GENETIC VARIATION OF WOOD DENSITY IN LUANTA FIR TESTED IN CENTRAL TAIWAN

Jenq-Chuan Yang
Director-General
Taiwan Forestry Research Institute
53 Nanhai Rd.
Taipei 100, Taiwan

Chen-Hui Lee
Professor
College of Natural Resources
University of Wisconsin
Stevens Point, WI 54481

and

Chih-Ming Chiu
Senior Scientist
Taiwan Forestry Research Institute,
53 Nanhai Rd.
Taipei 100, Taiwan

(Received September 2000)

ABSTRACT

Forty-nine wind-pollinated families representing 8 provenances of Luanta fir (*Cunninghamia konishii*) were sampled from the species' range in Taiwan. The study plantation was established in central Taiwan with 49 ten-tree linear plots in each of 5 blocks in the randomized complete block design. In July 1998 at plantation age 25, a 0.45-cm caliber increment core sample was extracted at breast height in the east cardinal direction from the best tree per plot; altogether 245 cores (1 core/family/plot × 49 families × 5 blocks) were sampled. From each core, only the 6 outermost growth rings (near the bark) were used to determine extracted specific gravity according to the maximum moisture content method. Genetic variations among provenances and among families within provenances were tested following a general linear model. There was no apparent geographic variation pattern, and the main source of specific gravity variation was attributable to differences among families within provenance. Overall specific gravity was 0.36 and the narrow-sense family heritability was 0.46. Wood specific gravity is strongly controlled by additive genetic variance, suggesting that this trait would respond to selection breeding. The importance of family selection was emphasized in the improvement of this wood property in Taiwan.

Keywords: *Cunninghamia konishii,* heritability, provenance, specific gravity.

INTRODUCTION

Paul (1953) and Mitchell (1955, 1960) were frequently credited for their recognition and emphasis on the importance of incorporating wood properties in a tree improvement program. Of the intrinsic wood properties, specific gravity (wood density) is by far the most important because it is a good indicator of yield and quality of both solid and fiber wood products. Van Buijtenen (1982) made a similar comment about wood specific gravity.

In general, this important wood property demonstrated a wide range of variation (Zobel and van Buijtenen 1989), moderate to high degree of genetic control or inheritance (Rozenberg and Cahalan 1997; Stonecypher and Zobel 1966; Van Buijtenen 1962; Zobel 1961; Zobel et al., 1972), and strong age-to-age (= juvenile to mature) correlation (Villeneuve et al., 1987).

Wood and Fiber Science, 33(3), 2001, pp. 486–491

Genetic information on wood properties is particularly limited in the tropical and subtropical tree species, and information on the inheritance pattern of wood properties is badly needed in Taiwan. Wood is the final product of forest growth, and any tree improvement program may not be successful unless the wood properties that meet the need of end product users are given consideration.

In our sampling scheme, we intentionally picked the best tree (usually the largest), instead of taking a random sampling of trees in the plot for increment boring. Our point of view is as follows: The test plantation will be kept for future measurement of mature traits. It is more likely that the best tree will remain to the end of the test period. If random samples are taken, the trees may not last through shading suppression, natural self-thinning, or artificial selective thinning. Secondly, the native forest management practice is to plant seedlings at a narrow spacing for better weed control and soil conservation. The young stand will be subjected to several thinnings before the final harvest. Results of the study using the best tree instead of a random sample tree, or an average tree, may better reflect field practice. Finally, the best tree has a better chance to recover from the boring wound.

However, readers need to be cautioned that statistical inference of the experiment is limited to a few growth rings sampled from the best trees, not to whole tree values or the average trees. In other words, our results are comparable to a test plantation that would have been thinned to the best trees in each plot. According to order statistics, population of the top rank individuals will have a higher mean and a smaller variance than the original population. Therefore, adjustment will be needed if results are to be converted to random samples (Kung 1977, 1980; Kung and Bey 1978; Kung and Liu 1978).

The objectives of this study were to determine the distribution and the magnitude of genetic variation in specific gravity of Luanta fir and to assess the size of its heritability for incorporation into a future tree improvement program in Taiwan.

