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Patterns of Genetic Variation of *Alnus formosana* in Taiwan

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ABSTRACT: Formosan alder (*Alnus formosana* (Burk.) Makino), a deciduous native tree in Taiwan, has dominant colonizing ability in open areas from lowland up to 2,500 m. The genetic structure of twenty-two populations of this species was studied by allozyme electrophoresis analysis. In the fifteen enzymes surveyed, 59.1 % of the loci was found polymorphic and the mean effective number of alleles per locus 1.21. The proportion of genetic diversity among the populations studied was 0.02 and the genetic distance among populations ranged between 0.000 to 0.019 with a mean of 0.004. Low genetic differentiation in *Alnus formosana* may be attributed to high degree of gene flow. However, the significant correlations between allelic frequencies in four loci and the altitude gradient revealed partial genetic variation that correlated with temperature differences.

KEY WORDS: ***Alnus formosana*, Allozyme, Allele frequency, Genetic diversity, Gene flow, Genetic variation, Altitude gradient.**

INTRODUCTION

Pioneer tree species play an important role in forest restoration in freshly demolished areas. Interest in land-use planning and environment management has stimulated a great effort in studying the effect of such species (Bousquet and Lalonde, 1991; Sharma, 1993). Formosan alder (*Alnus formosana*) is an early-successional indigenous species that can be found in disturbed areas including burned, eroded or freshly exposed places. Because of the symbiotic association with nitrogen-fixing actinomycetes *Frankia*, *Alnus* species survive in areas short of adequate supply of the available soil nitrogen (Tarrant, 1961; Tarrant and Trappe, 1971; Schubert, 1986). *A. formosana*, along with other alder species, is a nitrogen-fixing tree and is a common species in this subtropical island (Li, 1976; Liao, 1996). The reported studies of *A. formosana* dealt mainly with reforestation, land reclamation (Wu and Chen, 1989) and soil fertility improvement (Lee, 1986; Tang *et al.*, 1992). However, little is known about the genetic structure of formosan alder as compared with those species in other temperate areas (Bousquet *et al.*, 1987a, b, c; Bousquet *et al.*, 1988, 1990; Bousquet and Lalonde, 1991; Ager *et al.*, 1993). There was a study of the genetic variation of formosan alder dealt with early growth rate analyses (Chiang and Wang, 1986). The results from quantitative analyses indicated that the mean values of seedling growth differ significantly between the parent trees and seed sources. The results indicated that the genetic variabilities within and among populations in *A. formosana* may occur.

In terms of population genetics, life histories and ecological features contributed to the genetic structure of plant species. The distribution of genetic variation is determined by the

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breeding system, the amount of gene flow and the intensity of natural selection in plant populations. For woody angiosperm whose flowers and seeds are pollinated and dispersed by wind, the gene flow is expected to be extensive (Loveless and Hamrick, 1984; Hamrick, 1989; Hamrick and Godt, 1990). This is particularly true for alder species. For example, the genetic structure of green alder (*Alnus crispa*) and speckled alder (*A. rugosa*) among populations in central Quebec showed little genetic differentiation (F_{ST}=0.05) (Bousquet *et al.*, 1987a, 1988).

To understand the distribution and level on genetic variation of *A. formosana*, isozyme data were analyzed to examine the degree of microdifferentiation in local populations. In this study, we have examined the distribution of genetic variation of the species among the natural populations in Taiwan and the extent of genetic differentiation among various populations within different vegetation zones.

MATERIALS AND METHODS

Twenty-two populations along three transects were sampled (Fig. 1, Table 1). The localities and elevations of sampling sites were summarized in Table 1. Three transects, i. e., northern Taiwan, central Taiwan and southern Taiwan were selected for sampling. Of the twenty-two sampling sites studied, eight were sampled from northern Taiwan (1 - 8), eight from central Taiwan (9 - 16) and six from southern Taiwan (17 - 22). The selected transects were tested for the correlation between genetic differentiation and the linear geographic distance.

Based on Su's (1984a, b, 1992) classification, the distribution of forest in Taiwan can be divided into seven altitudinal vegetation zones ranging from lowland to alpine. Three of the sampling sites in this study are located at lowland with an elevation less than 500 m, six populations of 500 to 1,500 m. Meanwhile, eight populations are sampled at an elevation of 1,500 to 2,000 m and five of 2,000 to 2,500 m. These groupings were not only selected to test whether the level of genetic differentiation is associated with the vertical stratification of habitat types which correspond to temperature gradients, but to examine the distribution of the genetic diversity.

