

J. Agric. Sci. 41: 371–378 (1951). — GREEN, A. G., A. H. D. BROWN and R. N. ORAM: Determination of outcrossing rate in a breeding population of *Lupinus albus* L. (white lupin). Z.Pflanzenzüchtg. 84: 181–191 (1980). — HAGMAN, M.: Incompatibility in *Pinus*. Hereditas 52: 245 (1964). — HEDRICK, P. W., M. E. GINEVAN and E. P. EWING: Genetic polymorphism in heterogeneous environments. Ann. Rev. Ecol. 7: 1–32 (1976). — KING, J. N., B. P. DANCİK and N. K. DHIR: Genetic structure and mating system of white spruce (*Picea glauca*) in a seed production area. Can. J. For. Res. 14: 639–643 (1984). — LEE, G. J.: Allozyme analysis of lodgepole pine along elevational transects in Alberta. M. Sc. thesis. University of Alberta (1985). — LIBBY, W. F., R. F. STETTLER and F. W. SEITZ: Forest genetics and forest tree breeding. Ann. Rev. Gen. 3: 469–494 (1969). — MITTON, J. B., Y. B. LINHART, M. L. DAVIS and K. B. STURGEON: Estimation of outcrossing in ponderosa pine, *Pinus ponderosa* LAWS., from patterns of segregation of protein polymorphisms and from frequencies of albino seedlings. Silvae Genet. 30: 117–121 (1981). — MORAN, G. F. and A. H. D. BROWN: Temporal heterogeneity of outcrossing rates in alpine ash (*Eucalyptus delegatensis* R. T. BAK.). Theor. Appl. Genet. 57: 101–105 (1980). — NAMKOONG, G.: Inbreeding effects on estimation of genetic additive variance. For. Sci. 12: 8–13 (1966). — NEALE, D. B. and W. T. ADAMS: The mating system in natural and shelterwood stands of Douglas-fir. Theor. Appl. Genet. 71: 201–207 (1985). — RAO, C. R.: Linear statistical inference and its applications. Second Edition. John Wiley and Sons, New York (1973). — RIDGEWAY, G. J., S. W. SHERBURNE and R. D. LEWIS: Polymorphisms in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99: 147–151 (1970). — RITLAND, K. and S. JAIN: A model for the estimation of outcrossing rate and gene frequencies using n independent loci. Heredity 47: 35–52 (1981). — SARVAS, R.: Investigations on the flowering and seed crop of *Pinus sylvestris*. Commun. Inst. Forest.

Fenniae 53: 1–198 (1962). — SHAW, C. R. and R. PRASAD: Starch gel electrophoresis: A compilation of recipes. Biochem. Genet. 4: 297–320 (1970). — SHAW, D. V. and R. W. ALLARD: Estimation of outcrossing rates in Douglas-fir using isozyme markers. Theor. Appl. Genet. 62: 113–120 (1982). — SHAW, D. V., A. L. KAHLER and R. W. ALLARD: A multilocus estimator of mating system parameters in plant populations. Proc. Nat. Acad. Sci. USA 78: 1298–1302 (1981). — SICILIANO, M. J. and C. R. SHAW: Separation and visualization of enzymes on gels. pp 185–309. In: I. SMITH (ed.). Chromatographic and electrophoretic techniques. Vol. 2. Heimann, London (1976). — SORENSEN, F. C. Frequency of seedlings from natural self-fertilization in coastal Douglas-fir. Silvae Genet. 22: 20–24 (1973). — SORENSEN, F. C.: The roles of polyembryony and embryo viability in the genetic system of conifers. Evolution 36: 725–733 (1982). — SORENSEN, F. C. and R. S. MILES: Inbreeding depression in height, height growth, and survival of Douglas-fir, ponderosa pine, and noble fir to 10 years of age. Forest Sci. 28: 283–292 (1982). — SQUILLACE, A. E.: Average genetic correlations among offspring from open-pollinated forest trees. Silvae Genet. 23: 149–156 (1974). — SQUILLACE, A. E. and J. F. KRAUS: The degree of natural selfing in slash pine as estimated from albino frequencies. Silvae Genet. 12: 46–50 (1963). — WRIGHT, S.: The genetic structure of populations. Ann. Eugen. 15: 324–345 (1951). — YEH, F. C. and C. LAYTON: The organization of genetic variability in central and marginal populations of lodgepole pine (*Pinus contorta* ssp. *latifolia*). Can. J. Genet. Cytol. 21: 487–503 (1979). — YEH, F. C. and D. M. O'MALLEY: Enzyme variation in natural populations of Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO.) from British Columbia. I. Genetic variation patterns in coastal populations. Silvae Genet. 29: 83–92 (1980). — YEH, F. C., A. BRUNE, W. M. CHELIAK and D. C. CHIPMAN: Mating system of *Eurayptus citriodora* in a seed-production area. Can. J. For. Res. 13: 1051–1055 (1983).

