GENETIC GAINS FROM RED PINE
SEEDLING SEED ORCHARDS

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ABSTRACT.--Analysis of height growth data from 13-year old red pine family tests revealed significant differences among families and test locations, as well as a significant family by location interaction. Differences among families within stands accounted for 88% of the genetic variation observed, while variation among stands and regions accounted for 12% and 0% respectively. Family heritability estimates for height growth ranged between .40 - .50 and, coupled with planned thinning operations, yield expected genetic gains of 3-4% in height growth and 9-11% in stem volume. Analysis of wood specific gravity data revealed significant differences among test locations, but marginal or insignificant differences among families. Future breeding work with these populations should emphasize growth and volume traits; however, the more immediate need is to stimulate flowering and seed production.

Red pine (Pinus resinosa Ait.) is the principal conifer used for reforestation in the north central United States. Although red pine does not regenerate well naturally, its suitability for plantation culture, excellent form, and productivity on pine sites have made it a preferred species. State forest nurseries in the region produce 20-25 million seedlings annually for planting by public agencies, forest industry and private individuals.

From a genetic standpoint, red pine is anomalous among pines in possessing little genetic variation. Results of provenance studies indicate that small though significant differences in growth rate can be detected among red pine seed sources, but that the range of genetic variation observed is much less than that found in other pines (Buckman and Buchman, 1962; Fowler, 1964; Lester and Barr, 1965; Fowler and Lester, 1970; Park and Fowler, 1981). More extensive tests established in 1959 throughout the north central United States generally support earlier conclusions that little or no racial variation in growth rate is apparent in red pine, that faster growing provenances perform well across a range of sites, and that most seed sources contain fast as well as slow growing families (Wright et al., 1972; Sprackling and Read, 1975). Studies of wood specific gravity in red pine suggest that modest levels of variation exist for this character (Rees and Brown, 1945). Inbreeding studies (Fowler, 1965a, b), and a more recent survey of allozyme variation (Fowler and Morris, 1977) have confirmed that red pine is less variable genetically than most other pines.

Tree improvement and breeding efforts with red pine are somewhat controversial because of the obvious restrictions on potential genetic gain (e.g., Wright, 1964; Fowler, 1964). However, the extensive red pine planting program, and concomitant seed requirements, has led to the initiation of tree improvement programs for red pine in the north central region during the past 20 years. In Wisconsin, half-sib family test plantations were established at three locations in 1970 following the "seedling seed orchard" approach of Wright and Bull (1963). Lester (1971, 1976) reported on the early performance of the families included in these tests. In this paper, we present results on height growth and wood specific gravity from these tests 10 years after field planting, together with estimates of genetic gains possible in red pine using the seedling seed orchard approach.

MATERIALS AND METHODS

Between 1963 and 1967, cones were collected from 310 red pine trees in 46 naturally regenerated stands (average of 6.7 trees/stand) throughout Wisconsin (Fig. 1). In 1967, seed were sown in a randomized complete block design in the Wilson State Nursery, Boscobel, WI. Seedlings were lifted in 1970 as 3-0 stock and machine planted at 1.8 x 2.4 meter spacing at 3 locations in Wisconsin. These locations were chosen to represent the 3 climatic or floristic (southern climatic province, transition or "tension

Figure 1. Location of red pine stands from which trees were selected (•); and family test locations (*) in Wisconsin.

zone", and northern climatic province) regions of Wisconsin (Curtis, 1958; Fig. 1). The field planting design was randomized complete blocks with 10 replications per location and 4-tree row plots. Ten additional plots of nursery-run stock of unknown source were included in each replication to serve as a check on commercial seed.

Height growth

At age 10 years (13 years from seed), total height was measured to the nearest decimeter for the two tallest trees in each plot in the 5 most uniform replications at each location. Family means for each plantation were entered for missing plots in all analyses.

Analyses of variance were performed for the 310 families with results as shown in Table 1. Family heritabilities and expected genetic gain were calculated using the formulae given by Shelbourne (1969) and Wright (1976).

Age-age product moment correlations were calculated for height growth from 9 and 13 year measurements (Sokal and Rohlf, 1969) to determine whether the fastest growing families could have been selected at an earlier age.

Wood specific gravity

Wood specific gravity was determined 'for a sample of 3,335 trees representing 211-219 red pine families (number varied depending upon location) retained after the first thinning. A one-inch thick disc was cut from each tree at a position of 10-20 cm above the ground. Samples were debarked and wood specific gravity was estimated using the method of Heinrichs and Larson (1970). Data were analyzed using an analysis of variance similar to that described for height growth.

