitude. We propose a new hypothesis that life historical adaptation – that is, earlier resource allocation to reproduction at higher sites – is one of the reasons why trees are smaller at higher altitudes.

Keywords: elevational cline, life-history theory, maturation timing, reduction in tree size, reproductive effort.

INTRODUCTION

When an organism starts reproduction and the amount of resources it allocates to reproduction are major components of the life-history parameters that principally determine the organism's fitness (Stearns, 1992). Many theoretical and empirical

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studies have tried to explain the reproductive schedules of various organisms. For long-lived iteroparous organisms with indeterminate growth, life-history theory predicts that earlier investment of resources in reproduction should be selected in populations in which environmental conditions are severe, for example, where individuals exhibit a low growth rate and/or high mortality. On the other hand, in environments in which individuals can express a rapid growth rate and/or long life expectancy at maturation because of low mortality, a delay in investment of resources to reproduction can be expected (Kozlowski and Uchmanski, 1987; Charnov, 1993; Kozlowski and Teriokhin, 1999). These predictions suggest inter-population relationships as follows: first, the body size at reproductive onset should correlate with the asymptotic or typical final body size; second, the age at reproductive onset should correlate with typical life span. Such relationships have been observed in fishes, reptiles and aquatic invertebrates (Charnov, 1993).

However, investigations of life-history variants of plant species have concentrated on short-lived semelparous herbs, especially biennial plants. In studies on the reproductive timings of biennial plants, which flower once at the end of an individual's life, the size at reproductive onset is consistent with the optimum size that maximizes lifetime reproductive success (Kachi and Hirose, 1985; De Jong *et al.*, 1987) or maximizes population growth rate (Wesselingh *et al.*, 1997), as predicted by models based on life-history theory.

Forest trees are long-lived iteroparous plants with indeterminate growth that have received little attention in this context because of their long life spans and large body sizes. Only a loose correlation has been found between tree size at first reproduction and approximate life span (Harper and White, 1974; Franco and Silvertown, 1996) and between size at first reproduction and asymptotic size (Thomas, 1996) among species. Since there are strong phylogenetic effects on age and size at maturity in general (Stearns, 1992), a comparison within a species would be more informative. On the other hand, some intra-population studies of forest trees have reported results contrary to the predictions based on life-history theory (Kohyama, 1982; Nakashizuka, *et al.*, 1997; Shibata and Tanaka, 2002). These studies found that whether an individual was reproductive depended on its environmental conditions as well as body size, and that trees with high growth rates tended to reproduce at an earlier age and smaller size than the other trees in the population. Therefore, if trees of different populations still adopt the same rule for determining reproductive onset, trees in a population in which they generally experience a higher growth rate may show earlier maturation than trees in other populations. As mentioned above, however, life-history theory predicts that a higher growth rate delays maturation. There are few available data for judging whether trees have different rules for reproductive schedules in different populations under different environmental conditions (but see Silvertown and Dodd, 1999a).

Trees that grow on mountains are exposed to dramatic climatic changes with altitude. Tree size generally decreases with increasing altitude. Although this tendency is sometimes observed as a sequential change in canopy dominants from larger species to smaller species (Ohsawa *et al.*, 1985; Nakashizuka *et al.*, 1992; Lieberman *et al.*, 1996; Tang and Ohsawa, 1997; Pendry and Proctor, 1997; Buot and Okitsu, 1998), it is also common for tree size within the same species to decrease with altitude (Takahashi, 1978; Fusho and Makita, 1981; Koike *et al.*, 1990; Shibata and Ando, 1993; Pyrke and Kirkpatrick, 1994; Srutek and Leps, 1994; Raich *et al.*, 1997; Körner, 1998). Such size reductions have been investigated previously (e.g. Grubb, 1971; Körner, 1998; Vitousek, 1998), but not from an evolutionary point of view.

We explored altitudinal variations in the life-history schedule of *Abies mariesii* Masters (Pinaceae), which is the dominant conifer of the subalpine open forests in the northern part of Honshu, Japan. We chose three populations at different altitudes on Mt. Hakkoda where continuously regenerated stands of *A. mariesii* occur and compared their reproductive schedules. Based on life-history theory, we predicted that trees start reproduction earlier at higher altitude, where trees would have small final size due to the harsh environment. Life-history theory also predicts that such trees advance reproductive schedules in relation to resource allocation after maturation. That is, trees in a harsh environment should show higher reproductive effort than trees at a favourable site at the beginning of their reproductive stage in life. However, reproductive effort increases at a decelerating rate with size at a harsh site, whereas it increases at a constant or accelerating rate at a favourable site (Kozłowski and Uchmanski, 1987). To confirm these predictions, we investigated asymptotic maximum size, maturation timing (size, age and growth rate at reproductive onset) and size-dependent resource allocation to reproduction for the three populations, and also compared mortality tendencies between them. A basic assumption of life-history theory is the existence of a trade-off for resource use between reproduction and other functions, including vegetative growth (Stearns, 1992). Therefore, an advanced reproductive schedule may be one cause why trees are small at higher altitude. We thus investigated lifetime growth trajectories – that is, the size-dependent growth rate for a full range of tree sizes (taller than 1 m).

MATERIALS AND METHODS

Study organism and study site

Abies mariesii is a common conifer species distributed over a wide range of subalpine regions in central and northern Honshu, Japan. It usually co-dominates with other conifers, such as *A. veitchii* in central Honshu, but usually forms pure stands in northern Honshu. *Abies mariesii* is monoecious with conspicuous mast years synchronized within and between populations over large areas. Mast reproductive events occur every 2–3 years (Seki, 1994, 1997), with 1995, 1998 and 2000 being recognized as typical mast years in the study area. In such years, female and male cones appear and pollination occurs in May or June. Male cones wither just after their release of pollen, while seeds mature in female cones in autumn of the same year. The rachises of female cones remain after seed dispersal, at least until the next summer.

The study sites are in subalpine forests on Mt. Hakkoda in Aomori Prefecture in northern Honshu, Japan (40°40'N, 140°25'E). These forests extend from 900 to 1450 m in altitude on this mountain. They are almost completely composed of natural pure stands of *A. mariesii*, sometimes with *Betula ermanii* Cham. in the canopy layer and some deciduous shrubs such as *Sorbus commixta* Hedl. in the sub-canopy layer. The forest understorey is covered with dense shoots of *Sasa kurilensis* (Rupr.) Makino et Shibata at the low and middle altitudes of the subalpine zone, but is dominated by *Pinus pumila* (Pallas) Regel and deciduous shrubs at higher altitudes. Average annual maximum snow depth is around 3.5 m across a wide range of altitudes (Bokura and Fukuti, 1994). In winter, small trees are completely buried in snow and taller trees are covered with snow and ice. *Abies mariesii* takes on a flag-like form under severe weather conditions, but it never has a krummholz form or loses its apical stem in normal growth, even in the marginal parts of the distribution range.

