1979). In *G. arborea* the system appears to operate after the zygote is formed. The evidence for the post-zygotic incompatibility system is based on: (a) collapsed embryos in fruits resulting from self-pollinated flowers, and (b) retention of fruits on self-pollinated flowers well beyond the time it takes the pollen tubes to reach ovules. One might argue that in the strict sense the system should be termed a self-sterility rather than a self-incompatibility system, but it should be noted that complex post-zygotic incompatibility systems involving pollen/ovule interactions are not unknown in angiosperms (DE NETTANCOURT, 1977), and appear to be quite common in tropical plants (BAWA, 1979).

Self-incompatibility has also been reported in teak (*Tectona grandis* L. f.), perhaps the only other tree species in the *Verbenaceae* for which information on the breeding system is available (HEDEGART, 1976). The extent of self-incompatibility was reported to vary from 96 to 100%, although no explanation was offered concerning how these numbers were obtained.

This self-incompatibility in *G. arborea* in part defines the options available in future breeding programs. For example, open-pollinated seed orchards designed to take advantage of the general combining ability of superior individuals can be established, without incurring the problems associated with selfing. Self-incompatibility also precludes the development of homozygous inbred lines, and subsequent formation of hybrid varieties.

A major concern in tropical forest tree-breeding is the extent to which specialized pollination systems can be manipulated when the species is cultivated far away from the range of its pollinators (BAWA, 1976). Although we have not compared the fruit set of *G. arborea* trees in Costa Rica with those that occur in the natural range of the species, apparently the bees of the Guanacaste region, at least, can serve as pollen vectors.

In short, *G. arborea* is self-incompatible but despite obligate outcrossing, changed pollination conditions are not detrimental to fruit set in Costa Rica.

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Effects of Inbreeding and Genetic Variances in a Natural Population of Tamarack (Larix laricina (Du Roi) K. Koch) in Eastern Canada

By Y. S. PARK and D. P. FOWLER[1])

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Summary

A controlled pollination experiment in tamarack was done in four subpopulations of a natural stand in central New Brunswick, Canada, to define population structure. Estimates of relatedness among subpopulation trees were obtained by comparing self-pollination, neighbor, distant, long-distant, and unrelated polymix matings. The average relationship coefficient among neighbor (average 22 m between trees), distant (59 m), and long-distant (135 m) trees was found to be 0.167, 0.115, and 0.0, respectively. Self-pollination resulted in a significant reduction in seed set. Estimates of lethal equivalents for the selfed trees averaged 10.8 and ranged from 3.0 to 19.3. Relatively large specific combining ability variances were obtained for early seedling heights; however, interpretation and application of the variance components are complicated by the degree of relatedness among neighboring trees. Possible improvement procedures are discussed.

Key words: *L. laricina*, population structure, relationship, inbreeding, lethal equivalents, variance components, disconnected diallels and factorials.

Zusammenfassung

Ein Versuch mit kontrollierter Bestäubung wurde bei vier Subpopulationen von *Larix laricina* (DU ROI) K. KOCH eines natürlichen Bestandes in Zentral-New Brunswick, Canada, durchgeführt, um die Populationsstruktur zu definieren. Schätzwerte für den Verwandschaftsgrad von Bäu-

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[1]) Maritimes Forest Research Centre
Canadian Forestry Service
Department of the Environment
P O. Box 4000, Fredericton, N. B. E3B 5P7

men in Subpopulationen wurden durch den Vergleich von Selbstbestäubungen, Nachbar-, Entfernten-, Weitentfernten- und Polymix-Nichtverwandten-Kreuzungen erzielt. Der durchschnittliche Verwandtschaftskoeffizient zwischen Nachbar- (durchschnittlich 22 m zwischen den Bäumen), entfernten (59 m) und weitentfernten (135 m) Bäumen betrug 0,167; 0,115 bzw. 0,0. Selbstbestäubung bewirkte eine signifikante Reduktion im Samenansatz. Schätzwerte für Letaläquivalente geselbsteter Bäume betrugen im Durchschnitt 10,8 und reichten von 3,0 bis 19,3. Relativ große spezifische Kombinationseignungsvarianzen wurden nur für die frühen Sämlingshöhen erreicht, jedenfalls wird die Interpretation und Applikation der Varianzkomponenten durch den Verwandtschaftsgrad benachbarter Bäume kompliziert. Es wird diskutiert, wie züchterisch am besten vorgegangen werden kann.

