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Effect of High Summer Temperatures on Lammas Shoot Elongation and Flowering in Japanese Red Pine

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K e y w o r d s : Flowering, lammas shoots, leaf primordia, Japanese red pine (*Pinus densiflora* SIEB. & ZUCC.), summer temperature.

S u m m a r y

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The formation of lammas shoots and flowering in *Pinus densiflora* (SIEB. & ZUCC.) were investigated from 1990 to 2003, and their relationship with the temperature conditions prevailing during the months of July and August of each year, which is the leaf primordia differentiation phase, was investigated. Observations revealed that the longest lammas shoots developed during the months of July and August in 1995 when the highest mean temperature was recorded. In the years when the temperatures in July and August are high, a tendency to form longer lammas shoots is recognized. In addition, the number of leaf primordia differentiated per bud in late August was measured, and the relationships between the number of leaf primordia differentiated, the temperatures during July and August, and lammas shoots length were examined. The highest number of leaf primordia and the longest lammas shoots developed in 1995, when the temperatures were the highest. On the basis of these observations, it was inferred that the leaf primordia differentiation and the subsequent elongation of lammas shoots was facilitated in the years experiencing high temperatures during July and August, such as in 1995. On the other hand, since it was known that lammas shoots having length between 40 and 60 mm facilitated the differentiation of male flower, the relationship between the length of the lammas shoots and the male flowers that bloomed in the subsequent year was also investigated in the present study. The mean length of the lammas shoots differed greatly and was between 8 and 22 mm each year. Furthermore, the percentage of buds (lammas shoots) that contained male flowers was low, 0.0%–6.2%, and there was no difference among them. These observations can be attributed to the fact that the growth of lammas shoots having lengths between 40 and 60 mm was scarce between 1990 and 2003.

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Introduction

The Japanese red pine (*Pinus densiflora* SIEB. & ZUCC.) is a temperate evergreen conifer distributed widely from Kyushu to Hokkaido, in Japan. In the case of the Japanese red pine inhabiting central Japan, the flush period, which is the first elongation of the bud, generally starts in late March. In central Japan where the present study was undertaken, the flush period generally ends between late May and early June and is followed by bud formation at the apex of the shoot (HANAWA 1967, NAGATA 1968). The development of this bud continues till dormancy is induced in the autumn. This bud acts as the locus of growth in the following spring.

During the period from the beginning of bud formation through the end of September, the differentiation into leaf primordia, male cone initials, and female cone initials, which will increase in size and flower in the following spring, occurs inside the bud (HANAWA 1967). In other words, the Japanese red pine bud is a mixed bud; it possesses numerous leaf and flower buds within a single bud. Furthermore, after initiation of dormancy in the autumn and dormancy release on encountering low temperatures, a majority of the buds demonstrate internode growth and increase the size of needle leaves in the spring of the following year (NAGATA 1969). However, the internodes that develop inside certain buds elongate in the summer prior to the initiation of dormancy. In addition, an increase in the size of needle leaves is also observed in some buds (KUSHIDA & al. 1999a). These secondarily elongated buds are generally termed lammas shoots.

The growth mechanism of lammas shoots in the Japanese red pine has been examined in the study conducted by KUSHIDA & al. 1999a, in which the formation of lammas shoots was induced by heat treatment during spring, thus extending the period of leaf primordia differentiation in the summer. Therefore, when the number of leaf primordia, which successively differentiated inside a bud after the end of the spring flush, increased to approximately 90 to 100, it was ascertained that the lammas shoot of a Japanese red pine is a bud characterized by internode elongation as a reaction to the long day conditions (of over 14 hours).

Similar to *Camellia sasanqua*, in which a relationship between the lammas shoot formation and the growth and development of flower buds has been reported (NAKASHIMA & al. 1995, 1997), it has been shown that the increase in the lammas shoot length in the Japanese red pine hastens the differentiation of the male flower (KUSHIDA & al. 1999b). Furthermore, it has been observed that in the Japanese red pine, when the lammas shoot length exceeds 60 mm, the number of male flowers is small, and individuals that produce both male and female flowers are rare (KUSHIDA & al. 1999b).

The above findings suggest that there is a close relationship between the leaf primordia differentiation, the lammas shoot elongation, and the flowering in the following spring in the Japanese red pine. The present study monitored the summer temperature conditions pertaining to the leaf primordia differentiation and lammas shoot elongation along with the flowering data of the following year from 1991 through 2003 and analyzed their relationships.

Material and Methods

The experiments were carried out at two cultivated locations in Tsu City, Mie Prefecture, central Japan (lat 34°44'N, long 136°31'E and lat 34°42'N, long 136°23'E). It is known that the formation of the Japanese red pine lammas shoot varies according to locality and tree age. Hence, in this study, experiments were carried out every year using two-year-old Japanese red pine seedlings grown in Suzuka City, Mie Prefecture. Five seedlings were planted in each earthenware-pot measuring 270 mm in diameter and containing equal amounts by volume of pit sand, vermiculite, and compost. They were watered daily, and liquid fertilizer consisting of 0.04 ml each of N, P, and K was applied to each pot once every month. Surveys were conducted in 1990, 1991, 1993, 1995, 1996, and 1997 through 2003.

