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Author(s)	KADOMATSU, Masahiko
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Differences in Phenology of *Quercus* Collected from Northeastern China, Eastern Hokkaido and Western Honshu

by

Masahiko KADOMATSU*

中国東北部・北海道東部・本州西部産ナラ類のフェノロジーの相違

門松昌彦*

Summary

Differences in the phenology of *Quercus* from different provenances were investigated in spring and autumn. Acorns of *Quercus mongolica*, *Q. crispula*, *Q. serrata* and *Q. dentata* were collected from northeastern China, eastern Hokkaido and western Honshu. The seedlings from acorns of each provenance were nursed in a nursery located in northern Hokkaido. Differences among the families of each seed tree in the times of leafing and autumn leaf coloration were studied in two successive years. Variations in phenological traits were observed among different families within the same provenance and species. Variations between provenances and between species were also found. The traits showed the following tendencies in both years: 1) the time of leafing among provenances accorded with a certain order but not with geographical cline, and 2) the autumn leaf coloration was earlier for *Quercus* from high latitude regions. These phenological traits were thought to be under genetic control.

Key words: China, Hokkaido, Honshu, Phenology, *Quercus*

1. Introduction

Due to the long life of trees, the phenology of individual trees can be observed over a period of many years, and trees can therefore provide a suitable index for evaluating long-term environmental changes such as global warming. It is expected that the habitat of some species of trees will move north accompanying global warming, resulting in changes to the present ecosystem. Genetic breeding measures will be needed to deal with this expected change in the ecosystem. Therefore, it is important to investigate the genetic variation in phenology under present environmental conditions.

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*Wakayama Experimental Forest, The University Forests, Faculty of Agriculture, Hokkaido University
北海道大学農学部附属演習林和歌山地方演習林

In Japan, long-term phenological observations have been carried out on a national scale by the Meteorological Agency for *Prunus mume*, *Prunus x yedoensis* and *Acer palmatum*. There have also been many studies on other species, including investigations into the relationship of environmental factors to flowering and leafing phenomena: *Pinus densiflora* (KUSHIDA *et al.*, 1995), *Larix* (KURAHASHI, 1988; TADAKI *et al.*, 1994; KISANUKI and KURAHASHI, 1995), *Abies sachalinensis* (KURAHASHI and HAMAYA, 1983), *Fagus crenata* (HASHIZUME, 1994; KAJI, 1994; KURAHASHI and SHIBANO, 1994; NAKATA and NAKAYAMA, 1994; WATANABE and SHIBANO, 1994; HASHIZUME *et al.*, 1996), *Machilus thunbergii* (NAGATA, 1994), *Camellia sasanqua* (NAKASHIMA *et al.*, 1994, 1995).

There have also been several studies on the phenology of *Quercus* (MCGEE, 1974; KRIEBEL *et al.*, 1976; DICKE and BAGLEY, 1980; SCHLARBAUM and BAGLEY, 1981; SASAKI, 1983; KIMURA *et al.*, 1994; UBUKATA *et al.*, 1994; BACILIERI *et al.*, 1995). In the present study, variations in leafing and autumn leaf coloration of *Quercus* among provenances and among different families were investigated to obtain basic information concerning the phenology of *Quercus* in Japan.

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2. Materials and Methods

2.1 Collection of materials

In 1988, acorns of *Quercus mongolica* were collected in northeastern China (Dailing, Dongjingcheng in Heilungkiang). In 1989, those of *Q. crispula* were also collected in eastern Hokkaido (Ashoro). In 1990, acorns were collected from several *Quercus* species in western Honshu; i.e., *Q. crispula*, *Q. serrata* and *Q. dentata* in Sado, *Q. crispula* and *Q. serrata* in Daisen, and *Q. serrata* in Yamaguchi. In 1991, those of *Q. mongolica* were collected from Maoershan in northeastern China. Although *Quercus* in Ashoro shows *Q. mongolica* like elements (MIYAZAKI *et al.*, 1984), it was treated as *Q. crispula* in the present study. The acorns were sown in a nursery in Nayoro, northern Hokkaido, in the autumn of the year they were collected or in the spring of the following year, and they were grown under whole sky conditions. Therefore, the seedling age varied depending on the provenance. The maximum difference in seedling age was 3 years. The collection sites and location of the nursery are shown in Fig. 1.