Leaf samples were acquired in the spring of 1994. The leaves were collected from ca. 30 mature adult canopy trees within each population. The minimum distance between individuals was 10 m. The standard protocols for allozymes analysis was used (Soltis *et al.*, 1983). Leaf tissue was extracted by Tris buffer (Bousquet *et al.*, 1987a). The methods of interpretation of allozymic banding patterns and protein identification were developed by Gottlieb (1977, 1981) and Kephart (1990).

Fifteen surveyed enzymes included acid phosphatase (ACP, EC 3.1.3.2), cytosol aminopeptidase (CAP, EC 3.4.11.1), esterase (EST, EC 3.1.1.-), fructose-biphosphatase (FBP, EC. 3.1.3.11), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), isocitrate dehydrogenase (IDH, EC. 1.1.1.42), malate dehydrogenase (MDH, EC 1.1.1.37), malate dehydrogenase($NADP^+$) (MDHP, EC 1.1.1.40), menadion reductase (MDR, EC 1.6.99.2), peroxidase (PER, EC 1.11.1.7), phosphogluconate dehydrogenase (PGDH, EC 1.1.1.44), phosphoglucomutase (PGM, EC 2.7.5.1), shikimate dehydrogenase (SKDH, EC 1.1.1.25), superoxide dismutase (SOD, EC 1.15.1.1), and triose-phosphate isomerase (TPI, EC 5.3.1.1) (Soltis *et al.*, 1983; Murphy *et al.*, 1996).

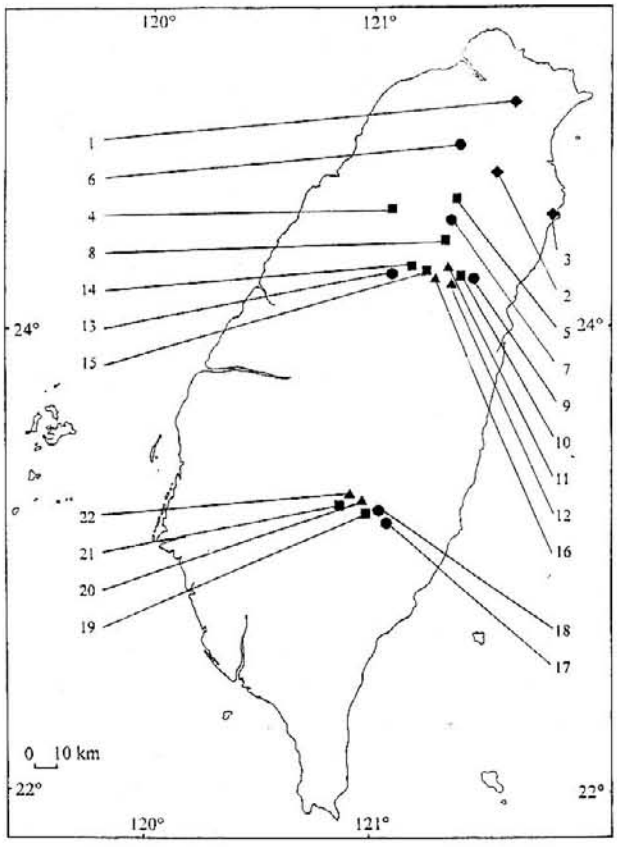

Fig. 1. Locations of populations sampled in this study. The numerical order for each symbol corresponds to population number in Table 1. ◆ < 500 m, ● 500 ~ 1500 m, ■ 1500 ~ 2000 m, ▲ 2000 ~ 2500 m.

Table 1. Locations of 22 populations of *Alnus formosana* in Taiwan.

