KLEINSCHMIT (at the Dept. of Forest Tree Breeding, Lower Saxony Forest Res. Inst. in Escherode, Germany) provided the computer facilities and a warm working environment during the final evaluation of the study, which was performed while KANI ISIK visited the Department as an ALEXANDER VON HUMBOLDT research scholar. Dr. TONY SHELBOURNE reviewed and provided valuable comments on the manuscript. We gratefully acknowledge the contributions of all these persons and institutions.

Literature

ARBEZ, M.: Distribution, ecology and variation in *Pinus brutia* in Turkey. Forest Gen. Res. Inf. **3**, FAO, 21–33 (1974). — BECKER, H. C.: Biometrical and empirical relations between different concepts of phenotypic stability. In: GALLAIS, A. (ed.): Quantitave Genetics and Breeding Methods. 307–314. I.N.R.A., Versailles (1981). — BECKER, H. C. and LÉON, L.: Stability analysis in plant breeding. Plant Breeding **101**, 1–23 (1988). — BREESE, E. L.: The measurement and significance of genotype-environment interactions in grasses. Heredity **24**: 27–44 (1969). — FINLAY, K. W. and WILKINSON, G. N.: The analysis of adaptation in a plant breeding programme. Aust. J. Agric. Res. **14**: 742–754 (1963). — GUNAY, T. and TACENUR, I. A. .: Turkiye'de mevcut kizilcam (*Pinus brutia* TEN.) fidanlarinin genel özellikleri ve uretilen fidanlarin fizyomorfolojik kaliteleri. (General features and physiological qualities of *Pinus brutia* seedlings produced in Turkiye) (In Turkish). In: Proc. International Symp. on *Pinus brutia.* Oct. 18 to 23, 1993, Marmaris-Turkiye. pp. 349–356 (1993). — HUEHN, M.: Nonparametric analysis of genotype x environment interaction by ranks. In: Genotype by Environment Interaction. Eds: M. S. KANG and H. G. GAUCH, JR. CRC Press, New York. pp. 235–271 (1996). — ISIK, K.: Altitudinal variation in *Pinus brutia* TEN.: Seed and Seedling Characteristics. Silvae Genetica **35**: 58–67 (1986). — ISIK, K., TOPAK, M. and KESKIN, A. C.: Kizilcamda (*Pinus brutia* TEN.) Orijin Denemeleri. (Genetic Variation Among and Within Six *Pinus brutia* TEN. Stands in Southern Turkey: Six-Year Results at Five Common Garden Plantations). OGM-Orman Agac. ve Tohum. Islah Enst. Yayini (Inst. of Forest Tree Seeds and Improvement Publ.) No: 3, Ankara. 139 pp. (1987). — KARA, N.: Investigation on isoenzyme variation in natural populations of Turkish red pine (*Pinus brutia* TEN.). M. Sc. Thesis, Akdeniz Univ., Fen Bilimleri Institute, 77 pp. (in Turkish, English summary). (1996). — MCKEAND, S. E., LI, B., HATCHER, A. V. and WEIR, R. J.: Stability parameter estimates for stem volume for loblolly pine families growing in different regions in the southeastern United States. Forest Science **36**(1): 10–17 (1990). — NASSAR, R., LÉON, J. and HUEHN, M.: Tests of significance for combined measures of plant stability and performance. Biometrical Journal **36**: 109–123 (1994). — NEYISCI, T.: Kizilcamin dogal yayilisi (Natural distribution of Turkish red pine). In: Kizilcam – El Kitabi Dizisi, Orm. Arast. Enst. Muht. Yayin. (Forest Res. Inst. Misc. Publ.) No. **52**, pp. 17–22 (1987). — PINTHUS, M. J.: Estimate of genotypic value: A proposed method. Euphytica **22**, 121–123 (1973). — POWELL, W., CALI GARI, P. D. S., PHILLIPS, M. S. and JINKS, J. L.: The measurement and interpretation of genotype by environment interaction in spring barley (*Hordeum vulgare*). Heredity **56**: 255–262 (1986). SAS: SAS/STAT Guide for Personal Computers. 6. Ed.. SAS Institute Inc., Cary, NC (1987). — SELIK, M.: Botanical investigation on *Pinus brutia,* especially in comparions with *Pinus halepensis.* Ist. Univ. Orman Fak. Derg. **8**(2) A: 161–198 (1958). — SHELBOURNE, C. J. A.: Genotype – Environment interaction: Its study and its implications in forest tree improvement. IUFRO Genetics -SABRAO Joint Symp., Tokyo, Oct. 1972, 27 pp. (1972). — SOKAL, R. R. and ROHLF, F. J.: Biometry: The Principles and Practice of Statistics in Biological Research. 3.rd Edn.. W. H. Freeman and Co., New York. 887 pp. (1995). — SWOFFORD, D. L. and SELANDER, R. B.: BIOSYS-1: A FORTRAN program for the comprehensive analyses of electrophoretic data in population genetics and systematics. The Journal of Heredity, **72**: 281–283 (1981). — WESTCOTT, B.: Some methods of analysing genotype-environment interaction. Heredity **56**: 243–253 (1986).

