

## Observations on the Genetic Structure of *Pinus densiflora* Sieb. et Zucc (I) : The Young-il Population<sup>1</sup>

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### 소나무의 遺傳的 構造에 관한 研究 (I) : 迎日 集團의 遺傳的 構造<sup>1</sup>

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#### ABSTRACT

Genetic structure of a *Pinus densiflora* population consisting of two subpopulations on the north- and south-facing slopes of a mountain was studied by allozyme analysis. Allozyme variants in aspartate aminotransferase (AAT), glutamate dehydrogenase (GDH) and leucine aminopeptidase (LAP) systems are encoded, at least, by eight loci : five for AAT, one for GDH and two for LAP. Average number of alleles examined over six loci was 3.33. Average heterozygosity and genetic diversity computed over six loci were, respectively, 0.19 and 2.76 for parental population, 0.17 and 2.22 for progeny population.

Differences in allelic frequencies between maternal sources at many of the investigated loci were found and between subpopulations on the north- and south-facing slopes. Allele frequencies of maternal origin at some of the loci were significantly different from each other between the two subpopulations. Thus it appears that the matings within and between subpopulations were not random and the mountain ridge that divides the north- and south-facing slopes isolate the two subpopulations reproductively to a great extent.

Some of the genotypes both in parental and progeny (embryo) groups deviate significantly from the Hardy-Weinberg equilibrium state. It appears from the result that the pine population is originated from a few limited ancestral trees and thus consanguineous matings are prevalent in this pine population.

*Key words* : Allozyme, micro-geographic variation, mating system, *Pinus densiflora*.

#### 要 約

同位酵素 分析에 의하여 慶尙北道 迎日地域 한 소나무 集團의 遺傳的 構造를 山의 南쪽과 北쪽의 小集團으로 區分하여 研究하였다. 同位酵素 AAT, GDH 및 LAP 등 에서 각각 5개, 1개 및 2개의 遺傳子座가 發見되었으며 詳細히 分析한 6개의 遺傳子座에는 平均 3.33개의 遺傳子가 있음이 確認되었다. 6개 遺傳子座의 average heterozygosity는 兩親集團의 境遇 0.19였고 次代集團의 境遇는 0.17이었다. 몇몇 遺傳子座에 있어서 南쪽 北쪽 小集團內 및 小集團間에 母系와 父系間 遺傳子頻度의 有意差가 있었고 남쪽 및 북쪽 小集團間에는 母系 遺傳子 頻度에 差異가 있었다. 이 結果로 보아 山의 북쪽과 남쪽에 位置한 소나무 小集團에 있어서 交配가 無作爲로 일어나지 않았으며 小集團間에도 自由롭게 交配가 이루어지지 않고있어 이들 小集團들은 最小한 生殖集團으로서 部分的으로 서로 격리되고 있음이 發見되었다.

兩親과 次代集團의 몇몇 遺傳子型들은 Hardy-Weinberg 平衡을 이루지 못하고 있었다. 이 소나무 集團의 遺傳的 構造로 보아 현재의 소나무 集團은 少數의 兩親樹에 의해 形成된 것으로 생각된다.

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## INTRODUCTION

*Pinus densiflora* Sieb. et Zucc. belongs to group lariciones, subsection pinaster of subgenus diploxylon.<sup>21)</sup> It is naturally distributed in eastern China, Korea and Japan and is the most common and important timber species in Korea. It often forms pure stands along the mountain ridges and slopes but sometimes forms mixed stands with hardwood species in Korea. Natural tree populations may show a continuous and clinal variation in many traits, however tree populations in mountain terrain may not show the same pattern of variation as in plain regions due to the differences in meteorological and ecological factors between the two regions that would affect the gene flow, population formation and natural selection.

In earlier work on a small pitch pine (*Pinus rigida* Mill.) stand originated and expanded rather rapidly from a few founder trees the author found marked differences in allelic and genotypic frequencies at some of allozyme loci between the initially colonized subpopulation on the south-facing slope and the lately colonized subpopulation on the north-facing slope of a hill.<sup>5)</sup> The differences in allelic and genotypic frequencies between the two pitch pine subpopulations at opposing sites of a hill found to be caused by the specific seed dispersal pattern at initial stages of colonization.

