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Age trends of genetic parameters of spiral grain in hybrid larch F₁ and implications for efficiency of early selection

Abstract Age trends in variance components and heritability were estimated from the spiral grain angle of rings 2–25, as counted from the pith in hybrid larch (*Larix gmelinii* var. *japonica × Larix kaempferi*) F₁. Age–age genetic and phenotypic correlations and the optimum selection age for spiral grain were also calculated. Wood samples were collected from 95 29-year-old trees belonging to 19 full-sib families in a progeny test plantation in Hokkaido, northern Japan. Spiral grain angle data were obtained by the splitting method. Mean grain angles at growth rings used for the analyses were calculated as the arithmetic mean of angles up to respective rings. Generally, the additive genetic variance for mean grain angle decreased with increasing ring number. Although dominance variance was comparatively high near the pith, it decreased to zero in subsequent growth rings. Highest heritability estimates of mean grain angle occurred at ring 4 and then declined with age, ranging from 0.45 down to 0.20. Age–age phenotypic correlations were higher than genetic correlations, especially those involving early growth rings. Optimum selection ages for spiral grain based on genetic and phenotypic correlations were estimated as 3 and 4 years (cambial age), respectively, in which maximum gain efficiency per year were obtained.

Key words Hybrid larch · Spiral grain · Heritability · Genetic correlation · Optimum selection age

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Introduction

Japanese larch (*Larix kaempferi*) is an extremely important tree for silviculture in Japan because it shows rapid growth and good adaptation in severe environmental conditions.[1] For that reason, Japanese larch has been planted in hilly areas of the northern half of Japan. Its afforestation area accounts for about 30% of all plantation forest areas in Hokkaido.[2] However, Japanese larch is susceptible to vole (*Clethrionomys rufocanus bedfordiae*) damage, which exerts serious influence on mortality of Japanese larch in Hokkaido.[3,4] In contrast, Kurile larch (*Larix gmelinii* var. *japonica*) exhibits high vole resistance and good wood quality, but its growth rate is slower than that of the Japanese larch.[3,5] Consequently, numerous studies on breeding by crossing with both species have been carried out over the past 50 years. Those studies have demonstrated that the hybrid larch F₁ (*L. gmelinii* var. *japonica × L. kaempferi*) shows higher vole resistance, faster growth, higher wood density, and higher strength than Japanese larch.[6–8] Actually, the amount of seedling production of the hybrid larch has increased recently; it is anticipated as a worthy species for silviculture in Hokkaido.[9]

Spiral grain is regarded as a major defect in Japanese larch, engendering serious problems of distortion and twisting in drying sawn timber, especially when the trees are young. In Japanese larch, the existence and importance of spiral grain have been well documented, but few definitive studies have reported the inheritance of spiral grain. Examining the relationship of the spiral grain between mother trees and clones of Japanese larch, Nakagawa[10] found that the estimates of the repeatability of spiral grain were 0.27 for the mean grain angle and 0.54 for the maximum grain angle. Oshima and Kuromaru[11] reported that narrow-sense heritability of spiral grain was 0.57 in 25 controlled pollinated families of 19-year-old hybrid larch.

The heritability of wood properties changes with tree age.[12] Consequently, knowledge of changes in heritability of traits and correlations between these traits assessed at different ages are necessary for determination of efficiencies of

early selection.[13] Nicholls et al.[14] reported on changes of heritability of some wood properties with the ring number from the pith in 10-year-old open-pollinated progenies of *Pinus radiata*; they showed that heritability of spiral grain decreased from 0.44 (fourth ring from pith) to 0.24 (seventh ring from pith). Mikami et al.[15] observed a similar trend among 8–9-year-old clones of Japanese larch in which broad-sense heritability based on grain angles for individual rings was within the range of 0.35–0.42. However, most of these studies were conducted with young trees. Hence, it remains unknown what change in heritability will be revealed at advanced age. Furthermore, there are few reports that assess age--age genetic correlations and the optimum selection age for spiral grains.

In Hokkaido, progeny tests of hybrid larch suitable for studying wood properties, including spiral grain, have only recently become available. Objectives of this study were to estimate the age trends of genetic parameters for the spiral grain and to determine the potential for early selection for spiral grain in hybrid larch F$_1$.

