

SELECTION FOR IMPROVED GROWTH AND WOOD DENSITY IN LODGEPOLE PINE: EFFECTS ON RADIAL PATTERNS OF WOOD VARIATION

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ABSTRACT

Changes in growth and wood density traits were investigated across annual rings of 12-year-old trees from four selected subpopulations in lodgepole pine (*Pinus contorta* Dougl. Ex Loud var. *latifolia* Engelm) based on X-ray densitometry profile data. Four subpopulations were constructed based on height growth and wood density as follows: 1) fast growth and high wood density (FH); 2) slow growth and high density (SH); 3) fast growth and low density (FL); and 4) slow growth and low density (SL). Annual ring density was initially high, declined with age until age 10, and then plateaued. Significant differences among subpopulations were found for ring density, earlywood and latewood densities, ring width, earlywood width, latewood proportion, and earlywood width after age 6. Wood density decreased less from the pith to the bark in both overall and earlywood densities in the FH subpopulation, resulting in denser, more homogeneous wood than in other subpopulations. This suggests that it may be possible to increase wood density and homogeneity in juvenile wood of this species by selecting FH families. Overall ring density may be better improved by selecting for earlywood and latewood components separately. The earliest age of which families combining fast growth and high wood density can be accurately identified is about 7 years.

Keywords: X-ray densitometry, wood density, density components, heterogeneity, radial pattern, early selection.

INTRODUCTION

Increased utilization of younger trees from managed fast-growing plantations will result in a higher proportion of juvenile wood, which in turn will influence the quality of wood products obtained (Zobel 1980; Kennedy

1995; Hatton 1997; Zobel and Sprague 1998). Juvenile wood differs from mature wood in most properties, among which lower wood density and mechanical properties are the most significant for hard pine species (Zobel and van Buijtenen 1989; Zobel and Sprague 1998). The low wood density reduces not only

strength, but also pulp yield (Zobel 1963; Harris et al. 1976; van Buijtenen 1982). The effects of shortening rotation age, and thus increasing the proportion of juvenile wood, increase the need to take wood properties, particularly juvenile wood density, into consideration when selecting breeding material.

The production of a juvenile-type wood results from normal physiological processes (Larson 1962). There is not much that foresters can do to avoid it. Nearly all the silvicultural activities that accomplish the objective of faster growth and earlier harvest will result in more juvenile wood (Larson 1969). However, it is possible to change the specific gravity of juvenile wood somewhat by breeding (Zobel and van Buijtenen 1989; Zobel et al. 1978; Ledig et al. 1975; Zobel and Jett 1995). For instance, the density gradient from the pith to the bark can be considerably reduced by clonal selection (Burdon and Harris 1973); and the age of transition from juvenile to mature wood formation can vary greatly among individual trees (Loo et al. 1985; Ladrach 1986), providing an opportunity to select trees with an earlier age of transition.

Wood characteristics within the juvenile zone are not uniform, but change rapidly throughout the zone from the pith outward (reviewed by Zobel and van Buijtenen 1989; Zobel and Sprague 1998). In lodgepole pine, Taylor et al. (1982) noted that specific gravity at most sampling heights decreases from a relatively high value in rings 1–5, to a minimum in rings 6–10, after which there is a slow increase to a maximum some 30–50 rings from the pith. Tree-to-tree variation was observed for the transition pattern from juvenile to mature wood. Although the materials were not genetically defined and the developmental pattern was not described by individual rings, this study sheds light on the possibility of exploring genotypic variation for this species. A detailed profile of juvenile wood development will also provide information regarding the earliest possible age for selecting genotypes with high wood density. This has previously

been attempted for several pine species (e.g., Reid 1963; Burdon and Harris 1973; Loo et al. 1984).

In our previous study of lodgepole pine (Wang et al. 1999), we found significant effects of selecting subpopulations using indices of height growth and Pilodyn pin penetration on overall growth and density parameters at age 12. In the present study, using X-ray densitometry profile data of genetically well-defined materials, we investigated developmental patterns from the pith to the bark of growth traits, wood density parameters, and wood heterogeneity, and analyzed the differences in these patterns among and within subpopulations. Changes in phenotypic correlations among these traits over time were also analyzed. The primary objectives of this study were 1) to investigate the possibility of changing the radial pattern of juvenile wood characteristics by genetic selection; and 2) to determine the earliest possible age for the selection of families combining fast growth and high wood density.

