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INTERVARIETAL HYBRIDIZATION IN SCOTCH PINE

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INTERVARIETAL HYBRIDIZATION IN SCOTCH PINE

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ABSTRACT

INTERVARIETAL HYBRIDIZATION IN SCOTCH PINE

By

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Height, flowering, stem form, winter foliage color, and susceptibility to the European pine sawfly were examined for 98 varietal combinations of Scotch pine. Height data were examined using analysis of variance and LSD procedures. Chi-square analysis was used for the remaining traits. Associations between mid-parent and hybrid values were examined with correlation analysis.

Variation was significant for two traits, height and sawfly resistance. Only the variation due to differences within varietal combinations was significant. The implications of such variation for breeding are discussed.

Inadvertant selection for early flowering among the parents resulted in hybrids which flowered at an early age.

Heterosis was generally lacking for all traits, however several hybrids exhibited combinations of desirable traits. Several explanations for the lack of heterosis are discussed.

Correlation was significant for winter foliage color only.

The study indicates that further selection among the varietal combinations is unwarranted.

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INTRODUCTION

Scotch pine (*Pinus sylvestris* L.) has long been Europe's most important timber species. Although it is the most important Christmas tree in the northeastern United States, the value of Scotch pine as a timber species has, until recently, been suspect. Much of the criticism of Scotch pine was due to the generally poor form of the varieties grown in this country before large provenance tests were established. Provenance studies established during the middle of this century (Wright and Baldwin, 1957; Hamilton and Frommer, 1962; Wright and Bull, 1963; Genys, 1965) demonstrated that some Scotch pine varieties grow as rapidly as native northeastern pines, while maintaining moderate to good form. The results of these tests, and the performance of some earlier plantings of unknown origin, lead to a renewed interest in Scotch pine as a timber tree. They also indicated that improvements could be made in selecting Christmas tree varieties.

The natural range of Scotch pine extends from west-central Spain to northern Italy and on into Turkey; north to Scotland and Finland, and east across Siberia. The range is continuous in the north, occurring in the mountains in the south (Wright and Bull, 1963). The geographic distribution and distinguishing characteristics of the Scotch pine varieties used in this study are listed in Table 1.

A large amount of genetic diversity across the range of Scotch pine has been demonstrated, including significant differences among varieties in growth rate, stem form, flowering, mineral nutrient uptake, susceptibility to insect attack, early survival, and various other characteristics (Wright and Baldwin, 1957; West and Ledig, 1963; Wright and Bull, 1963; Genys, 1965; Steinbeck, 1966; Steiner, 1974; Karfalt et al., 1975; Ruby and Wright, 1976; Van Haverbeke, 1978). These differences among varieties make up 70-85% of the total genetic variance of the species (Ruby and Wright, 1976).

Genetic diversity of the parents is necessary for the expression of heterosis in the cross of two varieties. The among varieties variation in Scotch pine was considered by some researchers to be large enough to support hybridization work within the species (Wright, 1963a; NC-51 Committee, 1964; Genys, 1965). Wright (1963a) noted that inter-racial hybridization in forest trees was very likely first attempted with Scotch pine by Dengler in 1926. Dengler crossed German, French, and Scottish origins, and at age twenty the hybrids were intermediate between their parents in height growth. In the same paper Wright suggested that inter-racial crosses in trees offer the same possibilities as crosses between varieties of a crop plant or animal

Table 1.--Geographic distributions and performance in Michigan of the Scotch pine varieties used in this study. Derived from Ruby and Wright (1976).

Variety	Description
Lapponica	Distributed north of 63° N in Norway, Sweden, Finland, and probably the USSR. Very slow growth, very yellow winter foliage, irregular crowns.
septentrionalis	Distributed between latitudes 59 and 63° N in Norway, Sweden, and Finland. Slow growth, yellow winter foliage, narrow regular crown.
rigensis	Distributed in southern Sweden, Latvian SSR, Estonian SSR. Moderate growth rate, yellow winter foliage, narrow regular crowns.
mongolica	Distributed between latitudes 50 and 55° N in Eastern Siberia, and 55 to 60° N in central Siberia. Slow growth.
polonica	Distributed in Poland. Slightly yellower during winter than var. hercynica and doubtfully distinct from that variety.
hercynica	Distributed in West Germany except for the Pfalz, East Germany, Czechoslovakia west of longitude 15° E. Rapid growth.
borussica	Distributed throughout the lowlands of northeastern East Germany. Slightly slower growing than var. hercynica and doubtfully distinct from that variety.
haguenensis	Distributed in the Vosges Mountains of eastern France, Pfalz, Land of adjacent West Germany, and many plantations in Belgium. More stem crooks than in other varieties, very rapid growth, heavy cone production on young trees, green foliage during the winter.
pannonica	Slower growth and coarser branches than in var. hercynica.

Table 1.--Continued.

Variety	Description
scotica	Distributed in four small areas in the Scottish highlands. Moderate growth rate, resembling southern varieties in foliage color.
'East Anglia'	Distributed in certain plantations in East Anglia, England. Rapid growth and heavy cone production at early ages.
iberica	Distributed in the mountains of Spain. Very dark green winter foliage color, moderate growth rate, and susceptible to winter cold in northern areas.
aquitana	Distributed in the Massif Central of southern France. Slight susceptibility to winter cold damage in northern Michigan, dark green foliage color during the winter, and very heavy cone and pollen production at early ages.
subillyrica	Distributed in the Trentino Province of Italy and possibly other parts of Italy and southern Switzerland. Resembling central European varieties in general appearance but slower growing and later flushing.
illyrica	Distributed in the mountains of central Yugoslavia. Resembles central European varieties in general appearance, and southern varieties in winter foliage color.
rhodopaea	Distributed in the mountains of southern Bulgaria and northern Greece. Moderate growth rate, and dark green winter foliage color.
armena	Distributed in the Crimean SSR, Turkey, Armenian SSR, and the Georgian SSR. Siminar to var. rhodopaea, but fruiting more heavily.

breeds, and that the F_1 hybrids may show hybrid vigor, or a combination of desirable traits, as well as furnishing the basis for a selection program. Genys (1965) suggested crossing Spanish provenances of Scotch pine with south German and Belgian provenances for improved Christmas trees. The NC-51 committee also recognized the possibilities of inter-racial hybridization in Scotch pine (NC-51 Committee, 1964). One of the principle objectives of the NC-51 provenance studies was to provide breeding material for inter- and intra-specific hybridizations.

Wright et al. (1966a) suggested that the variety, 'East Anglia' (var. scotica x German or southern European variety), demonstrates the possibilities of intervarietal hybridization followed by selection. In this case moderate to rapid growth rates appear to have been combined with dark green winter foliage color. In later years it has been shown that such inter-racial hybridizations are possible among most, or all, Scotch pine varieties (Demeritt et al., 1975; Karfalt et al., 1975; Zeaser, 1976). Karfalt et al. (1975) studied 189 inter-population combinations of Scotch pine and found seed yields comparable to those of intra-population combinations. As previously mentioned, significant differences among Scotch pine varieties have been detected for many characters. This suggests that there is a possibility that crosses between such varieties will result in heterosis in the offspring.

Manifestation of heterosis in the offspring resulting from inter-racial matings has generally not been demonstrated for species of pine or spruce (Morgenstern, 1975; Nilsson, 1975; Woessner, 1975; Zeaser, 1976; Hohn and Muhs, 1979; Park, 1979). However, hybrids expressing combinations of desirable traits were reported by both Zeaser (1976) with Scotch pine, and Morgernstern (1975) in black spruce.

The principle objective of this study was to determine to what extent intervarietal hybridization might be used in improving Scotch pine as both a timber and Christmas tree species.

MATERIALS AND METHODS

This study evaluated five plantations established between 1970 and 1974. Controlled pollinations were made by H. D. Gerhold, E. H. Palpant, and J. D. Murphy of the Pennsylvania State University, and J. W. Wright and W. A. Lemmien of Michigan State University. The controlled pollinations were performed in a large provenance test (MSFGP 2-61, 4-61) covering the natural range of Scotch pine, located at Michigan State University's W. K. Kellogg Forest in Kalamazoo County, Michigan. The trees were young (7-10 years from seed) when pollinated, and matings were restricted by the number of trees flowering. The 1969 and 1970 pollinations were performed using the mini-bag technique employed by Gerhold (1968), while the 1966 pollinations were made by spraying unbagged female flowers with pollen.

The hybrids produced were maternal half-sibs, with individual seed parents selected from several stands within each variety. Hybrids in plantations MSFGP 9-70 and 4-71 were produced by crossing females from twelve varieties with pollen mixes from two varieties. Hybrids in plantation MSFGP 8/9/10-72 consisted of inter- and intra-varietal half-sibs produced from crosses of nine female varieties with pollen bulks of males from eight varieties. In plantation MSFGP 6/7/8-73 the intra-varietal hybrids were produced within seven varieties, while the inter-varietal hybrids in this plantation were derived from eight varietal pollen bulks crossed with female parents from twelve varieties. Plantation MSFGP 1-74 was also established with inter- and intra-varietal hybrids. These hybrids were produced using eight varieties as females and seven as male parents. The matings for each plantation are illustrated in more detail in Tables 2 through 5.

All plantations were established with 2+0 stock except MSFGP 4-71 in which 3+0 stock was used. Three plantations (MSFGP 9-70, 8/9/10-72, and 6/7/8-73) were located in Ingham County, Michigan, and two (MSFGP 4-71 and 1-74) were established at the Kellogg Forest. Four plantations were established on old field sites, while one plantation had been a black locust grove prior to its establishment with Scotch pine. The Kellogg Forest plantations were established on low hills with up to 40% slope, while the Ingham County plantations were level. All plantations were established utilizing a randomized complete block design, with 4-tree plots and 5-10 replications. The planting was done by machine by Michigan State University crews at 8 x 8 ft. spacings. Weed control was practiced in all plantations either immediately before or after planting, using amitrole and simazine sprayed in 60 cm (2 ft) wide

Table 2.--Matings for hybrids in plantations MSFGP 9-70 and 4-71, performed in the spring of 1966.

Female	Male	
	HAG	IBE
BOR[a]	X[b]	-
AQU	X	X
IBE	X	-
RIG	X	-
SEP	X	-
HAG	X	X
SCO	X	X
EAN	X	-
HER	X	-
ARM	-	X
ILL	-	X

[a]BORussica, AQUitana, IBErica, RIGensis, SEPtentrionalis, HAGuenensis, SCOtica, 'East ANglia,' HERcynica, ARMena, ILLyrica.

[b]X indicates where crosses were made.