Materials and methods

Plant material

Wood samples were collected in a 29-year-old *Larix gmelinii* × *Larix kaempferi* progeny test stand, in Bibai, Hokkaido, northern Japan (43°28′N, 141°88′E; 250 m elevation). The progeny test included 19 full-sib families. They were derived from an incomplete factorial mating design involving four female and six male parent trees (Table 1). The parents were selected from among plus-trees; they originated from Hokkaido. The test was established in 1974 with 2-year-old seedlings and the families were planted in 21-tree plots at 2 × 2 m spacing according to a randomized complete block experimental design with two replicates.

In 2002, one to six sample trees were harvested from each of the families. Thereby, the number of sample trees was 95. A 1.8-m butt log was removed from each tree and a diametric flitch, 40 mm thick, was sawn from each log (Fig. 1). A 30-mm-long (longitudinal direction) section including the pith was cut from the top end of each flitch that was free from decay and knots, to determine the grain angle profile of the tree.

Grain angle measurement

Spiral grain angle was measured following a procedure outlined by Nakagawa.[16] A parallel base line passing through the pith was drawn on both cross sections. The specimen was split on one cross section through the base line; the distances from the base line on the other side were measured at each annual growth ring using a digitizer with an accuracy of 0.1 mm (Fig. 1). The grain angle of each ring was calculated as arctangent of the ratio of the distance from the base line to the specimen thickness (30 mm).

The final grain angles for individual growth rings in each specimen were expressed as the mean of values from both radii. Mean grain angle at each growth ring was calculated as the arithmetic mean of angles up to that ring, ignoring differences in sign.

Statistical analysis

The sample strips contained 25–27 growth rings reflecting their age and sampling height. The first annual ring was discarded because it was generally incomplete. The general stem pattern of spiral grain in conifers is that it shows its
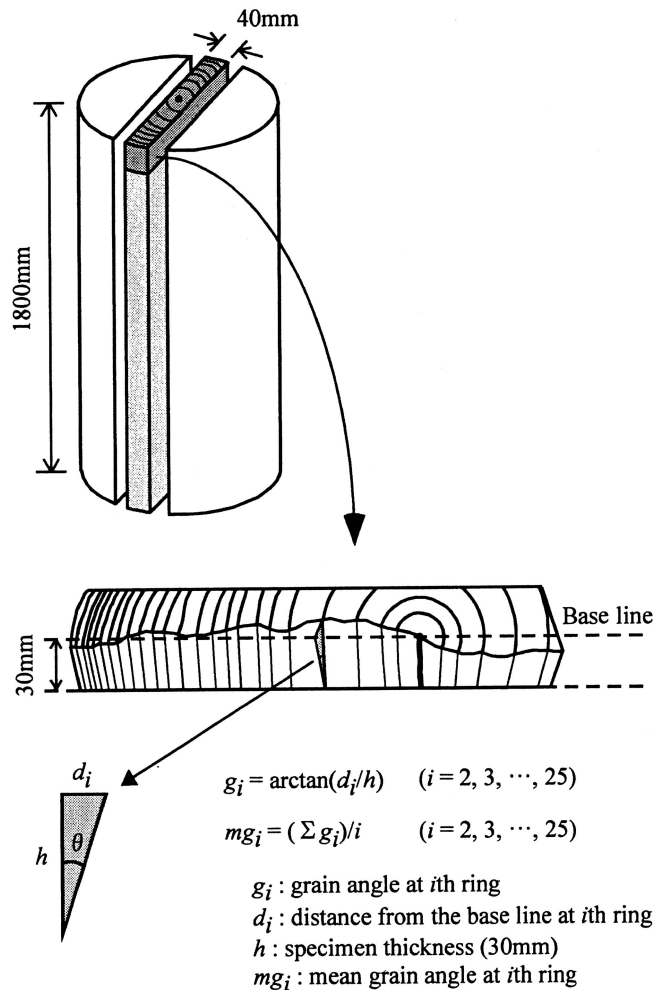
Table 1. Diagram of the mating design

