führt zu einer sterischen Hinderung der Zellulase (Schmie-
del, pers. Mitt.). Neben dem Verholzungsgrad der Kotyle-
donen spielt sicherlich auch der beginnende Sekundärstoff-
wechsel des Keimlings eine bedeutende Rolle. In Kiefern-
keimlingen werden nach dem Abwurf der Testa (Stadium
10) erste Harzkanäle nachgewiesen (Falz, 1981). Die bei
der Protoplastenisolierung dadurch möglicherweise frei-
werdenden toxischen Stoffe (z. B. Phenole) könnten Ein-
fluß auf die Lebensfähigkeit der Protoplasten haben. Bei
den Fusionsversuchen zeigen sich ebenfalls deutliche Un-
terschiede gegenüber den bisher mit elektrischem Feldim-
puls fusionierten pflanzlichen Protoplasten. So wurden im
Vergleich zu Protoplasten aus Gerste, Tomate, Tabak und
Saubohnen (Jacob et al., 1984; Zimmermann und Scheurich,
1981) sehr viel höhere Pulsspannungen und Pulslängen be-
nötigt, um Fusionen zu erreichen.

Die angeführten Ergebnisse unterstreichen somit einmal
mehr die Besonderheiten von Koniferen, die diese nicht
nur hinsichtlich der Protoplastenisolierung aufweisen.

Danksagung

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Mating System Dynamics of Lodgepole Pine in Alberta, Canada[1])

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Summary

The mating systems of three widely separated lodgepole
pine (Pinus contorta var. latifolia Dougl.) populations in
the Rocky Mountain foothills of Alberta, Canada, were
examined. Estimates of population multilocus outcrossing
rates ranged from 0.926 to 0.983. No significant differences
in outcrossing rates were found among stands, among pol-
lination years within stands, or among crown positions
within trees. However, a tentative temporal trend is sug-
gested in which selection against inbred seed is occurring
over time in the seed pool retained on the tree. Significant
heterogeneity was found among single-tree multilocus out-
crossing rate estimates in one stand.

Key words: Mating System, Outcrossing Rate, Pinus contorta var.
latifolia.

Zusammenfassung

Es wurde das Paarungssystem von 3 weit voneinander
getrennten Populationen von Pinus contorta var. latifolia
Dougl. in den Vorbergen der Rocky Mountains in Alberta,
Kanada, untersucht. Schätzungen der Fremdbefruchtungs-
rate anhand von Multilocusanalysen in den Populationen
ergaben Werte von 0,926 bis 0,983. Keine signifikanten
Differenzen in der Fremdbefruchtungsrate wurden zwi-
schen Beständen, Befruchtungsjahren des gleichen Bestan-
des oder Positionen innerhalb der Krone eines Baumes ge-
funden. Es wird jedoch auf einen zögernden, zeitlichen
Trend hingewiesen, bei dem eine Selektion gegen ingezüch-
teten Samen mit der Zeit im auf dem Baum verbleibenden
Samenbestand vorkommt. Significante Heterogenität wur-
de zwischen Einzelbäumen in einem Bestand gefunden,
die als Fremdbefruchtungsrate mit Hilfe der Multilocus-
analyse untersucht wurden.

Introduction

The mating system is an important determinant of plant
population genetic structure (Clegg, 1980). It is the genetic
link between generations and determines the initial zygotic
frequency distribution of each generation. Individuals of
a highly outcrossed species generally have higher levels of
heterozygosity than those of self-fertile species (Brown,
1979). Inbreeding can also induce gametic-phase disequili-
brium even among loci on different chromosomes (Allard,
1975; Mitton et al., 1981).

Knowledge of the mating system is also of practical sig-
nificance for forest tree breeders and those involved in re-
forestation. Selfed progeny of most coniferous forest species
display significant inbreeding depression in the form of
decreased survival and growth (Franklin, 1970; Sorensen
and Miles, 1982). In addition, the presence of inbreeding
violates some of the assumptions made in analysis of wind-
pollinated progeny tests, leading to overestimation of ad-

ditive genetic variance and genetic gain (Namkoong, 1966; Squillace, 1974).