2.2 Leafing survey

Leafing surveys were carried out in 1993 and 1994 for each seed-tree family. A total of 111 seed-tree families were surveyed: 10~30 families of *Q. mongolica*, 7~11 families of *Q. crispula*, 5~12 families of *Q. serrata*, and 3 families of *Q. dentata* (Table 1). The same families were surveyed in each year.

Leafing was ranked on a scale of 0 to 4 as shown in Table 2. A higher leafing rank represents a more advanced stage of leafing, indicating earlier flushing. Five indi-



Fig. 1 Sites of collection of acorns (●) and location of nursery (○).

viduals were mechanically selected from each seed-tree family on June 2, 1993, and the leafing rank of the bud that showed the most advanced stage of leafing in each individual was recorded. For comparison with the 1994 data, the maximum value of leafing rank for each family was taken as the representative value of that family. The leafing rank of each individual that showed the most advanced stage of leafing in each seed-tree family was also recorded at approximately 5-day intervals from May 26 to June 22 in 1994 in the same manner as in the 1993 survey. From among these data, the data for May 31 in 1994, which coincided approximately with the survey date in 1993, were selected as the representative leaf ranks of seed-tree families for 1994, and these ranks were compared with those for 1993. The author

Table 1 Number of families in each provenance for leafing survey.

species	provenance	number of families
<i>Q. mongolica</i>	Dailing	15
	Maoershan	30
	Dongjingcheng	10
<i>Q. crispula</i>	Ashoro	11
	Sado	8
	Daisen	7
<i>Q. serrata</i>	Sado	12
	Daisen	5
	Yamaguchi	10
<i>Q. dentata</i>	Sado	3
Total		111

Table 2 Leafing ranks.

- | |
|--|
| 0: not yet budded |
| 1: protrusion of leaf tips from tip of bud scale
~separation of leaf tips |
| 2: leaf blade recurved, but little extension |
| 3: extension |
| 4: leaf extension complete and leaf blade almost horizontal |

also investigated the number of days required from the first day of observation until the completion of leaf extension (leafing rank 4) for 1994. *Q. serrata* of Yamaguchi, which had not attained rank 4 at the end of the observation period, was excluded.

Based on previous reports (KURAHASHI *et al.*, 1966; SASAKI, 1983; KIMURA *et al.*, 1994; TADAKI *et al.*, 1994; UBUKATA *et al.*, 1994), the differences between mean daily air temperatures above 0°C and 5°C from January to May in both years and the respective tentative thresholds (0°C and 5°C) were added to obtain the "cumulative value of warmth". This value was compared with the leafing rank value for each year.

2.3 Autumn leaf coloration survey

Autumn leaf coloration surveys were carried out around October 20 in 1992 and 1993 for each seed-tree family. Panoramic photographs were taken of families with more than 5 individuals, and the seedlings were ranked according to the degree of red or yellow coloration and brown coloration. KADOMATSU *et al.* (1994) reported on autumn leaf coloration of the same samples, ranked into 11 stages including full coloration (5: leaves fully red or yellow, 11: leaves fully brown). In the present study, autumn leaf coloration was ranked into 9 stages (0~8), with stages above 5 representing brown coloration (Table 3). A higher rank represents a higher rate of coloration. In 1992, a total of 95 families were surveyed: 2~30 families of *Q. mongolica*, 7~11 families of *Q. crispula*, 5~12 families of *Q. serrata*, and 3 families of *Q. dentata* (Table 4). In the 1993 survey, the number of *Q. mongolica* families in Dailing and Dongjingcheng was increased to 10~15, making a total of 112 families. *Q. serrata* of Yamaguchi, which was not a sample in leafing time, was surveyed in both years.

