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Earlywood-Latewood Demarcation Criteria and Their Effect on Genetic Parameters of Growth Ring Density Components and Efficiency of Selection for End-of-Rotation Density of Radiata Pine

By S. KUMAR[1]

Abstract

Most commonly used components of the basic density of a growth ring are earlywood density, latewood density and latewood ratio. Various arbitrarily chosen criteria have been used as a demarcation of the earlywood-latewood boundary. The present study was conducted to compare genetic parameter estimates of ring density (RD) components using various demarcation criteria. Three criteria were considered: density of 400 kg/m^3 as a threshold; the average of the minimum and maximum density within the ring; two-thirds of the difference between the minimum and maximum density within the ring. Relative efficiency of selection using ring density and its components as selection criteria, for improving the average ring density at harvest age, was also evaluated. A pith-to-bark 5-mm increment core was taken from each of 8 or 9 trees from each of 50, 30-year-old, open-pollinated radiata pine families. Averages across each core, weighted according to ring width, were determined for overall RD, earlywood density, latewood density and latewood ratio, defined according to the above criteria.

Estimated individual-tree heritability of RD at ages 5 and 10 years were 0.71 and 0.81 respectively. Estimates of heritability and genetic correlations among growth ring density components varied considerably depending upon the demarcation criteria. The combination of low estimated heritability of latewood ratio and its non-significant genetic correlations with other traits argues strongly for discounting this variable for not contributing much information. Relative efficiencies of family selection for age-30 RD, based on RD at core ages 5 and 10 years as selection criteria, were calculated to be 82 and 93 percent, respectively. Index selection, involving ring density and its components, appeared to improve selection efficiency. Using the average of the lowest and highest density within a ring as the demarcation criterion gave the highest apparent relative efficiency of family selection. However, increased efficiencies of combined selection on densitometer-measured traits may not be worth the extra costs above selection for density of whole cores.

Key words: Ring density, heritability, family selection, genetic correlation, correlated response, index selection, *Pinus radiata*.

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Introduction

Wood basic density is probably the most important indicator of wood quality because of its important role in determining wood strength and stiffness, pulp digester yield and several other wood properties. Understanding the genetics of wood density is complicated by the composite nature of this trait. The wood produced early versus late in the annual growing season is termed as earlywood (EW) and latewood (LW) respectively (ZOBEL and JETT, 1995). Earlywood is formed when there are high auxin levels but the amount of photosynthesis available for cell wall formation is limiting (ZIMMERMAN and BROWN, 1971). Compared with LW, EW has shorter, wider tracheids with thinner cell walls while darker band of cells with longer, thicker-welled cells, in the outer part of the growth ring is referred to as being LW (ZOBEL and JETT, 1995).

The X-ray densitometry method (COWN and CLEMENT, 1983), which enables continuous records of density from pith-to-bark, is widely used for such ring by ring determination of wood density. The resulting cyclic density profiles are described in terms of minimum, maximum, earlywood and latewood density, latewood ratio and the average ring density. Because of the difficulty posed by EW intergrading with LW, various arbitrarily chosen thresholds (e.g. COWN and BALL, 2001) have been used to demarcate EW from LW.

A particular value of ring density (RD) can result from various combinations of its component traits and knowledge of the genetic control of these component traits may help in understanding the genetics of overall wood density. The most commonly used components of RD are earlywood density, latewood density and latewood ratio. Genetic control of RD components has been widely studied in various species including *Pinus radiata* (NICHOLLS et al., 1980; COWN and BALL, 2001), *Pinus sylvestris* (HANNRUP, 1999), *Pinus caribaea* (HARDING et al., 1991), *Pinus densiflora* (OHTA, 1989), *Picea abies* (WORRALL, 1975; HYLEN, 1999), *Picea mariana* (ZHANG and MORGENSTERN, 1995; ZHANG, 1998), *Pseudotsuga menziesii* (VARGAS-HERNANDEZ and ADAMS, 1991), Cryptomeria japonica (FUGISAWA et al., 1993) and *Eucalyptus nitens* (GREAVES et al., 1997). Different authors have used different demarcation criteria for EW and LW boundaries. Three main methods of determining the transition point have been used: first, an arbitrary threshold of wood density, say, 400 kg/m3 in radiata

pine (Cown and Ball, 2001); second, the average of the minimum and maximum density in a ring (Nicholls and Brown, 1971); third, two-thirds of the difference between the minimum and maximum within-ring density (Hylen, 1999).

