constituents of conifer needles. II. Pinifolic acid, a new diterpene acid isolated from *Pinus sylvestris* L. Acta Chem. Scand. **16**: 607—614 (1962). —— Gref, R.: Variation in isoabienol content in *Pinus sylvestris* needles. Can. J. Bot. **59**: 831—835 (1981). —— Gref, R. and Lindgren, D.: The inheritance of pinifolic acid in Scots pine (*Pinus sylvestris* L.) needles. Silvae Genetica **33**: 235—237 (1984). —— Gref, R., Rudin, D. and Lindgren, D.: Segregation patterns of isoabienol in *Pinus sylvestris* (L). Silvae Genetica **34**: 12—14 (1985). —— Gref, R. and Tenow, T.: Resin acid variation in sun and shade needles of Scots pine (*Pinus sylvestris* L.) Can. J. Bot. **17**: 346—349 (1987). —— Hiltunen, R.: Variation and inheritance of some monoterpenes in Scots pine (*Pinus sylvestris* L.). Planta Med. **28**: 315—323 (1975). —— Hiltunen, R., Tigerstedt, P. M. A., Juvonen, S. and Pohjola, J.: Inheritance of 3-carene quantity in *Pinus sylvestris* L.. Farm. Aik. **84**: 69—72 (1975). —— Newman, A. A.: Chemistry of terpenes and terpenoids. Academic Press, London and New York (1972). —— Rudloff, E. von: Inheritance of leaf oil terpene patterns in selfed progeny and some crosses of coastal Douglas-fir. Silvae Genetica **33**: 198—203 (1984). —— Tobolski, J. and Zinkel, D. F.: Variation in needle and cortex resin acids during shoot development in *Pinus sylvestris*, *P. nigra* and *P. strobus*. Forest Sci. **28**: 785—796 (1982). —— White, E. E.: Biosynthethic implications on terpene correlations in *Pinus contorta*. Phytochem. **22**: 1399—1405 (1983). —— White, E. E.: Mode of genetic control of monoterpenes in foliage of controlled crosses of *Pinus contorta*. Silvae Genetica **33**: 115—119 (1984). —— Zinkel, D., Magee, T. V. and Walter, J.: Major resin acids of *Pinus nigra* needles. Phytochem. **24**, 1273—1277 (1985).

Allozyme Variation in Four Populations of Taiwania cryptomerioides in Taiwan

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Summary

Genetic diversity within and genetic differentiation among 4 populations of Taiwania (*Taiwania cryptomerioides* Hay.) in Taiwan were investigated using 327 offspring growing in a 10-year-old provenance/progeny test plantation. Eight of the 15 loci examined were polymorphic. The average proportion of polymorphic loci per population was 50.2% (99% criterion for polymorphism). Mean expected heterozygosity was 0.145, ranging from 0.126 to 0.173 in the different populations. On average, the percent heterozygous loci/individual ranged from 12.3 to 19.4, the number of alleles/locus from 1.53 to 1.67, and the effective number of alleles/locus from 1.16 to 1.26. The slightly lower number of alleles/locus compared to other coniferous species probobly reflects the insular nature of Taiwania's distribution.

Partitioning the genetic variability into within- and among-population components with F-statistics led to an estimate of within-population variation amounting to 94.7% of total variation. This suggests a lack of barriers to gene flow among populations. Geographic distance and Nei's genetic distance appear to be positively related, except the Ta-Jiann population differs from the others in terms of genetic distance to a greater degree than they do among themselves. This may result from topographic isolation of the Ta-Jiann population.

Key words: Taiwania cryptomerioides, allozyme variation.

Introduction

A high proportion of the vascular plants of Taiwan overlap with the flora of mainland China (Keng, 1956). The presence of many endemic species, however, suggests a long evolutionary history since the isolation of Taiwan from the mainland. A landbridge may have existed during the late Miocene and early Pliocene periods (Huang, 1988). Taiwania (*Taiwania cryptomerioides* Hay.) appeared in the Miocene or Tertiary, as deduced from pollen analyses (Huang, 1988).

Numerous steep mountains occupy 4/5's of the island and raise the question of the apportionment of genetic variation within and among the populations which extend more or less continuously from north to south at an elevation of 1800m to 2600m (Liu, 1966).