The buds formed on the main axes of the test specimens were observed. The following details were studied: 1) The final bud (lammas shoot) length in late December when no further bud activity was observed, and 2) the percentage of the bud that contained male cone (hereinafter referred to as the male flower) and the female cone (hereinafter referred to as the female flower) in May of the subsequent year. Further, in order to compare the developmental degree of the buds in late August, in the surveys conducted in 1993, 1995, and 1996, a longitudinal section of the bud through the shoot apex was prepared and observed using an optical microscope, and the number of leaf primordia differentiated inside the bud was counted using the same method as a previous study (KUSHIDA & al. 1999a).

The number of test specimens and the number of buds observed were as follows: 23 specimens and 122 buds in 1990, 19 specimens and 111 buds in 1991, 20 specimens and 106 buds in 1993, 25 specimens and 146 buds in 1995, 30 specimens and 60 buds in 1996, 20 specimens and 108 buds in 1997, 20 specimens and 110 buds in 1998, 15 specimens and 83 buds in 1999, 15 specimens and 84 buds in 2000, 20 specimens and 114 buds in 2001, 20 specimens and 106 buds in 2002, and 20 specimens and 109 buds in 2003. The sample employed for the comparison of leaf primordia differentiated inside the bud was: 40 buds in 1993, 25 buds in 1995, and 60 buds in 1996.

Results and Discussion

Table 1 shows the lammas shoot lengths measured each year and the percentage of the buds that contain male and female flowers in the following year. The lammas shoot length was the greatest in 1995 and the least in 1993 ($p < 0.05$). Accordingly, it was ascertained that the lammas shoot length of Japanese red pines varies considerably from year to year. It has been ascertained that for the lammas shoots formation in Japanese red pine in central Japan, it is necessary that approximately 90 to 100 leaf primordia form inside the buds by the end of August, along with long day conditions of over 14 hours (KUSHIDA & al. 1999a). Corresponding to the period of leaf primordia differentiation in Japanese red pines (KUSHIDA & al. 1999a), a comparison was made with the temperature conditions in July and August of each year, when a strong relationship with lammas shoot elongation is expected. During the two months in each year, the mean temperatures in Tsu City, Mie Prefecture, (the mean temperature for 30 years is 26.5°C), showed a variance of 4.0°C, with the highest mean temperature recorded in 1995 and the lowest in 1993.

Fig. 1 shows the relationship between the final lengths of the buds measured each year and the mean temperature during the two months. It is observed that the lammas shoot lengths were greater in 1995 and 2000 when the temperatures were higher, and conversely, the shoot lengths were shorter in 1993 and 2003 when the temperatures were lower. Thus, a tendency toward the formation of longer

lammas shoots is recognized in years when the temperatures during July and August are high, suggesting the possibility of a correlation between lammas shoot formation and temperatures during July and August.

Table 1. Effect of mean temperature during July and August on lammas shoot elongation and flowering. The same letters indicate no significant difference at the 5% levels (Tukey-Kramer multiple comparisons test).

	Years					
	1990	1991	1993	1995	1996	1997
Lammas shoot length (mm)	18 ± 13^{b}	$21 \pm 14_{ab}$	8 ± 3^{d}	22 ± 14^{a}	15 ± 7^{c}	19 ± 10^{b}
Male flowering (%)	0.0	2.7	3.8	6.2	0.0	2.8
Female flowering (%)	0.0	0.0	14.2	10.3	6.7	6.5
Lammas shoots length between 40 and 50 mm (%)	5.7	6.3	0.0	10.3	8.3	3.7
Mean temperature (°C)	27.5	26.5	24.3	28.3	26.9	27.5
	Years					
	1998	1999	2000	2001	2002	2003
Lammas shoot length (mm)	$17 \pm 14_{bc}$	18 ± 12^{b}	21 ± 16^{a}	20 ± 10^{b}	18 ± 12^{b}	14 ± 10^{c}
Male flowering (%)	1.8	0.0	6.0	6.1	5.7	0.0
Female flowering (%)	7.3	6.0	2.4	10.5	5.7	7.3
Lammas shoots length between 40 and 50 mm (%)	1.8	0.0	8.3	7.9	5.7	0.0
Mean temperature (°C)	27.2	27.0	28.2	27.7	27.7	25.5

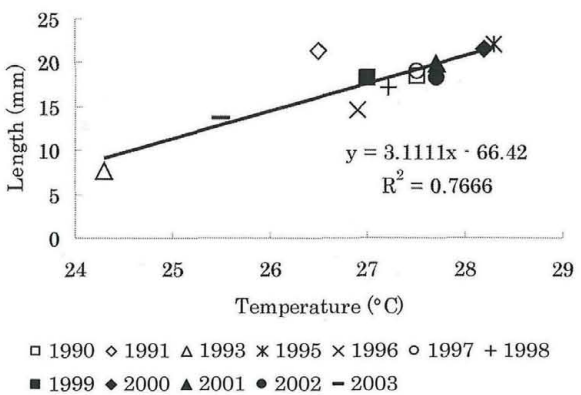

Fig. 1. The relationship between the mean temperatures during July and August and bud (lammas shoot) lengths.

