ASSESSMENT OF GENETIC VARIATION IN A MULTI-PLANTATION TEST OF HALF-SIB FAMILIES OF SCOTCH PINE

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
GEORGE EDWARD HOWE
1971

This is to certify that the

thesis entitled

Assessment of Genetic Variation in a
Multi-plantation Test of Half-sib
Families of Scotch Pine

presented by

George Edward Howe

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Forestry

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Date ~~April 26, 1971~~

O-7639

ABSTRACT

ASSESSMENT OF GENETIC VARIATION IN A MULTI-PLANTATION TEST OF HALF-SIB FAMILIES OF SCOTCH PINE

By

George Edward Howe

The objectives of this study were to determine relative amounts of within- and between-stand genetic variation, estimate gains from half-sib family selection, and make recommendations for future genetic improvement work in Scotch pine (Pinus sylvestris L.). The material used for the within-stand assessment was 140 open-pollinated half-sib families collected from nine stands in Norway, Belgium, and East Germany. Between-stand differences were assessed using bulked progenies from stands surrounding those from which the one-parent progenies were collected.

The 2-0 half-sib families were planted in nine randomized complete block experiments at each of three sites in Michigan in spring, 1961. The stand progenies were planted in the same spring in a provenance test at each of the same three sites.

Eight height measurements, age-11 diameter, and eleven other traits were analyzed in 1969 and 1970 for each of the nine groups. In addition to considering the five East German groups of half-sib families individually, all 100 East German families were analyzed together for each of four commercially important traits.

Eight traits displayed significant genetic variation among the Norwegian families, including total height, diameter, and frequency of Zimmerman moth attack. Expected gains from half-sib family selection were high for all of these traits, based on a selection intensity of 50% of the families. Parent-progeny correlations indicated that mass selection in this group would have been ineffective as an improvement technique. Between-stand differences were up to 18 times larger than within, and indicated that continued selection should be concentrated in the best stands.

There was little genetic variation in either of the Belgian groups from planted parental stands. One of these, however, was the fastest growing of all nine groups, but exhibited no significant within-stand variation in height, which made it of limited value to the tree breeder. In the third Belgian group there was usable genetic variation in total height and diameter. A 50% thinning of the shortest families will result in a predicted gain in height of 3.6% in the next generation. Parent-progeny

correlations were non-significant, showing that mass-selection would not have been effective in the Belgian population.

Between-stand differences were non-significant in East German Scotch pine, so all 100 East German families were analyzed together, as though sampled from one stand. This all-East German analysis provided a different picture of variation than did any one of the five East German groups by itself. Decisions based on 20-family results would have led to incorrect thinning of two of the groups, and Zimmerman moth attack would have been ignored because of non-significance. The all-East German analysis revealed significant differences in Zimmerman moth attack and indicated no differences in height growth, a trait which had shown differences in two of the five East German groups individually. It was concluded that small sample sizes lead to distorted assessment of populational variation.

Heritability estimates in forestry are strictly applicable only to the samples for which they are calculated, because sample sizes have been too small for broad application.

Genetic gains in forestry have come largely from sources of variation other than those recoverable by mass selection. These sources have been primarily provenance selection and family selection. Mass selection should

occupy only a small part of improvement programs in forestry.

The precision of genetic tests may be increased by improving cultural practices, increasing replication or otherwise modifying experimental design, and enlarging sample size. For a given sample size, improved cultural practices are usually less expensive than increasing replication.

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Forestry

1971

ACKNOWLEDGMENTS

I express my sincere gratitude to Professor Jonathan W. Wright (chairman) for providing the experimental material and the many intense hours of guidance for this study and training as a tree breeder. I am grateful to the other members of my committee--Professors M. W. Adams, Charles Cress, J. W. Hanover, and S. N. Stephenson--for their advice and critical review of this thesis, and to Dr. Wayne Myers of the Forestry Department for his help in computer usage. My thanks are extended to Myra Bair, Frances Howe, Timothy LaFarge, Hildegarde Lindsey, and David Reicosky for help in various phases of this study.

Financial assistance for this study was provided from funds for the NC-51 Project, and by the Michigan State University Forestry Department.

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INTRODUCTION

Scotch pine (*Pinus sylvestris* L.) is the most important planted Christmas tree species in the United States, and is widely planted as an ornamental. It holds potential as a pulp and lumber species in North America, as it does in its native Europe. For these reasons, Scotch pine has become one of our most widely-planted exotic tree species, and is receiving increasing attention from tree breeders in the northeastern U.S. and southeastern Canada.

In Scotch pine, as in any organism, genetic improvement is dependent upon the amount of genetic variation present in the population. Considerable variation between races of Scotch pine has been demonstrated by Langlet (1937), Wright and Bull (1963), Nanson (1968), and Wright *et al*. (1966). What accounts for race formation? What is the nature and extent of within-stand genetic variation and how does it relate to between-stand variation? These questions must be dealt with in assessing family selection as an improvement technique, which is the focus of the present study.

Specifically, the objectives of this study were (1) to determine the relative amounts of within- and

between-stand genetic variation in variable traits, (2) to make estimates of genetic gain by half-sib family selection, and (3) to make recommendations for a program for the future genetic improvement of Scotch pine. The term half-sib families is used throughout, although it is recognized that some open-pollinated family members may be full-sibs.

MATERIALS AND METHODS

The material used in this study is the same as in the study reported on by Wright (1963). One open-pollinated seedlot (family) from each of ten or twenty randomly-chosen trees in each of eight European stands of Scotch pine (Table 1) was collected in the fall of 1958. A ninth group, in Norway (Table 1), was represented by nine half-sib families from one stand and a six-tree bulked sample (#284) from a nearby stand. The latter was included by mistake. All parental stands were 8 to 10 acres in area and fully stocked.

All seedlots were sown in the Michigan State University (MSU) forest tree nursery in the spring of 1959. In the spring of 1961 the nine groups of families were planted in nine randomized complete block experiments at the MSU Fred Russ Forest, Cass County, southwestern Michigan (Figure 1). Each experiment contained five blocks (replicates), and each block contained one 4-tree row plot of each family.

The nine experiments were also planted in the same spring at the MSU W. K. Kellogg Forest, Kalamazoo County, south central Michigan (Figure 1), and the MSU Dunbar Forest, Chippewa County, eastern Upper Peninsula

Table 1. Identification number and origin information for 140 half-sib Scotch pine families from nine stands.

Family number	Seed received from	Parent stand			
		Location	Lat.N.	Long.E.	Origin
275-284[1]	T. Ruden	N. HØland, Norway	50°50'	11°34'	Native
285-294	A. de Jamblinne	Limburg, Belgium	51°17'	5°30'	Planted[2]
295-304	A. de Jamblinne	Limburg, Belgium	51° 7'	5°21'	[3]
531-540	A. Galoux	Campine, Belgium	-----	-----	Planted[2]
321-340	O. Schröck	Rövershagen, E. Germany	54°11'	12°15'	Native
341-360	O. Schröck	Neustrelitz, E. Germany	53°22'	13° 5'	Native
361-380	O. Schröck	Güstrow, E. Germany	53°48'	12°11'	Native
381-400	O. Schröck	Nedlitz, E. Germany	52° 5'	12°15'	Planted[2]
501-520	O. Schröck	Joachimsthal, E. Germany	52°58'	13°46'	Native

[1] #284 was a 6-tree bulked sample from a nearby stand.

[2] Origin of planted stands unknown.

[3] Natural regeneration from nearby 100-year-old planted stand.

Figure 1. Outline map of Michigan showing the locations of the Russ (R), Kellogg (K), and Dunbar (D) test plantations.

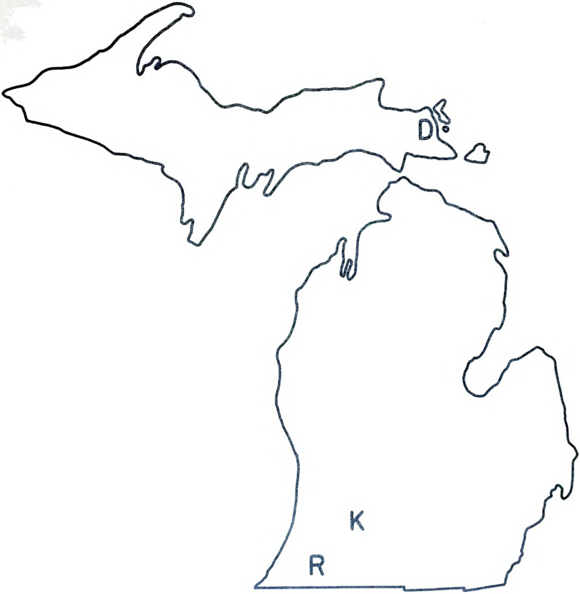

Figure 1

of Michigan, except that families #285 through #294 were not planted at Dunbar. The experiments were replicated ten times at Kellogg and five times at Dunbar, except families #295 through #304 which were replicated ten times at Dunbar.