In general, Taiwania grows in ultisol and aceptisol soils, with a pH in the range of 3.5 to 5.0. Stands occur on all exposures (N, E, S, W) when annual precipitation is around 3000mm. Taiwania is usually found in valleys or on hillslopes, but not on the ridge tops, and is mixed with varying proportions of broadleaved trees and other conifers (i. e., *Chamaecyparis, Tsuga, Picea,* and *Cunninghamia).*

Taiwania produces a valuable timber and has been widely used in reforestation in Taiwan over the past 10 years. Six natural populations have been compared in a provenance test. After 10 years, there was no difference in growth among provenances even though they differed in the first 1 to 2 years (Liu et al., 1985). Taking advantage of another younger provenance/progeny test plantation of Taiwania, we were able to quantitatively characterize the genetic structure within and among major populations using isozymes.

Materials and Methods

1. Sampling

Young leaf tissue of 327 offspring belonging to 34 families in 4 populations were collected from a provenance/progeny test plantation. The 4 populations were among the major seed sources of Taiwania collected for reforestation in Taiwan. The location of the original 34 seed trees is given in *Figure 1.* DBH varied from 120 cm to 380 cm, corresponding to an age roughly between 500 years to 1500 years (estimated from unpublished observations). Data on the seed trees is given in *table 1.* The plantation was planted in 1981 at Lien-Hwa-Chi branch station of the Taiwan Forestry Research Institute.

2. Electrophoresis methods

Horizontal starch gel electrophoresis was used to separate isozymes in 8 enzyme systems; namely, EST, F-EST, GOT, MDH, 6PGD, PGI, PGM, SKDH (GOT = glutamate oxalacetate transaminase, E.C.2.6.1.1; 6PGD = 6-phosphogluconate dehydrogenase, E.C.1.1.1.44; PGI = phosphoglucose isomerase, E.C.5.3.1.9; SKDH = shikimate dehydrogenase, E.C.1.1.1.25; PGM = phosphoglucomutase, E.C. 2.7.5.1; F-EST = fluorescent esterase, E.C.3.1.1.1; EST = esterase, E.C.3.1.1.1). Young needle tissue was ground with extraction buffer after Feret (1971). Electrophoresis and staining followed the procedures described in Cheliak and Pitel (1984).

3. *Measures of gene diversity*

Allele frequencies were calculated for each locus and for each population. The following 4 measures were used to quantify the amount of genetic variability within a population.

(a) The expected heterozygosity (Nei, 1975) at each locus was calculated as $He = 1 - \sum_{i=1}^{k} \chi_i^2$ Where χ_i is the frequency of the ith allele, summed over k alleles.

(b) The percentages of heterozygous loci per individual (Nei, 1973).

(c) The average number of alleles per locus was calculated by averaging over all polymorphic and monomorphic enzyme systems.

(d) The effective number of alleles per locus (n_e) (Crow and Kimura, 1970) is defined as : $n_e = 1 / \sum_i P_i^2$. The number of alleles is maximized when the allele frequencies at any locus are equal.

4. *Genetic differentiation*

Three methods were used to quantify the degree of differentiation among populations.

(a) $H_t = H_s + D_{st}$, was defined by Nei (1973, 1975). H_t is a measure of the mean heterozygosity expected under random mating. The total gene diversity, H_t, may be partitioned into average gene diversity within (H_s) and between (D_{st}) populations. The ratio D_{st}/H_t measures the relative degree of genetic differentiation (G_{st}).

(b) F-statistics were originally devised by Wright (1969) and extented by Nei (1977) to examine structuring in hierarchical populations by utilizing the correlation between uniting gametes within and among subpopulations and for the population as a whole. In other words, it is concerned with the distribution of genotype frequencies at single loci. F_{is} is the mean fixation index over all subpopulations and F_{st} is the correlation among random gametes within subpopulations relative to the total population. Fixation indices (F_{is} and F_{it}) were calculated according to the formulae of Nei (1977). F_{it} represents the overall fixation index, and can be estimated by $F_{it} = 1 - H_0/H_e$, here H_0 is observed heterozygosity and H_e is expected heterozygosity correlated for finite population size. F represents the deviation from Hardy-Weinberg proportions due to the combined effects of finite population size, selection, inbreeding, and other forces shaping the genetic structure of the population. For multiple allelic systems, F_{st} is equivalent to Nei's (1973) G_{st}. Contingency χ^2-tests (Li and Horvitz, 1953) were performed to test the homogeneity of allele frequency variation among populations.

(c) Nei (1972) devised a measure of genetic distance or differentiation (D) between all pairs of populations based on the gene identity between populations.