Table 3.--Matings for hybrids in plantation MSFGP 8/9/10-72, performed in the spring of 1967.

Female	Male								
	IBE	ILL	RHO	ARM	HER	SIB	AQU	HAG	POL
AQU[a]	X[b]	X	X	X	X	X	X	X	-
HAG	X	X	-	-	X	X	-	X	-
ARM	X	-	-	X	-	-	-	X	X
MON	-	-	-	-	-	X	-	-	-
ILL	-	X	-	-	-	-	-	-	-
EAN	X	-	-	-	-	X	-	X	-
HER	X	X	-	X	X	X	-	X	-
RIG	-	-	-	-	-	-	-	X	X
SUB	X	-	-	-	-	X	-	X	X

[a]AQUitana, HAGuenensis, ARMena, MONgolica, ILLyrica, 'East ANglia,' HERcynica, RIGensis, SUBillyrica, IBErica, RHOdopaea, POLonica.

[b]X indicates where crosses were made.

Table 4.--Matings for hybrids in plantation MSFGP 6/7/8-73, performed in the spring of 1969.

Female	Male					
	AQU	HAG	RHO	SUB	EAN	ARM
AQU[a]	X[b]	X	X	X	X	X
HAG	X	X	-	X	-	X
ARM	X	X	X	-	X	X
IBE	X	X	X	X	X	X
EAN	X	X	-	-	X	-
SUB	-	-	-	-	-	X

[a]AQUitana, HAGuenensis, ARMena, IBErica, 'East ANglia,' SUBillyrica, RHOdopaea.

[b]X indicates where crosses were made.

strips. Paraquat was used instead of amitrole and simazine in MSFGP 1-74.

The plantations were measured at the end of the 1978 growing season when the trees were 6-11 years old. All plantations were measured for height, flowering, and stem crooks. Height measurements were made on the two tallest trees in each plot, while flowering was recorded as the number of trees with female flowers per plot. The number of trees with severe crooks (those crooks involving more than a 5 cm (2 in) offset from center) was also recorded for each plot. The number of trees per plot with no distinct leader was used as an alternative measurement

Table 5.--Matings for hybrids in plantation MSFGP 1-74, performed in the spring of 1969 and 1970.

Female	Male						
	ARM	PAN	HAG	HER	AQU	IBE	SUB
EAN[a]	X[b]	X	X	X	X	-	-
SEP	X	-	X	-	-	-	-
ARM	X	X	X	-	X	X	-
SUB	X	-	X	X	-	-	-
IBE	X	-	X	X	X	-	X
AQU	-	-	X	-	X	X	-
LAP	X	-	X	X	-	-	-
SCO	X	-	X	-	X	-	-
HAG	-	-	-	-	X	-	-

[a]'East ANglia,' SEPtentrionalis, ARMena, SUBillyrica, IBErica, AQUitana, LAPponica, SCOtica, HAGuenensis, PANnonica, HERcynica.

[b]X indicates where crosses were made.

for stem form in plantation MSFGP 1-74 in which the trees were too young to show appreciable crook. Plantations MSFGP 1-74 and 8/9/10-72 were also scored for winter foliage color, which was rated from 0 (yellow) to 10 (green) based on live tree to tree comparisons. Two plantations (MSFGP 8/9/10-72 and 6/7/8-73) located in Ingham County, Michigan experienced a European pine sawfly (*Neodiprion sertifer* Geoff.) infestation in late spring of 1979. This provided an opportunity to determine the susceptibility of the hybrids to this insect. The percentage defoliation of each tree was measured and plot totals were recorded.

Parental values were calculated for the five traits examined in the hybrids (height, flowering, stem form, winter foliage color, and sawfly damage). Heights of parental trees were measured in four plantations in southern Michigan during the summer of 1979 by J. W. Wright and S. R. Homrich. The Kellogg plantation contained the parents of the hybrids, while the remaining three plantations were established with these same parental seedlots. Height values for each seedlot were averaged over plantations. For comparisons with hybrid heights these parental values were expressed as percents of the plantation mean. The plantation mean was derived from only those seedlots necessary for comparisons with the hybrid families within any one hybrid plantation. In this way the parental values centered around a mean of 100, which made them more suitable for comparisons with hybrid values, as they too had a mean of 100. Parental values for flowering, stem form, winter foliage color and European pine sawfly damage were calculated by averaging the parental seedlot values over plantations. Parental values were derived from six plantations in southern Michigan for flowering, two plantations from southern Michigan and one from the Upper Peninsula for stem form, three plantations from southern Michigan for winter foliage color, and a Kellogg Forest plantation for European sawfly damage. Flowering and stem form values were obtained from measurements made when these trees were the same age as the hybrids with which they were to be compared. Color and sawfly damage values were obtained from the most recent measurements using the same scales as those used to score the hybrids.

Data from each plantation were analyzed separately. A combined analysis of MSFGP 9-70 and 4-71 was also performed to investigate seedlot x plantation interaction. Height data was analyzed using analysis of variance calculations for irregular experiments. When the F-value was significant, the least significant difference (LSD) procedure was used to determine the differences among individual seedlots.

The analysis of data pertaining to flowering, stem form, winter foliage color, and sawfly damage was accomplished using chi-square analysis, as these are enumeration data and not suitable for standard analysis of variance procedures. The test criterion takes the form:

$$\text{Chi-square} = \frac{\Sigma(\text{Observed} - \text{Expected})^2}{\text{Expected}}$$

The expected value is the average number when the hypothesis is true.

Correlation analysis was used to investigate the correspondence of mid-parent and progeny values for height growth, flowering, stem form, winter foliage color, and European pine sawfly damage.

RESULTS AND DISCUSSION

Height

Plantations MSFGP 9-70 and 4-71

The plantations were in generally good condition when measured in 1978. The trees were growing well (60 cm/year, 2 ft/year) and crown closure was complete, except where trees or plots were missing. Missing trees were primarily the result of girdling by mice during the winter of 1975, which resulted in about 40% mortality in both plantations.

The heights of the slower growing seedlots were generally the same in both plantations, with the shortest seedlots being 3.2 m (10.7 ft) in height. The heights of the faster growing seedlots differed significantly, as the tallest seedlots in MSFGP 9-70 were 5.0 m (16.7 ft) in height compared with 4.0 m (13.3 ft) for the tallest seedlot in MSFGP 4-71.

This difference in height growth between the tallest seedlots in the plantations was most likely the result of establishing plantation MSFGP 4-71 with seedlings which were too large for that purpose. The faster growing varieties were up to 46 cm (18 in) tall and had large root systems when lifted as 3+0 seedlings. The faster growing 2+0 seedlings were much shorter (up to 23 cm, 9 in) and had smaller root systems. The large 3+0 seedlings suffered much more root damage than their 2+0 counterparts when lifted, and they had a larger shoot to support. This resulted in a reduced growth rate for the tallest seedlots in MSFGP 4-71 when compared with MSFGP 9-70. The lack of height differences between the slower growing seedlots in the plantations resulted because these slower growing seedlings were not large enough to suffer severe root damage when lifted from the nursery in either year. The use of large 3+0 stock cannot be recommended for the faster growing varieties of Scotch pine.

There was a question as to whether all of the progeny in these plantations were the hybrids intended. Female flowers were not bagged prior to or after the controlled pollinations, and the resulting seed might have been due to pollination from an older Scotch pine (probably var. _haguenensis_) stand about 1/8 mile away. Examination of families with the same female, but different male parents, indicates a significant effect on height growth due to the male parent (Table 6), as the families with the faster growing male parent were taller than those with the slower growing male. These results suggest that most, or all, of the trees in these plantations are indeed the hybrids that the controlled pollinations were intended to produce.

Table 6.--Mean heights of hybrids with the same female parent, and different male parents in plantations MSFGP 9-70 and 4-71.

Female Parent: Variety and Seedlot	Mean Height of Offspring Resulting from Pollination By:	
	haguenensis	iberica
aquitana		
212	107*	74, 96
238	114*	93, 85
haguenensis		
530	116*	111, 80
236	111*	---
241	112*	---
253	104*	---
318	111*	---
scotica		
265	---	79, 89
266	---	80, 93
267	110*	---

*Indicates that the attached mean is significantly larger at the 5% level than the mean for the hybrid with the var. iberica male, with LSD = 21.

The seedlots in these plantations were produced from the same set of controlled pollinations. There were 49 seedlots, 27 of them common to both plantations. Height data from the shared seedlots were used to determine the significance of seedlot x plantation interaction. From the analysis of variance such interactions were determined to be significant at the 5% level, however they were small relative to the variation due to seedlot alone (Table 7). Therefore, the height data for the two plantations were combined.

The mean heights and ranges for all of the varietal combinations in the two plantations are listed in Table 8. All but one of the varietal combinations with the

Table 7.--Analysis of variance for plantations MSFGP 9-70 and 4-71 showing the significance of seedlot x plantation interaction.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-Value
Total	259	18677	--	--
Seedlot	26	5864	222.5	4.47**
Plantation	1	5271	5271.0	104.58**
Seedlot x Plantation	26	1311	50.4	1.67*
Error	206	6231	30.25	--

*Significant at the 5% level.

**Significant at the 1% level.

Table 8.--Comparison of mid-parent and hybrid height for plantations MSFGP 9-70 and 4-71.

Varietal Combination	Relative Height	
	Mid-parent[a]	Hybrid Mean (Range)
BOR x HAG[b]	115	104 (--)
AQU x HAG	101	105 (88-118)
IBE x HAG	98	103 (99-107)
RIG x HAG	107	102 (--)
SEP x HAG	91	104 (95-113)
HAG x HAG	111	108 (90-119)
SCO x HAG	100	110 (110-110)
EAN x HAG	108	105 (104-106)
HER x HAG	112	104 (84-117)
SUB x HAG	106	88 (81-94)
AQU x IBE	90	88 (67-98)
ARM x IBE	83	81 (71-93)
ILL x IBE	91	90 (86-93)
HAG x IBE	94	98 (87-108)
SCO x IBE	85	85 (66-95)

[a]Mid-parent values were derived from seedlots of the parental variety in four plantations. Seedlot values were averaged over plantations and then expressed as a percent of the plantation mean. The plantation mean was derived from only those seedlots necessary for comparisons with the hybrid families within any one hybrid plantation.

[b]BORussica, HAGuenensis, AQUitana, IBErica, RIGensis, SEPtentrionalis, SCOtica, 'East ANglia,' HERcynica, SUBillyrica, ARMena, ILLyrica.

taller male parent were taller than all but one of the combinations with the shorter male parent. The only apparent difference among the varietal combinations with a slower growing male was between the shortest and tallest seedlots of such combinations. One should also note that all of the combinations with the shorter male parent contain families which performed better than the slower growing families within many combinations with the faster growing male.