We examined three *Abies* populations at different altitudes in the subalpine zone: 1000 m (low site), 1250 m (middle site) and 1400 m (high site). We selected study sites on gentle western-facing slopes of the mountain, where weather conditions are relatively mild, to avoid the effects of deformation of tree crowns due to wind and snow in winter. The plot areas of the low, middle and high sites were 2000 m² (50 × 40 m), 612 m² (a 70-m transect with irregular width to avoid gullies) and 625 m² (25 × 25 m), respectively. The densities of trees taller than 1 m were 515, 1029 and 1376 per hectare, and the sums of these basal areas were 127, 126 and 17 m³ · ha⁻¹ for the low, middle and high site, respectively.

Based on field observations and considerations of size and age distribution, we assumed that the studied populations had maintained stable structures by means of sequential regeneration with a tree-to-tree pattern, the dominant way in this region (Makita, 1997). There was no indication of synchronized wave-like regeneration or occasional regeneration, such regeneration probably depending on the mass death of *Sasa*.

Field methods

In 1996, we tagged all trees taller than 1 m and recorded the diameters (*D*) of the lowest parts of their boles (at 30 cm above the ground or just above the buttress if it reached over 30 cm). Diameter at breast height was also recorded for trees sufficiently large to measure. We also checked tree forms: most trees at the study sites were normal conical, while some had two stem axes, suggesting breakage in the past. If the point of separation was so low that two diameters were obtained at the same height of measurement, or if the treetop had been lost due to recent breakage, the tree was excluded from the analyses. Excluding eleven, six and nine such trees, the respective number of trees subjected to analysis were 103, 63 and 86 at the low, middle and high site, respectively. We measured tree height (*H*) with a tape measure by climbing sufficiently large trees, and with a measuring pole for the smaller trees. Height was recorded at the point of the last winter-bud scar of each tree trunk, and thus the heights of the trees in 1995 were recorded. Growth rates were measured for *H* and *D*: the distance between the first winter-bud scar and the eleventh scar on the trunk from the treetop was recorded as the height growth rate for 10 years (from the end of 1985 to the end of 1995). To estimate diameter growth rates, we collected short wood samples using increment borers and measured the widths of tree rings for the same 10 years. The wood samples were taken in four rectangular directions (two or three directions for small trees) from the lower part of boles, about 50 cm above the ground for all trees, excluding those too small for borers to be used, and the measured ring widths were averaged for each tree. There were 72, 52 and 69 trees for the low, middle and high site, respectively. To estimate the relationship between tree size and age for each study site, we collected a wood sample for each tree, the sample reaching the core of the bole. Because of difficulties in handling smaller trees to avoid damage, core samplings were mainly from relatively larger trees – that is, 22, 21 and 33 trees for the low, middle and high site, respectively.

In 1996, we counted the rachises of cones produced in 1995 for all trees to examine reproductive mode in relation to size. In 1998, to estimate reproductive biomass, we re-examined all trees for cones. We then selected 14, 13 and 5 various-sized trees with cones in the low, middle and high site, respectively, to estimate the dry mass of male cones per tree. We chose the sample trees on the basis of size, trying to obtain a full range of tree sizes that had male cones at each study site. For each of the sample trees, we harvested a 3-year-old shoot (i.e. the terminal part of a branch, including the last three inter-nodes and ramific-

ations) from each of four rectangular directions (two or three directions for small trees) of three heights of its tree crown in late May or early June 1998. Typically, 12 shoot samples per tree were collected. To estimate the dry mass of female reproductive organs, we counted the number of female cones for all trees with female cone(s), and harvested some of them (three cones from each of 9–11 trees) at each study site in September 1998.

Data analyses for growth pattern

To compare growth trajectories of trees between the studied populations, we calculated R^2H (the square of trunk radius at a height of 30 cm multiplied by tree height) as a measure of tree size. The increment rate of R^2H for the period between 1985 and 1995 was calculated from the increments of diameter and height, and arranged as a function of R^2H in 1995 for each population. Since trees apparently deformed due to disturbance had been excluded, this indicates the ideal growth pattern of individual trees when they are not disturbed. However, since this method was based on the growth rate of the last 10 years, we also used another method for whole growth rates of individual trees – namely, we counted annual rings on the wood samples extending to the bole centre and plotted R^2H against the number of rings. Because this wood sampling did not reflect the size distribution of each population and a large number of juveniles were less sampled, and because large variances existed suggesting that trees had experienced disturbances in the past and repaired tree forms were included, we referred to but did not use these data to detect age and size relationships in this study.

To estimate final body size, an important life-history component, we denoted the growth trajectory of each population as the regression function for the plots of the relative growth rate (*RGR*) of individuals against body size, and obtained the size at which the regression curve reached zero. Because the curve fittings were all significant, we regarded its size as the asymptotic maximum size, or the typical final body size of each population. We calculated relative growth rate for open growth trees using

$$RGR = \frac{\ln S_{1995} - \ln S_{1985}}{10} \quad (1)$$

Here, S_{1995} and S_{1985} denote observed and estimated tree size in each year. We fitted the Gompertz function, $a - b \ln S_{1985}$, and $\exp(a/b)$ was calculated as the asymptotic maximum size at each study site (Aiba and Kohyama, 1996).

Data analyses for reproduction

To detect the typical size at which trees start reproduction, we fitted a logistic regression function to binary data of reproductive status (1 for the trees having cones and 0 for the others) in 1995 for each study site:

$$p = \kappa / (1 + e^{\mu + \alpha x}) \quad (2)$$

where x is the logarithmic transformed tree height or diameter at a height of 30 cm and p is the cone production probability in 1995. The constants κ , μ and α were detected with the maximum-likelihood method. Here, κ , the parameter determining the maximum probability of reproduction, was fixed at 1 for the low and middle sites because larger trees

all had cones at these sites. The difference in the fitted curves for each of all combinations of the study sites was tested by the log-likelihood ratio test (Wesselingh and Klinkhamer, 1996). The inflection point of the function of the first derivative of equation (2) was defined as the typical threshold size of reproductive onset (Thomas, 1996).