Females (*Larix gmelinii*)	Males (*Larix kaempferi*)					
	L1	L2	L3	L4	L5	L6
G1		○		○	○	
G2	○	○	○	○	○	○
G3	○	○	○	○	○	○
G4		○	○	○	○	

Open circles indicate the sampling families

$$g_i = \arctan(d_i/h) \quad (i = 2, 3, \cdots, 25)$$
$$mg_i = (\Sigma g_i)/i \quad (i = 2, 3, \cdots, 25)$$

g_i : grain angle at ith ring
d_i : distance from the base line at ith ring
h : specimen thickness (30 mm)
mg_i : mean grain angle at ith ring

Fig. 1. Sample preparation and calculation of grain angle

maximum value within the first ten annual growth layers and decreases toward the bark.[17] Thus, the mean grain angle calculated for rings 2–25 counted from the pith was used in the following analyses, assuming that the relative impact of cambial age is largest near the pith.

Analyses of variance for all observed values for each ring were performed according to the models in Eq. 1 using the general linear model (GLM) procedure of the Statistical Analysis System (SAS):[18]

$$Y_{ijkl} = \mu + R_i + F_j + M_k + FM_{jk} + RFM_{ijk} + \varepsilon_{ijkl} \tag{1}$$

where Y_{ijkl} is the observed measurement of tree $ijkl$, μ is the general mean, R_i is the fixed effect of replicate i, F_j is the random effect of female j with variance σ_f^2, M_k is the random effect of male k with variance σ_m^2, FM_{jk} is the random interaction effect between female j and male k with variance σ_{fm}^2, RFM_{ijk} is the between-plot error, random effect with variance σ_{rfm}^2, and ε_{ijkl} is the within-plot error, random effect with variance σ_e^2. The model assumes that the random factors are distributed normally with expectation zero.

Variance components for each ring were estimated using the restricted maximum likelihood (REML) method of SAS VARCOMP procedure and estimates of the covariance between different rings were obtained from multivariate analysis of variance (MANOVA).[18] Variance components were expressed in terms of coefficients of variation to avoid potentially confounding scale effects.[19]

Estimates of additive and dominance variance were derived from the covariance between half and full-sibs, as described by Becker[20] and Cotterill et al.[21] The additive variance can be derived directly from female and male variance components when the coefficient of inbreeding among the parents is assumed to be zero and epistatic and maternal effects are assumed to be negligible:

$$\sigma_A^2 = 4\sigma_f^2 = 4\sigma_m^2 \tag{2}$$

where σ_A^2 is the variance caused by additive genetic effects, σ_f^2 is the random effect of the j-th female parent, and σ_m^2 is the random effect of the k-th female parent.

Similarly, dominance genetic variance was estimated as

$$\sigma_D^2 = 4\sigma_{fm}^2 \tag{3}$$

where σ_D^2 is the dominance genetic variance and σ_{fm}^2 is the random effect of the jk-th family.

The narrow-sense heritability is given by the following formula on an individual tree basis:[22]

$$h^2 = \frac{2\left(\sigma_f^2 + \sigma_m^2\right)}{\sigma_j^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_{rfm}^2 + \sigma_e^2} \tag{4}$$

where h^2 is the narrow-sense heritability, σ_{rfm}^2 is between-plot error variance, σ_e^2 is within-plot error variance, and σ_f^2, σ_m^2, and σ_{fm}^2 are defined as above.

The age–age genetic correlations for mean spiral grains between younger ages and the 25th ring were calculated as follows:[20]

$$r_g = \frac{cov_{fi,25} + cov_{mi,25}}{\sqrt{\left(\sigma_{fi}^2 + \sigma_{mi}^2\right) \times \left(\sigma_{f25}^2 + \sigma_{m25}^2\right)}} \tag{5}$$

where r_g is the genetic correlation, $cov_{i,25}$ is the covariance between the i-th and 25th ring, σ_i and σ_{25} are variance components of the i-th and 25th rings, and subscripts f and m indicate female and male parents, respectively. Standard errors of the heritability and additive genetic correlations were calculated respectively as in Becker[20] and Falconer and Mackay.[23]