The wide ranges in height for many of the combinations indicate significant variation due to families within varietal combinations (Table 9). Similar results were obtained by Park (1979) who worked with similar intervarietal Scotch pine hybrids. Large within varietal combination variation is a serious drawback to intervarietal hybridization, as the individual parent is more important than the variety in determining the performance of the hybrid. The result is an inability to predict the performance of hybrids from a varietal cross, which makes the task of producing useful hybrids much more difficult. Park (1979) also found significant variation among hybrid populations (i.e., varietal combinations), and he concluded that further breeding between hybrid populations would be useful. This conclusion was not supported by the findings of the current study, in which the variation among varietal combinations was not significant in four of the five plantations (Table 9). The lack of agreement between the two studies

Table 9.--Degrees of freedom and mean squares[a] showing the significance of within and among varietal combination variation in height for plantations MSFGP 9-70, 4-71, 8/9/10-72, 6/7/8-73, and 1-74.

Plantation MSFGP	Degrees of Freedom		Mean Square		
	Within Varietal Comb.	Among Varietal Comb.	Within Varietal Comb.	Among Varietal Comb.	Error
9-70	25	13	99.4**	209.0	43.2
4-71	25	14	38.8**	144.3**	16.0
8/9/10-72	18	32	84.9**	110.2	43.4
6/7/8-73	28	25	29.4**	27.3	13.0
1-74	16	27	27.8**	37.3	5.64

**Significant at the 1% level.

[a]The mean squares for plantation MSFGP 9-70 were as follows:

Source	Degrees of freedom	Expected mean square
Block	4	$\sigma_e^2 + 39\sigma_B^2$
Seedlot	39	
Among var. comb.	13	$\sigma_e^2 + 5\sigma_W^2 + 10\sigma_A^2$
Within var. comb.	25	$\sigma_e^2 + 5\sigma_W^2$
Error	96	σ_e^2

may be attributable to both the age of the trees when measured, and the uniformity of growing conditions. Park worked with three-year-old seedlings growing in nursery beds, while the current study examined six to ten-year old trees growing in plantations. Whereas age-age correlations for height growth in Scotch pine are usually fairly strong, the uniform growing conditions provided in the study by Park may have enabled him to detect differences that the current study was not able to detect. Genys (1970), reporting on the results of a Scotch pine provenance test, noted large intra-varietal diversity in many characters, and suggested that data from individual strains or trees may be more useful than varietal means for tree breeding.

Comparison of mid-parent and progeny heights indicated that the heights for varietal combinations tended to correspond well with those of their respective mid-parents. The correlation coefficient (r) for mid-parent and progeny heights was .68, which was significant at the 1% level. This was most likely due to the use of only two male parents that differed significantly in their ability to produce offspring with rapid growth. Mid-parent by progeny correlations for varietal combinations with the same male parent were nil. Of the varietal combinations, 64% were shorter than expected, and the largest deviations from the expected were also in this direction. The combination, var. _subillyrica_ x var. _haguenensis_ was much shorter than expected, while var. _scotica_ x var. _haguenensis_ was taller than expected and may exhibit hybrid vigor. There was no other evidence of useful hybrid vigor in these two plantations.

Plantations MSFGP 8/9/10-72, 6/7/8-73, and 1-74

These three plantations were in good condition when measured in 1978. Survival was fair (78%), most living trees appeared healthy, and the plantations could be easily traversed, as crown closure had only just begun in the oldest of the plantations. The trees in this plantation averaged 2.5 m (8.3 ft) in height, while those in MSFGP 6/7/8-73 averaged 2.3 m (7.7 ft), with the trees in MSFGP 1-74 averaging 1.3 m (4.3 ft).

Table 10 lists the mean heights and ranges for all of the varietal combinations in the three plantations. Of the 59 combinations only 24 contained more than one hybrid family, and a range of family means. These ranges were wide within many of the combinations, and most of the ranges overlapped. From the analysis of variance the variation due to families within varietal combinations was determined to be significant (Table 9). Again, this indicates that the individual parent is more important than the variety in determining the performance of the hybrid.

Hybrid heights were not strongly associated with those of their respective mid-parents. The correlation coefficient of $r = .37$ was significant at the 5% level. However a coefficient of determination of $r^2 = .14$

Table 10.--Comparison of mid-parent and hybrid height for plantations MSFGP 8/9/10-72, 6/7/8-73, and 1-74.

Varietal Combination	Relative Height		Varietal Combination	Relative Height	
	Mid-parent[a]	Hybrid Mean (Range)		Mid-parent	Hybrid Mean (Range)
AQU x IBE[b]	92	86(71-100)	ARM x SUB	95	75
AQU x ILL	98	103	ARM x PAN	107	88
AQU x RHO	94	102(87-126)	EAN x IBE	99	91
AQU x ARM	92	91(78-99)	EAN x HAG	114	118(79-133)
AQU x HER	104	107(78-128)	EAN x SUB	104	83(83-83)
AQU x SUB	100	92(73-114)	EAN x EAN	109	117
AQU x HAG	107	117(84-149)	EAN x AQU	103	94
AQU x AQU	96	100(83-117)	EAN x ARM	100	102(98-105)
AQU x EAN	103	105(96-116)	EAN x PAN	110	103
HAG x IBE	100	110(97-115)	EAN x HER	114	128
HAG x ILL	106	143	HER x ILL	103	77
HAG x HER	112	102	HER x ARM	95	104
HAG x SUB	112	97(80-117)	HER x SUB	98	110
HAG x HAG	117	122(116-128)	HER x HAG	116	90
HAG x ARM	101	109	HER x HER	107	88
HAG x AQU	108	116(109-123)	RIG x POL	103	104
ARM x HAG	104	96(52-133)	RIG x HAG	110	110
ARM x IBE	84	76(72-29)	SUB x SUB	99	84(78-90)
ARM x ARM	85	85(58-92)	SUB x IBE	95	74
ARM x POL	101	97	SUB x ARM	96	94
ARM x AQU	92	88(75-101)	SUB x HAG	112	104

Table 10.--Continued.

Varietal Combination	Relative Height: Mid-parent[a]	Relative Height: Hybrid Mean (Range)	Varietal Combination	Relative Height: Mid-parent	Relative Height: Hybrid Mean (Range)
ARM x RHO	90	109	SUB x HER	112	115
ARM x EAN	96	117	MON x SUB	95	103
ILL x ILL	99	92	IBE x HER	101	115
IBE x AQU	91	100(95-103)	SEP x HAG	94	108
IBE x RHO	89	91	SEP x ARM	79	109
IBE x HAG	100	110(90-133)	SCO x AQU	100	88
IBE x ARM	84	76(74-77)	SCO x ARM	93	55
IBE x EAN	95	109	SCO x HAG	110	98
IBE x SUB	94	88(86-91)			

[a]Mid-parent values were derived from seedlots of the parental variety in four plantations. Seedlot values were averaged over plantations and then expressed as a percent of the plantation mean. The plantation mean was derived from only those seedlots necessary for comparisons with the hybrid families within any one hybrid plantation.

[b]AQUitana, IBErica, ILLyrica, RHOdopaea, ARMena, HERcynica, SUBillyrica, HAGuenensis, 'East ANglia,' POLonica, PANnonica, RIGensis, MONgolica, SEPtentrionalis, SCOtica.

indicates that relatively little of the variation in hybrid height was due to its association with the mid-parent value. The varietal combinations which differed significantly from the mid-parent height were generally shorter than expected. These combinations and their respective mean and mid-parent heights are listed in Table 11.

All four combinations possibly exhibiting positive heterosis may be potentially useful hybrids. In three cases (var. armena x var. rhodopaea, var. armena x var. 'East Anglia,' and var. illyrica x var. haguenensis) the growth rate of slower growing varieties with good winter foliage color has been improved. The value of the remaining combination (var. septentrionalis x var. armena) is dubious unless the hybrid is better adapted to northern climates than the southern parent and exhibits better winter foliage color than the northern parent, or it shows more rapid height growth than the northern parent in a northern environment.

Zeaser (1976) found no evidence of heterosis for height growth among intervarietal Scotch pine hybrids. Similar results have been demonstrated in intervarietal hybridizations of loblolly pine (Woessner, 1975), Scotch pine (Nilsson, 1975), red pine (Holst and Fowler, 1975), black spruce (Morgenstern, 1975), and Norway spruce (Nilsson, 1975; Hohn and Muhs, 1979). Ying (1978) found that inter-provenance white spruce hybrids grew faster than trees of open-pollinated local controls and local x local,

Table 11.--Comparison of mid-parent and hybrid means of varietal combinations with means which differ significantly[a] from their mid-parent value for plantations MSFGP 8/9/10-72, 6/7/8-73, and 1-74.

Varietal Combination	Relative Height	
	Mid-parent[b]	Hybrid Mean
ARM x PAN[c]	107	88
ARM x SUB	95	75
EAN x SUB	104	83
HER x HAG	116	90
HER x HER	107	88
ILL x HAG	106	143
SCO x ARM	93	55
SEP x ARM	79	109
ARM x RHO	90	109
ARM x EAN	96	117

[a]A minimum difference of 20 was required for significance at the 5% level using LSD.

[b]Mid-parent values were derived from seedlots of the parental variety in four plantations. Seedlot values were averaged over plantations and then expressed as a percent of the plantation mean. The plantation mean was derived from only those seedlots necessary for comparisons with the hybrid families within any one hybrid plantation.

[c]ARMena, PANnonica, SUBillyrica, 'East ANglia,' HERcynica, HAGuenensis, SCOtica, SEPtentrionalis, RHOdopaea.

intra-provenance, crosses. He attributed these results to reduced inbreeding in the inter-provenance hybrids.

The results of species hybridization in the pines, undertaken by the Genetics Project of the Northeast Forest Experiment Station in 1947, are summarized by Garrett (1973). The hybrids were generally intermediate in height growth between the two parents, and rarely exceeded the height of the taller parent.

Park (1979) also reported a general lack of hybrid superiority in height growth for intervarietal Scotch pine hybrids. He felt that this may have been the result of inflated mid-parent values which were based on intra-population progenies. He suggested that the mating design exaggerated the outbreeding tendency of the species, and that the progeny were less inbred than if they had been produced from a natural population. Park's reasoning may explain in part the general lack of heterosis exhibited in the current study, as some of the seedlots were common to both studies.