If *Pinus densiflora* S. et Z. has the same pattern of migration as shown in *Pinus rigida* Mill., *Pinus densiflora* populations at different aspects of a mountain would have similar pattern of genetic variations as above at initial stages of migration and colonization. After the establishment of pine populations, the genetic structure of the subsequent generations can be affected by various factors such as mating systems and ecological components on which the tree populations are thriving. Also human activity that would affect the genetic structure of the tree populations can not be ignored.

The aim of this study was to investigate whether the subpopulations of *Pinus densiflora* located at different opposing aspects of a mountain have the same genetic structure or not.

## MATERIALS AND METHODS

### 1. Seed collection

Seeds materials were collected from randomly selected 99 and 102 trees respectively for the north- and south-facing slopes of a small mountain of about 500 meters high above sea level. The mountain is located in southeastern part of the Taeback Mountain Range at 36° 15' N and 129° 19' E. The mountain descends gradually to the north and rather steeply to the south. The area where the seeds were collected was occupied by a pure stand of about twenty-year old *Pinus densiflora* S. et Z. Seeds were germinated at room temperature (22°C ~ 26°C) on moist sands in petri dishes. Each megagametophyte and germinating embryos of eight seeds per tree were separated and analysed at the same time.

### 2. Electrophoresis

Aspartate aminotransferase (AAT, or glutamate oxaloacetate transaminase, GOT), glutamate dehydrogenase (GDH) and leucine aminopeptidase (LAP) were analysed by a horizontal starch gel electrophoresis in a discontinuous buffer system. Methods for enzyme extraction, electrophoresis and enzyme stainings are described elsewhere.<sup>4)</sup>

## RESULTS AND DISCUSSION

### 1. Allele frequencies

There are five zones of enzyme activity stained for AAT. Three of the five zones migrated anodally and two cathodally from the origin. Kim and Hong<sup>11)</sup> reported four zones of enzyme activity of AAT for the same species. Five zones of enzyme activity for AAT also found in *Pinus rigida* Mill.<sup>4)</sup> and in hybrid pine *Pinus rigida* × *Pinus taeda*.<sup>6)</sup> Alleles of the whole maternal population showed 1 : 1 segregation pattern at all loci of the three enzyme systems studied at present work.

There are two alleles at locus A, four at locus C for AAT (Fig. 1). Kim and Hong<sup>11)</sup>, and Son and his coworkers<sup>23)</sup> reported only one allele at locus A. Alleles B<sub>2</sub> are located very closely and thus often could not be separated clearly in embryos of heter

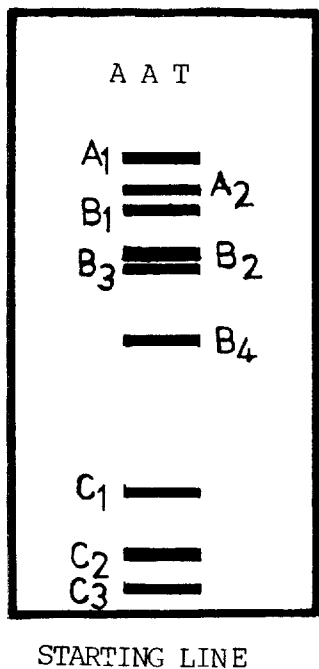


Fig. 1. Zymogram of aspartate aminotransferase in megagametophytes of *Pinus densiflora*.

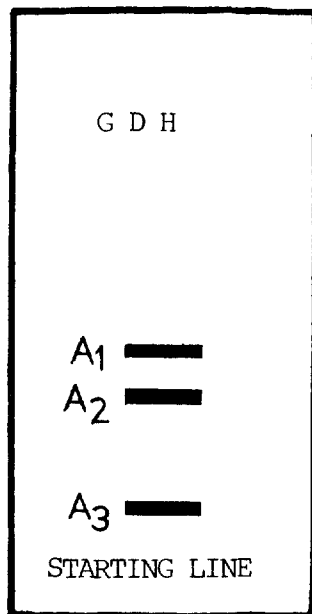


Fig. 2. Zymogram of glutamate dehydrogenase in megagametophytes of *Pinus densiflora*.