Total reproductive biomass was estimated for all reproductive trees in 1998. The estimation method used was as follows. First, we estimated total dry mass of male cones produced by a tree from the relationship between dry mass of male cones and needle leaves on the sampled shoots. Since the sampled shoots were 3 years old, it was necessary to know the allometric relationship between tree size and total amounts of current to 3-year-old needles on the tree to estimate the total dry mass of male cones. The allometric relationships among plant parts have previously been examined in *Abies veitchii* (Tadaki *et al.*, 1970), another subalpine conifer known to have allometric characteristics very similar to those of *A. mariesii* (Kimura, 1963). We adopted the relationship between total dry mass of current needles and tree size from Tadaki *et al.* (1970), covering the full range of tree sizes in this study. Furthermore, Kimura (1963) described the survivor curve of needles on canopy trees of *A. mariesii*. Using those data, we evaluated the total dry mass of current to 3-year-old needles as a function of tree size (R^2H), and then estimated the total dry mass of male cones produced by a tree for all trees with male cones. Second, for female organs, we measured the mean dry mass of female cones sampled at each study site. We estimated the total dry mass of female cones produced by a tree, calculating the product of the number of cones and the mean dry mass of cone for each tree. We defined the reproductive biomass as the sum of the estimated total dry mass of male and female cones produced by a tree.

RESULTS

Asymptotic maximum size

From the low (1000 m) to the middle (1250 m) to the high site (1400 m), heights and diameters became progressively shorter and smaller, respectively (Fig. 1). The observed maximum heights were 16.2, 12.6 and 5.9 m, and the observed maximum diameters were 63.4, 52.4 and 28.5 cm, at the low, middle and high site, respectively. The asymptotic maximum sizes estimated for zero relative growth rates on the Gompertz fitting curves (Fig. 2) and their 95% upper and lower confidence limits were 19.0 (23.5, 16.2), 13.4 (16.3, 11.6) and 5.5 (6.6, 4.8) m for height, and 65.4 (86.7, 53.9), 62.4 (87.5, 49.9) and 30.5 (45.7, 23.4) cm for diameter, for the low, middle and high site, respectively.

Reproductive schedule

Forty-nine of the 103 trees at the low site, 40 of the 63 trees at the middle site and 40 of the 86 trees at the high site produced cones in 1995. The trees with and without cones tended to be segregated in terms of height and diameter at each site (Fig. 1). The probability curves for reproduction (Fig. 3) were significantly different between the sites, although the differences between the low and middle sites for diameter were only marginally significant (the log-likelihood ratio test; degrees of freedom = 2): For tree height, $\Lambda^2 = 6.06$, $P < 0.05$ between the low and middle sites; $\Lambda^2 = 23.24$, $P < 0.0001$ between the low and high sites; and $\Lambda^2 = 6.44$, $P < 0.05$ between the middle and high sites. For tree diameter, $\Lambda^2 = 5.80$, $P = 0.055$

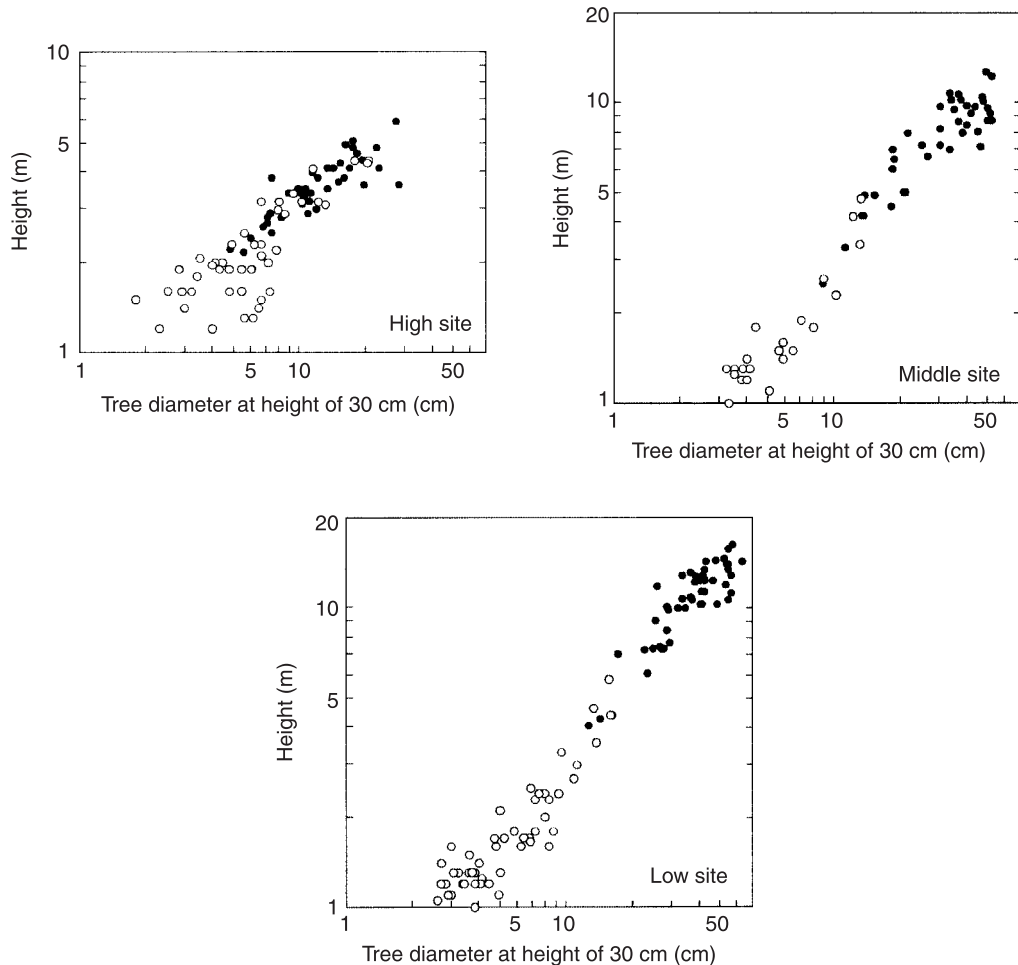


Fig. 1. Tree sizes of *Abies mariesii* in the three studied populations: low (1000 m), middle (1250 m) and high site (1400 m) on Mt. Hakkoda, northern Japan. Solid and open circles denote trees with and without cones, respectively, in 1995.

between the low and middle sites; $\Lambda^2 = 27.09$, $P < 0.0001$ between the low and high sites; and $\Lambda^2 = 9.62$, $P < 0.01$ between the middle and high sites. The peaks of the first derivative of the probability curves, which indicate typical sizes for first cone production, were 4.7, 3.2 and 2.3 m for height, and 15.4, 11.1 and 6.8 cm for diameter, at the low, middle and high site, respectively.

Total reproductive biomass (Fig. 4) increased consistently with tree size (Fig. 4a and 4b) and with growth rate (Fig. 4c) at all study sites. The slopes and intercepts of all regression lines were significantly different from each other with the exception that reproduction versus tree height was not different between the middle and high sites (Table 1). The smaller-sized trees or trees with a smaller growth rate tended to produce more cones at the higher sites than at the lower sites, while the larger trees or trees with a larger growth rate tended to produce more cones at the lower than at the higher sites.

