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A PRELIMINARY EVALUATION OF THE

PICEA GLAUCA x *PUNGENS* HYBRID

By

Gregory M. Kudray

A THESIS

Submitted to
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ABSTRACT

A PRELIMINARY EVALUATION OF THE

PICEA GLAUCA x *P. PUNGENS* HYBRID

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An evaluation of the white x blue spruce hybrid was undertaken with emphasis on commercial potential as a Christmas tree or ornamental. The average white x blue spruce cross yielded two seeds per cone with seed weight and speed of germination values between parental rates. F_1 hybrid seedling heights were intermediate to white and blue spruce seedlings but five to ten year heights were comparable or superior to the faster growing parent, white spruce. F_1 hybrids bore cones at early flowering ages with intermediate dimensions and appearance to white and blue spruce cones. Hybrid intermediacy was also noted for blue foliage color, needle sharpness, and growing season frost susceptibility. Many individual F_1 hybrid trees had desirable combinations of fast growth rate, blue color, and dull needles. A discriminant analysis using nine characteristics identified bud length as the best single factor in distinguishing species. Recommendations were made for continued breeding efforts. Methods of producing hybrid trees for public release were considered.

ACKNOWLEDGMENTS

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INTRODUCTION

Blue spruce, Picea pungens Engelm., is a widely planted ornamental throughout the North temperate zone. Because blue spruce is not commonly a timber species, few genetic improvement programs other than use of grafted varieties, have been undertaken (Cram, 1968; Dawson and Rudolph, 1966; Hanover, 1975). Nevertheless, there are several economically important traits in blue spruce amenable to improvement.

The valued blue foliage color varies greatly with seed source selection throughout the species' Rocky Mountain range (Bongarten, 1978). A slow growth habit means high production costs and long-term land commitments. Christmas tree suitability is also diminished by extremely sharp needles making handling difficult for the grower and consumer, although market value is high.

White spruce, Picea glauca (Moench) Voss, is considered to be in the same phylogenetic group but occupies a different range (Wright 1955b) than blue spruce. White spruce has a faster growth rate, soft foliage, and lacks the blue color of blue spruce. Hybridization as a method to combine valuable traits from these species was considered to have potential. Within this framework the Michigan State University spruce hybridization program began.

The first successful cross between white and blue spruce resulted from controlled pollinations in 1967 (Hanover and Wilkinson, 1969). Preliminary evidence of heterosis for early growth and seed germination encouraged further research. Controlled pollinations have been made annually since 1967 with the dual objectives of producing a superior hybrid and increasing knowledge of evolutionary patterns in the genus *Picea*.

The purpose of this study was to evaluate results and materials from 11 years of spruce hybridization with emphasis on the development of an improved hybrid for ornamental and Christmas tree use. Performance of the promising white x blue spruce hybrid, which we suggest designating the 'Spartan spruce,' will be compared with results from similarily grown white and blue spruce. The effectiveness of hybridization in combining desirable traits from the two parent species into a vigorous hybrid will be evaluated and recommendations for future study will be made.

MATERIALS AND METHODS

Trees evaluated in this study were the result of annual controlled pollinations in the spring from 1967-1978 involving *Picea glauca*, *P. pungens*, and their hybrids. Seed parents were located at Michigan State University or the Kellogg experimental forest in Kalamazoo County, Michigan. Sources of pollen included trees at the Michigan State University campus, Kellogg forest, a 1975 collection of blue spruce pollen in Colorado, and blue spruce pollen from trees selected for blue foliage in Cram's (1968) breeding program. Female strobili were isolated with sausage casing bags when reproductive buds became apparent and pollinated several days later when the scales were reflexed. Cones were collected in late summer and seed was extracted, cleaned, blown in an air column to eliminate empty seeds, counted, and weighed. Measurement of cone dimensions were made after extraction.

Seedlings were grown in containers in a greenhouse under accelerated-optimal-growth conditions utilizing optimum fertilization, temperature, and water regime with uninterupted light to ensure continuous growth (Hanover et al., 1976). During some years seedling height was recorded for various ages of trees.

Branch number counts were also made in one experiment involving a comparison between P. glauca, P. pungens, F_2 hybrids and backcrosses. On reaching plantable size, usually in 12 to 18 months, seedlings were hardened off and then outplanted. Planting sites at Kellogg forest underwent initial chemical weed control while the Michigan State University site received periodic fertilization and irrigation.

Shoot damage was counted on 3-year-old seedlings after an early spring frost in 1976. Measurements of foliage color, needle sharpness, and height were made on all trees 5 years or older in 1978. Correlation coefficients between 2-, 5-, and 9-year-old heights of the 1967 pollination crop were calculated. Foliage color and needle sharpness were qualitatively judged by the author on a numerical scale. Top whorl branch samples from 9- and 10-year-old trees were removed and several morphological features were measured for discriminant analysis. Measurements included branch diameter, bud length and width, foliage color and sharpness, and needle density, length, and angle to branch. A stepwise discriminant analysis program was run on Michigan State University's CDC 6000 computer using a subprogram routine (Klecka 1975).

RESULTS AND DISCUSSION

Seed Characteristics

Seed Yield In a hybrid breeding program, seed yield data are important in defining the taxonomic relationship among species through genetic compatibilities as well as in determining production feasibilities. Capturing F_1 hybrid vigor by mass generation of control pollinated seeds has been successful for Hyun (1976) with pines in the 1950's, but to do this economically, seed yields must be relatively high and labor inexpensive. Incompatibilities between species as reflected by zero or reduced seed yields indicate genetic diversity induced by isolation (Mikkola, 1969).

Table 1 presents a five year seed yield summary of controlled pollinations in Picea. Bagged but unpollinated controls were employed during this period and in the past to verify isolation of female strobili from foreign pollen. Most F_1 hybrid crosses were attempted using white spruce maternal parents. Blue spruce does not commonly reach reproductive maturity until it is 30 years old (Hanover, 1975). The difficulty involved in pollinating these large trees and the small quantities available locally necessitated greater emphasis on white spruce seed parents. White spruce flowers early under cultivation (Wright, 1964), are easily hand pollinated from the ground or a short ladder, and many good genetic sources are available locally.