Genetic Diversity and Structure of Natural Populations of *Pinus thunbergii* in Korea

By Z. S. KIM[1)3)], S. W. LEE[1)4)] and J. W. HWANG[2)]

(Received 10th January 1997)

Abstract

Thirteen natural populations of *Pinus thunbergii* were investigated by starch-gel electrophoresis. For 27 loci from 17 enzyme systems, the percentage of polymorphic loci (*P*; 99% level), the number of alleles per locus (*A*), the observed (H_o) and expected (H_e) heterozygosities and the effective number of alleles (A_e) were 71.3%, 2.2, 0.214, 0.212 and 1.443, respectively. 13 natural populations of *P. thunbergii* seemed to be in equilibrium of HARDY-WEINBERG expectation. Of the total variability, more than 95% was within populations. The mean value of NEI's (1978) unbiased genetic distance (*D* = 0.008) confirmed that the variation among populations was low. Weak correlation between genetic distance and geographic distance was found. Cluster analysis showed that the populations sampled from the east-coast region, except Samcheok, were distinguished from other populations in the west-coast and south-coast region.

Key words: *Pinus thunbergii*, natural populations, allozymes, genetic variation.

FDC: 165.3; 165.5; 174.7 *Pinus thunbergii*; (519.5).

Introduction

As its Korean name 'Haesong' means the maritime pine, *Pinus thunbergii* PARL. grows along the coastlines in South Korea. It also occurs along the coasts of three main islands of Japan (MIROV, 1967). As we consider its natural range, *P. thunbergii* seems to have a good resistance to salt and wind, consequently it has been partially planted for windbreak along the seacoasts in South Korea. It is generally known that the western boundary line of natural distribution reachs to Namyang, Kyunggi province (37°20' N. L.) and the eastern boundary line to Uljin, Kyungpook province (37° N. L.) (LEE, 1989).

[1)] Department of Forest Resources, Korea University, Seoul 136-701, Republic of Korea

[2)] Department of Forestry, Yeungnam University, Kyungsan 712-749, Republic of Korea

[3)] To whom correspondence should be addressed. Phone) 82-2-3290-3011, Fax) 82-2-953-0737

[4)] Present address: Forest Genetics Research Institute, Suwon 441-350, Republic of Korea

In these days, the natural populations of *P thunbergii*, have decreased owing to damages by harmful insects (pine leaf gall midge etc.) and subsequent deforestation. It is easily presumed that such changes in forest ecosystem could bring about the reduction of genetic variation. In consideration of the adaptable or sustainable forestry against these threats, the conservation of *P. thunbergii* is a urgent task.