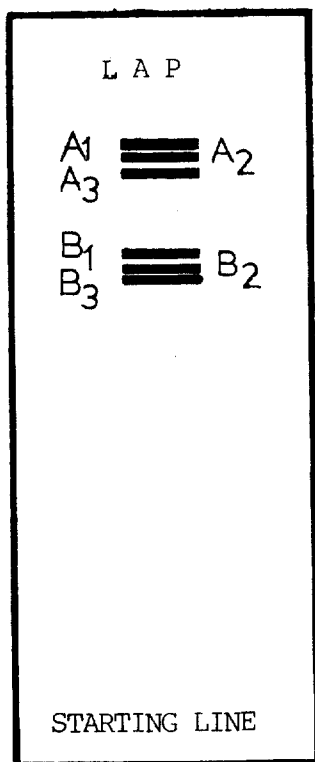


Fig. 3. Zymogram of leucine aminopeptidase in megagametophytes of *Pinus densiflora*.

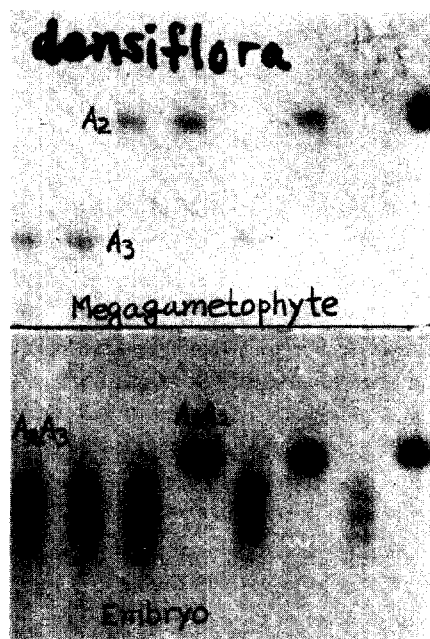


Fig. 4. Banding patterns of GDH in megagametophytes (upper side) and the corresponding embryos (lower side).

ozygotes by the buffer systems used in this study. Thus the rare allele B<sub>2</sub> is systematically regarded as allele B<sub>3</sub>. The alleles at loci D and E were excluded in statistical analyses due to poor separation of the alleles on these zones. The alleles at loci C and D for AAT appeared to be linked. Kim and Hong<sup>11)</sup>, Son and his coworkers<sup>23)</sup> reported the same pattern of allelic segregation at loci C and D for AAT in megagametophyte of the same species.

Alleles A<sub>2</sub>, B<sub>3</sub> and C<sub>2</sub> of AAT are the most common ones and the frequencies of those alleles are within the range of 0.85-0.99 at population level (Tab. 1). The reason why the alleles of AAT focused on to the common ones at each loci is not known. The most common alleles may have selective advantages for their ecological and/or physiological functions during growth and development under the conditions of natural habitats of the investigated species provided that the initial frequencies of the alleles at each loci were almost equal. The other rare alleles at each loci may have been developed recently by mutation within the species and/or they may have been introduced from closely related species and they are now at the initial stages of incorporation into the genetic systems of this species. Allele B<sub>4</sub> was very rare and found only in paternal source of the subpopulation on the south-facing slope. On the contrary, the rare allele C<sub>3</sub> was found in subpopulation on the north-facing slope.

Banding patterns of AAT in *Pinus densiflora* indicate that the enzyme is a dimer as it was found in other pine species.<sup>3,4,6,18)</sup> In the electrophenographs

of AAT, a hybrid band appears just between the parental ones in heterozygous loci.

Genes coding for GDH in *Pinus densiflora* appeared to be nearly monomorphic even though there are three alleles in one locus (Fig. 2). The rare allele A<sub>1</sub> was found only in paternal source of the south-facing subpopulation. Monomorphism in genes controlling for GDH of *Pinus rigida* Mill, was reported by the author.<sup>4,5)</sup> Judging from the banding patterns of GDH (Photo. 1) in *Pinus densiflora* S. et Z. the enzyme appears to be a tetramer.

