

Genetic Variation and Control of Intraspecific Crossability in Blue and Engelmann Spruce¹⁾

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(Received 6th January 1987)

Abstract

To assess the degree of genetic control for intraspecific crossability in blue and Engelmann spruce, two 20-parent partial diallel matings, one for each species, were conducted in the field during the spring of 1983. As measures of crossability, percent germinated and percent ungerminated-but-full seed were determined for the individual crosses. Best linear unbiased prediction (BLUP) was used to estimate the individual fixed and random effects of the mixed model, and restricted maximum likelihood (REML) methods were used to estimate general combining ability (GCA), specific combining ability (SCA), maternal effects and error variances. Engelmann spruce exhibited slightly higher intraspecific crossability than was observed for blue spruce. Viable seed yields from selfed crosses were approximately 50 percent less than control-pollinated biparental seed yields. Nonadditive sources of variation exerted major genetic influence in the production of viable seed in both species, and maternal effects were very important in the production of viable seed in blue spruce, but not so in Engelmann spruce.

Therefore, to maximize production of viable seed in seed orchards of both species, parents with desirable traits should be selected on the basis of specific cross combinations which produce proportionately high amounts of viable seed.

Key words: *Picea pungens*, *Picea engelmannii*, partial diallel, selfing, maternal effects.

Zusammenfassung

Um den Grad der genetischen Kontrolle für die intraspezifische Kreuzbarkeit bei *Picea pungens* und *Picea engelmannii* einzuschätzen, wurden für beide Arten im Frühjahr 1983 partielle Kreuzungsdiallele mit je 20 Eltern durchgeführt. Als Maß für die Kreuzbarkeit wurde der Prozentsatz gekeimter und ungekeimter, aber voller Samen bestimmt. Zur Schätzung der fixen und zufälligen Effekte in dem zugrunde liegenden gemischten Modell, wurde die Methode der Best Linear Unbiased Prediction (BLUP) angewendet, und die Restricted Maximum-Likelihood-Methode (REML) zur Schätzung der allgemeinen und spezifischen Kombinationseignung (GCA und SCA), sowie der Mutterbaumeffekte und von Fehlervarianzen.

Bei *Picea engelmannii* zeigte sich eine etwas höhere intraspezifische Kreuzbarkeit als bei *Picea pungens*. Bei Selbstungen war die Ausbeute an lebensfähigen Samen um annähernd 50% geringer als bei kontrollierten Kreuzungen zwischen verschiedenen Partnern. Bei beiden Arten waren nicht-additive Effekte (Dominanz) die wichtigste genetische Variationsursache. Mutterbaumeffekte waren sehr wichtig für die Bildung lebensfähiger Samen bei *Picea pungens*, nicht dagegen bei *Picea engelmannii*.

¹⁾ Michigan Agricultural Experiment Station Journal Article No. 12007.

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Um die Produktion an lebensfähigem Samen in Samenplantagen mit beiden Baumarten zu maximieren, sollten deshalb auf Grundlage der spezifischen Kreuzungskombination Eltern mit erwünschten Eigenschaften selektiert werden, die eine angemessene Ausbeute an lebensfähigem Samen produzieren.

Introduction

Phenotypic improvement of a trait requires an understanding of the genetic control governing the character of interest and how the environment influences its expression. Only then can appropriate selection and breeding methods be applied to the population or individuals to bring about the desired gains. In forest trees, as in all commercially important plant species, there is a wide variety of traits for which improvement is desired. In conjunction with these efforts, the improved plant material must be propagated either sexually—via seed—or asexually—via vegetative propagation—in large numbers for commercial use. Therefore, an important trait is how easily can individuals, selected on the basis of yield or some other trait, be propagated, and what is the genetic control of the propagation trait.

Many of the commercially important characters in forest trees are under polygenic control (WRIGHT, 1976). Therefore long-term gains are best realized through breeding programs and mass selection techniques which utilize the additive genetic variance associated with these traits (HALLAUER, 1981). Because of this, most forest trees in North America are propagated by seed rather than vegetatively. Also, vegetative propagation is not yet feasible on a commercial scale for many important forest tree species, especially among conifers (TIMMIS and RITCHIE, 1984; BONGA, 1981). In addition, because it takes so long for many tree species to reach commercial maturity (from 20 to 200 years), a variety of genotypes is generally more desirable than a monoculture (TIGERSTEDT, 1974).