Several methods have been employed in the study of mating systems of forest trees. Earlier estimates of outcrossing rates were largely based on mutant phenotype frequencies (Squillace and Kraus, 1963; Fowler, 1965; Franklin, 1971a; Sorensen, 1973) or on percentages of filled seed (Franklin, 1971b). With the advent of gel electrophoresis, allozyme polymorphisms have become commonly used gene markers for examining the mating systems of forest trees, because they provide many marker loci and alleles per locus, increasing the statistical precision of estimates (Moran and Brown, 1980; Fripp, 1982; Yeh et al., 1983; King et al., 1984; Farris and Mitton, 1984; Epperson and Allard, 1984). Single-locus (Brown et al., 1975; Shaw and Allard 1982; Cheliak et al., 1983) and multilocus models (Green et al., 1980; Ritland and Jain, 1981; Shaw et al., 1981) have been developed to estimate mating system parameters from allozyme data. These methods give an estimates of t, the proportion of viable progeny due to random outcrossing (outcrossing rate).

Gymnosperms are particularily convenient for isoenzyme studies. The haploid megagametophyte tissue is genetically identical to the maternal (gametic) contribution to the embryo. Therefore, by comparing the isoenzyme phenotype of the megagametophyte to that of the corresponding embryo, one may infer the paternal contribution at a given locus. This information may then be applied to an analysis of the mating system.

Coniferous species with serotinous cones provide a good opportunity to study temporal variation in the mating system, because they can retain seed within their cones for a number of years. Therefore, it is possible to collect seed from a number of different pollination years simultaneously.

In this study, both spatial and temporal aspects of the mating systems of three widely separated populations of lodgepole pine (Pinus contorta var. latifolia Dougl.) in Alberta, Canada were examined through allozyme analysis.

The objective was to determine whether the mating system of lodgepole pine varied among stands, among trees within a stand, among crown positions within a tree, and over time.

Methods

Seed Collection

Cones were collected from three widely separated, natural even-aged lodgepole pine stands in the Rocky Mountain foothills of Alberta, Canada, during the summer of 1983 (Table 1). A square grid of 49, 10m × 10m plots was laid out in each stand. Sample trees were selected in the 25 plots falling on the median and diagonal axes. The lodgepole pine tree closest to the center of the plot and having an adequate cone crop was sampled.

Five subsamples of cones were collected from most sample trees. Bulk upper crown (UC) and bulk lower crown (LC) cone subsamples were taken randomly with respect to cone age from upper third and lower third of the reproductive crown. In addition, cones from 1981, 1979, and 1977 pollinations were collected from the upper portion of the crown. It was not possible to collect 1977 samples from a few trees. Seed was extracted and stored separately by tree and subsample at 4° C until required for analysis.

Electrophoretic Methods

Seed was germinated in petri dishes until the radicle had emerged at least 2mm. The haploid megagametophyte and diploid embryo from approximately 10 seeds per subsample in each family were individually homogenized in 50μl of extraction buffer (Yeh and Layton, 1979) and assayed for six allozyme loci using starch gel electrophoresis (12.5% Connaught Hydrolysed Starch) (Table 2). The loci were chosen because they were consistently well resolved, polymorphic loci in which the embryo genotype could be interpreted unambiguously when compared to the corresponding megagametophyte. Inheritance and linkage relationships for these loci in lodgepole pine have previously been determined (Conkle, 1981; Yeh, unpublished data, Research Branch, British Columbia Forest Service, Victoria).

Table 1. — Description of lodgepole pine collection sites in the Rocky Mountain foothills of Alberta.

Population	Latitude	Longitude	Elevation (m)	Average Age (years)	Basal Area (m² / ha)
Robb	53°10'	117°15'	1300	84.2	11.85
Nordegg	52°30'	116°04'	1100	80.1	10.89
Cochrane	51°40'	115°12'	1300	89.3	12.55

Table 2. — Enzyme systems assayed in seed tissue of lodgepole pine.

