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Time Trends for Genetic Parameters in Progeny Tests of *Abies sachalinensis* (Fr. Schm.) Mast.

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Summary

Changes of genetic parameters for tree height with stand development were examined on 21-year performance data from 4 open-pollinated progeny tests of *Abies sachalinensis* in Hokkaido, Japan. Differences in tree height among families were significant on each site, while among regions were unclear. Large genotype-environment (GE) interaction was observed. Heritability was highest at the youngest age, and showed a tendency to decrease with stand development. Genetic juvenile-mature correlation was almost always higher than phenotypic correlation. Expected genetic gain in height by early selection was comparable to that by selection at 21 years.

Key words: Heritability, juvenile-mature correlation, stand development, genetic gain, early selection.

FDIC: 165.3; 165.5; 232.11; 174.7 *Abies sachalinensis*.

Introduction

Information on genetic parameters and time trends in them with stand development are important for decisions about breeding strategy and optimal selection age. Heritability and juvenile-mature correlations affect genetic gains and selection efficiency. These parameters have been estimated by many authors, and the possibility of early selection was discussed by them (TODA, 1972; GIERTYCH, 1974; SQUILLACE and GANSSSEL, 1974; NAMKOONG and CONKLE, 1976; FRANKLIN, 1979; LAMBETH, 1980; FOSTER, 1986; JIANG, 1987; COTTERILL and DEAN, 1988; REHFELDT, 1992; ERIKSSON et al., 1993). Genetic parameters at various ages are available for index selection based on assessment data at different ages (BURDON, 1989).

In progeny tests of *Abies sachalinensis* in Hokkaido, Japan, differences among progenies are obvious at an early stage for some traits. For example, susceptibility to Rhacodium-snow blight and winter desiccation damage

were observed on seedlings aged 2 and 7 years from seeds respectively (HATAKEYAMA, 1981). However, it remains unclear whether early selection in this species is possible for growth traits. In this paper, time trends of heritability and juvenile-mature correlation of tree height are investigated and the possibility of early selection, or of an effective way of selection is discussed.

Materials and Methods

Progeny test data

Plus trees of *Abies sachalinensis* have been selected from natural stands and plantations all over Hokkaido about 1958. Open pollinated seeds were collected from these in-

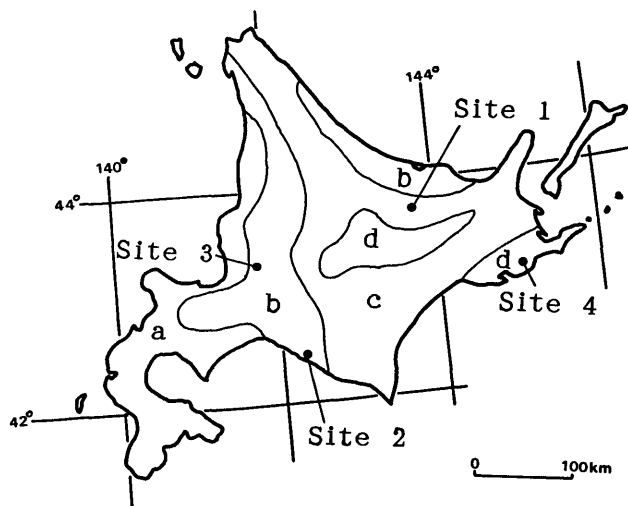


Fig. 1. — Locations of progeny test sites of *Abies sachalinensis* in Hokkaido. Four seed zones (a to d) of YANAGISAWA (1965) are also indicated.

Table 1. — General site descriptions for 4 progeny tests of *Abies sachalinensis*.

Test site	site 1	site 2	site 3	site 4
Annual mean temperature (°C)*	6.0	7.7	7.2	5.7
Annual mean precipitation (mm)*	815.3	1131.5	1204.4	1042.5
Maximum snow depth (cm)*	59	21	123	40
Elevation (m)	200	150	200	50
Number of families studied	59	62	50	29
Number of replications	2	3	3	3
Number of trees per plot at establishment	64	64	64	40

* Data from the nearest meteorological station to each test site. (Japan Weather Association, 1991, 30 year average from 1961 to 1990).

dividuals in 1958 or in 1959. They were sown and grown for 5 years in the nursery at Bibai, Hokkaido and then transplanted to each progeny test site.

Data from 4 progeny tests (sites 1 to 4) were used for analysis (Fig. 1). Few snow falls and cold winters are climatic characteristics of site 1 (Table 1). Climate is relatively mild in site 2. Heavy winter snow falls characterize site 3. Few snow falls, cold winters and cool summers caused by sea fog are characteristics of site 4.

The test design is randomized complete blocks with 2 or 3 replications at 1.5 m x 1.5 m spacing. Number of families studied and number of trees per plot are given in table 1. There were 87 different families in 4 tests and 21 families were common to all 4 tests.

