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GENETIC VARIATION OF STEM DIAMETER IN
RED PINE (<u>Pinus</u> <u>resinosa</u> Ait.)
IN MICHIGAN

presented by

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Dr.DANIEL E.KEATHLEY
Major professor

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GENETIC VARIATION OF STEM DIAMETER IN RED PINE

(*Pinus resinosa* Ait.) IN MICHIGAN

By:

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ABSTRACT

GENETIC VARIATION OF STEM DIAMETER IN RED PINE (*Pinus resinosa* Ait.) IN MICHIGAN

By:

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This study was undertaken to determine the genetic components of variation and to examine the potential for obtaining genetic gain in stem diameter in red pine (*Pinus resinosa* Ait.)

Red pine seeds were collected from 272 unselected trees, 58 from the Upper Peninsula and 214 from the Lower Peninsula of Michigan. In 1964, three-year-old stocks were used to establish four permanent plantations in Michigan. The plantations were arranged as randomized complete block design with four-tree row plots in one to eight replications. The spacing was 8 x 8 feet (2.4 x 2.4 m). In 1984, trees at the Allegan and Crawford plantations were measured for stem diameter.

The results of this study indicated that there were significant differences between plantations. There were also significant differences between the two seed collection regions. Seeds from the Lower Peninsula grew 6 to 9 %

faster than those from the Upper Peninsula. However, there were no significant differences among stands within regions. Differences among families within regions were significant. No genotype-plantation interaction was detected. The component of the total genetic variation attributable to regions, stands within regions and families within stands were 51.29, 16.01 and 32.69 %, respectively. Narrow-sense heritability of family means was found to be 0.227 $\pm$ 0.031. Immediate gains in diameter growth rate could be realized by using seed from the best region. More genetic gains could be realized by selection the best families and the best individuals within the best families. The progeny test could be converted into a seedling seed orchard using selected families or these selected families could be used for grafted orchards and clonal forestry.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Red pine (*Pinus resinosa* Ait.) is the primary conifer planted for reforestation in the north central United States. Its natural range extends from the northeastern coast to the Great Lakes region in the United States and across portions of southern Ontario, Quebec and New Brunswick in Canada. Twenty to twenty-five million red pine seedlings are planted annually in the north central United States for reforestation (Ager *et al.*, 1983). In the state of Michigan about 10 million red pine seedlings were produced for reforestation in 1981. It is projected that over 15 million seedlings will be produced in 1986 (Levenson and Hanover, 1985). The popularity of red pine among foresters is due to its good form and rapid growth on well drained loam and loamy soils. The principal uses of red pine are for the the production of lumber and pulpwood (James *et al.*, 1982)

Red pine has little or no genetic variation with respect to a wide array of characters including growth rate, morphology, and wood density (Flower and Lester, 1970). Provenance test studies on red pine indicate that little to no significant differences exist in survival rate (Rudolf, 1947), growth rate (Wright *et al.*, 1963; Lester and

Barr 1965), phenology (Rudolf, 1954; Rehfeldt and Lester, 1966), photoperiodic response (Vaartaja, 1962), wood quality (Ress and Brown, 1954; Peterson, 1966; Ager et al., 1983), frequency of lammas growth (Lester and Rehfeldt, 1967), and foliage polyphenols (Thielges, 1972). In a progeny test with red pine in Michigan there were significant differences in height growth (1 % level) among families (Yao et al, 1971). However, a similar study in Wisconsin by Ager et al.(1983) indicated that, although still significant at the 5 % level, the differences among families for height growth were smaller than reported by Yao et al. (1971), and no significant differences in wood density could be detected. Studies based on inbred population (Flower, 1964 b, 1965) and the examination of allozyme variation (Flower and Moris, 1977) have confirmed that red pine is less variable genetically than other pines.

Potential for genetic improvement is dependent upon the and type of genetic variation that is present in the species. The fact that red pine shows less genetic variation than most forest trees has lessened the effort, but not the need for a tree improvement program focused on red pine. The extensive red pine planting programs in the north central United States have led to the initiation of a tree improvement program for this species in that region. This study reports the results of individual measurements from two plantations established by Michigan State University in 1964 in Michigan. The objectives of this study were:

(1) to analyze the genetic components stem diameter stem diameter variation in red pine and

(2) to examine the potential for obtaining significantimprovement in stem diameter in red pine.

REVIEW OF LITERATURE

Work aimed at assessing the potential for improving growth rates and other characteristics in red pine through a breeding program was initiated by the Lake State Forest Experimental Station (now, North Central Forest Experimental Station) in 1928. This work began with the collection of seed from 37 different locations throughout the Lake States and New England. Seedlings from this seed were used to establish plantations in the Superior, Chippewa and Huron National Forests in 1931. In 1933 three additional plantations were established in the same areas using trees from 144 seed sources. The Allegheny Forest Experimental Station conducted a provenance test containing 50 different seed sources in the Kane Experimental Forest in 1937 (Hough, 1957; Rudolf, 1953). A plantation was established at Cass Lake, Minnesota in 1937 using 48 seed sources that wereleft over after the establishment of the 1931 and 1933 plantations (Rudolf, 1953; Buckman and Buchman, 1962). Due to a combination of drought, fire and other problems, among the 1931 and 1933 plantations, only those plantations in the Superior National Forest have survived (Rudolf, 1964; Hough, 1967).

In 1947, Rudolf (1947) reported on the surviving 1931 red pine plantation in the Superior National Forest. At 16 years, his results indicated that seedlots from northern Minnesota and northern Wisconsin had the highest rate of survival, and had more rapid height and diameter growth rates. Seedlots from central Wisconsin, Michigan and New England had poor growth. These results were only based upon the relative performance of the seedlots, no statistical analysis was performed. Wright _et al_. (1958) reanalyzed the same experimental data statistically, and found no significant differences among the Lake States origins growing in the Superior National Forest.