MATERIALS AND METHODS

Materials

Trees used in this study were sampled from a progeny test comprising 177 open-pollinated families, planted as one-year-old seedlings at three sites in the B.C. Ministry of Forests Willow-Bowron Seed Orchard Planning Zone in 1986. A randomized complete block design was used at each site with eight blocks and a single 4-tree row plot per entry per block. In our previous study (Wang et al. 1999), using the breeding value for height and the mean Pilodyn pin penetration value from two sites taken at age 11 as indices for these 177 families, we selected 10 families from each of the following combinations of height growth and wood density to construct four subpopulations: 1) fast growth and high wood density (FH), 2) slow growth and high density (SH), 3) fast growth and low density (FL), and 4) slow growth and low density (SL). For the present study, the classification of subpopula-

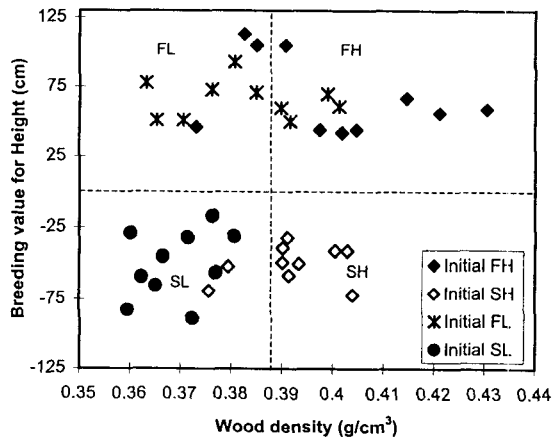


FIG. 1. Classification of subpopulations. The original classification was based on the breeding value for height and the indices of Pilodyn data over the two sites (see Wang et al. 1999). It was readjusted using wood density estimated from X-ray densitometry profiles instead of Pilodyn pin penetration. The dashed lines indicate the boundaries of the classification.

tions was adjusted using overall wood density estimated by X-ray densitometry (Fig. 1) replacing Pilodyn data. The breeding value for height was still used to characterize growth as height is not correlated with wood density (unlike diameter), but has a higher heritability than both diameter and stem volume. The predicted indirect genetic gain in stem volume due to selection on height is higher than gain predicted for direct selection on stem volume in this population (Wang et al. 1999).

As genotype-by-site interaction is relatively small for both height and Pilodyn pin penetration in these materials (Wang et al. 1999), wood samples were collected from only one test site, located at Indian-Point Creek in central British Columbia (Lat. 53°29'N Long. 121°34'W and Elev. 900 m). For each family, two trees were systematically selected and felled in each of six of the eight blocks, and 5-cm-thick wood disks sampled at 0.3 m above ground level. In total, 480 trees were sampled. In order to maximize the number of annual growth rings sampled, wood disks were taken from a relatively low position. As lodgepole pine tapers relatively little, and as little compression wood was observed at this

TABLE 1. Growth traits, wood density parameters, and wood heterogeneity parameters estimated from X-ray densitometry profiles.

Growth traits	RW—ring width EW—ring earlywood width LW—ring latewood width
Density parameters	RD—ring density ED—ring earlywood density LD—ring latewood density, and LP—ring latewood proportion
Heterogeneity parameters	IRVD—intraring variation of density CRVRW—cross-ring variation of ring width CRVEW—cross-ring variation of earlywood width CRVLW—cross-ring variation of latewood width CRVRD—cross-ring variation of ring density CRVED—cross-ring variation of earlywood density CRVLD—cross-ring variation of latewood density

height, this was considered a reasonable sampling height.

Growth traits and density parameters

One diametrical X-ray density profile was obtained for each sample (detailed methods were described in Wang et al. 1999). From the density profiles, ring growth, wood density, and heterogeneity parameters as listed in Table 1 were estimated for each annual growth ring using S-plus statistical software (Statistical Sciences 1993). In order to emphasize the radial pattern of wood development, all growth and density traits are expressed on a linear basis from the pith to the bark, rather than converting parameters to a ring-area basis.

Data analysis

As the wood samples differed somewhat in the number of growth rings sampled at a fixed height, we first needed to determine whether rings should be analyzed using cambial age (i.e., number of rings from the pith) at time of ring formation or using the calendar year in which the ring was formed as the time series

variable. We found that the calendar year of ring formation explained more variation than the cambial age for both ring width (RW) and ring density (RD). Thus, calendar year was used as the time series variable for all subsequent analyses of radial development of growth and wood density parameters. As 1988 was the earliest ring sampled for the majority of trees, data were analyzed for the period from 1988 to 1996.

To detect differences among the four subpopulations and among families within subpopulations for growth traits and wood parameters across all years examined, analyses of variance (Type III sum square of variance) were performed by year using the GLM procedures in SAS (1989) with the following linear model on the basis of individual trees:

$$y_{ijkl} = \mu + b_i + s_j + f_{jk} + bf_{ijk} + \epsilon_{ijkl} \quad (1)$$

where y_{ijkl} is an observation for the l^{th} individual in the k^{th} family in the j^{th} subpopulation in the i^{th} block, b_i is the fixed effect of the i^{th} block, s_j is the fixed effect of the j^{th} subpopulation, f_{jk} is the fixed effect of the k^{th} family within the j^{th} subpopulation, bf_{ijk} is the random interaction of the k^{th} family within j^{th} subpopulation with the i^{th} block, and ϵ_{ijkl} is the random error of the l^{th} individual of the k^{th} family within the j^{th} subpopulation in the i^{th} block.