F_1 hybrid crosses, using white and blue spruce seed parents, yielded an average of 1.7 and 1.9 seeds per cone, respectively. This represents an 8-fold fecundity reduction from intraspecific crosses. A great range

5

Table 1. Seed yield summary of 1974-1978 controlled pollinations involving *P. glauca*, *P. pungens* and their F_1 hybrids including 1978 germination rapidity.[1/]

Type of cross	Females (no.)	Males (no.)	Crosses (no.)	Successful crosses (%)	Cones (no.)	Filled seed/cone: Mean	Filled seed/cone: Max	1978 Germination rapidity
				Female parent, *P. glauca*				
Unpollinated	3	0	3	0	5	0.0	0.0	
Open pollinated	40	-	40	100	1188	2.2	12.6	
x *P. glauca*	39	15	75	96	619	15.9	90.0	17.4a
x *P. pungens*	57	54	265	72	1734	1.7	27.0	15.8ac
x (*P. glauca* x *pungens*)	1	1	1	100	8	21.6	21.6	
				Female parent, *P. pungens*				
Open pollinated	6	-	6	67	79	1.0	3.8	
x *P. pungens*	5	9	18	100	43	15.9	43	12.4d
x *P. glauca*	6	5	11	55	17	1.9	17	
				Female parent, (*P. glauca* x *pungens*)				
Unpollinated	3	0	3	0	5	0.0	0.0	
Open pollinated	25	-	25	96	505	6.1	31.7	
x *P. glauca*	24	13	61	97	358	24.6	93.5	19.4be
x *P. pungens*	19	51	55	64	325	2.7	36.5	17.0abc
x (*P. glauca* x *pungens*)[3/]	26	10	33	100	376	8.3	37.6	19.9e
x (*P. pungens* x *glauca*)[3/]	2	1	2	100	36	10.2	10.7	15.4ac
				Female parent, (*P. pungens* x *glauca*)				
x *P. glauca*	1	1	1	100	4	14.5	14.5	15.8ac
x *P. pungens*	1	2	2	50	9	6.3	11.4	14.7dc
x (*P. glauca* x *pungens*)[3/]	1	2	2	100	15	9.9	12.5	15.7ac

1/ Germination rapidity calculated as follows:

$$\text{Rapidity (days)} = \frac{\Sigma \text{ seedlots (days to germinate x number germinated seed)}}{\text{total number of germinated seed}}$$

(Hanover and Wilkinson, 1969).

2/ Means followed by the same letter are not significantly different at p = .05.

3/ Both parents of these crosses have a common male parent.

in seed yields was experienced with individual parental combinations. For example, 45% of the blue x white spruce crosses were not fruitful while crosses using a western source of white spruce pollen were particularily productive. The western white spruce pollen gave a maximum yield of 17 seeds per cone in one cross and high yields with other blue spruce females. A similar pattern occurred in white x blue and (white x blue) x blue spruce crosses. Pollen from Pp 15 gave maximum seed yields, 90% higher than average in both instances, while some other pollens were completely ineffective. In all cases described so far the superior performance can be mostly attributed to pollen effects, generally good results with other females were also achieved. Female parent and parental combination effects have also been observed. The maximum 93.5 seeds per cone yield for (white x blue) x white crosses was given by a pollen source which rated second lowest in overall seed yield effectiveness.

While parental selection is a critical factor in influencing seed yields, various other factors can modify results. Annual climatic conditions, individual worker's pollination technique, and incomplete crossing schemes confuse comparisons made between years. Fresh pollen used in two successive years gave widely varying average seed yields. Storage seemed to affect pollen differently, the best pollen one year was only average the next when compared with others treated similarly. Although results vary annually there are indications that some parents are superior in producing high hybrid seed yields.

Average and maximum seed yields from F_1 hybrids were generally higher than white or blue spruce seed yields when using comparable pollen. An exception to this effect is the low average seed yields with blue spruce pollen. While hybrid seed set with blue spruce pollen is slightly higher than that of the white spruce females, it is much lower than the intraspecific blue spruce cross. Blue spruce pollen has shown strong incompatibility effects with any female other than blue spruce throughout the study. Incompatibility is also strong in blue spruce females pollinated with white spruce. The average seed yield value for blue x white spruce crosses would be even lower, similar to results by Hanover (1969), if the western white spruce pollen discussed earlier had not been used. Backcrosses to white spruce averaged 9 times more sound seeds than backcrosses to blue spruce. This suggests that inheritance of reproductive behavior in the hybrid is influenced by either a white spruce maternal or dominant effect resulting in an incompatibility with blue pollen. Crosses involving F_1 blue x white spruces show a lower seed set with blue spruce pollen compared to white spruce pollen, suggesting a maternal effect was not present, although only a small number of these crosses have been made. A greater number of crosses involving a diverse genetic background must be completed to clarify the method of inheritance of reproductive behavior.

Seed Weight While seed weight is not generally considered to greatly influence mature performance, Bingham et al. (1956) found one and two year progeny heights directly correlated with average seed weight in hybrid pines. We have not investigated such a relationship in spruce hybrids, but there is much genetic information available from seed weight data. In a gymnosperm genus such as *Picea*, the endosperm and seed coat make up the greatest part of a seed and are both of maternal origin with only the embryo containing chromosomes from both male and female genomes. It could be expected that the main determinant of seed weight would be the genetic constitution of the seed parent.

Blue spruce seeds usually weigh slightly more than white spruce seeds (Cram, 1951). There can be confusion in determining accurate seed weights unless a rigorous separation of sound seed from empty seed is made. Seed weight data for parent species and hybrid combinations in 1976 are summarized in Table 2. 1976 data was chosen to represent general trends because of the relatively high seed weight, indicating rigorous separation of blind seed, and the wide range of crosses. Seed-lots were small and quite variable, but some trends can be seen. Seed from white spruce maternal parents was lightest, blue spruce heaviest, and hybrid seed intermediate. Male parents had little effect except in the hybrid, where white spruce pollen produced heavier seeds than blue spruce pollen. This unexpected behavior may be due to the low number of seeds available in each (white x blue) x blue spruce cross resulting in an unreliable value.

Germination Germination rapidity values (Hanover and Wilkinson, 1969) were calculated for the 1978 experimental sowing in the greenhouse (Table 1). Seeds were sown in containers, covered with fine sand to a depth of 1/2 inch, and watered regularly. Values for days to germinate were higher than generally experienced with *Picea* and probably comparable

Table 2. Mean seed weight of spruce species and hybrids derived from controlled pollinations during 1976 at Kellogg Forest.