Introduction

Tamarack, *Larix laricina* (Du Roi) K. Koch, has the widest range of any American conifer (Roe, 1957). Its range extends from Newfoundland to Alaska and from the northern limit of tree growth, south to Maryland and West Virginia. Tamarack although usually considered a bog or swamp species is capable of growing under a variety of climatic and edaphic conditions. In the southern part of its range it is usually confined to bogs or swamps but further north it occupies a wide range of sites.

Tamarack is one of the most rapid growing of the northeastern American conifers (Roe, 1957) and is reported to out-grow other native conifers in New York (Littlefield, 1939), the Lake States (Roe, 1952), New Brunswick (Maccgillivray, 1967), Ontario (Mead, 1978), and West Virginia (Cech *et al.*, 1977). Although planted on only a limited scale in the past, tamarack is now receiving attention as a potentially important reforestation species. It is one of four species chosen by the New Brunswick Tree Improvement Council for their tree improvement program (Coles, 1979).

There is little information available on the genetic variability of tamarack. Jeffers (1975) reported significant differences in 8-year survival, height, and possibly in susceptibility to late frost among 13 and 18 provenances planted at two locations in the Lake States. Local provenances and some distant provenances ranked among the best for survival and height growth. Cech *et al.* (1977), in a test of 16 tamarack provenances in West Virginia, found significant differences among provenances in survival and height and diameter growth. Growth was negatively correlated with latitude of origin but evidently not related to elevation. They suggested that the most northern provenance tested (Ontario) was from a different base population.

Significant differences among stands from within a a single geographic area (Wisconsin) with respect to budset, root pattern, and total height of 2-year-old seedlings were found by Rehfeldt (1970). He reported a high degree of variability within progenies derived from pollen mixes and inbreeding depression in progenies from self-pollination. Based on these findings, he suggested that tamarack is genetically highly variable at the intrapopulation level. High intrapopulation variation was also reported by Jeffers (1975).

An understanding of the genetic structure of natural populations is necessary for the development of effective breeding strategies. In this study, we examined the genetic structure of a natural tamarack population by means of a controlled mating experiment. In particular, the effects of inbreeding and the spatial distribution of related trees were examined.

Materials and Methods

The study was done at the Acadia Forest Experiment Station (AFES) in central New Brunswick where tamarack occurs in mixture with other conifers and intolerant hardwoods on the better drained sites, and in pure stands or in mixture with black spruce (*Picea mariana* (Mill.) B. S. P.), on poorly drained sites. Four accessible subpopulations of tamarack separated from one another by 1 to 6 km, were chosen. Within each subpopulation a center point was established and 11 trees were selected for controlled matings: five "neighbor" trees located within 25 m of the center point; three "distant" trees from between 25 and 75 m, and three "long-distant" trees from between 75 and 150 m.

Controlled pollinations were done in spring, 1974. The pollination procedures were similar to those used for white spruce and are described in detail by Nienstaedt and Teich (1971). The five neighbor trees of each subpopulation served as both seed and pollen parents whereas the distant and long-distant trees served only as pollen parents. The neighbor trees of each subpopulation were crossed in all possible combinations, including self-pollinations, to provide complete diallel sets of crosses. Also each neighbor tree received pollen from the distant and long-distant tree of the respective subpopulations, a polymix from one different subpopulation, and from open pollination. The average distance between seed parents and neighbor, distant, and long-distant pollen parents was 22 m, 59 m, and 135 m, respectively.

