

# Growth allocation between height and stem diameter in nonsuppressed reproducing *Abies mariesii* trees

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## Abstract

To understand the growth patterns with respect to competition and leaf-mass increase in reproducing trees, growth allocation between height and stem diameter was examined for nonsuppressed reproducing *Abies mariesii* trees in a subalpine forest in northern Honshu, Japan. The growth allocation was analyzed by dividing the relative growth rate of the stem volume into the relative contributions of height and stem-diameter growth. During a 9-yr period, height growth and seed-cone production showed obvious annual variation, while stem-diameter growth recorded moderate variation. For two of three years of seed-cone production during the 9-yr period, trees with larger seed-cone production were associated with less height growth in the following year of seed-cone production; however, there was no trend of height growth in the year of seed-cone production. In the following year of mast seeding, trees with larger stem-volume growth were associated with less height growth. This trend was also shown for the relationship between the cumulative stem-volume growth during the 9-yr period and growth allocation to height, suggesting that trees with a larger biomass increase depress the allocation of photosynthate to competition with a large expenditure for reproduction. In contrast to this, trees with a smaller biomass increase might allocate photosynthate to competition with surrounding trees. The results of this study suggest that an increase in reproductive organs during life history and annual variation in reproduction are closely associated with the growth patterns of the stem in *A. mariesii* trees.

*Keywords:* allometry, annual fluctuation, radial growth, relative growth rate, seed cone.

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## Introduction

Growth allocation is an important trait in woody plants for the acquisition of photosynthate. For the main stem in erect growth-formed trees, growth allocation to stem-volume growth consists of allocation to height growth and stem-diameter growth. Height growth is a competitive process of obtaining a better arrangement of leaves up to a sunlit space (Falster & Westoby 2003; Petit & Hampe 2006; Poorter *et al.* 2006). In woody plants, competition for

sunlit conditions is essential for canopy tree species in comparison with tree species that continue to survive under the canopy layer. On the other hand, stem-diameter growth is a component associated with the increase of leaf mass because the cross-sectional area of a stem is closely related to the amount of leaf mass supported by the stem (e.g. Shinozaki *et al.* 1964a,b; Mäkelä & Vanninen 2001; Kantola & Mäkelä 2004).

For growth allocation, the importance of height and stem-diameter growth changes under biomass increase during the ontogenetic development due to the difference in the role of these growth components. In growth rates, the relative growth rate of stem volume corresponds to the sum of the relative growth rate of height and that of stem diameter (Sumida *et al.* 1997). An analysis using the ratio of relative growth rate of height to that of stem

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volume, denoted as “height growth contribution,” in *Quercus glauca* indicated that this ratio gradually decreased from the seedling stage to later stages, especially in suppressed trees (Sumida *et al.* 1997). This example suggests that the increment in leaf mass predominates over height growth under conditions of low availability of photosynthate for growth. On the other hand, in trees competing with surrounding ones, height growth might predominate over the increment in leaf mass.

With respect to the availability of photosynthate for growth, reproduction is an important factor for growth allocation. In this sense, trade-offs between reproduction and some growth components have been detected in many woody plants (Obeso 2002), e.g. a trade-off between reproduction and shoot growth (Tappeiner 1969; Gross 1972; Silvertown & Dodd 1999), the number of shoots (Henriksson & Ruohomäki 2000; Hasegawa & Takeda 2001), and foliage (Powell 1977; Tuomi *et al.* 1982). Furthermore, many studies have indicated a decrease in stem-diameter growth in the year of intensive reproduction (e.g. Eis *et al.* 1965; El-Kassaby & Barclay 1992; but, see Despland & Houle 1997; Seifert & Müller-Starck 2009). In some tree species, a difference between growth components in response to reproduction (Obeso 1997; Silvertown & Dodd 1999) suggests the influence of reproduction on growth allocation.

As shown for growth allocation (Sumida *et al.* 1997), reproductive allocation also changes under biomass increase, as it is associated with life-history strategy. With respect to adaptation to some disturbance regimes, a shade-tolerant species allocates photosynthate to reproduction more under larger biomass increase after it has attained large size (e.g. Hirayama *et al.* 2008). In contrast, for a shade-intolerant species, it is considered to be advantageous to start reproduction earlier under smaller biomass increase or when it is smaller in size (Nakashizuka *et al.* 1997; Climent *et al.* 2008). To understand the life-history strategy, biomass increase may be an important factor for both growth and reproductive allocation.