The differences between minimum daily air temperatures below 5°C from August to October and the tentative threshold (5°C) were added to obtain the "cumulative value of coldness" (SASAKI, 1983). This value was compared with the autumn coloration rank for each year.

Table 3 Autumn leaf coloration ranks.

0: leaves are fully green
1: 1~25% of leaves are red or yellow
2: 26~50% of leaves are red or yellow
3: 51~75% of leaves are red or yellow
4: 76~100% of leaves are red or yellow
5: 1~25% of leaves are brown
6: 26~50% of leaves are brown
7: 51~75% of leaves are brown
8: 76~100% of leaves are brown

Table 4 Number of families in each provenance for autumn leaf coloration survey.

species	provenance	number of families	
		1992	1993
<i>Q. mongolica</i>	Dailing	2	15
	Maoershan	30	30
	Dongjingcheng	6	10
<i>Q. crispula</i>	Ashoro	11	11
	Sado	8	8
	Daisen	7	7
<i>Q. serrata</i>	Sado	12	12
	Daisen	5	5
	Yamaguchi	11	11
<i>Q. dentata</i>	Sado	3	3
Total		95	112

3. Results

3.1 Leafing time

The relationships between latitude of the provenance and leafing rank for each species and family in 1993 and 1994 are shown in Fig. 2. Figure 2 shows that the progression of leafing varies according to the provenance and species. Differences in leafing can also be seen between seed-tree families of the same species and of the same provenance. However, a relationship between latitude of the provenance and leafing time was not found. A comparison of mean leafing ranks shows almost the same trends for both years in the order of leafing among provenances and among species: the leafing of *Q. mongolica* was most advanced in Dongjingcheng ($43^{\circ} 54' N$); the leafing of *Q. crispula* was most advanced in Sado ($38^{\circ} 10' N$), followed by Ashoro ($43^{\circ} 18' N$) and Daisen ($35^{\circ} 23' N$); and the leafing of *Q. serrata* was most advanced in Sado, followed by Yamaguchi ($34^{\circ} 15' N$) and Daisen. Furthermore, the leafing rank of *Q. crispula* was higher than that of *Q. serrata* in both Sado and Daisen.

Figure 3 shows the relationship between the latitude of the provenance and the number of days needed to reach leafing rank 4 in 1994. There were variations in this

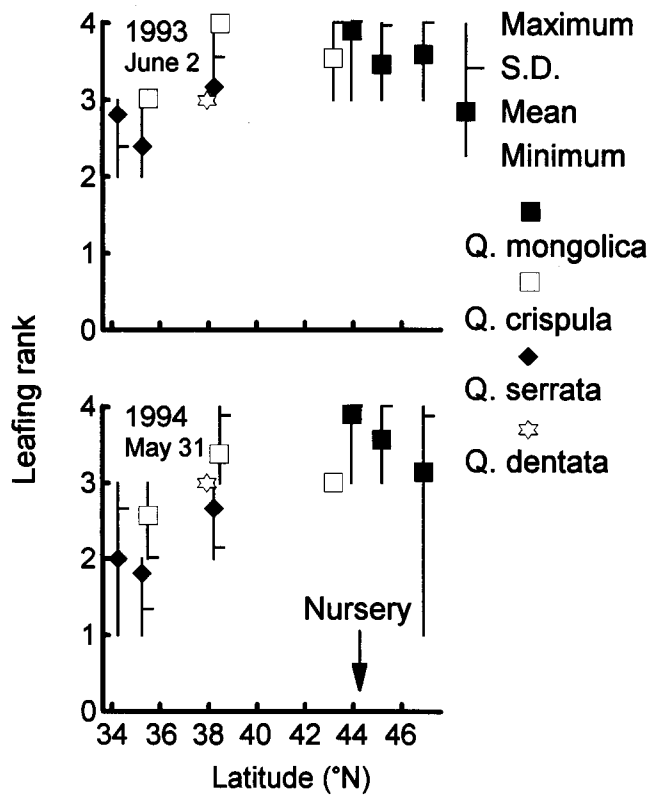


Fig. 2 Relationships between latitude of the provenance and leafing ranks for each species and family in 1993 and 1994. S. D., Standard deviation.