Population Hybridization in Scotch pine (*Pinus sylvestris* L.)¹): II. Combining Ability Comparisons

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Summary

Three-year height and needle length of interpopulation hybrids of Scotch pine (*Pinus sylvestris* L.), generated by three sets of modified matings, were evaluated in three nurseries in Pennsylvania. For both characters, particularly in the 7 × 8 factorial polycross experiment, females, males, and female × male interactions were significant sources of variation indicating the differences among both general and specific combining abilities. The rankings of general combining abilities of populations estimated from males were similar among different sets of matings, and they are expected to be consistent in population hybridization. Although a few large estimates of specific combining abilities were found, the differences among the population hybrids were accounted for mainly by general combining abilities of parents. The use of general combining ability seems reasonable in breeding of interpopulations of Scotch pine, just as in conventional breeding systems.

Key words: Scotch pine, population hybridization, combining ability, nested population diallel cross, factorial polycross.

Zusammenfassung

Nach einem modifizierten Kreuzungsplan in drei Gruppen erzeugte Populationshybriden von *Pinus sylvestris* L. wurden im Alter 3 auf Höhenwachstum und Nadellänge hin untersucht. Für beide Merkmale, besonders im 7 × 8 faktoriellen Polycross-Experiment, waren die Mütter, Väter und die Mütter × Väter-Interaktionen signifikante Ursachen der Variation, welche Unterschiede zwischen der allgemeinen und der spezifischen Kombinationseignung anzeigten. Die Ränge der allgemeinen Kombinationseignung von Populationen, errechnet nach den Vätern, waren in den verschiedenen Gruppen des Kreuzungsplanes ähnlich. Es wird erwartet, daß sie bei der Hybridisierung von Populationen konsistent sind. Obwohl einige große Schätzwerte der spezifischen Kombinationseignung gefunden wurden, erwiesen sich die Unterschiede zwischen den Hybrid-Populationen im wesentlichen als durch allgemeine Kombinationseignung der Eltern verursacht. Bei der Kiefer scheint die Nutzung der allgemeinen Kombinationseignung für die Erstellung von Hybridpopulationen bedeutungsvoll zu sein, wie dies auch aus der konventionellen Züchtung bekannt ist.

Introduction

Scotch pine (*Pinus sylvestris* L.) is an important timber species in northern Eurasia. In the northern United States, it is used mainly for ornamental and Christmas trees. The importance of genetic improvement in the economic traits of the species has been recognized by tree breeders and nurserymen to meet demands of markets (SCHRUM *et al.*, 1975). Population or provenance hybridization could be a

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feasible method for developing desirable genotypes because large genetic variation in several characters exists among the populations of Scotch pine (WRIGHT and BULL, 1963; GERHOLD, 1959; KING, 1965a, 1965b; STEINER, 1974), and controlled pollination among most of populations can be performed with relative ease (KARRFALT *et al.*, 1975). Possible benefits of an hybridization program may include heterosis, combination of desirable characters, and a wide range of adaptation.

A successful hybrid breeding program depends on genetic information, such as general (GCA) and specific combining abilities (SCA) and other genetic and environmental components of variability, as reported in a previous paper, (Part I) (PARK and GERHOLD, 1985). In this paper, we include extended information on general and specific combining abilities which was obtained from additional hybrids that were produced by two sets of "factorial population polycrosses" as well as those from the "nested population diallel cross" in Part I. The mating design used to produce the additional hybrids was a combination of factorial and polycross designs to obtain genetic parameters for populations and individual females. The parents included in these experiments are considered as a fixed set of breeding materials, and general and specific combining abilities of the parental populations and seed parents are estimated and compared.

Table 1. — Mating schemes used in producing population hybrids.

I. Nested population diallel cross (diallel).

Females	Males (pollen mixture)						
	212 FRA	250 GER	262 GEO	269 ENG	316 FRA	318 BEL	556 ITA
212 FRA 1 ^a	I	X	X	X	X	X	X
212 FRA 2	I	X	X	X	X	X	X
250 GER 1	X	I	X	X	X	X	X
250 GER 2	X	I	X	X	X	X	X
262 GEO 1	X	X	I	X	X	X	X
262 GEO 2	X	X	I	X	X	X	X
269 ENG 1	X	X	X	I	X	X	X
269 ENG 2	X	X	X	I	X	X	X
316 FRA 1	X	X	X	X	I	X	X
316 FRA 2	X	X	X	X	I	X	X
318 BEL 1	X	X	X	X	X	I	X
318 BEL 2	X	X	X	X	X	I	X
556 ITA 1	X	X	X	X	X	X	I
556 ITA 2	X	X	X	X	X	X	I

II. 7 x 8 factorial polycross

Females	Males (pollen mixture)							
	212 FRA	250 GER	262 GEO	269 ENG	316 FRA	318 BEL	556 ITA	243 GRE
201 NOR	X	X	X	X	X	-	X	X
238 FRA	X	X	X	X	X	X	X	X
240 FRA	X	X	X	X	X	X	X	X
214 TUR	X	X	X	X	X	X	X	X
242 YUG	X	X	X	X	X	X	X	X
268 SCO	X	X	X	X	X	X	X	X
245 SPA	X	X	X	X	X	X	X	X

III. 8 x 2 factorial polycross

Females	Males (pollen mixture)	
	213 TUR	SPA
221 TUR	X	-
242 YUG	X	X
250 GER	X	X
262 GEO	X	-
269 ENG	X	X
318 BEL	X	X
246 SPA	X	X
261 GEO	X	X

^a Abbreviations consisting of MSFG number and first three letters of country of origin followed by tree number.

