Research paper

No Clinal Variation in *Cunninghamia lanceolata* Wood Density Sampled from Thirteen Chinese Provinces

Jenq-Chuan Yang,[1,5] Chih-Ming Chiu,[2] Tsan-Piao Lin,[3] Fan-Hao Kung[4]

【Summary】

Seeds of China-fir were obtained from 42 provenances in 13 provinces of China. Height and diameter were measured at the ages of 11, 16, and 18 years. Wood density samples were taken by increment core at breast height and were assessed by the water displacement method. Isozyme frequencies of PGI, SKDH, and 6PGD were observed from electrophoresis. Wood density ranged from a high of 0.310 in Jiangsu Province to a low of 0.273 in Guizhou Province in southwestern China. The China-fir in these 2 provinces differed from those of their neighboring Provinces. Correlation between density and isozyme frequency was not significant for SKDH and 6PGD; it was weak for PGI. Since there were no linear geographic or climatic trends detected, random variation due to local factors appears to be a suitable description for wood density in China-fir.

Key words: provenance test, geographic variation, isozyme, wood property.

Yang JC, Chiu CM, Lin TP, Kung FH. 2001. No clinal variation in *cunninghamia lanceolata* wood density sampled from thirteen Chinese provinces. Taiwan J For Sci 16(2):65-80.

研究報告

源自中國十三省之杉木木材密度無連續性變異

楊政川[1, 5] 邱志明[2] 林讚標[3] 孔繁浩[4]

摘 要

杉木種子來自中國13省區之42個種源。樹高與胸徑生長資料分別於11，16及18年生時測定而得。生長木軸取自胸高部位，並應用排水法以測析木材密度。另以電泳技術測得PGI 、SKDH及6PGD等同功酶之頻率。木材密度最大值為0.310 ，來自江蘇省，而最小值為0.273 ，來自中國西南的貴州省。這兩個省區之密度值分別與其相鄰省區者比較，均有差異。木材密度值與SKDH及6PGD二同功酶頻

1) Director-General, Taiwan Forestry Research Institute. 53 Nanhai Rd., Taipei 100, Taiwan. 行政院農業委員會林業試驗所所長室， 100台北市南海路53號。

2) Divisions of Forest Management, Taiwan Forestry Research Institute. 53 Nanhai Rd., Taipei 100, Taiwan. 行政院農業委員會林業試驗所經營系，100台北市南海路53號。

3) Divisions of Forest Silviculture, Taiwan Forestry Research Institute. 53 Nanhai Rd., Taipei 100, Taiwan. 行政院農業委員會林業試驗所育林系，100台北市南海路53號。

4) Dept. of Forestry, Southern Illinois Univ. Carbondale, IL 62901-4411, USA. 美國南伊利諾州立大學森林系

5) Corresponding author 通訊作者

Received February 2001, Accepted April 2001. 2001年2月送審 2001年4月通過

率並無顯著之相關性存在，但與 PGI 同功酶卻顯出微弱之相關關係。由於無法測得直線型地理或氣候趨向之變異，我們認為杉木之木材密度係因地域局部因素而致呈現逢機型變異。

關鍵詞：種源測驗、地理變異、同功酶、木材性質。

楊政川、邱志明、林讚標、孔繁浩。2001。源自中國十三省之杉木木材密度無連續性變異。台灣林業科學 16(2)：65-80。

INTRODUCTION

Species with widespread ranges normally should have a higher level of diversity than more narrowly distributed species (Hamrick et al. 1990). As the distribution range increases, a species will encounter greater differences in ecological limiting factors. Geographic variation is then the result of long-term adaptation of a species to various selection pressures it has encountered.

Cunninghamia lanceolata (Lamb.) Hook. is one of the most important conifers growing in southern China. The geographic distribution center is near the Nanling Mountains and this species covers 13°of latitude (from 21°41' to 34°03'), 10° of longitude (from 101°30' to 121°53'), and 1,800 m of elevation (Yu 1996). The species has been cultivated for more than 2000 years by the local people for its different characters (Chen and Shi 1987). Because of the diversity of sites and climates where it is found, China-fir shows great geographic variation in tree height and diameter growth. Trees from the southern and the eastern provenances grow faster than those of the western and northern ones. However, none of the characteristics of needles, cones, or seeds were related to the latitude and longitude of the seed source (Yu 1996). At the age of 10 years, tree height, diameter, and volume growth of 42 China-fir provenances tested in 41 plantations were correlated with mean annual temperature and January temperature, but not with July temperature, nor with mean annual precipitation (Li 1994). However, the range-wide geographic variation of wood density in China-fir has yet to be studied.