The number of families in each subpopulation was too small for precise estimates of genetic variance components, and subpopulations were not selected randomly; thus heritability for individual traits and genetic correlations between traits could not be reasonably estimated. Pearson's correlation analysis was applied using SAS (1989) to examine the radial patterns in phenotypic correlations between growth traits and wood properties on the basis of individual tree data.

RESULTS

Radial variation in ring width and ring density

Disk annual ring width (RW) increased sharply from 1988 to 1989 and then decreased

continuously thereafter, with a particularly large drop in 1992 (Fig. 2A). The fast-growing, low-density (FL) subpopulation showed the greatest RW of all subpopulations after 1990. The economically desirable fast-growing, high-density (FH) subpopulation did not exhibit greater RW than other subpopulations as the fast volume growth of the families in this subpopulation is due to primarily faster height growth (not reflected in disk parameters). Differences in RW among the subpopulations generally increased with age, and were consistently significant ($P < 0.05$) after age 6 (1990) (Fig. 2A).

Ring density (RD) was initially high, then decreased until age 10 (1994) (Fig. 2B). The high-density subpopulations FH and SH had higher values for RD across the entire time series than the low-density FL and SL subpopulations. Interestingly, FH families outperformed SH families for RD after 1991 (age 7), and showed the highest RD values among the four subpopulations. Ring density differed significantly ($P < 0.05$) among subpopulations for all years examined (Fig. 2B).

Phenotypic correlations between annual RW and RD also showed a declining pattern with year, with considerable fluctuations from year to year (Fig. 3A). These fluctuations appeared to be associated with annual ring growth, i.e., the smaller the RW, the greater the correlation coefficient. Annual fluctuations in these correlations likely reflect variation in annual climate conditions. The development of the correlations over time also differed among the four subpopulations. The FH families had relatively smaller annual fluctuations in these correlations, but showed the strongest negative phenotypic correlation between RW and RD during the period from 1992 to 1994.

Variation in earlywood traits with age

Ring earlywood width (EW) was initially small, then increased to a maximum in two or three years, depending on the subpopulation (Fig. 2C). It fluctuated greatly from year to year and differed significantly among subpop-