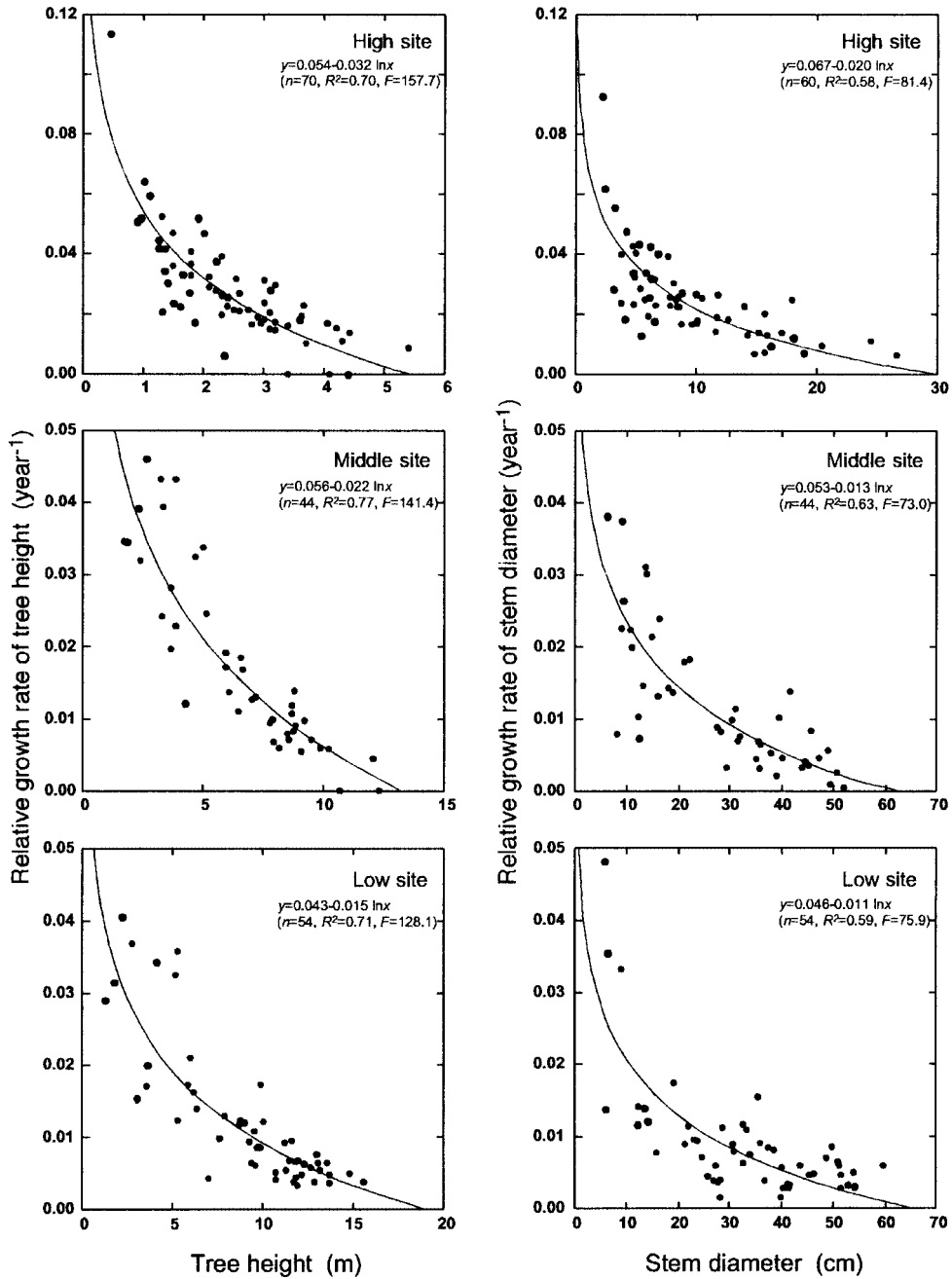


Fig. 2. Relative growth rates of open growth trees for the period 1985–95 in relation to tree height and diameter at a height of 30 cm for the three populations of *A. mariesii*. Data are plotted against the sizes in 1985 and fitted by the Gompertz functions (see text). All fits were significant ($P < 0.00001$).

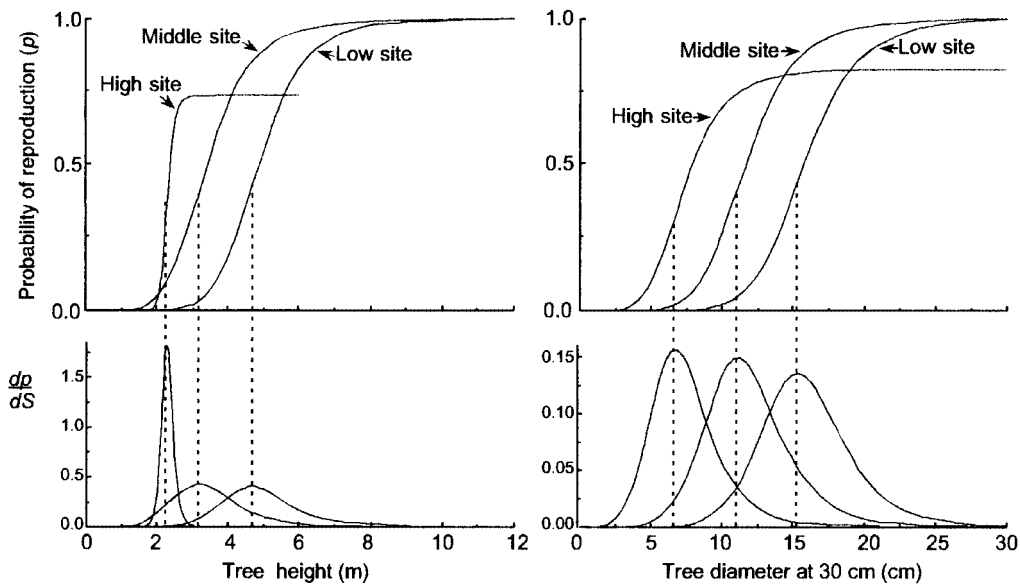


Fig. 3. The upper row of figures shows probabilities of reproduction (p) at a given height (m; h) and diameter (cm; d) calculated from binary data of the reproductive mode of all trees: $p = 0.73 / (1 + \exp(18.36 - 22.50 \ln h))$ and $p = 0.83 / (1 + \exp(10.16 - 5.09 \ln d))$ at the high site; $p = 1 / (1 + \exp(6.76 - 5.57 \ln h))$ and $p = 1 / (1 + \exp(16.66 - 6.79 \ln d))$ at the middle site; and $p = 1 / (1 + \exp(12.04 - 7.63 \ln h))$ and $p = 1 / (1 + \exp(23.18 - 8.41 \ln d))$ at the low site. These first derivatives are shown in the lower row of figures.