It is also possible that the means by which the parental values were calculated may have contributed to the failure to detect hybrid vigor. As previously mentioned the average values of trees from the parental seedlots were used, with these trees growing under different local conditions than those of the hybrids. Regardless of these drawbacks, it was felt that these 'parental values' might indicate the degree of progress achieved in the F_1 hybrids.

Several other possible explanations for the general lack of heterosis sometimes exhibited by hybrids have been proposed. Cress (1966) suggested that heterosis will not occur without genetic diversity, but that genetic diversity by itself may not result in a heterotic response. He further explained that with multiple alleles each locus will probably not contribute positively to the heterotic effect, even when alleles in pairs have partially dominant, completely dominant, or over dominant effects. Cress goes on to say that generally the positive contributions will be larger than those that are negative, but the breeder should not be surprised to find that in some crosses this is not the case. Another possible explanation may be that provided by Wallace (1955), from studies with inter-population hybrids of Drosophila melanogaster. He found that heterosis was the result of heterozygosity for integrated gene complexes, that recombination destroyed these complexes, and subsequently the heterosis dependent upon them.

Flowering

The hybrids in this study exhibited strong selection for precocious production of female flowers. Wright et al. (1966a), reporting on early flowering in Scotch pine, found 7% flowering of seven-year-old trees, and 22% flowering of eight-year-old trees among several plantations established in 1961 in southern Michigan. Six-year-old hybrids in the current study produced a larger percentage of trees with female flowers (28-36%) than the eight-year-old trees mentioned by Wright *et al*. Female flower production for the five plantations in this study is illustrated in Tables 12-14.

Differences among varietal combinations and within varietal combinations were not significant (5% level) as determined by chi-square analysis for all plantations. However plantations MSFGP 9-70 and 4-71 were also measured in 1974 and 1975 when the trees were six-years-old, and at this time differences among varietal combinations were significant (Table 15).

Only two male parents were used in these plantations, var. *haguenensis*, which exhibited the heaviest amount of early flowering in the study by Wright *et al*. (1966a), and var. *iberica*, which did not flower heavily in the same study. Combinations with the heavier flowering male produced more early flowering trees than did combinations with the lesser flowering male. The use of these two very different males with respect to this character was probably the major cause of the above mentioned differences.

Only one plantation (MSFGP 1-74) contained hybrids which did not exhibit a clearcut increase in flowering over that of their parents (Table 12). Of the 27 varietal combinations in this plantation, 8 produced fewer female flowers than expected, while 17 produced more than expected. More than half of these differences between the mid-parent and hybrid values were not large, however.

Table 12.--Comparison of mid-parent and hybrid flowering for plantation MSFGP 1-74.

Varietal Combination	Percent of Trees Flowering: Mid-parent[a]	Percent of Trees Flowering: Hybrid Mean (Range)	Varietal Combination	Percent of Trees Flowering: Mid-parent	Percent of Trees Flowering: Hybrid Mean (Range)
EAN x ARM[b]	16	11(0-15)	SUB x HER	13	54
EAN x PAN	10	47	IBE x HAG	16	22(0-43)
EAN x HAG	28	34(25-50)	IBE x HER	9	25
EAN x HER	18	30	IBE x AQU	12	0
EAN x AQU	20	60	IBE x ARM	12	25
SEP x HAG	16	0	IBE x SUB	6	10
SEP x ARM	16	0	AQU x HAG	26	14
ARM x HAG	27	27(12-60)	AQU x IBE	4	33
ARM x PAN	3	0	AQU x AQU	18	27
ARM x AQU	21	40(33-43)	SCO x AQU	14	50
ARM x IBE	12	60	SCO x ARM	14	14
ARM x ARM	19	13(0-50)	SCO x HAG	22	0
SUB x ARM	16	33	HAG x AQU	28	38
SUB s HAG	16	32			

[a]Mid-parent values were derived from seedlots of the parental variety in six plantations. Seedlot values were averaged over plantations.

[b]'East ANglia,' ARMena, PANnonica, HAGuenensis, HERcynica, AQUitana, SEPtentrionalis, IBErica, SUBillyrica, SCOtica.

Table 13.--Comparison of mid-parent and hybrid flowering for plantations MSFGP 9-70 and 4-71.

Varietal Combination	Percent of Trees Flowering		
	Mid-parent[a]	Hybrid	
		Mean	(Range)
BOR x HAG[b]	12	15	
AQU x HAG	16	51	(32-86)
IBE x HAG	10	48	(33-70)
RIG x HAG	12	25	
SEP x HAG	12	49	(17-63)
HAG x HAG	15	48	(21-78)
SCO x HAG	13	57	(26-88)
EAN x HAG	18	30	(9-50)
HER x HAG	14	50	(14-82)
SUB x HAG	14	64	(33-81)
AQU x IBE	10	24	(0-67)
ARM x IBE	2	29	(0-50)
ILL x IBE	4	3	(0-6)
HAG x IBE	20	22	(0-33)
SCO x IBE	4	15	(0-34)

[a]Mid-parent values were derived from seedlots of the parental variety in six plantations. Seedlot values were averaged over plantations.

[b]BORussica, HAGuenensis, IBErica, RIGensis, SEPtentrionalis, SCOtica, 'East ANglia,' HERcynica, SUBillyrica, AQUitana, ARMena, ILLyrica.

Table 14.--Comparison of mid-parent and hybrid flowering for plantations MSFGP 8/9/10-72 and 6/7/8-73.

Varietal Combination	Percent of Trees Flowering		Varietal Combination	Percent of Trees Flowering	
	Mid-parent[a]	Hybrid Mean (Range)		Mid-parent	Hybrid Mean (Range)
AQU x IBE[b]	8	82	ARM x HAG	6	74(25-100)
AQU x ILL	8	82	ARM x ARM	2	44(0-88)
AQU x HER	10	71(46-90)	MON x SUB	10	64
AQU x AQU	8	78(36-92)	ILL x ILL	0	83
AQU x EAN	14	81(64-100)	EAN x IBE	8	80
AQU x RHO	6	64(44-100)	EAN x SUB	14	67(57-86)
AQU x ARM	5	74(40-100)	EAN x EAN	21	88
AQU x SUB	8	81(70-100)	EAN x AQU	12	71
AQU x HAG	18	93(75-100)	EAN x HAG	21	83
HAG x IBE	12	79(50-92)	HER x ILL	7	31
HAG x ILL	12	83	HER x ARM	7	56
HAG x HER	20	47	HER x SUB	18	60
HAG x HAG	22	83(77-100)	HER x HAG	12	78
HAG x ARM	11	93	HER x HER	9	50
HAG x AQU	12	86	RIG x POL	4	100
HAG x SUB	24	75(67-97)	RIG x HAG	2	80
ARM x IBE	2	54	SUB x SUB	5	57
ARM x POL	2	71	SUB x IBE	2	25
ARM x AQU	5	97(94-100)	SUB x ARM	2	100
ARM x RHO	2	73	IBE x AQU	8	88(82-93)
ARM x EAN	11	100	IBE x RHO	2	56

Table 14.--Continued.

Varietal Combination	Percent of Trees Flowering		Varietal Combination	Percent of Trees Flowering	
	Mid-parent[a]	Hybrid Mean (Range)		Mid-parent	Hybrid Mean (Range)
ARM x SUB	2	91	IBE x HAG	10	100
IBE x ARM	0	69	IBE x SUB	2	86
IBE x EAN	10	88			

[a]Mid-parent values were derived from seedlots of the parental variety in six plantations. Seedlot values were averaged over plantations.

[b]AQUitana, IBErica, ILLyrica, HERcynica, 'East ANglia,' RHOdopaea, ARMena, SUBillyrica, HAGuenensis, POLonica, MONgolica, RIGensis.

Table 15.--Degrees of freedom and values of chi-square showing the significance of the variation in early flowering among varietal combinations in plantations MSFGP 9-70, 4-71, 8/9/10-72, 6/7/8-73, and 1-74.

Plantation MSFGP	Degrees of freedom	Chi-square Value	
		1974	1979
9-70	13	32.14**	7.76
4-71	11	51.82**	20.30
8/9/10-72	28		18.39
6/7/8-73	24		3.92
1-74	26		29.65

**Significant at the 1% level.

The general lack of clearcut precocity for flower production in MSFGP 1-74 was probably due to the age of the parent trees when the controlled pollinations were made. Most of the hybrids in this plantation were produced from trees which were 11-years-old, with a lesser number produced from 8-year-old trees. By age 11 a greater number of trees would be flowering, which would reduce the selection for trees exhibiting early flowering. Therefore one would not expect these hybrids to exhibit the degree of precociousness found in hybrids produced from earlier matings.

The hybrids in plantations MSFGP 9-70 and 4-71 showed a marked increase in early flowering over that of their parents (Table 13). After six years 39% of the trees produced female flowers compared with an average mid-parent value of 12%, and after ten years 78% of the trees were flowering.

The remaining two plantations (MSFGP 8/9/10-72 and 6/7/8-73) also contained hybrids exhibiting precocious flowering (Table 14). After eight years 74% of the hybrids were producing female flowers.

The above results clearly demonstrate strong selection for precocious flowering. Although it was not the intention of this study to select for precocious flowering, that is what resulted. As mentioned in materials and methods, hybrid parents were seven to seleven-years-old when the pollinations were made, and pollinations were restricted to those trees with enough female flowers to produce adequate amounts of seed. Even if parent trees were ostensibly selected for some other character, strong selection for early flowering could not be avoided.

Precocious flowering is one means by which the time barrier in the production of improved forest trees may be overcome. Gerhold (1966) suggested that efforts to exploit precocious flowering could be very rewarding without much risk of detracting from yield or quality if reasonable safeguards are incorporated. Both Wright (1966a) and Gerhold (1966) reported small positive correlations between the number of female flowers on a tree and height growth. Although these correlations were not statistically significant, they do indicate that selection for precocious flowering in Scotch pine may produce other beneficial results.

Early flowering may also be undesirable, especially for producers of Christmas trees. In the pines the male flowers occur in place of needles, therefore when many male flowers are produced large areas of the branch are left without needles. Christmas tree plantations which flower extensively at an early age would be greatly reduced in value.

The early flowering response of the hybrids did not correspond well with the mid-parent values. The correlation coefficient for plantations MSFGP 9-70 and 4-71 (.75, significant at the 5% level) indicates a fairly strong association between flowering of the hybrids and the mid-parent. However, this again is probably due to the use of only two male parents which differ markedly in their tendency to produce female flowers at an early age. Correlation coefficients for the remaining three plantations were low (.21, .10, .21), suggesting that the strong selection for early flowering may have hidden any associations that would have been present under less rigorous selection.