This study is an examination of growth and reproductive allocation in nonsuppressed *Abies mariesii* trees, which increase biomass during the ontogenetic development. In the study area, *A. mariesii* saplings are shade-tolerant, adapting to a disturbance regime, i.e. one with few chances of release from suppression by dwarf bamboos. For reproducing canopy trees, seed production should be continued for many years to ensure regeneration. This reproductive trait might be associated with larger reproductive allocation under larger biomass increase. In canopy trees, which indicate a large biomass increase, a temporal depression occurred in height growth after seed-cone production but not in elongation along the horizontally extending branch axis (Seki 2008),

suggesting obvious depression of growth allocation to height in comparison with stem diameter after reproduction. However, in trees with a small biomass increase, allocation to height growth might be important for the acquisition of a sunlit space. In this sense, the relationship between growth and reproductive allocation in trees with various degrees of biomass increase is an open question.

Here, we present and verify two hypotheses for reproductive and growth allocation in nonsuppressed *A. mariesii* trees during the ontogenetic development as follows: (i) reproductive allocation is larger in trees with a larger biomass increase; (ii) growth allocation to tree height is smaller in trees with a larger biomass increase. For these two hypotheses, shade tolerance and a disturbance regime will be considered for the former hypothesis, and the importance of competitive ability will be considered for the latter.

## Materials and methods

### Study site

The study site is located on a west-facing slope with an inclination of 15–20° (40°39'N, 140°52'E; 1080 m a.s.l.) on Mount Ioh (1360 m a.s.l.) in the Hakkoda Mountains in northern Honshu, Japan. The bedrock of the site is andesitic lava erupted from the Kita-Hakkoda volcanic group (Kudo *et al.* 2004). Since the ground surface is covered by snow from November to late May or early June, the growing season on the forest floor is from June to October. According to climate data recorded at Sukayu (890 m a.s.l.), 2 km west of the study site (Japan Weather Association Aomori Branch 1988, 1989, 1990, 1991, 1992, 1993, 1994), the mean monthly precipitation in each month from June to October is 120 to 250 mm. Due to the precipitation and matrix conditions, soil conditions for the canopy trees are humid, but the ground surface is not submerged during the growing season.

The dominant species of the study site are *A. mariesii*, *Betula ermanii* Cham., and *Fagus crenata* Blume. The *A. mariesii* trees form clusters with 5–10 canopy trees that are 10–18 m in height and 25–50 cm in stem diameter at breast height (DBH), i.e. 1.3 m in height. Within these clusters, the crowns of trees < 10 m in height are partly or entirely suppressed by surrounding trees. In *A. mariesii*, trees with suppressed crowns show low activity in reproduction even after the attainment of threshold reproductive size, as shown in other *Abies* species (e.g. Kohyama 1982; Greene *et al.* 2002). Around the clusters of canopy trees, *Sasa kurilensis* (Rupr.) Makino et Shibata develops a foliage layer from 1.5 to 2 m in height. Some *A. mariesii* trees > 3 m in height grow isolated from the clusters of canopy trees and develop lower branches of significant



Fig. 1 Bases of seed-cone rachises indicated by arrows on the surface of branches.

length over the foliage layer of *Sasa* scrubs. These isolated trees > 3 m in height produce both seed- and pollen cones.

#### Shoot elongation and seed-cone bearing of study species

In *A. mariesii*, shoot elongation in terminal leaders of the main stem and branches occurs once a year from late June to late July in the lower part of the subalpine forests (T. Seki, pers. obs., 2005). After the shedding of a vegetative-bud scale at shoot elongation, a ringed scar at the base of the bud remains for many years and thus enables tracing the year of shoot elongation.

Seed cones ripen in the following year of seed-cone bud development on the elongating shoots, as shown in several *Abies* species (e.g. Powell 1970; Singh & Owens 1981; Alista & Talavera 1994; Owens & Morris 1998). After seed dispersal, seed-cone rachises remain on the surface of shoots without abscission (Fig. 1; Kohyama 1982; Seki 1994, 2008; Sakai *et al.* 2003). The rachis bases are recognizable even after the decay of the upper part of the rachis because the bark of branches does not cover the remaining rachis base after the shedding of needles. Furthermore, at the study site, the branch surfaces are not abraded, and, thus, the rachises are recognizable up to 15 yr or more on the living branches.

According to the first seed-cone production record indicated by the rachis bases on several trees, the threshold size of seed-cone production of nonsuppressed *A. mariesii* trees at this study site might be c. 3 m in tree height and from 7 to 8 cm in stem diameter at BH (T. Seki, pers. obs., 1990).