Growth conditions

The increment rate of R^2H increased monotonically with size at decelerating rates that varied slightly among sites (Fig. 5), slowing more rapidly at the higher sites. The overall significance of differences between regression curves tested by the log-likelihood ratio test (degrees of freedom = 4) was $P = 0.053$ ($\Lambda^2 = 9.37$) between the low and middle sites, $P < 0.0005$ ($\Lambda^2 = 21.61$) between the low and high sites and non-significant ($\Lambda^2 = 3.94$) between the middle and high sites. Despite the partially significant differences, these trajectories were similar between the sites. The approximate age-size relationships in the sampled trees (Fig. 6) agreed with this tendency. The degrees of freedom (d.f.) and t -values for slope (t_s) and intercept (t_i) with P were: d.f. = 39, $t_s = 1.77^{NS}$ and $t_i = 0.58^{NS}$ between the low and middle sites; d.f. = 51, $t_s = 2.04$ ($P = 0.046$) and $t_i = 1.09^{NS}$ between the low and high sites; and d.f. = 50, $t_s = 0.53^{NS}$ and $t_i = 0.33^{NS}$ between the middle and high sites.

On the other hand, the right-hand side of Fig. 5 shows that the height increment of shorter trees increased with height but that of taller trees decreased for all sites. The log-likelihood ratio tests (degrees of freedom = 5) indicated that the fitting curves of the three sites were significantly different from each other: $P < 0.01$ ($\Lambda^2 = 16.71$) between the low and middle sites; $P < 0.0001$ ($\Lambda^2 = 29.42$) between the low and high sites; and $P < 0.0001$ ($\Lambda^2 = 28.27$) between the middle and high sites. With increased altitude, the height at which the growth rate changed from increase to decrease tended to become much less.

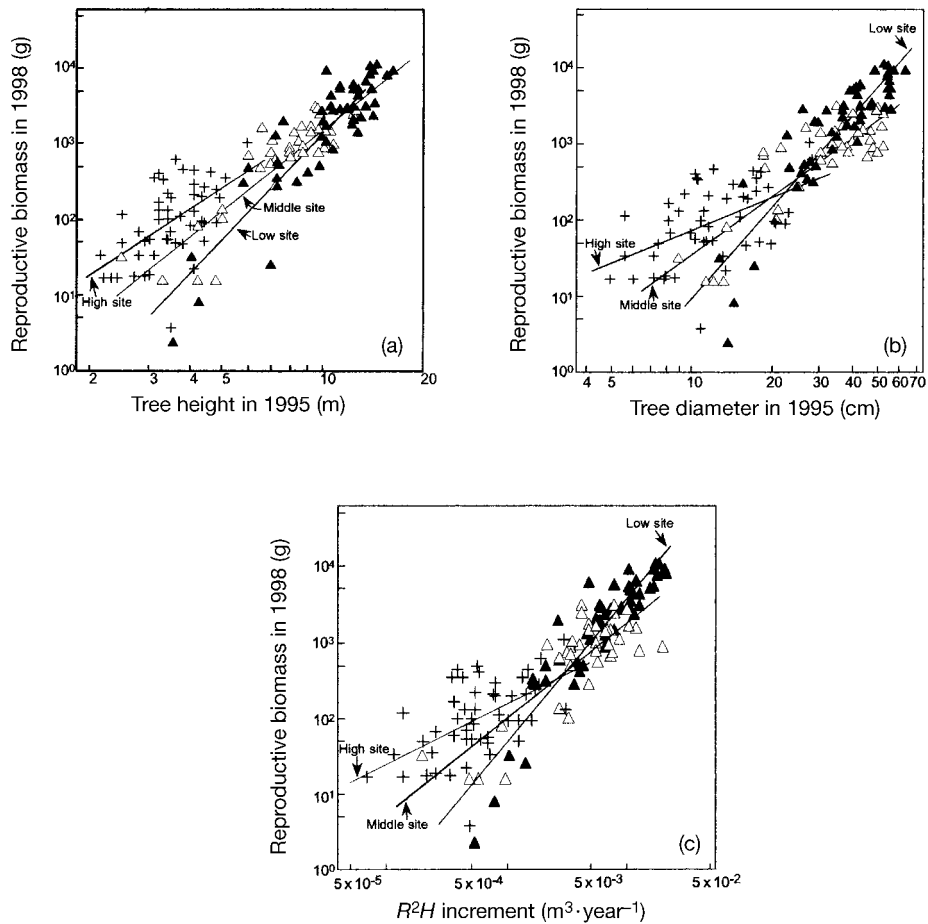


Fig. 4. Total dry weights of reproductive structures (female cones and male inflorescences) of *A. mariesii* in the three populations in 1998. Data are plotted against (a) tree height and (b) diameter at a trunk height of 30 cm in 1995, and (c) the size increment rate for the period 1985–95. All fittings were significant ($P < 0.0002$). In the order low, middle and high site: (a) $\log y = -1.50 + 2.02 \ln x$ ($n = 51$, $R^2 = 0.80$, $F = 192.7$), $\log y = -0.36 + 1.55 \ln x$ ($n = 38$, $R^2 = 0.77$, $F = 123.2$) and $\log y = 0.40 + 1.26 \ln x$ ($n = 50$, $R^2 = 0.32$, $F = 22.8$); (b) $\log y = -3.02 + 1.74 \ln x$ ($n = 51$, $R^2 = 0.79$, $F = 189.0$), $\log y = -0.98 + 1.10 \ln x$ ($n = 38$, $R^2 = 0.71$, $F = 89.6$) and $\log y = 0.43 + 0.62 \ln x$ ($n = 50$, $R^2 = 0.27$, $F = 17.6$); and (c) $\log y = 7.41 + 1.91 \log x$ ($n = 51$, $R^2 = 0.84$, $F = 256.1$), $\log y = 5.80 + 1.27 \log x$ ($n = 38$, $R^2 = 0.67$, $F = 71.8$) and $\log y = 4.57 + 0.79 \log x$ ($n = 50$, $R^2 = 0.33$, $F = 23.4$), respectively. +, high site; △, middle site; ▲, low site.

The size increment rate at the typical size at reproductive onset (Fig. 4) tended to be smaller in the order low, middle and high site: the means (plus positive and negative standard errors) for R^2H (m³·year⁻¹) calculated using the regression functions (Fig. 5) were 0.000829 (0.00132, 0.000521) for the low site, 0.000443 (0.000752, 0.000262) for the middle site and 0.000126 (0.000204, 0.000078) for the high site.