RESULTS

Growth performance

The distribution of family mean height at each location is shown in Fig. 2. Mean heights for the Oneida Co., Wood Co., and Iowa Co. locations were 45.2, 38.4, and 47.8 decimeters, respectively. The mean of the commercial seed lot was nearly identical

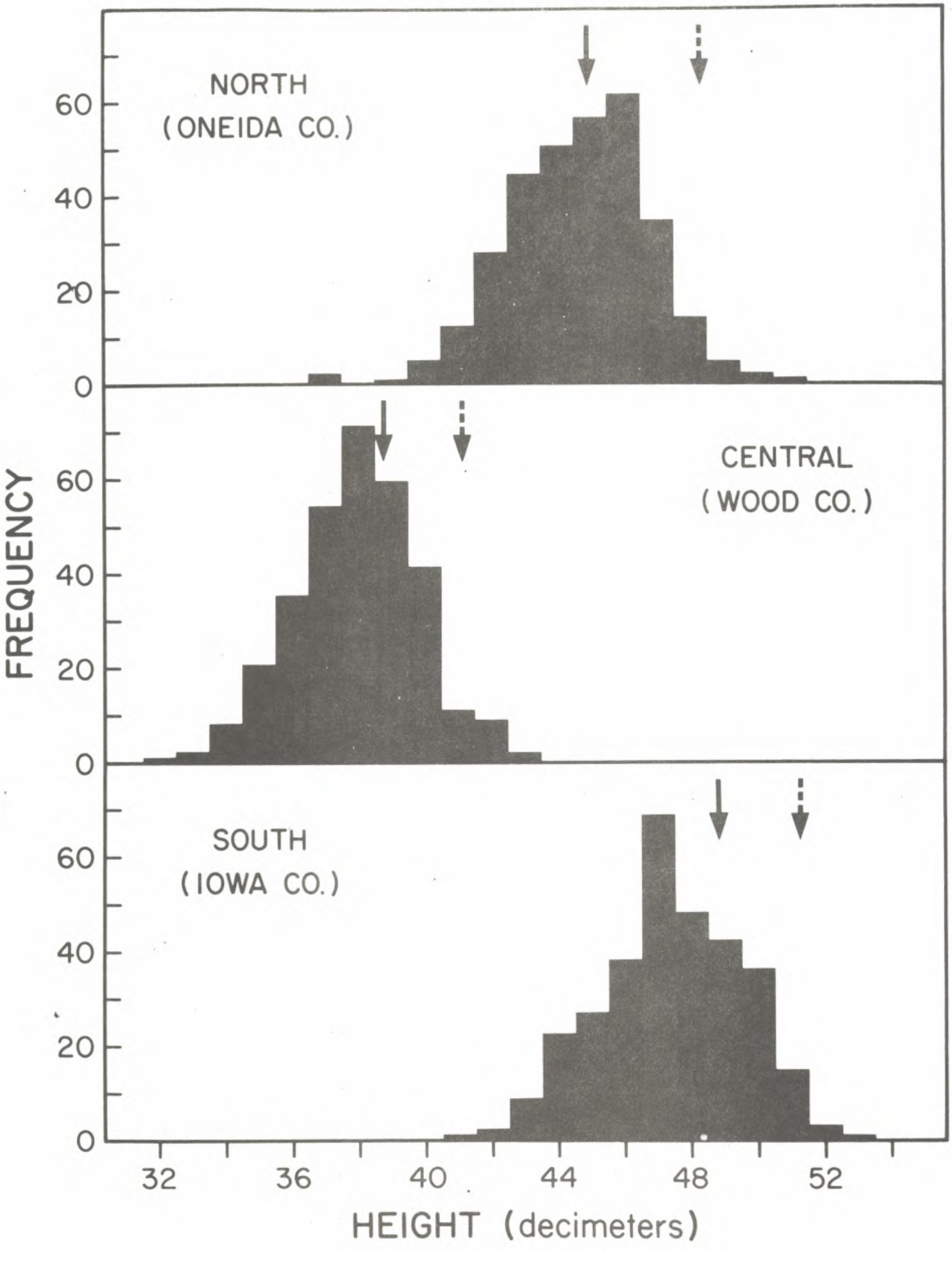

Figure 2. Distribution of mean family height (decimeters) at 13 years for 310 red pine families at 3 locations in Wisconsin. Solid arrow is plantation mean; dashed arrow is mean of 30 fastest growing families.

to the plantation mean at each location, while the best families were as much as 14% taller than the mean. The relatively short stature of the trees at the Wood Co. site is due to the droughty, infertile soil at this location.