Additional material included in this study was bulked stand progenies collected from stands near those from which the half-sib seedlots originated. These stand progenies were part of a range-wide provenance test also started in 1959 (Wright and Bull, 1963). Three of the provenance outplantings, which were planted in 1961, were located on the same sites as the half-sib progeny experiments just described. Data from this provenance material were used to assess between-stand genetic variation.

Fourteen traits plus mortality were measured on the half-sib families and appropriate provenance trees in the three Michigan plantations in the summer of 1969 and winter of 1969-70 (Table 2). Measurements were made in units approximating 1/20th of the range in a trait among individuals. In all analyses, plot means were used as the basic observation.

An AOV was run for each trait for each site separately. This included traits scored in one plantation only (Table 1):

Source	DF	MS	F	EMS
Total (T)	BF-1	---	---	---
Families (F)	F-1	MS1	$\frac{MS1}{MS2}$	V_E+bV_{FS}
Blocks (B)	B-1	---	---	---
Error	(B-1)(F-1)	MS2	---	V_E

Each trait which was scored in two or more plantations was subjected to analysis of variance of the following form:

Source	DF	MS	F	EMS
Total (T)	$(F\Sigma B_i)-1$	---		---
Families (F)	F-1	MS1	$\frac{MS1}{MS2}$	$V_E+bV_{FS}+bsV_F$
Sites (S)	S-1	---		---
Blocks/sites	$\Sigma(B_i-1)$	---		---
F x S	(F-1)(S-1)	MS2	$\frac{MS2}{MS3}$	V_E+bV_{FS}
Error	$(F-1)[\Sigma(B_i-1)]$	MS3		V_E

where B_i = number of blocks in the ith site
and b = harmonic mean of number of blocks.

The single-site analyses were performed so that comparisons could be made between single-site and multi-site results.

Provenance data were analyzed in the same way as were the half-sib families.

For 2- and 3-side analyses the additional ratios of $\frac{\text{Family MS}}{\text{Error MS}}$, and, for all analyses, the coefficient of

Table 2. Traits evaluated in the study of 140 half-sib families of Scotch pine from nine stands.

Description
Total height at age 2 in the nursery.
Total height at age 5 or 6.
Total height at age 9 or 10.
Total height at age 11.
Five-year height growth, 1965 through 1969.
Diameter at middle of fourth inter node below apex.
Number of branches in the 5th shorl below apex.
Number of trees bearing cones.
Number of cones per tree.
Number of trees attacked by Zimmerman pine moth (*Dioryctria zimmermani*).
Number of trees forked.
Number of trees damaged by the pine grosbeak (lateral buds plucked off).
Number of trees attacked by white pine weevil (*Pissodes strobi*).
Number of trees with tops broken out.
Mean branch angle of all branches in 5th whorl below apex.
Foliage color in midwinter on scale from 0 (yellowest) to 6 (bluest).
Needle retention, in years.

variation, in percent (C.V. = $\frac{\sqrt{V_E}}{\text{Mean}}$ X 100), were calculated. Simple correlations between traits were calculated. Differences between families within stands were contrasted with differences between stands, using provenance data for the latter.

AOV's of age-11 height, height growth the last 5 years, diameter, and Zimmerman moth attack for all 100 East German families together were run, on the hypothesis that they were representatives of the same population of Scotch pine and that the sampling of 100 parents from one stand would have been comparable to the sampling of the 100 parents from five stands. The same statistics were calculated for these analyses as for the previous ones.

Heritabilities of half-sib family means for traits measured on several sites were estimated from variance components using the following formula:

$$h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F} .$$

Heritabilities for traits measured at one site only were estimated by the formula:

$$h^2 = \frac{V_F}{V_E/b + V_F} .$$

The variance component ratios $\frac{V_F}{V_T}$, $\frac{V_{FS}}{V_T}$, and $\frac{V_E}{V_T}$ were computed, where $V_T = V_F + V_{FS} + V_E$.

RESULTS AND DISCUSSION

One or more of the nine groups displayed genetic variation in all of the traits measured except number of trees forked, number of trees attacked by the pine grosbeak, number of trees attacked by the white pine weevil, and mean branch angle (Table 2). Plantation means, mean square ratios, coefficients of variation, variance component ratios, heritability estimates, and simple correlation coefficients for traits displaying significant differences are presented in Tables 3 through 24. Family means for those traits are in Tables 25 through 37, Appendix. Other traits which were highly correlated with those whose values are tabulated, are discussed only in the text.

Appearance of the Plantations in 1969

The nine experiments at Russ Forest were located on two separated fields. Some of the East German families were located on the northernmost field, and they formed a closed stand in which mortality was so low that I found it difficult to keep located by keying on empty planting spots. There was very little variation in height in the stand and no other obvious gradients.

Table 3. Means, mean square ratios, coefficients of variation, variance component ratios and heritability estimates for height, diameter, and cone bearing in Norwegian families #275 to #284.

	Height at age 11			Diameter at age 11			Trees bearing cones		
Site	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
	Mean height Feet			Mean diameter Inches			% of trees		
	7.8	8.8	7.5	2.2	2.2	1.9	6	24	3
$\frac{\text{Fam MS}}{\text{Er MS}}$	6.95**			6.09**			4.81**		
$\frac{\text{F x Site MS}}{\text{Er MS}}$	1.40			1.43			1.36		
C.V. (%)	11.4			11.6			119.5		
$\frac{V_F}{V_T}$ (%)	22.4			19.4			15.9		
$\frac{V_{FS}}{V_T}$ (%)	0.5			0.5			0.4		
$\frac{V_E}{V_T}$ (%)	72.6			75.0			79.7		
h^2 (%)†	82			84			73		

** = significant at the 1% level.

† $h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 4. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for color, needle retention, and Zimmerman moth attack in Norwegian families #275 to #284.

	Winter foliage color			Needle retention			Zimmerman moth attack
Site	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ
	Grade			Years			% of trees
	3.6	2.2	2.3	1.4	1.8	1.7	17
$\frac{\text{Fam MS}}{\text{Er MS}}$	7.88**			10.11**			15.55**
$\frac{\text{F x Site MS}}{\text{Er MS}}$	2.72**			1.69*			---
C.V. (%)	33.1			15.9			79.4
$\frac{V_F}{V_T}$ (%)	21.8			29.5			74.5
$\frac{V_{FS}}{V_T}$ (%)	0.3			7.3			---
$\frac{V_E}{V_T}$ (%)	74.8			63.1			39.4
h^2(%)†	80			89			93

* and ** = significant at the 5% and 1% levels, respectively.

† $h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 5. Simple correlations among variable traits of families #275 to #284 grown from seed collected at N. Høland, southern Norway.

	Height at age 11	Height growth last 5 years	Height at age 5	Height at age 9
Height growth last 5 years	0.97**			
Height at age 5	0.79**	0.69*		
Height at age 9	0.83**	0.79**	---	
Diameter at age 11	0.82**	0.81**	---	0.72**
Degrees of freedom = 8				

* and ** = significant at the 5% and 1% levels, respectively.

Table 6. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for height, branching, and cone bearing in Belgian families #285 to #294.

Site	Age-6 height	Branches per 4 whorls		Trees with cones	
	Russ	Russ	Kell.	Russ	Kell.
	Feet	Number		% of trees	
	4.7	32	28	77	52
$\frac{\text{Fam MS}}{\text{Er MS}}$	4.32**	2.12*		5.29**	
$\frac{\text{F x Site MS}}{\text{Er MS}}$	---	0.28		1.45	
C.V. (%)	9.2	27.6		53.2	
$\frac{V_F}{V_T}$ (%)	39.8	12.7		20.4	
$\frac{V_{FS}}{V_T}$ (%)	---	10.0		4.7	
$\frac{V_E}{V_T}$ (%)	60.3	97.2		74.7	
h^2 (%)†	77	70		77	

* and ** = significant at the 5% and 1% levels, respectively.

† $h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 7. Simple correlations among variable traits of families #285 to #294 grown from seed collected at Achel, Limburg, Belgium.

	Height at age 11	Height growth last 5 years
Height growth last 5 years	0.92**	
Height at age 6	0.71*	0.51
Diameter at age 11	0.64*	0.70*
Degrees of freedom = 8		

* and ** = significant at the 5% and 1% levels, respectively.

Table 8. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for height, diameter, and needle retention in Belgian families #295 to #304.

	Height at age 11			Diameter at age 11			Needle retention			Age-6 height
Site	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ
		Feet			Inches			Years		Feet
	13	15	9	3.0	3.0	1.5	1.8	1.7	1.9	2.4
$\frac{\text{Fam MS}}{\text{Er MS}}$		3.24*			2.75*			7.99**		2.79
$\frac{\text{F x S MS}}{\text{Er MS}}$		0.63			0.85			1.25		---
C.V. (%)		14.9			9.0			12.5		10.8
$\frac{V_F}{V_T}$ (%)		3.4			7.5			55.2		25.6
$\frac{V_{FS}}{V_T}$ (%)		-1.4			-14.3			1.3		---
$\frac{V_E}{V_T}$ (%)		30.2			94.4			43.6		75.4
h^2 (%)†		76			67			75		62

* and ** = significant at the 5% and 1% levels, respectively.