The objectives of this study were to (1) assess the genetic variation and control of intraspecific crossability in blue and Engelmann spruce, and (2) generate full-sib progeny for future studies on the inheritance of a wide variety of traits in both species. The information on intraspecific crossability is desirable for two reasons. It will serve as a reference for studying the interspecific crossability between blue and Engelmann spruce (ERNST *et al.*, 1986). Also, it will provide information important to seed orchard selection and management techniques for the two species. Blue spruce is one of the most widely planted horticultural conifers in the world (HANOVER, 1975), and Engelmann spruce is a commercially valuable timber species in the Rocky Mountain region of North America (FOWLER and ROCHE, 1975).

Best linear unbiased prediction (BLUP), as developed by HENDERSON (1973) and described by MAO (1982), can be viewed in practice as an extension of generalized least-squares (GLS)—or more specifically, best linear unbiased estimation (BLUE)—techniques which allow for simultaneous estimation of fixed effects and prediction of random effects. While

BLUE is applicable only to fixed model analysis, BLUP was developed for analysis of mixed models which incorporate a mixture of random and fixed factors. In BLUP, *a priori* variances and covariances—from previous studies or estimates—associated with the different random factors are incorporated into the mixed model equations (MME) used to obtain the solutions. Using a maximum likelihood or restricted maximum likelihood (REML) technique such as described by SCHAEFFER (1976), new variance and covariance estimates can be obtained from the BLUP solutions, and the process is repeated until convergence. BLUP is especially well suited to unbalanced data situations, which are very prevalent in plant breeding experiments.

Materials and Methods

The Dolores River drainage in southwestern Colorado was selected as the study site because both blue and Engelmann spruce occur in the drainage, often in close proximity. Also, previous studies investigating the genetic variability in morphological and terpenoid characters of blue and Engelmann spruce have been conducted in the drainage (HANOVER, 1975; REED and HANOVER, 1983; SCHAEFER and HANOVER, 1985 and 1986).

The Dolores River was divided elevationally into five species-occupation zones, the middle three zones (2, 3 and 4) comprising the sample area for this study. Zone 2 extends from 2400 to 2590 meters (m) in elevation and blue spruce is the primary occupant relative to the occurrence of Engelmann spruce. Zone 3 extends from 2590 to 2770 m, an elevationally intermediate zone with respect to the habi-

tats of blue and Engelmann spruce. Both species occur in zone 3 and often in close proximity. Zone 4 extends from 2770 to 2960 m and is occupied primarily by Engelmann spruce relative to the presence of blue spruce. The respective parents in zones 2 and 4 represent “pure” species subpopulations and parents in zone 3 represent putative introgressed subpopulations. All parents were readily identifiable as to species.

During the spring of 1983, ten blue spruce trees each in zones 2 and 3, and ten Engelmann spruce trees each in zones 3 and 4—for a total of 40 trees, 20 of each species—were selected primarily on the basis of fecundity, accessibility and climbability to be used as parents in the controlled pollinations.

The partial diallel mating design was utilized in this study because it is theoretically efficient in regard to the amount of information per cross and accuracy of the estimates of the genetic parameters (NAMKOONG and ROBERDS, 1974; PEDERSON, 1972; GORDON, 1980). Empirical evidence has also shown the partial diallel design to be generally efficient (CHAUDHAREY *et al.*, 1977; ANAND and MURTY, 1969; MURTY *et al.*, 1967; KEARSEY, 1965). It has equal or higher efficiency and accuracy on a per cross basis than many other mating designs, including factorial and diallel, provided the number of half-sib families relative to full-sib families is maximized (NAMKOONG and ROBERDS, 1974).