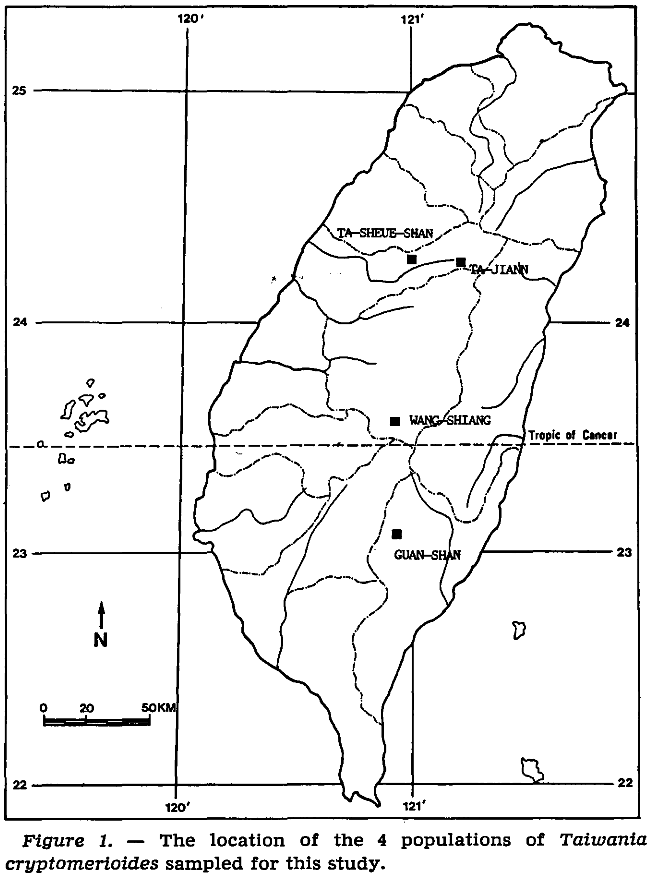

Figure 1. — The location of the 4 populations of *Taiwania cryptomerioides* sampled for this study.

Results

1. *Allele Frequencies*

The observed allele frequencies at each locus for each population, along with the overall mean allele frequencies, observed and expected heterozygosities and average heterozygosity are listed in *table 2*. Of the 15 loci that were consistantly scorable, 8 were polymorphic (99% criterion) in at least one population. EST-2, F-EST-1, MDH-1, MDH-2, MDH-3, and 6PGD-1, were monomorphic across all populations. A rare variant was recorded for MDH-1 at Ta-Sheue-Shan, and for PGM at Wang-Shiang. Guan-Shan had a rare variant at 6PGD-2 and SKDH-1. Of the 8 polymorphic loci, EST-1, 6PGD-2, F-EST-2, GOT-1, GOT-2, SKDH-2, had 2 alleles. The locus PGM had 3 alleles and PGI had 4 alleles. No allele is specific to Ta-Jiann.

2. *Genetic Diversity*

(a) Heterozygosity (*Table 2*)

For the 8 polymorphic loci, PGI is the only locus having a mean heterozygosity greater than 0.5 over oll populations. GOT-1 also has a moderate h_e (0.425). Two more loci (EST-1 and F-EST-2) had mean expected heterozygosities between 0.4 and 0.3. Two loci, PGM and SKDH-2, gave mean heterozygosities between 0.15 and 0.25. The final 2 polymorphic loci, GOT-2 and 6PGD-2 had mean expected heterozygosities of less than 0.1. At the population level, Guan-Shan has the lowest h_e (0.126); Ta-Sheue-Shan and Wang-Shiang have similar h_e (0.140 and 0.142); Ta-Jiann had the highest heterozygosity (0.173). The overall heterozygosity is 0.145 averaged over the 4 populations. Comparison of the observed and expected heterozygosities shows that in most cases there was very close agreement. Mean observed and expected heterozygosity

