Shoot growth chronology of alpine dwarf pine (*Pinus pumila*) in relation to shoot size and climatic conditions: a reassessment

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Abstract: Shoot growth chronology of alpine dwarf pine (*Pinus pumila*) was examined near the summit of Mount Norikura in central Japan, in relation to shoot size and climatic conditions. Shoot growth was investigated in 70 shoots with various shoot lengths between 18 and 273 cm, and the examined 70 shoots were divided into three size classes (shoot length <70 cm, 70–140 cm, and >140 cm). A shoot growth chronology was developed for each of the three size classes, but was not statistically different among them. It is suggested that the size dependency of shoot growth chronology was rather weak or negligible. Thus, a single shoot growth chronology was developed again, irrespective of shoot size. Climatic factors affecting the shoot growth were analyzed by using monthly climatic data (mean temperature, insolation duration and sum of precipitation). The shoot growth chronology was positively correlated with the June temperature of the current year, suggesting that the high temperature of this month increases the shoot growth by prolonging the growing season. The shoot growth chronology was also positively correlated with the temperatures from July to October of the previous year, suggesting that the growth of *P. pumila* largely depends on the photosynthetic production of the previous year. The mean temperature during July to October of the previous year explained 30% of the variation of the shoot growth chronology. These results showed that the shoot growth of *P. pumila* is largely regulated by temperature during the growing season, irrespective of shoot size.

key words: climatic conditions, Mount Norikura, *Pinus pumila*, shoot growth chronology

Introduction

High altitudes and high latitudes are harsh environments for plant growth and survival because of low temperature, strong winds, heavy snow and short growing season (Hadley and Smith, 1983, 1886; Körner, 1999; Kajimoto *et al.*, 2002). Therefore, climatic change will significantly affect plant communities in high altitudes and high latitudes (Henry and Molau, 1997; Chapin *et al.*, 2004; Takahashi, 2005). For example, many dendrochronological studies have revealed that radial growth of trees near timberline increased in mild years with higher than average temperatures (Ettl and Peterson, 1995; Gostev *et al.*, 1996; Buckley *et al.*, 1997; Peterson and Peterson, 2001; Wilson and Hopfmueller, 2001). Growth of plants is largely influenced not only by

climatic conditions but also by size (or age) and competition with neighboring plants (Weiner, 1984; Hara, 1993; Takahashi, 1996; Takahashi *et al*., 2003). Dendrochronology is effective for the evaluation of relationships between tree growth and climatic conditions because this method can remove effects of size (or age) and competition by well-established standardization techniques (Fritts, 1976; Cook and Peters, 1981). In terms of effects of tree age on growth-climate relationships, Szeicz and MacDonald (1995) showed that the radial growth response of *Picea glauca* (Moench) Voss to climatic conditions varied with tree age. Therefore, it is important for the analysis of climate-growth relationships to reduce effects of other factors than climatic conditions.

The alpine dwarf pine (*Pinus pumila* Regel) is widely distributed in the alpine zone in Japan (Tatewaki, 1958; Wardle, 1977). Although there is concern about the upward distribution shift of *P. pumila* due to global warming (*cf*. Kajimoto *et al*., 1996), information about the relationship between shoot growth of *P. pumila* and climatic conditions is still limited. Shoot growth of *P. pumila* has been observed to be positively correlated with summer temperatures of the previous year (Sano *et al*., 1977; Okitsu, 1988; Takahashi, 2003a). However, these studies examined the relationship between climatic conditions and shoot growth only in short periods (15 to 25 years). Short chronologies cannot give robust results. For example, Okitsu (1988) found few statistically significant relationships of the shoot growth chronologies of *P. pumila* with any climatic factors, probably due to its short shoot growth chronology (only 15 years). Thus, long shoot growth chronologies are necessary for the examination of effects of climatic conditions on the shoot growth of *P. pumila*. In addition, these previous studies did not take account of other factors than climatic conditions, such as competition and plant size (or age). However, the effect of competition on shoot growth of *P. pumila* seems to be small because *P. pumila* forms dwarf scrub without vertical stratification structure. Therefore, the effect of shoot size should be taken into account in evaluating the relationship between climatic conditions and shoot growth of *P. pumila*.