#### Sample trees

In September 1990, nine trees with a main stem originating from a sound terminal leader without apparent damage were selected for measurement (Table 1). Trees < 10 m in height were isolated trees (i.e. trees 1–3), and the others were selected from both isolated and clustered ones. In any sample tree, the tree crown had no sign of suppression by other trees for 30 yr or more, and, thus, the upper part of the tree crown was located under sunlight conditions at measurement. For seven of the nine trees, seed-cone bearing had been investigated in 1988. The heights of the sample trees and DBH ranged from 5.5 to 16.0 m and from 16.1 to 42.3 cm, respectively. The age at BH estimated from the stem diameter and the mean diameter growth in increment cores was from 76 to 179 yr (Table 1).

#### Measurement of stem growth

Annual height growth was defined as the terminal-leader length of the main stem in each growing season. The leader length was measured in 1990 using slide calipers on the crown top for the stem of elongation from 1980 to 1989. The years of elongation were determined using the times of branching from the main-stem terminal leaders in these years for branches directly developing from the main stem. Tree height was measured for the standing main stem of the sample trees using a steel tape measure temporarily attached to the main stem with adhesive tape.

The stem diameter for each sample tree was calculated from the circumference measured at BH in late September 1990. After the measurement, increment cores were sampled at BH from two directions perpendicular to each other.

The increment cores were mounted in the grooves of wood sticks with vinyl acetate emulsion and cut into 2.0-mm-thick cross sections. After the sections were seasoned in a conditioning room (20°C, 60% relative humidity), negatives of the sections were made by exposure to soft X-ray (18 kVp, 14 mA) in a soft X-ray apparatus (EMBW-S, SOFTEX). A series of ring widths was measured on the negatives using a stereomicroscope equipped with a magnet scale at 0.01 mm accuracy.

#### Estimation of seed-cone bearing

Seed-cone bearing in each tree was estimated by counting the number of bases of seed-cone rachises in all parts of the crown. Rachis bases corresponding to seed cones borne from 1980 to 1988 on each branch developing from the main stem were counted for each seed-cone-bearing year from the tree-crown top to the base on standing trees.

**Table 1** Tree size, estimated age at 1.3 m in height, and times of seed-cone production in the sample trees

Tree No.	Tree height in 1989 (m)	Diameter at 1.3 m in height in 1989 (cm)	Diameter at crown base in 1990 (cm)	Recognized number of tree rings	Mean stem-diameter growth (mm/yr)	Estimated age by mean stem-diameter growth (yr)	Times of seed-cone production from 1980 to 1988
1	5.5	16.1	16.9	68	1.05	76	3
2	7.6	22.6	22.4	56	1.42	80	5
3	9.9	20.4	20.8	100	1.02	100	2
4	12.9	27.1	26.2	122	1.00	135	3
5	13.2	39.5	38.1	77	2.11	93	4
6	13.5	26.5	24.7	145	0.85	156	3
7	14.5	26.6	21.5	159	0.74	179	4
8	14.7	41.7	41.7	123	1.65	126	4
9	16.0	42.3	39.5	82	2.53	84	3

The counting was conducted in October 1988 for seven of the nine sample trees and in September 1990 for the other two.

#### *Analysis for allocation to seed cones*

To clarify the relationship between the dry mass of living parts of trees and seed-cone production, allometric relationships between stem-volume increment and seed-cone weight were examined. In woody plants, since an increase in the proportion of nonliving structural tissues in large individuals may decrease the slope in an allometric relationship between vegetative and reproductive biomass (Weiner *et al.* 2009), a stem-volume increment was adopted as an appropriate measure for a living biomass at a developmental stage. For the estimation of seed-cone weight per tree, the mean seed-cone dry weight of 29.5 g/cone estimated in the study site (Seki 1994) was used.

To determine the slope of log-log linear relationships, if there were any, the Model Type II (standardized major axis, SMA) regression (Sokal & Rohlf 1995; Niklas & Enquist 2003; Niklas & Marler 2007) was used to avoid the underestimation of the slope originating from the procedure of the ordinary least squares regression (OLS). Before the determination of the slope, the relationship between growth and reproductive components was examined using the coefficients of determination by OLS ( $R_{OLS}^2$ ). The slope by Model Type II regression was calculated using a software package "smatr" (Warton & Ormerod 2007; see also Falster *et al.* 2006) in language R (R Development Core Team 2011).

#### *Analysis for height growth*

To examine the relationship between seed-cone production and height growth among trees of various sizes, an index consisting of relative growth rates was adopted.

Sumida *et al.* (1997) developed the procedure for the estimation of the index, "height growth contribution." In their analysis, for the relative growth rates in the stem volume ( $RGR_V$ ), cross-sectional area at BH ( $RGR_A$ ), and stem height ( $RGR_H$ ), the following equation was obtained:

$$RGR_H/RGR_V + RGR_A/RGR_V = 1 \quad (1)$$

In Equation 1, the height growth contribution was defined as the ratio,  $RGR_H/RGR_V$ .