The partial diallel design used in this study incorporated three intraspecific crosses—including selfs—and three interspecific crosses per parent (Figure 1). During the spring of 1983, female strobili were isolated before pollen shed. Also, pollen strobili were collected just prior to anthesis,

		ZONE II										ZONE III									
Male	Female	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	1	X					X					X									
Z	2		X					X					X								
O	3			X					X					X							
N	4				X					X					X						
E	5					X					X					X					
II	6	X					X										X				
	7		X					X										X			
	8			X					X										X		
	9				X					X										X	
	10					X					X										X
	11	X										X					X				
Z	12		X										X					X			
O	13			X										X					X		
N	14				X										X					X	
E	15					X										X					X
III	16						X					X					X				
	17							X					X					X			
	18								X					X					X		
	19									X					X					X	
	20										X					X					X

Figure 1. — A portion of the partial diallel mating design layout used to make the controlled pollinations (showing only the blue spruce intraspecific crosses here). An “X” denotes an attempted full-sib cross, and selfs are on the diagonal.

dried and the pollen extracted. Standard pollination methods for conifers were utilized and the trees were debagged following scale closure of the female strobili. The female strobili on a few of the blue spruce parents were beginning to close when pollinated, and therefore possible receptivity differences based on scale closure were recorded. Female strobili with scales completely open and fully receptive were scored as 1, strobili with up to 50 percent of the scales beginning to close were scored as 2, and strobili with more than 50 percent of the scales beginning to close scored as 3. The ages of the respective parents were also determined using increment cores taken from the bole at a height of one meter.

In the fall of 1983, control and open-pollinated cones were collected. The control-pollinated cones were kept separate by isolation bag. The cones were dried and seed extracted by hand, recording the total number of cones and the number of cones damaged by insects per isolation bag. The extracted seed was blown to separate empty and putatively full seed and both portions were counted and kept in cold storage (4° C).

During the summer of 1984, germination tests were conducted using a maximum of 30 seeds per isolation bag and for open-pollinated controls. Blue and Engelmann spruce seed do not have any special dormancy requirements (Herr, 1961). The seeds were germinated on filter paper discs in partial light, at a day-night temperature cycle of 27° C and 18° C, respectively. A solution of 2.5 g/l Captan and Benlate was used to keep the seeds moist and deter fungal growth during germination. The seeds were observed daily for 30 days, and the number of newly germinated seeds recorded each day. Upon germination, the seeds were removed and planted in 5 × 5 × 25 cm plant bands containing 3:1:1 (peat:vermiculite:perlite) soil mix. At the end of the 30-day germination period, the number of ungerminated seeds were counted and then dissected to determine the number of full but ungerminated seed and empty seed. The percentages of germinated and ungerminated-but-full seed were determined from the germination test (subsample), and these values were then extrapolated to a total seed basis—the total number of full and empty seed per isolation bag—to serve as the dependent variables in the analysis. Percent germinated seed on a total seed basis was used as a measure of intraspecific crossability because it measures the number of viable seed produced for a given cross. The percentage of ungerminated-but-full seed was determined primarily to detect postzygotic abnormalities.

The model equation used to account for the identified fixed and random factors was:

$$Y_{ijklmn} = c + L_i L_k + F_{ijm} + M_{kl} + (F_{im} M_k)_{jl} + R_m + b_a A + b_c C + b_d D + e_{ijklmn} \quad (1)$$

where:

- Y_{ijklmn} = the nth germination record (percent germinated or percent ungerminated-but-full seed on a total seed basis) of the cross between the jth female, found at location i and of receptivity class m and of age A, with male l of location k, that record (bag) having C cones and D (percent) of those cones damaged by insects;
- c = a constant common to all parents;
- F_{ijm} = the random effect of female j which resides in location i and of receptivity class m (j = 1, . . . , 20);