Optimum age for selection was estimated using the gain efficiency per year, which is the ratio of the genetic gain per year of indirect selection based upon early selection relative to direct selection for the breeding goal. Assuming equal intensities of selection between mature and young ages, gain efficiency per year was calculated as:[24]

$$E = \frac{h_j r_g T_m}{h_m T_j} \tag{6}$$

where E is the gain efficiency, r_g is the genetic correlation between the juvenile trait and mature (assumed to be 25 years) trait, and h_j and h_m are the square roots of individual tree heritability at juvenile and mature ages, respectively, and T_j and T_m are the respective generation intervals for juvenile and mature selection. In the present study, the generation interval was the selection age plus 5 years.[25]

Results and discussion

Population means

The grain angle for individual growth rings decreased gradually from the pith to the periphery (Fig. 2). Population means of maximum grain angles within each stem and the ring revealed maximum angle were 5.1° (3.7–8.3°) and 5.6 ring (2–25 rings), respectively. The mean grain angle decreased almost linearly for successive rings from 4.4° to 3.1°. The standard deviation of grain angle for individual growth rings and mean grain angle were constant at about 1.0° over the rings.

Although the age-associated changes of spiral grain resembled those of general patterns in conifers[17] with respect to population level, various developing patterns were found in each tree, as mentioned by Mikami.[1] Nakagawa[16] observed spirality patterns from pith to periphery in Japanese larch from a 49-year-old natural forest stand and classified it into five patterns. The present study, revealed some trees in which grain angles were constant or increased toward the periphery, rather than decreased. Large fluctuations at the outer parts of the stem resulted in a constant manner over the rings in standard deviations.

Variance components and heritability

The effects of both female and male parents were significant at $P < 0.05$ or $P < 0.1$ for mean grain angle at all rings, except
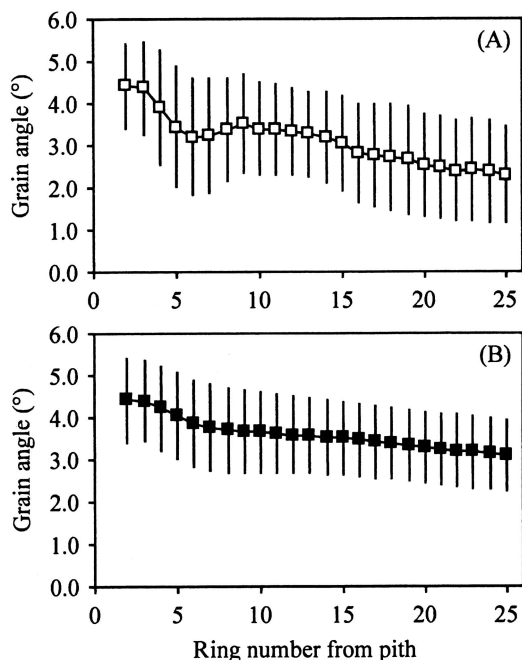
Fig. 2A,B. Age trends in population means for grain angle at individual growth rings (**A**) and mean grain angle (**B**). *Error bars* show the standard deviation. *Open squares*, grain angle; *filled squares*, mean grain angle

Fig. 3A,B. Age trends in variance components (**A**) and heritability (**B**) for mean grain angle. *Filled triangles*, phenotypic variance; *open diamonds*, environmental variance; *filled circles*, additive genetic variance; *open circles*, dominance variance; *filled squares*, individual tree heritability

for rings 10 and 11. The female × male parent interaction had no significant effect on mean grain angle at all rings. The coefficient of the phenotypic and environmental variance increased slight up to ring 6 and remained constant thereafter (Fig. 3). The coefficient of additive genetic variance increased to ring 4 and was followed by a steady decrease with increasing ring number until ring 9, then increased slightly in subsequent growth rings. The coefficient of dominance variance was comparatively high in the first several rings, but then decreased to zero for successive rings. The trend of heritability was similar to the trend of additive genetic variance. Namely, the highest heritability estimate of 0.45 occurred at ring 4 and declined to a value of 0.20 at ring 9, then increased to 0.30 toward the periphery. Standard errors of heritability estimates were high (0.17–0.22) because of the small number of progeny.