For the estimation of  $RGR_V$ ,  $RGR_A$ , and  $RGR_H$ , the following formula was used:

$$RGR_X = (\ln X_2 - \ln X_1)/(t_2 - t_1) \quad (2)$$

where  $X_n$  is the stem volume, the cross-sectional area, or the stem height at  $t_n$  (yr).

We examined the possibility of the influence of seed-cone production on the height growth contribution using the generalized linear model in language R (R Development Core Team 2011).

## Results

### *Annual variation in stem growth and seed-cone production*

The main-stem terminal-leader elongation varied annually (Fig. 2), with the largest elongation in 1981 and the smallest in 1983. The mean of the leader elongation in 1981 was  $17.5 \pm 7.4$  (mean  $\pm$  standard deviation) cm/yr, three times longer than that in 1983 ( $5.8 \pm 2.1$  cm/yr).

For the annual variation of the height growth contribution to stem volume, the variation pattern of the mean value was basically similar to that of the mean terminal-leader elongation (Figs 2,3). However, the variation of the index was not as large as that of the leader elongation, the

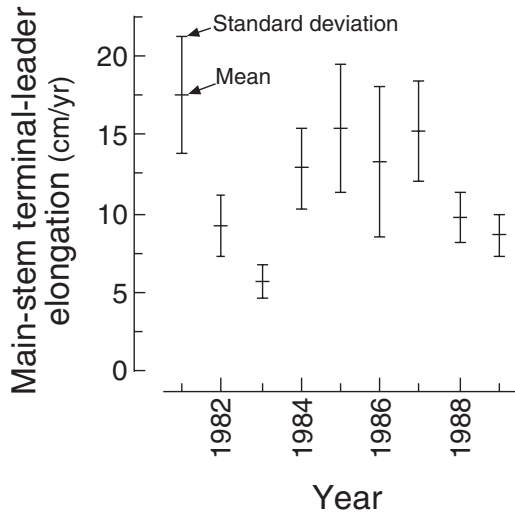


Fig. 2 Annual variation in main-stem terminal-leader elongation from nine sample trees from 1981 to 1989.

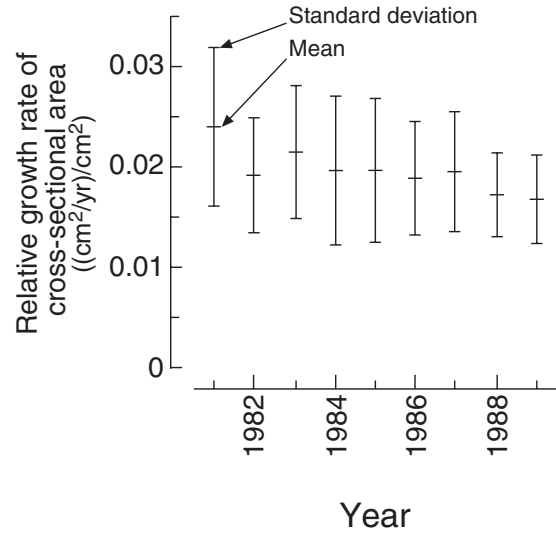


Fig. 4 Annual variation in the relative growth rate of a cross-sectional area at 1.3 m in height from nine sample trees from 1981 to 1989.

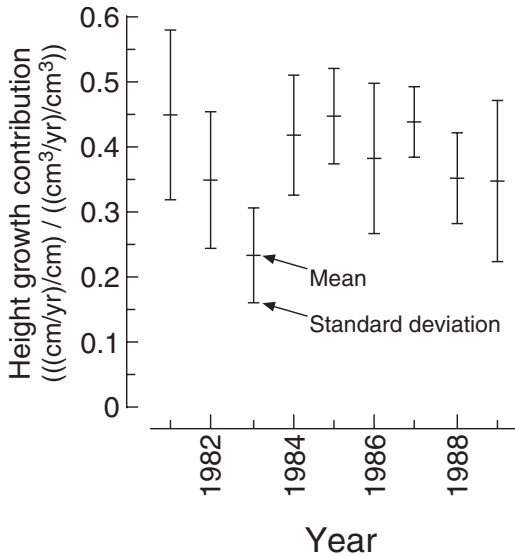


Fig. 3 Annual variation in height growth contribution, i.e. the ratio of the relative growth rate of height growth to that of stem-volume growth, from nine sample trees from 1981 to 1989.