† $h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 9. Simple correlations among variable traits of families #295 to #304 grown from seed collected at Hechtel, Limburg, Belgium.

	Height at age 11	Height growth last 5 years
Height growth last 5 years	0.89**	
Height at age 6	0.61	0.40
Diameter at age 11	0.84**	0.93**

Degrees of freedom = 8.

** = significant at the 1% level.

Table 10. Means, mean square ratios, coefficient of variation, variance component ratios, and heritability estimate for needle retention in Belgian families #531 to #540.

	Needle retention		
Site	Russ	Kell.	Dunb.
		Years	
	1.9	1.8	2.0
$\frac{\text{Fam MS}}{\text{Er MS}}$		2.84**	
$\frac{\text{Fam x Site MS}}{\text{Er MS}}$		0.46	
C.V. (%)		25.1	
$\frac{V_F}{V_F + V_{FS} + V_E}$ (%)		8.6	
$\frac{V_{FS}}{V_F + V_{FS} + V_E}$ (%)		0.0	
$\frac{V_E}{V_F + V_{FS} + V_E}$ (%)		97.1	
$h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ (%)		74	

** = significant at the 1% level.

Table 11. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for diameter and cone-bearing in East German families #321 to #340.

Site	Diameter at age 11			Trees bearing cones		
	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
		Inches			% of trees	
	2.9	2.9	1.3	24	28	0
$\frac{\text{Fam MS}}{\text{Er MS}}$		3.96**			2.70**	
$\frac{\text{F x Site MS}}{\text{Er MS}}$		1.72*			1.46	
C.V. (%)		10.6			122.8	
$\frac{V_F}{V_T}$ (%)		10.0			5.9	
$\frac{V_{FS}}{V_T}$ (%)		9.6			6.7	
$\frac{V_E}{V_T}$ (%)		80.4			87.2	
h^2 (%)†		62			50	

* and ** = significant at the 5% and 1% levels, respectively.

† $h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 12. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for color and needle retention in East German families #321 to #340.

	Winter foliage color			Needle retention		
Site	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
	Grade			Years		
	4.7	4.2	3.2	1.8	1.7	2.0
$\frac{\text{Fam MS}}{\text{Er MS}}$	3.60**			5.76**		
$\frac{\text{F x Site MS}}{\text{Er MS}}$	1.95**			2.18**		
C.V. (%)	19.6			12.8		
$\frac{V_F}{V_T}$ (%)	7.3			14.2		
$\frac{V_{FS}}{V_T}$ (%)	12.7			14.1		
$\frac{V_E}{V_T}$ (%)	79.8			71.6		
h^2 (%)†	53			69		

** = significant at the 1% level.

†$h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 13. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for color, branching, age-5 height, and age-9 height in East German families #341 to #360.

	Winter foliage color			Branches per 4 whorls			Age-5 height	Age-9 height
Site	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ	Dunb.
		Grade			Number		Feet	Feet
	4.9	4.2	3.9	30	30	28	2.4	5.4
$\frac{\text{Fam MS}}{\text{Er MS}}$		3.17**			3.79**		4.19**	2.42**
$\frac{\text{F x Site MS}}{\text{Er MS}}$		0.78			1.70**		---	---
C.V. (%)		21.6			22.1		8.7	18.1
$\frac{V_F}{V_T}$ (%)		12.0			9.4		39.0	22.1
$\frac{V_{FS}}{V_T}$ (%)		3.2			9.4		---	---
$\frac{V_E}{V_T}$ (%)		91.1			81.1		62.1	77.8
h^2 (%)†		73			61		76	59

** = significant at the 1% level.

$^\dagger h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks;

s = number of sites.

Table 14. Simple correlations among variable traits of families #341 to #360 grown from seed collected at Neustrelitz, East Germany.

	Age-11 height	Height growth last 5 years
Height growth last 5 years	0.55*	
Age-5 height	0.39	0.46*
Age-9 height	0.06	0.63**

Degrees of freedom = 18.

* and ** = significant at the 5% and 1% levels, respectively.

Table 15. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for cone bearing and foliage color in East German families #361 to #380.

	Trees bearing cones			Winter foliage color		
Site	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
	% of trees			Grade		
	16	30	0	4.3	4.3	3.4
$\frac{\text{Fam MS}}{\text{Er MS}}$		3.14**			5.09**	
$\frac{\text{F x Site MS}}{\text{Er MS}}$		1.51*			1.14	
C.V. (%)		134.1			20.2	
$\frac{V_F}{V_T}$ (%)		7.6			17.5	
$\frac{V_{FS}}{V_T}$ (%)		7.2			1.9	
$\frac{V_E}{V_T}$ (%)		85.1			80.5	
h^2 (%)†		57			79	

* and ** = significant at the 5% and 1% levels, respectively.

†$h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 16. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for needle retention and age-5 height in East German families #361 to #380.

	Needle retention			Height at age 5
Site	Russ	Kell.	Dunb.	Russ
		Years		Feet
	1.8	1.7	1.9	2.2
$\frac{\text{Fam MS}}{\text{Er MS}}$		5.13**		3.43**
$\frac{\text{F x Site MS}}{\text{Er MS}}$		2.03**		---
C.V. (%)		12.4		11.4
$\frac{V_F}{V_T}$ (%)		12.8		35.8
$\frac{V_{FS}}{V_T}$ (%)		12.7		---
$\frac{V_E}{V_T}$ (%)		74.3		64.4
h^2 (%)†		57		74

** = significant at the 1% level.

$^{\dagger}h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 17. Simple correlations among variable traits of families #361 to #380 grown from seed collected at Güstrow, East Germany.

	Age-11 height	Height growth last 5 years	Age-5 height	Age-10 height	Trees with cones
Height growth last 5 years	0.89**				
Age-5 height	0.69**	0.53*			
Age-10 height	0.43	0.72**	---		
Trees with cones	0.43	0.46*	0.11	0.04	
No. cones	0.37	0.39	0.11	0.04	0.89**

Degrees of freedom = 18.

* and ** = significant at the 5% and 1% levels, respectively.

Table 18. Means, mean square ratios, coefficients of variation, variance component ratios, and heritability estimates for height growth, needle retention, and age-10 height in East German families #381 to #400.

	Height growth last 5 years			Needle retention			Height at age 10
Site	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Dunbar
		Feet			Years		Feet
	10.4	10.8	6.0	1.9	1.7	2.0	7.0
$\frac{\text{Fam MS}}{\text{Er MS}}$		2.75**			4.08**		1.87*
$\frac{\text{F x Site MS}}{\text{Er MS}}$		1.39*			0.89		---
C.V. (%)	10.5			15.7			107.8
$\frac{V_F}{V_T}$ (%)		6.6			15.2		15.0
$\frac{V_{FS}}{V_T}$ (%)		5.7			0.0		---
$\frac{V_E}{V_T}$ (%)	87.8			86.2			85.3
h^2 (%)†	53			77			48

* and ** = significant at the 5% and 1% levels, respectively.

† $h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 19. Simple correlations among variable traits of families #381 to #400 grown from seed collected at Nedlitz, East Germany.

	Age-11 height	Height growth last 5 years
Height growth last 5 years	0.84**	
Age-6 height	0.80**	0.66**
Age-10 height	0.41	0.89**

Degrees of freedom = 18.

** = significant at the 1% level.

Table 20. Means, mean square ratios, coefficient of variation, variance component ratios, and heritability estimate for height growth in East German families #501 to #520.

	Height growth last 5 years		
Site	Russ	Kell.	Dunb.
		Feet	
	10.7	9.8	7.2
$\frac{\text{Fam MS}}{\text{Er MS}}$		3.58**	
$\frac{\text{Fam x Site MS}}{\text{Er MS}}$		1.50*	
C.V. (%)		11.1	
$\frac{V_F}{V_T}$ (%)		9.2	
$\frac{V_{FS}}{V_T}$ (%)		7.1	
$\frac{V_E}{V_T}$ (%)		83.8	
h^2 (%)†		61	

* and ** = significant at the 5% and 1% levels, respectively.

†$h^2 = \frac{V_F}{V_E/bs + V_{FS}/b + V_F}$ and b = harmonic mean of number of blocks; s = number of sites.

Table 21. Simple correlations among traits of families #501 to #520 grown from seed collected at Joachimsthal, East Germany.

	Age-11 height	Height growth last 5 years
Height growth last 5 years	0.79**	
Age-6 height	0.73**	0.55*
Age-10 height	0.29	0.59**

Degrees of freedom = 18.

* and ** = significant at the 5% and 1% levels, respectively.

Table 22. Variation in height, diameter and cone-bearing of Scandinavian provenances #543 to #546.