The results from the present study of flowering among the varietal combinations may also provide a clue regarding the lack of heterosis among the hybrids with respect to height growth. Performing controlled pollinations on the then young Scotch pines resulted in strong selection for precocious flowering. In effect this greatly reduced the selection differential for the second selected trait, which in this case was height growth.

Falconer (1960) noted that simultaneous selection for all of the component characters together would result in the most rapid improvement of economic value. These characters must be combined into an index, with selection applied to the index rather than the individual component characters. Characters are weighted by the product of their relative economic value and heritability, provided they are not correlated, or if there is no information concerning the genetic correlations. The efficiency of the index can be improved if such correlations are known.

Wright (1963b) suggested crossing families which are superior in each of two traits, growing the F_1 generation without selection, and then growing a segregating F_2 generation. Appreciable gain would not be evident for both traits in the F_1 generation, but from a reasonably sized F_2 population it would be possible to obtain segregates that nearly equalled the superiority found in one trait in the parent population in both traits.

Stem Form

The varietal combinations generally exhibited poorer stem form than expected, the exception being hybrids in plantations MSFGP 9-70 and 4-71. Of the fifteen varietal combinations in these two plantations, ten were straighter than expected. Hybrids in MSFGP 8/9/10-72 and 6/7/8-73 exhibited much poorer form than expected, as 34 of 47 varietal combinations had a greater proportion of crooked trees than the mid-parent value. Virtually all of the combinations in MSFGP 1-74 contained more trees without a leader or with multiple leaders than expected from the mid-parent value.

From the results reported above and examination of Tables 16 through 18 one would anticipate, at best, a weak association between progeny stem form and the mid-parent value, and, indeed, this is the case. The correlation coefficients were r = .35 (MSFGP 9-70 and 4-71), r = .13 (MSFGP 8/9/10-72 and 6/7/8-73), and r = .21 (MSFGP 1-74), all of which were not significant at the 5% level. Again, the effect of the use of only two male parents shows up in the correlation coefficient for MSFGP 9-70 and 4-71, as this value is much larger than that for the other groups of varietal combinations.

Several provenance studies and other reports have suggested that var. haguenensis generally exhibited the poorest form of all Scotch pine varieties (Wright and Baldwin, 1957; Wright and Bull, 1963; Ruby and Wright, 1976; Wright, 1976; Wright et al., 1976). It was not possible to determine from this study whether var. haguenensis passed this tendency for poor form on to its offspring among the intervarietal hybrids. Differences among the varietal combinations were generally not significant at the 5% level, using chi-square analysis (Table 19), and most varieties seemed to produce progeny from a varietal cross exhibiting both good and poor form. Variety haguenensis did appear to

Table 16.--Comparison of mid-parent and hybrid stem form for plantations MSFGP 9-70 and 4-71.

Varietal Combination	Percent of Trees with Stem Crooks	
	Mid-parent[a]	Hybrid Mean (Range)
BOR x HAG[b]	36	45
AQU x HAG	31	14 (0-43)
IBE x HAG	28	10 (0-17)
RIG x HAG	26	20
SEP x HAG	26	21 (0-50)
HAG x HAG	36	27 (16-43)
SCO x HAG	26	34 (12-56)
EAN x HAG	28	30 (25-36)
HER x HAG	34	28 (6-60)
SUB x HAG	34	18 (0-33)
AQU x IBE	14	24 (0-40)
ARM x IBE	23	17 (0-25)
ILL x IBE	16	0
HAG x IBE	28	21 (0-40)
SCO x IBE	16	30 (11-61)

[a]Mid-parent values were derived from parental seedlots in three plantations. Seedlot values were averaged over plantations.

[b]BORussica, HAGuenensis, AQUitana, IBErica, RIGensis, SEPtentrionalis, SCOtica, 'East ANglia,' HERcynica, SUBillyrica, ARMena, ILLyrica.

Table 17.--Comparison of mid-parent and hybrid stem form for plantations MSFGP 8/9/10-72 and 6/7/8-73.

Varietal Combination	Percent of Trees with Stem Crooks		Varietal Combination	Percent of Trees with Stem Crooks	
	Mid-parent[a]	Hybrid Mean(Range)		Mid-parent	Hybrid Mean(Range)
AQU x IBE[b]	19	18	ARM x HAG	26	16(0-33)
AQU x ILL	16	23	ARM x ARM	24	44(38-50)
AQU x HER	28	17(9-31)	MON x SUB	23	9
AQU x AQU	24	31(17-54)	ILL x ILL	14	50
AQU x EAN	19	30(7-40)	EAN x IBE	19	40
AQU x RHO	14	22(12-50)	EAN x SUB	20	62(43-71)
AQU x HAG	32	54(4-75)	EAN x EAN	18	25
AQU x SUB	20	28(11-50)	EAN x AQU	26	14
AQU x ARM	19	35(28-50)	EAN x HAG	44	17
HAG x IBE	26	58(50-62)	HER x ILL	14	15
HAG x ILL	23	25	HER x ARM	20	22
HAG x HER	30	27	HER x SUB	17	20
HAG x SUB	31	58(33-77)	HER x HAG	32	33
HAG x ARM	43	40	HER x HER	18	33
HAG x AQU	52	50	RIG x POL	18	25
HAG x HAG	62	33(0-46)	RIG x HAG	28	40
ARM x IBE	30	36	SUB x SUB	21	26
ARM x POL	18	0	SUB x IBE	20	0
ARM x AQU	20	40(31-50)	SUB x ARM	18	80
ARM x RHO	10	27	IBE x AQU	24	32
ARM x EAN	16	67	IBE x RHO	14	44

Table 17.--Continued.

Varietal Combination	Percent of Trees with Stem Crooks		Varietal Combination	Percent of Trees with Stem Crooks	
	Mid-parent[a]	Hybrid Mean (Range)		Mid-parent	Hybrid Mean (Range)
ARM x SUB	18	82	IBE x HAG	46	62
IBE x ARM	18	15	IBE x EAN	20	25
IBE x SUB	22	36			

[a]Mid-parent values were derived from parental seedlots in three plantations. Seedlot values were averaged over plantations.

[b]AQUitana, IBErica, ILLyrica, HERcynica, 'East ANglia,' RHOdopaea, ARMena, SUBillyrica, HAGuenensis, POLonica, MONgolica, RIGensis.

Table 18.--Comparison of mid-parent and hybrid stem form for plantation MSFGP 1-74.

Varietal Combination	Percent of Trees Without a Leader		Varietal Combination	Percent of Trees Without a Leader	
	Mid-parent[a]	Hybrid Mean (Range)		Mid-parent	Hybrid Mean (Range)
EAN x ARM[b]	10	33(23-60)	SUB x HER	5	32
EAN x PAN	6	37	IBE x HAG	10	40(28-71)
EAN x HAG	20	42	IBE x HER	7	38
EAN x HER	6	27	IBE x AQU	13	43
EAN x AQU	15	60	IBE x ARM	9	50
SEP x HAG	7	18	IBE x SUB	9	60
SEP x ARM	7	0	AQU x HAG	12	29
ARM x HAG	9	35(14-75)	AQU x IBE	6	50
ARM x PAN	4	17	AQU x AQU	16	18
ARM x AQU	14	30(0-43)	SCO x AQU	16	25
ARM x IBE	10	70	SCO x ARM	9	57
ARM x ARM	9	30(20-67)	SCO x HAG	8	25
SUB x ARM	10	42	HAG x AQU	14	50
SUB x HAG	10	45			

[a]Mid-parent values were derived from parental seedlots in three plantations. Seedlot values were averaged over plantations.

[b]'East ANglia,' ARMena, PANnonica, HAGuenensis, HERcynica, AQUitana, SEPtentrionalis, IBErica, SUBillyrica, SCOtica.

Table 19.--Degrees of freedom and values of chi-square showing the significance of the variation in stem form among the varietal combinations in plantations MSFGP 9-70, 4-71, 8/9/10-72, 6/7/8-73, and 1-74.

Plantation MSFGP	Degrees of Freedom	Chi-Square
9-70	13	14.89
4-71	11	18.90
8/9/10-72	28	57.74**
6/7/8-73	24	31.74
1-74	26	12.10

**Significant at the 1% level.

produce more offspring with poor form, but again this observation was not testable.

The stem form results for this study supported the statement made by Wright _et al_. (1976) in which they said that no one variety was guaranteed to grow straight under all circumstances. Wright (1976) noted that stem straightness in Scotch pine is a function of a seedlot's resistance to a damaging agent, and therefore Scotch pine tends to grow straight in the absence of such an agent. Wright and Baldwin (1957) found that almost all crooks occurred at nodes as a result of damage to the terminal bud by external agents. From these results one may conclude that the environment plays a large role in determining stem form in Scotch pine, with the genotype acting on stem form indirectly through resistance to such damaging agents as insects, birds, and cold temperatures.

Winter Foliage Color

Winter foliage color was scored for two plantations, MSFGP 8/9/10-72 in Ingham County, Michigan, and MSFGP 1-74 at the Kellogg Forest. The Ingham County plantation was scored in December, while the Kellogg Forest plantation was scored in March. Foliage was free of snow and there were cloudy skies on both occasions.

Differences among the seedlots with better (green) winter foliage color were generally not obvious from a distance in the field. The poorer (yellow) seedlots could be easily recognized, however. No differences among or within varietal combinations were detectable using chi-square analysis at the 5% level of probability (χ^2 = 25.77, df = 18 for MSFGP 8/9/10-72; χ^2 = 15.58, df = 26 for MSFGP 1-74).

In addition to the lack of significant differences among the varietal combinations in foliage color, all of the combinations had poorer color than the mid-parent value (Tables 20 and 21). Whether this resulted from observer differences is questionable. Schrum _et al_. (1975) reported that color measurements made by several observers were significantly different, while Wright _et al_. (1976) found that different people differed only plus or minus one-half color grade in judging a particular variety on a scale of one to ten. In the present study no means were employed

Table 20.--Comparison of mid-parent and hybrid winter foliage color for plantation MSFGP 8/9/10-72.

Varietal Combination	Color Grade, 0(yellow) to 10(green)	
	Mid-parent[a]	Hybrid Mean (Range)
AQU x IBE[b]	8.4	5.7
AQU x ILL	7.4	5.4
AQU x RHO	8.0	3.4(2.7-4.0)
AQU x ARM	8.1	7.5
AQU x HER	6.8	5.9(4.5-7.0)
AQU x SUB	7.5	3.5
HAG x IBE	7.6	5.7
HAG x ILL	6.6	4.7
HAG x HER	6.2	6.2
HAG x SUB	6.6	3.2
ARM x IBE	7.8	6.7
MON x SUB	4.0	3.0
ARM x POL	6.2	5.0
EAN x SUB	7.5	4.7
HER x ILL	6.0	4.8
HER x ARM	6.7	6.3
HER x HAG	6.1	5.0

Table 20.--Continued.

