

## Trends in Genetic Parameters with Age and Site for Early Implications of Genetic Improvement in Korean White Pine

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### 잣나무의 遺傳的 形質 改良의 早期檢定을 위한 樹齡 및 立地別 生長과 遺傳母數의 特性에 關한 研究

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#### ABSTRACT

Eighteen Korean white pine (*P. koraiensis* S. et Z.) families were tested in 3 different regions from age 5 to 9. Family and site were significant sources of variation for seedling survival and field growth, whereas the effects of family x site interaction were relatively small as compared with the former sources of variation. Variance components estimated from the separate and combined sites indicated that the most variabilities were associated with individual trees within plot. Family x site interaction components as a percentage of family variance decreased sharply with age. Heritability estimates varied with testing site and tree age. Combined analyses, however, showed a moderate change in heritability with increasing tree ages, and demonstrated high and stable trends of estimates, particularly in family heritabilities of tree height ( $h_F^2=0.789-0.798$ ).

The gains estimated from combined analysis have expected maximum or near-maximum efficiencies at age 6 or 7. Given equal intensity of selection, mass selection showed the most efficient gains within and across the sites. However, for the differences between mass and combined selections are small, selection made on the combination of family and within-family would be more effective in improving genetic gains. Indirect selection method indicated that 5-and 6-years height were all good predictors of 9-year-old height with little loss of relative efficiency (less than 10%) as compared with direct family selection at age 9. Phenotypic and genetic correlations computed on the basis of family mean values of height and diameter have shown predominantly high, positive, and statistically significant (1% level) relationships between all tested pairs of traits, which indicates that family growth maintained statistically consistent trends with age. The best families are those that maintained a stable superiority overall sites and ages in growth performance, therefore, it can be suggested that early identification of superior families at age 9 is feasible at age 5 or 6 in *Pinus koraiensis* S. et Z.

*Key words* ; variance components, heritability, genetic gain, selection, phenotypic and genetic correlations.

#### 要 約

잣나무(*Pinus koraiensis* S. et Z.)의 風媒次代檢定林을 忠北 永同郡, 京畿 廣州郡 및 加平郡의 3個 地域에 造成하고, 苗木의 生存率과 山地 5個年 동안(5年生-9年生)의 樹高 및 根元徑 生長을 調査하였다.

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山地植栽 後 苗木의 生存率과 生長은 家系와 植栽地에 따라 큰 差를 나타내었다. 生長의 變異를 나타내는 가장 큰 分散要因은 plot內的 個體木 間에 있음을 알 수 있었으며 家系分散에 대한 Family x Site 相互作用의 分散比는 樹齡이 증가함에 따라 현저히 감소하였다. 遺傳力은 地域과 樹齡에 따라 差를 나타내었으나 Combined analysis에 의한 樹高의 家系遺傳力( $h_e^2=0.789-0.798$ )은 높고 安定된 傾向을 보여주었다. 選拔에 의한 改良效果는 家系選拔과 家系內 個體選拔을 同時에 實施하는 Combined selection에 의하는 것이 바람직한 것으로 여겨진다. 家系選拔의 경우, 5, 6年生에서의 間接選拔은 9年生에서의 直接選拔에 比하여 90% 以上の 相對效率을 얻을 수 있었으므로 早期選拔의 可能性을 나타내었고, 5年生부터 9年生까지의 Age-age correlation을 구해본 결과 表現型 및 遺傳相關 모두 高度의 有意性を 認定할 수 있었다.

## INTRODUCTION

The long term of generation interval and the high variability of genetic and environmental conditions are the major considerations particularly in forest tree improvement programs. Therefore, efficiency of improvement effort can be increased by early testing and selection if adaptability or performance of mature trees can be reliably predicted from their performance at younger ages in a given area.

One way to reduce the generation interval in improvement programs is indirect selection which is a form of selection to improve the two traits simultaneously or to predict the correlated genetic gains from early selection (Falconer 1981). However, the use of genetic parameters to predict the gains may be seriously restricted by the fact that combined environmental and nonadditive genetic effects may exert a stronger, less predictable influence than additive gene action on quantitatively inherited traits of tree species (Hanover and Barnes 1969). The result obtained from any forest management operation therefore will be determined by both genetic makeup of the tree and its interaction with the environment in which it grow.

Thereupon, as a part of the improvement programs of *Pinus koraiensis*, half-sib progeny testing sites were established in three different regions.

The objectives of this study were to ;

1. examine the growth performance with different family, site, and tree age ;

2. determine and compare the estimates of genetic parameter and heritability for the growth traits ;

3. estimate the genetic gain and relative efficiency of different selection methods ;

4. determine the magnitude and tendency of correlations among the pairs of trials.