The purpose of this study was to examine the shoot growth chronology of *P. pumila* in relation to shoot size and climatic conditions by investigating various sized shoots for as long a period as possible.

Materials and methods

Study site

This study was carried out on Mount Norikura (36°06′N, 137°33′E, summit elevation 3026 m above sea level) in central Japan. *Betula ermanii* Cham. and four conifers (*Abies veitchii* Lindl., *Abies mariesii* Mast., *Picea jezoensis* var. *hondoensis* Rehder, and *Tsuga diversifolia* Mast.) were dominant between approximately 1600 m and 2500 m a.s.l. in the subalpine zone. Alpine dwarf pine scrub (*Pinus pumila*) was distributed in the alpine zone.

The study site was located at 2800 m a.s.l. near the summit of Mount Norikura. Mean annual temperature at this study site was estimated to be $-2.3°C$ from the temperature recorded at Nagawa Weather Station (1068 m a.s.l., approximately 11 km from the study site) using the standard lapse rate of $-0.6°C$ for each $+100$ m altitude.

Mean monthly temperatures in the coldest month of January and the hottest month of August were estimated to be -13.9 and $9.9°C$, respectively.

Field methods

Interannual fluctuation of shoot growth of *P. pumila* was examined from 13 to 15 September 2004. Annual shoot growth rate was measured from bud scars using a ruler. In order to examine the size dependency of shoot growth rate, shoot growth was investigated in a total of 70 shoots with shoot lengths between 18 and 273 cm. *P. pumila* regenerates by vegetative growth such as layering, and therefore, above ground shoots usually connect to other shoots (Kajimoto, 1992). In this study, shoot length was defined as the length from the shoot tip to the shoot base that appeared on the ground, *i.e.*, this study did not include the below ground shoot length.

Data analysis

The span of shoot growth chronologies differed among the examined 70 shoots from 6 to 52 years because of the large variation in the shoot length. Each shoot growth chronology was verified against a master dating series (mean of all series) for cross dating, on the basis of correlation coefficients. Of the examined 70 shoots, shoots that showed low correlations with the master dating series were eliminated from further analyses.

In order to examine whether the shoot growth of *P. pumila* in response to climate varies with shoot size, each shoot growth chronology was disaggregated into three size classes (shoot length <70 cm, 70–140 cm, and >140 cm, Fig. 1a). All of the shoot sections for each size class were then combined to produce a single chronology for each of the three size classes (Fig. 1b, c). Each size-corrected shoot growth chronology of each size class was developed by averaging shoot growth rates among the shoots examined in each year. The number of samples that were used to develop a size-corrected shoot growth chronology differed in each year because of the difference in the measured periods among the examined shoots. More than five shoots were used in each year for the development of each chronology. Shoot growth chronologies were determined for the periods 1973–2004, 1961–2004 and 1976–2004 for the small (shoot length <70 cm), the medium (70–140 cm) and the large size classes (>140 cm), respectively. Shoot growth chronologies were then compared among the three size classes by *t*-test for the period 1976–2004 that was common to all three size classes.

A simple correlation test was used to show what climatic factors affect the shoot growth of *P. pumila*. The nearest weather station was Nagawa ($36°05'$N, $137°41'$E, 1068 m a.s.l., *ca.* 11 km from the study area). However, the available meteorological data at Nagawa started in 1979 (*i.e.*, the recording period at Nagawa was shorter than shoot growth chronologies of *P. pumila*). In contrast, a long-term record was available at Matsumoto Weather Station ($36°15'$N, $137°58'$E, 610 m a.s.l., approximately 40 km from the study site). Thus, this study used climatic data recorded at Matsumoto for the correlation test. Monthly mean temperature, insolation duration and sum of precipitation were used. The shoot growth chronology of *P. pumila* was compared with the meteorological data from the beginning of the previous growth period to the end of the current growth period. The growing season of *P. pumila* at this study site