Use of different demarcation criteria may result in different genetic parameter estimates, which would complicate comparison of estimated parameters across various studies. It would also become difficult to make the appropriate choice for the selection of ring density components to improve average ring density. Use of various ring density components has been shown to improve the efficiency of early selection of overall wood density (Vargas-Hernandez and Adams, 1992). The first objective of the present study was to compare genetic parameter estimates of ring density components using various transition points. The second objective was to evaluate the relative efficiency of selection, using ring density and its components as selection criteria, for improving the average ring density at harvest age.

Materials and Methods

A progeny test of 600 open-pollinated (closely approximating half-sib) progenies of plus-trees of *Pinus radiata* D. Don was established in 1969 (Shelbourne and Low, 1980). The trial was established as 5 replications of 10-tree row-plots on a site in Northern Kaingaroa Forest (altitude 420 m, latitude 38° 17' S, longitude 176° 47' E) in the central North Island of New Zealand. The trial was thinned twice at different stages, leaving 3 to 4 trees per plot. At ages 5 and 10 years, the parents were ranked on the basis of their family performance for various traits including growth and form traits. The top 50 parents and their forwards selected offspring were deployed in seed orchards. In 1999, when the progenies were 30 years old, from each of the top 50 families, 8 to 9 trees were each sampled by one 5-mm breast-height pith-to-bark increment core for X-ray densitometry analysis (P. A. Jefferson and J. Lee, 1999; unpublished). Depending upon their availability, the number of trees sampled from each replication varied for different families.

Intra-ring density information was obtained for each core sample using X-ray densitometry. There were 28 annual rings identified and these were numbered from pith-to-bark. The first and last annual rings from each sample were discarded. For each of the remaining rings, minimum, maximum, average ring density (RD) and the ring width were recorded. Using three different definitions of transition point as explained earlier (*Method 1*: Cown and Ball, 2001; *Method 2*: Nicholls and Brown, 1971; *Method 3*: Hylen, 1999), the width and average densities for earlywood density, latewood density, as well as latewood ratio, were obtained for each ring. For *Method 1*, an arbitrary threshold of 400 kg/m³ was used as transition point. Weighted average values across the core were obtained for RD, earlywood density and latewood density, by weighting each individual ring value by its respective width. Weighted averages were obtained for each core at ages (in terms of number of rings from pith represented) 5, 10, and 27 years, representing values that would have been obtained for each tree at that age. The measurements taken at 27 years of core age represented harvest age (HA). Average latewood ratio across the core was obtained as the sum of the latewood width of individual rings divided by the length of the core sample.

Statistical analysis

Based on the trial design, the model for statistical analysis would include replicate, family, family by replicate interaction (or plot) and residual factors (or error). Preliminary analysis

using complete model revealed that replicate and plot effects were non-significant (p > 0.10). Thus, it was decided to merge replicate and plot effects with error component and the following simple model was used for single trait analysis of this experiment:

$$Y_{ij} = \mu + f_i + e_{ij} \tag{1}$$

where Y_{ij} is the phenotypic value for the jth individual in the ith family for a given trait; μ is the general mean; f_i is the random effect of ith family; e_{ij} is the random error effect. Cown et al. (1992), using age-20-years data from this same experiment, had used similar model for obtaining heritability estimates for wood density. Estimates of narrow-sense heritability ($\hat{h}^2$) and family-mean heritability ($\hat{h}^2_f$) for each trait were obtained using the family and error variance components as:

$$\hat{h}^2_f = 4\,\hat{\sigma}^2_f / (\hat{\sigma}^2_f + \hat{\sigma}^2_e) \tag{2}$$

$$\hat{h}^2_f = \hat{\sigma}^2_f / (\hat{\sigma}^2_f + \hat{\sigma}^2_e / n) \tag{3}$$

where $\hat{\sigma}^2_f$ ($= 0.25\,\hat{\sigma}^2_A$, the additive genetic variance) and $\hat{\sigma}^2_e$ are the estimated among-family and within-family variances, respectively; n is the effective number of half-sib offspring per family. The value of n used by the analysis model was 8.36. Approximate standard errors (SE) of heritability estimates were calculated following Falconer and Mackay (1996, page 180).