I Intrapopulation cross.

— Missing cross.

Materials and Methods

Plant Materials

Hybrid plants used in this experiment came from a set of "nested population diallel crosses" and two sets of "factorial population polycrosses" in 1969 and 1970 (KARRFALT *et al.*, 1975), involving a total of 18 populations. The nested population diallel cross (diallel cross) involved seven populations, as identified by Michigan State University designations, 212 from France, 250 from Germany, 262 from Georgian S.S.R., 269 from England, 316 from France, 318 from Belgium, and 556 from Italy (Table 1). The seven seed parents of the 7 x 8 factorial population polycross (7 x 8 polycross) represented seven populations, none of which was included in the diallel cross. These populations were 201 from Norway, 238 from France, 240 from France, 214 from Turkey, 242 from Yugoslavia, 268 from Scotland, and 245 from Spain (Table 1). The population males, represented by a pollen mixture from each of 8 populations, were the same as those used in the diallel cross with the addition of 243 from Greece. Detailed information on these populations is found in WRIGHT and BULL (1963). A pollen mixture contained equal volumes of pollen from three to nine individuals. Controlled pollinations were performed factorially using the "minibag technique" (GERHOLD, 1968) at Michigan State University's Kellogg Forest. Details of these pollination procedures are described in Part I and by KARRFALT *et al.* (1975). A total of 55 hybrid families was produced by these matings; one cross failed to produce enough seedlings for the experiment. The number of seedlings grown per hybrid family varied because of accidental losses in the greenhouse and some mortality after transplanting in the nurseries.

The other set of population hybrid families was obtained by an 8 x 2 factorial population polycross (8 x 2 polycross). Eight female parents, each representing a different population, were mated in 1970 with two pollen mixtures. The female populations were 221 from Turkey, 242 from Yugoslavia, 250 from Germany, 261 and 262 from Georgian S.S.R., 269 from England, 318 from Belgium and 246 from Spain; and the male populations were 213 from Turkey and a Spain Guadarram Mountains population growing near the Pennsylvania State University (Table 1). Four of these populations, 221, 246, 261, and the Spanish population used as a male were not used in any previously mentioned matings. A total of 14 families resulted; two crosses failed to produce sufficient seeds or seedlings.

Seeds were sown in mid-March 1974 in styrofoam block containers. The seedlings were grown in a greenhouse until June 1974, and then transplanted into nursery beds at three locations in Pennsylvania: Penn Forest Tree Nursery, Centre County; Carino Nurseries, Indiana County; and Strathmeyer Forests Nursery, York County. The seedlings remained in the nurseries until the end of the 1976 growing season. Measurements on individual tree heights and needle lengths were taken after growth was complete. Details of greenhouse, nursery, and measurement procedures were described in Part I.

Statistical Models and Analyses

Analyses of variance in height and needle length for the two factorial population polycrosses were performed using the model:

$$Y_{h(ij)k} = \mu + N_h + R_{hl} + F_i + M_j + FM_{ij} + NX_{h(ij)} + e_{hlijk} \quad (1)$$

where

$Y_{h(ij)k}$ = performance of k^{th} individual of the ij^{th} cross in l^{th} replicate of h^{th} nursery;

μ = overall mean;

N_h = h^{th} nursery effect, $h = 1, 2, 3$;

R_{hl} = l^{th} replicate effect in h nursery, $l = 1, 2$;

F_i = i^{th} female effect, $i = 1, 2, \dots, 7$ or $i = 1, 2, \dots, 8$;

M_j = j^{th} male (pollen mixture) effect, $j = 1, 2, 3, \dots, 8$ or $j = 1, 2$;

FM_{ij} = interaction effect of i^{th} female and j^{th} male (pollen mixture);

$NX_{h(ij)}$ = interaction effect of h^{th} nursery and ij^{th} population cross; and

e_{hlijk} = random error component.

Significance of the sources of variation was determined approximately by using the conventional F-test although the data were unbalanced (TIETJEN, 1974). Once the significance of females, males, and (or) female \times male interactions was found, combining abilities were estimated.

The GCA of an individual parent is defined as the average performance of the progeny of a parent in a series of matings, and it is expressed as the deviation from the overall mean. For example, estimations of GCA for both females and males based on mean of the crosses (Z_{ij}) were:

$$G_{i\phi} (G_{i\sigma}) = \frac{1}{p} Z_{i.} - \bar{Z} \quad (2)$$

where

$G_{i\phi} (G_{i\sigma})$ = estimated general combining ability of i^{th} female (male),

p = number of males (females) in the factorial population polycross,

$Z_{i.}$ = total mean performance of ij^{th} population crosses summed over males (females), and

\bar{Z} = overall mean of mean performance.