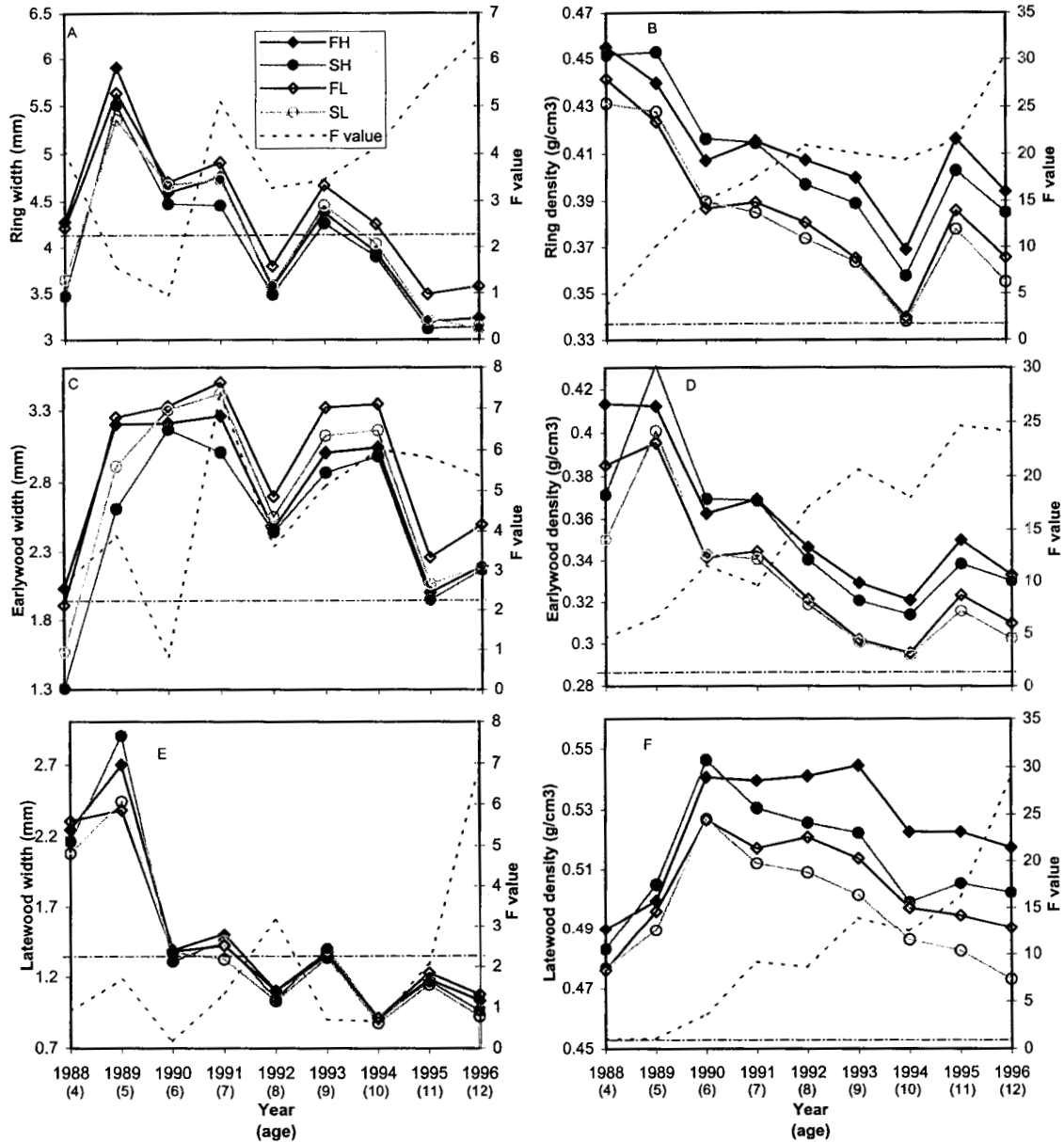


FIG. 2. Changes in annual ring width, ring density, and their components with year (age) for the four subpopulations. A) ring width; B) ring density; C) earlywood width; D) earlywood density; E) latewood width; and F) latewood density; Differences among the subpopulations for each ring width or density trait in each year are indicated with *F*-values (significant when above the horizontal dashed line representing $F = 2.25$, $P < 0.05$).

ulations in all years over the time series except in 1990. Similar to overall ring width, the FL subpopulation consistently had the highest EW, while the FH subpopulation was inter-

mediate for this trait. Changes in earlywood density (ED) with year (Fig. 2D) exhibited a very similar pattern to overall ring density. The FH subpopulation surpassed the SH sub-

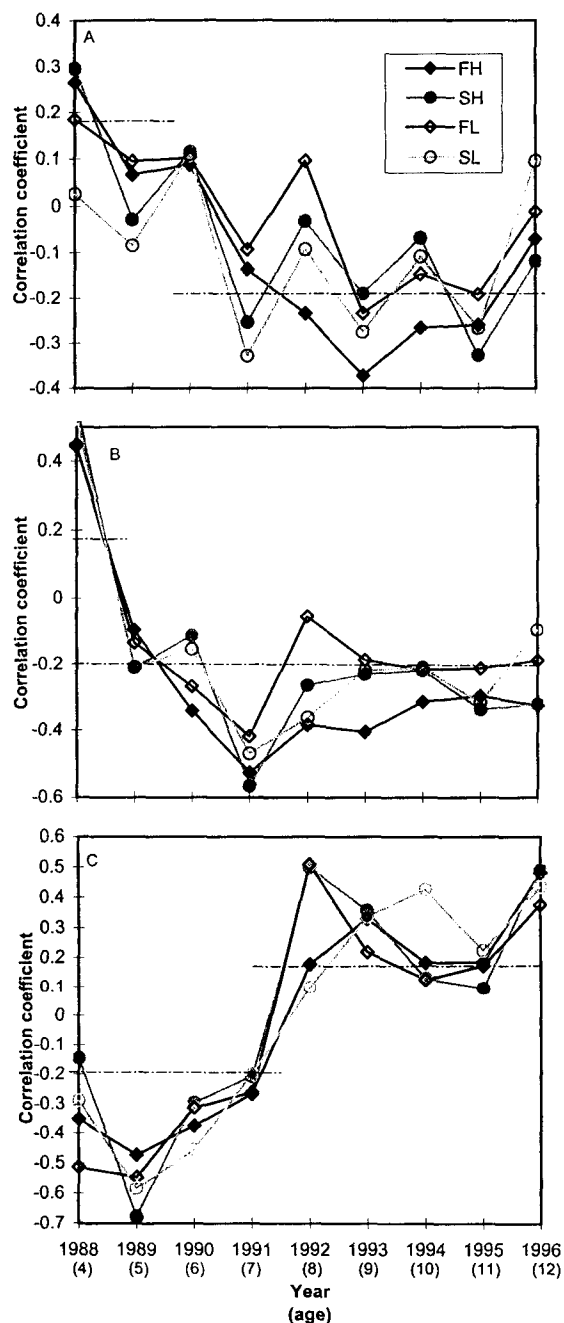


FIG. 3. Changes in phenotypic correlations between ring width and ring density components with year (age) for the four subpopulations. A) the correlation between ring width and ring density; B) the correlation between earlywood width and earlywood density; and C) the correlation between latewood width and latewood density. The correlation is significant if the correlation coefficient is either above the upper (positive) or below the lower (negative) dashed line ($P < 0.05$).

population for ED from 1992 on. The ED differed significantly among subpopulations through the entire period examined.

Phenotypic correlations between EW and ED were positive at the beginning of the series (1988), then became significantly negative and relatively stable for rest of the time series (Fig. 3B). The year-to-year fluctuation in these correlations appeared to be small in comparison with correlations between RW and RD. Again, the FH subpopulation showed less variation among years in these correlations than other subpopulations. However, no subpopulation had a consistently high or low correlation between EW and ED over the entire time series.