In comparison with those of *P. densiflora*, the most abundant Diploxylon pine in Korea, basic research, in particular genetic and breeding studies for *P. thunbergii* is relatively scarce. LEE (1989) reported the geographic variation of leaf and seed traits. SHIN (1987) and SHIRAISHI (1988a and b) studied the inheritance pattern and linkage of some isozymes of *P. thunbergii*. Recently, MIYATA and UBUKATA (1994) reported the genetic variation of 22 natural populations of *P. thunbergii* in Japan employing isozyme markers. KIM and LEE (1995) presented a brief outlook on the magnitude of genetic variation in 3 Korean native pines, *P. thunbergii*, *P. densiflora* and *P. koraiensis*.

The primary objectives of this study were to analyze the genetic diversity and structure and to describe geographical patterns for corresponding alleles and genetic diversity of thirteen natural populations of *P. thunbergii* in Korea.

Materials and Methods

Thirteen natural populations with the minimum area of 1 ha were sampled in Korea (*Fig. 1*): 3 (pop. 1 to 3) were located along the west-coast, 7 (pop. 4 to 10) along the south-coast, and 3 (pop. 11 to 13) along the east-coast.

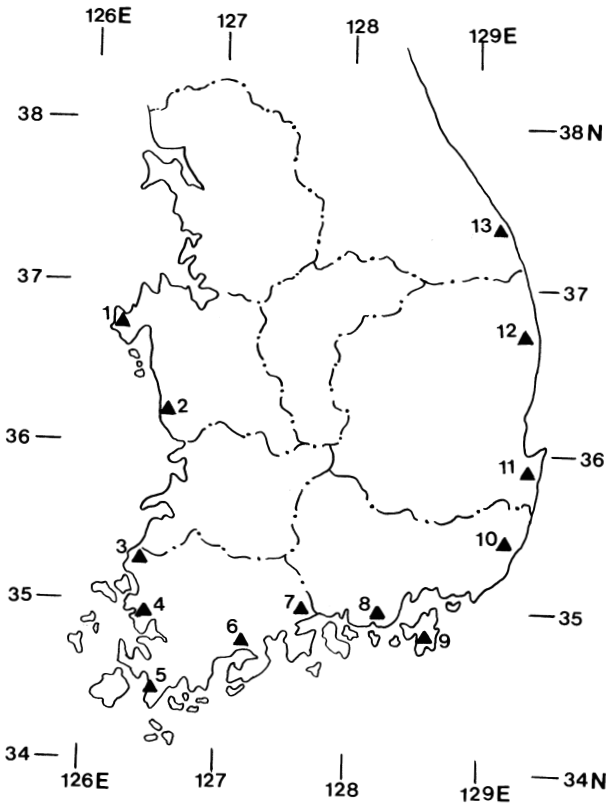

Fig. 1. – Distribution of the *Pinus thunbergii* natural populations examined in Korea (numerical codes as in *table 1*.)

Within each stand, 30 or more trees were selected for cone collection with a minimum distance of 30 m so as to decrease the risk of relatedness. Cones were taken from the top third of the crown and separated seeds were stored in freezer at –20 °C until used for electrophoresis. Seeds were soaked in 1% hydrogen peroxide for 3 days and then germinated on moist filter paper at 25°C for about 2 weeks. Germinated seeds (radicle extending at least 2 mm but less than 5 mm from the seed coat) were then used for isozyme analysis.

Seventeen enzymes were analyzed for the population survey (abbreviations and EC number / in parentheses): Aconitase (*ACO,* 4.2.1.3), acid phosphatase (*ACP*, 3.1.3.2), catalase (*CAT*, 1.11.1.6), fluorescent esterase (*FE*, 3.1.1.1), fumarase (*FUM*, 4.2.1.1), glutamate dehydrogenase (*GDH*, 1.4.1.3), glycerate dehydrogenase (*GLD*, 1.1.1.29), glutamate-oxaloacetate transaminase (*GOT*, 2.6.1.1), isocitrate dehydrogenase (*IDH*, 1.1.1.42), leucine aminopeptidase (*LAP*, 3.4.11.1), malic dehydrogenase (*MDH*, 1.1.1.37), menadion reductase (*MNR*, 1.6.99.2), mannosephosphate isomerase (*MPI,* 5.3.1.8), phosphoglucose isomerase (*PGI*, 5.3.1.9), phosphoglucomutase (*PGM*, 2.7.5.1), shikimate dehydrogenase (*SDH*, 1.1.1.25), and UDP-glucose pyrophosphorylase (*UGPP,* 2.7.7.9). Details of the electrophoretic procedures and staining recipes have been given by KIM et al. (1994). Studies on the inheritance patterns of some enzyme systems investigated here have been reviewed by SHIN (1987) and SHIRAISHI (1988b) and those of the other enzyme systems were surveyed in our lab (unpublished data).