Height growth differences among families were significant, though small, and the effect of planting location constituted a major source of variation (Table 1). The family x location interaction term was also significant indicating that family performance was not consistent between locations.

Region of seed collection and stands contributed little to the observed variation, while families within stands were a significant source of variation at the southern Wisconsin site (Table 2). Estimates of variance components indicate that families account for the bulk of the variation (88.3%) as compared to stands (11.7%) and regions (0.0%). The absence of regional differences is more easily seen in Table 3, where mean height of families from each of the three regions are shown for each planting locations. Somewhat different results were observed in Michigan where trees grown from seed collected in different stands and regions within Michigan differed significantly in height growth, especially in Lower Peninsula tests (Yao, et al., 1971). Although sizeable differences exist between different planting locations in Wisconsin, the average performance of families from different regions varied little at any one location. Despite the existence of family differences', and the family x location interaction noted earlier, we believe that movement of seed between regions entails minimal risk and results in little significant loss in growth rate. These findings are not contradictory to earlier studies which noted significant provenance or stand differences (Rudolf, 1964; Wright et al., 1972; and others); rather, these results simply reflect the limited range sampled within which appreciable genetic differentiation was not detected.

TABLE 1. Analysis of variance for red pine family, plantation location, and family x plantation location effects on 13 year height in Wisconsin.

Source of Variation	df	MS	F	Expected Mean Squares
Family	309	71.70	2.78*	$a2_E + ea^2FB + eba2_{FL}$ "4- &ps 2_F
Location	2	71780.75	43.09*	$GE^2 + ea^2$ + efa L + efbza2/9.-1
Family x Location	618	25.84	1.17*	$a2E + {}^{ea}FB^2$ + e"FL
Block/Location	12	1665.87	75.28*	${}^{a}E^2 + {}^{ea}FB^2$ 4- eLaB/L
Family x Block/Location	3708	22.13	2.72*	aE2 + eaFB
Error	4650	8.13		aE2

* Significant at the .01 level.

Table 3. Mean height (decimeters) of half-sib families from seed collected in three regions in Wisconsin and grown at three plantation locations.

Region of Seed Collection	Plantation Location Iowa Co.	Wood Co.	Oneida Co.	Mean
North	47.9	38.4	45.0	43.8
Transition	47.9	38.6	46.0	44.2
South	47.5	38.2	44.6	43.4
Mean	47.8	38.4	45.2	43.8

Wood specific gravity

Although differences in wood specific gravity were quite large between locations, differences among families were significant on an individual planting basis only at the Iowa Co. location (Table 4). On a combined analysis basis using families for which data was available for all three locations differences among families were not significant (Table 4). Given the high cost of measuring wood specific gravity, and the apparently low levels of variation for this character in red pine, further consideration of wood specific gravity in the Wisconsin program would probably not be cost effective.

Table 4. Summary ANOVA for wood specific gravity in red pine at three locations in Wisconsin.

Plantation Location	Source	df	SS	
Iowa Co.	Families	211	0.320	1.23
Wood Co.	Families	210	1.388	1.17^{ns}
Oneida Co.	Families	218	0.199	1.06^{ns}
Combined	Locations	2	1.805	346.61**
	Families	102	0.332	1.25ns
	Loc. x Fam.	201	0.416	.80ns

Significant at 0.05 level; ** Significant at 0.01 level

Wood specific gravity was negatively correlated with 13-year height at all locations (Table 5). Differences in mean wood specific gravity among locations are probably due to site factors; the site at Wood Co. (central) is a very well drained sand. Trees on such sites cease height growth earlier in the growing season and probably shift a larger proportion of their photosynthate into production of thick-walled summerwood tracheids.

Table 5. Summary of 13-year height-wood specific gravity correlations in red pine at 3 locations in Wisconsin.