Four alleles were found at each of the two loci A and B for LAP (Fig. 3). Both loci have silent alleles A<sub>0</sub> and B<sub>0</sub>. Kim and Hong<sup>11)</sup> Son and his coworkers<sup>23)</sup> reported two and three alleles respectively for loci A and B. Alleles A<sub>2</sub> and B<sub>2</sub> are the most common ones.

Test of allelic segregation patterns by Chi-square contingency tables indicated that the segregation ratios of alleles in megagametophytes of maternal origin was normal. However, in many cases, the alleles in embryos of paternal origin deviate significantly from those of maternal origin (Table 2). This means that embryos were developed from the egg-cells which fertilized by the pollens that have different allelic composition from those of maternal origin.

This fact also indicates that the gametic contribution for seed development in this pine population was not random. Differential gametic segregation as reported by Rudin<sup>18)</sup>, Rudin and Ekberg<sup>19)</sup>, Strauss and Conkle<sup>24)</sup> and post zygotic lethal factors may

**Table 1.** Allele frequencies for AAT, GDH and LAP in the maternal (megagametophytes), paternal (pollen) and the progeny (embryo) populations or subpopulations of the north-(N) and southfacing (S) slopes.

Source	Allele frequency																			
	A A T							G D H			L A P									
	A <sup>1</sup>	A <sup>2</sup>	B <sup>1</sup>	B <sup>3</sup>	B <sup>4</sup>	C <sup>1</sup>	C <sup>2</sup>	C <sup>3</sup>	A <sup>1</sup>	A <sup>2</sup>	A <sup>3</sup>	A <sub>0</sub>	A <sup>1</sup>	A <sup>2</sup>	A <sup>3</sup>	B <sub>0</sub>	B <sup>1</sup>	B <sup>2</sup>	B <sup>3</sup>	
Maternal	N	.01	.99	.15	.85	-	.06	.93	.01	-	.96	.04	.01	.01	.76	.22	.01	.05	.85	.09
	S	.03	.97	.18	.82	-	.06	.94	-	.98	.02	.05	.01	.96	.18	.01	.08	.85	.06	
	Sum	.02	.98	.16	.84	-	.06	.94	.00	-	.97	.03	.03	.01	.76	.02	.01	.06	.85	.08
Paternal	N	.01	.99	.11	.89	-	.03	.97	.00	-	.98	.02	-	.01	.83	.16	.00	.04	.88	.08
	S	.01	.99	.16	.84	.00	.04	.96	-	.01	.96	.03	.01	.00	.85	.14	.00	.11	.78	.11
	Sum	.01	.99	.14	.86	.00	.03	.97	.00	.00	.97	.03	.00	.01	.84	.15	.00	.08	.83	.09
Progeny	N	.00	1.00	.13	.87	-	.04	.95	.01	-	.97	.03	.00	.01	.81	.18	.01	.05	.86	.08
	S	.02	.98	.16	.84	.00	.04	.96	-	.00	.97	.03	.03	.01	.80	.16	.00	.09	.83	.08
	Sum	.01	.99	.15	.85	.00	.04	.96	.00	.00	.97	.03	.01	.01	.81	.17	.00	.07	.85	.08

- : non-occurrence, 0.00 : frequencies smaller than 0.005 (rounded off)

**Table 2.**  $\chi^2$  statistics evaluated by contingency tables for the differences in allele frequencies between maternal and paternal origins.

Enzyme loci and source		A A T			GDH		LAP	
		A	B	C	A	A	B	
N	$\chi^2$	0.11	4.75*	9.93**	2.77	19.17***	7.13	
	df.	1	1	2	1	3	3	
S	$\chi^2$	12.88**	1.51	5.52*	5.94	32.07***	15.12***	
	df.	1	2	1	2	3	3	
N+S	$\chi^2$	9.22**	4.89	15.40***	3.01	49.24***	10.40*	
	df.	1	2	2	2	3	3	

Significance at probability of 0.05 = \*, 0.01 = \*\*, 0.005 = \*\*\*

N : subpopulation on the north-facing slope, S : subpopulation on the south-facing slope.

**Table 3.** Differences in allele frequencies between the subpopulations on the north-facing (N) and south-facing (S) slopes.