Density is one of the most important of a wood's properties (Van Buijtenen 1982). For many years it was recognized that tree form and growth rates could all affect wood in several ways, so Zobel (1963) suggested that trees should be selected first for form, growth habits, pest resistance, volume, and finally for wood density. Selection for wood density is possible because heritability of wood density is moderate to high among many species (Zobel 1961, Stonecypher and Zobel 1966, Rozenberg and Cahalan 1997). Selection may be at the clonal level, for example, clonal variations in wood density are significant in aspen (Yanchuk et al. 1983); or, at the racial level, for example, geographic variations have been found among southern pines (Zobel and Van Buijtenen 1989). However, we need to be careful when looking at differing clones or races because density may also be controlled by site as well as by environmental and genetic interactions. For example, using subsets of 4 *Pinus oocarpa* and 5 *P. patula* subsp. *tecunumanii* provenances, Wright (1990a) assessed density at 1 site in each of Puerto Rico, Ecuador, Brazil, Zambia, South Africa, and Kenya. He found significant differences in density between sites ($p < 0.001$) and between provenances ($p < 0.05$). The site-by-provenance interaction term was not significant. In a similar study using 1 provenance of *P. caribaea* and 4 provenances of *P. patula* subsp. *tecunumanii*, Wright and coworkers found significant variations of stem volume and wood density at Nzoia, Kenya (Wright et al. 1992). Again, using 11 provenances of *Pinus caribaea* var. *hondurensis* at a total of 11 sites (in Puerto Rico, Zambia, Congo, Côte d'Ivoire, South Africa, Malaysia, Fiji, and Australia), analysis of variance revealed significant differences ($p < 0.001$) between sites and provenances for density, with site accounting for more of the variance than did provenance. The site-by-provenance interaction term was not statistically significant and accounted for none of the variance. However, when provenances were grouped, he found no significant differences between coastal and island provenances (Wright 1990b).

Wood density may be related to geographic races. For example, in Jack pine, *P. banksiana*, the northerly sources produced the highest specific gravity (King 1967). Remrod (1976) also found that northern provenances of *P. sylvestris* produced trees with a higher wood density in northern Sweden. On the contrary, Stahl found in the same species that the northern sources had lower basic density when grown in Sweden (Stahl et al. 1986). In *P. caribaea* var. *hondurensis*, Wright (1990b) found that trees in coastal provinces had lower wood density than those in inland ones. On the other hand, wood density may not be related to geographic races. For example, Rink and Thor (1973) found that specific gravity in *P. virginiana* was not affected by seed sources. Therefore, the objective of this paper is to test whether wood density in China-fir differs among the 13 southern provinces of China.

Instead of ecotypic variation, specific density may also display a clinal variation. Differences in wood density were evident among sources of *P. taeda* from Maryland to Texas (Strickland 1960). Strong correlations were found between density and latitude ($r = 0.98$) and between density and longitude ($r = 0.95$). Although Wright (1990 b) found that trees with low density were mainly from sites at a higher elevation (1,000 m), he did not indicate how density was related to other variables of the seed sources. Because geographic variation of wood density among provenances of China-fir has not been related to the effect of latitude and longitude, we decided to test the correlation between wood density and geographic variables.

Correlations of allelic frequencies with geographic and environmental variables are documented in conifers (e.g., Yeh and Layton 1979, Xie et al. 1992). Yet, a study based on 16 southeastern populations of China-fir showed that genetic variability did not correlate with geographic or climatic variables of those populations (Yeh et al. 1994). It would be interesting to know whether wood density in China-fir is correlated with genetic variables of the seed source, so that we may use such genetic information to screen for better seed origin.

Wood density usually decreases as growth rate increases; the correlation is weak but statistically significant (Beaudoin et al. 1992). On the other hand, Lee (1979) found no significant correlation between growth and wood properties in 27 black pine seed sources. In coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), it is possible to obtain substantial gains in bole volume without loss in (or even with a modest increase in) wood density (Vargas-Hernandez and Adams 1991). Therefore, we need to study the relation between growth and density among seed sources in China-fir to see if it is possible to select both traits independently at the same time.

It is well known that evidence of the environmental factors which modify the physiological and growth processes in trees is permanently deposited in the structure of the biomass being produced (Fritts 1959). By building growth rings, trees literally monitor the environmental status (Fritts 1966). Accordingly, the structure of tree rings allows the detection of captured climatic variations (Fritts 1960). This variability in the structure of tree rings that quantify the radial growth of stems has been studied by experts in the fields of dendrochronology, dendroclimatology, and dendroecology for a long time (Fritts 1972). The data thus obtained are analyzed and used for assessment of the tree-ring structure response to fluctuations in climate (Fritts and Shashkin 1994). However, it is not well know whether such acquired characteristics of tree-ring structure are inheritable. In the study we also test the correlation between wood density and climate factors among provinces of China where China-fir grows.

MATERIALS AND METHODS

The Taiwan Forestry Research Institute has obtained seeds of China-fir from 42 provenances in 13 provinces of China (Yang et al. 2000). The Lienhwachih plantation for China-fir was established on 14 May, 1981. The plantation is located at 23.56 ° N, 120.54 ° E at an elevation of 744 m. A randomized complete block design with 6 replicates was used. There were 4 trees per plot, and the spacing was 2 × 2 m.