- M_{kl} = the random effect of male l which resides in location k (l = 1, . . . , 20);
- $(F_{im} M_k)_{jl}$ = the random interaction effect common to all records (bags) of the subclass corresponding to the cross of female j (from location i and of receptivity class m) and male l (from location k);
- $L_i L_k$ = a subclass effect combining the fixed effects of the location of female j, the location of male l, and the location interaction (i, k = 1, 2 or 3 for zones, 2, 3 and 4, respectively);
- R_m = the fixed effect of the receptivity class of female j (m = 1, 2 or 3, as described previously);
- A = the age of female j in yeears;
- b_a = the regression coefficient corresponding to the age of female j;
- C = the number of cones in isolation bag n of cross $(F_{im} M_k)_{jl}$;
- b_c = the regression coefficient corresponding to the number of cones in record (bag) n of cross $(F_{im} M_k)_{jl}$;
- D = the percentage of cones in isolation bag n of cross $(F_{im} M_k)_{jl}$ that were damaged by insects;
- b_d = the regression coefficient corresponding to the percent of insect-damaged cones in record (bag) n of cross $(F_{im} M_k)_{jl}$;
- e_{ijklmn} = the random residual (error) associated with record y_{ijklmn} .

The model equation was rewritten in matrix form to facilitate the computation:

$$y = Xb + Zu + e \quad (2)$$

where:

- y = an a x 1 vector of the germination records, where a = 91 for blue spruce and 96 for Engelmann spruce intraspecific crosses;
- b = an unknown b x 1 vector containing the different levels of the fixed factors and the regression coefficients as described previously, where b = 11 for blue spruce and 8 for Engelmann spruce crosses;
- X = a known a x b matrix, its elements denoting the levels of the fixed factors and the values of the covariates in the b vector which are associated with a given y observation (record);
- u = an unknown c x 1 vector containing the different levels of the random factors — female, male and female x male effects — where c = 98 for blue spruce and 100 for Engelmann spruce crosses;
- Z = a known a x c matrix of ones and zeros, its elements denoting the levels of the random factors in the u vector which were associated with a given y observation (record);
- e = an unknown a x 1 vector of random residuals.

The two groups of intraspecific crosses were analyzed separately.

Assumptions pertaining to the operational model were: (1) the parents were unrelated; (2) the parents of each species were from a single, randomly mating population (and therefore shared common female, male and female × male variances for each trait); and (3) the control pollinations were made at random (no selection). Based on these assumptions, the mathematical expectations of the variances were:

$$\text{Var} \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{V} & \mathbf{ZG} & \mathbf{R} \\ \mathbf{GZ}' & \mathbf{G} & \mathbf{0} \\ \mathbf{R} & \mathbf{0} & \mathbf{R} \end{bmatrix} \quad (3)$$

where:

$\mathbf{G} = I\sigma_i^2$, where I is a $c \times c$ identity matrix, and $\sigma_i^2 = \sigma_F^2, \sigma_M^2$ or σ_{FM}^2 , corresponding to variances associated with the female, male and female \times male random effects, respectively;

$\mathbf{R} = I\sigma^2$, where I is an $a \times a$ identity matrix and σ^2 the error variance associated with the random residuals;

and $\mathbf{V} = \mathbf{ZGZ}' + \mathbf{R}$.

The fixed effects and covariates were considered to be "nuisance" factors because they were included in the model only to improve the accuracy of the variance estimates associated with the random factors. Estimation of the variances was the primary focus of this study.

To solve a set of mixed model equations (MME), restrictions must be imposed in order to obtain solutions for the fixed effects. For this model, the female, male and female \times male (random) effects have unique solutions but the fixed effects are not individually estimable (unique). However, certain linear contrasts between the levels of the fixed effects are best (minimum variance of the estimator), linear, unbiased and estimable or unique (BLUE) (MAO, 1982).

The solutions for the random factors in mixed model prediction (BLUP) are unique (MAO, 1982). However, nested predictands are the sum of fixed and random effects in mixed model prediction—e.g., location i + female j , and location k + male l —and are not unique. Therefore, direct comparisons of the female, male and female \times male predictands are possible only within a common location or receptivity class. If the effects of the nested fixed factors are accounted for (i.e., adjusted in linear combination), comparisons of parents or crosses from different locations or classes are estimable or unique.