Locus	E.C. Number	Buffer System[1]	Stain Reference
Aconitase (ACO)	4.2.1.3.	A	Yeh and O'Malley (1980)
Alcohol dehydrogenase (ADH)	1.1.1.1.	B	Shaw and Prasad (1970)
Isocitrate dehydrogenase (IDH)	1.1.1.42.	A	Yeh and O'Malley (1980)
Phosphoglucomutase (PGM)	2.7.5.1.	A	Yeh and O'Malley (1980)
Phosphoglucose isomerase (PGI-2)	5.3.1.9.	C	Yeh and O'Malley (1980)
6-Phosphogluconic dehydrogenase (6PG-1)	1.1.1.44.	C	Yeh and O'Malley (1980)

[1] Buffer systems:

A Tris-citrate pH 7.0 gel buffer; Tris-citrate pH 7.0 electrode buffer (Siciliano and Shaw, 1976). Run at 200 volts.

B Tris-citrate pH 8.5 gel buffer; lithium borate pH 8.1 electrode buffer (Ridgeway et al., 1970). Run at 300 volts.

C L-histidine-tris pH 7.0 gel buffer; Tris-citrate pH 7.0 electrode buffer (Florence, 1981). Run at 200 volts.

Table 3. — Population single-locus outcrossing estimates (t_s) and sample sizes for upper (UC) and lower (LC) crown, 1981, 1979, and 1977 pollinations, and pooled subsamples for three lodgepole pine populations in Alberta.

Population	Subsample	n	ACO	ADH	IDH	6PG-1	PGI-2	PGM	Mean[3]
Robb	UC[2]	250	0.864[1]	0.795[1]	-	1.052	1.033	-	0.936
	LC[2]	250	0.960	0.768[1]	0.917	-	1.033	1.025	0.941
	1981	240	0.940	1.037	1.009	0.918	1.043	-	0.989
	1979[2]	245	0.861[1]	0.892[1]	1.018	1.036	0.834	1.017	0.943
	1977[2]	250	0.899	1.401[1]	1.017	1.043	1.042	1.033	1.073
	Pooled[2]	1235	0.904[1]	0.911[1]	0.992	1.010	0.997	1.023	0.973
Nordegg	UC	250	0.978	-	1.017	-	-	1.033	1.009
	LC	250	1.055	-	1.025	-	-	-	1.040
	1981	240	0.856[1]	0.963	1.017	-	-	1.009	0.961
	1979	250	0.933	0.974	-	-	-	-	0.953
	1977	240	0.927	1.003	1.026	-	-	1.017	0.993
	Pooled[2]	1230	0.954	0.980	1.017	-	-	1.012	0.991
Cochrane	UC	240	0.871[1]	0.850	-	0.886	-	0.971	0.895
	LC[2]	247	0.880[1]	0.884[1]	-	1.091	-	-	0.952
	1981	241	0.944	0.934	-	0.948	-	0.948	0.944
	1979	240	0.993	0.972	-	1.005	-	0.943	0.975
	1977	240	0.932	0.971	-	0.973	-	-	0.959
	Pooled	1208	0.922[1]	0.928[1]	-	0.987	-	0.989	0.957

[1] Significant (P < 0.05) departure from H_0: ts = 1.0 (test not made for means).
[2] Significant (P < 0.05) heterogeneity among estimates within subsample.
[3] Unweighted mean over loci.

Statistical Methods

Genotypes of individual mother trees were inferred at the six loci based upon allozyme segregation in 35 to 50 megagametophytes per tree (mean = 49). With 35 megagametophytes the probability of misclassifying a maternal genotype at any one locus is exceedingly small (5.82 × 10^{-11}).

Single-locus (t_s) and multilocus (t_m) population estimates of outcrossing rates and outcross pollen pool allele frequencies were obtained using the maximum likelihood procedures and computer programs of NEALE and ADAMS (1985). Maximum likelihood estimators for t_s and t_m were described in SHAW and ALLARD (1982) and GREEN et al. (1980), respectively. Because of program limitations, to estimate t_s for loci with four alleles (ACO and ADH), it was necessary to combine the two least common alleles into a third synthetic class. Since a minimum of two maternal genotypic classes and a polymorphic pollen pool were required to estimate t_s, it was not possible to obtain estimates for all loci in all subsamples. A likelihood ratio test (RAO, 1973) was used to test the hypotheses H_0: $t_s = 1$ and H_0: $t_m = 1$ for the population estimates. Single-tree estimates of t_m were obtained for a random sample of six trees per population using data pooled over crown positions and years. Differences among outcrossing rates of populations, crown positions, pollination years and individual trees were tested using an H (homogeneity) test (RAO, 1973).