Variation in latewood traits with age

Latewood width (LW) was initially large, then sharply declined from 1989 to 1990 (Fig. 2E). It continued to decrease generally thereafter, however, it fluctuated somewhat from year to year. Significant differences among subpopulations were observed only in 1992 and 1996, and no subpopulation consistently ranked high relative to others. In contrast, latewood density (LD) differed significantly among the subpopulations after 1989, and this difference increased with year in general (Fig. 2F). Latewood density was initially low, but increased rapidly during the first few years, reached its maximum at age 6 (1990), then started to decline for most of the subpopulations. Interestingly, the LD of the FH subpopulation remained high for a few more years until 1993, and exhibited the highest LD among the four subpopulations after 1990. The SL subpopulation consistently had the lowest LD after age 4 (1998), and the differences between the SL and the other subpopulations increased with time.

The phenotypic correlation between LW and LD was generally negative for the first four years (1988 to 1991), and then became positive (Fig. 3C). The positive correlation indicated that trees with larger LW tend to have higher LD. The ranking of the correlation co-

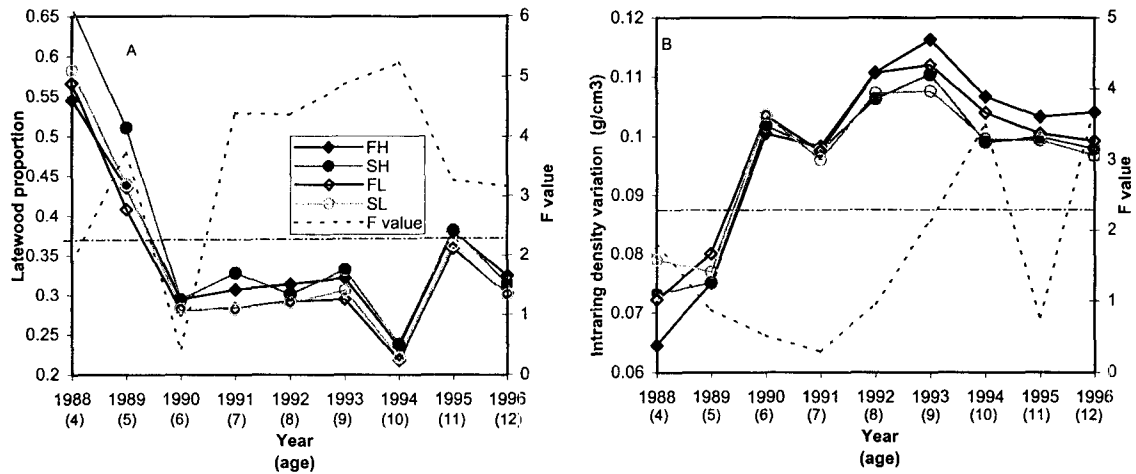


FIG. 4. Changes in annual ring latewood proportion (A) and intraring density variation (B) for the four subpopulations with year. Differences among the subpopulations for each trait in each year are indicated with F values (significant when F -values are above the horizontal dashed line representing $F = 2.25$, $P < 0.05$).

efficients among subpopulations changed from year to year.

Latewood proportion (LP) was high in the early growth rings, but declined sharply thereafter (Fig. 4A). It ranged between 0.54 and 0.63 in 1988, then dropped to less than 0.30 in 1990. Thereafter, no obvious general trend was observed up to age 12, although some year-to-year fluctuations were observed. A very low mean LP was observed in 1994 and a relatively high LP in 1995, which corresponded to density fluctuations in these years (Fig. 2B). This indicates that LP makes a considerable contribution to annual ring density, and is also strongly affected by annual climatic conditions. Differences among subpopulations were consistently significant after 1990, with the two high-density subpopulations (FH and SH) having a larger average LP than the low-density subpopulations.

Variation in wood heterogeneity with age

Annual intraring density variation (IRVD) was initially low, generally increased up to 1993 (age 9) (with the exception of 1991), then declined from 1994 to 1996 (Fig. 4B). The FH subpopulation showed higher IRVD values than other subpopulations after 1992.

However, the differences among the four subpopulations were generally small and not significant for most of the years examined.

Significant differences were found among subpopulations for cross-ring variation of both ring density (CRVRD) and earlywood density (CRVED) (Table 2). The FH subpopulation showed the smallest CRVRD and CRVED, and was significantly different from both the SH and SL subpopulations (Table 3). This is apparently due to a slower decline over time of RD and ED for the FH subpopulation than for the other subpopulations between ages 8 (1992) and 10 (1994). Heterogeneity of latewood width (CRVLW) exhibited the largest CV value, but showed no significant differences among subpopulations (Table 2).

Variation among families within subpopulations

Differences among families within subpopulations were generally small (Fig. 5) compared to the differences among subpopulations for most traits observed. Growth traits showed some significant differences only for the period from 1992 to 1994. For density traits, RD and ED did not show significant differences among families within subpopulations for the

TABLE 2. Variability of cross-ring heterogeneity traits among the pooled families, subpopulations, and among the families within subpopulations.