Type of cross	Crosses (no.)	g/100 seeds
P. glauca x glauca	27	.43a[1/]
P. glauca x pungens	38	.42a
(P. glauca x pungens) x pungens	12	.45a
(P. glauca x pungens) x glauca	32	.50b
P. pungens x pungens	17	.53b
P. pungens x glauca	5	.55b

1/ Means followed by a common letter are not significantly different at p = .05.

only within this trial. The slower rapidity rates may be attributed to the tendency of the sand to form a hard crust when watered, subsequently inhibiting emergence of the hypocotyl.

Hanover and Wilkinson (1969) reported a slight increase over both parent species in germination rapidity for F_1 hybrid seed. An intermediate value of 15.8 days, not significantly different from white spruce was recorded in 1978. Blue spruce seed germinated at the fastest rate, 12.4 days. Other values reflected the genomic constitution of the cross, i.e. F_1 hybrids backcrossed to blue germinated faster than those backcrossed to white, although in many cases there were no significant differences. The (white x blue) x (white x blue) spruce hybrid germinated slowest of all crosses with a rapidity value of 19.9 over 20% slower than either the (white x blue) x (blue x white) or (blue x white) x (white x blue) hybrids. While these rates may be confused due to inbreeding with only one blue spruce available, it is noteworthy that the sexual order of species in the F_1 hybrid parent makes such a significant difference. Presumably if inbreeding affects germination speed, all control pollinated F_2 crosses would be subject because of the common limited genetic base of their parents. The longest rate occurs only when white spruce is the maternal parent and blue spruce is the pollen parent in both F_1 hybrid parents. If this pattern holds true with a wide variety of hybrid crosses involving genetically diverse parentages, there would be indications of a sexual effect. This phenomenon is similar to the F_1 hybrid white x blue spruce seed yield behavior. As noted earlier, greatly increased compatibility with maternal pollen in F_1 backcrosses was noted.

Growth and Reproductive Traits

Greenhouse Growth All spruce seedlings were grown for at least 12 months in the greenhouse under accelerated-optimal-growth (AOG) conditions utilizing a 24 hour photoperiod to ensure continuous growth (Hanover, 1976). Height was measured periodically and a branch frequency index, expressed as number of branches per cm. stem, was calculated in one experiment.

Height growth of white and blue spruce, their control pollinated F_1 and F_2 hybrids, and backcrosses were compared in a greenhouse trial (Table 3). Previous AOG experience indicated a pattern of relatively slow white spruce early growth compared with the more rapid growth of blue spruce. This response was verified after 6 months in the greenhouse; blue spruce seedlings were 35% taller than white spruce, and significantly taller than all other crosses. Hybrids generally were intermediate but expressed some variation in the direction of their genomic constitution, that is, blue spruce backcrosses initially grew faster than white spruce backcrosses. By 12 months, differences were not significant between any crosses with one exception which was a severe case of inbreeding depression in the F_2 hybrid. The two F_2 hybrid crosses tested were a self and cross between full-sibs. Height growth rates for 6 and 12 month periods were about 50% lower than the F_1 hybrid.

This is an indication of deleterious recessive genes present in the parents and illustrates the necessity of a wide genetic base for advance generation hybrid breeding. A very slow growing cross such as this may,

Table 3. Mean height of 6-month and 12-month old *P. glauca*, *P. pungens* and their hybrids grown in a greenhouse under supplemental light.

Cross	Height(cm)	
	6 months	12 months
P. glauca x glauca	11.7a[1/]	43.7a
P. glauca x pungens	14.2ab	44.2a
P. pungens x pungens	18.1c	39.6a
(P. glauca x pungens) x glauca	11.3a	45.4a
(P. glauca x pungens) x pungens	15.0b	46.9a
(P. glauca x pungens) x (P. glauca x pungens)[2/]	7.2d	21.5b

1/ Means in the same column followed by the same letter are not significantly different at $p = .05$.

2/ This group includes a self and a cross between full-sibs.

if the trend continues with age, have potential as a dwarf horticultural variety.

Full-sib F hybrid trees, (TT5S59 x Pp1), were backcrossed with 7 pollen sources, four white spruce located in Michigan State University Forest Genetic Plantation 1-60 and three blue spruce growing on campus. Seeds were bulked by pollen source, sown in containers, and grown under AOG conditions in the greenhouse. There were no significant height differences between trees with different white spruce pollen sources after 6 months. However, seedlings from the two tallest sources TT10S49 and TT7S50, retained their status at 12 months (Table 4). Blue spruce pollen Pp7 produced the tallest 6 month progeny, about 20% superior to Pp15 and Pp22 progeny, but this difference diminished after 12 months of growth.

Height and branch frequency measurements were recorded for 8-month-old spruce seedlings (Table 5). Significant height differences were apparent only for the (white x blue) x (blue x white) spruce hybrid. Inbreeding depression is probable because the same blue spruce was used in both crosses. The (white x blue) x (white x blue) spruce hybrid performance may also not be indicative of potential because of inbreeding due to using full-sib F_1 hybrid parents.

A branch frequency index was formulated to express the dense branching habit of some hybrids. Blue spruce seedling form under AOG conditions in the greenhouse, has been observed to be very open with few branches. This was exemplified by the low (.2) branch frequency value

Table 4. Mean height of 6-month and 12-month-old backcrosses involving full-sib *(P. glauca x P. pungens)* hybrid seed parents[1/] with *P. glauca* and *P. pungens* pollen grown in the greenhouse under supplemental light.

Pollen parent	Height (cm)	
	6 months	12 months
P. glauca		
LL14S49[2/]	11.0a[4/]	50.1a
TT10S49	12.2a	58.3b
TT 7S50	12.1a	57.6ab
UU18S50	10.0a	51.2ab
P. pungens		
Pp 7[3/]	17.8b	59.2b
Pp 15	15.3c	55.0ab
Pp 22	15.0c	53.9ab

1/ Cross number TT5S59 x Pp1 located in Michigan State University Forest Genetic Plantation 21-70 in Kalamazoo County.

2/ Location number in Michigan State University Forest Genetic Plantation 1-60.

3/ Location number on Michigan State University Campus

4/ Means in the same column followed by the same letter are not significantly different at p = .01.

Table 5. Mean height and branch frequency for 8-month old spruce seedlings grown in the greenhouse under supplemental light.

Species	Mean height(cm)	Branch[2/] frequency
P. glauca	13.5a[1/]	.7a
P. pungens	12.2a	.2b
P. glauca x (P. glauca x pungens)	13.3a	.6a
(P. glauca x pungens) x (P. glauca x pungens)[3/]	11.9a	1.1c
(P. glauca x pungens) x (P. pungens x glauca)[4/]	8.9b	.6a

1/ Means followed by a common letter are not significantly different at p = .05.