Both t_s and t_m estimators rely upon the mixed-mating model (FYFE and BAILEY, 1951; SHAW and ALLARD, 1982), which assumes that each of the observed progeny is a result of either a random outcross (with probability t) or self-fertilization (with probability $1 - t = s$), that no selection occurs between germination and analysis of progenies, that the genotype of the maternal parent does not influence the probability of an outcross progeny, and that allele frequencies in the outcross pollen pool are homogeneous among maternal parents (SHAW et al., 1981). Independence among loci in the outcross pollen pool must also be assumed for multilocus estimation.

Wright's fixation index (F) (WRIGHT, 1951), a measure of the deviation of observed heterozygote frequency from that expected under Hardy-Weinberg equilibrium, was calculated for filial populations as:

$$F = 1 - H/h,$$

where H is the observed proportion of heterozygous individuals and h is the proportion of heterozygotes expected under panmixia. Expected heterozygosity was calculated as:

$$h = 1 - \Sigma p_i^2,$$

where p_i is the estimated frequency of the ith allele at the locus.

All tests of significance were conducted at the $p < 0.05$ level.

Results

Estimates of t_s ranged from 0.768 to 1.401 (Table 3), with significant heterogeneity among loci in five of the 15 subsamples and two of the three populations when subsamples were pooled. Population estimates of t_m ranged from 0.858 to 1.022 (Table 4), with no significant differences among estimates for different pollination years or crown positions within a population. Despite the lack of significant dif-

Table 4. — Population multilocus outcrossing estimates, t_m (standard errors in parentheses), for upper (UC) and lower (LC) crown, 1981, 1979, and 1977 pollinations, and pooled subsamples for three lodgepole pine populations in Alberta.

Subsample	Population					
	Robb		Nordegg		Cochrane	
UC	0.858[1]	(0.059)	1.014	(0.074)	0.899[1]	(0.052)
LC	0.874[1]	(0.061)	1.022	(0.073)	0.907	(0.054)
1981	0.948	(0.061)	0.935	(0.049)	0.907	(0.057)
1979	0.961	(0.061)	0.984	(0.047)	0.977	(0.051)
1977	1.007	(0.054)	0.984	(0.046)	0.934	(0.053)
Pooled	0.934[1]	(0.027)	0.983	(0.021)	0.926[1]	(0.024)

[1] significant (p < 0.05) departure from H_0: $t_m = 1.0$.

Population	Tree Number	t_m	
Robb	7	0.641	(0.277)
	11	0.739	(0.150)
	17	1.090	(0.222)
	23	0.993	(0.140)
	24	0.875	(0.116)
	39	1.025	(0.078)
Nordegg[1]	1	1.064	(0.139)
	7	0.745	(0.158)
	11	0.840	(0.120)
	13	1.188	(0.126)
	17	0.679	(0.114)
	24	1.146	(0.398)
Cochrane	4	0.796	(0.109)
	18	1.117	(0.120)
	27	0.962	(0.099)
	28	0.788	(0.134)
	32	1.110	(0.272)
	43	0.901	(0.053)

[1] estimates significantly heterogeneous (p $<$ 0.05) among trees within population.

ferences, UC subsamples consistently had slightly lower t_m estimates than LC subsamples. No trends were apparent among pollination years. Due to the lack of heterogeneity among subsamples, estimates based on data pooled across subsamples within a population were used as the best population estimates of t_m. These estimates ranged from 0.926 to 0.983 and were not significantly heterogeneous. Estimates of t_m for the Cochrane (0.926) and Robb (0.934) populations were significantly different from 1.0, while the estimate for the Nordegg population (0.983) was not.