Table 1. — Seed tree information for *Taiwania cryptomerioides.*

population	DBH (cm)	Height (m)	altitude (m)	aspect	slope	date of collection
1[1]	271	55	2,200	SW	15°	Nov 1979
1	275	50	2,490	W	—	Nov 1974
1	338	52	2,480	SW	32°	Nov 1979
1	168	35	1,850	W	15°	Nov 1979
1	286	65	1,850	NW	15°	Nov 1979
1	185	55	1,800	NW	15°	Nov 1979
1	166	48	2,000	SE	15°	Nov 1979
1	318	60	2,250	W	20°	Nov 1979
1	239	60	2,100	W	20°	Nov 1979
1	271	47	1,860	SW	20°	Nov 1979
1	172	58	1,900	N	25°	Nov 1979
2[1]	270	30	2,250	E	30°	Nov 1979
2	176	47	2,070	N	15°	Nov 1979
2	230	50	2,140	E	25°	Nov 1979
2	210	50	2,160	W	75°	Nov 1979
2	134	40	1,930	N	45°	Oct 1979
2	280	56	2,170	S	30°	Nov 1979
2	380	40	2,150	E	45°	Nov 1979
2	170	60	1,950	E	60°	Oct 1979
3[1]	160	70	2,160	W	40°	Oct 1979
3	—	60	1,900	W	10°	Nov 1979
3	240	90	1,850	NW	5°	Oct 1979
3	240	60	2,500	W	5°	Nov 1979
3	150	65	2,250	NE	30°	Nov 1979
3	180	57	2,250	W	35°	Nov 1979
3	146	35	2,100	NW	20°	Dec 1979
3	210	42	2,050	N	20°	Dec 1979
3	166	46	2,100	N	15°	Dec 1979
3	216	51	2,000	SW	25°	Dec 1979
4[1]	128	31	2,140	N	30°	Nov 1974
4	134	45	2,200	SW	40°	Nov 1979
4	132	35	2,080	SW	35°	Nov 1979
4	171	33	2,300	SE	30°	Nov 1979
4	114	30	2,260	SE	40°	Nov 1979

[1] 1. Ta-Sheue-Shan; 2. Ta-Jiann; 3. Wang-Shiang; 4. Guan-Shan.

were not significantly different except for F-EST-2 and 6PGD-2.

(b) Percentage of heterozygous loci per individual

Estimates of percent heterozygous loci/individual varies from 12.3% to 19.4% (*Table 3*). As might be expected, since observed and expected heterozygosity were very close, the population with the highest observed heterozygosity also had the highest percent of heterozygous loci/individual.

(c) Average number of alleles per locus

The average number of alleles/locus for the 4 populations was very similar, in a range of 1.53 to 1.67. Levels of heterozygosity did not necessarily relate directly to the number of alleles per locus because heterozygosity is sensitive to the evennes of allelic distribution in addition to the absolute number of alleles. Rare alleles contribute little to the measure of heterozygosity.

(d) Effective number of alleles per locus

The effective number of alleles show the same trend as heterozygosities, this is because both are functions of $\sum_i P_i^2$. Ta-Jiann has the highest effective number of alleles per locus owing to the more or less equal frequencies of alleles at several loci.

3. *Genetic differentiation*

(a) F-statistics are listed in *Table 4*. The F_{is} values for most enzyme systems were negative. The average F_{is} was —0.036 indicating that the observed distribution of genotypes within a population has a slight excess of heterozygotes. Treating the entire species as a random mating unit, estimates of the total fixation index F_{it}, are slightly larger on average than F_{is} for the loci surveyed.

To test whether F_{is} represented a significant deviation from panmixia within populations, one-tailed Chi-square values were calculated according to the formula of LI and HORVITZ (1953) : $\chi^2=F^2N(k-1)$ for $k(k-1)/2$ degrees of freedom where F is F_{is} for a population sample of size N, with k alleles. The analysis showed significant deviations from 0 at the F-EST-2 and 6PGD-2 loci, but gave no further information concerning the allocation of genetic diversity. The extent of genetic differentiation among

Table 2. — Allele frequencies and expected and observed heterozygosities for 10 loci with allelic variants. The average heterozygosity per population is the arithmetic mean of the h_e value over all loci.