The isolation bags containing the cones were harvested in August 1974. Each neighbor tree had the potential to provide 13 different families, including one from selfing, four from neighbor crosses, three each from distant and long-distant crosses and one each from the polymix and open-pollinations. The entire mating scheme resulted in a set of disconnected complete diallels with four subpopulations (*Table 1*) and two sets of disconnected factorials with three pollen parents from each set of distant and long-distant trees (*Table 2*).

The seeds were extracted, cleaned, and full and empty seeds separated by flotation in 95% ethyl alcohol. Numbers of full and empty seeds were recorded. In January 1976, up to 50 full seeds from each family were divided into two equal replications and germinated in petri dishes in a germinator at about 22^{0} C. Germination was recorded over four weeks and the germinated seeds were transplanted into number 8 styroblocks in a 2-replication greenhouse experiment. In the greenhouse, the seedlings were grown under an 18-hour photoperiod in a 1:1:1, peat: loam: vermiculite mix. Seedling height was recorded in late June 1976 when the seedlings were about 5 months old. At this time, the seedling were transplanted into a 2-replication nursery experiment at AFES at 15 × 15 cm spacing. Within each replication, families were planted at random in subpopulation blocks. Total seedling height was measured in September 1977 at the end of the second growing season.

Relative self-fertility (R) of each of the 20 neighbor trees was calculated:

$$R = \frac{\text{percent full seed from selfing}}{\text{percent full seed from outcrossing (polymix)}}$$

and used to estimate the number of embryonic lethal equivalents per zygote following Morton *et al.* (1956):

$$2B = -4 \ln R$$

where B is the average number of lethal equivalents per gamete. Inbreeding in the preceeding generation was assumed to be zero for this calculation.

Disconnected diallel analyses of variance for seedling heights were performed excluding selfed progenies, using the model:

$$Y_{hlijk} = \mu + R_h + S_l + g_{li} + g_{lj} + s_{lij} + m_{li} + m'_{lj} + r_{lij} + e_{hlijk},$$

where Y_{hlijk} is k^{th} observation of i^{th} and j^{th} cross of l^{th} subpopulation grown in h^{th} replicate; μ is overall mean; R_h is h^{th} replicate effect; S_l is l^{th} subpopulation effect; g_{li} (g_{lj}) is general combining ability effect of i^{th} (j^{th}) parents within l^{th} subpopulation; s_{lij} is specific combining ability effect of i^{th} and j^{th} parents within l^{th} subpopulation; m_{li} (m'_{lj}) is maternal effect of i^{th} female in l^{th} subpopulation such that $m_{li} = -m'_{lj}$; r_{lij} is reciprocal effect of i^{th} and j^{th} cross within l^{th} subpopulation; and e_{hlijk} is random error component. Similarly, disconnected factorial analysis combined over distant and long-distant males was performed, fitting the model:

$$Y_{hlijk} = \mu + R_h + S_l + F_{li} + M_{lj} + FM_{lij} + RS_{hl} + e_{hlijk},$$

where F_{li} is effect of i^{th} female in l^{th} subpopulation; M_{lj} is effect of j^{th} male in l^{th} subpopulation; FM_{lij} is interaction effect of i^{th} and j^{th} parents in l^{th} subpopulation; and RS_{hl} is interaction effect of h^{th} replication and l^{th} subpopulation.

For both disconnected diallel and factorial analyses, all the terms are assumed to be random effects. Because of imbalance in the data, general linear model analyses were performed. Expected mean square coefficients were obtained by the abbreviated Doolittle forward solution as explained by Gaylor *et al.* (1970) and Namkoong (1979).

Results

In general, the percent of sound seed was low, averaging only 19.2% for all pollinations and subpopulations combined. Subpopulations differed in percent sound seed, with the highest (28.1%) significantly greater than the other three (13.7, 15.1, and 19.2%). As expected, percent sound seed following self-pollination was low (1.6%) compared to the polymix (24.1%) and open-pollination (38.9%). Although differences among crosses with neighbor, distant, long-distant, and polymix males were not statistically significant, percent sound seed increased as the distance between parents increased (*Table 3*).