2/ Branch frequency = No. of branches per cm. stem.

3/ Parents are full sibs.

4/ Both F_1 hybrid parents of the cross had the same blue spruce parents.

(Table 5). White and hybrid spruce had fuller form, but the (white x blue) x (white x blue) spruce cross was very dense with nearly twice as many branches on a given length of stem.

It is not known if the dense branching form of the (white x blue) x (white x blue) spruce hybrid is a consequence of inbreeding, a reaction to the 24 hour photoperiod, or a peculiarity of the cross. If this juvenile character is retained as the tree matures, it may be of some value. Densely branched trees of good form are desirable for ornamental and Christmas tree use.

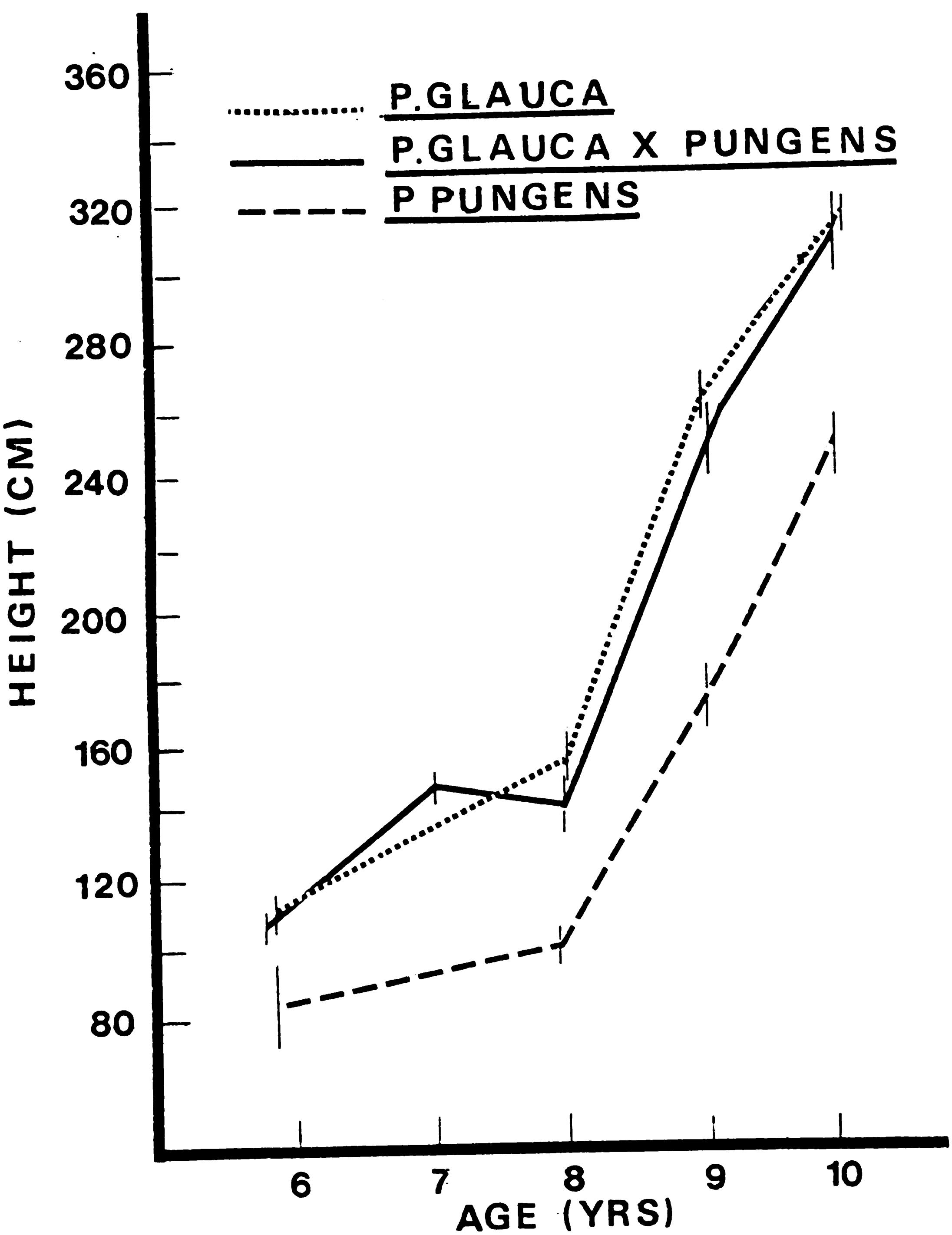
The (white x blue) x (blue x white) spruce hybrid was quite different in it's branching pattern with a value of .6, similar to white spruce and backcrosses to white spruce. Unfortunately, the number of crosses involved in these F_2 hybrids is too small to verify the cause of this behavior; it may be a manifestation of inbreeding or due to parental selection or order.

Field Growth Reports of heterotic height growth responses in interspecific conifer hybrids are numerous, (Bingham et al., 1956; Critchfield, 1963; Duffield et al., 1958; Hyun, 1976; Keiding, 1968; Langner, 1959; Rouland, 1971; Wright, 1955a; and Wright, 1959). Unfortunately, only early growth data is available in most cases. Duffield et al. (1958) has stressed the importance of long-term testing through the growing cycle. Differences in species' growth curves may cause the hybrid to exhibit a heterotic response during one period of development, but perhaps not at another phase. The oldest F_1 hybrid material we now have available in quantity is 10 years old. While not yet mature enough to evaluate as pulpwood material, we can consider its value for Christmas tree and ornamental use.

Figure 1 shows height growth of white, blue and the F_1 hybrid spruce growing at the Kellogg experimental forest. It should be noted that all measurments were taken in 1978 and the age values represent different annual pollination groups rather than one planting measured for several years. Each group was exposed to slightly different planting environments, cultural treatments, and growing conditions. Valid comparisons can only be made within a year.

Generally, white x blue spruce grew at similar rates to white spruce; there were no significant height differences in any given year. Both, however, were significantly faster growing than blue spruce when compared within a year, an increase of 30% was common. White spruce parents of hybrids and white spruce controls grown at Kellogg were selected from a variety of plantations, mostly located elsewhere in Kellogg Forest. Many sources were available, usually phenotypically superior and often from good genetic origins. Blue spruce pollen parents were few and of unknown genetic constitution. The importance of parental selection in hybrid progeny performance has been recognized (Bingham et al., 1956; Duffield, 1958; Hyun, 1976; Langner, 1956; Little and Trew, 1976; and Vidakovic, 1965). The differences in reported hybrid growth rates have been large enough to obscure hybrid potential if poor combining parents were used.