(a) Shoot growth chronology of each shoot

(b) Disaggregation into three size classes

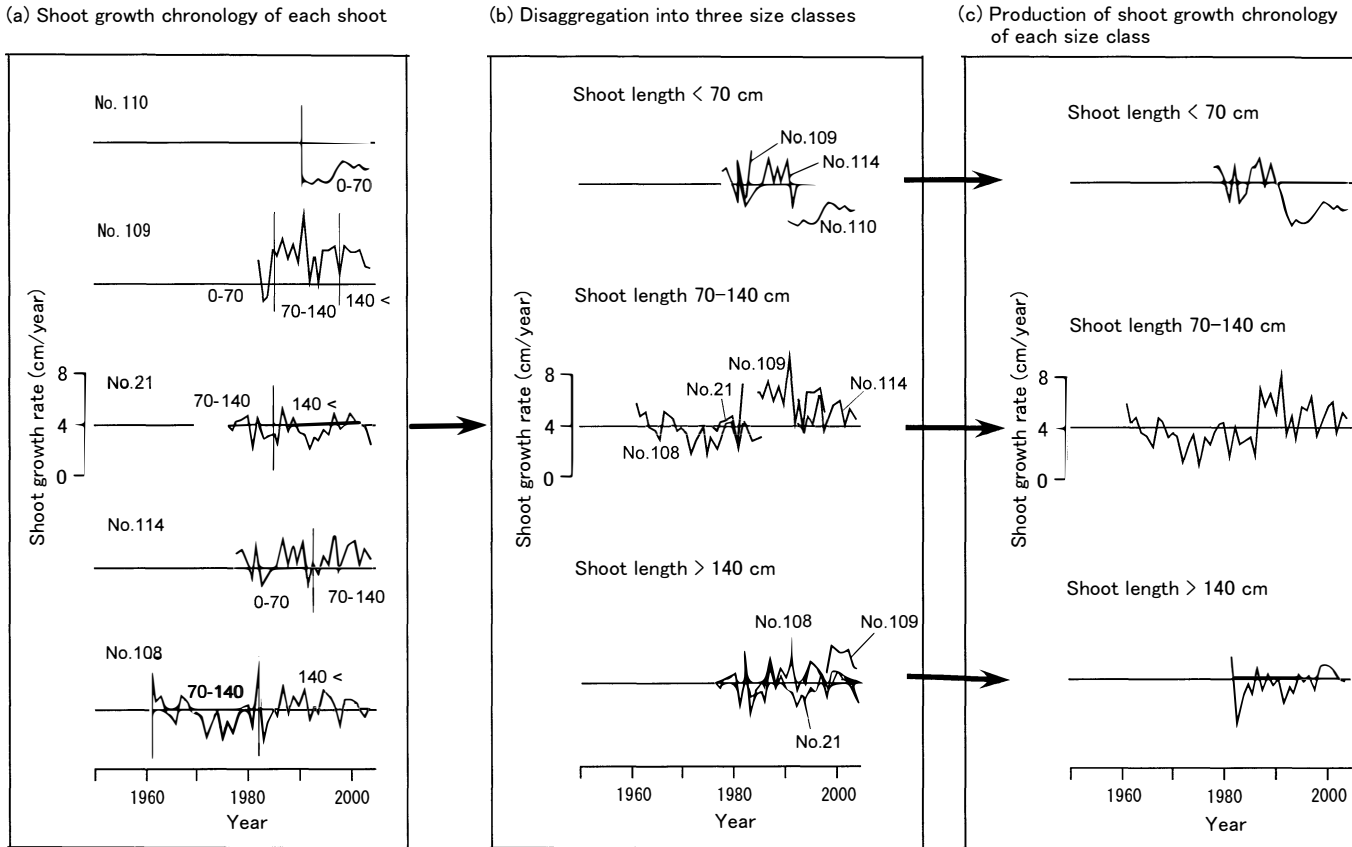**(c)** Production of shoot growth chronology of each size class

Fig. 1. Outline of methodology for the development of size-corrected chronologies from raw shoot growth measurements. Shoot growth chronologies of five shoots (Nos. 110, 109, 21, 114 and 108) are presented as examples. Each individual chronology was divided into three size classes as shoot length <70 cm, 70–140 cm, and >140 cm. Annual shoot growth rates of Nos. 21 and 108 could not be measured near the base of their shoots, therefore, the class 0–70 cm was not presented in those shoots in (a).

was determined as June to September because the mean monthly temperature exceeded 5°C, an effective temperature for plant growth (Kira, 1948), during this period (total 16 months). Bonferroni correction of *P*-values was done for the correlation tests.