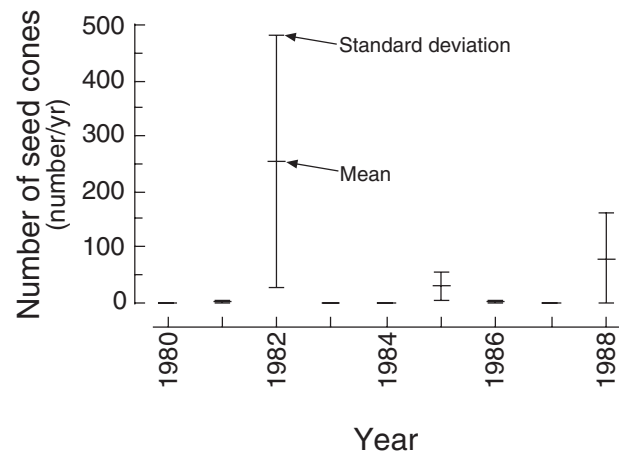


Fig. 5 Annual variation in the number of seed cones produced per tree based on nine sample trees from 1980 to 1988.

maximum mean value of 0.45 in 1981 being nearly twice the minimum of 0.23 in 1983.

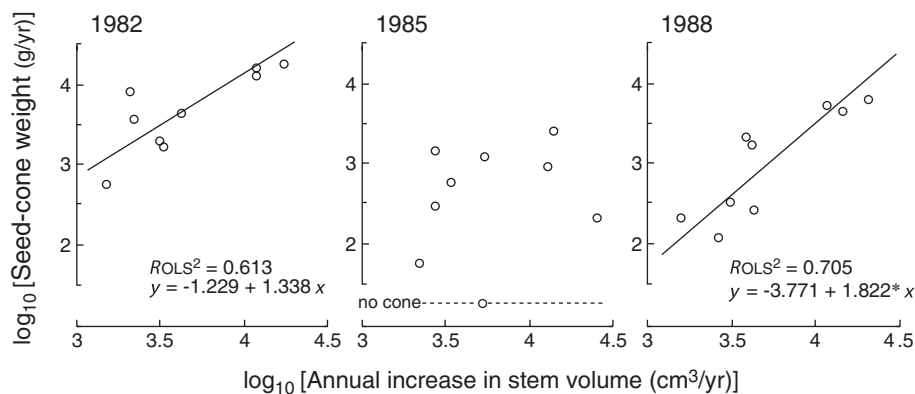
In comparison with height growth, stem-diameter growth showed moderate annual variation (Fig. 4). With respect to the relative growth rate of the cross-sectional area, no obvious depression occurred in 1983.

Obvious seed-cone bearing occurred in three of nine years (Fig. 5). Most seed-cone bearing occurred in 1982, followed by 1988 and 1985. On the other hand, no seed cone was borne on the sample trees in 1980, 1983, 1984 and 1987.

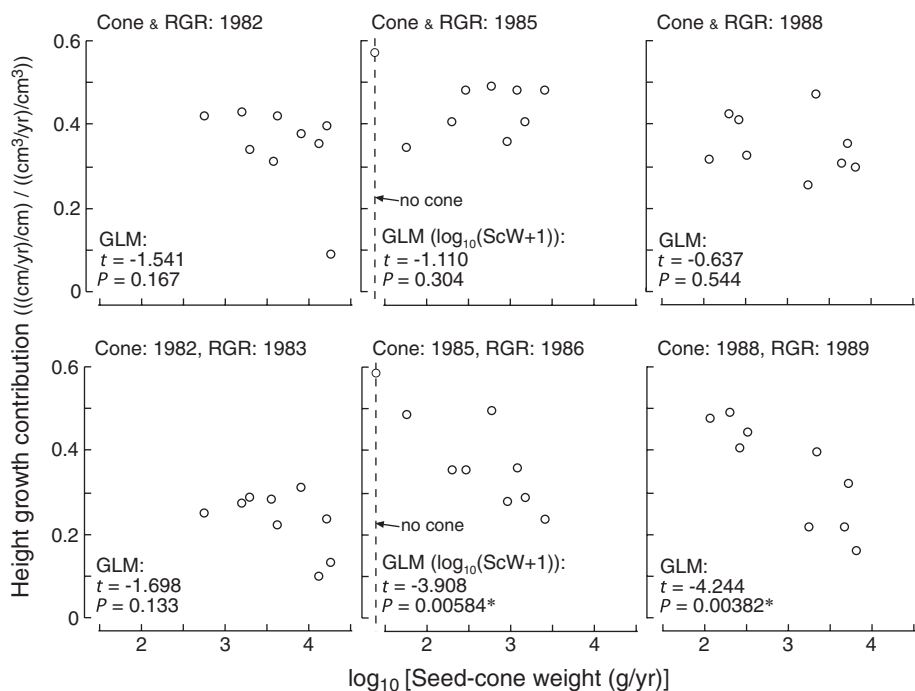
Of the three years of seed-cone bearing, there were allometric relationships between annual stem-volume growth and seed-cone weight per tree in 1982 and 1988 (Fig. 6). In 1982, seed-cone weight was almost proportional to the annual stem-volume growth of the individuals in that year. On the other hand, in 1988, seed-cone weight was proportional to the 1.82 power of the stem-volume growth. The slope of the log-log linear regression line in 1988 was significantly different from 1.