The standard error of the estimates was calculated assuming no covariances between plot means and overall mean. For example,

$$S.E.(G_{i\phi}) = \sqrt{\frac{1}{p^2} \text{Var}(Z_{i.}) + \text{Var}(\bar{Z})} \quad (3)$$

where

$S.E.(G_{i\phi})$ = standard error of GCA estimate of i^{th} female,

$\text{Var}(Z_{i.})$ = variance for i^{th} female total over all males, and

$\text{Var}(\bar{Z})$ = variance of overall mean.

The variance for i^{th} female total was calculated as the sum of plot mean variances over all males, i.e.;

$$\text{Var}(Z_{i.}) = \sum_j \sigma_{ij}^2 \quad (4)$$

where σ_{ij}^2 = variance of ij^{th} cross mean = $\frac{1}{n_{ij}} \sigma_e^2$,

where n_{ij} = number of observation for ij^{th} cross mean, and

σ_e^2 = error variance from analysis of variance.

Similarly,

$$\text{Var}(\bar{Z}) = \text{Var}\left(\frac{1}{pq} Z_{..}\right) = \frac{1}{p^2 q^2} \sum_i \sum_j \sigma_{ij}^2$$

where $Z_{..}$ = total cross means, and

$p (q)$ = number of males (females).

The SCA of cross is defined as the average performance of a cross between two particular parents after subtracting

GCA of the two parents. Therefore, once GCA of the maternal and paternal parents are estimated, SCA of a cross may be estimated as:

$$S_{ij} = Z_{ij} - G_{i\phi} - G_{j\sigma} - \bar{Z} \quad (5)$$

where

S_{ij} = estimated specific combining ability of i^{th} female and j^{th} population cross,

Z_{ij} = mean of ij^{th} cross,

$G_{i\phi} (G_{j\sigma})$ = estimated general combining abilities of i^{th} female (j^{th} male), and

\bar{Z} = overall mean of the means of all crosses.

The model and results of analyses of variance involving the nested population diallel cross were presented in Part I. General combining abilities of populations, females, and males (pollen mixture) were estimated using means of the crosses. The population general combining ability (G_i), excluding intrapopulation progenies, was estimated as:

$$G_i = \frac{1}{2(p-1)} (Z_{i.} + Z_{.i}) - \frac{1}{p(p-1)} Z_{..} \quad (6)$$

where

G_i = estimated general combining ability of i^{th} population,

p = number of populations,

$Z_{i.} (Z_{.i})$ = total mean performance of i^{th} population summed over all males (females), and

$Z_{..}$ = total of all mean performances.

The general combining abilities of females ($G_{i\phi}$) and males ($G_{i\sigma}$) were estimated as:

$$G_{i\phi} = \frac{1}{p-1} Z_{i.} - \bar{Z} \quad \text{and} \quad G_{i\sigma} = \frac{1}{p-1} Z_{.i} - \bar{Z}$$

where

$G_{i\phi} (G_{i\sigma})$ = estimated general combining ability of i^{th} population female (male), and other terms defined as previously.

The standard errors of estimates were calculated in a similar fashion as previously mentioned for GCA. An estimated combining ability value was declared significant if its absolute value exceeded twice the standard error, as 95% of the t - distribution fell within approximately two standard deviations.

Results

As reported in Part I, there were significant general combining ability effects both for height and needle length in the nested population diallel cross set.

In the 7×8 polycross experiment, all sources of variation, except for needle length among replicates, were significant (Table 2). In the 8×2 polycross experiment, nurseries, replicates, and females were the significant sources of variation for both height and needle length, while nursery \times cross interactions were significant only for height. There was no difference between the two pollen mixtures.

The mean height of population hybrids produced by the nested population diallel cross ranged from 218 mm (556 ITA \times 262 GEO, abbreviations consisting of MSFG numbers and first three letters of country of origin) to 378 mm (269 ENG \times 318 BEL).

Those produced by the 7×8 polycross ranged from 160 (214 TUR \times 269 ENG) to 371 mm (240 FRA \times 318 BEL). In the 8×2 polycross, the means of the hybrids ranged from 169 (252 GER \times 213 TUR) to 271 mm (250 GER \times SPA). Overall means for the diallel, 7×8 , and 8×2 polycross experiments were 288, 254, and 221 mm, respectively.

Table 2. — Analyses of variance of height and needle length in two sets of factorial population polycrosses.

Sources of variation	7 x 8 polycross			8 x 2 polycross		
	d.f.	Mean squares for		d.f.	Mean squares for	
		Height	Needle length		Height	Needle length
Nurseries (N)	2	1059884*	3040	2	190510*	4246*
Replicates in N	3	43139*	107	3	15411*	347*
Females (F)	6	16706*	2680*	7	16401*	826*
Males (M)	7	99456*	2299*	1	863	61
F x M	40 ^a	8797*	262*	5 ^a	3947	143
N x Crosses	91 ^a	9166*	173*	24 ^a	10549*	165
Error	502	4337	95	108	2235	119

^a Loss of degrees of freedom due to imbalance in the data.