Figure 7 shows size distributions of trees for the three populations. The high site had distribution patterns distinctive from the others. At the high site, we found that more

Table 1. The results of *t*-tests for the differences in regression lines among three populations of *Abies mariesii* (shown in Fig. 4) for the relationships between reproductive biomass in 1998 and (a) tree height in 1995, (b) tree diameter in 1995 and (c) R^2H increment

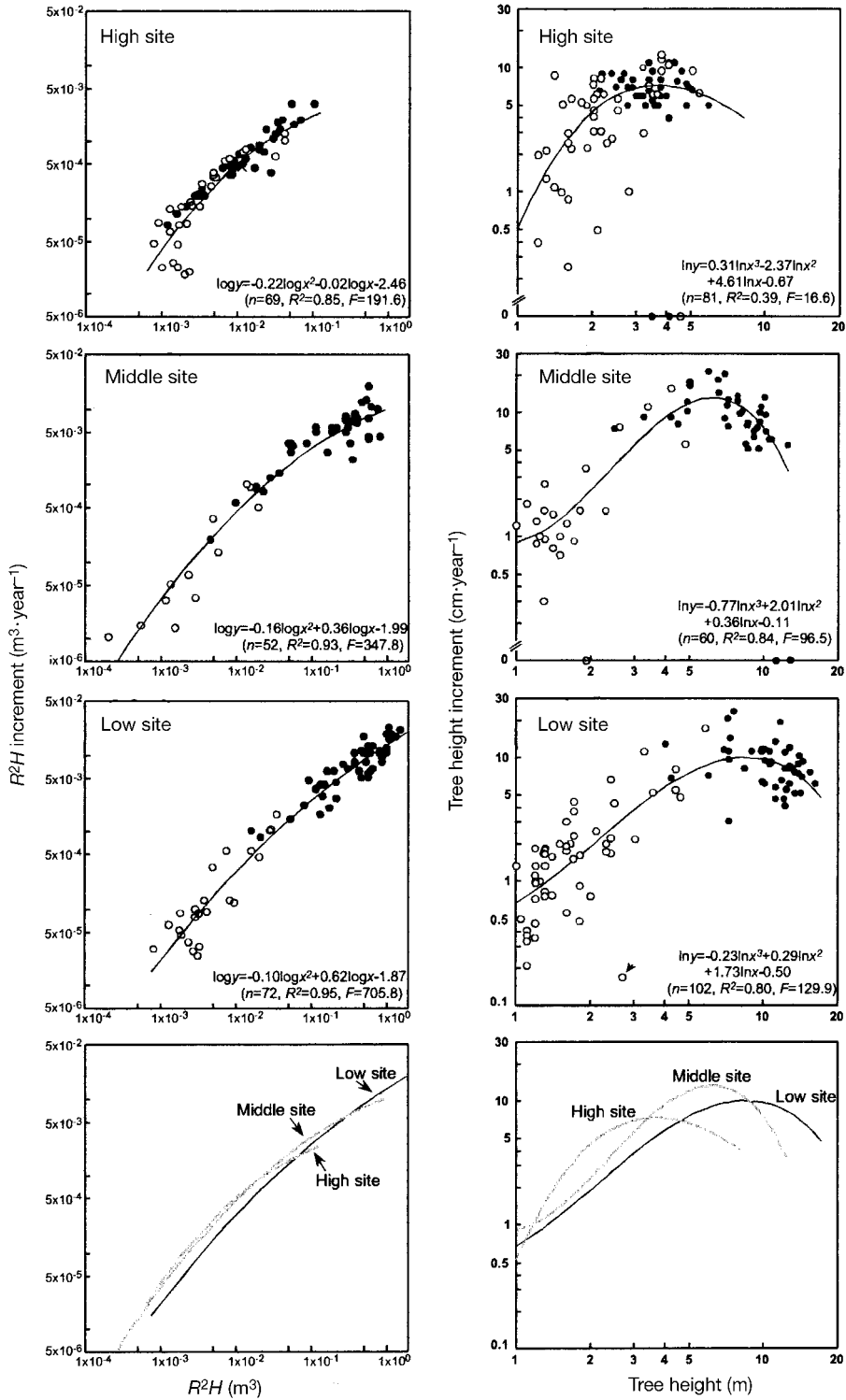
| | d.f. | <i>t</i> -values for slope | <i>P</i> | <i>t</i> -values for intercept | <i>P</i> |
|--------------------------|------|----------------------------|----------|--------------------------------|----------|
| (a) Tree height | | | | | |
| High vs middle site | 84 | 0.98 | 0.33 | 1.64 | 0.11 |
| High vs low site | 97 | 2.58 | 0.011 | 3.90 | 0.0002 |
| Middle vs low site | 85 | 2.28 | 0.025 | 2.53 | 0.013 |
| (b) Tree diameter | | | | | |
| High vs middle site | 84 | 2.50 | 0.014 | 2.45 | 0.016 |
| High vs low site | 97 | 5.70 | <0.0001 | 5.66 | <0.0001 |
| Middle vs low site | 85 | 3.69 | 0.0004 | 3.37 | 0.0011 |
| (c) Growth rate | | | | | |
| High vs middle site | 84 | 2.10 | 0.039 | 1.91 | 0.060 |
| High vs low site | 97 | 5.52 | <0.0001 | 4.97 | <0.0001 |
| Middle vs low site | 85 | 3.43 | 0.0009 | 3.66 | 0.0004 |

juveniles become established and participate in reproduction but that tree densities decrease gradually in all size classes, with more rapid decreases with increasing size. At the middle and low sites, on the other hand, the establishment of juveniles was relatively restricted and remarkable reductions were observed between the smallest and the next smallest classes, which mainly consisted of juveniles. Thereafter, trees tended to maintain similar densities until they reached the largest classes. This tendency, which is opposite to that of the high site, was more marked at the low site than at the middle site.

DISCUSSION

Timing of reproductive onset

The variation in reproductive schedules among the populations of *Abies mariesii* can be interpreted in terms of life-history theory. The typical height and diameter at reproductive onset changed in the same order as the asymptotic maximum height and diameter of the populations: in the order low, middle and high site, both the asymptotic sizes and the typical sizes when trees start to have cones tended to become smaller, although the difference in the asymptotic diameter between the low and middle sites was not statistically significant. The reproductive timings in terms of age tended to show a similar pattern. Applying 0.001 in R^2H ($\text{m}^3 \cdot \text{year}^{-1}$) as the reference size to the functions of the tree size increment rates (Fig. 5), relative age (the real age minus unknown years; that is, the age when a tree reached the size of 0.001 in R^2H) at the typical size of reproductive onset was calculated as 123, 60 and 24 years for the low, middle and high site, respectively. Similarly, 353, 277 and 132 years were estimated for the low, middle and high site, respectively, for the attainment of asymptotic maximum R^2H . Intra-population studies have found that earlier reproductive timing