Zobel et al.[26] reported on variation in spiral grains in 52 control-pollinated families of 4-year-old loblolly pine (*Pinus taeda*), and showed presence of a high proportion of nonadditive genetic variance. Thereby, they concluded that mass selection to reduce spiral grain would not be very effective if the pattern for older trees is similar. In this study, additive genetic variance was higher than dominance variance at all rings with the exception of the second ring, indicating that progeny testing for identification of trees with good general combining ability can rely on open-pollinated progenies, excluding the early year of growth.

Age trends of heritability estimates resembled those reported previously for spiral grains. In a 25-year-old clone of radiata pine, Nicholls[27] reported that estimates of broad-sense heritability decreased with increasing distance from
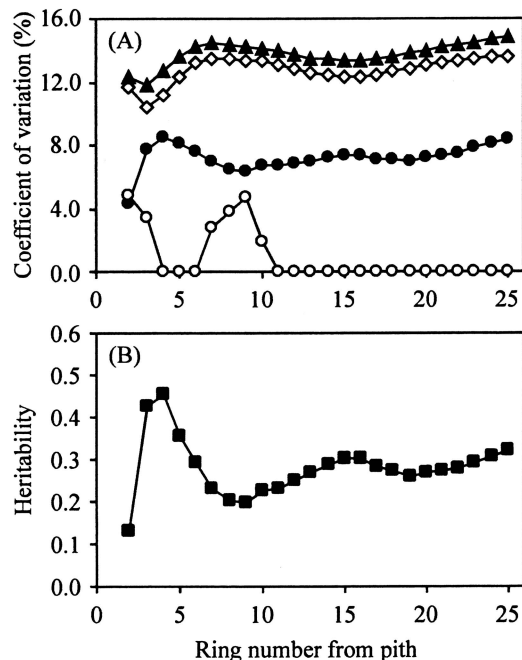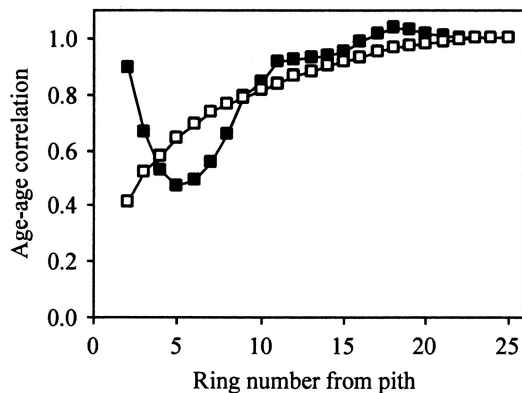

Fig. 4. Age–age genetic and phenotypic correlations between a mean grain angle at each ring and the corresponding mean grain angle at ring 25. *Open squares*, phenotypic correlation; *filled squares*, genetic correlation

pith, from 0.55 down to 0.08. Eisemann et al.[28] assessed the heritability of spiral grain angle in wood segments of different ages up to 15 years for hoop pine (*Araucaria cunninghamii*), and found that heritability of the spiral grain angle reached a maximum value of 0.35 near the pith where phenotypic expression of spiral grain was largest.

Age–age correlations

Genetic and phenotypic correlations for mean grain angle at different rings, with the respective values at ring 25, are presented in Fig. 4. Genetic correlations declined from

0.9 to 0.5 over the first four rings. Subsequently, they increased with age and were close to 1.0 after ring 17. The phenotypic correlations were higher than genetic correlations for early growth rings, except for the first two rings. Subsequently, both values traced each other after ring 9. While standard errors of genetic correlations were very high, especially at rings 4 to 8 (SE ≈ 0.3), the standard error declined as the differences in ring number decreased.