* Significant at $P < 0.05$.

The estimated general combining ability values of height for populations in the diallel cross based on female and male contributions, ranged from -30.2 (262 GEO) to 20.3 (318 BEL) (Table 3). The lowest and the highest estimates for females and males were also associated with the same populations, 262 GEO and 318 BEL, respectively. The number of relatively large estimates, exceeding twice their standard errors, were 2 for females, 6 for males, and 4 for combined estimates.

In the 7 x 8 polycross, estimated GCA of height associated with female parents ranged from -42.2 (201 NOR) to 24.2 mm (242 YUG) (Table 3). Four of these seven estimates exceeded twice their respective standard errors. GCA estimates among males ranged from -24.1 (262 GEO) to 28.4 mm (318 BEL), and only two of them were more than twice their respective standard errors. In the 8 x 2 polycross, GCA of females varied from -51.3 (262 GEO) to 43.8 mm (250 GER), and four of them were large relative to their respective standard errors (Table 3).

It may be noted that population 250 GER produced consistently positive estimates across the three sets of matings while 262 GEO produced consistently negative estimates. There were, however, a few inconsistencies between estimates for females and males; e.g., 212 FRA and 316 FRA had opposite signs between the two estimates.

In the 7 x 8 polycross, the largest specific combining ability value for height was 77.8 mm (201 NOR x 243 GRE) and the lowest was -65.7 mm (214 TUR x 269 ENG) (Table 5). Among the 55 population crosses, 31 estimates were positive and 24 were negative. Only five of these estimates were greater than twice their respective standard errors. It may be noted that the large SCA effects were associated in three cases with 318 BEL as the male parent. There were no significant SCA effects for height in the 8 x 2 polycross experiment.

For needle length, the means of population hybrids in the diallel cross ranged from 38 (556 ITA x 316 FRA) to 71 mm (318 BEL x 250 GER), with a grand mean of 52 mm.

Table 3. — General combining ability estimates (and standard errors) for height derived from three sets of polycross matings according to female and male contributions.

Population	Nested population diallel cross			7 x 8 polycross		8 x 2 polycross
	Female	Male	Combined	Female	Male	Female
212 FRA ^a	-10.5 (7.0)	23.8 (6.3)	6.6 (5.0)		-0.4 (9.2)	
250 GER	10.5 (6.6)	15.8*(7.3)	13.1*(5.2)		24.3 (12.7)	43.8*(13.3)
262 GEO	-26.0*(7.3)	-34.5*(7.3)	-30.2*(5.4)		-24.1*(9.5)	-51.4*(15.5)
269 ENG	16.8*(6.5)	5.1 (6.9)	10.9*(5.0)		-0.6 (12.9)	-13.1 (12.1)
316 FRA	6.6 (6.2)	-21.8*(6.4)	-7.6 (4.8)		-2.7 (8.3)	
318 BEL	12.8 (7.7)	27.9*(6.9)	20.3*(5.4)		28.4*(9.7)	-6.3 (17.6)
556 ITA	-10.2 (6.7)	-16.1*(6.9)	-13.1*(5.1)		-9.7 (11.8)	
243 GRE					-15.2 (10.6)	
201 NOR				-42.2*(13.6)		
214 TUR				-27.2 (14.9)		
221 TUR						2.8 (14.5)
238 FRA				-1.6 (8.0)		
240 FRA				23.8*(7.5)		
242 YUG				24.2*(8.7)		-8.5 (15.3)
245 SPA				15.7*(7.0)		
246 SPA						34.4*(11.6)
261 GEO						-26.2*(12.6)
268 SCO				7.3 (7.8)		
Grand mean:		288			254	221

^a Abbreviation of population composed of MSFG number and first three letters of country of origin; e.g., '212 FRA' is MSFG 212 from France.

* Absolute value of estimate exceeds twice standard error (range 4.8 to 17.6).

Table 4. — General combining ability estimates (and standard errors) for needle length derived from three sets of polycross matings according to female and male contributions.

Population	Nested population diallel cross			7 x 8 polycross		8 x 2 polycross
	Female	Male	Combined	Female	Male	Female
212 FRA ^a	-2.6*(1.0)	-2.7*(0.9)	-2.7*(0.7)		-1.8 (1.3)	
250 GER	8.7*(1.0)	5.4*(1.1)	7.1*(0.8)		10.2*(1.8)	9.1*(2.4)
262 GEO	-1.2 (1.1)	-2.5*(1.1)	-1.8*(0.8)		-1.9 (1.3)	-4.2 (2.8)
269 ENG	-2.3*(1.0)	4.3*(1.0)	1.0 (0.7)		5.8*(1.8)	-2.9 (2.2)
316 FRA	-3.9*(0.9)	-7.7*(1.0)	-5.8*(0.7)		-8.5*(1.2)	
318 BEL	6.3*(1.1)	3.2*(1.0)	4.7*(0.8)		-0.7 (1.4)	7.0*(3.2)
556 ITA	-4.9*(1.0)	0.0 (1.0)	-2.4 (0.8)		0.9 (1.7)	
243 GRE					4.0*(1.5)	
201 NOR				-4.2*(1.9)		
214 TUR				10.3*(2.1)		
221 TUR						1.9 (2.6)
238 FRA				-5.7*(1.1)		
240 FRA				-7.0*(1.0)		
242 YUG				9.9*(1.2)		5.8*(2.8)
245 SPA				-2.4*(1.0)		
246 SPA						-10.1*(2.1)
261 GEO						-7.7*(2.3)
268 SCO				-1.0 (1.1)		
Grand mean		52			48	50