MATERIALS AND METHODS

Discovered in 1905 by the Japanese botanist Konishi, Luanta fir is an important veneer-grade species in Taiwan. It is normally mixed with Taiwan red-cedar (*Chamaecyparis formosensis*), Taiwan Douglas-fir (*Pseudotsuga wilsoniana*), and pines at elevations between 1,300–2,000 m in northern and central Taiwan.

The study plantation located in central Taiwan (Yang et al. 1998) was established in 1973 with 2-0 seedlings grown from seeds collected from each of 49 wind-pollinated families representing 8 different provenances (Fig. 1) throughout the species range. It was hand-planted at a 2.0- × 2.0-m spacing with 5 replications, each containing 49 ten-tree linear plots arranged in the randomized complete block design. No thinnings have been administered since its establishment.

In late July 1998 at plantation age 25, a 0.45-cm caliber increment borer was used to remove 6 outermost growth rings near the bark (Lee and Wahlgren 1979; Yang et al., 1998) at breast height in the east cardinal direction from the best tree per plot (Lee 1974; Lee and Bey 1976). In conifers, the breast height sampling is generally satisfactory as a means of evaluating whole tree values (Zobel and van Buijtenen 1989). Furthermore, it was not intended to report values of interannual specific gravity (earlywood and latewood within a growth ring) because the boundary between the two wood zones was rather difficult to distinguish in Luanta fir, and it may cause consistently lower heritability estimates compared with those determined on the whole ring (Greaves et al. 1997). A mixture of 95% ethanol: benzene (1:2v/v) was used to remove the extractives from the wood sample. Extracted specific gravity was determined according to maximum moisture content method (Smith 1954) using all 6 outermost growth rings as an experimental unit to report wind-pollinated

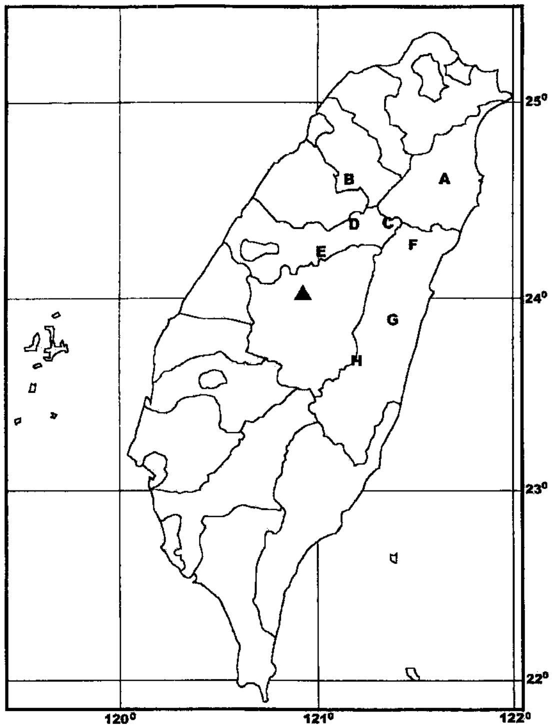

FIG. 1. Location of 8 provenances and test site.

family values. Altogether, 245 core samples (=1 core/family/plot × 49 families × 5 blocks) were analyzed. Two general linear models will be fitted; the first one is applicable to the whole experiment. Using Statistical Analysis System (SAS 1985), the general linear model can be expressed as:

Proc GLM;
Class provenance family;
Model density = provenance family;
Run;

The second one is applicable to an individual set of provenance data:

Proc GLM;
Class family;
Model density = family;
Run;

Family heritability is computed from the F-value in the second model by the following formula (Kung and Bey 1978):

$$H^2 = 1 - (1/F) \quad (1)$$

RESULTS AND DISCUSSION

Mean specific gravity of Luanta fir based on all 49 wind-pollinated families collected throughout the species range was 0.360, this figure being 5% lower than the published value of 0.379 (Wu and Wang 1967).