Phenotypic measurements obtained from the provenance tests were growth and wood density. Growth measurements included total height (H) and diameter at breast height (D) at the ages of 11, 16, and 18 years. For wood density measurement, a 0.45-cm increment core was extracted at breast height on the upper slope, because it has been shown for conifers that breast height sampling is generally satisfactory for evaluating wood density for the entire tree (Zobel and Van Buijtenen 1989). It is well known that wood density varies within a tree. Wood density tends to be high at the bottom of the tree, decreasing to a minimum at mid height, then increasing again near the top of the tree (Vargas-Hernandez and Adams 1991). They also found that in the radial direction, wood density is high near the pith (at all heights), decreasing, then increasing again in the mature wood zone (after rings 15-20+). Overall density is positively correlated with intra-ring density variation ($r = 0.72$) and negatively correlated with bole volume ($r = -0.52$) (Vargas-Hernandez and Adams 1991). Therefore, our sample of the outer 5 rings from the increment core may not give us a true reading of the whole tree density, but it is an effective indirect measurement of specific gravity, and it causes minimal tree damage (Lee and Wahlgran 1979). Density of the extracted sample was determined by the water displacement method according to Smith (1954).

Genotypic measurements were obtained by means of isozyme analysis. We collected shoot tips of current-year needles from each provenance. The leaf tissues were stored in a cooler kept at 4℃. and the collection was transported to the laboratory on the same day. Sample preparation, isozyme extraction, and electrophoresis followed standard procedures used in the past (Lin et al. 1993, 1994). Three isozyme systems were used for the study: phosphoglucose isomerase (PGI, EC 5.3.1.9), shikimate dehydrogenase (SKDH. EC 1.1.1.25), and 6-phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44). Segregation band patterns were interpreted to yield estimates for gene (allelic) frequency.

Geographic variables of seed sources used in the study were longitude, latitude, and elevation. These variables were found to be useful in developing a physiographic model for inland Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) (Campbell 1991, Rehfeldt 1991), and in the study of frost resistance and early growth of *Sequoiadendron giganteum* seedlings (Guinon et al. 1982). Climatic data about the seed source, were mean annual temperature (Mat), January mean temperature (Jant), July mean temperature (Jult), and annual precipitation (Pps). These variables were useful in defining *Cryptomeria japonica* seed sources for Taiwan (Yang et al. 1998). A combination of geographic and climate variables was previously used for a study of cold-hardiness of *Fraxinus americana* stem tissue (Alexander et al. 1984).

The software, Statistical Analysis System (SAS 1985), was used for data processing. A preliminary statistical analysis indicated that the block effect was not significant for wood density, therefore, we deleted this classification variable from the analysis of variance model. The entire experiment for testing density variation in 13 provinces was analyzed by a hierarchical model, nesting seed sources within provinces (Table 1). We also used a so-called "planned individual degree-of-freedom comparison of means in analysis of variance" (Sokal and Rohlf 1995) to test the high-density and low-density provinces against their neighbors (Table 1). The secondary statistical analysis included simple correlation analysis, canonical correlation analysis, and multiple regression analysis (Tables 2-8). The canonical correlation is useful for indicating the relationship between density and the whole group (e.g., growth), while the simple correlation can indicate the relationship between density and a given individual variable (e.g., height at age 11) within a group. For the correlation and regression analysis, we used province means as observations. Although there is no reason why adaptation should follow administrative borders, we used province means instead of provenance means because in a previous paper we found that growth among provinces was significant but growth among provenances within a province was not significant (Yang et al. 2000).

RESULTS AND DISCUSSION

Wood density ranged from 0.310 in Sichuan and Jiangsu Provinces to 0.273 in Guizhou Province in southwestern China (Table 6). In order to visualize geographic variation through a thematic map, we plotted standardized scores of density (e.g., Z-score = (province mean density − 0.28827) / 0.01207) on the map of southern China (Fig. 1). No consistent trends or patterns are evident from the thematic map. Clearly, we may consider that Jiangsu Province at the upper right corner of the map is unusual, because density scores of the other 5 southeastern provinces (Anhui, Zhejiang, Jiangxi, Fujian, and Guangdong) were all below average. When tested by analysis of

Table 1. General linear model for wood density in China-fir, with seed sources (SS) nested within a state and with planned individual degree-of-freedom comparison of means. The 1st contrast is for the Jiangsu seed sources against a group of southeastern seed sources in Anhui, Zhejiang, Jiangxi, Fujian, and Guangdong Provinces. The 2nd contrast is the Guizhou seed sources against a group of surrounding seed sources in Sichuan, Hunan, Guangxi, and Yunnan Provinces

		DF	Sum of squares	Mean square	*F* value	Pr > *F*
Source	Model	41	0.05628	0.001372	1.51	0.0448
	State	12	0.01893	0.001577	1.74	0.0672
	SS(State)	29	0.03794	0.001308	1.44	0.0893
	Error	117	0.10619	0.000907		
Total		158	0.16247			
			Contrast SS			
Contrast	Jiangsu vs. neighbors	1	0.007221	0.007221	7.96	0.0056
	Guizhou vs. neighbors	1	0.006146	0.006146	6.77	0.0105