^a Abbreviation of population composed of MSFG number and first three letter of country or origin; e.g., '212 FRA' is MSFG 212 from France.

* Absolute value of estimate exceeds twice standard error (range 0.7 to 2.8).

The means of hybrids in the 7 × 8 polycross ranged from 32 (238 FRA × 243 GRE) to 85 mm (214 TUR × 269 ENG), while their grand mean was 48 mm. In the 8 × 2 polycross, these means ranged from 39 (261 GEO × SPA) to 63 mm (250 GER × 213 TUR), and their grand mean was 50 mm.

The estimated GCA values combined within populations in the diallel cross ranged from -5.8 (316 FRA) to 7.1 mm (250 GER) (Table 4). In most cases the estimates were large

enough to exceed twice their standard error, and rather consistent with regard to males and females.

Needle length GCA estimates of female parents in the 7 × 8 polycross ranged from -7.0 (240 FRA) to 10.3 mm (214 TUR), and those of males were -8.5 (316 FRA) to 10.2 mm (250 GER) (Table 4). All the GCA estimates of females, except the one for 268 SCO, were large relative to their respective standard errors, and four of eight estimates for

Table 5. — Specific combining abilities (and standard errors) for height and needle length for the 7 × 8 factorial population polycross.

Females	Males							
	212 FRA	250 GER	262 GEO	269 ENG	316 FRA	318 BEL	556 ITA	243 GRE
	<u>Height (mm)</u>							
201 NOR	68.9*(23.5)	-40.7(72.2)	14.5 (28.7)	52.6 (36.5)	32.9(23.4)	-	33.9(52.6)	77.8(43.9)
238 FRA	-3.5 (21.6)	-23.5(24.2)	13.6 (21.3)	10.6 (23.3)	12.3(21.1)	49.6*(20.0)	-39.6(30.1)	-19.4(31.6)
240 FRA	2.6 (22.4)	12.9(25.9)	-9.5 (23.1)	-33.6 (23.2)	-22.6(20.2)	65.2*(20.8)	3.5(23.5)	-18.4(24.2)
214 TUR	-16.0 (44.0)	29.6(27.3)	48.8 (39.2)	-65.7 (72.5)	-24.8(29.0)	20.2 (52.5)	-1.3(44.6)	9.2(34.0)
242 YUG	-43.3 (24.0)	12.8(29.3)	13.9 (22.9)	15.0 (26.4)	33.6(29.1)	-9.1 (25.0)	29.7(27.7)	-52.6(27.2)
268 SCO	30.1 (22.5)	23.3(26.9)	-61.4*(29.3)	17.6 (23.7)	-13.2(20.0)	76.9*(22.7)	38.6(22.7)	34.6(23.0)
245 SPA	-38.8 (20.4)	-14.3(21.9)	-19.8 (21.8)	3.5 (22.3)	-18.2(22.4)	37.0 (20.3)	12.4(21.0)	38.2(22.3)
	<u>Needle length (mm)</u>							
201 NOR	7.0*(3.3)	16.2(10.2)	-0.6 (4.1)	7.4 (5.1)	0.1(3.3)	-	4.6(7.4)	8.1(6.2)
238 FRA	-0.0 (3.0)	-5.0(3.4)	5.4 (3.0)	-11.3*(3.3)	4.3(3.0)	13.6*(2.8)	-0.6(4.3)	-6.4(4.5)
240 FRA	-6.6*(3.2)	1.0(3.7)	0.2 (3.3)	-9.9*(3.3)	6.5*(2.8)	5.5 (2.9)	-1.1(3.3)	4.4(3.4)
214 TUR	8.4 (6.2)	-10.1*(3.8)	-5.4 (5.5)	21.1*(10.2)	-8.2 (4.1)	-4.3 (7.4)	6.4(6.3)	-8.1(4.8)
242 YUG	-6.3 (3.4)	0.3 (4.1)	0.9 (3.2)	-2.8 (3.7)	0.4 (4.1)	10.2*(3.5)	-1.4(3.9)	-1.3(3.8)
268 SCO	-0.2 (3.2)	4.8 (3.8)	-0.9 (4.1)	0.5 (3.3)	-1.1 (2.8)	6.8*(3.2)	-10.6*(3.2)	0.8(3.3)
245 SPA	-2.2 (2.9)	-7.3*(3.1)	0.4 (3.1)	-5.0 (3.1)	-2.1 (3.2)	11.0*(2.9)	2.7 (3.0)	2.4(3.1)

* Absolute value of the estimates exceeding twice the standard error.