	Height at age 11		Diameter at age 11		Cones per tree	
	Site		Site		Site	
Prov.	Russ	Kell.	Russ	Kell.	Russ	Kell.
	% of mean		% of mean		% of mean	
543	111	108	109	113	167	105
544	117	124	114	118	233	133
545	99	95	98	94	0	77
546	72	73	78	75	0	84
	Feet		Inches		Number	
All	7.2	8.6	1.7	2.6	12	57
$\frac{\text{Prov MS}}{\text{Er MS}}$	18.8**		21.6**		1.3	
$\frac{\text{P x S MS}}{\text{Er MS}}$	0.54		1.75		0.02	
C.V. (%)	21.4		18.2		164.5	

** = significant at the 1% level.

Table 23. Simple correlation among traits of Scandinavian provenances #543 to #546.

	Age-11 height	Height growth last 5 years	Age-6 height
Height growth last 5 years	0.99**		
Age-6 height	0.82	0.76	
Age-11 diameter	0.86	0.86	0.72

Degrees of freedom = 2.

** = significant at the 1% level.

Table 24. Mean, mean square ratio, coefficient of variation, variance component ratios, and heritability estimate for Zimmerman moth attack in East German families #321 to #400 and #501 to #520, grown at Russ Forest.

	% of trees attacked
	23
$\frac{\text{Fam MS}}{\text{Er MS}}$	1.31*
C.V. (%)	99.3
$\frac{V_F}{V_T}$ (%)	5.93
$\frac{V_E}{V_T}$ (%)	96.3
$h^2 = \frac{V_F}{V_E/b + V_F}$ (%)	2.40

* = significant at the 5% level.

By contrast, trees in the Norwegian families were far apart and averaged not much more than a man's height. They had shorter internodes and needles and yellower foliage, winter and summer, than the adjacent East German families. Mortality was low in this stand, too.

The remaining East German and Belgian families were planted in a large plantation near the south boundary of Russ Forest. Weed control apparently had not been as effective on this field as on the northern one, because there were frequent openings which were choked with multiflora rose, and the ground here was covered with wild blackberries. The Belgian trees were so large that the overlapping of the branches frequently made it impossible for me to push through between trees.

At Kellogg Forest all of the half-sib families except for four replicates of the Norwegian group were planted together on the top of a gentle hill. The first growing season after planting was a particularly dry one, and the trees highest on the hill suffered high mortality, which resulted in large openings.

None of the families formed closed stands at Dunbar Forest, although the Belgian families were distinctly the tallest here, as at Russ and Kellogg. The experiments were planted on three separate fields, two of them adjacent to one another near the northwest corner of the forest. One edge of these plantings and all of the

southeastern field were very wet, even in late summer. Flooding had caused high mortality in these areas, and the variation in heights of surviving trees was striking. The factors causing the high mortality here and at Kellogg Forest also resulted in high error variances among the surviving trees in the affected areas.

Families #275 to #284

The Norwegian families displayed significant differences in age-11 height, diameter, cone-bearing, winter foliage color, needle retention, and Zimmerman moth attack (Tables 3 and 4). There were significant differences in height growth the last 5 years, age-5 height, and age-9 height. All height measurements were highly correlated with one another and with diameter (Table 5). Number of cones per tree showed significant differences and was highly correlated with number of fruiting trees (Table 5).

Seedlot #284, which was the 6-tree bulked sample from a stand near the one providing the other nine Norwegian seedlots, in no case contributed enough to sums of squares to cause an otherwise low F value to become significant. It also did not change variance components enough to greatly distort heritability estimates. It did, however, provide the opportunity to compare the magnitude of error variance of bulked progenies with that of single-tree progenies, at least indirectly. Error variance

within a plantation was in part a measure of blocks by seedlots interaction, and so was a function of the range in plot means within each seedlot. This range for age-11 height and diameter for seedlot #284 never exceeded the maximum range for any of the other nine seedlots. This was true in each of the three plantations, indicating that the error variances for seedlot #284 did not exceed the error variances for the half-sib progenies. This suggests that for non-genetic experiments, e.g., fertilizer trials, the experimenter need not be concerned about having more error variance if he uses stand progenies than if he uses single-tree progenies.

Families #279, #282, #280, and #283 were the tallest at age 11; three of these also ranked in the top five in diameter, and three of them were the best families in number of fruiting trees. The height ranking of the families did not change appreciably with age. For example, family #279, which was tallest at age 2 (26% taller than average) was also tallest at age 11 (12% taller than average). Family #280 was also among the tallest at age 2 and 11, and #275 was the shortest at both ages. In other words, the nursery performance was a good predictor of age-11 height.

Winter foliage color differences were of little practical significance, because the group as a whole was quite yellow (Table 4 versus Table 13) and not satisfactory

for Christmas trees. The same was true of needle retention; growers will take interest in this trait only if three or more years' needles are held.

Zimmerman pine moth attack, present at Russ Forest only, was easily recognizeable by the presence of foamy-looking pitch masses full of frass at the union of branch and stem. The larvae bore into a tree at this point and mix saliva with the oleoresin to harden it rapidly. This gives the pitch masses a slightly foamy appearance, and the attacks are quickly identifiable.

A severely attacked tree might have had attacks at all branches at a node, with many branches broken off, or even the stem broken off at the damaged node. For this reason, I expected a high positive correlation between number of trees attacked and number of trees with tops broken out. However, the correlation was very low (non-significant) and negative. Apparently there were other, unrecognized, factors accounting for many of the broken tops.

A 50% thinning, removing the families most attacked by Zimmerman moth (Table 26, Appendix), will leave trees averaging 82% fewer attacks than the overall average. Applying a heritability of .93 (Table 4) I estimate that one generation of such selection could reduce the incidence of attack by 76%, from the present 17% to 4%.

Such selection for resistance to Zimmerman moth will not change growth rate appreciably.

However, the Norwegian families are of little commercial interest, anyway, because of their slow growth and undesirable color, but in the present study they were the only ones displaying substantial genetic variability in Zimmerman moth attack. They should be thinned on the basis of this trait, even at the sacrifice of high selection differentials in other traits, so that this apparent resistance may be available for future breeders.

Ruby (1964) found no significant correlations among families #275 to #284 and their parents, indicating that the best-looking parents in the stand in Norway did not produce the best offspring. This suggests that mass selection would be largely ineffective as an improvement regime in this Norwegian population. Because of the strong age-2/age-11 correlations in growth rate, it seems that this ineffectiveness is still true.

Mass selection produced mixed results in Nilsson's study (1968). The 15 tallest of 30 parent trees providing material for Trial no. 20 were 5.4% above average. The offspring of these 15 trees were 1.5% above average at age 18, so the approximate heritability (comparable to parent-progeny regression) was 1.5/5.4 = .28. Moreover, the parent-progeny correlation was high; that is, the

tallest parents produced the tallest offspring and the shortest parents the shortest offspring.

By contrast, the parent-progeny correlation in the Lunnaby trial (Nilsson, 1968) was low, even though the heritability calculated as above was 1.00. Offspring from superior mother trees were substantially taller in four of eight groups tested. In the other four, offspring from the taller parents were shorter than the average. If groups were tested individually, there would be as many showing no gain from mass selection as gain.

The mass selection practiced in the acquisition of the material used in Ehrenberg's study (1966) did not produce consistently superior (or inferior) offspring. Plus- and minus-tree performances were in some cases highly correlated with offspring performance, and in other cases were poorly or even negatively correlated with offspring performances. Mass selection has not been consistently effective in improving south Scandinavian Scotch pine.

The within-stand differences present in families #275 to #284 were contrasted with between-stand differences, using data from provenance stand progenies #543 to #546 (Table 22). These were collected from Norwegian and Swedish stands surrounding the stand from which the half-sib families came (Wright and Bull, 1963). In this provenance material there were significant between-stand differences in age-11 height, age-6 height, height growth

the last 5 years, age-11 diameter, and number of cones per tree (Zimmerman moth attack was not scored in the provenance material). F values were from 3 to 18 times larger between stands than within the parental stand of families #275 to #284, indicating that between-stand differences were greater than within. The best of these four provenance stands for all four traits was #544 and the poorest was #546. The average height for the four stand progenies was 7.9 feet (Table 22), as compared to 8.3 feet for the Norwegian half-sib progenies grown at Russ and Kellogg (Table 3). This suggests that the Norwegian stand providing families #275 to #284 was slightly above average but not among the best stands in the area.

In practical terms, future improvement work in the south Scandinavian Scotch pine should concentrate selection in the best stands in the area. This population was represented by collections from 17 stands in Sweden and Norway in the provenance test (Wright and Bull, 1963). The best four or five of these should be used as the sources for selections in future improvement work in the population.

Families #285 to #294

In the Belgian families #285 to #294, which were tested at Russ and Kellogg Forests only, the number of branches and number of trees bearing cones showed

significant differences (Table 6). The number of cones per tree also showed significant differences and was highly correlated with number of trees with cones (r = .90). All other correlations among traits were low. In none of the traits was the interaction between seedlot and plantation significant, indicating that the performance was consistent in the two plantations.

Family #290 contained 60% more fruiting trees than the average for other families from this stand. Families #286, #288, #289, and #292 all were in the range from 12 to 22% above the mean for all families from the stand. The ratio of family variance to total variance was 20.4% (Table 6). This means that about 20% of all of the variance was accounted for by the differences between families. These differences at age 11 were probably more a measure of earliness of fruiting than of differences which will remain throughout the life of the trees.