Table 2. Canonical structure and correlation between wood density and variables of growth, isozyme, GIS, and weather of the provinces

path	Canonical structure			Simple correlation	
	r	path	*r*	path	*r*
Density-Growth	-0.7290				
		Growth-H11	-0.2694	Density-H11	-0.1964
		Growth-D16	-0.2190	Density-D16	-0.1596
		Growth-H16	0.0686	Density-H16	0.0500
		Growth-D18	-0.3394	Density-D18	-0.2474
		Growth-H18	-0.1037	Density-H18	-0.0756
Density -PGI	-0.8433				
		PGI-*PGIA*	0.2884	Density-PGIA	-0.2432
		PGI-*PGIB*	0.0698	Density-PGIB	-0.0588
		PGI-*PGIC*	0.4027	Density-PGIC	-0.3396
		PGI-*PGID*	-0.2033	Density-PGID	0.1714
		PGI-*PGIE*	0.0642	Density-PGIE	-0.0541
Density-SKDH	0.4482				
		SK-*SK1A*	-0.0779	Density-SK1A	-0.0349
		SK-*SK2A*	-0.3911	Density-SK2A	-0.1753
		SK-*SK2B*	0.8793	Density-SK2B	0.3940
		SK-*SK2C*	-0.3507	Density-SK2C	-0.1571
		SK-*SK2D*	-0.1502	Density-SK2D	-0.0673
Density-6PGD	0.6371				
		6PGD-*6PGDA*	0.6802	Density-6PGDA	0.4333
		6PGD-*6PGDB*	0.0903	Density-6PGDB	0.0575
		6PGD-*6PGDC*	-0.5386	Density-6PGDC	-0.3431
		6PGD-*6PGDD*	0.2105	Density-6PGDD	0.1341
Density-GIS	0.2110				
		GIS-LAT	0.3416	Density-LAT	0.0720
		GIS-LONG	-0.8178	Density-LONG	-0.1725
		GIS-ELEV	0.3999	Density-ELEV	0.0843
Density -Weather	0.3546				
		WEATHER-MAT	0.1284	Density-MAT	0.0455
		WEATHER-JANT	0.2273	Density-JANT	0.0806
		WEATHER-JULT	-0.2253	Density-JULT	-0.0799
		WEATHER-PPS	-0.4795	Density-PPS	-0.1700

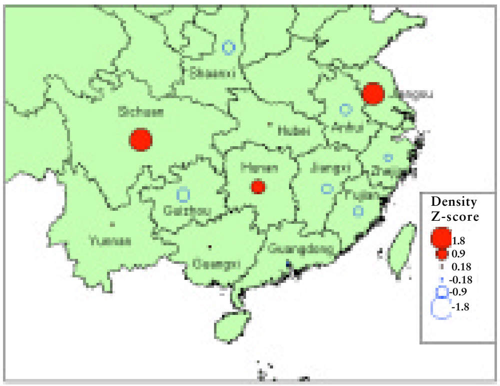

Fig. 1. Thematic map of wood density in China-fir. The Z-score is a standardized score which is the difference between a province mean and the population mean, divided by the standard deviation of province means.

variance, the contrast between Jiangsu and the group of southeastern seed sources was significant at the 0.01 level (Table 1). On the other hand, we may also consider the low density of Guizhou Province to be unusual because its neighbors all had densities higher than the population average. When tested by analysis of variance, the contrast between Guizhou and the group of Sichuan, Hunan, Guangxi, and Yunnan seed sources was significant at the 0.05 level (Table 1). Therefore, we may need to study these 2 odd provinces further in order to confirm whether the superior Jiangsu and the inferior Guizhou seed sources indeed are spe-

Table 3. Mean density, height, and diameter growth of China-fir from 13 provinces, and the result of a regression model using density as the dependent variable

Province	Density	H11	D16	H16	D18	H18
Sichuan	0.310	6.53	11.80	7.82	11.98	8.91
Jiangsu	0.310	6.59	12.72	8.02	13.23	8.77
Hunan	0.302	7.73	13.50	8.81	14.12	10.67
Yunnan	0.291	8.08	15.57	9.66	16.13	9.88
Hubei	0.290	6.67	12.95	7.84	13.94	9.84
Guangxi	0.290	7.82	15.67	10.31	16.14	11.21
Guangdong	0.287	7.55	14.92	8.70	15.96	11.86
Zhejiang	0.282	7.34	13.30	8.43	14.17	10.72
Fujian	0.280	7.89	14.12	8.18	14.77	9.39
Anhui	0.279	5.09	9.46	5.38	10.66	6.29
Jiangxi	0.278	7.65	13.55	8.61	14.39	10.27
Shaanxi	0.277	7.22	13.35	7.97	13.64	9.37
Guizhou	0.273	8.12	15.36	9.35	16.12	10.97

Analysis of variance

Source	DF	Sum of squares	Mean square	*F* value	Prob>*F*
Model	5	0.00093	0.00019	1.587	0.2787
Error	7	0.00082	0.00012		
Total	12	0.00175			

Root MSE = 0.01082 R^2 = 0.5314

Variable	DF	Parameter estimate	Standard error	T for H0: Parameter=0	Prob>|T|
INTERCEP	1	0.3401	0.03178	10.702	0.0001
H11	1	-0.0120	0.01070	-1.130	0.2959
H16	1	0.0117	0.01034	1.136	0.2933
H18	1	0.0026	0.00492	0.538	0.6071
D16	1	0.0117	0.01866	0.630	0.5485
D18	1	0.0174	0.01436	-1.214	0.2641

cial ecotypes of China-fir.

Density of China-fir was not related to any individual factors at the province level. All simple correlations in Table 2 were low and nonsignificant at the 0.05 probability of error, so we can assume that wood density and tree growth are independent in China-fir. This is good news for the China-fir tree improvement program, because now, we can select fast-growing seed sources without the fear that wood density will suffer. However, we may still need to be cautious, because 4 out of the 5 correlations between density and growth had negative signs, and the negative trend is common in many growth-density studies (Vargas-Hernandez and Adams 1991, Beaudoin et al. 1992).