Population No.	Location & Sample Size	Elevation (m)
1	Shih-ting (31)	310-530
2	Sung-lo (32)	170
3	Wu-shih Pi (30)	150-290
4	Kuan-wu (30)	1900-2000
5	Yuan-yang Hu (27)	1610
6	Pei-heng (27)	500-800
7	Nan Shan (31)	1300-1410
8	Ssu-yuan (30)	1650-1730
9	Lo-chao (24)	1200-1230
10	Sin-pal-yang (25)	1620-1730
11	Pi-lu (25)	2130-2230
12	Kuan-yuan (28)	2374
13	Ching Shan (27)	1140-1350
14	Li Shan (22)	1850
15	Ho-huan (18)	1950-2000
16	Sung-chuan Kan (30)	2250-2265
17	Li-tao (22)	900-1000
18	Mo-tein (26)	1350-1380
19	Li-yuan (27)	1680
20	Hsian-yang (23)	2312-2350
21	Li-kuan (28)	1650-1800
22	Tien-chih (30)	2370-2400

Allelic variation was analyzed using the program BIOSYS-1 (Swofford and Selander, 1989). For each population, the mean number of alleles per locus, the effective number of alleles per locus, the percentage of loci polymorphic, the expected and observed mean heterozygosity value (H_E and H_O) were computed. Chi-square test, *F*-statistics (Wright, 1965), Nei's genetic distance (Nei, 1972, 1978) and gene flow rate measure (Wright, 1931, 1943) were used to estimate population subdivision. The *F*-statistics (F_{XY}) for each level of the hierarchical analysis, the total gene diversity (H_T), the diversities within populations (H_C), within altitudes (D_{CS}) and among altitudes (D_{ST}) for each population, altitude transect and the total population levels were also calculated (Wright, 1978; Nei, 1973, 1977). An estimate of linkage disequilibrium for each possible pairwise comparison of polymorphic loci and chi-square tests for significance (Weir, 1979) was calculated using POPGENE (Yeh and Boyle, 1996).

RESULTS

Of all the fifteen enzymes analyzed, seventeen loci were found polymorphic. The mean number of alleles per locus (A) was 1.8 and the effective number of allele per locus (A_E) 1.21. The proportion of polymorphic loci (P) was 59.1% with H_O and H_E values of 0.181 and 0.175, respectively. The difference between the observed and expected values was not statistically significant ($p > 0.05$) (Table 2).

Inbreeding coefficients within population was negative (F_{IS} = -0.057). The result showed that the observed heterozygotes were in excess. The excessive heterozygotes were found in SOD, PER and MDR loci. The fixation index in overall populations was found barely below zero (F_{IT} = -0.017). The data revealed that most of the genotypes of formosan alder were distributed randomly in the populations studied (Table 3). The outcrossing rate for the species was estimated to be 0.956 ($\pm$0.013) with seven loci using Ritland's program (1990). Seven significant linkage pairs ($p < 0.05$) were observed for *Alnus formosana* (the pairs: *Cap – Pgm-1*, *Gpi-2 – Gpi-3*, *Gpi-2 – Est-3*, *Gpi-3 – Est-1*, *Gpi-3 – Acp-2*, *Gpi-3 – Acp-3*, *Pgm-1 – Gpi-1*). Significant disequilibria were found in thirteen of the twenty-two populations in which this combination of loci was studied.

The genetic structure of *A. formosana* in Taiwan was found poorly differentiated (F_{ST}= 0.038). The estimated F_{ST} value indicates that the amount of gene flow was high (average Nm = 6.329). The genetic diversity analysis indicated that ninety-eight percentage of the genetic variability occurred within populations as indicated by H_C values, and only two percentage among populations (Table 3). To examine patterns of various scale genetic structures, hierarchical analyses were used to specify population structure in different vegetation zones. Variance components of each hierachical arrangement of populations were shown in Table 4. It was found that the values of F-statistics at each hierarchy level was low (0.003 to 0.020). The genetic distance was found between 0.000 and 0.019 for pairwise comparisons between populations, and 0.000 to 0.007 between altitude transects. The results indicated that the difference in allele frequency between vegetation zones of the formosan alder forest was low (Table 5). Besides, of the seventeen surveyed polymorphic loci, the allele frequencies of *Sod*, *Pgm-1*, *Pgm-2* and *Est-1* were significantly different among vegetation zones and the genetic variations was associated with the elevation differences. Furthermore, the cline of allele frequency over elevational transect can be clearly demonstrated (Tables 6 & 7).

Table 2. Genetic variability at 23 loci in all populations (standard errors in parentheses).