Gene frequencies were analyzed using BIOSYS-1 (SWOFFORD and SELANDER, 1989). Average number of alleles per locus (A), average effective number of alleles (A_e), percentage of polymorphic loci (P), and average observed (H_o) and expected (H_e) heterozygosities were calculated on a population basis. Agreement of HARDY-WEINBERG proportions was tested using a chi-square test for goodness of fit (see KIM et al., 1994). Total genetic diversity was determined and partitioned into among and within populations (NEI, 1973) using polymorphic loci only. Genetic distances (NEI, 1978) were determined for all pairwise population comparisons. A dendrogram was constructed using SNEATH and SOKAL's (1973) unweighted pair grouping method (UPGMA).

Results

The distribution of the allele and genetic diversity

Four of the 27 loci at 17 enzymes were monomorphic (*Fe-1*, *Idh, Mpi-1,* and *Pgi-1*) and 23 were polymorphic. Most polymorphic loci were segregated for 2 or 3 alleles, but some loci, such as *Acp-1, Cat-1, Fe-2, Lap-1, Pgi-2,* and *Sdh-2*, segregated for 4 or 5 alleles. At 20 loci of 23 polymorphic loci, the most frequent allele was the common one in all populations. At the remaining 3 loci (*Aco, Mnr-1* and *Sdh-1*), an allele predominated in some populations, while the other allele predominated in other populations. Among the rare alleles present in many loci, 2 alleles, *Got-1*^{a} and *Got-1*^{c}, were found only in the populations Wolseong and Koseong, and Uljin, respectively. At *Gdh*, allele *b* was found only in 2 populations, Muan and Samcheok. While the frequency of this allele was very low in Samcheok, it exceeded 0.25 in Muan.

Summary statistics for the proportion of polymorphic loci at 95% and 99% level, the average number of alleles per locus, the effective number of alleles per locus, the average observed and expected heterozygosities are presented in *table 1*.

Genetic structure and genetic differentiation

Out of the 247 tests performed to compare the observed genotypic frequencies at each locus with those under the HARDY-WEINBERG expectation, 13 indicated a significant departure from the expected distribution (data are not shown). Thus, on the whole, 13 natural populations of *P. thunbergii*

Table 1. – Genetic diversity at 27 loci in 13 populations of *Pinus thunbergii* (standard errors in parentheses).

Population	N	A	A_e	P_{95} (%)	P_{99} (%)	H_o	H_e
1. Seosan	32.6(0.2)	2.1(0.2)	1.50	51.9	66.7	0.230(0.047)	0.220(0.045)
2. Seocheon	38.6(0.2)	2.0(0.2)	1.45	51.9	70.4	0.208(0.045)	0.205(0.043)
3. Youngkwang	34.3(0.4)	2.1(0.2)	1.32	55.6	70.4	0.190(0.039)	0.186(0.036)
4. Muan	35.7(0.2)	2.0(0.2)	1.43	59.3	66.7	0.198(0.042)	0.211(0.040)
5. Haenam	18.7(0.3)	1.7(0.2)	1.32	40.7	55.6	0.178(0.048)	0.158(0.039)
6. Boseong	44.8(0.6)	2.3(0.2)	1.41	59.3	74.1	0.204(0.043)	0.201(0.039)
7. Kwangyang	38.3(1.0)	2.1(0.2)	1.41	59.3	70.4	0.193(0.039)	0.200(0.039)
8. Koseong	40.3(0.4)	2.4(0.2)	1.51	55.6	77.8	0.242(0.046)	0.238(0.042)
9. Keoje	19.1(0.5)	2.1(0.2)	1.51	55.6	66.7	0.246(0.045)	0.232(0.045)
10 .Yangsan	40.7(0.2)	2.3(0.2)	1.45	55.6	74.1	0.240(0.045)	0.220(0.040)
11. Wolseong	41.6(0.2)	2.3(0.2)	1.45	51.9	81.5	0.206(0.037)	0.218(0.040)
12. Uljin	34.4(0.3)	2.2(0.2)	1.45	55.6	70.4	0.191(0.044)	0.202(0.042)
13. Samcheok	34.5(0.2)	2.4(0.2)	1.56	66.7	81.5	0.253(0.044)	0.261(0.041)
Mean		2.2	1.44	55.3	71.3	0.214	0.212