Locus	allele	Ta-Sheue-Shan	Wang-Shiang	Guan-Shan	Ta-Jiann	Mean
EST-1	a[1]	0.807	0.724	0.900	0.596	0.757
	b	0.193	0.276	0.100	0.404	0.243
	observed h	0.303	0.469	0.156	0.515	0.361
	expected h	0.312	0.400	0.180	0.482	0.344
F-EST-2	a	0.853	0.708	0.911	0.654	0.782
	b	0.147	0.292	0.089	0.346	0.219
	observed h	0.294	0.438	0.178	0.662	0.393
	expected h	0.251	0.413	0.162	0.452	0.320
GOT-1	a	0.451	0.308	0.170	0.553	0.371
	b	0.549	0.692	0.830	0.447	0.630
	observed h	0.473	0.410	0.295	0.561	0.435
	expected h	0.495	0.426	0.283	0.494	0.425
GOT-2	a	0.949	0.983	0.966	0.956	0.964
	b	0.051	0.017	0.034	0.044	0.037
	observed h	0.103	0.035	0.068	0.059	0.066
	expected h	0.097	0.034	0.066	0.084	0.070
MDH-1	a	0.008	0.000	0.000	0.000	0.002
	b	0.992	1.000	1.000	1.000	0.998
	observed h	0.017	0.000	0.000	0.000	0.004
	expected h	0.017	0.000	0.000	0.000	0.004
6PGD-2	a	0.000	0.000	0.133	0.000	0.033
	b	1.000	1.000	0.867	1.000	0.967
	observed h	0.000	0.000	0.133	0.000	0.033
	expected h	0.000	0.000	0.231	0.000	0.058
PGI	a	0.176	0.105	0.022	0.206	0.127
	b	0.269	0.237	0.356	0.132	0.249
	c	0.542	0.579	0.622	0.662	0.601
	d	0.013	0.079	0.000	0.000	0.023
	observed h	0.529	0.621	0.467	0.515	0.533
	expected h	0.603	0.591	0.486	0.502	0.546
PGM	a	0.000	0.026	0.000	0.000	0.006
	b	0.954	0.938	0.856	0.882	0.908
	c	0.046	0.036	0.144	0.118	0.086
	observed h	0.059	0.125	0.289	0.206	0.170
	expected h	0.088	0.119	0.247	0.208	0.166
SKDH-1	a	1.000	1.000	0.989	1.000	0.997
	b	0.000	0.000	0.011	0.000	0.003
	observed h	0.000	0.000	0.022	0.000	0.006
	expected h	0.000	0.000	0.022	0.000	0.006
SKDH-2	a	0.134	0.083	0.122	0.250	0.147
	b	0.866	0.917	0.878	0.750	0.853
	observed h	0.252	0.125	0.244	0.412	0.258
	expected h	0.233	0.153	0.215	0.375	0.244
	average h_e	0.140	0.142	0.126	0.173	0.145

[1] Alleles a, b, c, d were designated according to their migration distance away from the origin.

populations (F_{st}) ranged from 0.005 to 0.103 among loci and averaged 0.053. Thus, more than 94% of the genetic variation resided within populations.

(b) Gene diversity statistics for 15 loci in Taiwania are presented in *table 5*. Averaged over all loci, the total gene diversity (H_t) was 0.153. For any locus, the largest proportion of this diversity was attributable to the within-population component (H_s = 0.145). G_{st} averaged over all loci was 0.052, indicating that there was approximately 5.2% as much variation between populations as there was within populations.

(c) Estimates of the genetic identity function, I, and genetic distance, D, are given in *table 6*. Values of I ranged from 0.995 to 0.982. A rough correlation exists between genetic and geographic distances, except that the difference between the Ta-Jiann population and the others is somewhat greater than expected based on geographic distance.

Discussion

The level of heterozygosity in Taiwania is lower than the values reported for many other conifers, the H_s of 0.160 was estimated based on 56 taxa (Hamrick and Godt, 1989). This may be due to our choice of loci and number of enzyme systems. However, Guries and Ledig (1982) showed that estimates of observed heterozygosity based upon 20 or more loci are in the range 0.123 to 0.161 for several wide-ranging conifers. Because populations of long-lived organisms can be genetically differentiated both temporally and spatially (Linhart *et al.*, 1981), the level of heterozygosity observed in this study, which represent survivors in a man-made plantation, may not be the same as in the natural state.

Genetic heterogeneity is often attributed to local adaptation to environmental variations. Lofty mountains and valleys divide Taiwan into many isolated pockets. Also Taiwania grow on all exposures and occur over a 800m range in elevation (*Table 1*). This environmental heterogeneity might be expected to favor genetic heterogeneity in Taiwania. However, the overall F_{st} value of 0.053 and G_{st} of 0.052 indicate that slightly more than 5% of the genetic variability occurs among the 4 populations. The majority of the variation resides within populations. It is

Table 3. — Proportion of polymorphic loci, percentage of heterozygous loci per individual, average number of alleles per locus, effective number of alleles per locus, mean heterozygosity observed and mean heterozygosity expected for each population. Standard errors are given in parentheses for h_o and h_e.