Location	Mean wood sp. gravity	Mean 13-year height (dm)	Correlation coefficients
Iowa Co.	.355	47.8	-.186*
Wood Co.	.419	38.4	-.242**
Oneida Co.	.334	45.2	-.021

* Significant at 0.05 level

Significant at 0.01 level

DISCUSSION

Heritability estimates and genetic gain

Family heritability estimates were calculated using appropriate variance components and equating these with components of genetic variance (Shelbourne, 1969; Namkoong, 1979). The third analysis of variance, provided estimates of variance components (Table 6). Heritability of height growth for half-sib families was calculated as

$$h_f^2 = \frac{\sigma_F^2}{\frac{\sigma_E^2}{eb} + \frac{\sigma_{FB}^2}{b} + \sigma_F^2}$$

and ranged from 0.40 - 0.50 (Table 7). These estimates are somewhat higher than those calculated for red pine in Michigan (Yao, et al. 1971). However, some individuals within the open-pollinated families may be more closely related than half-sibs, resulting in a slight over-estimate of heritabilities (Namkoong, 1966).

Table 7. Family heritability estimates for 13-year height growth for red pine in Wisconsin

	Plantation Location		
	Iowa Co.	Wood Co.	Oneida Co.
Heritability (h_f^2)	.396	.501	.482
S.E. of h_f^2 estimate*	.039	.048	.048
Family CV (%)	19.7	18.6	17.2

Calculated according to Wright, 1976, p. 244.

Estimates of genetic gain expected from thinning each plantation were calculated as

$$\Delta G = h_f^2 \, i \, \sigma_p$$

where AG is the increment in height, h_f^2 the family heritability estimate, i the standardized selection differential, and σ the phenotypic standard deviation of family means. Expected gains from thinning are provided for several selection intensities in Table 8.

TABLE 6. Analysis of variance for estimation of variance components used in heritability calculations.

		Mean Square				Component Estimate		
	df	Iowa Co.	Wood Co.	Oneida Co.	Expected Mean Squares	Iowa Co.	Wood Co.	Oneida Co.
Block	4	3328.35	564.80	1104.31	$\sigma^2_E + e\sigma^2_{FB} + ef\sigma^2_B$	5.33	0.88	1.75
Family	309	44.54	35.16	43.67	$\sigma^2_E + e\sigma^2_{FB} + eb\sigma^2_F$	1.77	1.76	1.75
Block x Family	1236	26.90	17.53	21.95	$\sigma^2_E + e\sigma^2_{FB}$	8.73	5.19	7.07
Error	1550	9.43	7.15	7.80	σ^2_E	9.43	7.15	7.80

TABLE 8. Expected genetic gain in height growth in red pine for a range of selection differentials (i) resulting from removal of 50%, 80%, or 90% of original families.

			i = .8 (50% retained)		i = 1.4 (20% retained)		i = 1.75 (10% retained)	
Plantation Location		h^2	AG*	% Gain	AG	% Gain	AG	% Gain
Iowa Co.	2.11	.396	.668	1.380	1.170	2.4	1.460	3.0
Wood Co.	1.88	.501	.752	1.958	1.315	3.3	1.645	4.1
Oneida Co.	2.12	.482	.818	1.812	1.431	3.2	1.788	3.8

AG represents height increment (decimeters) in offspring produced from matings among selected parents.

Removal of the slowest growing 50% of the families from each planting was completed during the winter of 1980. Genetic gains of only 1.4-2.0% are expected for this selection intensity, but at final conversion we anticipate retaining only 10% of the original families with an expected gain of 3-4% for height growth (Table 8). We believe these estimates are conservative and likely will be higher due to within-family selection resulting from retaining only the best tree per plot. Expected genetic gains for height growth are similar to those obtained for red pine in Michigan (Yao et al. 1971).

Cubic volume rather than height growth is the important measure by which producers gauge yield. Expected volume gains from thinning these red pine seed orchards are provided in Table 9 for a range of selection intensities. Retention of the best 30 families results in an expected volume gain of 11%. While small relative to volume gains possible with other species, modest gains multiplied via a large planting program represent a sizeable economic gain. We have not completed a formal economic analysis of red pine tree improvement in Wisconsin, but it is obvious that yield increments of 9-12% are substantial given an annual Lake States harvest of 167,000 cords of red pine pulpwood (Blyth and Smith, 1977).

Table 9. Volume gains expected from thinning red pine family tests at three selection intensities.

	Volume Before	Volume After	AG	% Gain
Remove 50%	32.95	34.79	0.184	5.29
Remove 80%	32.95	36.19	0.324	8.95
Remove 90%	32.95	37.00	0.407	11.00

[*] Volumes expressed for individual trees in cubic meters x 10

Diameter calculated by D = .324 x (Height)$^{1.\ 1017}$ Ek, 1974);

Volume approximated by V = .31416 x D^{2} x Height.