Results and discussion

The shoot growth rate was positively correlated with shoot length ($P < 0.001$, Fig. 2). Thus, larger shoots tended to grow faster. However, the variation in the shoot growth rate was large, and the shoot length could explain only 14% of the variation. Of the examined 70 shoots of *P. pumila*, 59 shoots were well correlated with the master dating series, and were used to develop the shoot growth chronology for each of the three size classes (shoot length < 70 cm, 70–140 cm, and > 140 cm). Uncorrelated shoots varied in shoot length from short to long shoots. Therefore, low correlations of these shoots were ascribed to measurement errors. The shoot growth chronology was not significantly different among the three size classes for the period 1976–2004 (*t*-test, $P > 0.05$), although the shoot growth rate in the smallest size class seems to be lower during 1995 to 2004 compared with the two other size classes (Fig. 3). It is suggested that the size dependency of the shoot growth chronology was rather weak or negligible.

This study showed that the shoot growth chronology did not differ among the three size classes. In order to produce the shoot growth chronology of the smallest size class, data of "current small shoots" and those of "past small shoots" were combined. Growth rates of current smaller shoots were actually lower than those of larger shoots after 1995 (Figs. 2, 3a), suggesting the size dependency of shoot growth. However, the growth of "past" small shoots was similar to that of current large shoots before 1995 (Fig. 3a). Although the data of current small shoots were taken from isolated seed-derived seedlings, those of the past small shoots (*i.e.*, current long shoots) were taken
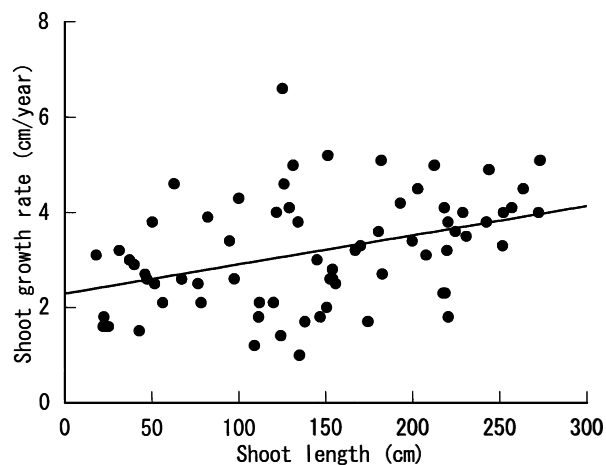