## REVIEW OF LITERATURE

Determining the variations within a species is necessary for tree improvement programs to be successful. However, not many studies to find out the kind, amount, cause, and nature of variation have been made for *Pinus koraiensis* until recent years (Chon 1976 ; Chon and Kim 1983 ; Kim and Chon 1987 ; Lee 1977). Intensive genetic testing to improve this species may have been started for some two decades ago in Korea. Since then some studies (Chon 1985, 1987 ; Chon and Kim 1986 ; Han and Choi 1985 ; Han *et al.* 1984, 1987, 1988) were made to develop the genetic control of growth traits under various conditions, and indicated that magnitudes of variance components were varied with experimental conditions, and which resulted in various estimates of heritability and expected genetic gain.

Variation in tree populations can be partitioned into genetic and environmental components, and considerable amount of work has been done on the variation commonly occurs within a species. Statistically significant differences in growth traits have been reported in provenance studies by such foresters as Bongarten and Hanover (1986a, for

Blue spruce), Falkenhagen (1978, for Sitka spruce), Griffin (1978, for Douglas-fir), Khalil (1987, for Red spruce), and Melchoir and Herrman (1987, for Giant sequoia).

Genetic testing in growth traits of forest trees has been made to determine the magnitude and probability of improvement for tree breeding. Bongarten and Hanover (1986b) indicated highly significant family differences in height growth of Blue spruce. Clair and Kleinschmit (1986) stated that analysis of variance for ten year height growth indicated a highly significant clone x site interaction in Norway spruce. Rockwood and Goddard (1980) found considerable variation among family means in volume, and suggested that genetic potential for improving volume trait appears good in Sand pine. Loo *et al.* (1985) determined the age of transition from juvenile to mature wood in Loblolly pine. In Black pine (Matziris 1984), ten morphological and anatomical needle characteristics showed significant differences between clones.

Heritability, the ratio between genetic and phenotypic variances, is not a fixed value for a given trait of a given species. This variability has been indicated by previous studies (Chon and Kim 1986; Graham *et al.* 1985; Samuel and Johnstone 1979; Shim *et al.* 1985) in which heritabilities were varied enough to demonstrate differences between families (genotypes), sites (environments), and testing years (tree ages). Nienstaedt and Riemenschneider (1985) noted that heritability estimates for height increased markedly between age 9 and age 15, however, Ying and Morgenstern (1979) found increased heritability estimates for height from age 8 to age 22 in only one of the four tests in White spruce. Lambeth's assumption (1980) was that heritability did not change significantly with age. Dean *et al.* (1986) indicated that there were no consistent changes in the heritability of height in *Pinus caribaea* var. *hondurensis*, but in stem diameter.

Previous attempts to develop juvenile-mature correlations have shown no consistent suggestions in early selection age and/or optimum gains per

unit of time. Many studies have suggested that selection for mature growth performance can be accomplished reliably at early ages in pine species, such as Loblolly pine (Lambeth *et al.* 1983; Waxler and van Buijtenen 1981), Japanese red pine (Noh and Yim 1979), Slash pine (Squillace and Gansel 1974), and Shortleaf pine (Tauer and McNew 1985). On the other hand, Wakeley's study (1971) in 4 coniferous species indicated that trees that would be of superior size at age 30 could be identified with a high degree of certainty at age 20 and in some instances at age 15, however, growth performance at age 10 or earlier should be accepted with reservations, particularly as guides to the rouging of seed orchard. Kang (1985) also concluded that extremely early selection time such as earlier than one third of rotation age should be used with caution, and Franklin (1979) suggested that accurate selections might be made after half the rotation age. Others (Namkoong and Conkle 1976; Namkoong *et al.* 1971) indicated extremely large changes in the relative magnitude of genetic and environmental effects on height growth during stand development.

## MATERIALS AND METHODS

Seed source and establishment procedures have been described in detail in the previous report (Chon and Kim 1986). Many seedlings died in the first year of outplanting due to the combined effects of drought and planting check. Therefore, from the end of the second growing season (Dec. 1984), the trees had completed five years of growth from seed, measurements have been made annually on all existing trees in each plot. Tree height and stem diameter at root-collar were measured. Of the 25 families, 18 test families where more than 8 individuals survived in each plot were checked, and 8 trees selected at random for analysis. This random selection aimed to reflect the soil diversity in each plot. A total of 1,296 test trees was selected and used in this study.

**Statistical analysis**

Analysis of variance and calculation of variance components were conducted on height and diameter from the data of each test separately and combined over sites, and heritabilities were estimated using the variance components and the formulas (Wright 1976 ; Zobel and Talbert 1984).