Tree height at 1, 6, 11, and 16 years after planting was measured for all trees at all sites, except for height at 1 year in site 3. Tree height at 21 years was measured for all trees on sites 1 and 4. On sites 2 and 3, tree height at 21 years was measured for half of the trees in each plot, and stem diameter at breast height was measured for all trees. In these 2 sites, tree height at 21 years was estimated from the allometric relationship between stem diameter and tree height on each site. No significant differences among progenies was observed in the allometric relationships.

On sites 1 and 3, apparently tree height changed directionally in a block along a slope. This environmental effect was evaluated by simple or multiple regression of the plot mean height on column and/or row number of the plot (AKASHI et al., 1971). Regression was significant at 6, 11, 16, 21 years in site 1 ($r^2 = 0.36, 0.38, 0.33, 0.33$), and at 11, 16, 21 years in site 3 ($r^2 = 0.63, 0.76, 0.81$). Data was adjusted before analyses, by removing environmental effects as evaluated based on the regression from each individual tree height.

Statistical analyses

Families of plus trees of *Abies sachalinensis* show large genotype-environment (GE) interactions in some traits, for example, resistance to snow damage, desiccation damage in winter, and Rhacodium-snow blight (HATAKEYAMA, 1981). The breeding program should therefore be established in each region separately whereby GE interaction might be reduced. In this paper, genetic parameters were at first estimated in each progeny test site. In addition, to clarify the effect of GE interaction on height growth, genetic parameters for the 4 test sites were estimated from the unbalanced data consisting of 87 families. Analyses of variances were carried out using SAS (SAS Institute Inc.,

1989). SAS PROC GLM (general linear model) was used to test for significance of models. SAS PROC VARCOMP was used to estimate variance components.

The linear model used for analysis of variance in each test site is:

$$Y_{ijkl} = \mu_i + r_{ij} + F_{ik} + P_{ijk} + w_{ijkl}$$

where

μ_i = the mean height for the i th test;

r_{ij} = random effect of j th block within i th test,

$$E(r_{ij}) = 0, \text{Var}(r_{ij}) = \sigma_r^2;$$

F_{ik} = random effect of k th family on the i th test,

$$E(F_{ik}) = 0, \text{Var}(F_{ik}) = \sigma_F^2;$$

P_{ijk} = random plot error of k th family in j th block of i th test, $E(P_{ijk}) = 0, \text{Var}(P_{ijk}) = \sigma_P^2;$

w_{ijkl} = random tree error of l th tree in a plot of k th family in j th block of i th test, $E(w_{ijkl}) = 0, \text{Var}(w_{ijkl}) = \sigma_w^2;$

and the covariances between all pairs of factors are assumed to be zero.

The linear model used for analysis of variance including all test sites is:

$$Y_{ijkl} = \mu + t_i + r_{ij} + f_k + ft_{ik} + P_{ijk} + w_{ijkl}$$

where

μ = a fixed general mean height;

t_i = random effect of i th test environment,

$$E(t_i) = 0, \text{Var}(t_i) = \sigma_t^2;$$

f_k = random effect of k th family,

$$E(f_k) = 0, \text{Var}(f_k) = \sigma_f^2;$$

ft_{ik} = random interaction effect of k th family with the i th test, $E(ft_{ik}) = 0, \text{Var}(ft_{ik}) = \sigma_{ft}^2.$

$\sigma_F^2, \sigma_P^2, \sigma_t^2, \sigma_{ft}^2$ were estimated based on plot means, and σ_w^2 were calculated separately.

Single-site heritability h_s^2 , heritability for 4 sites h^2 , genetic juvenile-mature correlation r_g , and type B genetic correlation r_B were calculated as below.

$$h_s^2 = 4 \sigma_F^2 / (\sigma_F^2 + \sigma_P^2 + \sigma_w^2), h^2 = 4 \sigma_f^2 / (\sigma_f^2 + \sigma_{ft}^2 + \sigma_P^2 + \sigma_w^2)$$

$$r_g = \sigma_{ft(x,21)} / \sqrt{\sigma_{ft(x)} \cdot \sigma_{ft(21)}}, r_B = \sigma_f^2 / (\sigma_f^2 + \sigma_{ft}^2)$$

where

$\sigma_{ft(x,21)}$ = covariance component of family between height at age x and height at age 21;

$\sigma_{ft(x)}^2$ = variance component of family at age x ;

$\sigma_{ft(21)}^2$ = variance component of family at age 21.

Type B genetic correlation is a measure of genotype-environment interaction (BURDON, 1977). Standard errors of h_s^2, h^2 and r_g followed BECKER (1984).