Because no published genetic information on Luanta fir wood properties has been available based on whole tree values, results of our study will have to be compared with data published elsewhere. This approach may involve discrepancies in tree species studied, the age of the study materials selected, sampling technique employed, and the test environment chosen. Between-provenance differences in this wood property were not statistically significant (Table 1). The range in mean specific gravity among provenances was from 0.342 to 0.393. The difference was 0.051 or about 14% of the species mean (Table 2). No provenance effect (V_p = 0%) was found to contribute toward the total variation in Luanta fir specific

TABLE 1. *The anova for provenance and families of specific gravity.*

Source variation	SS	df	MS	F value	Expected MS
Provenance	0.0151027	7	0.002158	0.891	$V_e + RV_{f:p} + RnV_p$
Families within provenance	0.0992629	41	0.002421	1.858**	$V_e + RV_{f:p}$
Error	0.2553704	196	0.001303		V_e
Total	0.369736	244			

Note: R: Block = 5. n: harmonic means of no. of families = 3.4
**: significant at the 1% level.

TABLE 2. *Description of seed source data.*

Provenances	No. families sampled	Latitude (°N)	Longitude (°E)	Altitude (m)	Wood density	Family heritability
A: Tayuan Shan	3	24.57	121.63	1900	0.366	
B: Kuanwu	6	24.52	121.10	2250	0.360	
C: Sheng Kuang	8	24.37	121.33	1900	0.357	
D: Tahsueh Shan	8	24.33	121.12	2200	0.368	
E: Pahsien Shan	3	24.17	121.02	2050	0.342	
F: Yenhai	5	24.18	121.53	2200	0.350	
G: Lintien Shan	1	23.78	121.38	2250	0.393	
H: Tanta	15	23.60	121.20	2200	0.360	
Species range					0.360	0.462

gravity. In addition, when specific gravity was related to the latitude and longitude (Table 2) at seed origins in a multiple regression analysis, both variables jointly accounted for only 17% of the total variation in specific gravity. This figure (=17%) is far less significant than 51% reported for slash pine (*Pinus elliottii*) by Goddard and Strickland (1962). It appears that no between-provenance differences existed or even expected with the small number of families available in Luanta fir.

Published data indicated that genetic variations in specific gravity among provenances (seed origins, seed sources, or geographic sources) are usually small or slight; however, the north-to-south and east-to-west trend may exist but does not always occur. Take loblolly pine (*Pinus taeda*), a major southern United States pine species, for example, the Maryland source (sp. gr. = 0.47) is 0.11 lower in specific gravity than the Florida source (sp. gr. = 0.58) and along the identical latitude, the Piedmont (or inland) source is 0.03 lower than the coastal source (Zobel et al. 1972). The magnitude of provenance difference (0.051) in Luanta fir specific gravity is only one half the size of the north-to-south variation found in loblolly pine. Hall (1984) found no geographic trend of wood density in black spruce (*Picea mariana*), nor was there significant provenance effect found on other tree species such as *Araucaria cunninghamii* wood specific gravity (Harding and Woolaston 1991).

Breeding tactics have to be adjusted according to the genetics of tree species. In the absence of geographic variation in Luanta fir, selection of any seed sources is not expected to result in any benefit. Matziris (1979) made a similar conclusion in his wood density study of 10-year-old progeny of 4 seed sources of Monterey pine (*Pinus radiata*) established in 2 sites in Greece.

Between-family variation is more important and effective than the between-provenance difference in improving wood specific gravity (Rees and Brown 1954). In sycamore (*Platanus occidentalis*), between-family variation accounted for as high as 78.6% of the total variation in wood density, while the regional variation accounted for only 21.4% (Nebgen and Lowe 1982). This is also the case with Luanta fir in which genetic differences in specific gravity between families within provenance were statistically significant at the 1% level [F (41,196) = 1.858**]. Of the total variation in this wood property, the effect of family differences within provenance contributed 15% ($=V_{f:p}$). Family means in wood density varied from 0.318 (a family from Tanta provenance) to 0.421 (a family from Tahsueh Shan provenance), the difference being 0.103 or about 29% of the species mean (Table 2).

Geographically, Taiwan is a small island about 400 km long and 140 km wide, and all the 8 provenances studied for the genetic variation in specific gravity were sampled from an area of no more than 200 km apart in latitude and 80 km apart in longitude. Besides, the north-to-south mountain range in Taiwan did not seem to function as a geographic barrier for free migration of pollen between provenances. Because of this geographic condition, there has been no effective mechanism to prevent members of the species from migration in response to glacial climatic change. A study at the enzymatic level involving 4 provenances of Luanta fir from central Taiwan also confirmed that between-provenance variation was much smaller than the within-provenance variation (Chang 1988). Young shoots of 120 clones of Luanta fir from 5 geographic areas were analyzed by starch-gel electrophoresis by Lin et al. (1998). They also expressed their concern over the continual loss of species heterozygosity in Taiwan.