Varietal Combination	Color Grade, 0(yellow) to 10(green)	
	Mid-parent[a]	Hybrid
		Mean (Range)
RIG x HAG	5.2	3.5
SUB x SUB	7.1	5.3(5.0-5.7)

[a]Mid-parent values were derived from parental seedlots in three plantations. Seedlot values were averaged over plantations.

[b]AQUitana, IBErica, ILLyrica, RHOdopaea, ARMena, HERcynica, SUBillyrica, HAGuenensis, MONgolica, POLonica, 'East ANglia,' RIGensis.

Table 21.--Comparison of mid-parent and hybrid winter foliage color for plantation MSFGP 1-74.

Varietal Combination	Color grade, 0(yellow) to 10(green)		Varietal Combination	Color grade, 0(yellow) to 10(green)	
	Mid-parent[a]	Hybrid Mean(Range)		Mid-parent	Hybrid Mean(Range)
EAN x ARM[b]	7.8	4.6	SUB x HER	6.2	3.7
EAN x PAN	6.9	5.0	IBE x HAG	7.6	5.7(5.3-6.5)
EAN x HAG	7.1	4.7(4.6-5.5)	IBE x HER	7.3	5.6
EAN x HER	6.8	4.4	IBE x AQU	8.2	5.5
EAN x AQU	8.0	6.0	IBE x ARM	7.8	5.8
SEP x HAG	5.1	5.0	IBE x SUB	7.6	4.5
SEP x ARM	5.6	4.0	AQU x HAG	7.6	5.2
ARM x HAG	6.9	4.9(3.9-7.5)	AQU x IBE	8.5	3.3
ARM x PAN	6.8	3.3	AQU x AQU	8.4	5.5
ARM x AQU	7.8	5.0(4.7-5.5)	SCO x AQU	8.0	6.0
ARM x IBE	8.0	5.2	SCO x ARM	7.6	5.0
ARM x ARM	7.5	5.2(5.0-6.5)	SCO x HAG	7.0	4.5
SUB x ARM	7.2	3.8	HAG x AQU	7.3	5.5
SUB x HAG	6.6	3.3			

[a]Mid-parent values were derived from parental seedlots in three plantations. Seedlot values were averaged over plantations.

[b]'East ANglia,' ARMena, PANnonica, HAGuenensis, HERcynica, AQUitana, SEPtentrionalis, IBErica, SUBillyrica, SCOtica.

whereby the effects of observer differences could be quantified. Zeaser (1976) reported a similar reduction in color grade among intervarietal Scotch pine hybrids, some of which were produced from the same pollinations as in this study. These similar results between the two studies reduce the plausibility of observer differences as a major factor contributing to the observed results.

While color values for the progeny were lower than those of the mid-parent, these values appeared to be associated (Tables 20 and 21). The correlation coefficients for plantations MSFGP 8/9/10-72 and 1-74 support this observation, as they were significant at the 5% level (r = .46, n = 19; r = .70, n = 27 for plantations MSFGP 8/9/10-72 and 1-74 respectively).

Five varietal combinations exhibited winter color which was at least one color grade above average. These combinations were var. haguenensis x var. hercynica, var. armena x var. iberica, var. hercynica x var. armena, 'East Anglia' x var. aquitana, and var. scotica x var. aquitana. Of the above combinations var. haguenensis x var. hercynica is the only combination exhibiting good color which was not expected. Both varieties are of central European origin and exhibit average to slightly above average color in provenance tests. The generally average color exhibited by even the best varietal combinations in the hybrid plantations does not lend them to use as Christmas trees, as trees with better color characteristics can be produced from existing varieties.

Susceptibility to the European Pine Sawfly

Scotch pine is subject to attack by many insects and other pests. Such attacks often result in stem crooks, reduced growth rates, or a loss of foliage. The larvae of the European pine sawfly feed on the old needles of Scotch pine in late May and early June (Wilson, 1977). Since the larvae feed on old foliage the trees are rarely completely defoliated, however any amount of defoliation in a Christmas tree plantation can be serious.

Two plantations (MSFGP 8/9/10-72 and 6/7/8-73) experienced heavy infestations of the European pine sawfly in the spring of 1979. The plantations were one year apart in age and had similar numbers of living trees. Plantation MSFGP 6/7/8-73 suffered the most severe attack with approximately 50% defoliation, while MSFGP 8/9/10-72 was subjected to 29% defoliation.

The hybrid plantations were defoliated much more than the parental plantations, so the mid-parent values could not be used as expected values for the hybrids. Tables 22 and 23 support this observation. A further indication that mid-parent values did not serve as good indicators of expected hybrid performance was provided by correlation analysis, which demonstrated only a weak positive association between mid-parent and progeny values ($r = .30$

Table 22.--Comparison of mid-parent and hybrid resistance to damage by the European pine sawfly in plantation MSFGP 8/9/10-72.

Varietal Combination	Percent of Branches Defoliated: Mid-parent[a]	Percent of Branches Defoliated: Hybrid Mean (Range)	Varietal Combination	Percent of Branches Defoliated: Mid-parent	Percent of Branches Defoliated: Hybrid Mean (Range)
AQU x IBE	8	19	ARM x ARM	8	2
AQU x ILL	8	25	MON s SUB	7	15
AQU x HER	6	26 (10-40)	ILL x ILL	11	15
AQU x RHO	4	30 (20-41)	EAN x IBE	10	44
AQU x HAG	10	12	EAN x SUB	10	45 (44-48)
AQU x SUB	8	27	HER x ILL	12	58
AQU x ARM	6	20	HER x ARM	10	28
HAG x IBE	14	36 (22-42)	HER x SUB	10	48
HAG x ILL	13	44	HER x HAG	21	36
HAG x HER	10	40	HER x HER	9	5
HAG x SUB	10	8	RIG x POL	10	54
ARM x IBE	10	56	RIG x HAG	9	39
ARM x POL	9	16	SUB x SUB	12	38
ARM x HAG	2	29 (19-40)	SUB x IBE	11	10

[a]Mid-parent values were derived from parental seedlots in a large provenance test at the Kellogg Forest. Seedlot values were averaged over replications.

[b]AQUitana, IBErica, ILLyrica, HERcynica, RHOdopaea, HAGuenensis, SUBillyrica, ARMena, POLonica, MONgolica, 'East ANglia,' RIGensis.

Table 23.--Comparison of mid-parent and hybrid resistance to damage by the European pine sawfly in plantation MSFGP 6/7/8-73.

Varietal Combination	Percent of Branches Defoliated		Varietal Combination	Percent of Branches Defoliated	
	Mid-parent[a]	Hybrid		Mid-parent	Hybrid
		Mean(Range)			Mean(Range)
AQU x AQU[b]	5	54(48-67)	ARM x SUB	8	62
AQU x EAN	16	45(40-50)	ARM x HAG	10	51(37-78)
AQU x RHO	4	51(34-83)	ARM x ARM	4	41
AQU x HAG	9	62(42-75)	EAN x EAN	26	24
AQU x SUB	9	42(31-55)	EAN x AQU	16	58
AQU x ARM	5	57(49-69)	EAN x HAG	20	46
HAG x ARM	8	72	SUB x ARM	8	25
HAG x AQU	10	41	IBE x AQU	8	36(30-42)
HAG x HAG	14	64(55-79)	IBE x RHO	6	41
HAG x SUB	14	31(26-37)	IBE x HAG	12	30
ARM x AQU	4	44(38-50)	IBE x ARM	7	70
ARM x RHO	3	53	IBE x EAN	18	38
ARM x EAN	15	52	IBE x SUB	16	32

[a]Mid-parent values were derived from parental seedlots in a large provenance test at the Kellogg Forest. Seedlot values were averaged over replications.

[b]AQUitana, 'East ANglia,' RHOdopaea, HAGuenensis, SUBillyrica, ARMena, IBErica.

and .35 for plantations MSFGP 8/9/10-72 and 6/7/8-73 respectively).

There was a large amount of variation among the varietal combinations in their susceptibility to European pine sawfly attack. Chi-square analysis indicated that this variation was highly significant, as was the variation among hybrid families within varietal combinations (χ^2 = 355.69, df = 27 for MSFGP 8/9/10-72 and χ^2 = 144.79, df = 24 for MSFGP 6/7/8-73). The variation appeared to be random both among and within varietal combinations. As pointed out with height growth, large variation within combinations considerably impairs the production of useful intervarietal hybrids in Scotch pine.

Several studies have shown that Scotch pine varieties differ in their susceptibility to attack by various insects including the European pine sawfly (Wright et al., 1966b; Wright et al., 1967; Genys, 1970; Wright and Wilson, 1972; Steiner, 1974; Wright et al., 1975). Wright et al. (1975) found that resistance to insect attack is more or less specific for particular insects.

Wright et al. (1967) found that the taller trees in a Scotch pine plantation were generally attacked more than shorter trees by the European pine sawfly. The results of the current study do not support this finding. The correlation between tree height and percent defoliation was essentially zero for both plantations (r = -.03 and -.04 for MSFGP 8/9/10-72 and MSFGP 6/7/8-73 respectively). The lack of an association between these traits in this study may be due to the severity of the sawfly infestation. Both of the hybrid plantations suffered much heavier infestations than the plantations which Wright *et al*. (1967) studied. As the severity of the infestation increases so too will the likelihood of the sawfly spreading to shorter trees. This may have occurred in this study to the extent that any correlations between tree height and sawfly resistance were effectively eliminated.

Combinations of Desirable Traits

The best examples of combinations of desirable traits were found in varietal combinations expressing rapid height growth with relatively few stem form problems. Such combinations are illustrated in Table 24. At least one of the parents was a fast growing variety (var. *haguenensis*, var. *hercynica*, or 'East Anglia') in every instance. Not surprising was the fact that almost all of the varietal combinations in Table 24 also exhibited a high early flowering response. This was no doubt due to the strong selection practiced for early flowering in the parental stands.

None of the combinations included in Table 24 exhibited either good winter color or high resistance to the European pine sawfly. Color was generally poor for all of the hybrids in the plantations so it was not surprising that good color was not exhibited by hybrids with good growth rates and form. Some varietal combinations appeared

Table 24.--Height, flowering, and stem form values for varietal combinations exhibiting desirable combinations of these traits.