— Missing cross.

males were relatively large. The highest GCA for females in the 8 × 2 polycross was 9.1 mm (250 GER), and the lowest was -10.0 mm (246 SPA) (Table 4). Five of these estimates exceeded twice their respective standard errors.

The range of specific combining abilities of needle length was from -11.3 (238 FRA × 269 ENG) to 21.1 mm (214 TUR × 269 ENG) for the 7 × 8 polycross (Table 5). Twenty-nine of the 55 estimates were positive and 26 were negative, and the absolute values of 13 estimates were larger than twice their respective standard errors. Again, there were no significant SCA effects for needle length in the 8 × 2 polycross experiment.

Discussion

The general combining abilities of females and males are the average contributions of individuals and pollen mixtures, respectively, in hybrid combination. The specific combining abilities, however, represent interactions between individuals and pollen mixtures on the basis of average performances of the two "parents". Since each pollen mixture contains several individuals, these interactions are expected to be mainly non-additive effects involving seed parents and the average effects of populations.

Both females and males were important sources of variation in the 7 × 8 polycross, indicating that there were real differences among general combining abilities associated with both the female parents and the population males. The estimated GCA values represent the additive deviations of the parental means from the overall mean. However, it should be noted that estimated general combining ability values of females may contain maternal effects if they were present. Perhaps the inconsistent GCA estimates for height of females and males of the 212 and 316 FRA populations may be accounted for by such maternal effects.

Because seven males in the 7 × 8 polycross were identical to males in the diallel cross and four females in the 8 × 2 polycross were identical to females in the 7 × 8 matings

and parental populations in the diallel cross, GCA estimates resulting from the three sets of mating designs were compared. The rankings of the estimated GCA values were similar for both height and needle length, especially when they were based on males (Table 6). Actual differences in GCA estimates for populations do not seem particularly large, especially if allowances are made for different sets of females. The GCA estimates for males were based on pollen mixture of three to nine individuals from the same population crossed with 14 females in the diallel cross and seven in the factorial polycross. The estimates for males may be considered as an average of the population. This consistency in the rankings indicates that GCA estimates associated with pollen mixtures are useful in screening populations for population hybridization. It is evident that the populations evaluated on the basis of males' GCA were different in their genetic make up, and that GCA associated with populations may indicate their average breeding values.

While GCA estimates for males are very consistent across the sets of matings, the estimates for females are variable. The female estimates are based on two and one trees per population in the diallel cross and factorial polycrosses, respectively. Therefore, female GCA may not be based on sufficient number of samples to represent the population. Significant variation in GCA of individuals, as demonstrated in Part I, indicated large differences among individuals within the populations.

Utilization of specific combining ability in plant breeding implies breeding for hybrid or clonal varieties, where heterosis or desirable combinations of characteristics may be the major factors under consideration. The interpopulation specific combining abilities resulting from the present experiment are rather a specific type of interaction between the seed parents and average effects of males from genetically diverse populations, and may be influenced considerably by the individual genotypes represented in the females and pollen mixtures. Therefore, inter-population specific combining abilities based on polycrosses may be taken

Table 6. — Comparisons of rankings (descending order) in GCA of populations estimated from three sets of polycross matings.

Population	Comparison between				Comparisons among				
	7x8 vs Male	Diallel			7x8 vs Male	Diallel			vs 8x2 Female
		Male	Female	Combined		Male	Female	Combined	
<u>Height</u>									
212 FRA	3	2	6	4					
250 GER	2	3	3	2	2	2	3	2	1
262 GEO	7	7	7	7	4	4	4	4	4
269 ENG	4	4	1	3	3	3	1	3	3
315 FRA	5	6	4	5					
318 BEL	1	1	2	1	1	1	2	1	2
556 ITA	6	5	5	6					
<u>Needle Length</u>									
212 FRA	5	6	5	6					
250 GER	1	1	1	1	1	1	1	1	1
262 GEO	6	5	3	4	4	4	3	4	4
269 ENG	2	2	4	3	2	2	4	3	3
316 FRA	7	7	6	7					
318 BEL	4	3	2	2	3	3	2	3	3
556 ITA	3	4	7	5					

only to indicate an average degree of non-additivity on a population basis.

Some possibilities for utilizing interpopulation specific combining abilities are indicated from the 7×8 polycross experiment. Five population SCA estimates for height were relatively large, i.e., the absolute values exceeded twice their respective standard errors; four of these estimates were positive and were larger than GCA values. Also, three of the large SCA estimates were associated with the pollen mixture of the Belgian population. For example, a desirable SCA for 3-year height growth may be identified by 240 FRA \times 318 BEL from the 7×8 factorial population polycross. It is not the highest SCA, but the progenies have better quality in other Christmas trees traits. One method of capturing these non-additive effects is to identify desirable specific combining ability pairs, and then vegetatively propagate them to produce planting stock. Perhaps, successive rooted cuttings of juvenile plants as described by ARMSON *et al.* (1980) may be used.