Note: N, mean sample size per locus; A, mean number of alleles per locus; A_e, mean number of effective alleles; P_{95}, percentage of polymorphic loci at 95% level (A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95); P_{99}, percentage of polymorphic loci at 99% level; H_o, mean observed heterozygosity; H_e, mean expected heterozygosity.

investigated seemed to be in equilibrium of HARDY-WEINBERG expectation.

The average gene diversity in total populations (H_T) and the average gene diversity within populations (H_S) were 0.255 and 0.245, respectively (*Table 2*). Therefore, 4.4% of the gene diversity (G_{ST}) was distributed among populations. G_{ST} values for each locus ranged from 0.1% (*Sdh-3*) to 24.8% (*Gdh*).

The mean NEI's (1978) genetic distance (D) was 0.008, showing that the differentiation between populations was low as shown in the analyses of NEI's hierarchical gene diversity and typical of the level of differentiation observed between local populations of pines (HAMRICK et al., 1992).

To better visualize the above results, a dendrogram produced by the UPGMA clustering method is presented in *figure 2*. It showed that 13 populations could be classified into three groups. Namely group I consisted of Seosan, Seocheon (located along the west-coast), Keoje, Koseong, Kwangyang (south-coast), and Samcheok (east-coast). Group II was composed of Yeongkwang, Muan (west-coast), and Haenam, Boseong, Yangsan (south-coast) and this group clustered with group I. Finally, Wolseong and Uljin (east-coast) made up group III which was distinct from other 2 groups.

Discussion

The amount of genetic diversity observed here is relatively large. HAMRICK and GODT (1989) indicated that long-lived woody plant species tend to maintain higher levels of allozyme variation within populations and within species than other plant species. The averages and standard deviations of genetic parameters within populations of long-lived woody plants were as follows: P, 49.3 ± 1.8%; A, 1.76 ± 0.04; A_e, 1.20 ± 0.01; H_e, 0.148 ± 0.006; and H_{es}, equivalent to H_T over all the loci in this study, 0.177 ± 0.006 (HAMRICK et al., 1992). These values were lower than those we found for *P. thunbergii* in Korea (P = 55.3%; A = 2.2; A_e = 1.44; H_e = 0.212; H_T = 0.255). Additionally, genetic variation maintained in *P. thunbergii* at the species level (H_{es}) and the population level (H_e) were high relative to those reported for both gymnosperms (H_{es} = 0.169; H_e = 0.151) in general and pines (H_{es} = 0.157; H_e = 0.136) in particular (HAMRICK et al., 1992).