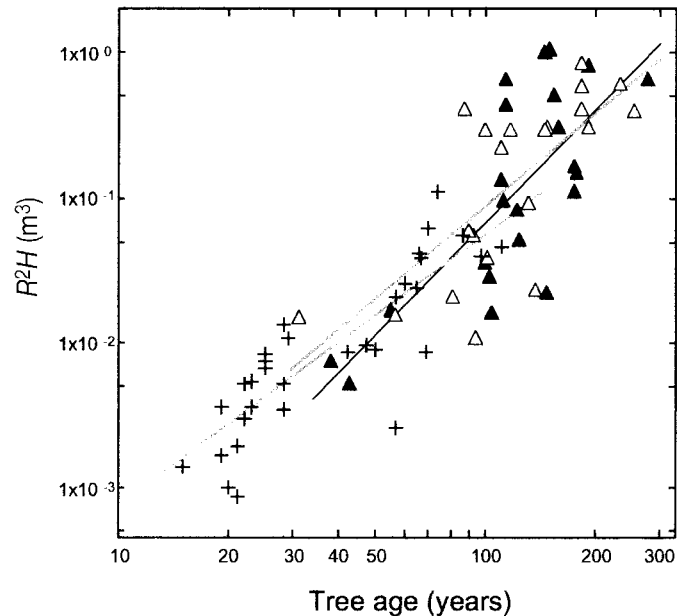


Fig. 6. Relationship between observed age at a trunk height of about 50 cm and tree size for the three populations of *A. mariesii*. The fit lines were all significant ($P < 0.0002$): $\log y = 2.58 \ln x - 14.58$ ($n = 22$, $R^2 = 0.56$, $F = 25.3$) at the low site; $\log y = 2.12 \ln x - 12.21$ ($n = 21$, $R^2 = 0.53$, $F = 21.3$) at the middle site; and $\log y = 1.88 \ln x - 11.53$ ($n = 33$, $R^2 = 0.70$, $F = 73.9$) at the high site. + high site; Δ , middle site; \blacktriangle , low site.

occurs in individuals with higher growth conditions within populations (Kohyama, 1982; Nakashizuka *et al.*, 1997; Shibata and Tanaka, 2002). In the present inter-population study, however, the earlier reproductive onset was not related to a higher growth rate: overall growth rate of the whole tree (R^2H) was similar among the populations (Fig. 5), and the growth rate at the typical size at reproductive onset was also smaller in the order low, middle and high site. This suggests that the studied populations are differentiated in terms of the rules for determining reproductive onset.

Life-history theory explains that the balance between the cost and benefit of reproduction, which varies depending on size and age, determines the lifetime schedule of resource allocation to reproduction. The benefits of earlier maturation are shorter generation times and higher survival to maturity because the juvenile period is shorter (Stearns, 1992). Kozłowski and Uchmanski (1987) developed a theoretical model for reproductive schedules of iteroparous indeterminate growth organisms and showed that the optimal

Fig. 5. Size increment rates of trees for the period 1985–95 in the three populations of *A. mariesii* in terms of whole growth rate (left-hand side) and height growth rate (right-hand side). Solid and open circles denote trees with and without cones, respectively. Data are plotted against sizes in 1995. All fits were significant ($P < 0.0001$). For the height growth rate, trees recorded as zero growth and a tree indicated by an arrow were excluded from the fittings. Whole growth rate of those trees is not shown (not calculated).

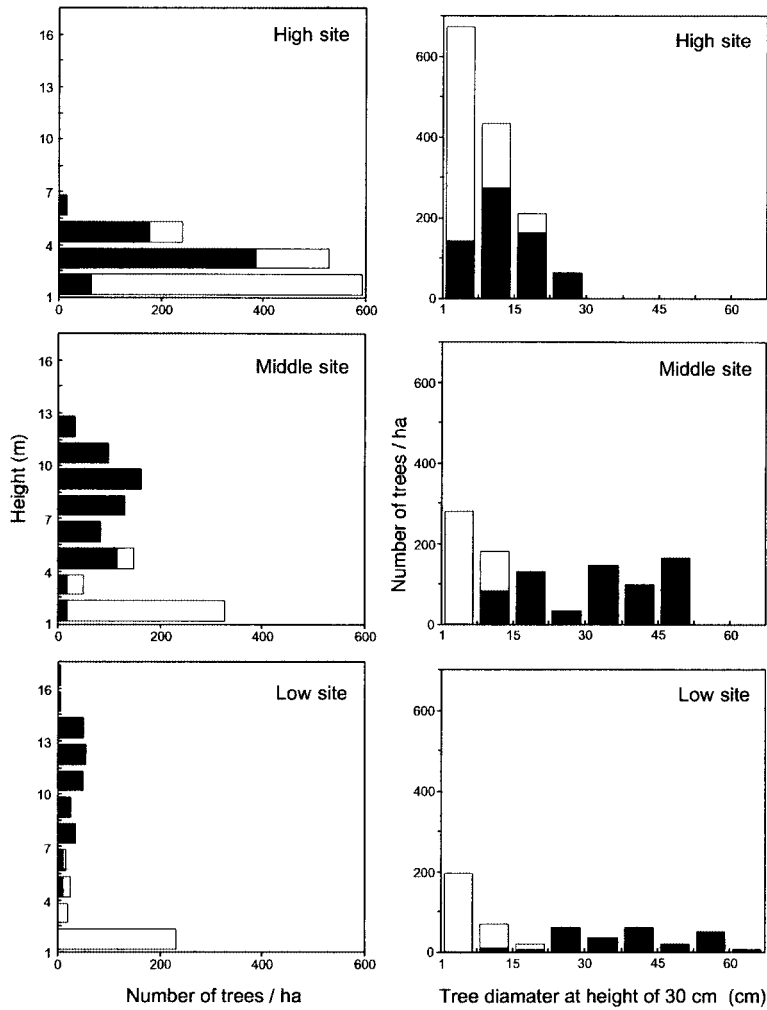


Fig. 7. Size distributions of *A. mariesii* for the three populations. Solid and open bars show trees with and without cones, respectively.

maturation age is younger with higher yearly mortality even if the production rate (potential growth rate) is the same. This appears to explain the advanced reproductive schedule observed at the high site. Since overall growth rates were not too different between the populations, size distribution at the high site (Fig. 7) suggests that the mortality rate is relatively high overall and that as trees become larger, the mortality rate increases much more. Although not investigated directly in this study, disturbance and stress, such as ice- and snow-storms, are probably important mortality factors (Ishizuka, 1981). These effects are usually stronger at higher sites, and taller trees within a population would be more strongly disturbed and older trees exposed to stress for a longer time. Moreover, trees at the high site may produce softer wood, allowing faster growth (since overall growth rates were very similar among the populations, although production rate may be smaller with increasing altitude). This may result in much higher mortality at the high site. Delayed

maturation, however, is potentially selected where long life expectation at maturation is expected. This can explain the observed delayed maturation at the lower sites. At the lower sites, tree death tended to be concentrated in the smallest size classes before maturation (Fig. 7). On the other hand, the size distribution suggests that trees enjoy considerably low mortality with long life expectancy after maturation, probably owing to relatively mild climatic conditions. The main cause of juvenile death is probably over-topped covering by large trees with wide crowns. It appears that trees delay reproductive onset to concentrate resources on vegetative growth until they reach a safe size.