Family #293 was 17% below average in number of branches; families #285, #288, and #291 were in the range from 1 to 10% below the mean. Families #287 and #290 were 20% above the mean. The establishment of a seed orchard using family #290 because of its fruiting ability would mean the inclusion of one of the poorest families in branchiness. However, this relationship for this family was not part of a trend; that is, there was not a high positive correlation between number of fruiting trees

and branchiness. Selections based on low number of branches would not include more low- than high-fruiting families.

These Belgian families showed significant differences in winter foliage color at age 1 and age 3 (Wright, 1963). The differences were not discernible at age 11. In the nursery study the seedlots were grown very close to one another, which permitted the observer to distinguish between color differences which could not be picked up by an observer walking between plots in a large test plantation. It is also probable that some of the early color differences had disappeared by age 11.

Wright (1963) found no other significant differences among traits which were scored in both studies. He did find differences in date of bud formation, presence of primary and secondary leaves, and leaf length. These were traits which were very difficult to measure precisely in large trees, and were considered to be of less importance than any of the other traits which are listed in Table 2.

There were significant differences in total height at age 6 at Russ Forest (Table 6). The differences were still significant at age 11 at Russ, but when the data were included with the Kellogg data, the differences disappeared. This was one of many demonstrations in this

study that the results at one site were not consistent with multi-site results.

Families #295 to #304

Belgian families #295 to #304 showed significant differences in age-11 height, age-6 height, age-11 diameter, and needle retention (Table 8). Height growth in the last 5 years also showed significant differences and was highly correlated with age-11 height (r = .89, Table 9); age-6 height was not highly correlated with either of the other height measurements (Table 9). This trait was scored at one plantation only and again shows the inconsistency of single- versus multi-site results. Performance was consistent throughout all plantations for all of these traits, as shown by the non-significance of the seedlot by plantation interaction terms (Table 8).

Family #301 was the tallest at age 11 and was 11% above the mean; #297, #298, #300, and #302 were 4% to 5% above average. Family #298 was 5% above the mean in diameter; #297 and #302 were 3% above the mean. A 50% thinning of the shortest families at age 11 will result in a selection differential of 4.8% for total height, 2% for diameter, and 12.5% for needle retention.

The half-sib family heritability of age-11 height was .76 (Table 8), so the expected gain in height in the next generation among open-pollinated families coming

from the thinned plantations is 3.6% of the present mean, or .47 foot.

The families from this Belgian stand were the second fastest-growing group in the study (statistical comparisons were not made). The high heritability of height among these families offers ample opportunity for improvement in an already outstanding origin, which is of great practical importance.

Wright (1963) found significant differences in height among the families at ages 1 and 2. The six tallest families at age 2 were still the top six families at age 11, which indicated that nursery growth was a good predictor of later height growth.

Ruby (1964) found no significant correlations for any traits between these families and their parents growing in Belgium. This means that had the best-looking parent trees been consciously selected they would not have produced the best offspring. Mass selection in this stand would have been a waste of time.

Families #531 to #540

Belgian families #531 to #540 were the tallest group at age 11 (15.0 feet, average) of those included in the study, but displayed practically no within-stand genetic variability. This absence of genetic variation is regrettable because of the outstanding commercial

potential of the group. It offers no opportunity for genetic improvement in any trait except needle retention (Table 10), which is of little practical importance until needles are retained three years or more. It is doubtful that Scotch pine anywhere achieves this. Wright (1963), too, found very little genetic variation among these families.

Height differences were significant at ages 1 and 2 but not at ages 6, 10, or 11. The ratios of family variance to total variance were in all cases quite small (this was true even for needle retention, Table 10), and error variance to total variance quite large. But in Wright's data for the Belgian families these ratios were 34% and 66%, respectively for age-1 height. This indicates that error variances have increased substantially since the nursery study, reducing the sensitivity of the tests. It is not evident what factors are operating in this particular group of families to increase error variance.

It is also possible that these families came from parents (planted trees of unknown origin) which were genetically similar for all traits except early height growth, which in some populations may be controlled by genes other than the ones controlling later height growth. If the parental seed had been collected in such a population, the offspring might display this kind of variation pattern.

All Belgian Families

The two Belgian stands displaying the least genetic variability (#285 to #294 and #531 to #540) were the two planted stands. The seed for the parent stands might have come from commercial seed dealers who probably collected from a wide area and from diverse sources. The offspring from such a plantation would be expected to display increased genetic variability. The results suggest the opposite, that is, the parent plantations originated from a narrowed genetic base. Nanson (1969) demonstrated that offspring from plantations originating from a few trees displayed little genetic variability. This reconfirms the necessity for establishing seed-orchards from a broad genetic base, if effective continued selection is to be practiced.

There is little opportunity for improvement in resistance to Zimmerman pine moth attack among the Belgian families. The number of Belgian trees attacked by the pest ranged from 13 to 25% in the Russ plantation, so it poses a serious threat to the growing of Belgian Scotch pine in southern Michigan and in many other areas where it is planted in the U.S. Either resistance will have to come from other sources (e.g., the Norwegian families) or it will be necessary to look to chemical or biological pest control.

Families #321 to #340

East German families #321 to #340 were significantly different in age-11 diameter, number of fruiting trees, winter foliage color, and needle retention (Tables 11 and 12). For all four traits the seedlot by plantation interaction was significant; that is, the best families at Russ were not the best at Kellogg or Dunbar and the worst at each plantation were not the worst at the others. Interaction means that individuals or groups of related individuals perform differently with respect to one another in different environments. Interactions make it difficult to recommend thinning which will result in a satisfactorily high selection differential at all sites. Often, interaction is a measure of the failure of a majority of the individuals or families to perform consistently, yet several perform well at all sites. For example, family #323 ranked in the top nine at all three sites in age-11 diameter; families #326, #327, #330, and #338 also ranked in the top nine (Table 31, Appendix). A selection intensity of 75%; saving these five families, will result in a selection differential of 7%. Using a heritability of .62 (Table 11), the expected gain in the next generation is 4.3% of the present mean, or .12 inch in diameter.

However, present and anticipated crown closure necessitates a thinning of 50% rather than 75%, so families #321, #328, #329, #335, and #336 will be saved also. This reduces the selection differential to 4% and the gain to 2.5%

The alternative would be to thin each plantation separately. But since I wish to recommend families for planting over a broad area of the U.S., it will be necessary to either (1) produce material which is superior at all sites where Scotch pine may be planted, or (2) identify the environmental factors accounting for the interaction at the three test sites, grow material suited to those factors, identify the factors at potential planting sites, and plant the appropriate material. Those environmental factors are not yet identifiable, so approach (1) is the only feasible one. This means the same families will be thinned at all three test plantations and low selection differentials will have to be accepted.

Wright (1963) found significant height differences at ages 1, 2, and 3, and significant differences in winter foliage color in all three years in the nursery. The environmental uniformity in the nursery made it possible to distinguish small differences in heights. This is a trait which is sensitive to environmental influences and for this reason small height differences in the test plantations could not be detected. It is also possible

that height differences disappeared with age, as a result of genetic influences, as discussed in a preceeding section.

Families #341 to #360

Height differences were significant at ages 1, 2, and 3 in the nursery (Wright, 1963) and still significant at age 5 at Russ Forest and at age 9 at Dunbar Forest in the East German families #341 to #360 (Table 13). However, the differences had disappeared by age 11 at each of these plantations, and were not present in the combined analysis. The test at Dunbar had become much more insensitive because flooding of the planting site had caused high variability and mortality among these families, as reflected by an unusually high error variance. At Russ Forest the age-11 family mean heights ranged from 11.8 to 15.1 feet, which means that differences of approximately 9% were not detectable, even in the most precise of the three tests.

There was no correlation between nursery height performance and later height performance at either Russ or Dunbar plantations. Likewise, there was no correlation between height ranking at Russ at age 5 and Dunbar at age 9 (Table 32, Appendix); the best agreement was in family #348, which ranked among the shortest three in the nursery, at Russ (age 5), and at Dunbar (age 9). Also family #352

was among the tallest five both in the nursery and at age 5 at Russ Forest (not included in the Dunbar data).

These data suggest that planting or other environmental influences caused differences in height among these families which were unrelated to their genetic potential in this trait. These influences were not outgrown by age 9, as shown by the Dunbar analyses and by the nonsignificance of height-growth differences in the last 5 years in the combined analysis. This stand should not be thinned on the basis of height data presntly available, but should be thinned on the basis of height growth after age 9, if significant differences appear.

These East German families offer opportunity for improvement in branchiness and in winter foliage color (Table 13), which was greener in this group than in any of the others included in this study. When thinning on the basis of height growth after age 9, the selection differential which is produced for winter foliage color should also be considered. Color is of little importance to pulp and lumber growers, but is of great interest to the Christmas tree industry. The East German origins are faster-growing than Spanish origins, but not as blue-green (Wright and Bull, 1963).