The genetic parameters estimated from the test were used for predicting the genetic gains ( $\Delta G$ ) with different selection methods ; i) mass selection, ii) family selection, iii) within-family selection, and iv) combined (family plus individuals within-family) selection (Falconer 1981 ; Jain 1982) :

$$\Delta G = ih^2\sigma_p$$

where

i =intensity of selection

$h^2$  =heritability

$\sigma_p$  =phenotypic standard deviation.

In computing the expected gains, top 10% of trees or families were retained for selection (i.e.,  $i=1.75$ ).

Since the former equation for direct selection does not apply to indirect selection, correlated gain for more mature trait is estimated by (Falconer 1981)

$$CG_m = i_j h_j h_m r_{gjm} \sigma_{Pm}$$

where

$CG_m$  =correlated gain

$i_j$  =selection intensity

$h_j$  =square root of heritability for the juvenile trait

$h_m$  =square root of heritability for the mature trait

$r_{gjm}$  =genetic correlation between the juvenile and mature trait

$\sigma_{Pm}$  =phenotypic standard deviation for the mature trait.

Phenotypic and genetic correlations were estimated by using family mean values of each site in the cross-products analysis of variance (Falconer 1981). Each family was ranked by height, and any changes in family ranking over time were noted. Spearman's rank order correlation coeffi-

cient (Snedecor and Cochran 1967) was used to test the consistency of family performance over time and site in field experiment.

**RESULTS AND DISCUSSION**

**Survival**

The original data expressed as percentage were converted into a new data set using the arcsin $\sqrt{p}$  transformation to make the data more amenable to the ANOVA. Seedling survival after five growing seasons in the field (8-year-old) differed with both site and family (Table 1). Statistically, however, survival of Kapyoung site (75.9%) was only significantly higher than those of Youngdong (65.4%) and Kwangju (68.8%) sites. Survival differences were also significant between families (1% level) ; ranged from a low of 59.3% (Fam. 17) to a high of 82.7% (Fam. 8), and averaged 70.06%. Non-significant effect of interaction indicates that families did not perform erratically with site in seedling survival. Family-mean heritability could be calculated for survival since the trait is measured on a plot basis. This result of 0.53 is consistent with that of Foster (1986) in Loblolly pine. Many papers have appeared on seedling survival (Farmer *et al.* 1983 ; Shim *et al.* 1985 ; Tak *et al.* 1986 ; van Haverbeke 1983 ; Williams *et al.* 1987), and these papers have shown that survival has a various trend. Considering that survival is attributed to various causes, e.g., site preparation, season and methods of planting, and weeding, etc., improvement of survival seems to be a difficult problem. However, the efforts to improve the survival through family selection would yield some progres-

**Table 1.** Analysis of variance for seedling survival.

Source of variation	df	MS	Family -mean heritability
Site	2	1007.42**	
Family	17	229.52**	0.53
F × S	34	107.00 <sup>ns</sup>	
Error	162	87.64	

\*\* ; significant at 1% level.

<sup>ns</sup> ; non-significant.

sive results since the family variation was noted significantly and heritability estimate on a family-mean basis was not so low as to relinquish an effort.

#### Analysis of variance

Analyses of variance for height and diameter measured from 5 to 9 years of growth from seed are evaluated in Table 2. When each site was analyzed separately, those traits indicated highly significant differences between families (1% level). Family x block interactions were also significant (5 to 1% level) with 3 exceptions. The uniformity of replications within the sites resulted in non-significant differences of growth among the blocks in Youngdong and Kapyoung sites. Whereas, Kwangju site having split replications showed significant differences between blocks. The high significance of replications confirms the existence of interreplication soil variation and sensitivity of *Pinus koraiensis* to it. In the multiplantation test, effects of family, site, and family x site interaction were highly significant at 1% level for all ages (Table 2). These results indicate that significant variations for height and

diameter occur in all sources of variation. Though the family x site interactions had a significant effect on the growth of progenies, their magnitudes were relatively small as compared with other sources. Magnitude of variance components will be discussed closely in the part of variance components.

Most tree species contain great variabilities that can be grouped into some categories of variation (Zobel *et al.* 1960), and previous studies have demonstrated that pine species such as Korean white pine (Chon and Kim 1983; Lee 1977), Ponderosa pine (Graham *et al.* 1985), Eastern white pine (Han *et al.* 1986), and Red pine (Lester and Barr 1966) were genetically variable in their growth characters. Han and Choi (1985) stated that total height of 10-year-old *Pinus koraiensis* showed highly significant differences (1% level) between sites, but did not show the differences between families. However, Han *et al.* (1988) reported significant differences between families at age 5, 8, and 10, respectively, when data on three sites were combined for analyses. If strong genotype x environment interactions are found, then it might be desirable to develop