Trait	Pooled families			Subpopulations F value (P value)	Families within subpopulations F value (P value)
	Mean	CV (%)	Range		
CRVRW (mm)	1.10	17.7	0.80–1.71	1.24 (0.3092)	2.04 (0.0011)
CRVRD (g/cm ³)	0.033	10.8	0.026–0.040	5.44 (0.0035)	1.01 (0.4610)
CRVEW (mm)	0.86	13.5	0.70–1.25	1.24 (0.3090)	1.67 (0.0150)
CRVED (g/cm ³)	0.045	15.6	0.033–0.060	4.51 (0.0087)	1.58 (0.0275)
CRVLW (mm)	0.77	26.1	0.33–1.12	1.02 (0.3971)	1.35 (0.1056)
CRVLD (g/cm ³)	0.039	7.9	0.032–0.045	1.32 (0.2826)	1.39 (0.0840)

entire time series. Variation among families in LD fluctuated around the significance level $P = 0.05$ with age. This indicates that the majority of variation in these traits was utilized in the initial selection of subpopulations. One exception was intraring density variation (IRVD), which exhibited considerable amount of variation among families within subpopulations in most years examined. Significant differences were revealed among families within subpopulations for cross-ring variation of ring width (CRVRW), earlywood width (CRVEW), and earlywood density (CRVED) (Table 2).

Changes in family ranking for growth and density with age

Age-age correlations between annual family ranking and family ranking in the last year studied (1996) for growth and density traits are shown in Fig. 6. These correlations for RW, EW, and LW fluctuated considerably among years across the entire time series, although they generally increased with year. The correlations for RD and ED were initially significant and, together with LD, sharply in-

creased during the first few years up to 1991, but leveled off thereafter. This indicates that the family ranking was stabilized for these traits at age 7 (1991). Annual fluctuations were generally smaller for density traits than for growth traits. Latewood traits LW and LD in both cases showed the strongest annual fluctuations in family ranking.

DISCUSSION

Radial patterns of growth and density

This study investigated the radial patterns of annual ring growth and ring density, as well as their components, in juvenile wood of lodgepole pine. As would be expected with increasing tree diameter, ring width showed a clear decline with age, although fluctuation occurred from year to year (Fig. 2A). While earlywood width initially increased substantially with age, latewood widths decreased dramatically, resulting in a sharp decline in latewood proportion from age 4 to age 6. Year-to-year fluctuations in latewood width appeared to occur on a regular cycle, i.e., a relatively large value was always followed by a relatively

TABLE 3. Comparisons among subpopulations for cross-ring heterogeneity traits including cross-ring variations of ring width, ring density, and their components. FH = fast-growing, high-density, SH = slow-growing, high-density, FL = fast-growing, low-density, and SL = slow-growing, low-density.

Subpopulation	CRVRW (mm)	CRVEW (mm)	CRVLW (mm)	CRVRD (g/cm ³)	CRVED (g/cm ³)	CRVLD (g/cm ³)
FH	1.20	0.91	0.80	0.033b*	0.041c	0.039
SH	1.02	0.83	0.83	0.038a	0.052a	0.039
FL	1.10	0.86	0.72	0.035b	0.045bc	0.037
SL	1.06	0.84	0.72	0.037a	0.046b	0.040

* Means with the same letter are not significantly different at $\alpha = 0.05$.

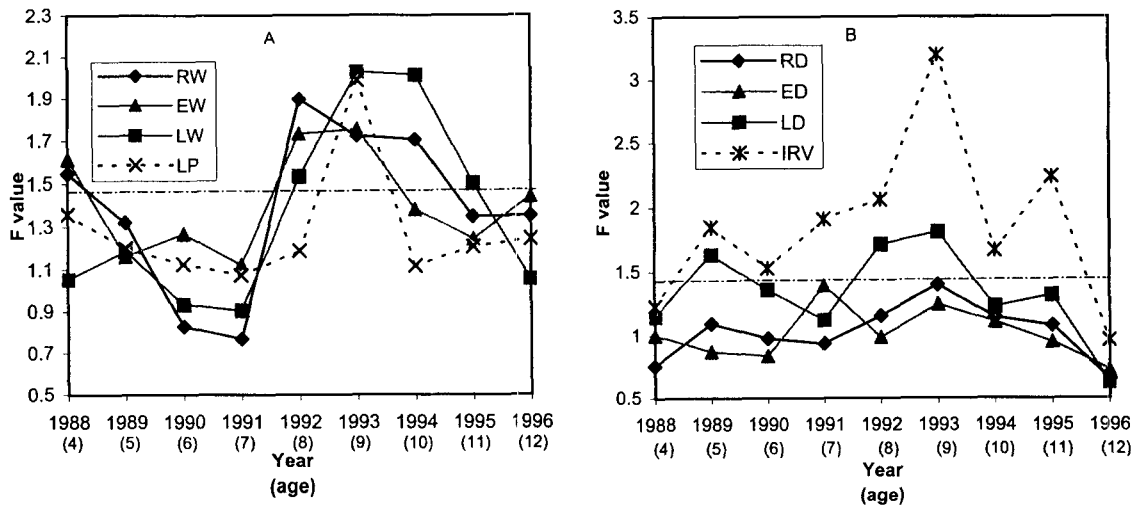


FIG. 5. Changes in variation of ring width (A) and ring density parameters (B) among families within subpopulations with year. Differences are significant when F values are above the horizontal dashed line ($F = 1.48$, $P < 0.05$).

small value. This suggests a possible influence of the amount of latewood produced in one year on the amount of latewood produced in the following year.