Figure 1. Mean heights for blue, white, and the white x blue F_1 hybrid spruce grown at Kellogg Forest. The vertical bars at each age represent standard errors. All measurements were taken in 1978.


P.GLAUCA
P.GLAUCA X PUNGENS
P PUNGENS
HEIGHT (CM)
360
320
280
240
200
160
120
80
6
7
8
9
10
AGE (YRS)

Mean height differences of over 20% in 5-year-old hybrid progeny of the same white spruce seed parent pollinated with different blue spruce sources have been observed. 50% height differences were recorded in a larger 5-year-old trial varying white spruce seed parents while retaining a constant blue spruce pollen source. Although this information was compiled from relatively small quantities of trees, parental selection can be seen to be crucial in producing a fast growing hybrid.

Another important variable to be considered in hybrid evaluation is planting site conditions. One explaination of heterosis asserts that a hybrid habitat, different from that of the parent species, was available and could be utilized best by the hybrids (Anderson, 1953). While this hypothesis usually refers to natural hybridization, artificial hybrids often show variable performance when tested in a variety of areas (Bingham et al., 1956; Hyun, 1976; Little and Trew, 1976). They may be heterotic in one location but not in another. The genetic diversity contained in a hybrid may enable more efficient physiological use of good conditions or greater adaptation to rigorous environments.

White, blue and F_1 hybrid spruce were also grown in nursery beds on the Michigan State University campus to the age of 5 years. Cultural practices included fertilization, irrigation and weeding when necessary. The parentage of the hybrid was more diverse than the Kellogg forest spruce plantation described earlier, i.e., a larger number of blue spruce pollen parents were available. F_1 hybrids grew vigorously, 20% taller than white spruce controls planted in the same beds. Only a few blue spruce progenies were available for comparison. Many hybrids were particularily vigorous, up to 2.5 times taller than average trees and exhibiting desirable morphological qualities such as good form and blue color.

This superior performance may be attributed to the wider genetic base in the hybrids or their increased ability to utilize optimal conditions. Probably both of these contributed to the heterotic behavior.

The necessity of understanding the genotype-environment interaction has been recognized and these hybrids will be outplanted at a variety of sites throughout Michigan. Their performance under a wide range of conditions will be evaluated for pulpwood, Christmas tree, and ornamental uses.

Correlation Coefficients Length of improvement programs can be shortened if early selection of juvenile trees is possible. For this technique to be feasible, early performance rankings must correlate very closely with rotation age rankings. This will enable the breeder to eliminate poor material early and concentrate on higher potential trees, increasing overall program efficiency.

An important selection parameter is height growth rate. Correlation coefficients were calculated between 2-, 5-, and 9-year height measurements on white, blue and the F_1 white x blue spruce hybrid (Table 6). There was an indication of increased stability with age, as correlations between 5- and 9- year heights were higher than those between 2-

Table 6. Correlation coefficients between 2-, 5-, and 9-year height measurements on blue and white spruces and their F_1 hybrid.

Age(yrs)	Species	Age(yrs)	
		5	9
2	*P. glauca*	.70[1/]	.55
	P. pungens	.84	.70
	P. glauca x pungens	.65	.50
5	*P. glauca*		.80
	P. pungens		.90
	P. glauca x pungens		.74

1/ $r_{.01;\ 40\ d.f.} = .49$

and 5-year values. The relationship between 2- and 9-year-heights, although significant, was too low to consider early selection possibilities.

Blue spruce heights gave the highest correlations followed by white spruce and the F_1 hybrid. The relatively low correlation coefficient of the F_1 hybrid indicates variability in the early growth curve. This stresses the importance of testing throughout the rotation age to guarantee hybrid performance.

Flowering Response Breeding work in trees is often limited by late flowering ages leading to long generation times. Blue spruce, which does not usually reach reproductive maturity in nature until 30 years of age (Hanover, 1975), is difficult to work with for this reason. Additionally, the female strobili are normally borne high in the crown, making controlled pollinatons difficult. There is evidence that hybridization can stimulate precocious flowering. Some pine hybrids have produced cones earlier than their comparably grown parent species (Critchfield, 1963; Fowler and Heimburger, 1958;), others flowered at similar dates to the parent with the earlier age of sexual maturity (Wright, 1955a; and Wright et al., 1969). This may imply dominance of early fruiting behavior in certain F_1 hybrids (Wright, 1955a).

White spruce can reach reproductive maturity in 4 years (Sutton, 1969; Young and Hanover, 1976) with significant cone crops on trees 6-to 10-years-old in breeding orchards (Wright, 1964). There is evidence that F_1 hybrids have retained the early flowering characteristics of white spruce in some instances, although relevant data is available for only a few years. The hybrid crop of sufficient age to examine contains two crosses, TT5S59 x Ppl, and R4-14 x Ppl, both having the same male parent but exhibiting different flowering responses. After 6 years, 50% of TT5S59 x Ppl offspring had produced female strobili with 7% bearing male strobili. 89% had flowered by the age of 10 years with heavy, 30 per tree, cone crops. The 11% that had not responded were below average trees in growth and quality. Male strobili production was widespread by this time although precise data are not available.

Conversely, only 5% of the R4-14 x Ppl offspring bore flowers at age 8, their earliest flowering age, with 20% productivity by age 10. Male strobili generation was similarily delayed. R4-14 x Ppl, in addition to a later age of reproductive maturity, also had other blue spruce characteristics such as: sharper needles, shorter height, and bluer foliage when compared to TT5S59 x Ppl.

Unfortunately, flowering data is not available from the white spruce maternal parents for comparison. Even with the same male parent, physiological and morpological trait expression in the hybrid was greatly influenced by the combining ability of the *P. glauca* parent. This emphasizes the importance of including good combining parents as well as selecting on the basis of external characteristics.

Flower initiation age at Kellogg forest can probably be considered typical for an untreated breeding orchard. Flowering may possibly be increased with fertilization, girdling, or cultural treatments.

Cone Characteristics Cone characteristics are used extensively in hybridization studies because of their many distinguishing features and resistance to environmental effects (Khalik, 1974; Weaver, 1963). Blue and white spruce cones are readily differentiated, the latter being shorter, more narrow and lighter in color. White spruce cones also have thin orbicular scales with rounded or slightly emarginate apex compared to the elongated erose apex of the blue spruce scales (Sargent, 1922). F_1 hybrid cones are darker than white spruce cones and tinted orange or light brown. The cone scales are intermediate with slightly erose, undulating apex.