Fig. 2. Relationship between shoot growth rate and shoot length in 2004. The regression equation is $Y = 0.0061\,X + 2.29$ ($F_{1,68} = 11.9$, adjusted $r^2 = 0.136$, $P < 0.001$), where Y is the shoot growth rate (cm/year) and X is the shoot length.
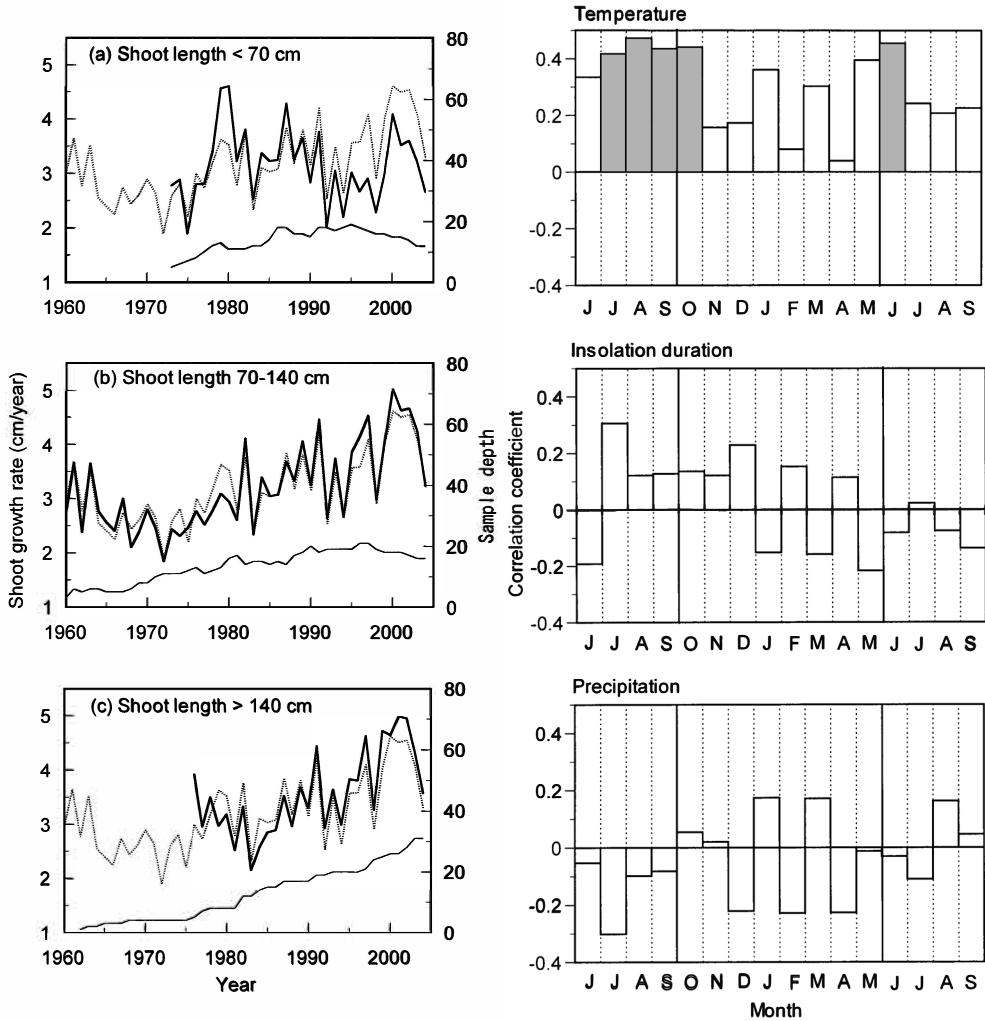
Fig. 3. Size-corrected shoot growth chrono-
logies of *Pinus pumila* (thick solid lines) for
the shoot length <70 cm (a), 70–140 cm (b),
and >140 cm (c). A dotted line in each fig-
ure indicates the overall mean chronology
without the size correction. A thin line in
each figure represents the sample depth.

Fig. 4. Correlation coefficients between annual
shoot growth of *Pinus pumila* (1959–2004)
and monthly climatic data (temperature, inso-
lation duration and precipitation). Shaded
bars indicate significant correlations ($P < 0.05$
by the Pearson correlation test with Bonfer-
roni correction).

from shoots in scrub. Shoots in scrub were probably vegetative-growth individuals.
One of the possible reasons for the lack of a significant difference in the shoot growth
chronology among the three size classes was due to this methodology. Generally,
growth rate of shoots derived from vegetative reproduction, such as sprouts and root
suckers, is higher than that of seed-derived individuals because vegetative sprouts are
supported by mother plants in terms of water, nutrients and photosynthetic production

(Stuefer *et al*., 1994). Okitsu and Ito (1983) found that shoot growth rate was higher in the vegetative-growth shoots than in the seed-derived shoots. Therefore, the lack of significant difference in the shoot growth chronology among the three size classes was attributable to the vegetative growth trait of *P. pumila*, and this result does not mean the absence of size-dependent growth rate for seed-derived individuals of *P. pumila*.

A single shoot growth chronology was developed again by using the 59 shoots that showed good correlations with the master dating series, irrespective of size, for the period 1959–2004. The 46-year span of the chronology is considerably longer, as compared with previous studies (15–25 years) (Sano *et al*., 1977; Okitsu, 1988; Takahashi, 2003a). Climatic factors affecting shoot growth were analyzed by the simple correlation test. However, no significant correlations were detected with the insolation duration and precipitation of any months (Fig. 4). In terms of precipitation, Takahashi (2003b) observed that drought stress hardly occurred in summer for *P. pumila* because of frequent rain events in the alpine zone.