Population no.	Mean sample size per locus	Mean no. of alleles per locus	Mean effective no.of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity	
					Direct-count	HdyWbg expected**
1	29.9	1.6	1.19	43.5	.180	.158
	(.4)	(.2)			(.059)	(.044)
2	31.7	1.7	1.21	56.5	.201	.171
	(.1)	(.2)			(.062)	(.046)
3	29.3	1.7	1.19	47.8	.165	.163
	(.2)	(.2)			(.056)	(.046)
4	29.0	1.9	1.22	60.9	.169	.178
	(.3)	(.2)			(.049)	(.045)
5	26.5	2.0	1.24	65.2	.185	.193
	(.2)	(.2)			(.049)	(.048)
6	26.6	1.9	1.19	60.9	.161	.163
	(.2)	(.2)			(.047)	(.043)
7	30.5	1.8	1.21	60.9	.182	.172
	(.2)	(.2)			(.057)	(.046)
8	29.6	1.9	1.23	60.9	.194	.186
	(.2)	(.2)			(.053)	(.046)
9	23.7	1.8	1.22	52.2	.185	.183
	(.1)	(.2)			(.057)	(.046)
10	24.6	1.7	1.19	56.5	.175	.162
	(.2)	(.1)			(.050)	(.040)
11	24.6	1.9	1.20	60.9	.164	.164
	(.2)	(.2)			(.047)	(.041)
12	26.9	1.8	1.19	60.9	.167	.163
	(.3)	(.2)			(.047)	(.042)
13	26.3	1.8	1.24	60.9	.209	.195
	(.2)	(.2)			(.057)	(.044)
14	22.0	1.7	1.20	60.9	.193	.170
	(.0)	(.1)			(.056)	(.045)
15	17.8	1.7	1.21	52.2	.171	.173
	(.1)	(.2)			(.055)	(.046)
16	28.3	2.0	1.24	69.6	.189	.192
	(.5)	(.2)			(.054)	(.046)
17	21.5	1.8	1.22	65.2	.207	.183
	(.2)	(.1)			(.057)	(.046)
18	25.5	1.7	1.21	60.9	.174	.175
	(.2)	(.1)			(.051)	(.044)
19	26.6	1.8	1.22	65.2	.183	.179
	(.2)	(.2)			(.053)	(.046)
20	22.9	1.9	1.21	60.9	.179	.172
	(.1)	(.2)			(.056)	(.047)
21	26.0	1.9	1.22	60.9	.171	.178
	(.5)	(.2)			(.050)	(.044)
22	27.7	1.8	1.21	56.5	.175	.171
	(.5)	(.2)			(.053)	(.047)
Mean	26.3	1.8	1.21	59.1	.181	.175
	(.7)	(.0)			(.003)	(.002)

* A locus is considered polymorphic if the frequency of the most common allele does not exceed .99

** Unbiased estimated (see Nei, 1978)

Table 3. Result of the Chi-square contingency test, F-statistics, gene flow and gene diversity at polymorphic loci in 22 populations of *Alnus formonsana* in Taiwan.

Locus	Chi-square	F_{IS}	F_{IT}	F_{ST}	$Nm^{(1)}$	$H_T^{(2)}$	$H_C^{(3)}$	$D_{CS}^{(4)}$	$D_{ST}^{(5)}$
Cap	36.463*	.156	.181	.030	8.083	.18270	.18047	.00256	-.00033
Skdh	22.758	- .058	- .036	.021	11.655	.06681	.06666	.00035	-.00020
Sod	53.814***	- .422	- .355	.048	4.958	.41254	.40029	.00737	.00488
Per	8.966	- .348	- .338	.007	35.464	.49803	.49866	.00000	-.00063
Pgm-1	70.307***	.544	.576	.071	3.271	.61531	.61531	.01973	.00000
Pgm-2	131.249***	.480	.502	.043	5.564	.12348	.12348	.00254	.00040
Gpi-1	31.400	-.081	-.053	.026	9.365	.09494	.09415	.00000	.00079
Gpi-2	61.063*	-.098	-.067	.028	8.679	.26759	.26525	.00364	-.00130
Gpi-3	109.343***	-.121	-.079	.038	6.329	.49868	.48937	.01251	-.00320
Mdh-1	42.684**	-.056	-.019	.035	6.893	.03594	.03535	.00053	.00005
Est-1	140.462***	.051	.092	.043	5.564	.50741	.49533	.01277	-.00069
Est-3	131.293***	.211	.262	.065	3.596	.12813	.12240	.00552	.00021
Tpi-2	55.929***	-.061	-.012	.047	5.069	.02277	.02214	.00074	-.00011
Pgdh-2	31.463	.438	.454	.027	9.009	.06803	.06740	.00076	-.00013
Mdr	88.110*	-.513	-.484	.019	12.908	.51321	.51367	.00048	-.00094
Acp-2	27.267	- .051	- .026	.024	10.167	.04917	.04888	.00018	.00011
Acp-3	17.131	- .019	- .004	.015	16.416	.00848	.00850	.00000	-.00002
Total	1159.702***					4.09322	4.01153	.06969	.01200
Percentage							98.01 %	1.70 %	0.29 %
Mean		- .057	-.017	.038	6.329	0.241	0.236	0.004	0.001