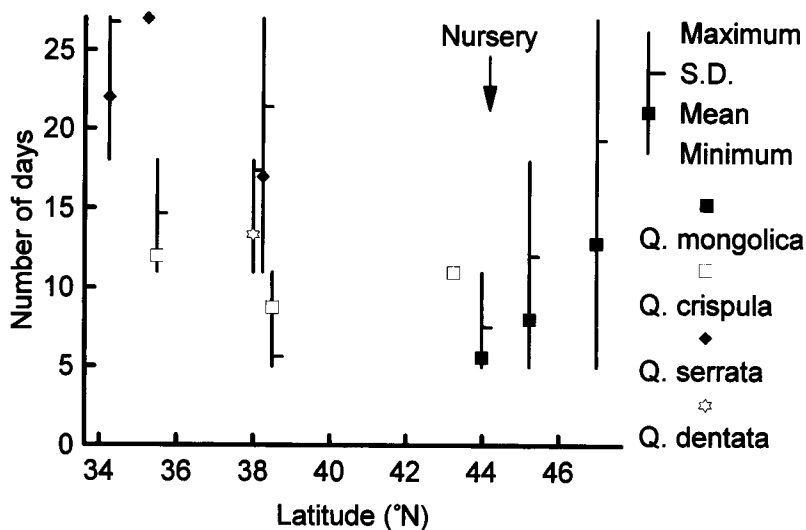


Fig. 3 Relationship between latitude of the provenance and number of days to reach leafing rank 4 in 1994. Calculation was started on the first day of observation (May 26). S.D., Standard deviation.

trait among families within the same provenance and species. The average number of days needed to reach leafing rank 4 (i. e., completion of extension) for each provenance and species was as follows: *Q. mongolica* required the least number of days to reach rank 4 in Dongjingcheng; *Q. crispula* required the least number of days to reach that rank in Sado, followed by Ashoro and Daisen; and *Q. serrata* required the least number of days to reach the rank in Sado, followed by Yamaguchi and Daisen.

However, as shown in Fig. 4, although the correlation between the leafing ranks for each family in both years was statistically significant at the 1% level, the coefficient of correlation was only 0.49. The regression coefficient for both years was also only 0.66.

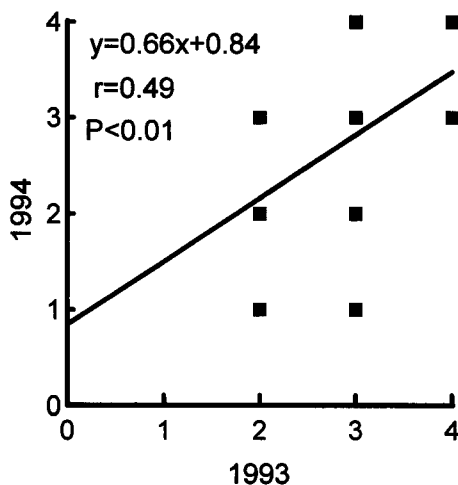


Fig. 4 Relationships between leafing ranks for each family in 1993 and 1994.

As for the daily mean air temperatures in both years, the cumulative values of warmth obtained by setting the tentative thresholds at 0°C and 5°C are shown in Figs. 5 and 6, respectively. A comparison of these cumulative values shows that there was not a great difference between 1993 and 1994 regardless of the tentative threshold value.