For multivariate analysis, there are assumed to be f groups (half-sib families) each of size n (number of offspring per half-sib family), and p traits are recorded on each individual. It was further assumed that the observations are multivariate normally distributed, with among- and within-group effects independent of each other. Estimates of covariance components were obtained using genetic variance-covariance matrix calculated from multivariate analysis of variance (MANOVA). PROC GLM of the SAS™ package (SAS Institute Inc., 1989) was used to obtain Type III sums-of-squares and cross-products matrices.

An estimate of a genetic correlation was obtained as:

$$\hat{r}_g = \hat{\sigma}_{xy} / \sqrt{\hat{\sigma}^2_x \times \hat{\sigma}^2_y} \tag{4}$$

where $\hat{\sigma}_{xy}$ is estimated additive genetic covariance between two traits; $\hat{\sigma}^2_x$ and $\hat{\sigma}^2_y$ are estimated additive genetic variances for the two traits. Approximate standard errors (SE) of estimated genetic correlation were calculated following Falconer and Mackay (1996, page 316).

Predicted genetic gain

Average ring density, obtained by weighting the value for each individual ring component by its width, at the harvest age was assumed to be the target trait to improve. The ratio of genetic gain in the target trait expected from an early age selection, relative to gain expected when the selection is made directly on the target trait, was called the relative efficiency of indirect or early selection. The genetic gain in the target trait by direct selection can be calculated as (Falconer and Mackay, 1996):

$$\Delta_g = ih^2\sigma_p \tag{5}$$

where σ^2_p is the phenotypic variance for the target trait.

The correlated response (Δ_{g*}) in the target trait (y) from indirect selection based on trait x will be:

$$\Delta_{g*} = ih_x h_y r_g \sigma_{p(y)} \tag{6}$$

where $\sigma^2_{p(y)}$ is the phenotypic variance for the target trait.

The ratio of genetic gain obtained from Eq.6 to that obtained from Eq. 5, expressed in percentage, was calculated for core

age 5 and 10 years. Relative efficiency (%) presented in this study is for parental selection. When selection criteria contained more than one trait (called index selection), the correlated response (Δ_{g**}, in the unit of measurement) in the target trait was calculated following WHITE and HODGE (1989, page 244):

$$\Delta_{g**} = i \sqrt{(\boldsymbol{b'Pb})} \tag{7}$$

where $\boldsymbol{b} = \boldsymbol{P^{-1} c,}$

$\boldsymbol{P}$ = Estimated phenotypic variance-covariance matrix among selection criteria traits (ring density, earlywood and latewood density, and latewood ratio),

$\boldsymbol{c}$ = is vector of estimated genetic covariance between selection criteria traits and the target trait (ring density at harvest age).

Selection intensity (i) was assumed to be 1 in all calculations. The estimated relative efficiency of index selection was calculated as the ratio of genetic gain obtained from Eq. 7 to that obtained from Eq. 5

Results and Discussion

The average ring density (RD) was found to be 331, 349 and 380 kg/m³ at core ages 5, 10 and 27 years, respectively. The average value of ring density components was calculated using three different methods (*Table 1*). It shows that the average value of each component increased as the age of trees increased. Different methods of setting EW and LW boundary resulted in different average values of ring density component traits. Using *Method 1* (COWN and BALL, 2001), the average earlywood density increased from 310.29 kg/m³ at core age 5 years to 324.06 kg/m³ at harvest age (HA). Similarly, latewood ratio increased from 0.15, at core age 5 years, to 0.32 at the harvest age. The average values of earlywood density and latewood density were highest when calculated using *Method 3* (HYLEN, 1999). *Method 1* and *Method 2* gave very similar average value of latewood ratio at core age 5 years but at the harvest age it was 0.32 and 0.25 for *Method 1* and *Method 2*, respectively (*Table 1*).