When analyzed at 25 years from seed, the 1933 red pine plantation yielded results that were similar to those of 1931 plantation reported by Rudolf (1947). When the seed sources were ranked based on cubic feet of volume per 100 trees planted, all of the sources in the top 20 % were from localities in Minnesota, northern Wisconsin and the Upper Peninsula of Michigan. None of the sources from central Wisconsin, Michigan's Lower Peninsula or the northern states was included in this category (Rudolf, 1964). Based upon these results, Rudolf (1964) concluded that the local and near local sources performed best at this age, and those from a farther distance performed more poorly.

Hough (1957) reported on the results of the 1937 plantation from the Kane Experimental Forest. At five years of age, survival and height growth did not differ significantly among seed sources. Differences in height growth among seed sources were, however, found to be significant at 10 years. Hough (1967) reanalyzed this plantation at 20 and 25 years. In both cases his results indicated that there were small but significant differences for height growth among seed sources. Seedlots grown from seed collected from southern latitudes had better height growth than those from northern latitudes. The best seedlots were from the Lower Peninsula of Michigan and eastern Wisconsin.

Peterson (1966) analyzed the 1937 plantation in the Kane Experimental Forest at 27 years of age. He analyzed 10 of the 50 sources, and found that differences among seed sources were highly significant for increment width of stem diameter and wood specific gravity.

Rees and Brown (1954) measured and analyzed the 1937 plantation in the Cass Lake Forest, Minnesota at 17 years. They analyzed 19 of the 48 seed sources. The results showed that the following traits were not significantly affected by seed source: percentage of summer wood, average diameter inside the bark at 82 inches (2.10 m) above ground, height growth and volume index. The same experiment was reanalyzed by Buckman and Buchman (1962) at 27 years of age. They found that there were no significant differences in average tree height between the eight regional groupings. They concluded that red pine exhibited less racial variation in height growth than did other pines.

In 1949, the University of Wisconsin in cooperation with the Wisconsin Conservation Department initiated a tree improvement program for red pine. The program was started by collecting seed from 72 individual trees in 10 locations in Wisconsin and Canada. Seedlings from this collection were used to establish two plantations in 1952 and four plantations in 1954 using lattice designs (Lester and Barr, 1965).

The 1952 and 1954 plantations were measured and analyzed by Lester and Barr (1965) at the ages of nine and 11 years, respectively. The results showed significant family effects for the following traits: height growth, stem-diameter, volume, and and mortality. They indicated that it would be possible to attain genetic gains for growth rate, but selection would have to be based upon a progeny test with very high precision.

In 1957, a provenance test with red pine was established in Wisconsin. This test contained 18 seedlots collected from Canada. At eight years of age, shoot elongation was measured andanalyzed. The results showed that there were significant differences in the following characteristics associated with shoot elongation: total height, total elongation, bud length and the termination, duration and growth rate of elongation. Differences in the date of the initiation of elongation, however, were not significant (Rehfeldt and Lester, 1966)

Wright *et al*. (1963) published a provenance test study on red pine using nursery data involving 77 different seed sources. At three years from seed, the results for height growth indicated the presence of significant differences among progenies, both within and between regions. They also reported that there were no significant differences among progenies for other traits such as foliage color, foliage length, bud type and hardiness. These differences in height growth, however, were relatively small in comparison to those found in other pines. In the provenance test of red pine studied by Wright et al. (1963), the tallest seedlot grew two times as fast as the slowest one. In comparison, the corresponding figure at the same age in scotch pine (Pinus sylvestris) was six times (Wright and Bull, 1963), and three times in jack pine (Pinus banksiana) (Canavera, 1969).

The above planting stocks studied by Wright et al. (1963) with additional 14 seed sources were tested in eight locations in the north central states in 1963. The results of this experiment were reported by Wright et al. (1972). For height growth, seedlots from Michigan's Lower Peninsula were found to grow the fastest at all sites except one. On average they were 8 % the all-plantation average at 11 years of age. Seedlots from New Brunswick, Manitoba, and western Ontario grew the slowest at all sites. Their average growth was 8 % less than the all-plantation average. Wright et al. (1972) also observed that there were significant differences in height growth among the regions of seed collection.

In 1964, Michigan State University established an open-pollinated progeny test at four locations in Michigan. This test contains 272 seedlots from unselected individual trees from the Upper and Lower Peninsula of Michigan. Yao et al. (1971) reported statistically significant differences among the offspring of different stands in the same peninsula and between the progeny of trees in the same stand for height growth. The experiment also showed the presence of genotype-enviroment interactions for height growth. In the Lower Peninsula plantations, trees grown from seed collected in the Lower Peninsula were 10 % taller than trees grown from seed collected in the Upper Peninsula. In the Upper Peninsula plantations, however, trees grown from seed collected in the Lower Peninsula were only 3 % taller than trees grown from seed collected in the Upper Peninsula. The narrow-sense heritability of family means for height growth was found to be 0.204 for the Lower Peninsula data, while the corresponding heritability, calculated from the Upper Peninsula data was 0.124. Based upon the retaining of 25 tallest families in the last thinning, Yao et al. (1971) estimated that the genetic gains for height growth were 3.6 and 2.5 % for the Upper Penisula and Lower Peninsula plantations, respectively. They recommended that seed should be used where it was produced.