Furthermore, the number of leaf primordia differentiated inside the bud by the end of August, which is considered to be a necessary condition for lammas shoot formation in Japanese red pine, was studied in 1993, 1995, and 1996, and the relationships between the number of leaf primordia differentiating each year, the mean temperatures during July and August, and lammas shoot formation was investigated.

The estimated numbers of leaf primordia differentiated inside the bud by August were 92.9 ± 10.6 in 1995, which was the maximum, followed by 72.7 ± 17.0 in 1996, and 43.2 ± 11.0 in 1993, which was the least (Fig. 2). In 1995, the year of maximum leaf primordia differentiation, the amount of leaf primordia differentiated was more than double of that observed in 1993. It was evident that a statistically significant difference existed in the numbers of leaf primordia ($p < 0.05$).

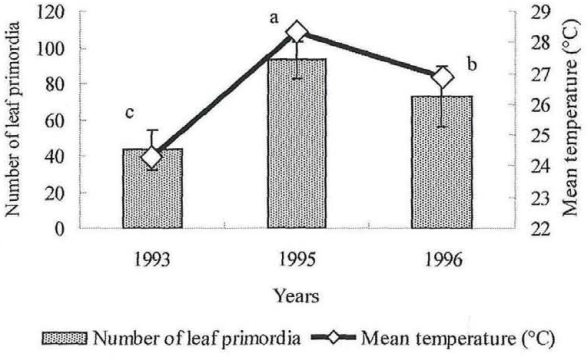

Fig. 2. Number of leaf primordia and mean temperature during July and August in 1993, 1995, and 1996. The same letters indicate no significant difference at the 5% levels (Tukey-Kramer multiple comparisons test).

By studying the relationships between the number of leaf primordia differentiated inside the buds in late August of each year, the mean temperatures during July and August, and the occurrence of the lammas shoots, it was ascertained that not only was the leaf primordia differentiation maximum in 1995, when mean temperatures were high, but also lammas shoot lengths were longer. In 1993, the year with a low mean temperature, it was also observed that leaf primordia numbers were low and lammas shoot lengths were shorter. On the basis of these results, it was inferred that July and August temperatures influence the processes of leaf primordia differentiation, which is followed by lammas shoot elongation. Measurements indicate that in years such as 1993, in which the temperatures during July and August were lower, leaf primordia differentiation was inhibited, and lammas shoot elongation was also suppressed. Conversely, measurements also indicate that in years such as 1995 and 2000, when the July and August temperatures were high,

leaf primordia differentiation was hastened, and lammas shoot elongation was also accelerated. These test results in which it was ascertained that higher summer temperatures stimulate increased leaf primordia differentiation suggest that Japanese red pine makes efficient use of the high temperature and long day conditions of over 14 hours in the summer for leaf primordia differentiation.

Table 1 shows the percentage of the buds that contain male and female flowers each year. The percentage of the buds that contained male flowers each year was low at 0.0%-6.2%; no difference was detected in the male flowering. This is considered to be due to the fact that lammas shoots of lengths between 40 and 60 mm, which is known to be the length at which male flower differentiation is stimulated (KUSHIDA & al. 1999b), were hardly produced during 1990 through 2003 (Table 1). On the other hand, the percentage of buds that bloomed into female flowers each year was also low at 0.0%-14.2%, however, no relationship was observed between the blooming of female flowers, lammas shoot lengths, and the temperatures recorded during July and August.

The above results are important findings in providing indicators for growth predictions under environmental fluctuations as well as for forestry resources management. This is similar to other studies that have considered the impact of environmental changes on the physiological reactions of woody plants (EMBERLIN & al. 2002, KOIKE & al. 1996, HEIDE 2003). This study was conducted within a temperature range of 24.3°C (1993) and 28.3°C (1995) measured during July and August. However, the average temperature during July and August in Tsu City, Mie Prefecture, in central Japan is 26.5°C. Based on these points, it is possible to infer that if the temperatures during this period fluctuate ±2°C due to environment changes, such as global warming, an increase in the amount of second elongation in the Japanese red pine may occur. On the other hand, this fluctuation in temperature is not anticipated to have any significant impact on the blooming of male and female flowers in the following year.

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