Table 1. – Average values (kg/m³) of ring density, earlywood density, latewood density, and latewood ratio obtained using three different methods at different core ages including harvest age (HA).

Method	Trait	Core age (years)		
		5	10	HA
Method 1	Earlywood density	310	318	324
	Latewood density	457	474	499
	Latewood ratio	0.15	0.21	0.32
Method 2	Earlywood density	310	321	336
	Latewood density	448	476	518
	Latewood ratio	0.16	0.18	0.25
Method 3	Earlywood density	317	330	347
	Latewood density	477	506	548
	Latewood ratio	0.09	0.11	0.17
	Ring density	331	349	380

The gradual increase in average RD from pith-to-bark confirms the trend observed by COWN and BALL (2001) in radiata pine. Average RD at harvest age was 31 kg/m³ higher than that observed at core age 10 years. Average RD (349 kg/m³) in first 10 growth rings observed in this study is very close to that reported by COWN and BALL (2001). The difference in the average value of ring density components, especially latewood ratio, obtained using various methods, highlights the need to draw a clear distinction among the various methods.

Estimates of individual-tree heritability (*Table 2*) of average ring density (standard error in parenthesis) at core ages 5, 10 and 27 years were 0.71 (0.19), 0.81 (0.20) and 0.95 (0.21), respectively. High heritability estimates were obtained for most component traits. There were, however, large differences in the heritability estimates especially for latewood density and latewood ratio for various earlywood-latewood demarcation criteria. For example, heritability of latewood density at core age 5 years was 0.51, 0.75 and 0.71 and at age 10, was 0.44, 0.82 and 0.77, for *Method 1*, *Method 2* and *Method 3*, respectively. Heritability estimates of latewood ratio at core ages 5 and 10 years (0.53 and 0.75, respectively) obtained using *Method 1* were much higher than that obtained using *Method 2* (0.10 and 0.12, respectively) and *Method 3* (0.11 and 0.19, respectively).

Table 2. – Estimates of individual-tree heritability of ring density components for different methods of setting transitional point. Figures in parentheses are approximate standard error of heritability estimates.

Method	Trait	Core age (years)		
		5	10	Harvest age
Method 1	Earlywood density	0.75 (0.20)	0.76 (0.20)	0.76 (0.20)
	Latewood density	0.51 (0.17)	0.44 (0.16)	0.38 (0.16)
	Latewood ratio	0.53 (0.18)	0.75 (0.20)	0.89 (0.21)
Method 2	Earlywood density	0.75 (0.20)	0.77 (0.20)	0.83 (0.21)
	Latewood density	0.75 (0.20)	0.82 (0.20)	0.72 (0.20)
	Latewood ratio	0.10 (0.12)	0.12 (0.12)	0.23 (0.14)
Method 3	Earlywood density	0.75 (0.20)	0.81 (0.20)	0.90 (0.21)
	Latewood density	0.71 (0.19)	0.77 (0.20)	0.65 (0.19)
	Latewood ratio	0.11 (0.12)	0.19 (0.13)	0.33 (0.15)
	Ring density	0.71 (0.19)	0.81 (0.20)	0.95 (0.21)

Increases in heritability estimates from core age 5 to 10 years could be because of less environmental 'noise' at later age as a result of less competition after thinning. The families used in this study were those selected for growth and form traits. Given a moderate negative genetic correlation between growth and wood density, estimates of heritability obtained from a selected subset of families could be biased. However, heritability estimates for RD obtained in this study are very similar to that reported earlier for radiata pine (BURDON and LOW, 1992) in New Zealand. Minimal family-site interactions for wood density are reported (BURDON and LOW, 1992) and thus heritability estimates obtained from a single site should not be seriously upwardly biased. Heritability estimates for earlywood density were similar for all three methods. However, some of the differences in the h^2 estimates of latewood density and latewood ratio are very large. In general, heritability estimates of ring density components, especially latewood ratio, were consi-