Steiner (1979) studied the Kellogg Forest plantation of the provenance test described by Wright et al. (1972) for bud-bursttiming. He found that there were no significant differences among seed sources. Steiner (1979) also analyzed similar studies for seven other north-temperate pines at the same location test. All seven species showed significant differences in bud-burst timing among seed sources.

In 1970, the University of Wisconsin conducted a similar open-pollinated progeny test with red pine using 310 seedlots from natural stands throughout Wisconsin. The experiment was established at three locations in Wisconsin. Height growth and wood density were measured and analyzed in these plantations at 13 years of age by Ager et al. (1983). The analysis of the height growth data indicated that significant differences were present among families and test locations. Significant family-plantation interactions were detected. Differences among families within stands accounted for 88 % of the total genetic variation, while stands within regions and regions accounted for 12 and 0 %, respectively. Narrow-sense heritability of family means for height growth were calculated to be between 0.40 and 0.50. The genetic gains were predicted to be 3 to 4 % for height growth and 9 to 11 % for stem volume.

Attempts have been made to increase the amount of genetic variation in red pine through interspecific hybridization. Thus far the results have not been promising due to strong interspecific barriers. Wright and his coworkers made 55 species crosses of the hard pines, series Sylvestres during the period 1948 to 1956. Thirty-one of the species tested failed to cross to other species. One of those unsuccessful species was red pine (Wright and Gabriel, 1958).

Many attempts have been made to cross red pine with Austrian pine, since the latter species has been successfully crossed with several other pines. For example, Wright and his coworkers pollinated more than 300 female strobili in an attempt to make this cross. Both species were used as the female parent. All the crosses failed (Wright and Gabriel, 1958). At the Institute of Forest Genetics in California, the cross between red pine and Austrian pine was attempted using more than 500 strobili from 30 different trees. The results have not been successful so far (Critchfield, 1963). In Canada, Flower (1964) reported a number of crosses between red pine and Austrian pine using more than 700 female strobili from 24 different trees. None of those crosses was successful.

Out all of the attempts at hybridization, only one cross, *Pinus nigra* var. austriaca x *P. resinosa*) made at the Institute of Forest Genetics in 1955 yielded interspecific hybrids (Critchfield, 1963; Flower and Lester, 1970). The hybrids are intermediate between their parents in most characteristics, such as size of conelet and cone, flowering time, leaf dimension and leaf anatomy but they exceed either parents in height growth.

Morris *et al*. (1980) used isozyme variation to analyze the genotype of the putative hybrids at the Institute of

Forest Genetics. The results of this study indicated that they were not red pine hybrids, but rather hybrids between Austrian pine and other unidentified species.

Moulalis *et al*. (1976) obtained 23 putative hybrids of *Pinus nigra* x *P. resinosa* and 21 of *P. heldreichii* x *P. resinosa*. However, the authenticity of these hybrids has not been verified yet.

MATERIALS AND METHODS

Seed Procurement.- Seed was collected in 1960 from natural stands of red pine in Michigan. The collection effort was coordinated by J.W. Wright and W.I. Bull of Michigan State University. The collections were made by personnel of the United States Forest Service and the Division of Forestry, Michigan Department of Natural Resources. Seeds were collected from and maintained in individual tree seedlots. Seed collections were made from unselected 272 trees, 58 from the Upper Peninsula and 214 from the Lower Peninsula of Michigan (Figure 1). Seeds were accompanied by data on the location, relative height and stem diameter, and stem form of the parent trees.

Nursery Practice.- All seeds were sown in the Michigan State University Experimental Nursery in East Lansing, Michigan in 1961. The seedlots were sown in a randomized complete block design with each seedlot replicated four times. Nursery plots were four feet long and six inches apart. There was an average density of 50 seedlings per square foot in the plots. Two years after sowing the seedlings were transplanted using the same design. The average density of the transplants was 10 seedlings per square foot.

Plantation Establishment.- In 1964, four permanent plantations (Figure 1) were established using 2-1 planting stocks. The experiment used a randomized complete block design with four-tree row plots and spacing of 8 x 8 feet (2.4 x 2.4 m). Due to the low number of seedlings in some of the seedlots, seedlots are not represented in all locations or in the full number of blocks in each plantation.

Further details concerning the establishment of the individual plantations are as follows:

MSFGP-1/2/3/-64:

Planted 4/13/64 at Allegan County : eight replicates, randomized complete block designs, four-tree row plots; site level, sandy soil, sparce weed cover; no herbicide treatement before planting.

MSFGP-5/6/7-64:

Planted 5/6/64 at Crawford County: eight replicates, randomized complete block design, four-tree plots; site nearly level, a loamy sand with a dense quack sod; plowed and disked before planting, treated with a simazin and amino triazole spray after planting.

MSFGP-8-64:

Planted 5/11/64 at Delta County: three replicates, randomized complete block design, four-tree row plots; sandy soil with dense sod; plowed disked, and treated with aldrin before planting.