Although there was a wide range in individual tree estimates of t_m within a population (e.g., 0.641 to 1.090 in the Robb population), significant heterogeneity among estimates occurred only in the Nordegg population *(Table 5)*.

No significant deviations from Hardy-Weinberg expectations occurred at ACO, IDH, 6PG-1, PGI-2 or PGM in any of the filial subsamples. Significant deviations were observed in two subsamples (Robb UC and Robb 1977) at the ADH locus. When subsamples were pooled, significant deviations occurred only at ADH in the Robb population and

ACO in the Cochrane population. All significant deviations from Hardy-Weinberg genotype frequencies were due to an excess of homozygotes, as indicated by the positive F values in these cases *(Table 6)*. Another trend that is suggested by the F estimates at both ACO and ADH is an apparent decrease in F from UC to LC subsamples within a population.

Discussion

The results of this study indicate that lodgepole pine populations in the Rocky Mountain foothills of Alberta are highly outcrossing. These results are in close agreement with those of EPPERSON and ALLARD (1984), in which t_m for two populations of lodgepole pine in northeastern Washington did not differ significantly from 1.0. High outcrossing rates have been found in the majority of conifers examined (CHELIAK et al., 1985; KING et al., 1984; MITTON et al., 1981; SHAW and ALLARD, 1982).

Significant heterogeneity among single-locus outcrossing estimates has often been observed in predominantly outcrossing plants (BROWN and ALLARD, 1970; BROWN et al., 1975). Since in this study all estimates for a subsample or population were made from the same set of embryos, the observed variability must be due either to random variation or violations of the assumptions of the mixed-mating model (SHAW and ALLARD, 1982). Multilocus estimates of outcrossing are likely to be more accurate than single-locus estimates, because the utilize a larger amount of information and are less susceptable to violations of assumptions of the mixed-mating model. Single-locus estimates of outcrossing are expected to be biased downward by consanguineous matings other than selfing (ELLSTRAND and FOSTER, 1983; SHAW and ALLARD, 1982). Such a bias was not evident in this study, in which the majority of means of single-locus estimates were larger than the corresponding multilocus estimates. This observation suggests a lack of family structuring within the maternal populations studied, contrary to the common assumption that most conifers have some degree of family structuring within populations (LIBBY et al., 1969). Relationships among maternal trees were not directly measured in this study, and their dispersion would likely have masked any family structure. However, LEE (1985)

Table 6. — Estimates of WRIGHT's Fixation Index (F) for filial subpopulations from three lodgepole pine populations in Alberta.

Population	Subsample	Locus					
		ACO	ADH	IDH	6PG-1	PGI-2	PGM
Robb	UC	0.067	0.123[1]	-0.016	-0.033	-0.017	-0.008
	LC	0.040	0.101	0.107	-0.025	-0.018	-0.012
	1981	0.031	0.006	-0.017	-0.026	-0.023	-0.011
	1979	0.084	0.073[1]	-0.032	-0.032	-0.019	-0.004
	1977	-0.031	-0.019	-0.025	-0.027	-0.025	-0.016
	Pooled	0.038	0.060[1]	-0.011	-0.028	-0.020	-0.010
Nordegg	UC	-0.018	0.071	-0.010	-0.016	-0.009	-0.014
	LC	-0.023	0.014	-0.016	-0.018	-0.013	-0.012
	1981	0.080	0.053	-0.014	-0.013	-0.011	-0.006
	1979	0.061	0.061	-0.012	-0.010	-0.012	-0.010
	1977	-0.005	0.052	-0.019	-0.013	-0.002	-0.012
	Pooled	0.019	0.055	-0.014	-0.014	-0.009	-0.011
Cochrane	UC	0.090	0.075	–	-0.055	-0.006	0.061
	LC	0.051	0.066	-0.004	-0.049	-0.004	-0.036
	1981	0.072	0.116	-0.005	0.105	-0.015	-0.030
	1979	-0.087	0.122	–	-0.039	–	0.105
	1977	0.031	-0.015	-0.002	-0.054	-0.011	-0.041
	Pooled	0.032[1]	0.072	-0.002	-0.004	-0.007	0.012

[1] significant deviation (p $<$ 0.05) from H_0: F = 0.0.

found evidence of family structure within these same stands.