Plantation MSFGP	Varietal Combination	Relative Height	Percent of Trees Flowering	Percent of Trees with Crooks
9-70	AQU x HAG	106	81	14
	IBE x HAG	102	78	11
	RIG x HAG	102	30	20
	SEP x HAG	104	83	21
	EAN x HAG	106	100	25
4-71	HAG x HAG	112	95	22
	SCO x HAG	110	88	12
	HER x HAG	105	97	22
8/9/10-72	HAG x ILL	143	83	25
6/7/8-73	EAN x HAG	117	83	17
	EAN x EAN	117	88	25
	IBE x EAN	109	88	25
1-74	EAN x HER	128	30	27
	SUB x HER	115	54	32

to harbor some resistance to the European pine sawfly, but these same combinations exhibited either poor height growth or form. As Wright (1963b) noted, achieving appreciable gain when selecting for two or more traits is much more difficult than when selection is for one trait. This most likely explains the lack of varietal combinations with good performance in more than three traits.

CONCLUSIONS

Where similar traits were considered, the results of this study generally agreed with the results of previous studies of intervarietal hybridization in forest trees. Specifically, there was an apparent lack of heterosis for all traits measured, and variation within varietal combinations was large.

The failure of the F_1 generation to exhibit hybrid vigor for height growth has been demonstrated in several different studies since the mid 1970s (Holst and Fowler, 1975; Morgenstern, 1975; Nilsson, 1975; Woessner, 1975; Zeaser, 1976; Hohn and Mush, 1979). There is no doubt a genetic basis for this occurrence, however in the present study and in a previous study by Zeaser (1976), parental values were averaged over several trees within the parental stand, and were therefore approximations of the true parental values. This most likely affected the parent by hybrid comparisons, and may have hidden any heterotic response.

The value of this study would have been greatly enhanced had the experimental design included a sufficient number of control crosses, so that true mid-parent values could have been calculated. As it was there were too few such crosses to be of any use. Another drawback appears to have been the age at which the trees in this study were mated. The strong selection for early flowering ability that resulted made it much more difficult to select for other, perhaps more desirable, traits.

There did not appear to be sufficient variation to support further selection among the varietal combinations. Most of the variation was associated with differences among hybrid families within varietal combinations, so any future matings should be made among selected hybrid families rather than varietal combinations.

This study indicates that the production of F_1 intervarietal Scotch pine hybrids may not be desirable as there are naturally occurring varieties which outperform them. If the production of such hybrids is undertaken, matings should be between selected trees within selected stands, thereby taking advantage of both the variation found within varieties and among varieties.

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APPENDIX

Table 25.--Summary data for plantations MSFGP 9-70 and 4-71.

MSFG ♀ ♂	Number of Plots			Number of Trees				Total Height			Number of Trees with Cones				Number of Trees with Crooks		
	9-70	4-71	Σ	1974	9-70	4-71	Σ	9-70	4-71	Σ	1974	9-70	4-71	Σ	9-70	4-71	Σ
BOR x HAG:6012)210 x HAG	4	-	-	13	11	-	-	191	-	-	2	7	-	-	5	-	-
AQU x HAG:6018)212 x HAG	5	8	13	18	16	24	40	245	308	553	7	12	23	46	3	1	4
6036)235 x HAG	5	2	7	18	12	7	19	271	70	341	9	6	7	13	0	3	3
6043)238 x HAG	3	7	10	16	6	16	22	161	276	437	12	5	16	21	0	1	1
6136)316 x HAG	5	7	12	15	10	16	26	203	242	445	6	10	15	25	2	3	5
6146)320 x HAG	4	-	-	19	14	-	-	190	-	-	6	14	-	-	3	-	-
IBE x HAG:6022)218 x HAG	2	7	9	15	3	19	22	99	258	359	5	1	12	13	0	2	2
6054)245 x HAG	3	-	-	10	6	-	-	137	-	-	7	6	-	-	1	-	-
RIG x HAG:6029)224 x HAG	4	-	-	12	10	-	-	187	-	-	3	3	-	-	2	-	-
SEP x HAG:6034)230 x HAG	2	-	-	6	6	-	-	101	-	-	1	6	-	-	3	-	-
6150)522 x HAG	2	-	-	7	7	-	-	104	-	-	3	2	-	-	2	-	-
6154(524 x HAG	3	-	-	11	6	-	-	153	-	-	5	6	-	-	0	-	-
6155)524 x HAG	5	-	-	19	10	-	-	219	-	-	12	10	-	-	1	-	-
HAG x HAG:6041)236 x HAG	4	8	12	20	13	21	34	201	321	522	11	10	21	31	4	4	8
6051)241 x HAG	4	8	12	15	11	19	30	209	312	521	4	9	17	36	4	3	7
6060)253 x HAG	4	4	8	12	9	11	20	165	170	335	6	5	10	15	2	4	6
6141)318 x HAG	3	-	-	12	7	-	-	153	-	-	7	7	-	-	3	-	-
6177)530 x HAG	-	4	-	-	-	9	-	-	166	-	-	-	9	-	-	2	-
SCO x HAG:6083)267 x HAG	4	6	10	19	9	17	26	202	234	436	5	8	15	23	5	2	7

Table 25.--Continued.

MSFG ♀ ♂	Number of Plots			Number of Trees				Total Height			Number of Trees with Cones				Number of Trees with Crooks		
	9-70	4-71	Σ	1974	9-70	4-71	Σ	9-70	4-71	Σ	1974	9-70	4-71	Σ	9-70	4-71	Σ
EAN x HAG:6090)269 x HAG	5	5	10	19	12	11	23	243	187	430	8	12	10	22	3	4	7
HER x HAG:6107)305 x HAG	4	5	9	16	12	10	22	214	180	394	4	9	10	19	2	1	3
6114)308 x HAG	2	-	-	7	5	-	-	102	-	-	1	4	-	-	2	-	-
6118)309 x HAG	4	7	11	15	11	27	38	165	235	400	8	10	27	37	3	6	9
6121)310 x HAG	5	8	13	13	13	16	29	242	296	538	7	9	15	24	2	1	3
6126)311 x HAG	5	-	-	15	9	-	-	245	-	-	9	8	-	-	4	-	-
6159)525 x HAG	3	7	10	20	6	11	17	116	257	373	11	2	11	13	1	1	2
6161)526 x HAG	4	6	10	16	9	8	17	215	237	452	4	6	7	13	5	2	7
6169)528 x HAG	3	6	9	17	10	13	23	161	230	391	7	5	13	18	6	5	11
6171)529 x HAG	4	7	11	14	8	19	27	184	291	475	7	8	18	26	3	7	10
SUB x HAG:6281)555 x HAG	-	8	-	-	-	16	-	-	269	-	-	-	16	-	-	2	-
6283)556 x HAG	-	5	-	-	-	9	-	-	160	-	-	-	7	-	-	3	-
6284)556 x HAG	-	2	-	-	-	3	-	-	58	-	-	-	3	-	-	0	-
AQU x IBE:6288)212 x IBE	3	4	7	17	5	6	11	112	95	207	5	5	4	9	2	2	4
6289)212 x IBE	2	8	10	10	4	19	23	90	267	357	1	1	15	16	0	5	5
6292)238 x IBE	-	8	-	-	-	18	-	-	262	-	-	-	15	-	-	4	-
6293)238 x IBE	2	5	7	13	3	11	14	87	151	238	0	1	6	7	1	1	2
SCO x IBE:6300)265 x IBE	2	8	10	14	3	20	23	65	251	316	1	3	12	15	2	4	6
6301)265 x IBE	4	4	8	13	8	9	17	162	128	290	0	5	5	10	1	1	2

Table 25.--Continued.

MSFG ♀ ♂	Number of Plots			Number of Trees				Total Height			Number of Trees with Cones				Number of Trees with Crooks		
	9-70	4-71	Σ	1974	9-70	4-71	Σ	9-70	4-71	Σ	1974	9-70	4-71	Σ	9-70	4-71	Σ
6302)266 x IBE	3	2	5	9	5	7	12	92	66	158	2	4	5	9	3	2	5
6303)266 x IBE	3	8	11	12	4	29	33	131	260	391	1	3	17	20	2	6	8
ARM x IBE:6290)221 x IBE	3	4	7	8	4	6	10	98	133	231	2	1	2	3	1	0	1
6291)221 x IBE	-	2	-	-	-	4	-	-	61	-	-	-	2	-	-	1	-
HAG x IBE:6298)250 x IBE	-	3	-	-	-	6	-	-	115	-	-	-	2	-	-	0	-
6299)250 x IBE	-	7	-	-	-	15	-	-	266	-	-	-	10	-	-	1	-
6305)318 x IBE	-	8	-	-	-	23	-	-	276	-	-	-	7	-	-	7	-
6306)318 x IBE	-	8	-	-	-	26	-	-	292	-	-	-	20	-	-	3	-
6308)530 x IBE	3	-	-	9	7	-	-	153	-	-	2	3	-	-	1	-	-
6309)530 x IBE	4	7	11	15	5	14	19	135	216	351	5	5	12	17	2	3	5
ILL x IBE:6294)242 x IBE	5	3	8	16	9	6	15	198	99	297	1	4	2	6	0	0	0

Table 26.--Summary data for plantations MSFGP 8/9/10-72.

MSFG ♀ ♂	# Plots, Color	# Plots	# Trees	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Color	Total, Sawfly
AQU x SPA:4797)212 x 4901	3	3	11	101	9	2	17	23
AQU x ILL:4798)212 x 242	5	7	22	242	18	5	27	69
AQU x RHO:4800)212 x 243	4	5	16	176	7	2	16	81
4852)316 x 243	3	5	17	160	9	3	8	40
AQU x ARM:4801)212 x 221	2	3	12	92	9	4	15	24
AQU x HER:4802)212 x 209	2	3	11	132	8	1	9	32
4803)212 x 209	-	2	7	86	6	1	-	8
4817)235 x 525	4	5	13	132	6	4	24	79
4825)239 x 525	2	3	10	119	9	1	14	15
AQU x SUB:4804)212 x 556	2	3	9	93	7	1	7	32
AQU x HAG:4806)212 x 302	-	2	8	99	8	6	-	10
AQU x O.P:4807)212 x O.P.	7	8	30	254	17	4	32	140
4808)212 x O.P.	3	4	13	141	11	6	18	37
4820)235 x O.P.	4	4	12	122	10	5	21	48
4855)316 x O.P.	6	8	34	298	20	5	35	59
4856)316 x O.P.	-	2	6	70	4	1	-	5
HAG x SPA:4857)318 x 4901	-	2	6	65	3	3	-	18
4874)531 x 4901	3	4	13	155	12	8	17	68
HAG x ILL:4875)531 x 242	3	4	12	194	10	3	14	11
HAG x HER:4876)531 x 525	4	6	15	172	7	4	25	97

Table 26.--Continued.