**Table 2.** Test of significance for height and diameter growth.

S.V.	df	Height					Diameter				
		5	6	7	8	9	5	6	7	8	9
Youngdong											
Family	17	**	**	**	**	**	**	**	**	**	**
Block	2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
F x B	34	**	**	**	**	**	**	**	**	**	**
Kwangju											
Family	17	**	**	**	**	**	**	**	**	**	**
Block	2	**	**	**	**	**	**	**	**	**	**
F x B	34	ns	ns	*	*	**	*	ns	**	*	**
Kapyoung											
Family	17	**	**	**	**	**	**	**	**	**	**
Block	2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
F x B	34	*	**	**	**	**	*	**	*	**	**
Combined over sites											
Family	17	**	**	**	**	**	**	**	**	**	**
Site	2	**	**	**	**	**	**	**	**	**	**
B / S	6	**	**	**	**	**	**	**	**	**	**
F x S	34	**	**	**	**	**	**	**	**	**	**
F x B/S	102	**	**	**	**	**	**	**	**	**	**

\*, \*\* : significant at 5% and 1% level. ns ; non-significant.

special genotypes suited for each environment. In general, the existence of this interaction is main reason for replicating experiments in space and time (Wright 1973).

Considering the results of this study, those significant differences for all sources of variation confirm the existence of intra- and inter-site environmental variations and the sensitivity of *Pinus koraiensis* to them. Therefore, the tests to determine the proper genotypes on a given environment are necessary trials.

**Growth performances**

The results of ANOVA (Table 2) showed that there were significant family differences for height and diameter growth within and across the sites.

At the end of 5th growing season from seed germination (Dec. 1984), the families ranged from 26.08cm (F3) to 38.33cm (F8) in Youngdong, 27.29cm (F5) to 46.96cm (F8) in Kwangju, and 29.

08cm (F21) to 46.83cm (F8) in Kapyoung site, and averaged 33.51cm (Table 3). Family rankings were slightly changed in each site. After 6 years in the field (9-year-old), the total height averaged 131.70cm and ranged from the worst of 73.75cm (F18) in Youngdong to the best of 198.2 cm (F8) in Kapyoung site; 56.0% and 150.5% of the family mean of 131.70cm (C.V.=25.65%). Family 8 showed consistently excellent performance over all the testing years and sites. Family variations were also observed in diameter growth (Table 4). At age 9, families averaged 26.55mm (C.V.=29.89%) and ranged from the maximum of 42.49mm (F8) in Kapyoung to the minimum of 13.86mm (F18) in Youngdong.

Of the 3 test sites, height growth has been worst in Youngdong, whereas, trees in Kapyoung site have shown outstanding performance with a mean of 9-years height of 162.04cm, about two times higher than the poorest site of Youngdong

**Table 3.** Family means of height growth in 3 test sites.

		unit ; cm				
Site \ Age	5	6	7	8	9	
Youngdong						
Range	26.08-38.33	35.17-54.13	45.67-70.21	56.71-87.18	73.75-110.0	
Mean	29.56a <sup>2</sup>	40.94a	53.02a	66.80a	84.74a	
Kwangju						
Range	27.29-46.96	42.54-74.54	62.00-106.3	86.96-141.2	122.2-176.6	
Mean	35.53b	56.28b	83.13b	113.47b	148.31b	
Kapyoung						
Range	29.08-46.83	46.13-77.54	69.71-110.3	101.1-152.8	138.3-198.2	
Mean	35.43b	57.64b	84.72b	120.95c	162.04c	
Grand mean	33.51	51.62	73.62	100.41	131.70	

<sup>2</sup>: Values are not significantly different at 5% level if followed by the same letter.

**Table 4.** Family means of diameter growth in 3 test sites.

		unit ; mm				
Site \ Age	5	6	7	8	9	
Youngdong						
Range	5.42- 7.46	6.52- 9.50	7.48-11.29	10.25-14.71	13.86-20.60	
Mean	6.47a	7.89a	9.02a	11.92a	16.24a	
Kwangju						
Range	7.53-10.29	9.81-13.18	12.99-18.37	17.49-26.04	24.49-35.53	
Mean	8.44b	11.27b	15.53b	21.41b	28.71b	
Kapyoung						
Range	6.82- 9.49	9.40-14.24	12.47-20.50	19.40-29.15	29.73-42.49	
Mean	7.97c	11.29b	16.08c	23.35c	34.70c	
Grand mean	7.63	10.15	13.54	18.89	26.55	

(Table 3). This result is the same trends as diameter growth (Table 4).