Families #361 to #380

In these East German families there were significant height differences at age 5 at Russ Forest (Table 15), and these differences were significantly correlated with nursery performance ($r = .52$, $p > .05$ $r = .444$); the height differences at ages 1 and 2 were significant (Wright, 1963). However, the low correlation did not permit accurate prediction, as the tallest and shortest families in the nursery were not the tallest and shortest, respectively, at age 5 at Russ Forest. Height differences were still significant at age 11 at Russ, but the correlation between age-5 and age-11, although significant, was not high ($r = .69$, Table 17), again suggesting that environmental influences accounted for much of the height difference.

There was little consistency in fruiting between Kellogg and Russ, the only two plantations which had high fruiting. This was measured by the significant seedlot by plantation interaction term (Table 16). Of all the groups showing significant differences in the number of trees with cones in this study, these families were the only ones showing significant interaction. This means that selection based on 3-site average family performance may not produce high selection differentials at all three sites.

None of the traits showing significant differences is important enough commercially to be used as a selection criterion. It is recommended that, as in families #341 to #360, height growth measurements after age 9 be acquired and, if significant differences appear, selection be based on this character.

Families #381 to #400

These East German families showed significant differences in age-10 height at Dunbar Forest (F = 1.87, Table 18); the significance of the differences had decreased by age 11 (F = 1.61, significant at the 10% level only). Furthermore, the correlation between age-10 and age-11 heights was only r = .41 (Table 19). However, these families grew an average of 1.9 feet in that one year, and this was 27% of their average age-10 height. Obviously, differences among the families in height increment in that one year could drastically change prior relationships. These increment differences might be related to genetic potential, but might also be conditioned by environmental influences present in a particular year.

There was low correlation (r = .34) between height in the nursery and height growth the last 5 years for the combined data (Table 35, Appendix), and between nursery heights and age-10 heights at Dunbar (Table 35, Appendix). The significant interaction term for height growth

supports the contention that the performance in this trait was unstable in changing environments.

These families came from the only planted stand among the five East German groups. There was no distinctly different pattern of genetic variation in this group than in any of the other four. Apparently the parents did not originate from either widely diverse sources or from a very narrow genetic base.

Families #501 to #520

There was very little genetic variability among these East German families; the only trait showing significant differences was height growth in the last 5 years (Table 20). Because of high seedlot by plantation interaction, selection for height growth on the basis of average height over all test sites would not produce a high selection differential at all three plantations. However, selection on this basis is not recommended, because this trait, as in other East German stands, was not highly correlated with nursery performance (r = .39) or with any other height measurements, except height at age 11 (r = .79, Table 31). The latter did not show significant differences, so the correlation is probably chance.

There is no apparent explanation for this lack of variability in this one of the five East German groups, except that by chance trees were picked which grouped

near the mean. A 10- or 20-tree sample of a forest stand is probably not likely to provide a good estimate of the genetic variability of that stand. It was for this reason that the 100 East German families were analyzed together, as though sampled out of one stand.

The All-East German Analysis

LaFarge (1971) tested between-stand differences in age-11 height, height growth the last 5 years, and age-11 diameter among the five East German parental stands represented in the present study. He treated the Russ, Kellogg, and Dunbar plantations as three replications of stands and found no differences between stands in any of these three traits. Likewise, I found no significant differences in any of nine traits measured in stand progenies collected from East German Scotch pine stands for the provenance test (Wright and Bull, 1963). I concluded that the East German population of Scotch pine was fairly uniform and that the 100 families from five stands might be considered as though sampled from one stand.

Including all East German families in one analysis showed significant differences in Zimmerman moth attack (Table 24). The 51 least-attacked families averaged 13.3% attack, which represented a selection differential of 42.5%. However, the heritability estimate for this trait in this group was very low (h^2 = .024, Table 24), so in the next

generation I expect 22.78% instead of 23.00% of the trees to be attacked. The low predicted gain results from the very low heritability estimate. It demonstrates that the practical limits for producing high selection differentials inevitably cause commercially meaningless gains when heritabilities are low.

Age-11 height, height growth, and age-11 diameter all showed no significant differences in the all-East German analysis. Wright (1963) found significant height differences among these families in a similar analysis performed on the nursery material at ages 1 and 2. This supports the contention that height is a trait sensitive to the relatively larger environmental influences present in test plantations than present in a nursery; that is, the influences of the three different test sites created non-genetic differences, but they cancelled each other out when the data were subjected to combined analysis.

The decision not to thin any of the East German groups on the basis of present height data was supported by the results of the all-East German analyses; the important commercial traits so far measured (except Zimmerman moth attack) displayed no genetic variation. The absence of genetic variation in East German Scotch pine was further evidenced by the lack of significant between-stand differences found by LaFarge (1971) and myself.

The East German Scotch pine is in the variety hercynica (Ruby, 1964; Wright and Bull, 1963), in which substantial genetic variation has been demonstrated (Wright and Bull, 1963; Wright, et al., 1966). The apparent absence of substantial genetic variation within and between stands in East Germany suggests that varietal boundaries may have been too broadly drawn in the earlier studies.

All East German Families

Genetic variation was minimal among the five East German groups in the commercially important traits height and diameter. This was confirmed by the all-East German analyses. The putative desirability of thinning families #381 to #400 and #501 to #520 on the basis of height growth in the last 5 years was not supported by the all-East German analysis, which showed those differences to be non-significant for all groups.

Zimmerman moth attack differences became significant in the all-East German analysis, whereas they were not in any one of the groups individually. This makes East German Scotch pine of more commercial interest to the tree breeder.

The all-East German versus the individual groups analyses suggest that 20-tree samples may not permit precise estimates of within-stand genetic variation, and may lead to incorrect selection recommendations. In the

present study, I would have been tempted, on the basis of single-group analyses, to recommend thinning families #381 to #400 and #501 to #520 on the basis of height growth, and to ignore Zimmerman moth attack differences altogether.

All analyses of these groups showed that nursery performances were not good predictors of later height growth. This trait in the East German material appeared to be much more sensitive to environmental influences than the same character in either the Belgian or Norwegian populations. By contrast, the winter foliage color differences were less sensitive, for they remained consistent from age 1 and 2 to age 11.

HERITABILITY ESTIMATES IN FORESTRY

Sewell Wright (1921) demonstrated that the measurable genetic variance among half-sibs was only 1/4 of the additive genetic variance present in the parents. Thus, heritability estimates applicable to the present generation should correctly contain $4V_F$ in the numerator. But the next generation of offspring, because they will be half-sibs, will contain only 1/4 of the genetic variance present in the present generation, so it will be necessary to divide by 4 again. For convenience, the 4 in the numerator was omitted in the formulae on page 10. To make the heritabilities applicable to selection based on family rather than plot means it was necessary to divide the error variance by the number of sites and number of replicates per site, and to divide the family by site interaction by number of replicates.

Heritability estimates vary because, in the abscence of estimates verified by realized gain in forestry, tree breeders are not in agreement about the components to be included in heritability estimates. Namkoong, Snyder, and Stonecypher (1966) published a summary of all forest tree heritability estimates they considered to be reliable. The report demonstrated that family

heritabilities had been calculated in various ways, resulting in a range of estimates. None was verified by realized gain, so heritability estimation cannot be regarded as an absolute.

Heritability estimates for a particular trait in a particular species vary from study to study, too, because most improvement programs in forestry to date involve too few samples of a population. In the present study, no one of the five East German groups provided the same estimate of the genetic variability in East German Scotch pine as did the five groups combined. Examples of variation in heritability estimates appear in studies of the inheritance of specific gravity in slash and loblolly pine:

Species	Age	Number of parents	h^2 half-sib	h^2 full-sib	h^2 clonal	Author
slash pine	>14	8	.73			Squillace, <u>et al</u>. (1962)
slash pine	>14	6		.56		Squillace, <u>et al</u>. (1962)
slash pine	>12	7			.48[1]	Squillace, <u>et al</u>. (1962)
slash pine	7	13	.43			Goddard and Cole (1966)
loblolly pine	2	100	.56			Stonecypher <u>et al</u>. (1964)
loblolly pine	3	100	.72			Stonecypher, <u>et al</u>. (1964)
loblolly pine	5	100	.73			Stonecypher and Zobel (1966)

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[1] Broad sense heritability.

The only estimates which were consistent were the two involving 100-tree samples, and much of that consistency was because the two reports were on the same material. With small sample sizes, heritability estimates must be regarded as parameters of the individual tests, and useful only within those boundaries. They cannot be considered to be parameters of larger populations.

THE EFFICACY OF MASS SELECTION

The parent-progeny correlations reported for the Norwegian and Belgian populations included in this study showed that mass selection would not have been effective for growth traits in those parental stands. Comparable work in Scandinavia and Belgium was cited which also showed that mass selection in Scotch pine was not consistently effective. Obviously, mass selection would not have been effective in the East German material included in the present study, as there was no detectable genetic variation present in growth traits.