Numerous studies of other species have revealed that age–age genetic correlations for wood properties, such as wood density, were higher and more stable than the corresponding phenotypic correlations.[25,29,30] These results indicate that using age–age phenotypic correlations rather than genetic correlations to evaluate efficiency of early selection will underestimate potential gains from early selection. Contrary to this, phenotypic correlations were higher than genetic correlations at rings 4–8 in the present study. This fact might be attributable to high standard errors of genetic correlations at these rings, giving a less precise estimate of genetic correlations. It has been suggested that phenotypic correlations could replace genetic correlations, particularly when small sample sizes are used, because estimation errors of genetic correlations in such cases are large.[31]

Genetic and phenotypic correlations between early rings and ring 25 from pith for mean grain angle were comparatively high. Autocorrelation effects could upwardly bias these estimates from remeasurements of the same sample strips.[32] However, Vargas-Hernandez and Adams[29] found that the age–age genetic correlations for whole core density determined as an aggregate of observed individual ring densities were similar to those of individual rings, suggesting that age–age genetic correlation of core densities was not merely caused by autocorrelations. Similarly, Borralho et al.[33] observed little difference between genetic parameters for absolute and incremental growth traits. In this study, genetic correlations estimated between grain angles of individual growth rings at different ages were almost as strong as the age–age genetic correlations for the corresponding mean grain angle, but there were some fluctuations in the grain angles of individual rings.

Relative efficiency of early selection

Optimum selection age for mean grain angle based on genetic correlations was estimated to be 3 years (cambial age) in which the maximum gain efficiency per year of 2.9 was obtained (Fig. 5). This figure indicates that the genetic gain per year was about three times higher when selection was carried out at age 3 than when it was carried out at age 25. The optimum selection age based on phenotypic correlations was estimated as 4 years, and the gain efficiency per year was lower than that based on genetic correlations.

Few reports address the optimum selection age for spiral grain angle. Johnson et al.[34] examined the height and diameter of Douglas fir (Pseudotsuga menziesii) and found that the optimum selection age was 10 years for height and 13 years for diameter. Gwaze et al.[25] estimated the optimum selection age for wood density in loblolly pine (Pinus taeda)
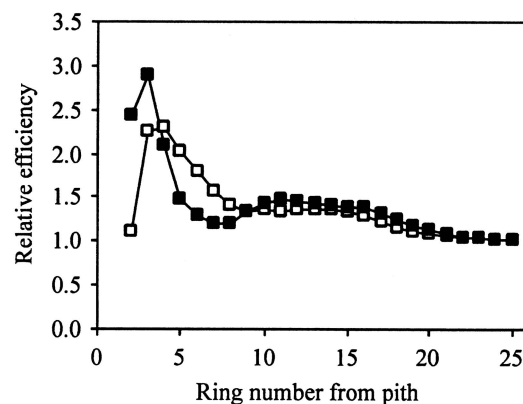

Fig. 5. Relative efficiency of selection for grain angle at different ages. *Open square*, gain efficiency per year calculated from phenotypic correlation; *filled squares*, gain efficiency per year calculated from genetic correlation

and obtained 5 years when calculations were based on genetic and phenotypic correlations. It should be noted that sample strips in the present study were taken at a height of about 2 m. Thereby, the optimum selection age for grain angle may be older than that predicted in the present study. Sampling should be made at a height below 2 m to determine the actual optimum selection age.

The present study confirms that selection at a very young age is effective for spiral grain, as suggested by Zobel,[12] Nicholls,[27] and Mikami.[1] However, a prerequisite for including trees of this early age in a breeding program is that early flowering be inducible.[30] Mikami[1] pointed out that the propagation of superior genotypes by cuttings seems to be the best method of obtaining practical effects on decreasing grain angle in Japanese larch. Kuromaru and Kita[35] also stated that it is practically possible to propagate the hybrid larch F_1 by rooted cuttings of young seedlings, considering the effects of age of stock plants and the time of transplanting.

Conclusions

Age trends of variance components and heritability indicate that spiral grain is under genetic control in the early growth phase in hybrid larch F_1. Additive genetic variance was higher than nonadditive genetic variance for all ages, except for near the pith. This fact suggests that progeny testing for selection of trees with good general combining ability could rely on open-pollinated progenies, but specific combining ability should be considered if the selection is applicable to very young trees.

Genetic correlations between early rings and ring 25 from the pith for grain angle were comparatively high – greater than 0.5. The genetic gain per year for grain angle was about three times larger when selection was performed at cambial age 3 than at age 25. These results suggest that early tests for spiral grain should increase the efficiency of the hybrid larch tree-breeding program.

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