* $p < .05$, ** $p < .01$, *** $p < .001$

(1) $F_{ST} = 1 / (1 + 4Nm)$

(2) H_T: total gene diversity (= total limiting variance)

(3) H_C: gene diversity within populations (= total limiting variance minus variance component-population-total)

(4) D_{CS}: gene diversity within altitudes (= variance component-population-altitude)

(5) D_{ST}: gene diversity among altitudes (= variance component-altitude-total)

Table 4. Variance components and F-statistics combined across loci.

Comparison		Variance component	F_{XY}
X	Y		
population	– altitude	.06969	.017
population	– total populations	.08169	.020
altitude	– total populations	.01200	.003

Table 5. Matrix of genetic distance coefficients between four vegetation zones in elevational transects of *Alnus formosana*.

	Altitude (m)	1	2	3	4
1	< 500	–			
2	500 ~ 1500	.002	–		
3	1500 ~ 2000	.005	.000	–	
4	2000 ~ 2500	.007	.001	.000	–

Table 6. Allele frequencies of four polymorphic loci with significant Chi-square value at four elevational transects of *Alnus formosana*.

Locus	Elevational transect (m)	Allele frequency A	B	C	D	Chi-square
Sod	< 500	.418	.582			22.373***
	500~1500	.321	.679			
	1500~2000	.272	.728			
	2000~2500	.221	.779			
Pgm-1	< 500	.624	.129	.247		67.999***
	500~1500	.500	.327	.173		
	1500~2000	.426	.426	.148		
	2000~2500	.422	.469	.109		
Pgm-2	< 500	.000	.011	.925	.065	24.284**
	500~1500	.013	.045	.896	.045	
	1500~2000	.005	.015	.960	.020	
	2000~2500	.008	.023	.953	.016	
Est-1	< 500	.553	.435	.012		45.575***
	500~1500	.617	.370	.013		
	1500~2000	.630	.344	.026		
	2000~2500	.574	.320	.107		

** $p < .01$, *** $p < .001$

Table 7. Coefficient of determination (R-square) between allele frequency and elevation.

Locus	R-square Allele	A	B	C	D
Sod		1.000	1.000		
Pgm-1		0.948	0.982	0.996	
Pgm-2		0.270	0.040	0.304	0.950
Est-1		0.180	0.994	0.575	

DISCUSSION

The genetic variation of *Alnus formosana* at the population level (H_E= 0.175) is higher than the average heterozygosity of woody plants (0.149, Hamrick and Godt, 1990) and other alders in the temperate zone in which H_E for *A. crispa*, *A. rugosa* and *A. sinuata* were 0.140, 0.160 and 0.160, respectively (Bousquet *et al.*, 1987a,b, 1988; Bousquet *et al.*, 1990). The overall expected diversity value (H_T) of *A. formosana* is 0.241, which is higher than that of *A. rugosa*, *A. sinuata* and *A. crispa* (0.110 - 0.170, Bousquet and Lalonde, 1991).

Of the investigated twenty-two natural populations of *A. crispa* across Quebec, Canada using sixteen genetic loci, Bousquet *et al.* (1987a) obtained similar values of heterozygosity and found that nearly all of populations were in Hardy-Weinberg equilibrium. Also the mean outcrossing rate of eight loci was estimated to be 0.95 . Meanwhile, there was no genetic differentiation among the populations in all the alder species studied (F_{ST} = 0.04-0.05). A low value of F_{ST} implied that the selection due to the spatial and elevation distribution did not influence the population genetic structure of *Alnus* species.