On the other hand, previous study of *P. thunbergii* in Japan (MIYATA and UBUKATA, 1994) revealed that this species is one of the most polymorphic in the genus, *Pinus*. The number of populations surveyed and the number of polymorphic loci examined were 22 and 14, respectively. We compared the genetic diversities between Japanese and Korean populations using the parameters of A and H_e, although the differences in electrophoretical procedures and isozyme loci investigated in 2 studies prevented the accurate comparison. Our comparison indicated that the genetic diversity (A = 3.9; H_e = 0.240) of Japanese *P. thunbergii* was somewhat higher than that of Korean *P. thunbergii*. Similarly, when only loci commonly employed in both studies (*Got-1, Got-2, Got-3, Lap-1* and *Lap-2*) were considered, A, P (95% level), and H_e of Japanese populations, 2.3, 42.7%, and 0.174 respectively, were higher than those found in Korean populations (2.0, 38.5%, and 0.127). It is quite interesting to interpret this difference in connection with the different distribution pattern of *P. thunbergii* in both countries. *P. thunbergii* is known to occur along the coasts of almost whole country in Japan, while its distribution along the coastlines in Korean peninsular is restricted to South Korea. It is generally known that the more widespread species has more polymorphic loci, more alleles per locus and allele frequencies are less skewed (HAMRICK et al., 1992). *P. thunbergii* in Japan with larger geographic ranges had

Table 2. – NEI's (1973) gene diversity estimates within and among populations at 23 polymorphic loci in *Pinus thunbergii*.

Locus	H_T	H_S	D_{ST}	G_{ST}
Aco	0.519	0.502	0.018	0.034
Acp-1	0.144	0.141	0.003	0.023
Cat-1	0.244	0.230	0.014	0.056
Fe-2	0.202	0.200	0.003	0.013
Fum-1	0.061	0.060	0.001	0.019
Gdh	0.044	0.033	0.011	0.248
Gld-1	0.029	0.027	0.002	0.067
Got-1	0.006	0.006	0.000	0.010
Got-2	0.034	0.033	0.001	0.021
Got-3	0.032	0.031	0.000	0.015
Lap-1	0.189	0.183	0.006	0.030
Lap-2	0.388	0.371	0.017	0.044
Mdh-2	0.247	0.239	0.008	0.033
Mdh-3	0.048	0.046	0.001	0.025
Mnr-1	0.460	0.439	0.021	0.045
Mnr-2	0.544	0.507	0.037	0.068
Mpi-2	0.579	0.547	0.032	0.055
Pgi-2	0.266	0.251	0.014	0.054
Pgm-1	0.589	0.577	0.012	0.021
Sdh-2	0.513	0.487	0.026	0.051
Sdh-3	0.060	0.060	0.000	0.001
Ugpp-1	0.281	0.275	0.006	0.022
Ugpp-2	0.395	0.379	0.015	0.039
Mean	0.255	0.245	0.011	0.044

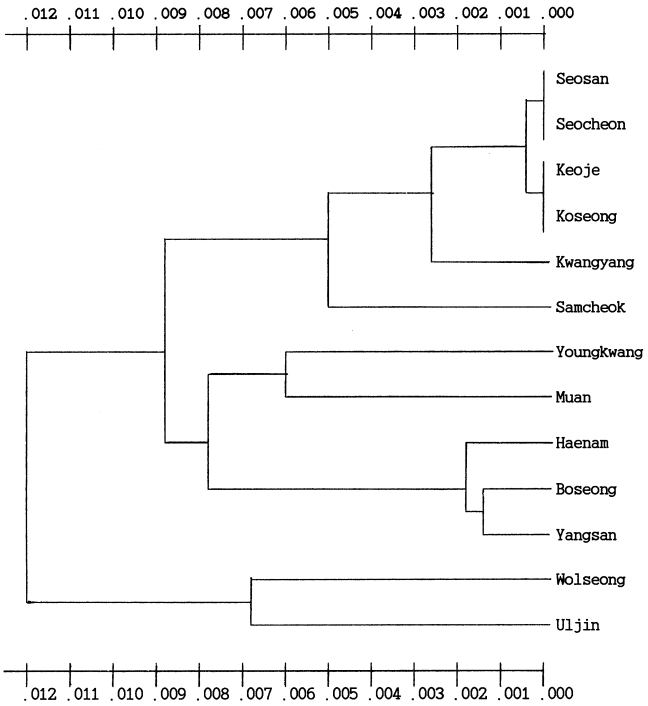

Fig. 2. – Dendrogram showing the clustering of the 13 natural populations of *Pinus thunbergii* based on NEI's (1978) unbiased genetic distance coefficient.

higher level of genetic diversity than that in Korea. However, under the present circumstances where the evolutionary history of this species have not been well studied, systematic researches should be needed to get more detailed information on genetic architecture of *P. thunbergii* in Japan and Korea.