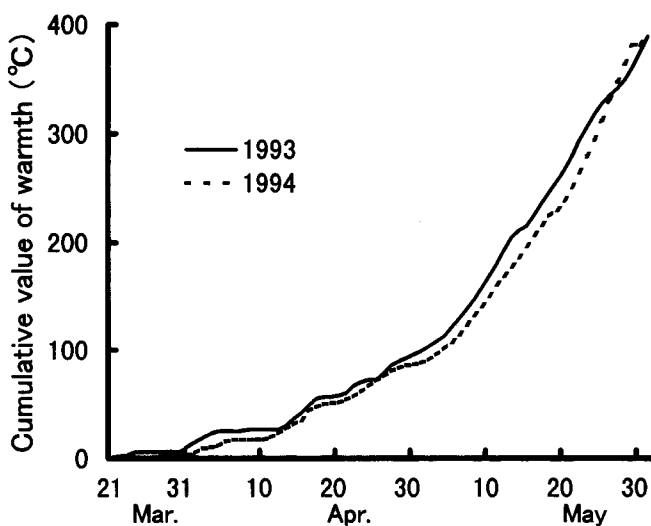


Fig. 5 Cumulative values of warmth in 1993 and 1994.
cumulative value of warmth = $\Sigma(t-0)$ t = daily mean temperature over 0°C

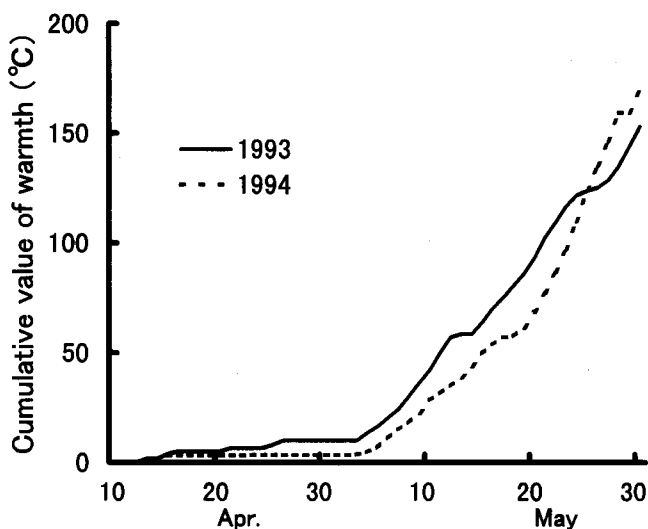


Fig. 6 Cumulative values of warmth in 1993 and 1994.
cumulative value of warmth = $\Sigma(t-5)$ t = daily mean temperature over 5°C

3. 2 Autumn leaf coloration time

The relationships between latitude of the provenance and autumn leaf coloration rank for each species and family in 1993 and 1994 are shown in Fig. 7. As was the case with leafing time, the degree of autumn leaf coloration progression varied according to the provenance and species. Differences in the progression of coloration were also seen between seed-tree families of the same species and of the same provenance. In contrast to leafing time (Figs. 2 and 3), the autumn leaf coloration of *Quercus* tended to

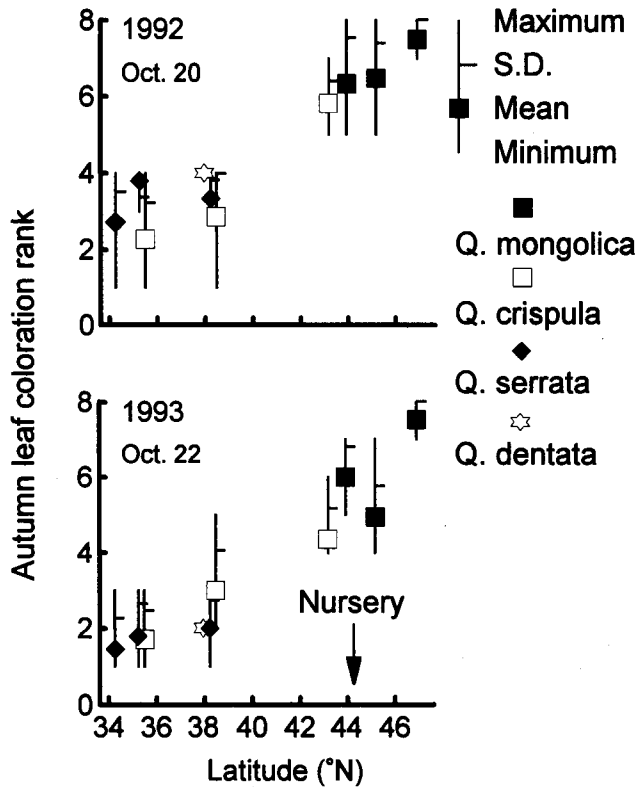


Fig. 7 Relationships between latitude of the provenance and autumn leaf coloration ranks for each species and family in 1992 and 1993. S.D., Standard deviation.