A small sample of mature unopen cones from controlled pollinations at Kellogg Forest was measured in 1978 (Table 7). F_1 hybrid cones were significantly longer and wider than white spruce cones.

This reflects an intermediate value because blue spruce cones are commonly 5-10 cm long (Den Ouden and Boom, 1965) and over 20 mm wide (personal observation). Flowering hybrids were all from one cross (TT5S59 x Ppl), previously identified as having relatively more white spruce morphological characteristics. This particular combination could also disproportionately resemble white spruce in cone features.

Morphological and Physiological Traits

Blue Color The ornamental value of blue spruce resides in it's unique blue foliage coloration. This highly valued trait is considered to be a result of surface wax deposition (Hanover and Reicosky, 1971). The degree of foliage color depends primarily on the quantity and physical structure of the wax and is influenced by a number of factors both genetic and environmental (Hanover and Reicosky, 1971; Reicosky and Hanover, 1978).

Table 7. Length and width measurements of mature unopen spruce cones from 1978 controlled pollinations at Kellogg Forest.

Species	Cones(no.)	Length(cm.)	Width(mm.)
P. glauca	126	4.5 1/	13.1
P. glauca x pungens	129	5.4	13.5

1/ Means in the same column are significantly different at $p = .05$.

Nurserymen have commonly grown blue spruce using seed from geographic origins known to yield trees of good color. Hanover (1975) and Bongarten (1978) identified several of these areas. Cram (1968) has had some success in a selection program for blue color but the inheritance pattern does not seem to be simple.

Moisture and nutritional regimes affect expression of genetic capability for blue foliage color (Hanover and Reicosky, 1971). Fertilizer is commonly recommended to enhance ornamental color. Surface waxes are also influenced by weathering, first year needles are more glaucous than older foliage, with best color on newly flushed needles.

White spruce also possesses surface waxes similar to blue spruce but in much lesser amounts (Hanover and Reicosky, 1971). Some variation in color can be seen although white spruce foliage never reaches the degree of glaucousness present in blue spruce.

Foliage color ratings for 6 to 10 year old spruce indicate good retention of blue color in the F_1 white x blue spruce hybrid (Table 8). A subjective evaluation revealed a 5 year mean of 2.3 (4.0 = very blue foliage, 0.0 = green foliage) for the hybrid, slightly lower than blue spruce (2.6), but much higher than white spruce (1.2).

A wide range in yearly means of foliage color for blue spruce was observed, extending 73% of the overall mean, compared to 25% for the hybrid and white spruce. This may reflect the smaller sample size and the small number of blue spruce parents used in several years. Often within a year, the blue and F_1 hybrid white x blue spruce means were not significantly different. While hybrid means did not vary extensively,

Table 8. Foliage color and needle sharpness of *P. glauca*, *P. pungens*, and the *(P. glauca x P. pungens)* hybrid spruce.

Species	Trees(no.)	Foliage color[1/]		Needle sharpness[2/]	
		5 yr. mean	Range in yearly means	5 yr. mean	Range in yearly means
P. glauca	738	1.2	1.1 - 1.4	0.6	0.2 - .7
P. pungens	142	2.6	1.6 - 3.5	2.6	2.3 - 2.7
P. glauca x pungens	915	2.3	2.0 - 2.6	1.5	1.0 - 1.8

1/ Color rating as follows: 0 = no blue, 4 = very blue

2/ Needle sharpness rating as follows: 0 = soft, 3 = sharp means of individual crosses within a year reflected much variability. Values ranged from .5 to 3.5 depending on the parental combination. Diversity within a cross was also considerable, it was common to find foliage color ratings from maximum to minimum when there were numerous members in the cross.

Foliage color ratings were also scored for 5-year-old hybrids grown in nursery beds on the Michigan State University campus. Cultural conditions were excellent with fertilization and irrigation, promoting full expression of foliage color. The F_1 hybrid spruce average color rating was 2.3, even higher than the value for a small sample of blue spruce present. Many individual hybrids had very good blue color. This higher overall rating may reflect good cultural conditions and choice of blue spruce pollen sources, which included pollen received from Cram, and resulting from a selection program for blue color (Cram, 1968).

Needle Sharpness Blue spruce are often difficult for nurserymen to handle and unpopular as Christmas trees because of their extremely sharp foliage. A tempering of this quality could lead to increased use and value for the species.

Needle sharpness is dependent on three factors: rigidity, acuteness of tip, and angle of the needles to the branch. Blue spruce has very rigid, acute needles extending at an angle of 75° to 90° from the branch. White spruce needles are more appressed to the branch and are usually soft and flexible. Intermediacy for this trait occurs in the F_1 hybrid although some variation is present.

A subjective scoring of needle sharpness was undertaken for spruce 5 years and older. Individual tree foliage was rated in late summer from 0, very soft, to 3, very sharp (Table 8). The F_1 hybrid 5-year mean needle sharpness value was 1.5, almost exactly intermediate to the parent species. The relatively small range in yearly mean values for blue and white spruce reflect the consistency of the trait. Hybrid yearly means ranged slightly larger. Values within a year and within a cross generally showed little variation except in the hybrid with slightly larger deviations.

Five-year-old spruce grown in nursery beds gave similar results to field plantations indicating increased moisture and nutritional levels have little effect on foliage sharpness.

Correlation coefficients between needle sharpness and blue color indicate a positive correlation between the two blue spruce characteristics, sharp needles and blue color. However, r is only .6 implying a relatively weak correlation. Simultaneous selection for blue foliage color and duller needles should be possible in a breeding program.

Frost Injury Growing season frost is the most critical limiting factor when northern species are grown south of their native range (Wright, 1976). Frost injury can result in growth retardation and malformed trees which is especially damaging for ornamentals or Christmas trees. White spruce, with its predominantly boreal range, is susceptible when grown in lower Michigan or farther south (Wright, 1977). Blue spruce, native to the Rocky Mountains, is not usually injured by growing season frosts.

Table 9. Spring frost injury on the white and blue spruces and their F_1 hybrid growing at East Lansing, Michigan in 1976.

Species	No. of trees	Percent damaged shoots per tree
P. glauca	61	41.6[1/]
P. pungens	62	3.5
P. glauca x pungens	50	12.4

[1/] All means are significantly different at p = .05.