Ring density was high initially, then continuously declined with age up to 10 years, at which time it appeared to reach a minimum, and showed some increase thereafter. The development of overall ring density found in the present study (Fig. 2B) is in agreement with previous observations in the same species (Taylor et al. 1982; Kennedy 1995). Earlywood density followed a very similar pattern to ring density. Latewood density exhibited a different pattern, starting low, continuously increasing up to age 6, and then declining. The early increase in latewood density did not compensate for the decline in overall ring density as it was associated with a sharp decline in latewood proportion. The results also suggest that both earlywood and latewood densities, individually and combined, change greatly with age, having different radial patterns in the juvenile wood of lodgepole pine. We also observed that intraring density variation started low, increased rapidly during the first few years, and then stabilized.

The effect of selection on development of juvenile wood variation

The significant differences in ring density components and wood heterogeneity parameters among subpopulations across almost the entire time series demonstrate the effects of selection of subpopulations on wood density parameters. It is worth noting that significant differences in cross-ring density heterogeneity among subpopulations were not statistically detectable in our previous study (Wang et al. 1999) before subpopulations were redefined using X-ray density instead of Pilodyn data. In addition to higher overall density and rapid height growth, the select FH families showed higher mean values for all density parameters after age 7, less marked declines in both earlywood and overall ring densities, and a longer period of producing high density latewood, as well as smaller cross-ring heterogeneity in ring density and earlywood density, than other subpopulations. On the other hand, the SL subpopulation consistently had the lowest earlywood, latewood, and overall ring densities. These results suggest that radial patterns of juvenile wood formation can be improved through genetic selection. This can be

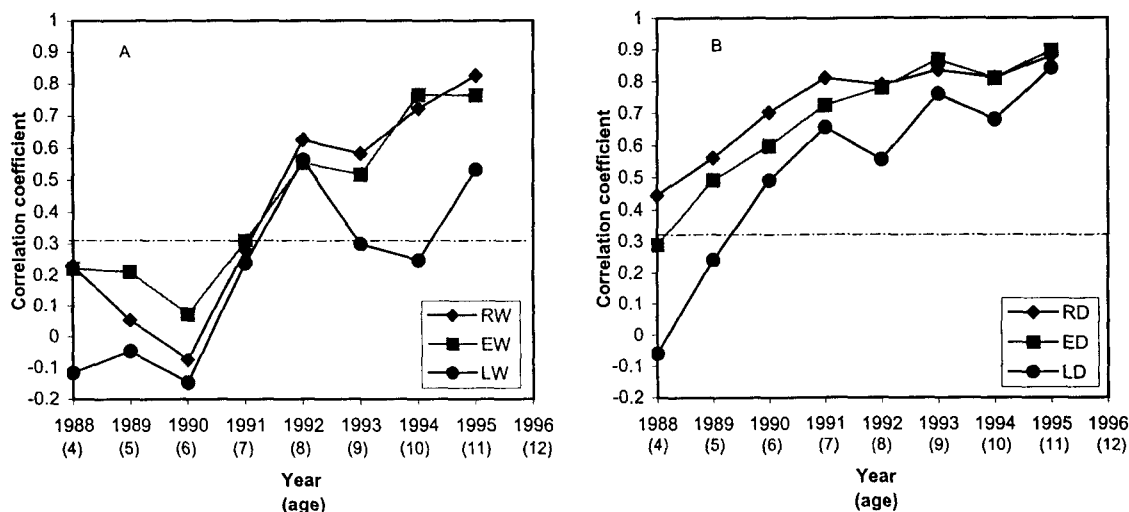


FIG. 6. Changes in correlations between annual family ranking and family ranking in the final year (1996) for ring width parameters (A) and ring density parameters (B). The correlation is significant if the correlation coefficient is above the dashed line ($r = 0.31, P < 0.05$).

achieved either by selecting FH families or by purging SL families from the breeding populations.

The effect of selection for fast growth on ring width was consistent only in the FL subpopulation, not in FH. The rapid diameter growth of the FH subpopulation in the first two years resulted in a relative large diameter core and this will reduce ring width in subsequent years if the cross-sectional area of wood production stays constant. In addition, increased growth was achieved through selection on height, not on diameter or volume, and wood density is negatively correlated with diameter growth (Wang et al. 1999).

Intraring density variation did not differ significantly among the four subpopulations during any of the years studied. This indicates that the selection using breeding values for height and wood density will not affect the intraring homogeneity. However, considerable variation exists among families within subpopulations for this trait. If the breeding goal is to increase intraring homogeneity, a different selection approach may be applied to utilize this among-family variation. Selection for intraring homogeneity could also follow the

selection of FH families in a second stage of selection.