*Relationship between seed-cone production and height growth under annual variation*

There were negative relationships between seed-cone production and height growth in the following year of seed-



**Fig. 6** Relationship between stem-volume growth and seed-cone production in 1982, 1985 and 1988. The asterisk beside the numerical value indicates a significant difference from 1 at  $P = 0.05$ .



**Fig. 7** Relationship between seed-cone production and height growth contribution, i.e. the ratio of the relative growth rate of height growth to that of stem-volume growth. In analyses using the generalized linear model, the logarithm of the dry weight of seed cones was adopted as an explanatory variable. For seed-cone production in 1985, the logarithm of the dry weight of seed cones was calculated after adding 1. The asterisks beside the  $P$ -values indicate a significant relationship at  $P = 0.05$ .

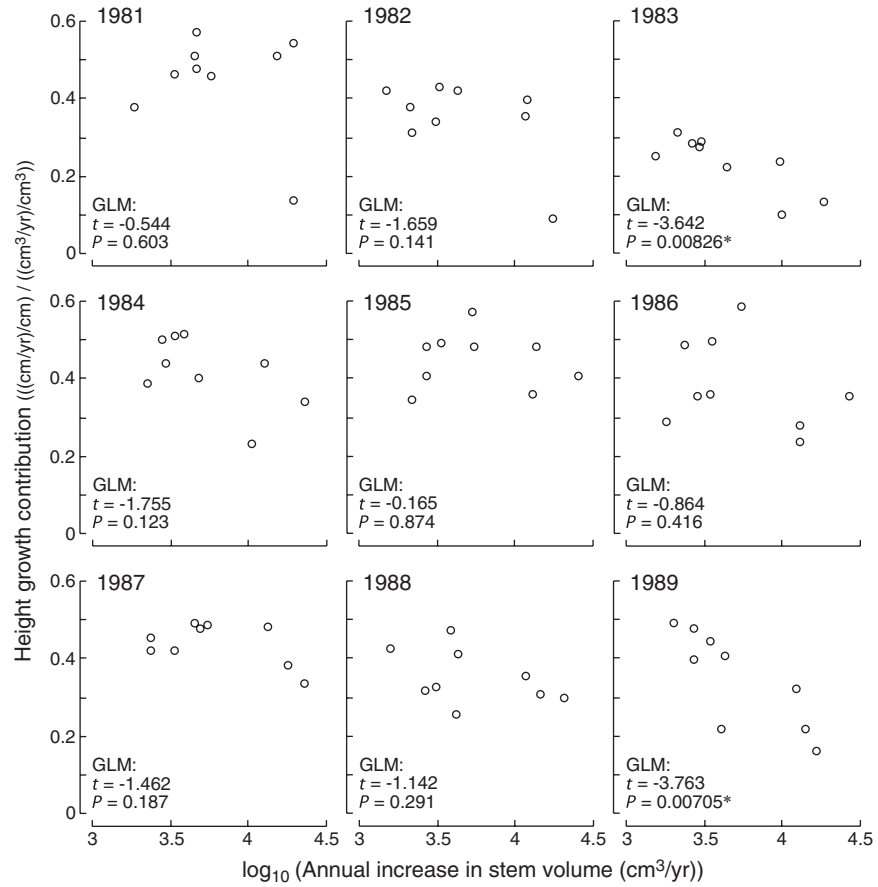
cone production for two of three times of seed-cone production (Fig. 7). In 1986 and 1989, the height growth contributions to stem volume were lower for the trees that had produced large amounts of seed cones in the previous years. In 1983, the following year of mast seeding, there was no relationship between seed-cone production and height growth. However, the height growth contribution in all the sample trees was generally low in that year (Figs 3,7). In contrast to the following years of seed-cone production, there was no relationship between seed-cone production and height growth in the years of seed-cone production (Fig. 7).