The mean G_{ST} value (0.044) for Korean *P. thunbergii* was low compared with those of woody species with similar life-history and ecological characteristics in general as well as that of other pines in particular (see HAMRICK et al., 1992). For long-lived woody species, genetic variation among populations is most strongly influenced by geographic distribution (HAMRICK et al., 1992). Namely, tree species with widespread and continuous distributions have retained lower gene differentiation among populations than trees with isolated scattered distributions. Japanese populations of *P. thunbergii* that are distributed widely, gene differentiation among populations is small (0.073), but slightly larger than that of Korean *P. thunbergii*. The difference in G_{ST} values among the 2 countries might be due to the difference in distribution. Although the distribution of Japanese populations was wider than that of the present study, some populations of Japanese *P. thunbergii* were geographically isolated. That is to say, out of 22 populations studied, 18 populations were sampled from Honshu island – the biggest island of Japan, and the rest of them were separately sampled from Shikoku and Kyushu islands. This might have made a contribution to increasing the degree of genetic differentiation among populations of Japan.

A positive correlation existed between genetic and geographic distance although the value of correlation coefficient was very low. Accordingly, adjacent populations tended to cluster into the same group. However, this grouping pattern was not exact. For instance, population Samcheok of the east-coast group was clustered more closely to the populations of the west- and south-coast group. This population is located higher than the eastern boundary of natural populations of *P. thunbergii* according to other reports (LEE, 1989). Thus we could suppose that this population was established artificially by the seeds or trees originated from the trees of the west- or south-coast populations. However, we could not ascertain whether this hypothesis was true or not, due to the absence of any records on the origin of this population.

Acknowledgment

This research was financially supported, in part, by Korea Science and Engineering Foundation (KOSEF). The authors thank unknown reviewer for reading and making substantial comments on the manuscript.

References

HAMRICK, J. L. and GODT, M. J. W.: Allozyme diversity in plant species. In: Plant population genetics, breeding, and genetic resources. Edited by A. H. D. BROWN, M. T. CLEGG, A. L. KAHLER and B. WEIR. Sinauer Associates Inc., Sunderland. pp. 43–63 (1989). — HAMRICK, J. L., GODT,

M. J. W. and SHERMAN-BROYLES, S. L.: Factors influencing levels of genetic diverse in woody plant species. New Forests **6**, 95–124 (1992). — KIM, Z. S. and LEE, S. W.: Genetic diversity of three native *Pinus* species in Korea. In: Population genetics and genetic conservation of forest trees. Edited by PH. BARADAT, W. T. ADAMS and G. MÜLLER-STARCK. SPB Academic Publishing, Amsterdam, The Netherlands. pp. 211–218 (1995). — KIM, Z. S., LEE, S. W., LIM, J. H., HWANG, J. W. and KWON, K. W.: Genetic diversity and structure of natural populations of *Pinus koraiensis* (SIEB. et ZUCC.) in Korea. Forest Genetics **1**, 41–49 (1994). — LEE, D. H.: Geographic variation in leaf and seed characteristics of natural populations of *Pinus thunbergii* PARL. in Korea. M. A. thesis. Yeungnam University. (in Korean). (1989). — MIROV, N. T.: The genus *Pinus*. The Ronald Press Company, New York (1967). — MIYATA, M. and UBUKATA, M.: Genetic variation of allozymes in natural stands of Japanese black pine. (in Japanese). J. Jpn. For. Soc. **76**, 445–455 (1994). — NEI, M.: Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. **70**, 3321-3323 (1973). — NEI, M.: Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583–590 (1978). — SHIN, D. H.: Inheritance and linkage of allozymes in *Pinus thunbergii* PARL. M. A. Thesis. Korea University (1987). — SHIRAISHI, S.: Linkage relationships among allozyme loci in Japanese black pine, *Pinus thunbergii* PARL.. Silvae Genetica **37**, 60–66 (1988a). — SHIRAISHI, S.: Inheritance of isozyme variations in Japanese black pine, *Pinus thunbergii* PARL.. Silvae Genetica **37**, 93–100 (1988b). — SNEATH, P. H. A and SOKAL, R. R.: Numerical Taxonomy. W. H. Freeman and Co., San Francisco, CA (1973). — SWOFFORD, D. L. and SELANDER, R. B.: BIOSYS-1: A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. Illinois Natural History, Survey, IL (1989).