In 1976 a late spring frost caused extensive damage to the campus nursery spruce planting. The percentage of damaged shoots on each three-year-old tree was recorded (Table 9). White spruce, as expected, experienced the most severe injury, 41.6% of the shoots were damaged. Only 3.5% of the blue spruce shoots were damaged. Hybrid frost resistance was intermediate with 12.4% of the shoots damaged. Individual F_1 hybrid trees showed great variability, some injured as much as white spruce, while others were as resistant as blue spruce.

Multivariate Analysis

Discriminant Analysis Discriminant analysis is a multivariate technique which can be used to statistically distinguish related groups of taxa. Discriminant analysis weights and combines various characters to best "discriminate" between groups by means of a series of linear equations (Fisher, 1936). These equations are of the form:

$$D_i = d_{i1}Z_1 + d_{i2}Z_2 + \dots + d_{ip}Z_p$$

where D_i is the score on discriminant function i, d's are weighting coefficients, and Z's are the standardized values of the p discriminating variables used (Klecka, 1975).

A discriminant analysis can be separated into two objectives. Effectiveness of the equations and the involved variables in discriminating between the groups is calculated first. Next, the relative classification of the groups is established enabling unknowns to be assigned to groups (Kleca, 1975).

First applied in forestry to distinguish between clones of locust (Hopp, 1941), discriminant analysis has proved useful in introgression and hybridization studies (Clifford and Binet, 1954; Dancik and Barnes, 1975; Ledig et al., 1969; Mergen et al., 1966; Mergen and Furnival, 1960; Namkoong, 1966; Sharik and Barnes, 1971). Discriminant analysis was recognized as being particularly efficient in selecting discerning characteristics (Dancik and Barnes, 1975) and in separating species (Namkoong, 1966). Mergen and Furnival (1960) saw special benefits for a beginning hybridization breeding program. Individual features and their relationships can be examined and the best diagnostic characteristics to isolate the hybrid can be identified.

A particularily useful form of discriminant analysis uses a stepwise procedure to add or delete variables on the basis of their discriminating power. During the process, previously selected variables may lose their discriminatory power with the addition of a new variable and be removed from the equation. Often a relatively small number of variables will define the species with sufficient accuracy and the entire model need not be used.

Stepwise discriminant analysis was performed on a CDC 6000 computer for 9- and 10-year-old white, blue, and F_1 hybrid spruce growing at Kellogg forest. Results were kept separate by age class. Variables entered were as follows: height, twig diameter, bud length and width, foliage color and sharpness, and needle density, length and angle to branch. All branch measurements were taken from top whorl samples.

Two discriminant functions were necessary to define horizontal and vertical dimensions. The functions, while using the same variables, weigh them differently with coefficients to maximize distance between groups that was not explained by a previous function. The importance of the two equations is expressed as the relative percentage of trace they contain. With the spruce data, 92.3% of trace was covered by the first function, indicating the second equation is of little value. Standardized coefficients are computed to weigh the comparative value of each variable's discriminating power in the equation.

Table 10 lists standardized discriminant function coefficients for samples of 9-year-old spruce including their relative rank. The data for 9-year-old spruce was chosen to typify this discriminant analysis because a greater variety of crosses were available. The only difference in the coefficients for 10-year-old spruce was a juxtaposition of two variables in rank for the first discriminant function.

Bud length was the best single factor in differentiating white, blue, and the F_1 hybrid spruce. Other variables also significantly contributed with the exception of needle density, which was removed from the analysis during the stepwise procedure. The coefficient rankings were different for the second discriminant function, as expected, but the small amount of trace explained renders this set relatively unimportant.

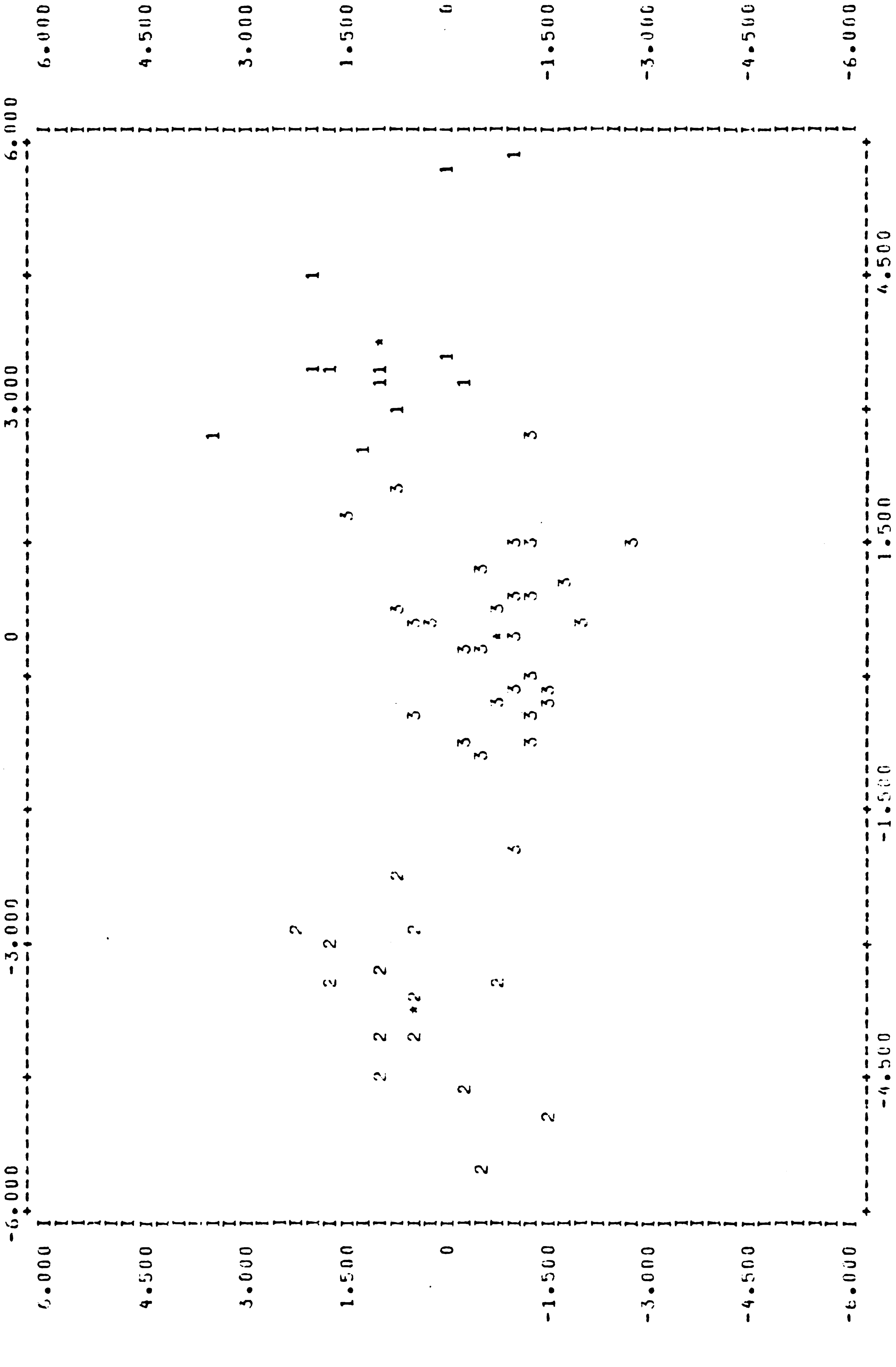
The function equations defined individual tree values and expressed them in a 2-dimensional plot (Figure 2). The greater amount of discrimination possible with the first function, expressed as horizontal distance, is readily apparent. Small vertical differences reflect the