	Population			
	Ta-Sheue-Shan	Wang-Shiang	Guan-Shan	Ta-Jiann
Proportion of polymorphic loci[1]	0.47	0.47	0.60	0.47
Percent heterozygous loci / individual	13.4	14.5	12.3	19.4
Average number of alleles / locus	1.67	1.67	1.67	1.53
Effective number of alleles / locus[2]	1.20	1.21	1.16	1.26
Mean heterozygosity observed	0.135 (0.048)	0.148 (0.056)	0.124 (0.038)	0.195 (0.066)
Mean heterozygosity expected	0.140 (0.051)	0.142 (0.053)	0.126 (0.038)	0.173 (0.057)

[1] The frequency of the most common allele is $\leq$ 0.99.

[2] The average effective number of alleles per locus per population is the geometric mean of the n_e values for all loci (Lundkvist, 1979).

Table 4. — Results of the χ^2 contingency tests and F-statistics for each locus. The average values for F_{is}, F_{it} and F_{st} over all the loci were calculated according to Nei (1977).

	χ^2	d_f	F_{is}	F_{it}	F_{st}
EST-1	0.549	1	-0.050	0.022	0.068
F-EST-2	36.261*	1	-0.229	-0.151	0.064
GOT-1	0.175	1	-0.024	0.068	0.090
GOT-2	5.320	1	0.061	0.066	0.005
MDH-1	0.000	0	-0.008	-0.002	0.006
6PGD-2	56.046*	1	0.423	0.483	0.103
PGI	0.565	6	0.023	0.048	0.026
PGM	0.212	3	-0.025	-0.002	0.023
SKDH-1	0.000	0	-0.011	-0.003	0.008
SKDH-2	1.062	1	-0.060	-0.024	0.031
average			-0.036	0.019	0.053

*) 1% significance level

Table 5. — Analysis of gene diversity and degree of differentiation at 15 loci among the 4 populations of *Taiwania cryptomerioides*. The mean of H_t, H_s and D_{st}, was the arithmetic average of H_t, H_s and D_{st}, respectively, for 15 enzymes.

Locus	No. of allele	Total gene diversity (H_t)	Gene diversity within populations (H_s)	Gene diversity among populations (D_{st})	Proportion of interpopulation gene differentiation (G_{st})
EST-1	2	0.368	0.344	0.024	0.065
EST-2	1	0.000	0.000	0.000	0.000
F-EST-1	1	0.000	0.000	0.000	0.000
F-EST-2	2	0.341	0.320	0.021	0.062
GOT-1	2	0.467	0.425	0.042	0.090
GOT-2	2	0.071	0.070	0.001	0.014
MDH-1	2	0.004	0.004	0.000	0.000
MDH-2	1	0.000	0.000	0.000	0.000
MDH-3	1	0.000	0.000	0.000	0.000
6-PGD-1	1	0.000	0.000	0.000	0.000
6-PGD-2	2	0.064	0.058	0.006	0.094
PGI	4	0.559	0.546	0.013	0.023
PGM	3	0.169	0.166	0.003	0.018
SKDH-1	1	0.005	0.004	0.001	0.200
SKDH-2	2	0.251	0.244	0.007	0.028
Mean	1.8	0.153	0.145	0.008	0.052

Table 6. — NEI's measures of genetic identity (below the diagonal) and genetic distance (above the diagonal) for 4 populations of *Taiwania cryptomerioides*.

Population	Ta-Sheue-Shan	Wang-Shiang	Guan-Shan	Ta-Jiann
Ta-Sheue-Shan	—	0.005	0.011	0.016
Wang-Shiang	0.995	—	0.008	0.019
Guan-Shan	0.989	0.992	—	0.045
Ta-Jiann	0.984	0.982	0.958	—

clear that the populations of Taiwania come close to approximating a single panmictic unit. This conclusion is consistent with data on many other conifers which generally indicate relatively little interpopulation differentiation (HAMRICK *et al.*, 1989; HARTL, 1980).