Genetic gain from selection, ΔG was estimated by:

$$\Delta G = i r_g h_{(x)} h_{(21)}$$

where

i = selection intensity;

$h_{(x)}$ = square root of heritability at age x ;

$h_{(21)}$ = square root of heritability at age 21.

In this paper, it is assumed that $i = 1$ regardless of stand age, and $h_s^2, r_g = 1$ when they are larger than 1.0.

Results and Discussion

Family mean tree heights at 21 years in 4 test sites are shown in figure 2. For convenience, all families are assigned to 4 regions (a to d, Fig. 1) based on seed zones of YANAGISAWA (1965). In site 4, differences among regions are obvious. Families originating from regions c and d showed better growth than those from region b. This differentiation of height growth on regional level coin-

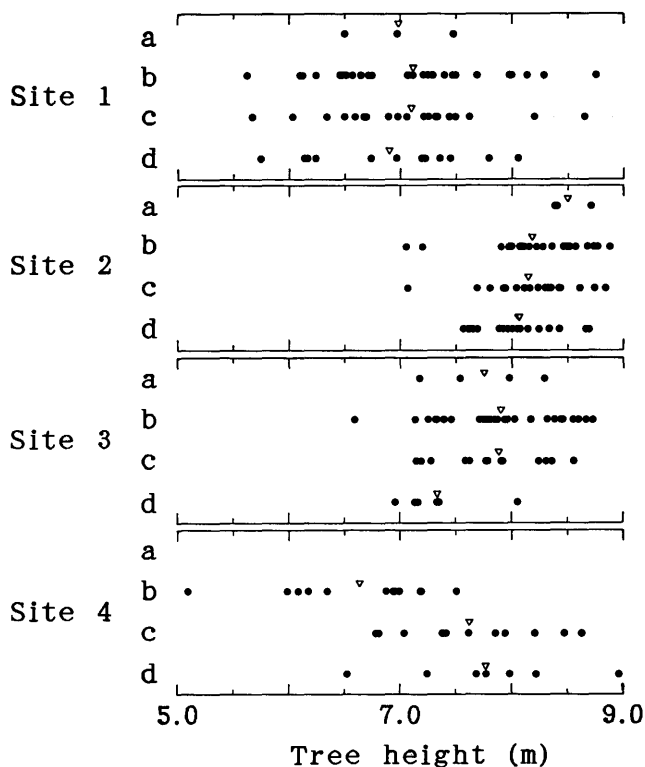


Fig. 2. — Family mean tree height of *Abies sachalinensis* on 4 test sites. They are classified into 4 regions (a to d, Fig. 1) based on seed zones of YANAGISAWA (1965). — In sites 1 and 3, they were adjusted by removing environmental effects (see materials and methods). Open triangles indicate means on tree height in each region.

cides with that of winter desiccation damage at age 2 years (HATAKEYAMA, 1981). It appears that desiccation damage at a younger stage affected tree height at 21 years on site 4. On the other hand, scatter within a region is large on all sites, and differences among regions were generally low at all ages in sites 1 to 3. Differences in tree height on

Table 4. — Expected genetic gain in height at 21 years (meters) by selection at various ages.

Stand age (year)	site 1	site 2	site 3	site 4	4 sites
1	0.52	0.19	—	0.55	-0.16
6	0.29	0.12	0.28	1.01	0.14
11	0.34	0.19	0.40	0.81	0.12
16	0.25	0.17	0.44	0.87	0.12
21	0.34	0.12	0.30	0.92	0.07

regional level are not so clear as in susceptibility to *Rhacodium*-snow blight, winter desiccation damage, and snow damage (HATAKEYAMA, 1981). In the present analysis, effects of regions were not included in the models.

Variance among families of tree height at 21 years was significant on each site ($P < 0.04, 0.05, 0.007$ and 0.01 on sites 1, 2, 3 and 4 respectively). But it was not significant, and GE interaction was significant ($P < 0.0001$), when the 4 test sites were analysed together.

Heritabilities for height (both single-site heritability and heritability for 4 sites) decline with age (Table 2). This is due to increase of plot error variance σ_p^2 , and/or within-plot variance, σ_w^2 .

FRANKLIN (1979) distinguished 3 developmental phases in 4 conifer species. Heritability decreased in the juvenile genotypic phase, abruptly increased in the mature genotypic phase, and decreased again in the codominance suppression phase. He considered that inter tree competition causes an increase of additive genetic variance and leads to the mature genotypic phase. FOSTER (1986) and HODGE and WHITE (1992) reported an increase of heritability in loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* E.), respectively. But in *Abies sachalinensis*, little increase of heritability can be seen, in spite of narrower spacing compared to FRANKLIN'S (1979) and FOSTER'S (1986), and canopy closure at about 11 to 16 years. The reason for this difference is not clear. However, it seems reasonable that plot error variance and within-plot variance increase

Table 2. — Single site heritabilities (h_s^2), heritabilities for 4 sites (h^2), and type B genetic correlations (r_B) for height trait at various ages in progeny tests of *Abies sachalinensis*. Standard errors of heritabilities are in parentheses.