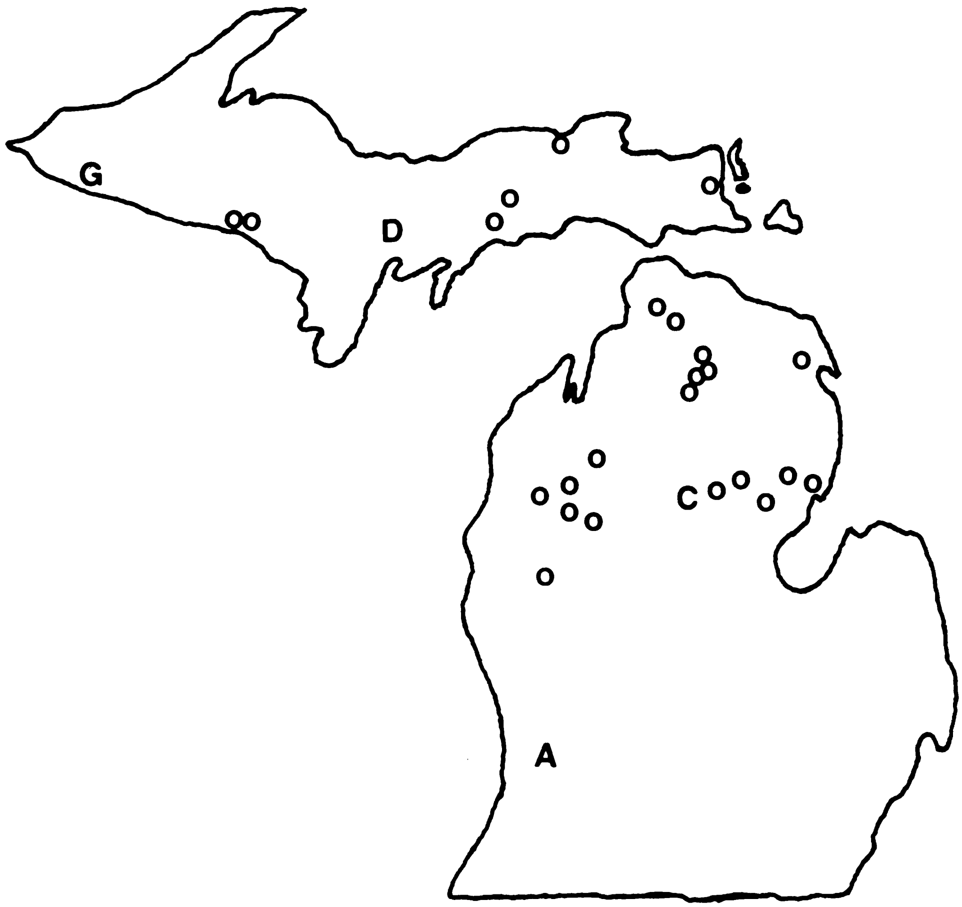

Figure 1. Location of seed collection areas (circles) and of the four red pine plantations in Michigan. A- Allegan C- Crawford, D- Delta, G- Gogebic.

MSFGP-9-64:

Planted 5/13/64 at Gogebic County: one replicate, randomized complete block design, four-tree row plots; site rough; furrowed prior to planting.

This study only deals with the Allegan and Crawford County plantations. Further details about site conditions in those two plantations are depicted in Table 1.

Table 1. Site Conditions in two test plantations 1)

Name of plantation	Mean of temperature Jan. (°C)	July (°C)	Ann. (°C)	Ann.prec. (mm)	Soil
Allegan	- 5.32	21.78	8.79	942	Sandy
Crawford	- 8.68	19.60	6.27	741	Sandy loam

1) Climate data: thirty years average (1954 - 1983), National Climatic Center, United States Department of Commerce.

Stem diameter measurements were taken in July and August 1984 for the Allegan and Crawford plantations, respectively.The measurements were made on individual trees at breast height to the nearest millimeter using a diameter tape. Four replicates were measured for each plantation.

An analysis of variance was conducted according to the model presented in Table 2. Plantations, replicates, stands within regions and families within stands were considered to be random. Regions was considered to be fixed. Plot mean

Table 2. Form of analysis of variance

Source of variation	DF	MS	EMS
Rep.(Plant.)	(bp - p)	MSB	------------
Plantations	(p - 1)	MSP	$\sigma^2_E+b\sigma^2_{FP}+bm\sigma^2_P$
Families	(m - 1)	MSF	$\sigma^2_E+b\sigma^2_{FP}+bp\sigma^2_F$
Regions	(r - 1)	MSR	$\sigma^2_E+b\sigma^2_{F(R)P}+bg\sigma^2_{RP}+$ $+bp\sigma^2_{F(R)}+bpg\sigma^2_R$
Fam.(Reg.)	(m - r)	MSF(R)	$\sigma^2_E+b\sigma^2_{F(R)P}+bp\sigma^2_{F(R)}$
Stands(Reg.)	(n - r)	MSS(R)	$\sigma^2_E+b\sigma^2_{F(S)P}+bf\sigma^2_{S(R)P}+$ $+bp\sigma^2_{F(S)}+bpf\sigma^2_{S(R)}$
Fam.(Stands)	(m - n)	MSF(S)	$\sigma^2_E+b\sigma^2_{F(S)P}+bp\sigma^2_{F(S)}$
Fam.x Plant.	(m-1)(p-1)	MSFP	$\sigma^2_E+b\sigma^2_{FP}$
Reg.x Plant.	(r-1)(p-1)	MSRP	$\sigma^2_E+b\sigma^2_{F(R)P}+bg\sigma^2_{RP}$
Fam.(Reg.)x Plant.	(m-r)(p-1)	MSF(R)P	$\sigma^2_E+b\sigma^2_{F(R)P}$
Stands(Reg.)x Plant.	(n-r)(p-1)	MSS(R)P	$\sigma^2_E+b\sigma^2_{F(S)P}+bf\sigma^2_{S(R)P}$
Fam.(Stands)x Plant.	(m-n)(p-1)	MSF(S)P	$\sigma^2_E+b\sigma^2_{F(S)P}$
Error	by subtraction	MSE	σ^2_E
Total	(mbp-1-missing plots)		

where b = number of replicates
p = number of plantations
m = total number of families tested
n = total number of stands tested
r = total number of regions tested
f = harmonic mean number of families/stand
g = harmonic mean number of families/region

values were used as entries in the analysis of variance. However, attempts have been made to use individual measurements as entries in the data analysis. Due to the difficulty in finding an appropriate statistical package program which is able to handle the available data, the efforts have not succeeded so far.