High winds during the season of pollen dispersal, February to March, may favor gene flow. Typhoons, which occur during late summer or early fall, contribute to the distribution of seeds. The longevity of Taiwania (DBH larger than 3 meters, suggesting that age probably exceeds 1500 years) and its height (perhaps >70m) would facilitate temporal and spatial dispersal. Taiwania has the lightest seed weight of any coniferous species in Taiwan (CHUNG and CHANG, 1990); about 1000 seeds in 1.01 g or 116 g in 1 l volume of seeds. In addition to this, a continuous distribution and high outcrossing rates also may prevent genetic drift and play a significant role in the observed low level of differentiation. The calculated mean value for F_{is} is —0.036, which reflects a slight excess of heterozygotes. The calculated F_{it} value of 0.019 suggests that most loci are probably in HARDY-WEINBERG equilibrium or that there is only a slight heterozygote deficiency in the total population. Thus, no evidence for inbreeding was found in any population. Another reason for the lack of differentiation may be that the enzymes studied are not subjected to environmental selection (FALKENHAGEN, 1985).

The Guan-Shan population, located at the margin of Taiwania's range, appears to have the lowest level of heterozygosity, lowest effective number of alleles/locus, and lowest percentage of heterozygous loci per individual. Data for other plant species (YEH and LAYTON, 1979; GURIES and LEDIG, 1982; SCHUMAKER and BABBEL, 1980) suggests that marginal populations may exhibit reduced variability, perhaps due to genetic drift, greater inbreeding in small, isolated populations, or more rigorous selection in ecologically marginal environments.

Generally, a positive correlation exists between genetic and geographic distance, except that the Ta-Jiann population deviates to a greater degree from the other populations than they do among themselves. However, the geographic distances of Ta-Sheue-Shan, Wang-Shiang and Guan-Shan from Ta-Jiann agree well with the corresponding genetic distances between them. Ta-Jiann is located within a deep valley between 2 more or less parallel, east-west oriented, alpine ridges of 3000m to 3500m elevation which act as orographic barriers. Ta-Jiann is, thus, topographically isolated from other populations, even from the nearest population, Ta-Sheue-Shan.

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Literature Cited

Cheliak, W. M. and Pitel, J. A.: Techniques for starch gel electrophoresis of enzymes from forest tree species. Petawawa National For. Institute, Can. For. Serv. Information Rep. PI-X-42. p. 19—45 (1984). —— Chung, Y. L. and Chang, N. H.: Technical Report for Important Tree Seeds in Taiwan. Publication no. 35, Taiwan Forestry Research Institute, Taipei. 130 pages. (in Chinese). (1990). —— Crow, J. F. and Kimura, M.: An Introduction to Population Genetics Theory. Harper and Row, New York (1970). —— Falkenhagen, E. R.: Isozyme studies in provenance research of forest trees. Theor. Appl. Genet. **69**: 335—347 (1985). —— Feret, P. P.: Isozyme variation in *Picea glauca* (Moench) Voss seedlings. Silvae Genet. **20**: 46—50 (1971). —— Guries, R. P. and Ledig, F. T.: Genetic diversity and population Structure in Pitch pine (*Pinus rigida* Mill.). Evolution 36(2): 387—402 (1982). —— Hamrick, J. L. and Godt, M. J. W.: Allozyme diversity in plant species. In: A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Wier (ed.): Plant population genetics, breeding and genetic resources. Sinauer Associates, Inc., Sunderland, Mass. p. 43—63 (1989). —— Hartl, D. L.: Principles of Population Genetics. Sinauer Associates Inc., Sunderland, Mass. p. 164—165 (1980). —— Huang, T. C.: The vegetational history of Taiwan as reflected by geopalynological studies. In: Edward K. Y. Chen (ed): The Palaeoenvironment of East Asia from the Mid-Tertiary. Vol. 1. pp. 528—559. Centre of Asian Studies, Univ. Hong Kong (1988). —— Keng, H.: The floristic relationship of Taiwanese plants and adjacent neighboring plants. (In Chinese). Bull. Exp. Forest., Nat. Taiwan Univ. **4**: 102 (1956). —— Li, C. C. and Horvitz, D. G.: Some methods of estimating the inbreeding coefficient. Amer. J. Hum. Genet. **5**: 107—117 (1953). —— Linhart, Y. B., Mitton, J. B., Sturgeon, K. B. and Davis, M. M.: Genetic variation in space and time in a population of ponderosa pine. Heredity **46**: 407—426 (1981). —— Liu, T.: Study on the phytogeography of the conifers and taxads of Taiwan. (In Chinese). Bull. Taiwan For. Res. Inst. no. 122. 33 pages (1966). —— Liu, Y. C., Cheng, T. Y., Ho, C. P., Ou, C. H., Chu, C. P. and Lu, K. C.: Provenance study of *Taiwania*. (In Chinese). Quart. J. Chin. For. **18** (1): 1—8 (1985). —— Lundkvist, K.: Allozyme frequency distributions in 4 Swedish populations of Norway spruce (*Picea abies* K.). II. Estimations of genetic variation within and among populations, genetic linkage and a mating system parameter. Hereditas **90**: 127—143 (1979). —— Nei, M.: Genetic distance between populations. The American Naturalist **106**: 283—292 (1972). —— Nei, M.: Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. USA **70** (12) Part I: 3321—3323 (1973). —— Nei, M.: Molecular population genetics and evolution. In: A. Neuberger and E. L. Tatum (eds). Frontiers of Biology. Vol. **40**. Am. Elsevier, N. Y. (1975). —— Nei, M.: F-statistics and analysis of gene diversity in subdivided populations. Ann. Human Genet. London **41**: 225—233 (1977). —— Schumaker, K. M. and Babbel, G. R.: Patterns of allozymic similarity in ecologically central and marginal populations of *Hordeum jubatum* in Utah. Evolution **34**: 110—116 (1980). —— Wright, S.: Evolution and the genetics of populations. Vol. 2. The theory of gene frequencies. Univ. Chicago Press, Chicago (1969). —— Yeh, F. and Layton, C.: The organization of genetic variability in central and marginal populations of lodgepole pine (*Pinus contorta* spp. *latifolia*). Can. J. Genet. Cytol. **21**: 487—503 (1979).