Stand age (year)	h_s^2				h^2	r_B
	site 1	site 2	site 3	site 4		
1	1.05(0.14)	0.51(0.09)	0.39(0.08)	0.73(0.13)	0.32(0.05)	0.32
6	0.12(0.03)	0.31(0.06)	0.34(0.07)	0.72(0.09)	0.21(0.03)	0.63
11	0.20(0.05)	0.30(0.06)	0.32(0.07)	0.41(0.08)	0.13(0.02)	0.41
16	0.09(0.03)	0.25(0.05)	0.38(0.07)	0.45(0.07)	0.13(0.02)	0.43
21	0.16(0.04)	0.09(0.03)	0.18(0.04)	0.47(0.03)	0.04(0.01)	0.24

Table 3. — Genetic correlations (r_g) and phenotypic correlations (r_p) between height at various age and height at age 21. Standard errors of r_g are in parentheses.

Stand age (year)	site 1		site 2		site 3		site 4		4 sites	
	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p
	1	0.63(0.08)	0.33	0.67(0.09)	0.25	—	—	0.48(0.13)	0.28	-0.83(0.04)
6	1.25(-0.09)	0.57	0.53(0.13)	0.31	0.68(0.08)	0.38	0.90(0.03)	0.72	0.93(0.02)	0.42
11	0.91(0.03)	0.83	0.91(0.03)	0.68	0.99(0.004)	0.59	0.96(0.01)	0.86	1.06(-0.02)	0.70
16	1.04(-0.02)	0.91	0.89(0.04)	0.81	1.03(-0.01)	0.79	0.98(0.01)	0.93	1.03(-0.01)	0.83

with stand development because of the accumulation of microenvironmental effects and inter tree competition.

An increase of heritability might occur when suppressed trees in a plot die and consequently the within-plot variance decreases. If it were so, the causes of difference of our tests' results with others' might lie in a species difference. Since *Abies sachalinensis* is a shade-tolerant species, suppressed trees survive longer in the understory. Should intensive thinning be carried out or stands developed further till suppressed trees die, the within-plot variance might decrease.

Type B genetic correlation r_B is comparable to that in slash pine (HODGE and WHITE, 1992) from 6 to 16 years but lower at 1 and 21 years. It is believed that relatively large GE interaction operates for height growth at all ages. This agrees with the result of the test for family variance as mentioned above.

Genetic correlations between height at various ages and height at age 21 in single sites are always higher than phenotypic correlation (Table 3). They reach more than 0.9 at age 11 on all sites. Genetic correlations estimated for the 4 sites together showed a high positive value from 6 years to 16 years, while negative correlation was observed at year 1.

Genetic gains in height at 21 years expected from selection at early stages on each site are comparable to that expected from selection at 21 years (Table 4). It is considered that early selection for *Abies sachalinensis* is possible in view of the genetic gain in height, similarly as was shown for other tree species in many researches (SQUILLACE and GANSEL, 1974; FRANKLIN, 1979; LAMBETH, 1980; FOSTER, 1986; COTTERILL and DEAN, 1988; REHFELDT, 1992; ERIKSSON et al., 1993). On the other hand, some researchers have reported the negative phenotypic juvenile-mature correlations for the more aged progeny tests and risks of early selection (TODA, 1972; GIERTYCH, 1974). In *Abies sachalinensis*, age 21 is about a half to one third of rotation age. There is a possibility that negative genetic age-age correlations are observed for our tests with further investigations continued. But in practice, precise estimation of genetic parameters for more aged stands will be difficult in our tests if plot error variance and within-plot variance become still larger.

In *Abies sachalinensis*, accelerated flowering is not developed as yet. Therefore it is impossible to shorten the breeding generation for the present. Nevertheless early

assessment data is useful for selection because the expected genetic gain is high. The best use of data at various ages to maximize the genetic gain needs to be examined.

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Genetics of Rubber Tree (*Hevea brasiliensis* (Willd. ex ADR. de Juss.) Müll. Arg.)

I. Genetic Variation in Natural Populations*

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Summary

Electrophoretic analyses were effected in 2 populations of rubber trees (*Hevea brasiliensis*) for the enzymatic systems MDH, SKDH and LAP, with the objective of drawing inferences on the genetic structure of the populations. Four loci (LAP-1, LAP-2, SKDH and MDH-1), with 5, 4, 5, and 3 alleles/locus, respectively, were identified. The estimated variability parameters exhibit a high

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