Regardless of these SCA effects however, it is clear that the largest differences among the hybrid families were due to additive effects of the two parents in combination, since a general lack of useful specific combining ability was found. Therefore, conventional breeding techniques that utilize general combining ability seem appropriate for breeding of Scotch pines of different provenances for juvenile height and needle length.

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Literature Cited

- ARMSON, K. A., M. FUNG and W. R. BUNTING: Operational rooting of black spruce cuttings. *J. For.*, 341–343 (1980). — GERHOLD, H. D.: Seasonal variation of chloroplast pigments and nutrient elements in the needles of geographic races of Scotch pine. *Silvae Genet.* 8: 113–123 (1959). — GERHOLD, H. D.: Minibag for tree breeding. *Silvae Genet.* 17: 31–32 (1968). — KARRFALT, R. P., H. D. GERHOLD and E. H. PALPANT: Inter-racial hybridization in Scotch pine: geographic flowering patterns and crossability. *Silvae Genet.* 24: 107–110 (1975). — KING, J. P.: Seed source \times environment interactions in Scotch pine. I. Height growth. *Silvae Genet.* 14: 105–115 (1965a). — KING, J. P.: Seed source \times environment interactions in Scotch pine. II. Needle length and color. *Silvae Genet.* 14: 141–148 (1965b). — PARK, Y. S. and H. D. GERHOLD: Population hybridization in Scotch pine (*Pinus sylvestris* L.). I. Genetic variance components and heterosis. *Silvae Genet.* 34 (in press). — SCHRUM, G. M., H. D. GERHOLD, R. F. WEST and L. S. HAMILTON: Genetic variances of Scotch pine: Environment and age effects. *For. Sci.* 21: 330–339 (1975). — STEINER, K. C.: Genetic differences in resistance of Scotch pine to eastern pine shoot borer. *Great Lakes Entomologist* 7: 103–107 (1974). — TRETJEN, G. L.: Exact and approximate tests for unbalanced random effects design. *Biometrics* 30: 537–581 (1974). — WRIGHT, J. W. and W. I. BULL: Geographic variations in Scotch pine. *Silvae Genet.* 12: 1–25 (1963).

Strobilus Production in a Clonal White Spruce Seed Orchard: Evidence for Unbalanced Mating

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Summary

Two important genetic objectives of clonal seed orchards are the minimization of self-fertilization and the production of seed reflecting the genetic diversity of all represented clones. As part of a study of the mating system of a clonal seed orchard of white spruce, *Picea glauca* (MOENCH) Voss, male and female strobilus production was investigated during two successive years. Within years, one third of the clones produced the vast majority of the male and female strobili; clonal means of male and female strobilus numbers were positively correlated; and the seed germination rate was negatively correlated with clonal male strobilus numbers. The results are concordant with the hypothesis that a few clones make a disproportionately large genetic contribution to the seed crop of a given year, and that clones which produce the largest numbers of male strobili also yield seed resulting from higher than average levels of self-fertilization. Between years, clone means of female strobilus numbers are negatively correlated, suggesting that the genetic diversity of the seed crop may be significantly increased by combining the seed harvest of the two separate years. If upheld by genetic marker studies of the mating system, the results imply that white spruce seed orchards should be monitored for strobilus production levels, and if necessary, modified mechanically or hormonally to foster more equitable flowering.

Key words: seed orchard, *Picea glauca* (MOENCH) Voss, male strobili, female strobili, mating pattern, gamete production, self-fertilization.

Zusammenfassung

Zwei wichtige Ziele von Klon-Samenplantagen sind die Minimierung der Selbstbefruchtung und eine Samenproduktion, die die genetische Vielfalt aller repräsentierten Klone widerspiegelt. Als Teil einer Studie über die Pollenverteilung bei Weißfichten [*Picea glauca* (MOENCH) Voss] in einer Klon-Samenplantage wurde die Produktion männlicher und weiblicher Blüten während zweier Jahre untersucht. Jeweils innerhalb eines Jahres produzierte ein Drittel der Klone den Großteil der männlichen und weiblichen Blüten. Die Durchschnittswerte der Anzahl männlicher und weiblicher Klon-Blüten waren positiv korreliert, und die Keimrate des Samens verschiedener Klone war mit der Anzahl männlicher Klon-Blüten negativ korreliert. Die Ergebnisse stützen die Hypothese, daß nur wenige Klone den genetischen Hauptbeitrag zur Samenproduktion eines Jahres leisten, und daß Klone, die die höchste Anzahl männlicher Blüten produzieren, Samen hervorbringen, die das Resultat überdurchschnittlich hoher Selbstbefruchtung sind. Vergleicht man die beiden Jahre, so sind die Durchschnittswerte der Anzahl weiblicher Klon-Blüten negativ korreliert, was darauf hinweist, daß die genetische Vielfalt