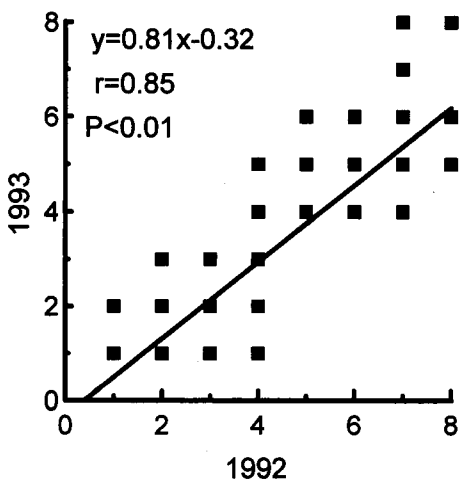


Fig. 8 Relationships between autumn leaf coloration ranks for each family in 1992 and 1993.

occur earlier if their origin was at a relatively high latitude. This tendency was especially clear in *Q. crispula*. The tendency was also the same in both 1992 and 1993, and the correlation coefficient of autumn leaf coloration rank for each family, although slightly lower than that reported previously (KADOMATSU *et al.*, 1994), was significantly high (0.85) (Fig. 8).

The autumn leaf coloration in 1992 was generally earlier than that in 1993 (Fig. 8). The progression of autumn leaf coloration in Sado in 1992 was in the order of *Q. dentata*, *Q. serrata*, and *Q. crispula*, while in 1993 *Q. crispula*

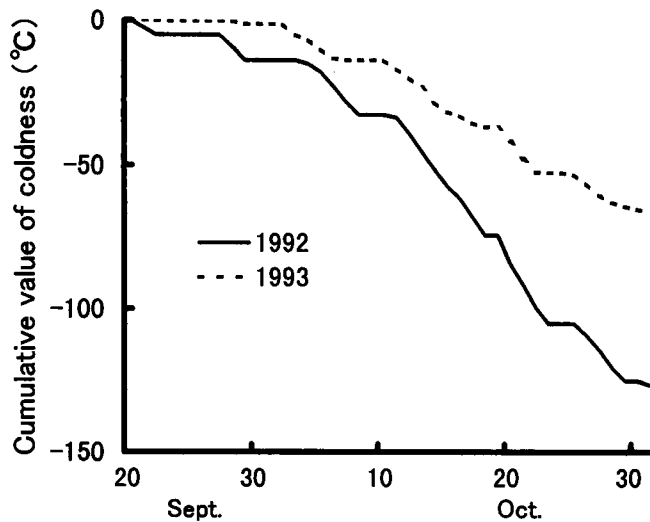


Fig. 9 Cumulative values of coldness in 1992 and 1993.

cumulative value of coldness = $\Sigma(t-5)$ t = daily minimum temperature under 5°C

changed color earlier than *Q. dentata*, and *Q. serrata*. In Daisen, the autumn leaf coloration was earlier for *Q. serrata* than for *Q. crispula* in both years. Furthermore, a comparison of the autumn leaf coloration ranks of *Q. serrata* for each provenance in 1992 showed the progression of autumn leaf coloration to be in the order of Daisen, Sado, and Yamaguchi, and no relationship was found with latitude. The results also showed that autumn leaf coloration of *Q. mongolica* in Maoershan started later in 1993 than that of *Q. mongolica* in Dongjingcheng, which is located at a lower latitude. Thus, there were slight differences between 1992 and 1993 in the order of autumn leaf coloration between species of the same provenance and in the relationship between latitude of the provenance and autumn leaf coloration rank for two species (Fig. 7).