Table 3. – Estimates of genetic correlations of ring density components, at early ages, with average ring density at harvest age. Figures in parentheses are approximate standard error of correlation estimates.

| Method | Trait | Core age (years) | |
		5	10
Method 1	Earlywood density	0.84 (.05)	0.93 (.02)
	Latewood density	0.83 (.06)	0.79 (.08)
	Latewood ratio	0.80 (.07)	0.90 (.03)
Method 2	Earlywood density	0.83 (.05)	0.94 (.02)
	Latewood density	0.90 (.03)	0.93 (.02)
	Latewood ratio	-0.22 (.35)	0.02 (.33)
Method 3	Earlywood density	0.84 (.05)	0.94 (.02)
	Latewood density	0.89 (.04)	0.94 (.02)
	Latewood ratio	-0.00 (.35)	0.04 (.28)
	Ring density	0.87 (.04)	0.96 (.01)

derably lower than that of RD. The use of arbitrary thresholds for the earlywood-latewood boundary may be increasing the residual variance of ring density components, and would thus reduce the apparent heritability relative to the RD (VARGAS-HERNANDEZ and ADAMS, 1991; GREAVES et al., 1997).

Average ring density at harvest age (HA) was considered as the target trait in this study. Estimates of genetic correlation of RD at core ages 5 and 10 years with average RD at harvest age were 0.87 and 0.96, respectively. Estimates of genetic correlation of earlywood density, latewood density and latewood ratio at core ages 5 and 10 years with RD at harvest age (*Table 3*) were very low for latewood ratio for *Methods 2* and *3*. In general, very high genetic correlations were obtained between earlywood density and latewood density at early ages, with RD

at harvest age using all three methods. Estimated genetic correlation of latewood ratio at core age 10 with RD at harvest age was very high (0.90) for *Method 1*, but very low (0.02 and 0.04, respectively) for *Method 2* and *Method 3*. Estimates of genetic correlations among ring density, earlywood density, latewood density and latewood ratio at core ages 5 and 10 years for each method are shown in *Table 4*. Estimated genetic correlation among ring density, earlywood density and latewood density were very high (>0.90) for all three methods. On the other hand, estimated genetic correlations of latewood ratio with ring density, earlywood density, and latewood density were insignificant (and often negative) for *Methods 2* and *3* but high for *Method 1*.

High genetic correlations of RD at core ages 5 and 10 years with RD at harvest age indicate that early selection would be effective for improving overall ring density harvest age. Estimated genetic correlations among ring density, earlywood density and latewood density were very high irrespective of the method used for setting the earlywood-latewood boundary. Latewood ratio obtained using *Method 1* had very high positive correlation with RD, while non-significant correlation was observed for the other two methods. It seems that using 400 kg/m³ as a demarcation criterion in *Method 1* has resulted in some spuriously high genetic correlations with ring density. Using a fixed threshold of 400 kg/m³ makes the earlywood and latewood ratio co-vary with ring density and thus could cause spurious correlation. These striking differences in estimates of heritability and genetic correlations for variously defined latewood ratio highlights its unreliability as a predictor of ring density at harvest age.

In this study, latewood ratio (using *Method 2* and *Method 3*) was found to be under poor genetic control and estimated genetic correlations between latewood ratio and other traits were also non-significant. NICHOLLS et al. (1980) also reported poor heritability of latewood ratio and also non-significant genetic correlation of this trait with average ring density in radiata pine. The low estimated heritability of latewood ratio indicates that this trait makes a negligible contribution to tree-to-tree variation in ring density. The combination of low estimated heritability of latewood ratio and its non-significant genetic correlations with other traits argues strongly for rejecting this trait for combined selection for ring density at harvest age or indeed for selecting for high corewood density.