The differences among single-tree t_m estimates in the Nordegg population may be due to variable levels of self fertility. A prefertilization mechanism is unlikely, since cytological studies in lodgepole pine have shown that self-pollination does not reduce pollen germination, growth of the pollen tube or fertilization capacity (HAGMAN, 1964). Polyzygotic polyembryony, a post-fertilization factor, has been reported in the genus *Pinus* (DOGRA, 1967), providing an opportunity for selection among embryos of unequal vigor during early embryo development (SORENSEN, 1982). Therefore, variation among trees in the numbers of embryonic recessive lethals and deleterious alleles, or even in the degree of polyzygotic polyembryony, may account for the observed tree-to-tree variation in t_m. Such heterogeneity may complicate the analysis of data from wind-pollinated progeny tests. Progeny of trees with low outcrossing rates may contribute to an overestimation of additive genetic variance and potential genetic gains and, if inbreeding depression is pronounced, could conceivably result in a maternal tree, which is genetically superior in other respects, being excluded from a breeding program.

Higher levels of outcrossing have been observed in seed collected from the upper crown than that from the lower crown in Douglas-fir *(Pseudotsuga menziesii* [MIRB.] FRANCO) (SHAW and ALLARD, 1982), jack pine *(Pinus banksiana* LAMB.) (FOWLER, 1965), loblolly pine *(Pinus taeda* L.) (FRANKLIN, 1971b), and Scots pine *(Pinus silvestris* L.) (SARVAS, 1962). This is usually attributed to a higher concentration of male strobili in the lower crown. The contradictory, although non-significant, results reported here, with lower outcrossing rates in the upper crown, may be more accurately described as temporal rather than spatial, since we observed many more older, weathered cones in the lower crown than the upper crown and 1981 cones were rare in the lower reproductive crown. Of course, many of these old, weathered cones from the lower crown position likely occupied an upper crown position when originally formed.

Temporal heterogeneity has been found in mating systems of other forest tree species. CHELIAK et al. (1985) found evidence of a temporal trend in jack pine, a closely related conifer, in which selfing apparently decreased with cone age. A similar trend was found by MORAN and BROWN (1980) for a population of alpine ash *(Eucalyptus delegatensis* R. T. BAK.), where significant differences in outcrossing rates of three seed crops were found, with the oldest crop having the highest outcrossing rate and the most recent having the lowest. Since both species retain their seed for many years, these temporal shifts have been attributed to selection against selfs in the embryo populations. The apparent decrease in F from upper to lower crown observed in the lodgepole pine populations studied here indicates such a mechanism may be operating, but may be obscured partially by the presence of some new seed in the bulk lower crown subsamples and some relatively old seed in the bulk upper crown subsamples. If selection against inbred seed is occurring over time in the seed pool retained on the tree, it is not strong enough to become evident during the time interval between the 1977 and 1981 cone subsamples. Since there was only a small initial proportion of selfed embryos available on which such a mechanism could operate, the time period necessary for the trend to be observable would likely be increased, and the chance of such a trend ever having statistical significance would be remote.

The high outcrossing rates observed in these lodgepole pine populations may help maintain genetic variation that may be required by a species to cope with a spatially and temporally heterogeneous environment (CAMPBELL, 1979; HEDRICK et al., 1976). Of practical significance to foresters, the high observed outcrossing rates indicated that wind-pollinated lodgepole pine seed from extensive, even-aged stands with densities similar to these populations may be used for reforestation purposes in the foothills with little risk of inbreeding depression. Although statistically significant tree-to-tree variation in outcrossing rates was encountered in only one of three stands studied, it may be wise to proceed with caution when using estimates of additive genetic variance and gain obtained through wind-pollinated lodgepole pine progeny tests. The magnitude of the tentative temporal trend observed in this study is not great enough to suggest that preference be given to older seed for reforestation or testing purposes.

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

By H. D. Gerhold and Y. S. Park[2])

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