It is unfortunate that none of the enzyme systems we have studied were related to density; otherwise, we might use allelic frequencies of PGI, SKDH, or 6PGD to facilitate selection. It is also regrettable that density in China-fir is independent of latitude, longitude, and elevation of the seed source. Furthermore, we found that weather items such as mean an-

Table 4. Mean density and frequency in pgi from 13 provinces of China-fir, and the result of a regression model using density as the dependent variable

Province	Density	Isozyme frequency				
		PGIA	PGIB	PGIC	PGID	PGIE
Sichuan	0.310	0.000	0.165	0.000	0.830	0.000
Jiangsu	0.310	0.000	0.165	0.000	0.830	0.000
Hunan	0.302	0.042	0.124	0.000	0.832	0.000
Yunnan	0.291	0.063	0.313	0.000	0.475	0.145
Hubei	0.290	0.000	0.208	0.000	0.790	0.000
Guangxi	0.290	0.063	0.313	0.000	0.625	0.000
Guangdong	0.287	0.057	0.250	0.000	0.637	0.057
Zhejiang	0.282	0.017	0.104	0.000	0.836	0.042
Fujian	0.280	0.042	0.292	0.125	0.542	0.000
Anhui	0.279	0.000	0.000	0.000	1.000	0.000
Jiangxi	0.278	0.058	0.291	0.100	0.516	0.033
Shaanxi	0.277	0.000	0.125	0.000	0.875	0.000
Guizhou	0.273	0.042	0.222	0.000	0.735	0.000

Analysis of variance

Source	DF	Sum of squares	Mean square	*F* value	Prob>*F*
Model	5	0.00124	0.00025	3.448	0.0687
Error	7	0.00051	0.00007		
Total	12	0.00175			

Root MSE = 0.00849 R^2 = 0.7112

Variable	DF	Parameter estimate	Standard error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	5.489	1.5073	3.642	0.0083
PGIA	1	-5.132	1.4364	-3.573	0.0091
PGIB	1	-5.204	1.5247	-3.413	0.0112
PGIC	1	-5.273	1.4954	-3.526	0.0096
PGID	1	-5.211	1.5091	-3.453	0.0106
PGIE	1	-5.341	1.5446	-3.458	0.0106

nual temperature, January temperature, July temperature, and precipitation were not useful for studying density variation in China-fir, because there are no significant correlations as shown in Table 2.

Not only does density have no significant correlation with any individual item, it also has no significant relationship with any group collectively. The highest canonical correlation was found between density and isozyme frequency in PGI (r = -0.84), yet it was significant only at the 0.1 level but not at the 0.05 level. Canonical correlations between density and other groups (growth, SKDH, 6PGD, GIS, and weather) were not significant at the 0.1 level. The levels of significance for canonical correlations are not listed in Table 2, but we discuss them in the section on the multiple regression model. It is interesting to point out the path relationship between canonical correlations and simple correlations. This can be expressed as.

Path(density to group) × Path(group to item) = Path(density to item).

Table 5. Mean density and isozyme frequency in SKDH from 13 provinces of China-fir, and the result of a regression model using density as the dependent variable

State	Density	Isozyme frequency				
		SK1A	SK2A	SK2B	SK2C	SK2D
Sichuan	0.310	0.500	0.313	0.313	0.375	0.000
Jiangsu	0.310	0.625	0.125	0.125	0.688	0.063
Hunan	0.302	0.563	0.156	0.250	0.594	0.000
Yunnan	0.291	0.500	0.375	0.063	0.500	0.063
Hubei	0.290	0.444	0.163	0.063	0.775	0.000
Guangxi	0.290	0.688	0.063	0.125	0.813	0.000
Guangdong	0.287	0.458	0.083	0.250	0.667	0.000
Zhejiang	0.282	0.588	0.285	0.079	0.634	0.000
Fujian	0.280	0.475	0.408	0.117	0.475	0.000
Anhui	0.279	0.750	0.250	0.000	0.750	0.000
Jiangxi	0.278	0.525	0.175	0.125	0.650	0.051
Shaanxi	0.277	0.503	0.188	0.313	0.500	0.000
Guizhou	0.273	0.583	0.250	0.042	0.625	0.083

Analysis of variance

Source	DF	Sum of squares	Mean square	F value	Prob>F
Model	5	0.00035	0.00007	0.352	0.8660
Error	7	0.00140	0.00020		
Total	12	0.00175			

Root MSE = 0.01413 R^2 = 0.2009

Variable	DF	Parameter estimate	Standard error	T or H0: Parameter=0	Prob > |T|
INTERCEP	1	2.705	8.2629	0.327	0.7529
SKDH1A	1	0.019	0.0535	0.356	0.7322
SKDH2A	1	-2.444	8.2699	-0.296	0.7761
SKDH2B	1	-2.376	8.2517	-0.288	0.7817
SKDH2C	1	-2.436	8.2588	-0.295	0.7765
SKDH2D	1	-2.372	8.2018	-0.289	0.7808

Taking density and height growth at age 11 years for example, we have 0.7290 × (-0.2694) = -0.1964. In other words, the canonical correlation is the largest common denominator among items within a specific group. Therefore, in our study we found that no variables, individually or collectively, could explain the trend of density. Without further study, random error may be the only logical explanation.