Five independent variables, such as mean, maximum, and minimum temperature, total precipitation, and sunshine hours were checked to test the influence of climatic conditions on tree growth. Some portion of the variability in height and diameter was explained by the size of  $R^2$  values of 0.756 and 0.696, respectively. However, both multiple linear regressions were not significant at 5% level. With such low level of influence, the estimated regression equation would not be useful in estimating the size of annual growth. However, these non-significances may be caused by a short term observation; subsequent examination should help to characterize the influence of climatic conditions in growth performance of *P. koraiensis*.

Consequently, both height and diameter showed reliable variation and significant difference between the trials. Therefore, it is recommended that genetic testing layout established with different genotypes and environments should be used to get the more advanced forest productivity.

### Heritability

Heritability estimates for height and diameter in each site are listed in Table 5. The variance components indicated that family was a significant source of variation in all ages, especially in Kapyoung site, although the most variability was associated with individual trees within plot.

Magnitudes of heritabilities estimated on the

basis of individual tree and half-sib family were decreased with increasing tree ages in Youngdong and Kwangju sites, whereas Kapyoung site showed less remarkable changes with age than the other sites. This can be explained by relatively small family x block interaction and high level of additive genetic variance in Kapyoung site. The difference of estimates with site clearly indicates that a reliable heritability should be based on genetic tests established in multiple environments. With two exceptions for the first five years, heritability estimates of diameter were lower than those of height (Table 5), whereas the fluctuation of the estimates has shown no clear trends with age.

Estimates of heritability in both height and diameter were relatively high beyond those indicated in other reports (Merrill and Mohn 1985; Zobel and Talbert 1984). This result may be caused by intensively controlled extraneous environmental variance that resulted in reduced experimental errors.

Estimated variance components and heritabilities for a multiplantation test are shown in Table 6. In tree height, components of variance for family x site interaction as a percentage of family variance were 26.46, 30.02, 22.76, 12.19, and 4.38% from 5- to 9-year-old height, respectively (Table 6). The magnitude of these small interactions implies moderate change in height ranking with different sites. Therefore, F x S interaction can be expected to be weak and family effect to be appreciable, in which case selection should be

**Table 5.** Estimates of heritability for height and diameter growth in 3 test sites.

Site	Height					Diameter				
	5	6	7	8	9	5	6	7	8	9
Youngdong										
$h^2_i$	.295	.414	.310	.252	.192	.185	.220	.187	.151	.145
$h^2_F$	.513	.621	.534	.457	.288	.407	.420	.370	.327	.350
Kwangju										
$h^2_i$	.750	.652	.538	.431	.280	.341	.244	.189	.225	.200
$h^2_F$	.798	.784	.711	.653	.527	.593	.576	.414	.488	.408
Kapyoung										
$h^2_i$	.505	.566	.566	.516	.517	.385	.401	.549	.340	.332
$h^2_F$	.708	.700	.693	.659	.688	.644	.596	.738	.568	.578

Note:  $h^2_i$  and  $h^2_F$  indicate the individual tree and family heritabilities, respectively.

**Table 6.** Estimates of variance component and heritability from combined ANOVA.

	Height					Diameter				
	5	6	7	8	9	5	6	7	8	9
$\sigma^2_W$	74.554	210.716	429.000	766.203	1141.59	2.5433	6.6212	14.152	32.513	62.973
$\sigma^2_{F \times B}$	5.834	17.305	44.529	88.106	120.550	0.2060	0.5979	1.2926	3.2609	6.9596
$\sigma^2_{F \times S}$	2.713	8.829	12.930	11.407	5.234	0.1499	0.4220	0.7711	1.1838	1.3558
$\sigma^2_F$	10.255	29.412	56.802	93.599	119.529	0.0952	0.1991	0.8190	1.4443	2.6138
$\sigma^2_A$	41.020	117.648	227.208	374.396	478.116	0.3808	0.7964	3.2760	5.7772	10.455
$h^2_i$	0.439	0.442	0.418	0.390	0.345	0.127	0.102	0.192	0.150	0.141
$h^2_F$	0.798	0.791	0.789	0.794	0.794	0.468	0.400	0.578	0.544	0.554

**Table 7.** Spearman's rank correlations for family mean height between the test sites.

Age	Site	Youngdong	Kwangju	Kapyoung
5	KJ	.237 <sup>ns</sup>		
	KP	.509*	.558*	
	Mean	.586*	.814**	.835**
6	KJ	.195 <sup>ns</sup>		
	KP	.499*	.601**	
	Mean	.571*	.781**	.895**
7	KJ	.283 <sup>ns</sup>		
	KP	.579*	.630**	
	Mean	.642**	.744**	.948**
8	KJ	.296 <sup>ns</sup>		
	KP	.649**	.598**	
	Mean	.734**	.767**	.917**
9	KJ	.195 <sup>ns</sup>		
	KP	.636**	.624**	
	Mean	.690**	.763**	.940**