Age-age correlations

A continuing problem in tree improvement programs is the need to delay final selection of the best genotypes or families until reliable estimates of performance are available (Franklin, 1979). Highly significant correlations between measurements of a variable at different ages provides some degree of assurance that relative rankings of families have not changed over time. For these three red pine plantings measured at 9 and 13 years of age (from seed), the family mean height correlations were .734 for Iowa Co.; .490 for Wood Co.; and .727 for Oneida Co. These correlations are statistically significant from zero at the 1% level and are in good agreement with correlations of height in red pine on similar materials (Wright et al., 1972). While these correlations are positive and moderately high, they are not so high as to warrant complete reliance upon the accuracy of our family rankings up to age 13. Final choice of the families and individuals to be retained for seed production will be made at about age eighteen.

Future directions for red pine breeding

The choice of the seedling seed orchard approach for improvement of red pine was predicated on the assumptions that genetic gains would be limited due to a paucity of genetic variation, that large replicated family tests would be required to detect the expected small differences among families, and that additional information was needed on the extent of genotype-environment interactions. We now have evidence that heritabilities for height growth are large enough to permit identification of superior families with a reasonable degree of accuracy. Expected first generation genetic gains of 3-4% for height growth and 9-11% for volume, though modest, are attractive enough to warrant continued breeding efforts. Genotype-environment interactions are present, but are relatively small, and a number of families performed above average at all test locations.

A major concern of many tree improvement programs involves compromises resulting from maintaining a broad genetic base to avoid the deleterious effects of inbreeding in future generations while imposing high selection intensities needed to produce genetic gain. For red pine, concern for the effects of relatedness may be negligible, as even selfing results in little or no loss in seed production or progeny vigor (Fowler, 1965; Holst and Fowler, 1973).

Squillace (1973) has shown that despite the generally negative effects attributed to inbreeding in pines the inclusion of relatives to a limited degree in advanced generation selections permits a greater emphasis to be placed upon family versus within family selection. This appears to be especially true when heritabilities are relatively low and most gain is expected from family rather than within-family selection. Use of a combined selection index (family + within family) with some restriction on the number of relatives chosen from any family will likely lead to higher gains as a result of including two or more members from the very best families. Red pine appears to be an excellent candidate for employing such a scheme.

For an advanced generation breeding program with red pine a crossing sequence using the nested polycross design suggested by Burdon and Shelbourne (1972) should be initiated using individuals from the present family tests. Burdon and Shelbourne (1972) discuss the pros and cons of several polycross variations relative to more elaborate (and costly) mating designs. We wish to emphasize here that the major disadvantage to the use of a polycross design in most tree breeding programs,the loss of a large effective population size leading to deleterious inbreeding effects in later generations, may be relatively unimportant in red pine. The advantages of a nested polycross scheme, including low cost, ease of completion, and the estimation of general combining ability (GCA), are attractive features for a small program with limited resources. Burdon and Shelbourne recommmend inclusion of 20-30 clones per nest to maintain a moderate effective population size. For red pine, we believe that nests as small as 10-15 individuals would be adequate for estimating GCA and would permit more intensive selection to be practiced in the present tests.

Although natural stands of red pine are being replaced by plantations, especially in southern Wisconsin, there are a large number of plantations in the 15-30 year age class throughout the Lake States that could serve as additional sources of selections. The uniformity of such plantations relative to natural stands should permit efficient selection even if single-tree heritabilities are relatively small. While parentage would be unknown for such selections, state nurseries have used seed of local origin for almost all stock produced in the past. Such selections could easily be incorporated into the program described above as additional nests to be mated as flowering and resources permit. Red pine programs in other north central states and Canadian provinces could also provide unrelated materials if larger base populations are deemed necessary or desirable in the future.

In order to achieve maximum improvement in the short term, small clonal seed orchards comprised of the best 10-15 individuals from the best families could be established. Red pine, unlike other northern conifers, does not produce frequent, abundant cone crops, and a major consideration in the management of these tests upon conversion to seedling seed orchards will be flower promotion and regular seed production. Inclusion of only 10-15 clones would likely lead to genetic gains similar to those shown in Table 8; while heritabilities calculated on an individual tree basis would be lower, the reduction in expected genetic gain would be offset by a greater selection intensity.

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