As shown in Fig. 9, the cumulative value of coldness for 1992 was much larger than that for 1993, indicating that 1992 had a cool autumn.

4. Discussion

4.1 Leafing time

The facts that all the seedlings were grown in the same area and that the leafing rank order between seedlings from different provenances was almost the same in both years of the survey suggest that the difference in the leafing time seen between seedlings from different provenances is genetic. This speculation is supported by the results of provenance tests carried out on *Quercus rubra* by KRIEBEL *et al.* (1976). The results of a study by UBUKATA *et al.* (1994) on *Q. crispula* in Hokkaido also showed a significant difference between provenances. CHIBA and NAGATA (1973), based on a high genetic correlation between mother tree clones and their progeny of *Populus maximowiczii*, also reported that leafing is a genetic character. EL-KASSABY and PARK (1993) reported that, in a narrow sense, the heritability of flushing for *Pseudotsuga*

menziesii was very high (0.69) compared to the heritability of the character of growth and biomass (0.06~0.18). They also reported that flushing is not affected by spacing.

Also, the fact that a relationship between leafing and latitude was not found agrees with the report by SCHLARBAUM and BAGLEY (1981) for *Q. rubra*. In an earlier report for the same species, KRIEBEL *et al.* (1976) also stated that among trees of northern origin, there was a tendency for trees of western provenance to bud earlier, and among trees of central and southern provenance, there was a tendency for trees of southern origin to flush earlier. Tests conducted on clones of *Populus balsamifera* collected from regions at almost the same longitude but different latitudes showed that clones collected from regions north or south of the planting site budded earlier than clones collected from near the planting site, indicating that there is no relationship between flushing and latitude (FARMER, 1993).

On the other hand, despite little difference in the temperature during the spring of the two years, the leafing rank for each family varied between years and the correlation was rather weak. According to a report by KIMURA *et al.* (1994) on a *Q. crispula* tree, flushing time is closely related to fluctuations in the spring temperature. Thus, it can be inferred that if there are not large fluctuations in spring temperature, there will be little annual variation in the leafing of each family. Considering the results of the present study along with the above assumption, annual variations in leafing ranks for each family may be attributed to such factors as a delay in flushing due to the death of terminal buds, which was observed in this survey.

4. 2 Autumn leaf coloration time

A difference in the degree of autumn leaf coloration was seen between provenances and species. Although the variation within the same provenance for *Q. rubra* was reported to be small (KRIEBEL *et al.*, 1976), a variation was seen between seed-tree families within the same provenance for the *Quercus* investigated in the present study. Also, unlike the leafing time, autumn leaf coloration was earlier for *Quercus* from high latitude regions.

The autumn phenology of many species of trees is affected by the photoperiod and temperature (SATO and TSUTSUMI, 1978). However, in the case of *Q. rubra*, the autumn leaf coloration time is genetically controlled and a strong correlation with latitude of the provenance has been reported (KRIEBEL *et al.*, 1976; SCHLARBAUM and BAGLEY, 1981). Similar relationships with the provenance have also been reported for other species. For example, in the case of *Acer rubrum*, while young trees of northern sources show intense autumn leaf coloration, those of southern sources do not cease growing until very late and autumn leaf coloration is difficult to achieve (TOWNSEND *et al.*, 1979). Regarding the cold tolerance of leaves, it was reported that for plus-trees of *Pinus sylvestris* in Sweden, not only was there a variation among clones within the same population but the autumn cold acclimation of the southernmost population was slower than that of the central and northern populations (NILSSON and WALFRIDSSON, 1995). In the present study, the facts that seedlings were grown in the same area and that there was no large annual variation suggest that the difference in autumn coloration

tion time seen between provenances and between families is genetic.