\*\*\* : significant at 5% and 1% level  
<sup>ns</sup> : non-significant

based upon a family's average performance in all 3 test sites (Wright 1976). This implication can be supported somewhat by the result of rank correlation test (Barnes and Schweppenhauser 1979) presented in Table 7. It showed consistent family performance between the sites, however, significant changes of family ranking were found between Youngdong and Kwangju sites ( $r_s=0.195-0.296$ ). Comparing the family rankings obtained in each site with combined over sites, there were no significant changes ( $r_s=0.571-0.948$ ) between them. According to the results of this study, F x S interaction for height of *Pinus koraiensis* might be caused by environmental errors rather than different performance of individual families which showed relatively small changes of family ranking for height with site.

The interactions for diameter were comparative-

ly larger than those for height (Table 6). This result indicates that genetic effect on diameter growth is more weakly influenced than height growth by the extraneous environmental conditions.

Heritability estimates of tree height ( $h^2_i=0.345-0.442$ ;  $h^2_F=0.789-0.798$ ) showed high and stable trends in combined analysis for overall sites, and those of diameter were relatively small (Table 6). Family heritabilities of combined analysis were higher than the individual site estimates because the family x site interaction variances were proportionally small.

A trend of decreasing heritability estimates for height growth with increasing tree age is a contrast to other reports. Nienstaedt and Riemenschneider (1985) found increased heritability between age 9 and age 15 in White spruce. Samuel and Johnstone (1979) indicated that the estimates of narrow-sense heritability fell in years 2 and 3 in the forest and then rose through to year 6. Tauer and McNew (1985) also found that family-mean heritability estimates were relatively high at age 10 for height and diameter. However, Han and Choi (1985) indicated that heritabilities of height estimated from combined site analyses at age 10 were very low ( $h^2_i=0.002$ ;  $h^2_F=0.004$ ) in Korean white pine. A major assumption made by Lambeth (1980) was that heritabilities do not change significantly with age in Pinaceae, and was that the average height increment in the younger ages is genetically reliable indicator for more mature tree performance.

The heritabilities estimated in this study were probably inflated because of the intensive site



management, and also overestimated because the open-pollinated families are likely to contain some products of inbreeding (Namkoong 1966; Sorensen 1973). Although the estimates of genetic parameters are needed for meaningful breeding strategy, the progeny test values could not be applied to selection in natural stands because heritability in natural stands would be different due to the heterogeneous conditions of establishment spacing, and competition (Leding and Whitmore 1981). In this study, however, the most variabilities for height and diameter were associated with individual trees within family and with families.

#### Genetic gain

The estimated genetic parameters were used for predicting genetic gains with different selection methods; mass, family, within-family, and combined selections. Relative effectiveness of genetic gain evaluated for height and diameter is shown in Table 8.

Mass selection simply involves the selection of best trees solely on the basis of their phenotypes. In this method, maximum or near-maximum efficiencies of 20.8% (YD), 36.4% (KJ), and 31.6% (KP) for height growth were expected at age

6 when best 10% of trees ( $i_m=1.75$ ) were retained for selection. The gains have started to decline with increasing tree ages, and this transition was almost the same trend with other selection methods. Family selection resulted in the least successful efficiencies. The gains ranged from 12.7% to 20.0% at age 6. This method generally may lead to increased rates of inbreeding, rarely used in practical operations. Within-family selection is a method of selection in which individuals are chosen on the basis of their deviation from the family mean. The expected gains based on a selection intensity of  $i_{w_f}=1.75$  ranged from the maximum efficiency of 29.0% (KJ) at age 5 to the minimum of 7.89% (YD) at age 9. Combined selection consists of choosing the best families along with the best individuals in them. For a family selection of 0.316, and a within-family selection of 0.316, a combined selection intensity of 0.0998 (about 10%), i.e.,  $i_c=1.75$  is derived. Gains expected from combined selection were larger than those expected from family or within-family selection methods; ranged from a low of 10.1% (YD) at age 9 to a high of 32.2% (KJ) at age 5 (Table 8). According to the results, mass selection showed the best efficiencies in a given equal intensity of selection. However, it can be

**Table 8.** Relative efficiency of expected genetic gains for height and diameter in different sites and tree ages with selection method.