The female, male and female \times male predictands correspond to general and specific combining ability estimates of the respective parents and crosses in the partial diallel mating design. Under the assumptions that the population was sampled at random, it is randomly mating, and there is no inbreeding, linkage or epistasis, the general combining ability variance (σ_G^2) corresponds to one-fourth the total additive genetic variance ($1/4 \sigma_A^2$) for that trait, and the specific combining ability variance (σ_S^2) corresponds to one-fourth the total nonadditive (dominance) variance ($1/4 \sigma_D^2$) in the partial diallel mating design (KEMPTHORNE and CURNOW, 1961). Maternal effects were contained within the female general combining ability estimate, and therefore the maternal effect variance (σ_{ME}^2) is estimable by subtracting the male general combining ability variance from the female general combining ability variance: $\sigma_{ME}^2 = \sigma_{GF}^2 - \sigma_{GM}^2$.

Variance component estimates were obtained using iterative expectation maximization restricted maximum likelihood (EM-REML) algorithms (BANKS *et al.*, 1985) under the assumption of normality of female, male and female \times male effects. The EM-REML algorithms used were:

$$\hat{\sigma}^2 = (\mathbf{y}'\mathbf{y} - \tilde{\mathbf{b}}'\mathbf{x}'\mathbf{y} - \hat{\mathbf{u}}'\mathbf{z}'\mathbf{y}) / (n - 1) \quad (4)$$

$$\hat{\sigma}_i^2 = (\hat{\mathbf{u}}_i'\hat{\mathbf{u}}_i - \hat{\sigma}^2 \text{tr}(\mathbf{C})) / (p_i - 1) \quad (5)$$

where $\tilde{\mathbf{b}}$ and $\hat{\mathbf{u}}$ were the solutions to the MME. The vector $\hat{\mathbf{u}}_i$ corresponds to the female, male or female \times male portion of $\hat{\mathbf{u}}$ used to estimate the respective variances. The \mathbf{C} matrix is the portion of the inverse matrix from the MME pertaining to female, male or female \times male effects. The value n is the total number of records, and p_i is the number of parents or crosses associated with the female, male or female \times male effects in each set of intraspecific crosses. The variance estimates were incorporated into the MME, and new solutions for \mathbf{b} and \mathbf{u} and variance estimates were obtained. Iterations were carried out until the estimated variances changed less than one percent from the previous iteration.

Results

Viable seeds were obtained from 46 blue spruce and 56 Engelmann spruce full-sib families, out of a total 60 possible full-sib families for each species. Mean values of the percent germinated and percent ungerminated-but-full seeds from open-pollinated and control-pollinated selfed and biparental collections are given in *Table 1*. Viable seed yields for open-pollinated crosses exceeded those for control-pollinated biparental crosses by a factor of two or more. Larger yields for open-pollinated collections were expected because only one pollen parent was used in each pollination bag and each bag was pollinated only once, whereas there is a diverse mixture of pollen genotypes over an extended period of time under open-pollinated conditions. Viable seed yields for selfed crosses in both species were 80 to 90 percent less than those for open-pollinated accessions, and approximately 50 percent less than control-pollinated biparental cross yields. Slightly higher intraspecific crossability was observed for Engelmann spruce than for blue spruce among both open and control-pollinated collections (*Table 1*).

The proportion of ungerminated-but-full seed yields, compared to percent germinated values, was consistent across all pollination types for both species (*Table 1*). There was only a slight proportionate increase in full-but-ungerminated seed among the selfed crosses relative to open-pollinated and biparental crosses.

All variance component estimates converged rapidly using restricted maximum likelihood techniques. Due to the small magnitude of the ungerminated-but-full male general combining ability variance in Engelmann spruce, iterations for this variance component were terminated after a change of less than five percent rather than one percent. The variance component and narrow-sense heritability estimates are given in *Table 2*. Among the blue spruce crosses, general combining ability (GCA) variance accounted for only one percent of the total variance observed in percent germination (*Table 2*). Maternal effects and specific combining ability (SCA) variances greatly exceeded the GCA variance for this trait, accounting for 56 and 15 percent of the total variance, respectively. For percent germi-

Table 1. — Mean values of percent germinated (% Germ) and percent ungerminated-but-full (% Ungf) seed on a total seed basis for open-pollinated (Open) and control-pollinated (Self and Biparental) collections.