MSFG ♀ ♂	# Plots, Color	# Plots	# Trees	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Color	Total, Sawfly
HAG x SUB:4877) 531 x 554	5	6	13	162	9	10	16	20
HAG x O.P:4829) 252 x O.P.	-	3	12	123	10	3	-	20
4878) 531 x O.P.	5	6	19	226	12	4	24	115
4881) 531 x O.P.	6	7	23	253	11	8	23	76
ARM x HAG:4831) 261 x 258	-	2	5	67	4	0	-	15
4834) 263 x 258	-	2	4	35	1	0	-	32
ARM x O.P:4832) 261 x O.P.	2	3	11	121	6	3	12	25
4837) 263 x O.P.	3	4	14	120	4	2	15	22
4839) 264 x O.P.	2	3	10	102	8	2	9	30
ARM x SPA:4833) 263 x 4901	3	4	11	97	6	4	20	90
ARM x ARM:4835) 263 x 221	-	2	4	62	0	2	-	2
ARM x POL:4838) 264 x 211	4	5	14	163	10	0	20	31
MON x SUB:4812) 234 x 556	2	3	11	104	7	1	6	18
ILL x ILL:4827) 242 x 242	-	2	6	62	5	3	-	12
EAN x SPA:4840) 270 x 4901	-	2	5	61	4	2	-	35
EAN x SUB:4842) 270 x 556	-	2	7	56	6	3	-	38
4843) 270 x 554	3	4	14	112	8	10	14	70
EAN x O.P:4844) 270 x O.P.	4	5	16	205	11	1	30	11
HER x ILL:4846) 312 x 242	4	5	13	130	4	2	19	116
HER x ARM:4847) 312 x 221	3	3	9	105	5	2	19	34

Table 26.--Continued.

MSFG ♀ ♂	# Plots, Color	# Plots	# Trees	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Color	Total, Sawfly
HER x SUB:4849) 312 x 554	-	2	5	74	3	1	-	38
HER x HAG:4859) 525 x 236	2	3	9	91	7	3	10	43
HER x HER:4861) 525 x 207	-	2	6	59	3	2	0	4
HER x O.P:4862) 525 x O.P.	4	5	16	174	8	2	16	87
4873) 529 x O.P.	-	2	8	84	5	1	-	16
RIG x POL:4882) 541 x 211	-	2	8	70	8	2	-	43
RIG x HAG:4883) 541 x 253	2	3	10	111	8	4	7	47
SUB x SUB:4891) 556 x 556	3	3	10	91	8	2	17	30
4898) 557 x 556	3	4	13	105	5	4	15	76
SUB x SPA:4890) 556 x 4901	-	2	4	50	1	0	-	8
SUB x O.P:4896) 556 x O.P.	4	5	14	171	8	4	22	35

Table 27.--Summary data for plantation MSFGP 6/7/8-73.

Penn. 70-	MSFG: ♀	♂	# Plots	# Trees	# Trees, Sawfly	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Sawfly
AQU x AQU:201)	212 x	212	4	11	12	75	9	3	64
218)	316 x	316	4	15	16	93	13	5	83
386)	238 x	212	3	9	12	61	7	3	62
423)	240 x	316	4	11	12	74	4	6	61
431)	240 x	316	3	12	12	68	11	2	58
450)	316 x	212	4	12	12	104	11	3	80
AQU x HAG:243)	212 x	250	2	11	12	53	9	4	64
235)	212 x	250	3	12	12	76	9	1	81
251)	212 x	250	6	20	12	143	17	8	79
365)	212 x	318	6	21	12	143	20	9	98
388)	238 x	250	4	11	12	77	11	4	50
420)	240 x	250	2	7	8	38	5	2	42
424)	240 x	318	2	8	8	48	7	1	60
428)	240 x	250	4	9	8	75	7	4	50
AQU x RHO:360)	212 x	243	3	12	12	74	12	4	100
387)	238 x	243	4	12	12	86	11	6	58
419)	240 x	243	6	16	20	117	10	3	67
444)	316 x	243	4	14	16	112	10	2	81
AQU x SUB:366)	212 x	556	4	16	12	99	13	8	37
401)	238 x	556	4	10	8	65	7	4	33

Table 27.--Continued.

Penn. 70- MSFG: ♀ x ♂	# Plots	# Trees	# Trees, Sawfly	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Sawfly
425) 240 x 556	5	17	8	106	15	7	44
449) 316 x 556	3	10	12	58	10	5	55
AQU x EAN: 382) 212 x 269	3	10	8	65	10	4	34
390) 238 x 269	3	10	12	61	8	4	48
422) 240 x 269	4	14	16	86	9	1	73
447) 316 x 269	5	19	16	129	16	7	80
AQU x ARM: 389) 238 x 262	2	7	8	37	6	9	45
413) 240 x 262	2	6	8	35	2	2	55
446) 316 x 262	3	6	12	66	6	3	59
HAG x HAG: 208) 250 x 250	2	5	8	57	5	0	63
540) 250 x 318	4	13	12	103	10	6	66
HAG x ARM: 537) 250 x 262	4	15	12	97	14	6	87
HAG x SUB: 541) 250 x 556	3	11	12	77	10	5	31
641) 318 x 556	3	9	12	71	6	3	44
HAG x AQU: 546) 250 x 316	4	14	12	98	12	7	49
ARM x ARM: 211) 262 x 262	2	8	8	41	7	3	33
ARM x AQU: 557) 262 x 212	5	16	16	113	15	5	80
561) 262 x 316	4	14	16	86	14	7	61
ARM x RHO: 558) 262 x 243	3	11	12	73	8	3	64
ARM x HAG: 559) 262 x 250	5	18	16	126	16	6	51

Table 27.--Continued.

Penn. 70-	MSFG: ♀	♂	# Plots	# Trees	# Trees, Sawfly	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Sawfly
562)	262 x	318	3	9	12	76	9	3	93
ARM x EAN:560)	262 x	269	2	6	8	51	6	4	42
ARM x SUB:563)	262 x	556	4	11	12	67	10	9	74
IBE x AQU:526)	245 x	212	4	14	12	85	13	4	50
531)	245 x	316	3	11	12	69	9	4	36
IBE x RHO:527)	245 x	243	3	9	12	61	5	4	49
IBE x HAG:528)	245 x	250	2	8	8	44	8	5	24
IBE x ARM:529)	245 x	262	4	13	8	66	9	2	56
IBE x EAN:530)	245 x	269	4	16	12	94	14	4	46
IBE x SUB:533)	245 x	556	4	14	12	78	12	5	38
EAN x EAN:215)	269 x	269	2	8	8	51	7	2	19
EAN x AQU:618)	269 x	316	5	14	12	112	10	2	69
EAN x HAG:630)	269 x	250	2	6	8	52	5	1	37
SUB x ARM:673)	556 x	262	2	5	8	37	5	4	20

Table 28.--Summary data for plantation MSFGP 1-74.

Hybrids are MSFG #s in 4000 series, or Penn. #s in 71- series	MSFG: ♀ ♂	# Plots	# Trees	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Color
EAN x ARM:4112)	269 x 262	6	13	78	2	3	26
449)	269 x 213, 220-1	2	5	28	0	3	11
EAN x PAN:4113)	269 x 552	8	19	110	9	7	40
EAN x HAG:4114)	269 x 533	10	37	181	13	18	46
445)	269 x 318	2	2	21	1	1	11
452)	269 x 318	3	8	44	2	1	14
EAN x HER:4115)	269 x 529	10	33	170	10	9	44
EAN x AQU: 435)	269 x 212	3	5	37	3	3	18
SEP x HAG:4123)	201 x 533	3	11	43	0	2	15
SEP x ARM:4124)	201 x 262	2	3	29	0	0	8
ARM x HAG:4125)	264 x 533	10	38	177	9	12	39
375)	261 x 250	2	5	23	3	2	11
377)	261 x 318	4	8	44	1	4	22
385)	261 x 318	2	7	30	3	1	11
404)	262 x 318	2	4	27	1	3	15
ARM x PAN:4127)	264 x 552	3	6	35	0	1	10
ARM x AQU: 373)	261 x 212	3	7	32	3	3	14
381)	261 x 212	2	3	20	1	0	11
ARM x SPA: 379)	261 x SPA	4	10	42	6	7	21
ARM x ARM: 376)	261 x 261-2	3	5	23	1	1	15

Table 28.--Continued.

Hybrids are MSFG #s in 4000 series, or Penn. #s in 71- series	MSFG: ♀ ♂	# Plots	# Trees	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Color
384)	261 x 261-2	2	4	23	2	1	10
388)	261 x 262	2	3	17	0	2	13
401)	262 x 213, 220-1	3	5	35	0	1	15
403)	262 x 261-2	2	6	19	0	2	10
SUB x ARM:4128)	556 x 262	10	33	139	11	14	38
SUB x HAG:4129)	556 x 533	9	31	129	10	14	39
SUB x HER:4130)	556 x 529	7	22	102	12	7	26
IBE x HAG:4131)	245 x 533	8	29	146	5	8	45
331)	245 x 250	2	5	28	0	3	13
333)	245 x 318	2	5	28	2	3	11
344)	246 x 250	3	9	43	2	3	16
346)	246 x 318	3	7	36	3	5	17
IBE x HER:4132)	245 x 529	5	16	77	4	6	28
IBE x AQU: 342)	246 x 212	2	7	27	0	3	11
IBE x ARM: 355)	246 x 261-2	4	12	41	3	6	23
IBE x SUB: 357)	246 x 556	4	10	46	1	6	18
AQU x HAG: 465)	316 x 318	5	14	64	2	4	26
AQU x SPA: 312)	240 x SPA	3	6	19	2	3	10
AQU x AQU: 461)	316 x 212	4	11	54	3	2	22
SCO x AQU: 413)	268 x 212	3	4	35	2	1	18

Table 28.--Continued.

Hybrids are MSFG #s in 4000 series, or Penn. #s in 71- series	MSFG: ♀ ♂	# Plots	# Trees	Total Height	# Trees w/Cones	# Trees w/Crooks	Total, Color
SCO x ARM:	415) 268 x 261-2	3	7	22	1	4	15
SCO x HAG:	416) 268 x 318	2	4	26	0	1	9
HAG x AQU:	481) 318 x 212	2	8	33	3	4	11