Multiple regression analysis also failed to find a suitable model for density using growth, allelic frequency, geographic, or climatic elements as independent variables (Tables 3-8). It is interesting to point out here that R^2 for the multiple regression model is also the square of the canonical correlation for the group of interest. For example, since the R^2 for the regression model in Table 3 is 0.5314, and the canonical correlation between density and growth in Table 2 is 0.7290, we can see that the square of 0.7290 is 0.5314. Furthermore, the probability of the *F*-value for the multiple regression model is the same as the probability of the canonical correlation. The multiple regression model in Table 3 has an *F*-value of 1.587, which is not significant at the 0.05

Table 6. Mean density and isozyme frequency in 6PGD from 13 provinces of China-fir, and the result of a regression model using density as the dependent variable

State	Density	Isozyme frequency			
		6PGDA	6PGDB	6PGDC	6PGDD
Sichuan	0.310	0.083	0.228	0.250	0.438
Jiangsu	0.310	0.125	0.313	0.188	0.375
Hunan	0.302	0.114	0.614	0.063	0.208
Yunnan	0.291	0.148	0.290	0.210	0.350
Hubei	0.290	0.094	0.350	0.150	0.406
Guangxi	0.290	0.000	0.188	0.313	0.500
Guangdong	0.287	0.083	0.417	0.292	0.208
Zhejiang	0.282	0.079	0.242	0.402	0.276
Fujian	0.280	0.075	0.308	0.333	0.283
Anhui	0.279	0.000	0.438	0.438	0.125
Jiangxi	0.278	0.050	0.282	0.458	0.208
Shaanxi	0.277	0.000	0.313	0.188	0.500
Guizhou	0.273	0.109	0.345	0.083	0.457

Analysis of variance

Source	DF	Sum of squares	Mean square	*F* value	Prob>*F*
Model	4	0.00071	0.00018	1.366	0.3269
Error	8	0.00104	0.00013		
Total	12	0.001			

Root MSE = 0.01140 R^2 = 0.4059

Variable	DF	Parameter estimate	Standard error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	-3.202	2.1669	-1.478	0.1777
6PGDA	1	3.628	2.1990	1.650	0.1376
6PGDB	1	3.483	2.1681	1.607	0.1467
6PGDC	1	3.466	2.1627	1.603	0.1476
6PGDD	1	3.497	2.1704	1.612	0.1457

level, so the canonical correlation between wood density and tree growth (*r* = 0.729) in Table 2 is also non-significant. However, the multiple regression coefficient is not the same as the simple correlation coefficient because of the scale factor and the inter-relationship among items in a group. We may point out here that if we had chosen the significance level at 0.1 instead of the commonly used 0.05, then the PGI isozyme system may have been useful in predicting density among the 13 provinces of China-fir "seed origins". All 5 allelic frequencies of PGI were significant for the model, and they are comparable to each other in terms of parameter estimate, standard error, and significance level (Table 4). Since there were significant relations between PGI isozyme patterns and wood strength of *Castanea sativa* (Frascaria et al. 1992), further study is required to show whether density is actually controlled by PGI in China-fir.

Because the combined contribution of latitude, longitude, and elevation to the total variation is less than 0.05 (Table 7), more than 95% of the variance in the geographic modeling of density by provinces is due to random

Table 7. Mean density and geographic data of China-fir from 13 provinces, and the result of a regression model using density as the dependent variable

State	Density	Geographic variables		
		Lat.	Long.	Elev.
Sichuan	0.310	28.83	103.27	1622
Jiangsu	0.310	31.92	118.97	23
Hunan	0.302	27.88	112.21	364
Yunnan	0.291	24.44	104.28	1423
Hubei	0.290	30.31	112.56	302
Guangxi	0.290	24.69	110.34	762
Guangdong	0.287	23.27	112.32	706
Zhejiang	0.282	29.04	119.21	968
Fujian	0.280	27.08	118.28	711
Anhui	0.279	31.53	117.38	475
Jiangxi	0.278	27.77	115.21	366
Shaanxi	0.277	33.17	107.00	504
Guizhou	0.273	26.53	108.96	848

Analysis of variance

Source	DF	Sum of squares	Mean square	*F* value	Prob>*F*
Model	3	0.00008	0.00003	0.140	0.9336
Error	9	0.00167	0.00019		
Total	12	0.00175			

Root MSE = 0.01363 R^2 = 0.0445

Variable	DF	Parameter estimate	Standard error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	0.3219	0.1211	2.658	0.0261
LAT	1	0.0005	0.0014	0.359	0.7281
LONG	1	-0.0004	0.0009	-0.459	0.6569
ELEV	1	0.0000051	0.00012	0.042	0.9677

error. Again, in Table 8, the combined contribution of annual temperature, January temperature, July temperature, and precipitation to density variation is less than 0.13, so that 87% of the variance in the climatic modeling of density is due to random error. Since random error is so prominent, we may now consider differences in density in China-fir as random variations. Such a conclusion may seem to be an exception to the common understanding of geographic variation of forest trees, i.e., that most traits will follow a north-south trend or a wet-dry trend. Although random variation may be a rare occurrence, we may accept it when no geographical or climatic trends can be found. For example, in a study of phenotypic variation in cones and seeds of 15 Spanish provenances of *Pinus sylvestris* from natural stands, the provenances exhibited highly significantly different values for cone size and shape, for seed weight, and the percentages of full, empty, and undeveloped seeds, but there were no geographical or climatic groupings. Thus, random variation due to local factors appeared to explain most of the behavior of these characters in the Spanish provenances of *P. sylvestris*