F tests were performed as indicated by arrows in Table 2, except that synthetic F tests and degrees of freedom were computed by the method of Cochran (1951) to test the effect of stands within regions and regions.

The estimate of heritability on family mean basis was calculated according to Wright (1976):

$$h_f^2 = \frac{\sigma_F^2}{\sigma_F^2 + \sigma_{FP}^2/p + \sigma_E^2/bp}$$

where h_f^2 = narrow-sense family heritability, σ_F^2 = variance component of family, σ_{FP}^2 = variance component of family-plantation interactions, σ_E^2 = variance component of error, p = number of plantations, and b = number of replicates per plantation. The standard error of the family heritability was calculated as $4\sigma t$ from the intraclass correlation equation according to Becker (1984) :

$$\sigma_t^2 = \frac{2(n.- (1 - t)^2 [1 + (k - 1)t]^2}{k^2 (n.- S)(S - 1)}$$

and

$$k = \frac{1}{S-1}\left(n. - \frac{\Sigma n_i^2}{n.}\right)$$

where $t = 1/4\, h^2$ for half-sib families, S = number of families, n = number of plots for i^{th} family and n.= total number of plots.

Estimates of genetic gains in stem diameter expected from thinning were calculated using the formula :

$$Gs = h_f^2\ i\ \sigma p$$

where Gs = genetic gain, h_f^2 = heritability, i = selection intensity, and σp = phenotypic standard deviation of family means.

The association between stem diameter of stand means and north latitudes was determined using simple linear regression. Finally, correlations between ages of 15 and 20 years for stem diameter of family means were calculated.

RESULTS AND DISCUSSION

Test of Significance

Based upon the grouping of families according to stands and origins (Table 3), an analysis of variance was conducted. A test of homogeneity indicated that the variance among families across the two regions was homogeneous. The analysis of variance was then performed as shown in Table 4. The results indicated that there were highly significant +ifferences between the Allegan and Crawford plantations. Trees in the Allegan plantations grew more slowly than those in the Crawford plantation (Table 3). This was due to the lower soil fertility at the Allegan site, since other site conditions were more favorable for growth than bhose found in the Crawford plantation (Table 1).

The differences due to regions of seed collection were significant (Table 4). Trees from seed sources in the Lower Peninsula had stem diameters that were 6 to 9 % larger than those from seed sources in the Upper Peninsula (Table 3). Similar results for height growth were reported by Yao *et al.* (1971) from the same experiment. The red pine forest of the Lower Peninsula is separated from that of forest in the Upper Peninsula by the Straits of Mackinac which form a natural barrier to crossing so that natural selection could

Table 3. Relative 20-year stem diameter of red pine grown from seed collected in 19 Michigan Counties at two location tests.

County of origin	North Lat. (degree)	Relative stem diameter when planted Allegan (percent of plantation mean)	Crawford
Upper Peninsula			
Schoolcraft	45.9	91	96
Iron	46.0	95	95
Luce	45.7	103	98
Chippewa	46.3	83	89
	Average	93	95
Lower Peninsula			
Grand Traverse	44.5	102	101
Alpena	44.2	105	98
Otsego	45.0	102	98
Cheboygan	45.5	106	102
Cheboygan	45.2	102	103
Cheyboygan	45.3	101	107
Ogemaw	44.6	103	103
Crawford	44.6	95	95
Crawford	44.6	105	107
Crawford	44.6	97	102
Alcona	44.6	105	100
Newagyo	43.7	102	101
Oscoda	44.6	99	101
Maniste	44.3	101	101
Wexford	44.3	100	100
	Average	102	101
Actual mean stem diameter (mm)		149	166

Table 4. Analysis of variance of 20-year stem diameter data for red pine grown at two plantations

Source of variation	df	MS	F value	EMS 1/
Reps(Plant.)	6	3395.84	____	
Plantations	1	82253.086	168.90**	$\sigma^2_E+4\sigma^2_{FP}+652\sigma^2_P$
Families	162	731.75	____	
Regions	1	15808.09	36.85*	$\sigma^2_E+4\sigma^2_{F(R)P}+4g\sigma^2_{RP}+8\sigma^2_{F(R)}+8g\sigma^2_R$
Fam.(Reg.)	161	638.11	1.31*	$\sigma^2_E+4\sigma^2_{F(R)P}+8\sigma^2_{F(R)}$
Stands(Reg.)	17	1163.19	1.95ns	$\sigma^2_E+4\sigma^2_{F(S)P}+4f\sigma^2_{S(R)P}+8\sigma^2_{F(S)}+8f\sigma^2_{S(R)}$
Fam.(Stands)	144	576.12	1.19ns	$\sigma^2_E+4\sigma^2_{F(S)P}+8\sigma^2_{F(S)}$
Fam.xPlant.	162	576.97	____	
Reg.xPlant.	1	279.12	0.57ns	$\sigma^2_E+4\sigma^2_{F(R)P}+4g\sigma^2_{RP}$
Fam.(Reg.)x Plant.	161	488.26	0.95ns	$\sigma^2_E+4\sigma^2_{F(R)P}$
Stands(Reg.)x Plant.	17	506.095	1.04ns	$\sigma^2_E+4\sigma^2_{F(S)P}+4f\sigma^2_{S(R)P}$
Fam.(Stands)x Plant.	144	486.150	0.95ns	$\sigma^2_E+4\sigma^2_{F(S)P}$
Error	849	511.60		σ^2_E
Total	1181			

*, ** = significant at 5 and 1 percent level, respectively
1/ f, g = harmonic mean number of familes/stand, families/region were 12.87, and 108.91, respectively.

result in the development of distinct races (Wright *et al*., 1972). In contrast, there were no significant differences among progenies of trees from different stands within regions or among progenies of trees from different families within stands. Differences among families were significant, when the effect of stands was confounded into the family effect. This indicates that differences among families within regions exist. No genotype-environment interaction was detected. Trees grown from seed collected from different regions, stands or families grew at the same relative rates in in the Allegan and Crawford plantations. Somewhat different results in height growth were reported by Yao *et al*. (1971) from the same experiment. In that study, differences among families within stands, among stands within regions, as well as family-plantation interactions in height growth were significant.