Enzymes Alleles	A A T				GDH			L A P		
	A <sub>1</sub>	A <sub>2</sub>	B <sub>1</sub>	B <sub>3</sub>	C <sub>3</sub>	A <sub>0</sub>	A <sub>3</sub>	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>
Maternal	***	***	-	-	***	***	*	**	-	*
Paternal	N<S	N>S	***	***	N>S	N<S	N>S	N<S	***	N>S
Progeny	-	-	N<S	N>S	-	-	-	N<S	N<S	N<S
	***	***	**	**	***	***		**	**	
	N<S	N>S	N<S	N>S	N>S	N<S	-	N<S	N>S	-

Designation the same as in Table 2. Evaluated by 2x2 contingency table.

play a partial role for the non-random mating. Differential gamete productivity within and/or between individual trees<sup>1,18,19,20)</sup>, and factors affecting the pollination such as differences in flowering time between individuals within the population<sup>2)</sup>, distance between individual trees, physical barriers for pollen flight, aspects of wind during the flowering time ect., appeared to be the major reason for the result. In this respects Shen and his coworkers<sup>22)</sup> described an interesting pollination pattern in a Scots pine seed orchard. In case of LAP the differences in allele frequencies between maternal and paternal origins appeared due partly to the silent alleles A<sub>0</sub> and B<sub>0</sub> that were masked under heterozygous conditions by functional alleles.

Differential gametic contribution for seed development between gametes of maternal and paternal origins within populations were also found in *Pinus sylvestris* L.<sup>14)</sup> and in *Pinus rigida* Mill.<sup>4,5)</sup> Müller-Starck reported that gametic contribution of Scots pine clones investigated in two successive years in a seed orchard significantly differ from one another.<sup>14)</sup> As discussed by Müller-Starck<sup>14)</sup> and Ziehe<sup>26)</sup> sexually asymmetric selection appears to affect the genetic structure of tree populations in succeeding

generations.

There are differences in allele frequencies between subpopulations on the north-facing and south-facing slopes (Table 3). Mountain ridge which divides the north-facing and south-facing slopes where trees of the two subpopulations inhabit appears to function as barriers for an effective gene flow between the two subpopulations. Sample trees of the two subpopulations are located within radius a of 800 m from the center of the mountain ridge. However the two subpopulations have different allelic frequencies both in maternal and paternal origins at many loci. The progeny groups of the north-facing and south-facing slopes also have different allelic structure at all loci.

It is most probable that the trees on the cooler north-facing slope flower comparatively later than those on the warmer south-facing slope. Hence, trees of the two subpopulations can be, at least, partially isolated reproductively. Mountain ridge can be an effective physical barrier that may prevent free exchange of pollens between the two subpopulations. Differences in frequencies of alleles originating from pollen strongly suggest the possible role of the above two factors for their isolating mecha-

nisms.

2. Genotypic frequencies

In general, with a few exceptions, genotypic frequencies in parental population or subpopulations were under Hardy-Weinberg equilibrium state. significantly smaller numbers of genotype of B<sub>1</sub>B<sub>3</sub> for LAP were found respectively for the subpopulation on the north-facing slope ( $\chi^2=4.71^*$ ,  $df=1$ ) and the parental population as a whole (N and S subpopulations combined,  $\chi^2=6.65^{**}$ ,  $df=1$ ). Significantly ( $\chi^2=6.56^*$ ) larger number of B<sub>1</sub>B<sub>1</sub> genotype for LAP were observed in parental population as a whole.

In case of progeny population or subpopulations, there were more genotypes for LAP that deviate from the expectations of Hardy-Weinberg equilibrium state (Table 4) than in the parental population.

The cause of deviation of genotypic frequencies from the Hardy-Weinberg equilibrium state is not known. The genetic structure of this pine population at present work is very similar to the pitch pine population that colonized recently by a few founder trees.<sup>5)</sup> Therefore, it is suspected that the pine population was established by a few founder trees that remained in this site after a catastrophic destruction of this pine stand during and after the Korean War. Actually the author observed a few exceptionally large and crooked trees that are suspected to be the parental seed trees of the pine stand.