In a study of black wattle, Moffett and Nixon (1963) found significant differences in only one of four traits between offspring from parents selected for (1) high values and (2) low values in each of the traits:

Diameter	not significant
Bark thickness	not significant
Percent tannin	significant at the 1% level
Percent gummosis	not significant.

The authors concluded, "For diameter and bark thickness, phenotypic selection has had a negligible or only slight effect, . . ." (p. 5). Webb and Barber (1965)

found non-significant correlations between selected slash pine mother trees and their open-pollinated offspring in test plantations in height, diameter and volume at age 8. Barber (1964) provided data from a progeny test in slash pine which permitted the calculation of parent-progeny correlations for age-7 heights and diameters. The height correlation was r = .25 and the diameter correlation was r = .15, which means that the parents selected for superior height and diameters did not necessarily produce the tallest or thickest offspring. This was further supported by the observation that the four tallest of fifteen parents produced offspring which were only .2 foot above the overall progeny mean of 20.1 feet. In another test involving some of the same parents, the offspring from the tallest three parents averaged 2.6 feet taller than the overall progeny mean of 21.0 feet. However, this information was of limited use because the differences among the progenies were not significant.

In a study of specific gravity in slash pine, Goddard and Cole (1966) calculated a parent-progeny correlation of r = .488, so relative parental performance was a poor predictor of relative progeny performance; the same was true for the specific gravity study conducted by Squillace, Echols, and Dorman (1962). Stonecypher (1966) found no correlations in height between randomly-selected loblolly pine parents and their open- or

control-pollinated 1- and 2-year-old offspring. Canavera (1969), who practiced intense selection in even-aged stands of jack pine in Michigan, found that offspring from phenotypically superior mother trees were no better than those from average trees. Also, phenotypically inferior mother trees did not produce relatively poorer offspring.

Six other studies reviewed did not permit a precise estimate of the effectiveness of mass selection because (1) control material against which the selected-tree progenies were compared originated from other populations that those represented by the selected parents, and (2) no parental data were given, so that parent-progeny correlations might be calculated. Only by testing selections against average material from the same population is it provable that gain comes from the genetic improvement recoverable by mass selection and not from other sources of genetic differences or from improved cultural treatment.

Genetic gains in forest tree species are being provided by sources of genetic variation other than those recoverable by mass selection. The two major sources have been provenance selection and family selection. This means that the initial phase of an improvement program can be cheaper and more efficient because (1) random selection of parent trees is always much faster than phenotypic selection, (2) provenance selection permits bulking of seedlots, (3) the time saved in (1) and (2) permits a much

larger number of parent trees to be sampled, and (4) provenance selection continues to be cheaper, because individual tree progenies are kept separate in testing.

It must be recognized, however, that mass selection is the only form of selection practiced by nature, and the genetic variation present within species (e.g., provenance differences) attests to the effectiveness of mass selection in nature. There must be genetic differences present within stands or there would not be genetic differences present between stands or between populations. But natural selection can operate on very subtle differences and has available to it immense periods of time to make changes; wood users are less patient with tree breeders. Nevertheless, since single-tree genetic differences are surely present within stands, a judicious amount of time might be devoted to single-tree selection within the framework of an improvement program whose main emphasis is on provenance or family selection.

INCREASING PRECISION OF GENETIC TESTS

Genetic gain in growth traits in the East German population will not be possible in the present test. Genetic differences between families were masked by uncontrolled variation. The breeder interested in East German Scotch pine will be faced with these alternatives: (1) forget about getting gain in growth traits, (2) assume that a 100-tree sample was insufficient to assess the genetic variation present in a population, and include more selections in the test, recognizing that there will be increased costs, (3) increase the precision of the test by improving nursery practice, providing better weed control, supplying irrigation, or increasing the number of replications or otherwise modifying the experimental design. At Russ Forest, the present test permitted distinction of 18% differences in family mean heights. To distinguish 9% difference, the number of replications would have to be increased from 5 to 20. The costs of increasing precision in this way will usually be greater than the costs of improving cultural practices.

Those portions of the Kellogg and Dunbar plantations which, when I was working in them, gave me the impression of being unusually variable did in fact produce

the highest error variances. Mortality was high in those portions and the factors causing the mortality caused much variation among the surviving trees. The high mortality at Dunbar was caused by flooding which could have been avoided by choice of a more suitable planting site, had one been available. The high mortality at Kellogg was caused by insufficient water in the first growing season, which might have been avoided by irrigating once or twice during the summer.

Population samples of 20 trees will not provide the same picture of genetic variability of a population as will 100-tree (or larger) samples. Assessment based on small samples may lead to erroneous management decisions even within the confines of a particular study. Heritability estimates calculated for a test involving a small sample size apply only to that test. The range in heritability estimates for a particular trait in the present study are more likely due to inadequate sample sizes than to great differences in the frequencies of the genes controlling the trait.

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APPENDIX

APPENDIX

Table 25. Variation in height, diameter and cone-bearing in families #275 to #284 grown from seed collected in N. Høland, southern Norway.

	Height at age 11			Diameter at age 11			Trees bearing cones		
Family	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
	% of mean			% of mean			% of trees		
275	92	91	92	88	93	96	0	10	0
276	98	101	92	102	107	97	0	18	0
277	99	102	83	100	113	87	3	38	0
278	100	97	93	96	93	88	5	15	0
279	105	110	121	107	107	119	3	25	0
280	109	104	106	114	107	107	10	38	10
281	99	95	98	99	93	102	3	25	0
282	100	110	116	103	106	108	15	45	20
283	109	97	106	99	91	107	13	10	0
284	92	93	93	90	97	95	3	18	0

Table 26. Variation in color, needle retention and Zimmerman pine moth attack in families #275 to #284 grown from seed collected in N. Høland, southern Norway.

	Winter foliage color			Needle retention			Zimmerman moth attack
Family	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ
		Grade			Years		% of trees
275	2.8	1.7	2.4	1.4	1.7	1.6	0
276	4.2	2.8	3.2	1.5	1.8	1.6	5
277	2.8	2.0	1.6	1.4	1.6	1.9	0
278	3.8	1.5	1.0	1.1	1.4	1.5	15
279	3.8	3.0	3.0	1.6	1.7	1.7	25
280	3.2	2.2	2.4	1.2	1.6	1.6	10
281	3.2	1.9	2.2	1.6	2.0	1.8	20
282	3.8	3.3	2.8	1.5	2.1	1.9	80
283	4.0	1.2	2.2	1.6	2.2	1.9	0
284	4.0	1.9	2.6	1.6	1.9	1.8	15

Table 27. Variation in height, branchiness and cone-bearing in families #285 to #294 grown from seed collected at Achel, Limburg, Belgium.

	Age-6 height	Branches per 4 whorls		Trees with cones	
Families	Russ	Russ	Kell.	Russ	Kell.
	% of avg.	Number		% of trees	
285	90	29	29	65	64
286	107	33	29	80	78
287	115	38	34	70	64
288	87	30	24	99	58
289	105	32	29	90	61
290	97	36	--	100	--
291	90	29	27	75	50
292	115	34	31	99	58
293	92	27	23	45	0
294	98	32	29	50	36

Table 28. Variation in height, diameter, and needle retention in families #295 to #304 grown from seed collected at Hechtel, Limburg, Belgium.

	Height at age 11			Diameter at age 11			Needle retention			Age-6 ht.
Fam.	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ
	% of mean			% of mean			Years			% $\overline{X}$
295	96	96	96	97	98	102	1.7	1.6	1.9	94
296	91	96	90	95	97	95	1.8	1.8	1.9	88
297	103	106	99	103	102	103	2.0	1.9	1.9	102
298	99	104	105	103	104	108	1.6	1.7	1.8	107
299	99	98	--	103	103	--	1.9	1.9	--	90
300	101	102	102	92	99	105	2.0	1.8	1.9	100
301	102	105	126	101	103	99	1.9	1.8	2.1	103
302	111	103	102	106	100	103	2.0	1.9	1.8	114
303	94	90	86	99	93	91	1.6	1.6	1.7	96
304	104	100	94	103	100	96	1.5	1.5	1.8	103

Table 29. Variation in needle retention in families #531 to #540 grown from seed collected at Campine, Belgium.

Family	Needle retention		
	Russ	Kell.	Dunb.
		Years	
531	1.9	1.6	2.0
532	1.6	1.5	1.8
533	1.9	1.8	2.0
534	2.1	1.7	1.9
535	2.1	1.9	2.0
536	1.6	2.6	1.9
537	1.9	1.8	2.2
538	1.6	1.7	1.8
539	2.0	1.7	2.2
540	2.0	2.1	1.7

Table 30. Variation in diameter and cone-bearing in families #321 to #340 grown from seed collected in Rövershagen, East Germany.