The genetic variation in stem diameter reported here was in agreement with that observed by Lester and Barr (1965) from a similar study in Wisconsin. However, they were able to detect differences among families when the data were analyzed in lattice designs. When the same data were analyzed in a randomized complete block design the differences among families in stem diameter growth were not significant.

Association between Stem Diameter Growth and North Latitudes

Correlations between stem diameter growth and north latitudes were calculated for each plantation using the data in Table 3. The results indicated that the association between stem diameter growth and north latitudes was significant at the 1 % level for both plantations. The coefficients of correlation (r) were calculated to be - 0.57 and - 0.59 for the Allegan and Crawford plantations, respectively. Trees grown from seed collected at more southern latitudes had greater stem diameter growth than those from northern latitudes. These results were in accordance with those reported by Hough (1967) from a progeny test with red pine in Wisconsin, but he did not mention the magnitude of the coefficient of correlation.

Components of Variance

The amount of genetic variation in stem diameter that can be attributed to regions, stands within regions, and families within stands was estimated using components of variance derived from the analysis of variance in Table 4. Variance components are expressed as a percentage of the total genetic variation (Table 5). Knowledge of the amount of variation associated within each component indicates in which level selection will achieve the greatest genetic gain per generation. The total genetic variation attributable to regions represented the biggest portion of the total genetic variation in stem diameter growth (51.29 %). Families within stands and stands within regions accounted for 32.69 and 16.01 % of the total genetic variation, respectively.

Table 5. Variance component estimates of stem diameter growth in red pine

Sources	Component estimate	% of total
Regions	17.65	51.29
Stands (Regions)	5.51	16.01
Families (Stands)	11.25	32.69

Ager _et_ _a_. (1983) reported different results for height growth of red pine in Wisconsin. Regions of seed collection did not contribute to the total genetic variation, while the components of variance attributable to families and stands were 88.3 and 11.7 %, respectively. In that study the absence of region contribution to the total genetic variation was apparently due to the limited sample of regions.

The distribution of the genetic variation among regions, stands, and families has an important implication from a practical standpoint. This information can be valuable indirecting further improvement work for stem diameter with red pine in Michigan. Over one-half of the potential genetic gain in stem diameter growth could be realized by selection from the best region. The Lower Peninsula is the best seed source for collecting seeds used for reforestation in this peninsula. Further gains could be realized by selection from the best families within the best regions. From an economic viewpoint selection between regions is the most desirable because the expected gain can be realized immediately without waiting for the more expensive and time-consuming family selection.

Heritability and Genetic Gain Estimation

Narrow-sense heritability of family means in stem diameter were calculated using components of variance derived from the analysis of variance in Table 4. The family heritability was found to be 0.227 ± 0.031. This family heritability is low in comparison to values for other conifers (Table 6). This heritability was similar to that value for height growth reported in red pine from the same plantations (Yao *et al.*, 1971). Since there have been no other studies of this type reported in red pine, comparison within this species cannot be done.

Table 6. Narrow-sense family heritability estimates in stem diameter from other conifers

Species	Age (yr.)	h_f^2	Reference
E. white pine (*Pinus strobus* L.)	8	0.83	desBordes and Thor (1979)
E. white pine	9	0.84	Mullins (1983)
Caribbean pine (*Pinus caribaea* Morelet)	8	0.65	Ledig and Whitmore (1981)
Jack pine (*Pinus banksiana* Lamb.)	12	0.31	Ernst *et al.* (1983)
White spruce (*Picea glauca* (Moench)Voss)	20	0.35	Merrill and Mohn (1985)

Estimates of genetic gains were calculated for several selection intensities expected from thinning among families (Table 7). The expected genetic gains in stem diameter were found to be small in comparison to those reported by Yao et al. (1971) for height growth from the same experiment. A genetic gain of 3.29 % would be expected if 1 % of the original families were retained. These expected genetic gains would likely be higher when within family selection was practiced. They might also have been higher, if a different experimental design had been used. Lester and Barr (1965) reported from a study on a red pine test that lattice designs had 111 to 126 % better precision than randomized complete block designs in detecting differences among families for stem diameter growth. However, they did not calculate the expected genetic gains for this trait in their study.

Table 7. Genetic gains expected from thinning in red pine for different selection intensities

Selection intensity	% Gain in stem diameter	Volume (cubic meter/ha) Before	After	Increase
25 % retained	1.66	185.63	194.86	9.23
10 % retained	2.30	185.63	198.47	12.80
1 % retained	3.29	185.63	204.26	18.63

1/ Cubic feet per tree = $[(dbh./2)-1)]^2$ and assuming there are 1500 trees per hectar.

The concern for the effect of relatedness due to imposing high selection intensities might be negligible, since inbreeding has little or no loss in seed production or progeny vigor in red red pine (Flower, 1965).