Species	Open		Self		Biparental	
	%Germ	%Ungf	%Germ	%Ungf	%Germ	%Ungf
Blue spruce	43.1	4.9	4.8	1.0	11.9	2.2
Engelm. spruce	48.7	8.0	9.5	2.3	19.7	3.6

Table 2. — Variance component and narrow-sense heritability estimates for production of viable and abnormal full-sib seed in blue and Engelmann spruce. Numbers in parentheses represent percentages of the respective variance components as compared to the total observed variance for that trait.

Trait ^a	Species ^b	Variance Component				h ²
		GCA	SCA	Maternal	Error	
%Germ	BS	1.890 (1)	30.992 (15)	118.482 (56)	57.796 (28)	0.04
	ES	3.987 (1)	135.299 (47)	-0.02 ^c	150.086 (52)	0.06
%Ungf	BS	2.642 (28)	1.028 (11)	-0.357 ^c	5.711 (61)	1.12
	ES	0.687 (3)	2.712 (13)	2.834 (13)	15.000 (71)	0.12

^a %Germ = percent germinated, %Ungf = percent ungerminated-but-full seed on a total seed basis.

^b BS = blue spruce, ES = Engelmann spruce.

^c Not calculated due to small, negative variance components (assumed to be zero).

nation in Engelmann spruce, GCA variance was also much smaller than SCA variance, each accounting for one and 47 percent of the total variance in this trait, respectively (Table 2). The most striking difference observed between the species was that the variance due to maternal effects was essentially zero in Engelmann spruce. These results suggest maternal influences are very important in the production of viable seed in blue spruce but are not in Engelmann spruce. In both species, sources of nonadditive (dominance) variance apparently exert a great deal more control over viable seed yields than do additive sources of genetic variation, and this is reflected in the very small narrow-sense heritability estimates for this trait in both species (Table 2). GCA and SCA variances were both relatively large for percent ungerminated-but-full seed yields in blue spruce, accounting for 28 and 11 percent, respectively, of the total variance observed in this trait (Table 2). However, GCA variance was disproportionately large, resulting in a narrow-sense heritability estimate exceeding unity. Maternal effects variance was essentially zero for this trait in blue spruce. In Engelmann spruce, GCA variance was relatively small, accounting for only three percent of the total variance. However, both SCA and maternal effects variance were moderately large and approximately equivalent in magnitude for percent ungerminated-but-full seed yields in Engelmann spruce, each accounting for 13 percent of the total observed variance (Table 2). In both species, the number of full but nonviable seed may also be under the control of nonadditive sources of variation. Only for Engelmann spruce was there any evidence of maternal effects in the production of ungerminated-but-full seed.

Product-moment correlations between the two germination traits, calculated using parental means or GCA estimates, were somewhat contrasting for the two species (Ta-

Table 3. — Product-moment correlations between percent germinated and percent ungerminated-but-full values when parents served as females or males, derived using parental means and general combining ability evaluations (BS = blue spruce, ES = Engelmann spruce).

	Females		Males	
	BS	ES	BS	ES
Parental means	0.46	-0.01	0.24	-0.15
GCA estimates	0.40	-0.30	0.44	-0.33

ble 3). The blue spruce parents—serving as either female or male—which produced higher viable seed yields also tended to produce higher ungerminated-but-full seed yields. However, for Engelmann spruce there was no correlation between the two germination traits, or possibly a slight negative association when Engelmann spruce parents served as males.

Product-moment correlations between male and female mean responses for percent germination in both species were also calculated to evaluate the consistency of male and female parental responses. Both blue and Engelmann spruce indicated only a slight degree of positive association between male and female responses on a parental mean basis ($r = 0.28$ for blue spruce and 0.23 for Engelmann spruce).

Discussion

In both blue and Engelmann spruce, the production of viable seed is primarily under the control of nonadditive (dominance) sources of genetic variation. A large amount of the total variance observed in both species for percent germination on a total seed basis was attributable to SCA variance, while very little was accounted for by GCA variance. Therefore, very little gain will be achieved in the production of viable intraspecific seed in blue and Engelmann spruce by using half-sib selection techniques. Rather, selection must be based on specific cross combinations which show high crossability rates as measured by germination tests.