Resource allocation to reproduction after maturation

We found that reproductive schedules were different among the populations not only for the reproductive onset but also for subsequent fecundity pattern (Fig. 4): trees tended to have large reproductive biomass immediately after the onset of reproduction in the higher sites. On the other hand, the increment rate of reproductive biomass against size (Fig. 4a,b) and thus age was smaller at the higher sites. Notably, the disproportionately large reproductive outputs of smaller trees at the higher sites is not caused by an increase in tree productivity (\equiv increment of tree size), but rather by a large allocation of resources to reproduction or reproductive effort (Fig. 4c). This result is also consistent with the predictions based on life-history theory. Kozłowski and Uchmanski (1987) theoretically drew an optimal timetable of reproductive effort and showed that optimal reproductive effort increases monotonically with age with various patterns depending on mortality: when yearly mortality is high, the increment rate of optimum reproductive effort is high at the beginning and decelerates with ageing. When mortality is low, however, the increment rate of optimum reproductive effort is low at the beginning and then tends to be constant or to accelerate.

A monotonic increase in reproduction biomass throughout life has, however, not always been observed in forest tree species (Harper and White, 1974; Watkinson and White, 1985; Greene and Johnson, 1994). For example, Kohyama (1982) examined the fecundity pattern of *Abies veitchii* growing in a wave-regenerated forest and found that its reproductive effort reached the maximum just after commencement of reproduction and decreased with tree height. Theoretical models for life-history strategies do not generally deal with competition among individuals (those are usually not game models). However, forest trees sometimes experience severe competitive conditions (e.g. in dense stands which undergo self-thinning) until the late stage of life. Also, there are usually other co-occurring tree species with various life-history traits, which form more complex competitive conditions. In such cases, trees may not simply increase reproductive biomass or reproductive effort with increasing size and age. In this study, the populations form mono-species sparse forests with less competitive open canopies, the common structure of the forests in this region. Seki (1994) also reported a monotonic increase in female cones with increasing tree size at another site on Mt. Hakkoda. Whether the predicted pattern in reproductive schedules among populations appears may depend on stand conditions of the habitats.

Altitudinal reduction in size from the viewpoint of life-history strategy

The asymptotic maximum size estimated for the study sites decreased with increasing altitude. Decreases in height and diameter of canopy trees of this species have also been reported on Mt. Hakkoda (Fusho and Makita, 1981) and on another mountain (Shibata

and Ando, 1993). The reduction in tree size along altitudinal gradients is a worldwide phenomenon, and its proximate factors, such as disturbance, stress, carbon balance and limited growth due to cold temperatures, have been investigated in ecophysiological studies (Körner, 1998). Although our results can be interpreted using some of these proximate factors, we propose another hypothesis based on life-history theory, which would at least partially explain the reduction in size of trees with increasing altitude.

As mentioned above, the reduction in asymptotic maximum size with increasing altitude in this study is mainly due to the shorter life span. However, we also found that relative growth rate gradually decreased and became nearly zero in the largest trees for all populations (Fig. 2). This indicates that a substantial reduction in growth in the late stage of life also regulates the maximum size of the trees in the studied populations. Life-history theory principally assumes the existence of a trade-off between current reproduction and vegetative growth and/or survival rate, both of which influence future reproduction (Stearns, 1992; Jönsson and Tuomi, 1994). The trade-off between growth and reproduction is the best-confirmed broad-sense phenotypic trade-off (Kozłowski, 1992; Stearns, 1992; Ryan *et al.*, 1997). Increases in seed and cone production have been reported to reduce size increments and to cause crown deterioration (ageing) in various forest trees, including other *Abies* species (Eis *et al.*, 1965; Linhart and Mitton, 1985; Woodward *et al.*, 1994; Ryan *et al.*, 1997). At higher sites, in addition to the direct effects of a harsh environment, a disproportionately large allocation of resources to reproduction in young plants may promote ageing and thus may result in an earlier reduction in growth.

In this study, the tendency for an earlier reduction in growth at higher sites was more clearly reflected in height growth rate than in whole growth rate (R^2H) of trees (Fig. 5). The height growth rate, which was increasing, began to decrease at around the height at which most trees produced cones. This may be because reproductive organs are strongly concentrated on treetops in this species. We confirmed that every female cone was on the uppermost 20% of the tree crowns on average. Male flowers were widely distributed, but their densities were also higher on the upper part of the crowns (A. Sakai *et al.*, unpublished). Resource transport for reproductive organs within a tree body may be relatively limited (Watson and Casper, 1984; Marquis, 1992; Obeso, 1997), and a large part of resources used for reproduction may be supplied to the portion near the treetop, which may enhance a gradual reduction in height growth.

Nevertheless, for exact certification, the costs of reproduction on growth rate should be measured quantitatively. There are many difficulties in detecting the reproductive costs for long-lived plants (Silvertown and Dodd, 1999b). Recently, however, Silvertown and Dodd (1999b) succeeded in evaluating the cost of reproduction to growth rate and survival ratio using demographic analysis in wave-regenerated *Abies balsamea* in North America.

A large part of the study area is protected and fieldwork is regulated. Therefore, we were only allowed access to three study sites and thus there was no replication in the study. We could not estimate mortality directly because of small sample sizes (only a few trees died during 1996 and 2002). Because the cutting down of trees was impossible, we had to use other species' data and apply the same allometric relations to all populations at different altitudes to estimate reproductive outputs. Replicated data sets with larger sample sizes, direct mortality measurements and direct estimates of the trade-off between growth and reproduction are necessary to help prove our hypothesis that the small size of trees at high altitude is at least partially the result of adaptation by the trees – namely, a change in the lifetime resource allocation plan.

ACKNOWLEDGEMENTS

We are indebted to Takeshi Seki for important information on the study sites and materials, particularly that on the reproductive behaviour of this species. We would like to thank K. Kikuzawa, T. Nakashizuka, N. Kachi, C. Körner, D. Robinson, B. Kunin, T. Fujiwara and anonymous referees for providing thoughtful comments and helpful suggestions on the manuscript. We are grateful to E. Kasuya for his statistical advice. We also appreciate valuable discussions with colleagues and students of our laboratories as well as their help with the fieldwork.

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