Height growth was lower for trees of higher stem-volume growth in two of nine years (Fig. 8). In 1983 and 1989, the years following those in which there were

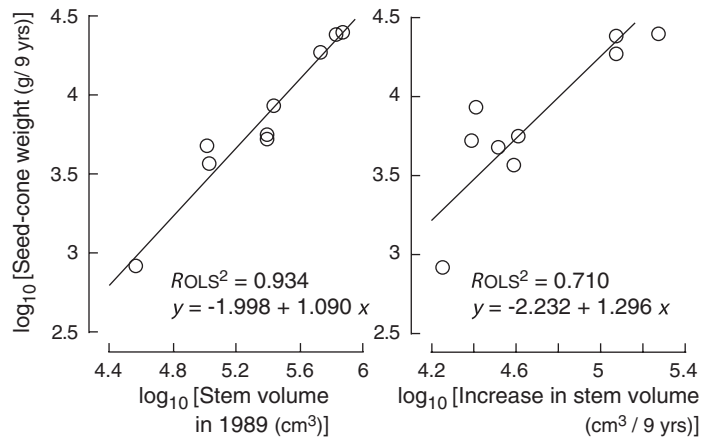
allometric relationships between stem-volume growth and seed-cone production, the height growth contributions were lower in trees of higher stem-volume growth. In the other 7 yr, no trend was detected for height growth contribution.

*Relationship between seed-cone production and height growth during the study period*

For the cumulative seed-cone production during a 9-yr period, there was an allometric relationship between stem volume and seed-cone production as well as a relationship between stem-volume growth and seed-cone production (Fig. 9). For both log-log linear regression lines, the slope was not significantly different from 1.



**Fig. 8** Relationship between stem-volume growth and height growth contribution, i.e. the ratio of the relative growth rate of height growth to that of stem-volume growth. In analyses using the generalized linear model, the logarithm of the annual increase of stem volume was adopted as an explanatory variable. The asterisks beside the  $P$ -values indicate a significant relationship at  $P = 0.05$ .



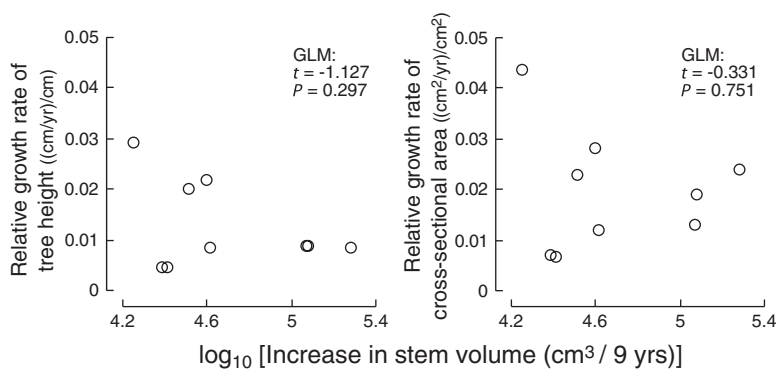
**Fig. 9** Relationship between stem volume or stem-volume growth and seed-cone production for 9 yr.

No relationship between the stem-volume growth and relative growth rate was detected (Fig. 10), but a negative relationship was found between stem-volume growth and height growth contribution to stem-volume growth (Fig. 11). On the other hand, there was no relationship between tree-size components, i.e. tree height and stem volume, and height growth contribution (Fig. 11).

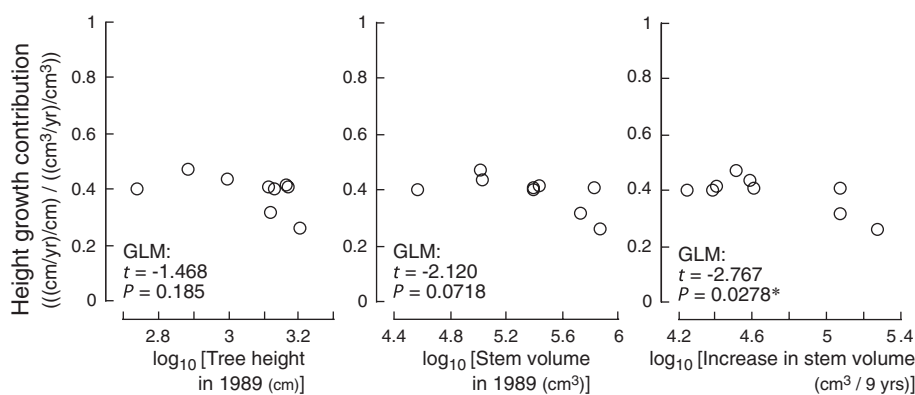
## Discussion

### *Reproductive allocation*

The reproductive allocation pattern in this study is similar to that of shade-tolerant species (e.g. Hirayama *et al.* 2008) rather than that of shade-intolerant ones (e.g. Nakashizuka *et al.* 1997; Climent *et al.* 2008), with a larger repro-



**Fig. 10** Relationship between stem-volume growth and relative growth rate of tree height or cross-sectional area for 9 yr.