Age-Age Correlations

The only data on stem diameter available from the previous measurements were the 1979 data. These 1979 and 1984 data were used to calculate coefficients of correlation between ages for each plantation. The associations were highly significant. The phenotypic coefficients of correlation (r) were found to be 0.865 and 0.872 for the Allegan and Crawford plantation, respectively. Thus far, no other studies of this type have been done in red pine. Several studies, however, have been conducted in other species. For comparison, Table 8 presents age-age correlations in stem diameter from other species.

Table 8. Age-age correlations in stem diameter reported from other pines (Wakely, 1971)

Species	Measurement ages correlated	r
Slash pine (*Pinus elliottii* Engelm. var. *elliotii*)	10, 30	0.75 - 0.93
	15, 30	0.88 - 0.96
	20, 30	0.97 - 0.98
Longleaf pine (*Pinus palustris* Mill.)	10, 30	0.70 - 0.90
	15, 30	0.80 - 0.96
	20, 30	0.81 - 0.98
Loblolly pine (*Pinus taeda* L.)	10, 30	0.74 - 0.88
	15, 30	0.88 - 0.96
	20, 30	0.96 - 0.97
Shortleaf pine (*Pinus echinata* Mill.)	10, 30	0.67 - 0.76
	15, 30	0.87 - 0.90

Conclusions

This study indicates that a significant amount of genetic variation in stem diameter exists in red pine in Michigan. The major components of this variation were found to be whether the seed was collected in the Upper or Lower Peninsula, the stand within that region where it was collected, and the family within the stand. The regions accounted for the biggest portion followed by families within stands and stands within regions. The Lower Peninsula of Michigan is the better region for seed collection for use in the Lower Peninsula. Trees grown from seeds collected in more southern latitudes had greater stem diameter growth when tested in the Lower Peninsula of Michigan.

The heritability estimate and genetic gains were low compared to those reported from other pines. More efficient experimental designs should be considered to increase the amount of genetic gain in progeny tests with red pine. Although the expected genetic gain is small, this gain will have a considerable impact in increasing wood production in Michigan, since this state has an extensive red pine planting program. More than 10 million red pine seedlings are planted annually in Michigan.

The present results indicate that collecting seed from the best region would give immediate genetic gains in diameter growth. The combined family and within-family selection was probably the most promising approach to obtain more genetic gains for diameter growth in red pine. The progeny test then could be converted into a seedling seed orchard using the best families and the best individuals within the best families. However, it might be desirable to use the selected families for grafted orchards and clonal forestry. It was not possible to ascertain non-additive genetic variance from the present data, therefore the possibility to exploit the existance of non-additive variance should be considered in the improvement program with red pine in the future.

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APPENDICES

Appendix A. Stem diameter means for regions, stands within regions and families within stands

Region	Stand	Family	Stem diameter mean(mm) Crawford	Allegan
L.Peninsula			168	152
	Grand Traverse		167	152
		301	177	143
		302	185	142
		303	169	143
		304	158	144
		306	173	143
		307	166	140
		308	168	158
		309	178	159
		310	148	143
		311	167	154
		312	175	158
		313	174	159
		314	158	155
		315	179	160
		316	160	157
		317	177	147
		321	170	151
		322	156	153
		323	178	149
		324	170	154
		325	159	211
		326	161	136
		327	147	148
		328	157	156
		329	184	148
		330	175	147
	Alpena		162	156
		351	175	161
		352	157	147
		354	170	151
		358	144	165
	Otsego		162	152
		399	164	146
		401	164	159
		402	171	157
		405	167	154
		407	167	146
		408	169	159
		409	154	151
		410	158	152
L. Peninsula	Cheboygan		170	158
		428	163	135
		430	192	153
		431	175	201
		432	182	140

Appendix A (continued)

Region	Stand	Family	Stem diameter mean (mm) Crawford	Allegan
L. Peninsula	Cheboygan		171	152
		433	176	156
		435	171	148
		436	175	150
		437	161	153
	Cheboygan		171	151
		438	188	148
		439	184	159
		440	154	153
		445	183	144
		447	176	151
	Ogemaw		171	153
		460	183	142
		461	171	162
		464	177	169
		465	153	147
		466	154	156
		467	161	138
		468	182	154
	Crawford		157	142
		473	155	151
		474	164	141
		475	174	151
		480	166	137
		481	126	132
		482	157	136
		484	162	149
	Alcona		166	156
		514	182	160
		516	155	161
		518	153	151
		520	180	158
		521	173	155
		523	145	123
		524	163	170
		527	186	163
		528	173	154
		530	146	154
L. Peninsula	Newagyo		168	152
		531	167	151
		532	171	194
		534	154	158
		535	186	154
		536	170	157
		537	178	153
		538	184	141
		539	196	146
		540	159	143

Appendix A (continued)

Region	Stand	Family	Stem diameter mean (mm) Crawford	Allegan
	Newagyo	542	173	148
		543	144	144
		544	183	147
		545	157	150
		546	157	157
		547	149	139
		548	183	141
		549	170	150
		552	166	158
		555	151	146
	Oscoda		167	148
		557	172	151
		559	153	146
		560	177	155
		562	169	140
	Crawford		177	157
		563	173	160
		564	179	159
		565	180	152
	Crawford		169	145
		566	158	142
		567	176	139
		569	178	131
		570	172	156
		571	182	139
		572	159	143
		573	145	138
		574	179	166
		575	162	152
		576	161	143
		577	189	144
		578	157	145
		579	175	141
		581	179	138
		586	161	153
		587	157	157
L. Peninsula	Maniste		167	151
		594	167	144
		595	177	145
		597	157	151
		598	181	147
		600	154	166
	Wexford		166	149
		608	173	140
		612	181	150
		614	155	154
		616	154	145
		618	168	155
		588	178	142