Buchbesprechungen

Biotechnology in Agriculture and Forestry. 11. Somaclonal Variation in Crop Improvement. I. By Y. P. S. Bajaj (edited). 1990. Springer Verlag, Berlin, Heidelberg, New York. 685 pages. Hardcover DM 578,—.

Somaclonal variation, that is, variation originating in tissue culture, has been observed in a large number of plant species. This variation could be transient or heritable. From the standpoint of genetics and breeding, it is the heritable somaclonal variation that has importance. Of course, the genetic changes could be undesirable or may be useful for crop improvement. This volume on somaclonal variation is divided in 4 sections. Section I contains 10 chapters that deal with the origin and implications of somaclonal variation, chromosomal genetic and molecular variability, gene amplification, mosaics and chimeras, and variability for tolerance to salinity and nematodes. Section II to IV (containing 20 chapters) are case histories of somaclonal variation in cereals (rice, maize, barley), vegetable and fruits (potato, tomato, eggplant, cucurbits, sugerbeet, chicory, strawberry, peach) and ornamental and forage plants (*Pelargonium*, *Fuchsia*, carnations, *Haworthia*, *Wiegela*, *Nicotiana sylvestris*, alfalfa). This is an informative volume on somaclonal variation of plants. How far has somaclonal variation contributed to genetic improvement of crop species remains to be seen. Other than perhaps some libraries, I wonder who could afford to buy this volume costing DM 578.00 The price is too high.

M. R. Ahuja (Grosshansdorf)

Biotechnology in Agriculture and Forestry. 16. Trees III. By Y. P. S. Bajaj (Edited). 1991. Springer Verlag, Berlin, Heidelberg, New York. 520 pages with 179 figures. Hardcover DM 498,—.

This is continuation of the series on tissue culture of trees by Y. P. S. Bajaj. How many more trees and how many more volumes? To what purpose? This could be an endless series of contributions. One must pause and think where this series Biotechnology in Agriculture and Forestry is heading towards? Perhaps churning up more volumes? And all very expensive. As in the previous two volumes on trees, there are angiosperm trees and gymnosperm trees. All sound very familier and rather mundane. The purpose of the present volume is to add another 28 case histories on tissue culture of woody plants, to already reported 23 species in Trees I, and 31 in Trees II. Section I on Angiosperm Trees contains tissue culture of black cherry, sour cherry, pomegranate, loquat, *Ficus* spp., yellow-poplar, horse chestnut, eastern redbud, linden, Saskatoon, Taiwan sassafras, plane trees, rattans, and bamboos. Section II on Gymnosperm trees deals with tissue culture of jack pine, caribbean pine, eldarica pine, slash pine, eggcone pine, maritime pine, ponderosa pine, eastern white pine, loblolly pine, Engelmann spruce, white spruce, larch, hinoki cypress, and western red cedar. By employing tissue culture technology, it is possible to vegetatively propagate a large number of woody plants. However, mostly from juvenile tissues. This is especially true in the case of gymnosperms. What remains to be done is the mass cloning of tested superior tree genotypes by tissue culture.

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