Narrow-sense heritability is used to measure the amount of a given trait to be passed from parents to offsprings and is expressed as the ratio of additive genetic variance to the total variance. In general, wood density has a high proportion of additive variance (Zobel and Jett 1995), implying that this wood property is responsive to selection breeding. Heritability figures vary from 0.4 to 0.7 (Zobel and van Buijtenen 1989), and mean progeny values assessed at early ages may serve as a good predictor at later ages (Stonecypher and Zobel 1966).

The heritability determined for Luanta fir wood density was 0.46, this figure being assessed at a given cambial age of 20 to 25 years. Therefore, it provides a relative indicator rather than an absolute value because the environmental variance included in the heritability formula will change with tree ages and other factors.

To calculate genetic gains, heritability figures (=0.46) must be multiplied further by two more factors: selection intensity (=2.665 at 1% when infinite population size is assumed) and phenotypic standard deviation (=0.0391 derived from an analysis of variance). Thus, a genetic gain of 0.048 was obtained; it means an increase of 48 kg/m^3 in wood production and a 13% increase (0.048/0.360) over the species mean. In slash pine (*Pinus elliottii*), another important southern United States pine species, Einsphar et al. (1964) found the corresponding values: 0.56 for average wood density, 0.07 (corresponding to 70 kg/m^3 increase in wood production) for the amount of genetic gain and 12.5% as the size of improvement over the mean density.

We recognize the advantages of using a larger increment core sample (10–12 mm caliber) and sampling of more trees to represent a family in our future work. Under the current scope of sampling scheme, it was not possible to explore the differences in specific gravity values among trees within a family.

CONCLUSIONS

Forty-nine wind-pollinated families representing 8 provenances of Luanta fir (*Cunninghamia konishii*) were sampled from the species range in Taiwan. Genetic variation among provenances and among families within provenance were tested following a general linear model. There was no apparent geographic variation pattern, and the main source of specific gravity variation was attributable to differences among families within provenance. The range in mean specific gravity among families was from 0.318 to 0.421. Overall specific gravity was 0.36 and the narrow-sense family heritability was 0.46. Wood specific gravity is strongly controlled by additive genetic variance, suggesting that this trait would respond to family selection.

ACKNOWLEDGMENTS

This study was funded by a grant, NSC 87-2316-B-054-001 from the National Science Council, Taipei, Taiwan. Contribution No. 171 of Taiwan Forestry Research Institute.

REFERENCES

CHANG, K. C., 1988. Isozyme variation in different provenances of *Cunninghamia konishii* Hay. M.S. thesis, Natl. Taiwan University, Taipei, Taiwan, 64 pp.

EINSPAHR, D. W., R. E. GODDARD, AND H. S. GARDNER. 1964. Slash pine wood and fiber property heritability study. Silvae Genet. 13:103–109.

GODDARD, R. E., AND R. K. STRICKLAND. 1962. Geographic variation in wood specific gravity of slash pine. Tappi 45(7):606–608.

GREAVES, B. L., N. M. G. BORRALDHO, C. A. RAYMOND, R. EVANS, AND PH. WHITEMAN. 1997. Age-age correlation in, and relationships between, basic density and growth in *Eucalyptus nitens.* Silvae Genet. 46(5):264–270.

HALL, P. J. 1984. The relationship between wood density and growth rate and the implications for the selection of black spruce plus tree. Info. Rep. N-X-244, Newfoundland For. Res. Ctr. Can. For. Serv. 22 pp.

HARDING, K. J., AND R. R. WOOLASTON. 1991. Genetic parameters for wood and growth properties in *Araucaria cunninghamii.* Silvae Genet. 40(5–6):232–237.

KUNG, F. H. 1977. Adjustment and interpretation of progeny tests when only the best tree in each plot is measured. Silvae Genet. 16(2–3):117–119.