Table 4. – Estimates of genetic correlation between ring density, earlywood density, latewood density, and latewood ratio at core ages 5 and 10 years for different methods. Figures in parentheses are approximate standard errors of correlation estimates.

| Method | Trait | Core age 5 years | | | Core age 10 years | | |
		Earlywood density	Latewood density	Latewood ratio	Earlywood density	Latewood density	Latewood ratio
Method 1	Ring density	0.99 (0.0)	0.95 (.02)	0.87 (.05)	0.98 (.01)	0.84 (.06)	0.93 (.02)
	Earlywood density		0.94 (.02)	0.82 (.07)		0.77 (.09)	0.86 (.05)
	Latewood density			0.79 (.09)			0.80 (.08)
Method 2	Ring density	0.99 (0.0)	0.97 (.01)	-0.21 (.38)	0.99 (0.0)	0.97 (.01)	0.03 (.35)
	Earlywood density		0.96 (.01)	-0.28 (.37)		0.95 (.02)	-0.11 (.36)
	Latewood density			-0.26 (.37)			0.01 (.35)
Method 3	Ring density	1.00 (0.0)	0.98 (.01)	-0.14 (.37)	0.99 (0.0)	0.99 (0.0)	0.01 (.29)
	Earlywood density		0.96 (.01)	-0.19 (.37)		0.97 (.01)	-0.11 (.29)
	Latewood density			-0.06 (.38)			0.16 (.29)

Ring density (RD) and its components were used as selection criteria to make family selections at core ages 5 and 10 years. Average ring density at harvest age (HA) was assumed to be the target trait for improvement. Relative efficiency (RE) of using RD alone as a selection criterion was 82 and 93 percent at core age 5 and 10 years, respectively. Calculated RE of index selection, using earlywood density and latewood density as selection criteria, varied from 83.4 to 87.0 percent and 91.7 to 94.4 percent at core age 5 and 10 years, respectively (*Table 5*) for various methods. There was small increase (less than 2 percent) in relative efficiency when ring density was also included along with earlywood and latewood density in an index selection (*Table 5*).

Table 5. – Relative efficiency (%) of index selection, using ring density (RD) and its components (Earlywood density: EW; Latewood density: LW) as selection criteria, at core ages 5 and 10 years. Efficiency of direct selection for RD at harvest age (HA) was assumed to be 100 percent.

Core age (years)	Method	Selection criteria	
		EW and LW	RD, EW and LW
5	*Method 1*	83.4	84.0
	Method 2	87.0	88.3
	Method 3	85.7	87.1
10	*Method 1*	91.7	93.5
	Method 2	94.0	94.8
	Method 3	94.4	94.7

The difference in the relative efficiency of using RD for family selection at core ages 5 and 10 years was about 11 percent. It would be worthwhile to evaluate whether early selection at age 5 years is more economical in dollar terms. Index selection, especially for *Method 2* and *Method 3*, was slightly more efficient than using RD alone for selecting families. In general, relative efficiencies of using index selection, following *Method 1*, was similar to using RD alone. Results shown in *Table 5* revealed that index selection could be more efficient compared to selection based on RD alone particularly at an early age. *Method 2* was found to be about 3.6 and 4.3 percent more efficient than *Method* 1 when different selection criteria were used at core age 5 years. The differences in relative efficiency of various methods, for different selection criteria, were very small at core age 10 years.

None of the three methods of earlywood-latewood boundary demarcation considered in this study provides "true" expression of ring density components. *Method 1* might indicate that there is no latewood in first-10 annual growth rings and no earlywood in the outerwood zone, because of the 400 kg/m³ definition used to define the earlywood-latewood boundary. HYLEN (1999) observed that the minimum-maximum density midpoint (*Methods 2*) gave unusual high latewood ratio for most of the rings in their material and thus used two-thirds of the density range (*Method* 3). However, there can be some errors in the maximum and minimum points measured in the X-ray densitometry profile (HYLEN, 1999) depending upon the resolution, and thus some error could occur in demarcating earlywood-latewood boundary in *Method 2* and *Method 3*. This study demonstrated that the sensitivity of genetic parameter estimates to choice of criterion should be evaluated.