In a diallel cross of seven black spruce (*Picea mariana* (MILL.) B.S.P.) parents, MORGENSTERN (1974) observed that SCA variance accounted for six times the total variance observed for percent germination than did GCA variance. Morgenstern attributed this to the fact that percent germination and percent survival, for which similar results were obtained, are fitness or survival traits, which are less likely to be controlled by additive sources of variation (FALCONER, 1960). MORGENSTERN (1974) observed in the same study that for traits related to growth and size—rate of germination, first and second-year height—additive sources of variation were of primary importance. In a six parent diallel cross of flax (*Linum usitatissimum* L.), percent germination was also controlled primarily by genes showing dominance (GUPTA and BASAK, 1983). However, both additive and nonadditive sources of variation were important in low-temperature germination percentages in cucumber (*Cucumis sativus* L.) (WEHNER, 1984), and additive sources of variation were more important than nonadditive sources in seed yield of tall fescue (*Festuca arundinacea* SCHREB.) (NGUYEN and SLEPER, 1983). It is not known why these results vary, but the species represent a wide array of plant groups.

Maternal influences were very important in the production of viable seed in blue spruce, but of no apparent importance in Engelmann spruce. Large maternal influences in seed germination have also been observed in black spruce (MORGENSTERN, 1974), Virginia pine (*Pinus virginiana* MILL.) (BRAMLETT *et al.*, 1983), and Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) (Greathouse 1966). FALCONER (1960) has interpreted maternal effects as common environmental influences of a given female parent. BRAMLETT *et al.* (1983) have further subdivided maternal effects for members of *Pinaceae* into the effect of the local environment of the female parent and the effect of the seedcoat and megagametophyte tissue—both maternally derived—of the germinating seed. The megagametophyte seed tissue in mem-

bers of *Pinaceae* is haploid and identical in genetic composition to the female egg nucleus. Therefore, the only paternal influence in the developing seed is through the embryo. Whether the observed difference between blue and Engelmann spruce in maternal influence of seed set is due only to how each species responds to the local environment or species-specific responses to seed coat and megagametophyte effects is uncertain. As BRAMLETT *et al.* (1983) suggested, the only way to test the relative importance of the two effects would be to replicate given crosses in clonally derived seed orchards located on a variety of sites. The effect of local environment only on the production of viable seed could be assessed by replicating given crosses in separate seedling seed orchards located on two or more sites, each orchard made up of the same half-sib or full-sib families. The magnitude of maternal effects should be investigated further for seed orchards of blue spruce.

The variance of female parental means for percent germination in blue spruce was 75 percent greater than that observed among male responses. In Engelmann spruce the variance of female means exceeded that observed among males by 37 percent. The large maternal influences observed in blue spruce may account for some of the increased variance observed among females of both species.

Selfing reduced viable seed yields approximately 50 percent relative to biparental controlled crosses in both blue and Engelmann spruce. This is consistent with other reports on the effect of selfing in blue spruce (CRAM, 1984). Conifers are generally intolerant of inbreeding, resulting in reduced levels of seed set and poor survival and growth of selfed seedlings (FRANKLIN, 1970; SHAW and ALLARD, 1981). While selfed crosses in both species did have lower yields of viable seed, they did not produce proportionately more ungerminated-but-full seed relative to the proportions observed among biparental controlled crosses. Therefore reductions in seed set due to selfing in blue and Engelmann spruce were probably the result of prezygotic incompatibility mechanisms that prevented normal fertilization, as has been reported for other conifers (FECHNER, 1979). Some loss of seed may occur between fertilization and early embryo development (CECICH, 1979; KOSSUTH and FECHNER, 1973; ALLEN and OWENS, 1972). Both prezygotic incompatibility and postzygotic inviability have been observed among members of *Pinaceae* (FECHNER, 1979).

For some as yet unknown reason, there was slight tendency for blue spruce parents which produced more viable seed on average to also produce greater numbers of non-viable full seed. There was no such trend—or possibly a slight reversal—observed among Engelmann spruce parents. This species difference is apparently not due to the maternal effects observed to influence seed set in blue spruce, as the trend was consistent in both species when the parent served as either male or female. Also, it does not account for the slightly higher intraspecific crossability observed for Engelmann spruce, as the proportion of ungerminated-but-full seed relative to viable seed was the same in both species for the respective pollination types.