Selection method	Site	unit : %									
		Height					Diameter				
		5	6	7	8	9	5	6	7	8	9
Mass	YD	13.5	20.8	16.6	14.0	10.5	6.50	9.00	8.98	7.47	8.37
	KJ	38.7	36.4	29.3	23.3	14.0	14.2	11.2	9.21	12.7	11.4
	KP	26.2	31.6	30.9	25.8	22.8	15.2	21.0	30.6	19.1	17.4
Family	YD	8.93	12.7	10.9	9.46	7.48	4.79	6.21	6.32	5.54	6.53
	KJ	20.0	20.0	16.8	14.4	9.60	9.36	8.61	6.83	9.29	8.15
	KP	15.5	17.6	17.1	14.6	13.1	9.79	12.8	17.7	12.4	11.5
Within-family	YD	10.1	15.6	12.4	10.5	7.89	4.95	6.72	6.65	5.62	6.28
	KJ	29.0	27.3	22.0	17.5	10.5	10.7	8.43	6.89	9.48	8.57
	KP	19.7	23.7	23.2	19.3	17.1	11.4	15.8	23.0	14.4	13.1
Combined	YD	12.6	18.6	15.3	13.1	10.1	6.34	8.49	8.54	7.30	8.44
	KJ	32.2	31.1	25.5	20.9	13.2	13.2	11.2	9.01	12.3	11.0
	KP	23.1	27.1	26.5	22.3	19.9	13.9	18.8	26.7	17.6	16.2

**Table 9.** Expected genetic gains from combined analysis of 3 test sites.

Selection method	unit : %									
	Height					Diameter				
	5	6	7	8	9	5	6	7	8	9
Mass	22.2	24.5	23.2	21.1	17.1	5.11	4.93	10.3	8.63	8.02
Family	15.0	16.4	15.9	15.0	13.0	4.85	4.83	8.86	8.21	7.95
Within-family	16.6	18.3	17.4	15.8	12.8	3.80	3.65	7.68	6.46	6.03
Combined	20.7	22.8	21.9	20.3	16.9	5.64	5.62	10.9	9.63	9.19

recognized that the differences of relative effectiveness are small between mass and combined selection methods, which suggests that it would be more efficient to emphasize the selection of family plus individuals within-family.

Gains for root-collar diameter in each site are also presented in Table 8. It is the same tendency as height that gains obtained at 6 or 7 years of age were almost larger than those obtained at other ages, and that the most efficient gains could be obtained by mass selection and followed by combined selection. Assuming that height is highly correlated with diameter (Table 11), additional gains in diameter may be obtained through independent selection for height.

Estimates of genetic gains from the combined ANOVA are evaluated in Table 9. Gains for height have expected greatest efficiency at age 6, ranging from 16.4% by family selection to 24.5% by mass selection, while diameter showed greatest efficiency at age 7; ranged from 7.68% by within-family selection to 10.9% by combined selection. According to Shelbourne (1972), the effect of genotype x environment interaction is to reduce genetic gains. One way assessing the effect

**Table 10.** Expected gain and relative efficiency for 9-year height by indirect selection at younger ages.

Trait	H9	H8	H7	H6	H5
Gain	16.56 <sub>cm</sub>	16.53	16.44	16.05	15.31
R.E.	100.0%	99.82	99.28	96.92	92.45

of G x E interaction is to compare the genetic gains achieved by selection of the best families for the trait at each site with those achieved by the best families averaged over all sites (La Farge and Kraus 1981). In Tables 8 and 9, it can be seen that the difference is small, which means that interaction effect on family height is not considerably large.

With gain in total height at age 9 as the goal of selection, the efficiencies of indirect selection were compared to direct selection. Indirect gains for 9-year height by selection at each younger age yielded relative efficiencies of 99.82, 99.28, 96.92, and 92.45%, respectively (Table 10). These results indicate that 5- and 6-year height are all good predictors of 9-year height with little loss of relative efficiency (less than 10%) as compared with direct selection.

Genetic gains are often calculated from the data

**Table 11.** Phenotypic (top right corner) and genetic (bottom left corner) correlations for height and diameter between various tree ages.

Trait	H5	H6	H7	H8	H9	D5	D6	D7	D8	D9
H5	1	.949**	.896**	.845**	.795**	.842**	.847**	.816**	.787**	.747**
H6	.986	1	.981**	.954**	.925**	.891**	.939**	.936**	.914**	.885**
H7	.951	.986	1	.989**	.969**	.906**	.962**	.971**	.957**	.927**
H8	.934	.981	1.00	1	.992**	.879**	.955**	.979**	.977**	.961**
H9	.922	.971	.996	.998	1	.857**	.946**	.978**	.984*	.978**
D5	1.05	1.02	.996	1.01	1.01	1	.944**	.912**	.884**	.817**
D6	1.14	1.12	1.13	1.14	1.13	1.10	1	.978**	.961**	.924**
D7	1.03	1.03	1.03	1.05	1.06	1.02	1.06	1	.986**	.959**
D8	1.10	1.10	1.12	1.13	1.13	.991	1.04	1.04	1	.982**
D9	.994	.999	1.03	1.04	1.04	.961	1.07	1.03	1.01	1

\*\* : statistically significant at 1% level

that are based only on the performance of younger trees. Robinson and van Buijtenen (1979) have reported that, despite a drop in growth, meaningful gains of outstanding seedlings were still evident in 15-year-old Loblolly pine. However, Franklin (1979) indicated that gains estimated on data from young trees have been expected that are unreliable because growth characteristics usually cannot be reliably determined until about half of the rotation age. Selection age strongly influences the breeding interval, which in turn impacts the amount of genetic gains realized per unit of time (Squillace and Gansel 1974).