Table 10. Standardized discriminant function coefficients for 9-year-old *P. glauca*, *P. pungens*, and their F_1 hybrid. Relative ranking is in terms of discriminative efficiency.

	First discriminant function		Second discriminant function	
Variable	Rank	Coefficient	Rank	Coefficient
Bud length	1	-.977	2	-.768
Needle sharpness	2	-.897	5	-.542
Bud width	3	.853	3	.741
Needle length	4	-.625	1	.872
Height	5	.582	7	-.424
Needle angle	6	-.507	4	.698
Blue color	7	.483	8	-.227
Twig diameter	8	.197	6	-.536
Needle density[1]	9	-.111	9	-.139

[1]Not significant for inclusion in stepwise discrimant analysis by change in Rao's V at P = .05

Figure 2. Plot of discriminant score 1 (horizontal) vs. discriminant score 2 (vertical) for nine-year-old spruce growing at Kellogg Forest. Each number designates a tree's score, 1 = white, 2 = blue, and 3 = white x blue F_1 hybrid spruce. * indicates a species' centroid.


-6.000
-4.500
-3.000
-1.500
0
1.500
3.000
4.500
6.000

minor contribution of the second function, predominantly useful in increasing distance between the hybrid and the pure species. The plot for discriminant analysis of 10-year-old spruce, not shown, is similar with the exception of a slightly closer relationship expressed between the hybrid and white spruce.

Prediction results were calculated on the success of discriminant group assignations compared to known parentage. 100% of white and blue spruce and 90% of the F_1 hybrids were correctly identified in the analysis of 9-year-old spruce. 6.7% of the hybrids were incorrectly classified as white spruce and 3.3% as blue spruce. Prediction results from ten-year-old spruce were similar, but incorrectly classified hybrids were catergorized as white spruce.

Discriminant analysis presents a clear pictorial representation of hybrids relative to parental species. Patterns in hybrid inheritance for traits studied can be easily recognized. Discerning characteristics of high value are identified and can be used in further research.

RECOMMENDATIONS

Nurserymen and Christmas tree growers have already expressed interest in obtaining hybrid spruces. Unfortunately, up to the present, all hybrids produced have been needed to continue research and breeding work. The generation of hybrids for public release may be accomplished through several methods.

Mass production of F_1 hybrid pine seed by controlled pollination was successfully done by Hyun (1976) in the 1950's, but this approach is

economically unfeasible with our low seed yields and expensive labor. Another approach, vegetative reproduction by grafting or rooted cuttings has the advantage of perpetuating preferred genotypes, thereby eliminating variability present in F_1 hybrids.

Varieties of blue spruce are commonly grafted, but this approach is expensive with variable success rates (Wells, 1953). Similar problems may be expected in grafting hybrids. Vegetative propagation by rooted cuttings has been undertaken for hybrid spruce in Europe (Rouland, 1971) with large clonal variations in performance. Some easy rooting clones gave 82% success rates while others were difficult to root. Mist chamber rooting of spruce at Michigan State University has given good results with some species (personal observation). Rooting ability decreases with the stock age, but a small scale F_1 hybrid production may be possible if young stock is used. This method is likely to be of limited usefulness due to expense and topophysis effects. At present, F_1 hybrid availability will probably be confined to the Michigan State University research program and initial testing by large growers in the Michigan Cooperative Tree Improvement Program.

Greenhouse seedling growth of backcrosses has been vigorous under AOG conditions. Backcrosses may have commercial potential if this growth rate continues. Unfortunately backcross production must be by controlled pollination, encountering the same difficulties as F_1 hybrid mass production.

The most workable approach to mass production of hybrids may be an F_2 hybrid seed orchard. F_1 hybrids would be isolated from sources of contaminant pollen and allowed to wind pollinate. Unfortunately there is no guarantee of hybrid vigor extension beyond the F_1 generation. Although Wright (1955a) and Hyun (1976) have reported encouraging early results with F_2 hybrids, our data is preliminary. The only F_1 hybrid spruce presently flowering are of similar parentage and the intercrossed progeny have been severely stunted in growth trials in the greenhouse. In the next few years F_1 hybrids of diverse parentage will be flowering, enabling F_2 crosses of sufficiently wide genetic base to be made. If these F_2 hybrids show early vigorous growth and retain the desirable features of the F_1 hybrid, a grafted F_2 hybrid seed orchard should be considered. By this time good combining F_1 hybrid parents could be identified. Grafting would ensure that the superior combining performance of the selected F_1 hybrids would continue into the F_2 seed orchard. Intensive culture would aid good growth, and early flowering would probably ensue with significant seed production within 10 years.

An alternative to this approach would involve orchard establishment with untested F_1 hybrids. Mild selection could be practiced with combining ability judged after F_2 hybrid production and growth. The savings in time with this method may be offset by the unknown performance of F_2 hybrids.

Present work should concentrate on ensuring a diverse genetic base for F_1 hybrids, and making a wide variety of F_2 crosses. Selection of superior parents has been emphasized earlier. A selection score has been computed for all spruce examined, on the basis of growth rate, blue color, and needle sharpness. Phenotypically superior trees can be used in further crosses.

Blue spruce pollen should be collected in the native range from areas known for high genetic value. If phenotypically desirable blue spruce can be found locally, their value would be high for control pollination work. More blue spruce females should be pollinated with white spruce to learn about parental sex effects in inheritance.

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