Significant differences in genotypic frequencies between subpopulations on the north-facing and south-facing slopes both in parental and progeny

Table 4. Deviations of observed(O) genotypic frequencies for LAP loci from the expected(E) under Hardy-Weinberg equilibrium.

Genotype	A <sub>0</sub> A <sub>0</sub>	A <sub>2</sub> A <sub>3</sub>	A <sub>3</sub> A <sub>3</sub>	B <sub>1</sub> B <sub>1</sub>	B <sub>1</sub> B <sub>2</sub>	B <sub>1</sub> B <sub>3</sub>	B <sub>2</sub> B <sub>2</sub>	B <sub>2</sub> B <sub>3</sub>
N	-	-	-	O>E	O<E	-	-	O>E
S	-	O<E	O>E	O>E	O<E	O<E	-	*
N+S	O>E	O<E	O>E	O>E	O<E	O<E	O>E	O>E

Designation the same as in Table 2. Evaluated by 2×2 contingency table.

Table 5. Genotypic frequencies in the subpopulations on the north-facing(N) and south-facing(S) slopes of the parental(M) and progeny(F) groups.

Enzyme Genotype	n	A A T										G D H			
		A <sub>1</sub> A <sub>2</sub>	A <sub>2</sub> A <sub>2</sub>	B <sub>1</sub> B <sub>1</sub>	B <sub>1</sub> B <sub>3</sub>	B <sub>3</sub> B <sub>3</sub>	B <sub>3</sub> B <sub>4</sub>	C <sub>1</sub> C <sub>1</sub>	C <sub>1</sub> C <sub>2</sub>	C <sub>2</sub> C <sub>2</sub>	C <sub>2</sub> C <sub>3</sub>	A <sub>1</sub> A <sub>2</sub>	A <sub>2</sub> A <sub>2</sub>	A <sub>2</sub> A <sub>3</sub>	A <sub>3</sub> A <sub>3</sub>
M N	99	.01	.99	.01	.28	.71	-	.02	.08	.88	.02	-	.93	.07	-
M S	102	.07	.93	.01	.33	.66	-	.01	.10	.89	-	-	.96	.04	-
M N+S	201	.04	.96	.01	.31	.68	-	.01	.09	.89	.01	-	.95	.05	-
F N	790	.01	.99	.03	.21	.76	-	.00	.08	.90	.02	-	.95	.05	.00
F S	813	.04	.96	.03	.27	.70	.00	.00	.08	.92	-	.01	.94	.05	.00
F N+S	1603	.02	.98	.03	.23	.74	.00	.00	.08	.91	.01	.00	.95	.05	.00

	A <sub>0</sub> A <sub>0</sub>	A <sub>0</sub> A <sub>2</sub>	A <sub>0</sub> A <sub>3</sub>	A <sub>1</sub> A <sub>2</sub>	A <sub>1</sub> A <sub>3</sub>	A <sub>2</sub> A <sub>2</sub>	A <sub>2</sub> A <sub>3</sub>	A <sub>3</sub> A <sub>3</sub>	B <sub>0</sub> B <sub>0</sub>	B <sub>0</sub> B <sub>2</sub>	B <sub>0</sub> B <sub>3</sub>	B <sub>1</sub> B <sub>1</sub>	B <sub>1</sub> B <sub>2</sub>	B <sub>1</sub> B <sub>3</sub>	B <sub>2</sub> B <sub>2</sub>	B <sub>2</sub> B <sub>3</sub>	B <sub>3</sub> B <sub>3</sub>
M N	-	.02	-	.01	-	.60	.30	.07	-	.02	-	.04	.02	-	.75	.16	.01
M S	-	.10	-	.02	-	.57	.27	.04	-	.01	-	.05	.07	-	.74	.13	-
M N+S	-	.06	-	.02	-	.58	.29	.05	-	.02	-	.05	.04	-	.75	.14	.00
F N	-	.01	.00	.01	-	.66	.27	.05	.00	.01	.00	.03	.04	.00	.78	.12	.02
F S	.01	.04	.00	.01	.00	.69	.19	.06	.00	-	-	.05	.07	.00	.71	.16	.01
F N+S	.00	.02	.00	.01	.00	.68	.23	.06	.00	.00	.00	.04	.05	.00	.76	.14	.01