———. 1980. Estimate heritability of sprouting from a partially thinned plantation. Proc. Northeastern Forest Tree Improvement Conference, 27:233–239.

———, AND C. C. LIU. 1978. Quantitative study of the remaining trees after thinning. Quart. J. Chinese Forestry 11(1):1–6.

———, AND C. F. BEY. 1978. Heritability construction for provenance and family selection. Proc. Lake States Forest Tree Improvement Conference, 13:136–146.

LEE, C. H. 1974. Effect of partial measurement on statistical precision and efficiency in a nursery study of *Pinus ponderosa.* Silvae Genet. 23:124–126.

———, AND C. F. BEY. 1976. Sampling efficiency for 1-year-old white ash seedlings. Proc. 10th Central States Forest Tree Improvement Conference, 105–108.

———, AND H. E. WAHLGREN. 1979. Specific gravity sampling with minimal tree damage—A study of red pine. Wood Sci. 11(4):241–245.

LIN, T. P., C. T. WANG, AND J. C. YANG. 1998. Comparison of genetic diversity between *Cunninghamia konishii* and *C. lanceolata.* J. Heredity 89(4):370–373.

MATZIRIS, D. I. 1979. Variation of wood density in radiata pine grown from four seed sources at two sites in Greece. Silvae Genet. 28(2/3):104–106.

MITCHELL, H. L. 1955. Breeding for high quality wood. U.S. Forest Prod. Lab. Rep. No. 2050, 13 pp.

———. 1960. Development of an adequate concept of wood quality for the guidance of geneticists and forest managers. 5th World Forestry Congr. Seattle, WA. Pp. 1341–1348.

NEBGEN, R. J., AND W. J. LOWE. 1982. Inheritance of growth, branch angle, and specific gravity in three American sycamore populations. Silvae Genet. 31:86–89.

PAUL, B. H. 1953. Forest genetics in relation to wood property. Proc. Lake States For. Genet. Conf. Misc. Rep. 22:55–59.

REES, L. W., AND R. M. BROWN. 1954. Wood density and seed sources in young plantations of red pine. J. Forestry 52:662–665.

ROZENBERG, PH., AND CH. CAHALAN. 1997. Spruce and wood quality: Genetic aspects. Silvae Genet. 46(5): 270–279.

SAS. 1985. SAS Users' Guide: Statistics. Version 5 ed. SAS Inst. Inc., Cary NC. 975 pp.

SMITH, D. M. 1954. Maximum moisture content method for determining specific gravity of small wood specimens. Forest Prod. Lab. Rep. No. 2014, Madison, WI. 8 pp.

STONECYPHER, R. W., AND B. J. ZOBEL. 1966. Inheritance of specific gravity in 5-year-old seedlings of loblolly pine. Tappi 49(7):303–305.

VAN BUIJTENEN, J. P. 1962. Heritability estimates of wood density in loblolly pine. Tappi 45(7):602–605.

———. 1982. Fibers for the future. Tappi 65(8):10–12.

VILLENEUVE, M., E. K. MORGENSTERN, AND L. P. SEBASTIAN. 1987. Variation patterns and age relationships of wood density in families of jack pine and black spruce. Can. J. For. Res. 17:1219–1222.

WU, S. C., AND H. WANG. 1967. Important wood species of Taiwan. Chinese For. Assoc, Taipei, Taiwan. 2 pp.

YANG, J. C., C. H. LEE, AND C. M. CHIU. 1998. Precision of estimating Luanta fir specific gravity by a few outer growth rings. Taiwan J. For. Sci. 13(4):251–257.

ZOBEL, B. J. 1961. Inheritance of wood properties in conifers. Silvae Genet. 10:65–70.

———, R. C. KELLISON, M. F. MATTHIAS, AND A. V. HATCHER. 1972. Wood density of the southern pines. Tech. Bul. No. 208, North Carolina Agric. Exp. Sta. N.C. State Univ., Raleigh, NC. 56 pp.

———, AND J. P. VAN BUIJTENEN. 1989. Wood variation—its causes and control. Springer-Verlag, New York, NY. pp. 33–55, 249–261.

———, AND J. B. JETT. 1995. Genetics of wood production. Springer-Verlag, New York, NY. pp. 98–124.