The results obtained in this study demonstrated that expected gains varied with site and selection method, and decreased with increasing tree ages. The most obvious features of expected gain were that the maximum or near-maximum gains could be achieved at age 6, and that mass selection almost always expected the most efficient gains. However, because the differences between mass and combined selections were small, selection made on the combination of family and individuals within-family would be more efficient in improving genetic gains of *Pinus koraiensis*. Though the trees are still very young such that on optimum selection age could not be determined, early indirect selection was very effective. When selecting for height at age 9, families could be selected at age 5 or 6 with little loss (less than 10%) of relative efficiencies.

### Correlation

Simple correlations used to compare parental phenotype with progeny performance in the nursery and test sites were very low and demonstrated rather negative signs in most pairs of traits. These relationships indicate that good parental phenotypes (taller height and larger DBH) did not produce larger progenies in both nursery and field progeny trials. Most correlations between nursery and field performances also did not show significant relationships until age 9, however, the values were increased slightly with

increasing tree ages. Only correlation of height at age 3 (nursery) with age 8 height ( $r=0.470$ ) was statistically significant at 5% level. Result of this study indicates that parental phenotype and nursery performance are not the reliable indicators of subsequent field growth, therefore, selection of families based upon only parental phenotype and nursery performance should be done cautiously.

Phenotypic and genetic correlations estimated on the basis of family means in each site are presented in Table 11. All phenotypic correlations between the traits were positive and highly significant in field trials; ranged from 0.747 to 0.992 (d.f.=52). Correlation coefficients were not changed significantly during the test for 5 years in the field, though the magnitude was decreased with age interval, which indicates the consistency of family performance for height and diameter growth with age. Genetic correlations of 45 combination of traits were very high ( $r_c=0.922-1.0$ ), and higher than the phenotypic correlations (Table 11). This strong association between tree ages implies that selection for 9-year performance can be made at more younger ages with relatively small errors. On the other hand, many values were estimated greater than 1.0 due to relatively high sampling errors associated with the components of variance for the traits. Since the genetic correlations greater than 1.0 are meaningless, those of height growth estimated less than 1.0 are particularly noticeable.

Since the effectiveness of phenotypic selection becomes known only after offspring of selected trees have been grown in experiments, phenotypic selection is generally used as a prelude to family selection or the others. However, many studies have suggested the effectiveness of early selection. Williams *et al.* (1987) found strong positive simple and rank order correlations among the different ages, and stated that family selection at 4 years from outplanting should be possible for height performance at age 13 in Black spruce. This result is also corresponding to those of Khalil (1985), Lambeth *et al.* (1983), Tauer and McNew (1985), and Waxler and van Buijtenen

(1981); the early family selection is an effective control of mature trait expression. Noh and Yim (1979) also suggested that age-age correlations of height growth in Japanese red pine were significantly high, thereby early selection seems to be possible at age 8. Squillace and Gansel (1974) indicated that less-than-mature trees (about age 10) could be selected for mature performance in Slash pine, and Bey (1979) suggested that selection made for either height and diameter at age 5 would hold well for selections made for either trait at age 10 in Black walnut. On the other hand, some studies (Namkkong *et al.*, 1972; Namkoong and Conkle 1976; Wakeley 1971) indicated that early selection for height based on growth of younger ages may not be reliable, because of extremely large changes in the relative magnitude of genetic and environmental effects during stand development, especially with crown closure. Despite these some uncertainties, it is emphasized that selection should be made at relatively young ages in genetic tests (Foster 1986; Meier and Goggans 1977).

Because of these various suggestions, selection age and probability should be evaluated only with the greatest caution and after complete testing has indicated the juvenile-mature relationships.

In this study, high correlations for both height and diameter with age may be large enough to be of concern. Although the data base in this evaluation is limited, and the trees are still young such that optimum selection age could not be determined, strong and consistent age-age correlations after outplanting in the field imply that early family selection may be possible. And, taller trees tend to have larger diameter (Chon and Kim 1983), selection for taller height will result in increased indirect gains for diameter in *Pinus koraiensis* S. et Z.

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