As were discussed on leafing time, slight annual differences were also seen in the relationship of autumn leaf coloration rank with provenance latitudes and in the leaf coloration order between species. Leaf coloration for most families was also earlier in 1992 than in 1993. A comparison of accumulated temperatures indicated that the autumn in 1992 was cooler than that in 1993. Therefore, it was speculated that temperature is a factor causing annual variation in the autumn leaf coloration. This hypothesis does not agree with the report by KIMURA *et al.* (1994). In the autumn phenology of the genus *Larix*, a clear relationship with the distribution latitude was not found, and it was pointed out that the climate of the origin appears to be a significant factor (KISANUKI and KURAHASHI, 1995). Further detailed investigation of the relationship with temperature of the provenance is needed.

4. 3 General discussion

Variations in leafing and autumn leaf coloration of *Q. mongolica*, *Q. crispula*, *Q. serrata* and *Q. dentata* were observed between provenances and between families. The variations between provenances and between families of *Quercus* have been confirmed in the character of growth (MATSUURA and TANAKA, 1987; KADOMATSU, 1989; KURAHASHI and OGASAWARA, 1989; MIYAZAKI *et al.*, 1989; ORITA and KOONO, 1989; TANAKA and MATSUURA, 1989; HIURA *et al.*, 1992; OHSHIMA, 1992). The start and cessation of growth are closely related to the avoidance of stunting in vegetative growth due to such factors as frost (FARMER, 1993; SKRØPPA and MAGNUSSEN, 1993) and the growth period. Thus, as MA (1989) pointed out variations among provenances are thought to result from adaptation to the local natural selection pressure. Natural environmental factors include the photoperiod and temperature, which are related to latitude.

In the present study, although there was no clear relationship between leafing and latitude, a relationship was found between autumn leaf coloration and latitude. In their phenology, it is not clear whether the photoperiod or temperature plays the most significant role. However, as bud and leaf development of *Quercus* has been shown to be correlated with altitude (MCGEE, 1974), temperature must have some effect. SCHLARBAUM and BAGLEY (1981) reported that temperature appears to play a secondary role in growth cessation. The mean annual temperature in the neighborhood of the provenance in this study is as follows: 3.3°C at Harbin (45° 45' N), 6.1°C at Obihiro (42° 55' N), 13.1°C at Sado, 14.4°C at Matsue (35° 27' N), and 15.0°C at Hiroshima (34° 22' N). There is a tendency for mean annual temperature to be related with latitude of each provenance. Therefore, variation between provenances in autumn leaf coloration of *Quercus* is thought to correlate with the temperature of the provenance.

5. Conclusions

Several findings were obtained concerning the leafing and autumn leaf coloration of *Quercus*. Difference between the seed-tree families were seen in phenological traits. Variations between provenances of same species were also observed. These differences were thought to be heritable. Although there was no clear relationship between leafing

and latitude, a relationship was found between autumn leaf coloration and latitude. Leafing time accorded with a certain order.

These results were obtained for trees grown in only one nursery in northern Hokkaido and under the same environmental conditions. Therefore, the behavior of *Quercus* under various environmental conditions is not clear. To clarify this, investigation of the phenology of seed trees at the sites where acorns were collected is needed. The phenology of interspecific hybrids is also important.

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* : in Japanese, ** : in Japanese with English title, *** : in Japanese with English title and summary.

要 旨

本報では、産地の異なるナラ類について、春季と秋季におけるフェノロジーの違いを明らかにしようと試みた。中国東北部・北海道東部・本州西部からモンゴリナラ・ミズナラ・コナラ・カシワの堅果を収集し、北海道北部にある苗畑で養成した。そして、2ヶ年にわたり母樹系統別に開葉と紅葉の状況を調べた。その結果、開葉時期・紅葉時期ともに、同一樹種・同一産地内の母樹系統間で差異が認められた。また、産地間・樹種間にも変異があった。そして、年次を問わず、開葉時期および紅葉時期にそれぞれ一定の傾向がみられた。すなわち、開葉では地理的勾配はなかったが、産地の開葉順位がほぼ決まっていた。紅葉については、高緯度産のナラ類が早く紅葉する傾向があった。そして、これらのフェノロジーは遺伝的支配を受けていると推察された。