Table 8. Mean density and climatic data of China-fir from 13 provinces, and the result of a regression model using density as the dependent variable

State	Density	Climatic variables			
		Mat	Jant	Jult	Pps
Sichuan	0.310	16.8	7.2	25.6	1129
Jiangsu	0.310	15.2	2.3	27.7	1030
Hunan	0.302	16.4	4.0	28.2	1493
Yunnan	0.291	16.0	6.9	24.2	1365
Hubei	0.290	15.8	3.3	27.4	1284
Guangxi	0.290	19.6	9.6	28.1	1526
Guangdong	0.287	21.6	12.7	28.6	1784
Zhejiang	0.282	16.4	5.0	28.7	1531
Fujian	0.280	18.2	7.9	28.1	1743
Anhui	0.279	15.1	2.5	28.0	1066
Jiangxi	0.278	16.2	4.0	27.1	650
Shaanxi	0.277	13.2	-0.4	26.6	736
Guizhou	0.273	16.4	5.1	25.9	1321

Analysis of variance

Source	DF	Sum of squares	Mean square	*F* value	Prob>*F*
Model	4	0.00022	0.00005	0.288	0.8780
Error	8	0.00153	0.00019		
Total	12	0.00175			

Root MSE = 0.01382 R^2 = 0.1257

Variable	DF	Parameter estimate	Standard error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	0.2963	0.09215	3.216	0.0123
MAT	1	-0.0012	0.01345	-0.091	0.9296
JANT	1	0.0023	0.00767	0.302	0.7702
JULT	1	0.0010	0.00617	0.170	0.8696
PPS	1	-0.000021	0.000021	-0.988	0.351

(Agundez et al. 1992).

In conclusion, we found no supporting evidence to consider that density variation follows a graded sequence of differences in growth, isozyme frequency, geographic, or climatic issues. Random variation may have caused trees grown from seeds originated in Jiangsu to have a higher and those from
Guizhou to have a lower density than their neighbors.

ACKNOWLEDGMENT

The competitive grant provided by National Science Council (NSC 88-2313-B- 054-014) is gratefully acknoweledged.

LITERATURE CITED

Agundez D, Alia R, Diez R, Gil L, Pardos JA. 1992. Variation of *Pinus sylvestris* in Spain: characteristics of cones and seeds. Investig Agraria Sist Recursos For 1(2):151-62.

Alexander NL, Flint HL, Hammer PA. 1984. Variation in cold-hardiness of *Fraxinus americana* stem tissue according to geographic origin. Ecology 65(4):1087-92.

Beaudoin M, Hernandez RE, Poliquin J, Koubaa A. 1992. Interclonal, intraclonal and within-tree variation in wood density of poplar hybrid clones. Wood Fiber Sci 24(2):147-53.

Campbell RK. 1991. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglasfir in southwestern Oregon. For Sci 37 (4):973-86.

Chen YW, Shi JS. 1987. Genetic variation and improvement program of Chinese-fir. J Nanjing Inst For 4:1-21.

Frascaria N, Chanson B, Thibaut B, Lefranc M. 1992. Genetic diversity and wood mechanical properties of chestnut (*Castanea sativa*). Analysis of one factor concerning ring shake. Ann Sci For 49(1):49-62.

Fritts HC. 1959. The relation of radial growth to maximum and minimum temperatures in three tree species. Ecology 40 (2):261-5.

Fritts HC. 1960. Multiple regression analysis of radial growth in individual trees. For Sci 6(4):334-49.

Fritts HC. 1966. Growth rings of trees: their correlation with climate. Science 154(3752):973-9.

Fritts HC. 1972. Tree rings and climate. Sci Am226(5):92-100.

Fritts HC. Shashkin AV. 1994. Modeling tree-ring structure as related to temperature, precipitation, and day length. In: Lewis TE, editor. Tree rings as indicators of ecosystem health. Boca Raton (FL): CRC Press. p. 17-57.

Guinon M, Larsen JB, Spethmann W. 1982. Frost resistance and early growth of Sequoiadendron giganteum seedlings of different origins. Silv Genet 31(5/6):173-8.

Hamrick JL, Godt MJ, Sherman-Broyles SL. 1990. Factors influencing levels of genetic diversity in woody plant species. In: Adam WT, Strauss S, Copes D, Griffin AR, editors. Population genetics of forest trees. Proceedings of the International. Symposium of Population Genetics of Forest Trees; 1990 Jul 31-Aug 2. Corvallis, OR. p 95-124.

King JP. 1967. Seed source variation in tracheid length and specific gravity of five-year-old jack pine seedlings. Eighth Lake States Forest Tree Improvement Conference. US. For. Ser., St. Paul, MN Res. Pap. NC-23, p 6-9.