Predominant outcrossing of *A. formosana* can be manifested by the negative value of

inbreeding coefficient (F_{IS} = -0.057) and the high outcrossing rate (t = 0.956). Linkage was observed in seven pairs of loci studied in formosan alder. These loci also showed departures from Hardy-Weinberg expected frequencies. Pairwise linkage disequilibrium can reveal selection operating on pairs of genes (Hartl and Clark, 1989). Furthermore, some factors that were found to contribute to the departure from Hardy-Weinberg proportion at the single locus level also affected the linkage disequilibrium (Roberds and Brotschol, 1985). These factors for the natural populations of formosan alder remained to be identified.

Comparison of variance components in each altitude transect indicated that the level of variance within population was higher than those within and among transects (Table 4). Also, the gene diversity analysis showed that the proportion of genetic variability among populations was less than two percent. Most of the genetic variability occurred within populations (Table 3). The results were consistent with the fact that high levels of genetic variations distributed within the population rather than among populations of the wind - pollinated trees (Hamrick and Godt, 1990). The genetic differentiation among populations (F_{ST} = 0.038) and the distribution of genetic diversity among populations were low, and the level of gene flow among populations was high (Nm = 6.329). Kimura and Maruyama (1971) demonstrated that populations will be strongly differentiated if Nm is much less than 1 and they behave as a single panmictic unit if the value is higher than 4. The results of this work indicated poor genetic differentiation and high rates of gene flow in all the formosan alder populations studied. The genetic distances between the populations or different vegetation zones were also found low. Wind dispersal of the small winged seed and pollen over relatively long distances should contribute significantly to the absence of subpopulation structure and the random union of gametes within population. Moreover, we have found that the genetic differentiation among different elevational transects were much lower than that among the populations studied (0.003 vs. 0.020) and ninety-eight percentage of the total genetic diversity occurred within the population. Thus, the formosan alder populations investigated seem to be a member of the larger homogeneous panmictic population.

Nevertheless, of the seventeen polymorphic loci surveyed, the allelic frequencies of seven loci are significantly different between elevational transects. And four of them, *Sod*, *Pgm-1*, *Pgm-2* and *Est-1*, showed allelic and genotypic frequencies change along the altitude gradient. In general, the favorable alleles increase in frequency in the population and more of the fitter genotypes are formed. The types and frequencies of alleles in the population will change gradually so as to promote greater adaptation to the environment (Hartl and Clark, 1989). The result of this work implied that the force of natural selection through climatic variables exerted on these loci. Because of the selectivity within the vegetation zones, a great amount of genetic variations existed within the formosan alder population. Furthermore, both microgeographic differentiation and genotypic differentiation were reportly correlated, clines of gene frequency over elevational transects were revealed in a number of conifer species at some loci (Bergmann, 1978; Mitton *et al.*,1980, 1989; Moran and Adams, 1989). Although formosan alder populations in different vegetation zones may have their specific genetic patterns as a result of microgeographic variations, there is a substantial mixing of genetic sources through pollen and seed dispersal. The possible ecological and life-history natures may contribute to maintaining the high level of genetic variability and low level of genetic differentiation in formosan alder.

This study provides preliminary knowledge for further understanding the relationship within the population of formosan alder forest. The information gives valuable genetic insight into the species that provides practical knowledge for forest conservation programs.

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臺灣赤楊族群遺傳變異性之研究

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摘　　要

臺灣赤楊(*Alnus formosana* (Burk.) Makino)，為落葉樹種，在臺灣地區分布很廣，由低海拔至中高海拔山區均有其蹤跡。本研究是利用澱粉膠體電泳探討臺灣赤楊二十二個族群之遺傳結構，共檢視十五種同功酵素，其中多型性基因座約佔 59.1 %，每一基因座之有效對偶基因數為 1.21；族群間的歧異度為 0.02，族群間的遺傳距離由 0.000 到 0.019，平均為 0.004。臺灣赤楊族群間分化的程度很低，可能是由於其花粉和種子均是靠風力傳播，以致族群間有大量的基因流傳而使遺傳變異性呈現均質化的分佈。此外，由實驗結果中發現有四個基因座其對偶基因的頻率與海拔梯度有顯著的相關性，顯示臺灣赤楊的遺傳變異性可能與高低海拔棲地的溫度差異有關。

關鍵詞：臺灣赤楊，同功酵素，對偶基因頻率，遺傳歧異度，基因流傳，遺傳變異性，海拔梯度。

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