The three methods were compared in context of the radiata pine wood grown in New Zealand conditions. The all three methods considered here might not be directly relevant for other species or the same species grown in different climatic conditions. The purpose of this study was, however, to make researchers aware about the effect that earlywood-latewood demarcation criterion could have on the estimates of genetic parameters, irrespective of the type of wood being analysed. In this study, there is some indication of a slight gain in efficiency from determining density components and using the information for index selection. The high estimated relative efficiency of multi-component selection is because of high estimated heritabilities of component traits, and also high genetic correlation with RD. However, there should be consideration of whether one would put cores through the full densitometric scan, or just use a quicker and cheaper method of determining density. With the latter, one could screen more candidates for a given budget, and thus allow higher selection intensity. The cost-efficiency of using the latter approach needs to be determined.

Acknowledgements

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Allozyme Variation in Eight Natural Populations of *Pinus roxburghii* SARG. in India

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Abstract

Seeds collected from eight populations of Chir pine (*Pinus roxburghii* SARG.) from the natural distribution range of the species in Himachal Himalayas in India were analysed isozymatically at 11 enzyme systems. For the enzyme systems studied, 25 gene loci were identified out of which 18 were polymorphic. The observed mean values for genetic variation were slightly lower than mean values reported for *Pinus* species (number of alleles: 1.65 compared to 2.36; effective number of alleles: 1.13 compared to 1.26; observed heterozygosity: 0.153 compared to 0.179). A small differentiation among populations and large variation within populations were reflected by small value of GST (0.04). Considering the different genetic parameters three populations seem favourable for gene conservation measures.

Key words: *Pinus roxburghii*; allozymes, differentiation, multilocus diversity, genetic distance, variation.

Introduction

Owing to its economical and ecological importance, *Pinus roxburghii* has outnumbered all other species in afforestation programmes in its natural zone of occurrence. Selecting superior *P. roxburghii* stands/genotypes and their mass multiplication can increase its productivity many fold as significant variation could be expected on the basis of its natural distribution under diverse environmental conditions which include heterogeneous areas of the Shiwaliks and western Himalayas. Hence, there is an immediate need to conserve and manage genetic resources of this species. However, establishing priorities for gene conservation (*in situ* and *ex situ*), management and use of tree genetic resources for breeding programmes as well as efficient and successful plantation require an understanding of the degree of diversity within and between populations of a species as geographically separated populations have different genes and their frequencies due to mutation, different selective forces and genetic drift. Within each tree species the amount and pattern of genetic variation determine its adaptability and are consequently essential parameters of the long term stability of the forest ecosystem.

The scientific methods used to distinguish levels of variation are the working tools for shaping the decisions on management and tree improvement policies. Studies conducted in the past on provenance testing of *P. roxburghii* have revealed significant variation in growth parameters, and biochemical contents (QURESHI and SINGH, 1967; SINGH *et al.*, 1970; SAGWAL, 1978; GHOSH *et al.*, 1982; SHARMA, 1986). However, provenance trials, based on quantity measurements often give an incomplete picture about the population structure as these measurements are subjected to environmental influences (BROWN and MORAN, 1978). There is an urgent need to supplement the selection procedure by the modern techniques for detecting systematic differences between populations of this species. The method which has been proved suitable for characterisation and demarcation of subspecific groupings of plant/animal species is the analysis of isoenzymes.

Since there is no report based on isoenzyme data in *P. roxburghii* in India, aim of the present study is to assess the genetic variation at isoenzyme level present within and between its populations growing under different environmental conditions and hence to describe the genetic architecture of the species (SHARMA, 1999). HUSSAIN (1995) studied twelve populations of *P. roxburghii* of the species' natural distribution westward of India.

Material and Methods

Seeds collected from eight natural populations of *P. roxburghii* viz., Sulyali (P1), Aghar (P2), Banethi (P3), Gagret (P4), Nauni (P5), Nihari (P6), Shilly (P7) and Shalaghat (P8) covering Shiwalik and Himalayan ranges of species' distribution in Himachal Pradesh in India (*Figure 1*) were used for these studies. The distance between the populations varied from 4 to 233 km.

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