Lee CH. 1979. Absence of growth-wood property correlation in twenty-seven black pine seed sources. Wood Fiber 11:22-8.

Lee CH, Wahlgren HE. 1979. Specific gravity sampling with minimal tree damage - a study of red pine. Wood Sci 11:241-5.

Li XC. 1994. Study on relationship between superior Chinese-fir provenances and climatological ecology. For Res Mem 7:78-84.

Lin TP, Lu CS, Chung YL, Yang JC. 1993. Allozyme variation in four populations of *Taiwania cryptomerioides* in Taiwan. Silv Genet42:278-84.

Lin TP, Lee TY, Yang LF, Chung YL, Yang JC. 1994. Comparison of the allozyme diversity in several populations of *Chamaecyparis formosensis* and *Chamaecyparis taiwanensis*. Can J For Res 24:278-84.

Rehfeldt GE. 1991. A model of genetic variation for *Pinus ponderosa* in the inland Northwest (U.S.A.): applications in gene resource management. Can J For Res 21(10):1491-500.

Remrod J. 1976. Choosing Scots pine (*Pinus sylvestris*) provenances in Northern Sweden - analysis of survival, growth and quality in provenance experiments planted in 1951. Skogshogsk Stockholm Inst Skogssgen Rapp Upps 19. 132 p.

Rink G, Thor E. 1973. Inheritance and gains of three wood properties in Virginia pine. Twelfth Southern Forest Tree Improvement Conference; 1973 June 12-13. Baton Rouge, LA, p 24-30.

Rozenberg P, Cahalan C. 1997. Spruce and wood quality: genetic aspects. Silv Genet 46(5): 270-9.

SAS. 1985. SAS user's guide: statistics. Ver. 5. Cary, NC: SAS Inst. 975 p.

Smith DM. 1954. Maximum moisture content method for determining specific gravity of small wood specimens. For Prod Lab Rep No. 2014, Madison, WI. 8 p.

Sokal RR, Rohlf SJ. 1995. Biometry. 3rd Ed. New York: W H Freeman.887 p.

Stalh EG, Persson A, Persson B. 1986. Timber quality in northern latitudes - implications for forest tree improvement. Sveriges Lantbruksuniversitet, Rep 6 (Frans kempe Symp. In Umea) p 149-77.

Stonecypher RW, Zobel BJ. 1966. Inheritance of specific gravity in 5-year-old seedlings of loblolly pine. Tappi 49(7):303-5.

Strickland RK. 1960. Geographic variations in specific gravity and tracheid length of loblolly pine. [MS Thesis]. Athens (GA): Univ Georgia. 68 p.

Van Buijtenen JP. 1982. Fibers for the future. Tappi 65(8):10-2.

Vargas-Hernandez J, Adams WT. 1991. Genetic variation of wood density components in young coastal Douglas-fir: implications for tree breeding. Can J For Res 21(12):1801-7.

Wright JA. 1990a. Variation in wood properties of *Pinus oocarpa* and *P. patula* ssp. *tecunumanii* provenances at six sites. Silv Genet 39(1):1-4.

Wright JA. 1990b. Provenance variation in wood properties of *Pinus caribaea* var. *hondurensis*. New Zealand J For Sci 20 (2): 220 -30.

Wright JA, Gibson GL, Barnes RD. 1992. Variation of stem volume and wood density in provenances of *Pinus oocarpa* and *P. patula* ssp. *tecunumanii* at Nzoia, Kenya. Commonwealth For Rev 71(3-4):203-6.

Xie CY, Dancik BP, Yeh FC. 1992. Genetic structure of *Thuja orientalis*. Biochem Syst Ecol 20: 433 - 41.

Yanchuk AD, Dancik BP, Micko MM. 1983. Intraclonal variation in wood density of trembling aspen in Alberta. Wood Fiber Sci 15(4): 387-94.

Yang JC, Cheng CC, Kung FH. 1998. Defining *Cryptomeria* seed sources useful for Taiwan by superimposing probabilities of good provenance results over climatic data maps. Silv Genet 47(4):190-6.

Yang JC, Lin TP, Kung FH. 2000. Geographic variation of China-fir (*Cunninghamia lanceolata* (Lamb.) Hook.) in Taiwan: analysis of provenance division by ecotype and by province. Taiwan J For Sci 15(3):303-15.

Yeh FC, Layton C. 1979. The organization of genetic variability in central and marginal populations of lodgepole pine *Pinus contort* ssp. *latifolia*. Can J Genet Cytol 21:487-503.

Yeh FC, Shi J, Yang R, Hong J, Ye Z. 1994. Genetic diversity and multilocus associations in *Cunninghamia lanceolata* (Lamb.) Hook. from the People's Republic of China. Theory

Appl Genet 88:465-71.
Yu ST. 1996. Provenance test and geographic variation of China-fir. Contemp Silv 11(3):41- 8.
Zobel BJ. 1961. Inheritance of wood properties in conifers. Silv Genet 10:65-70.
Zobel BJ. 1963. Breeding for wood properties in forest trees. Stockholm, Sweden: World Consultation Forest Genetics Tree Improvement. 31 p.
Zobel BJ, Van Buijtenen JP. 1989. Wood variation-its causes and control. New York: Springer Verlag. 363 p.