The shoot growth chronology was positively correlated with the June temperature of the current year (Fig. 4). June is the start month of the growing season. The growth period for plants is rather short in the alpine zone, and therefore, high temperature in early summer is effective for the tree growth and production by prolonging the duration of growing season (Camarero *et al*., 1998; Menzel and Fabian, 1999; Grace *et al*., 2002). Gostev *et al*. (1996) and Solomina *et al*. (1999) also showed that early summer temperature of the current year was positively correlated with the tree-ring growth of Dahurican larch (*Larix cajanderi* Mayr.) on the Kamchatka Peninsula, the
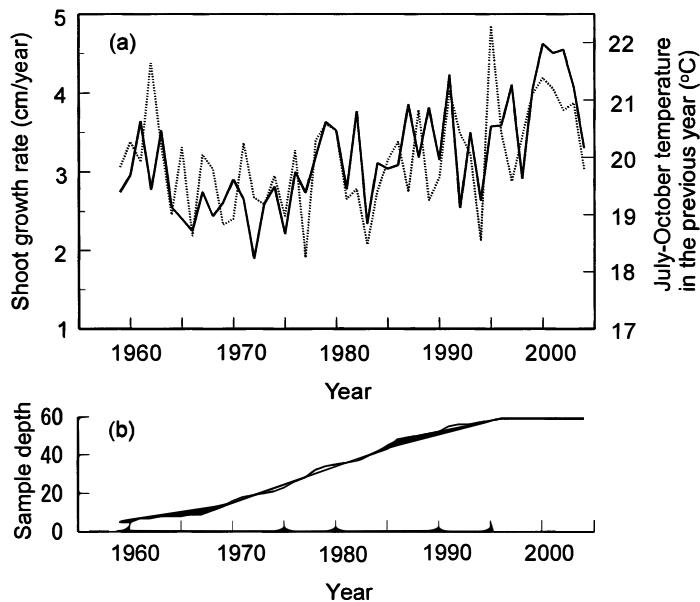

Fig. 5. (a) Fluctuation of annual shoot growth rate of *Pinus pumila* during 1959 to 2004 (solid line) and mean temperature between July and October of the previous year (dotted line), and (b) the sample depth of the shoot growth chronology.

Russian Far East.   Thus, it is suggested that high temperature in June increases the growth of *P. pumila* by prolonging the growing season.

The shoot growth chronology was positively correlated with the temperatures from July to October of the previous year (Fig. 4).   This is because *P. pumila* grows using the photosynthetic production accumulated in the previous year (Kibe and Masuzawa, 1992).   The previous studies also revealed that the shoot growth rate of *P. pumila* was positively correlated with the summer temperatures of the previous year (Sano *et al*., 1977; Okitsu, 1988; Takahashi, 2003a).   Therefore, the result of the long chronology of this study was in accordance with that of the short chronology of the previous studies. Therefore, it is suggested that a relationship between the shoot growth of *P. pumila* and summer temperature of the previous year is evident.   Annual fluctuation of the shoot growth rate of *P. pumila* and that of mean temperature during July to October of the previous year were synchronousl (Fig. 5).   The mean temperature during July to October of the previous year explained 30% of the variation of the shoot growth chronology by the regression model $Y = 0.425X - 5.318$ ($F_{1,44} = 20.4$, adjusted $r^2 = 0.301$, $P < 0.001$), where Y is the shoot growth rate (cm/year) and X is the mean temperature during July to October of the previous year.

This study concluded that the size-dependency of shoot growth chronology was rather weak or negligible, and that the shoot growth rate of *P. pumila* was strongly regulated by the summer temperature of the previous year, irrespective of shoot size. The results of this study will contribute to the prediction of shoot growth of *P. pumila* in future, *i.e.*, global warming can increase the shoot growth of *P. pumila* by increasing temperatures during the growing season and by prolonging the growing season.

Acknowledgments

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