Appendix A (continued)

Region	Stand	Family	Stem diameter mean (mm) Crawford	Allegan
U. Peninsula			157	138
	Schoolcraft		159	135
		363	154	125
		364	165	144
		365	152	131
		366	159	140
		367	151	140
		369	158	128
		370	159	147
		371	160	126
		375	173	130
		377	163	140
		378	153	131
		379	162	129
	Iron		158	141
		380	156	149
		381	152	150
		382	157	147
		383	158	132
		384	150	134
		387	149	136
		388	161	140
		390	145	145
		393	176	138
		394	178	141
	Luce		163	154
		448	156	161
		450	167	211
		451	165	150
		452	150	149
		453	175	149
		454	121	138
		455	170	147
		456	164	146
		457	172	142
		459	182	143
	Chippewa		148	123
		487	136	126
		491	174	123
		492	134	119

Appendix B. Familiy ranks in stem diameter growth in two plantations

Crawford		Allegan	
Family number	Stem diameter (% of plant. mean)	Family number	Stem diameter (% of plant. mean)
539	118.1	450	141.6
577	113.8	325	141.6
438	113.3	431	134.9
535	112.0	532	130.2
527	112.0	524	114.4
302	111.4	464	113.4
538	110.8	600	111.4
329	110.8	574	111.4
439	110.8	358	110.7
445	110.2	527	109.4
460	110.2	461	108.7
544	110.2	448	108.1
548	110.2	351	108.1
514	109.6	516	108.1
468	109.6	563	107.4
432	109.6	315	107.4
571	109.6	514	107.4
459	109.6	564	106.7
598	109.0	313	106.7
612	109.0	439	106.7
565	108.4	309	106.7
520	108.4	408	106.7
564	107.8	401	106.7
581	107.8	520	106.0
574	107.8	308	106.0
315	107.8	312	106.0
309	107.2	552	106.0
537	107.2	534	106.0
394	107.2	587	105.4
323	107.2	402	105.4
588	107.2	536	105.4
569	107.2	546	105.4
595	106.6	316	105.4
464	106.6	466	104.7
317	106.6	433	104.7
560	106.6	570	104.7
301	106.6	328	104.7
567	106.0	521	104.0
433	106.0	560	104.0
393	106.0	618	104.0
447	106.0	314	104.0
579	105.4	614	103.4
351	105.4	405	103.4
453	105.4	528	103.4
330	105.4	324	103.4

Appendix B (continued)

Crawford		Allegan	
Family number	Stem diameter (% of plant. mean)	Family number	Stem diameter (% of plant. mean)
436	105.4	311	103.4
312	105.4	530	103.4
431	105.4	535	103.4
475	104.8	468	103.4
313	104.8	537	102.7
491	104.8	322	102.7
528	104.2	586	102.7
608	104.2	437	102.7
521	104.2	440	102.7
563	104.2	430	102.7
542	104.2	565	102.0
375	104.2	410	102.0
306	104.2	575	102.0
457	103.6	321	101.3
570	103.6	531	101.3
557	103.6	475	101.3
461	103.0	557	101.3
435	103.0	447	101.3
402	103.0	518	101.3
532	103.0	409	101.3
354	102.4	597	101.3
536	102.4	473	101.3
455	102.4	354	101.3
549	102.4	549	100.7
321	102.4	436	100.7
324	102.4	612	100.7
408	101.2	381	100.7
562	101.2	545	100.0
303	101.2	451	100.0
618	101.2	453	100.0
308	101.2	323	100.0
594	100.6	452	100.0
407	100.6	484	100.0
450	100.6	380	100.0
311	100.6	435	99.3
531	100.6	542	99.3
405	100.6	329	99.3
480	100.0	438	99.3
552	100.0	327	99.3
307	100.0	317	98.7
451	99.4	465	98.7
364	99.4	382	98.7
399	98.8	352	98.7
401	98.8	544	98.7
456	98.8	370	98.7
474	98.8	330	98.7

Appendix B (continued)

Crawford		Allegan	
Family number	Stem diameter (% of plant.mean)	Family number	Stem diameter (% of plant. mean)
524	98.2	598	98.7
428	98.2	455	98.7
377	98.2	399	98.0
575	97.6	555	98.0
379	97.6	539	98.0
484	97.6	456	98.0
586	97.0	559	98.0
467	97.0	407	98.0
388	97.0	390	97.3
437	97.0	616	97.0
326	97.0	578	97.0
576	97.0	595	97.0
371	96.4	445	96.6
316	96.4	543	96.6
370	96.8	364	96.0
540	95.8	594	96.0
325	95.8	304	96.0
572	95.8	306	96.0
366	95.8	540	96.0
304	95.2	572	96.0
369	95.2	459	96.0
314	95.2	576	96.0
410	95.2	303	96.0
566	95.2	577	96.0
383	95.2	310	96.0
546	94.6	301	95.3
597	94.6	588	95.3
328	94.6	457	95.3
587	94.6	566	95.3
545	94.6	302	95.3
482	94.6	460	95.3
352	94.6	579	94.6
382	94.6	474	94.6
578	94.6	548	94.6
380	94.0	538	94.6
322	94.0	394	94.6
448	94.0	562	94.0
516	93.4	307	94.0
614	93.4	367	94.0
473	93.4	608	94.0
466	92.8	377	94.0
600	92.8	366	94.0
616	92.8	432	94.0
363	92.8	388	94.0
409	92.8	547	93.3
440	92.8	571	93.2