groups were found at present work (Table 5). In many cases subpopulations on the south-facing slope have more heterozygous genotypes. Thirty five point four % and 24.5% respectively for the trees on north-facing and south-facing slopes in parental population were homozygous all over the six investigated loci. And 39.2% and 37.5% respectively for the progenies of north-facing and south-facing tree groups were homozygous all over the six loci examined. The proportion of homozygous individuals all over the six loci in progeny population (38.4%) is significantly ( $\chi^2=5.53^* \text{ df}=1$ ) higher than that of the parental one (29.9%) the population as a whole. The proportion of homozygous individuals all over six loci in the progenies of the trees on south-facing slope is much higher than that of the parental one ( $\chi^2=6.65^{**}$ ). It appears from this result that viability selection against the homozygous individuals all over the six loci during the stand development in this pine population is very severe.

Fixation indices<sup>8)</sup> ranged from -0.12 (AAT B) to 0.26 (LAP B) and from 0.00 (AAT A) to 0.34 (LAP B) respectively for parental and progeny subpopulations on the north-facing slope, and from 0.00 (AAT A and GDH A) to 0.25 (LAP B) and from 0.00 (AAT A and C) to 0.24 (LAP A and B) respectively for parental and progeny subpopulations on the south-facing slope. A relatively higher levels of homozygotes than those of expected ones at LAP A and B loci in this species appears to be maintained by matings of the same alleles of neighbouring trees rather than selfings.

### 3. Heterozygosity and genetic diversity

Average number of alleles examined all over the six loci was 3.33. The values for average heterozygosity<sup>15,16)</sup> and genetic diversity<sup>9)</sup> were presented in Table 6. Gregorius<sup>9)</sup> developed new method for measuring genetic diversity. The calculation is made according to the following formula.

$$V(p) = \left\{ \frac{1}{\sum_{i=1}^n P_{2i}^2} \dots \dots \dots \frac{1}{\sum_{i=1}^n P_{2i}^2} \right\} - 1$$

i = allele (ij = 1...nj) at j-th locus (j = 1...l)

P<sub>il</sub> = allele frequency (P<sub>ij</sub> = P<sub>1ij</sub>...P<sub>lij</sub>)

**Table 6.** Average heterozygosity (H) and genetic diversity (V<sub>p</sub>) of the parental (M) and progeny (F) groups computed over six enzyme loci.

Source	n	H	V <sub>p</sub>
M	N	99	0.18
	S	102	0.21
	N+S	201	0.19
F	N	990	0.16
	S	813	0.18
	F+S	1603	0.17

n : number of parental trees or embryos.  
 N : subpopulation on the north-facing slope.  
 S : subpopulation on the south-facing slope.

**Table 7.** Average heterozygosity (H) in some pine species.

Species	H	Authors
<i>Pinus attenuata</i>	0.14	Conkle 1980
<i>P. contorta</i>	0.19	"
<i>P. jeffreyi</i>	0.26	"
<i>P. lambertiana</i>	0.26	"
<i>P. ponderosa</i>	0.27	Nicolic and Tucic 1983
<i>P. "</i>	0.33	Mitton et al 1977
<i>P. radiata</i>	0.13	Woods et al 1977
<i>P. rigida</i>	0.12	Moran and Bell 1987
<i>P. rigida</i>	0.24	Chung 1984
<i>P. "</i>	0.27	"
× <i>P. rigida</i>	0.39	Chung and Jo 1986
<i>P. sylvestris</i>	0.33	Rudin et al 1974
<i>P. "</i>	0.30	Cung 1981
<i>P. "</i>	0.31	Gullberg et al 1985
<i>P. taeda</i>	0.34	Conkle 1980

The largest value for average heterozygosity is 0.5 while the value for V(p) is larger than 1.

The average heterozygosity of *Pinus densiflora* is smaller than those of *Pinus sylvestris* and *Pinus nigra* that belong to the same group of laticiones (Table 7).

Isozyme study on *Pinus densiflora* indicates that tree populations growing in montane region with complicated terrain reproductively partially subdivided into small subpopulations due to ecological and topographical factors.

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