The feasibility of selection on wood density components

Selection on individual density components (i.e., earlywood and latewood density and proportion) may be more effective than selection on overall ring density. Earlywood density showed a very similar radial pattern to overall ring density. This is consistent with our earlier finding that the phenotypic correlation between wood density and earlywood density is the strongest of all possible correlations between overall density and its components (Wang et al. 1999). This indicates that overall ring density is determined primarily by earlywood density, probably due to greater variation in, and a greater proportion of, earlywood than latewood in the annual ring. Thus, selection on overall density can achieve the objective of increasing earlywood density, or vice versa. Latewood density, on the other hand, had a very different radial pattern (Fig. 2F) from overall ring density or earlywood density. Because of the small proportion of

latewood in juvenile rings, this pattern was not reflected well in the profile of overall ring density. Thus, additional gains might be achieved through genetic selection on this trait. Furthermore, latewood density is the only density parameter that is not negatively correlated with any growth traits (Wang et al. 1999).

Latewood volume, rather than proportion, has previously been shown to be a promising trait for simultaneously improving growth and wood density (Wang et al. 1999). The subpopulations appeared to have no differences in latewood width before age 11. However, a relatively large amount of variation in this trait was revealed among families within subpopulations in the present study, suggesting that this remains a potential trait for improvement within subpopulations.

Correlations between growth and wood density components

This study revealed weak, negative correlations between ring width and ring density, as well as between earlywood width and earlywood density, after age 4 (1988), although these relationships fluctuated from year to year. In contrast, the correlation between latewood width and latewood density switched from negative to positive at age 8, and remained positive thereafter. The negative correlation between ring width and ring density after this age is purely attributable to the negative correlation between earlywood width and earlywood density. The FH subpopulation exhibited relatively small annual fluctuations in the correlation between ring width and ring density, and between earlywood width and earlywood density, compared to other subpopulations, indicating that changes in growing conditions between years or possibly sites will likely have less impact on these relationships for this subpopulation than for others.

Age of earliest identification of FH families

An indicator of high wood density that can be assessed when trees are very young is desirable for tree selection and breeding pro-

grams; however, highly variable juvenile wood properties reduce the chance of finding such a trait. The earliest possible age for selecting desirable FH families depends on how early differences among genotypes in growth and wood quality traits are significant and the age after which the ranking of genotypes is relatively stable. The four subpopulations investigated displayed significant differences throughout the chronology from the first ring studied (age 4) for ring density and its components earlywood and latewood densities. The two high-density subpopulations showed higher values for the three density parameters densities from age 6 (1990) on. Meanwhile, family rankings for density traits were well stabilized at age 7 (1991). These results, therefore, suggest that the earliest possible age for identifying high-density families is around 7. If selection for fast height growth is possible at this age, FH families can then be identified. Strong genetic correlations between height at age 7 and at age 24 (Xie and Ying 1996) support this possibility. For ring-width parameters, however, family rankings varied to a much greater extent from year to year, suggesting a stronger genotype-by-year interaction than for density parameters. A longer observation period may be necessary to determine the earliest reliable selection age for this trait.

Early prediction of mature wood density from juvenile wood properties has been attempted for many hard pines. In the closely related species *Pinus banksiana*, King (1967) noted that the specific gravity of 3-year-old material is not useful in predicting the density of mature trees. In *Pinus radiata*, Reid (1963) found that the specific gravity of juvenile wood is significantly correlated with mature wood, while Burdon and Harris (1973) reported that even the first five growth rings give a good indication of the density of outer rings. Loo et al. (1984) also suggested that the juvenile wood density could be an indicator of mature wood density in *Pinus taeda*. Fries (1986) was worried by the low correlation between earlywood and latewood densities in

published reports in determining the relationship between juvenile and mature wood densities in lodgepole pine, as the juvenile wood is dominated by earlywood, while the influence of latewood greatly increased with age. However, we found that the FH subpopulation was superior for both earlywood and latewood densities after age 6. The fact that the FH subpopulation had a higher average density than other subpopulations for both earlywood and latewood increases the possibility that FH families will have high mature wood density according to the literature. Earlywood dominates juvenile wood, while a higher proportion of latewood is produced in mature trees (Harris 1971; Person and Gilmore 1980). The less desirable SL families showed the lowest earlywood, latewood, and overall density from age 7 on, suggesting that it is possible to purge SL families from breeding populations at this age. Thus, it appears likely the changing relative amounts of earlywood and latewood from juvenile to mature wood would not greatly reduce the efficiency of early selection. In fact, we noted a very strong phenotypic correlation between earlywood and latewood densities for this species (Wang et al. 1999). In the near future in the remaining trees in the progeny test sampled for this study there will be a transition to mature wood production as crown closure occurs and the live crowns recede, and it would be advisable to follow-up on this study at that time to assess the transition age and correlations between juvenile and mature wood density components.

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