Balancing Gain and Relatedness in Selection

By D. LINDGREN[1]) and T. J. MULLIN[2])

(Received 23rd January 1997)

Summary

A population merit criterion, B_ω, for a set of genotypes, ω, is formulated as $B_\omega = \bar{g}_\omega - c\Theta_\omega$ where, c is a weighting constant, $\bar{g}_w$ is the average of their breeding values, and Θ_ω is the average coancestry of the considered genotypes, which is a measure of their relatedness. The breeding objective studied here is selecting the set ω that maximises B_ω. An iterative search algorithm is proposed for finding this maximum under a given breeding-population size. This algorithm was applied to an example using simulation techniques. Results were presented as graphs where the gain was plotted against the status effective number, which was used to quantify the degree of relatedness as an inverse function of average coancestry. For all except extreme c values the algorithm gave markedly better combinations of gain and average coancestry when compared with a conventional method to control relatedness by restricting contributions from individual parents.

Key words: computer simulation, diversity, effective population size, inbreeding, genetic base, status number, selection response, coancestry, kinship.

FDC: 165.3/.4; 165.6

Introduction

Breeders always face a trade-off between 2 basic desiderata. While they are expected to produce genetic gain, they are also expected to control relatedness so that genetic diversity is conserved. The challenge is first to formulate a breeding objective considering both gain and relatedness, and then to apply a selection procedure that somehow affords an optimal trade-off.

The problem of balancing genetic gain and diversity of the genetic base by including relatedness in selection decisions has been approached by several investigators (e.g., TORO and PÉREZ-ENCISO, 1990; QUINTON and SMITH, 1995; WEI, 1995; BRISBANE and GIBSON, 1995). QUINTON *et al*. (1992) introduced comparisons of breeding methods at the same level of inbreeding, and it seems to be common to regard inbreeding as the entity that must be compromised in the pursuit of gain (e.g., CABALLERO *et al*., 1996). Recently, combining consideration of breeding value and relatedness among selections has been suggested as a way to achieve that goal (WRAY and GODDARD, 1994). BRISBANE and GIBSON (1995) developed a selection algorithm amounting to the estimated breeding values of the selected individuals, minus their assumed influence on average coancestry, in order to maximise gain in relation to the genetic base maintained.

WEI (1995) showed how gain and diversity may be pursued for a single breeding cycle, assuming a symmetric population structure with all individuals equally inbred. For deployment of unrelated clones in forestry, either as parents in seed orchards or as mass-propagated clonal mixtures, the problem has a simple solution, requiring only that the frequencies of deployed genetic entries vary in linear relationship to their predicted genetic values (LINDGREN, 1986; LINDGREN *et al*., 1989). While this method was also shown to serve as a good approximation for families (WEI and LINDGREN, 1995), where a similar optimising method can be used LINDGREN *et al*., 1993), such methods are only applicable in simple situations (which, however, are of major practical importance in forest tree breeding) and are somewhat complicated to use.

The aims of the current study were to formulate an expression for the merit of a given set of genotypes considering their relatedness in conjunction with their breeding values as a composite breeding objective, and to suggest a way to optimise the approach to that objective.

[1]) Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

[2]) Genesis Forest Science Canada Inc., C. P 64, Succursale Haute-Ville, Québec (QC) G1R 4M8, Canada