**Fig. 11** Relationship between tree height, stem volume or stem-volume growth and height growth contribution, i.e. the ratio of the relative growth rate of height growth to that of stem-volume growth, for 9 yr. The asterisk beside the *P*-value indicates a significant relationship at *P* = 0.05.

ductive allocation in smaller trees. During the period including three times of seed-cone production, reproductive allocation may be basically constant irrespective of biomass increase (Figs 6,9). In addition to this, a larger reproductive allocation is also suggested in trees with larger biomass increase in some years (e.g. 1988; Fig. 6).

Constant reproductive allocation, irrespective of the biomass increase, might be suitable for nonsuppressed trees to increase the chance of forest regeneration by their offspring in the study area, with few chances of release from suppression by dwarf bamboos. This reproductive allocation pattern enables reproducing trees to increase seed production monotonically with tree size (Seki 1994) even after the attainment of a forest-canopy layer (cf. Kohyama 1982). However, with regard to the life-history strategy, reproductive allocation in the largest trees, whose height growth had already stopped, remains an open question.

#### *Growth allocation in reproducing trees*

According to the relative growth rate of stem diameter with a small annual variation under the obvious annual variation of seed-cone production (Figs 4,5), this study indicates no trade-off between stem-diameter growth and seed-cone production (cf. Eis *et al.* 1965; Silvertown &

Dodd 1999). With respect to no trade-off between reproduction and stem-diameter growth in conifer species, there are several lines of thought, e.g. a trait of population in the limit of distribution (Despland & Houle 1997), no influence of the amount of accumulated photosynthate and nutrients on stem-diameter growth (Seifert & Müller-Starck 2009), and a large amount of accumulated photosynthate at the beginning of mast seeding (Seifert & Müller-Starck 2009). With regard to the first line of thought (Despland & Houle 1997), the study site is located at the lower part of a subalpine forest (Seki 1994, 2008), and thus the reproductive trait is not the one at the limit of distribution. For the latter two, the source of photosynthate for stem-diameter growth in *A. mariesii* is an open question, as is the photosynthate for reproduction. However, in this species, a drastic increase in stem-diameter growth might not occur even in years when a large amount of photosynthate is accumulated in a tree.

Regarding the relationship between the whole vegetative growth and reproduction within a tree, there is some extent of trade-off in this study, suggested by smaller allocation to height growth in trees of larger seed-cone production (Fig. 7). In addition to this, a closer negative relationship between seed-cone production and height growth than any other relationship between climatic factor and height growth (Seki 2008) is supportive of the



trade-off. However, the lesser height growth in trees of larger reproduction is not necessarily explained by the deficit of photosynthate. First, if the amount of photosynthate for height growth is depressed, depression of height growth in the year of seed-cone production (e.g. Silvertown & Dodd 1999) should also occur. Second, if the deficit of photosynthate is the only cause of the height-growth depression, a depression should also occur in stem-diameter growth (see Fig. 4). The height-growth depression and obscure change in stem-diameter growth at reproduction might rather be due to a growth allocation pattern, in which a leaf-mass increase is more important than competitive ability.

Among trees with various degrees of biomass increase, trees with a larger biomass increase may lower the growth allocation to competitive ability, as it is associated with the reproduction (Figs 7,8). For these trees, an increase in leaf mass through stem-diameter growth, suggested by a relatively constant horizontal crown expansion (Seki 2008), may be more important than height growth after mast years, but it may not necessarily be associated with larger reproductive allocation (e.g. Figs 6,8). In this regard, the height-growth depression after reproduction might not be simply due to larger reproductive allocation but, rather, to some kinds of physiological processes associated with seed-cone production. In contrast to trees with a larger biomass increase, the importance of acquiring sunlit space through height growth may be greater for trees with smaller biomass increase rather than stem-diameter growth and horizontal crown expansion, irrespective of the absolute relative growth rates in height and stem diameter (Figs 10,11). This might reflect the importance of height growth for future survival in trees of lower productivity.

This study suggests that biomass increase and reproduction are associated with growth allocation to tree height. For trees with small biomass increase, a weak influence of reproduction on height growth means a small possibility of depression in competitive ability and is thus important for the survival. This idea should be proved by the examination of various-sized trees, including those in a nonreproductive stage to the stage just after the attainment of the reproductive threshold. To understand the relationship between the growth rate and reproductive allocation through the life history of trees, canopy trees in which height growth has stopped should also be investigated.

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