Acknowledgements

We would like to thank the many individuals who assisted in the field and laboratory work of this project. Also, appreciation is extended to Dr.'s J. F. HANCOCK, P. MOORE and P. R. SCHAEFFER for their careful review and comments on earlier versions of this manuscript.

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Growth of Hybrid Fir Trees in Connecticut

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(Received 27th April 1987)

Summary

Crosses were made between various species of fir in the spring of 1960 and 1962. Progeny of successful crosses were sown in Connecticut in 1962 and measured for diameter, height, and crown profile when the trees were 17 years old. In addition, branch samples were collected for classification according to needle tip morphology.

In almost all cases, interspecific crosses grew better than intraspecific crosses. Crosses between species of neighboring geographic ranges tended to grow better than crosses between species of widely separated ranges.

There were growth depressions as a result of selfing, and, on average, characteristics of selfed progeny were less variable than those of hybrids. The needle tips of the hybrid crosses exhibited a range of variability. The most variable crosses in this respect were those from widely separated natural ranges.

Key words: *Abies* hybrids, height, diameter, crown area, needle tip morphology.

Zusammenfassung

Im Frühjahr 1960 und 1962 wurden mit 10 *Abies*-Arten intra- und interspezifische Kreuzungen durchgeführt. Von den erfolgreichen Kombinationen, die 1962 in Connecticut ausgesät wurden, konnten nach 17 Jahren Durchmesser, Höhe und Kronenprofil gemessen werden. Zusätzlich wurden Zweigproben für klassifikatorische Zwecke entnommen.

In fast allen Fällen wuchsen die interspezifischen besser als die intraspezifischen Kreuzungen. Kreuzungen zwischen Arten, die benachbarte Verbreitungsgebiete haben, tendierten zu besserem Wachstum als die Kreuzungen zwischen Arten mit entfernten Verbreitungsgebieten.

Als Folge der Selbstung wurden Wachstumsdepressionen und geringere Variabilität der Nachkommen gegenüber den Hybridnachkommenschaften beobachtet. Die Nadelspitzen der Hybridkreuzungen zeigten eine beträchtliche Variabili-

tät, wobei die größte Variabilität bei Hybriden aus weit entfernten Verbreitungsgebieten zu beobachten war.

Schlagwörter: *Abies*-Arten, Höhe, Durchmesser, Kronenfläche, Nadelspitzenmorphologie.

Introduction

During the spring of 1960 and 1962, control crosses were made between various species of fir growing in the George P. Brett Pinetum of Yale University at Fairfield, Connecticut.

The growth characteristics of the progeny surviving in 1981 are presented in this report. This study is part of ongoing research on the cytological, developmental, and growth characteristics of this genus. Previous studies dealt with the staminate flower phenology and pollen formation in four species (MERGEN and LESTER, 1961a), on the induction of polyploidy by colchicine in nine species (MERGEN and LESTER, 1961b), crossability (MERGEN *et al.*, 1964), and the karyotypes of seven species (MERGEN and BURLEY, 1964).

The compatibility between species and species evolution in the genus *Abies* have not been widely studied. A search of the literature provided few references on hybridization with fir beyond those described by KLAEHN and WINIESKI (1962) and by MERGEN *et al.* (1964). A citation by SILEN *et al.* (1965) showed that there was no significant genetic barrier to crossing *A. procera* and *A. magnifica* where the ranges overlap in southern Oregon and northern California. KORPEL *et al.* (1982) described 8 spontaneous hybrids of *A. sp.* including *A. borisii regis* MATTF. (*A. alba* × *A. cephalonica*), and *A. nebrodensis* MATTEI (*A. cephalonica* × *A. alba*). The former occurs in the southern Balkan Peninsula and the latter occurs in Sicily. KANTOR and CHIRA (1971, 1972) crossed *A. cephalonica* with pollen of six other species, including *A. alba*, and all crosses were compatible.

Data on total height, diameter at breast height, and crown area of putative hybrid progeny, along with observations on their needle tip morphology, are given in this report.

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