	Diameter at age 11			Trees bearing cones		
Family	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
	% of mean			% of trees		
321	102	99	103	35	65	0
322	100	99	93	15	32	0
323	111	112	102	25	28	0
324	100	101	92	25	45	0
325	96	96	84	15	12	0
326	109	102	111	5	2	0
327	103	100	127	20	35	0
328	103	100	102	25	22	0
329	98	100	95	35	25	0
330	101	101	106	5	4	0
331	97	94	92	15	30	0
332	89	105	98	20	38	0
333	89	105	112	40	15	0
334	104	104	86	35	35	0
335	103	101	95	35	38	0
336	101	100	112	35	22	0
337	92	88	103	10	22	0
338	109	105	108	25	15	0
339	99	97	93	35	40	0
340	97	91	87	15	22	0

Table 31. Variation in color and needle retention in families #321 to #340 grown from seed collected at Rövershagen, East Germany.

	Winter foliage color			Needle retention		
Family	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
		Grade			Years	
321	5.4	4.0	4.2	1.7	1.6	2.0
322	3.8	3.5	2.6	2.0	1.7	2.0
323	5.2	4.9	3.6	1.7	1.9	1.9
324	5.4	4.6	2.6	1.7	1.6	1.7
325	4.8	4.7	3.6	1.6	1.5	1.8
326	5.0	4.1	3.4	1.7	1.7	2.1
327	5.0	4.2	4.2	2.0	2.0	2.3
328	4.6	4.0	3.6	2.0	1.7	1.9
329	4.8	3.9	3.2	2.2	2.0	2.3
330	5.0	4.7	4.0	1.7	1.8	1.9
331	4.4	4.3	2.2	1.9	1.5	1.9
332	4.8	4.1	3.0	1.6	1.8	1.9
333	4.2	5.2	2.6	2.0	1.7	2.1
334	4.8	4.1	3.2	1.8	1.8	1.8
335	4.2	4.2	3.8	2.0	1.9	1.9
336	4.8	4.5	2.2	1.5	1.8	2.1
337	4.2	3.6	2.4	1.7	1.5	2.0
338	5.0	4.2	4.0	1.8	1.6	1.7
339	4.6	4.2	2.6	1.9	1.6	1.9
340	5.0	4.0	2.4	1.9	1.9	1.7

Table 32. Variation in color, branchiness, height at age 5, and height at age 9 in families #341 to #360 grown from seed collected at Neustrelitz, East Germany.

	Winter foliage color			Branches per 4 whorls			Age-5 ht.	Age-9 ht.
Family	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Russ	Dunb.
		Grade			Number		% $\bar{X}$	% $\bar{X}$
341	5.0	4.6	4.6	27	29	25	104	91
342	5.2	4.0	4.2	28	37	29	105	91
343	5.0	4.4	3.4	33	36	26	109	108
344	4.8	4.7	3.4	28	32	25	105	99
345	4.2	3.9	3.2	28	33	29	94	104
346	5.4	---	4.6	29	--	28	98	102
347	5.2	4.0	4.0	26	26	24	110	97
348	4.6	4.2	4.0	26	26	22	91	89
349	5.6	4.9	4.6	32	31	25	109	101
350	4.6	4.0	3.4	31	27	24	83	77
351	5.0	3.9	3.2	30	27	26	102	85
352	5.0	4.3	---	26	28	--	107	--
353	5.4	---	---	25	--	--	104	--
354	4.4	3.8	3.8	28	28	23	104	91
355	5.2	4.0	4.2	33	27	33	93	104
356	5.0	4.0	4.2	39	30	34	109	112
357	4.4	4.5	4.0	31	40	33	87	89
358	3.8	3.8	2.8	33	29	28	93	119
359	5.0	4.4	3.6	31	28	31	97	124
360	4.8	---	5.2	33	--	33	97	115

Table 33. Variation in cone-bearing and color in families #361 to #380 grown from seed collected at Güstrow, East Germany.

	Trees bearing cones			Winter foliage color		
Family	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.
	% of trees			Grade		
361	30	36	--	4.4	4.1	---
362	5	36	0	4.0	3.8	3.4
363	20	18	5	4.0	4.3	3.4
364	5	25	0	3.8	4.1	2.8
365	30	43	0	4.2	4.3	2.8
366	25	43	0	4.4	4.6	4.8
367	0	4	0	4.2	3.8	3.2
368	15	--	0	3.6	---	3.4
369	15	18	0	3.6	3.6	2.4
370	25	36	0	4.4	4.6	3.0
371	15	61	0	4.2	4.6	4.0
372	0	14	0	4.6	4.7	4.2
373	10	18	0	4.8	4.6	2.6
374	20	25	0	4.4	4.8	3.4
375	5	4	0	4.4	3.6	2.6
376	10	14	0	4.6	4.3	4.0
377	20	43	0	4.4	4.1	3.4
378	5	29	0	4.6	4.0	3.4
379	40	54	0	4.8	4.8	4.4
380	10	54	0	4.6	4.6	3.2

Table 34. Variation in needle retention and age-5 height in families #361 to #380 grown from seed collected at Güstrow, East Germany.

Family	Needle retention			Height at age 5
	Russ	Kell.	Dunb.	Russ
		Years		% of mean
361	1.7	1.7	---	104
362	1.8	1.8	1.9	96
363	1.5	2.0	2.1	99
364	1.9	1.7	1.9	93
365	1.5	1.7	1.9	103
366	1.6	1.2	1.7	101
367	2.0	1.9	1.8	99
368	2.1	---	1.8	89
369	1.7	1.6	1.7	85
370	2.0	1.7	2.1	100
371	1.8	1.8	1.9	108
372	1.8	1.7	1.9	120
373	1.8	2.0	2.1	96
374	1.9	1.8	2.3	97
375	1.8	1.7	1.8	106
376	1.6	1.8	2.0	106
377	1.7	1.5	1.8	112
378	2.0	1.8	2.0	103
379	1.9	1.9	2.0	103
380	1.7	1.6	1.9	81

Table 35. Variation in height growth, needle retention, and age-10 height in families #381 to #400 grown from seed collected at Nedlitz, East Germany.

	Height growth last 5 years			Needle retention			Height at age 10
Family	Russ	Kell.	Dunb.	Russ	Kell.	Dunb.	Dunbar
	% of mean			Years			% of mean
381	108	95	114	2.0	1.8	1.9	184
382	98	100	94	1.8	1.7	2.0	45
383	104	103	90	2.1	1.6	2.0	20
384	110	109	105	1.9	1.9	2.1	120
385	92	102	95	2.0	1.8	2.0	85
386	95	101	98	2.1	1.8	2.3	30
387	96	93	98	1.8	1.5	2.1	80
388	96	101	93	1.5	1.1	1.8	90
389	108	109	97	1.7	1.7	2.0	65
390	103	106	113	1.8	1.5	2.0	150
391	102	101	113	1.7	1.6	2.1	180
392	103	104	92	2.0	1.8	2.1	35
393	102	95	104	1.7	1.5	1.9	115
394	97	98	94	1.7	1.4	1.8	45
395	104	104	111	1.8	1.6	2.1	190
396	107	94	120	2.1	1.7	2.1	254
397	97	96	90	2.0	1.9	2.1	50
398	91	100	101	1.8	1.9	2.0	160
399	102	94	83	1.8	1.7	1.9	60
400	94	98	96	2.0	1.6	1.9	45

Table 36. Variation in height growth in families #501 to #520 grown from seed collected at Joachimsthal, East Germany.

	Height growth last 5 years		
Family	Russ	Kell.	Dunb.
		% of mean	
501	94	98	94
502	113	108	109
503	104	---	101
504	99	106	96
505	105	102	109
506	103	94	100
507	99	106	104
508	108	101	94
509	99	107	104
510	101	103	95
511	96	100	98
512	97	89	93
513	99	---	110
514	110	92	101
515	88	98	92
516	102	97	97
517	98	96	107
518	105	105	108
519	97	104	108
520	86	93	83

Table 37. Variation in Zimmerman moth attack among East German families #321 to #400 and #501 to #520, grown at Russ Forest.

Family and trees attacked		Family and trees attacked		Family and trees attacked		Family and trees attacked	
Fam.	%	Fam.	%	Fam.	%	Fam.	%
321	35	346	35	371	10	396	25
322	30	347	20	372	20	397	5
323	35	348	20	373	30	398	33
324	20	349	35	374	20	399	0
325	20	350	5	375	45	400	40
326	30	351	40	376	20	501	15
327	50	352	15	377	45	502	15
328	5	353	25	378	20	503	15
329	25	354	30	379	30	504	15
330	30	355	10	380	0	505	50
331	30	356	20	381	5	506	35
332	20	357	15	382	20	507	35
333	25	358	10	383	25	508	40
334	5	359	10	384	45	509	5
335	30	360	20	385	15	510	30
336	35	361	35	386	23	511	40
337	30	362	15	387	15	512	15
338	25	363	5	388	40	513	20
339	30	364	15	389	15	514	15
340	35	365	10	390	8	515	35
341	25	366	20	391	25	516	30
342	25	367	10	392	25	517	20
343	15	368	10	393	38	518	15
344	5	369	15	394	15	519	40
345	5	370	25	395	15	520	30

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Publications:

Gabriel, Wm. J. and G. E. Howe. 1968. Practical problems of a sugar maple selection program. N.E. Forest Tree Impr. Conf. Proc. 15: 72-74.

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