Percent sound seed (*Table 4*) from self- and polymix pollination of the neighbor trees varied from 0.0 to 7.6% and 3.1 to 45.4%, respectively. Relative self-fertility estimates ranged from 0.0 to 0.47. Based on these estimates and procedures used by Morton *et al.* (1956) and Sorensen (1971), the number of lethal equivalents per zygote varied from 3.0 to 19.3 with a mean of 10.8 (*Table 4*).

Table 1. — Mating scheme of four subpopulation disconnected diallel crosses including selfs and reciprocals.

		I[1]					II					III					IV				
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
I	1	s	x	x	x	x															
	2	x	s	x	x	x															
	3	x	x	s	x	x															
	4	x	x	x	s	x															
	5	x	x	x	x	s															
II	1						s	x	x	x	x										
	2						x	s	x	x	x										
	3						x	x	s	x	x										
	4						x	x	x	s	x										
	5						x	x	x	x	s										
III	1											s	x	x	x	x					
	2											x	s	x	x	x					
	3											Δ	x	s	x	x					
	4											x	x	x	s	x					
	5											x	x	x	x	s					
IV	1																s	x	x	x	Δ
	2																x	s	x	x	Δ
	3																x	x	s	x	x
	4																x	x	x	s	x
	5																x	x	x	x	s

[1] : Roman numerals indicate subpopulation number.

s : Self-pollination.

Δ: Pollination unsuccessful, isolation bags lost.

Table 2. — Mating scheme of four subpopulation disconnected factorial crosses with distant and long-distant pollen parents and of polymix and open- pollination.

		Distant pollen												Long-distant pollen												Mix[2]	O.P.[3]
		I[1]			II			III			IV			I			II			III			IV				
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X		
I	1	x	x	x										x	x	x										x	x
	2	x	x	x										x	x	x										x	x
	3	x	x	x										x	x	x										x	x
	4	x	x	x										x	Δ	x										x	x
	5	x	x	x										x	x	Δ										x	x
II	1				x	x	x										x	x	x							x	x
	2				x	x	x										Δ	x	x							x	x
	3				x	x	x										x	x	x							x	x
	4				x	x	x										x	x	x							x	x
	5				x	x	x										x	x	x							x	x
III	1							x	x	x										Δ	x	x				x	x
	2							x	x	x										x	x	x				x	x
	3							x	x	Δ										x	x	x				x	x
	4							x	Δ	x										x	x	x				x	x
	5							x	x	x										x	x	x				x	x
IV	1										Δ	x	Δ										Δ	x	x	x	x
	2										x	x	x										x	x	x	x	x
	3										x	x	x										x	x	Δ	Δ	Δ
	4										x	x	x										x	x	x	x	Δ
	5										x	x	x										x	x	x	x	x

[1] Roman numerals indicate subpopulation number.

[2] Polymix of different subpopulation.

[3] Open-pollinated.

Δ Pollination not successful, isolation bags broken from tree.

Table 3. — Mean distances between parents, percent sound seed, percent germination and percent early survival with respective standard deviations in parentheses.

Cross type	Distance (m)	Percent sound seed	Percent germination	Percent survival
Self	0	1.63 (1.83) A[1]	80.84 (25.27) A[1]	63.2 (25.96) A[1]
Neighbor	22	18.37 (11.97) B	91.39 (9.97) B	79.2 (13.64) B
Distant males	59	19.05 (11.84) B	90.37 (9.62) B	73.9 (16.50) B
Long distant males	135	21.61 (15.07) B	89.70 (9.62) B	74.1 (16.97) B
Pollen mix	3260	21.51 (13.24) B	90.10 (7.87) B	75.8 (17.74) B
Open pollination	-	38.94 (14.54) C	84.33 (13.33) A	75.0 (12.35) B
Overall mean		19.19	89.36	75.1

[1]) Mean separation by cluster analysis [Scott, A. J. and M. Knott (1974), and Gates and Bilbro (1978)]. Means followed by the different letters fall into different, discrete, non-overlapping groups.

Table 4. — Percent of sound seeds obtained from various types of crosses relative self-fertility, and lethal equivalents.

Subpopulation	Female	Cross type of: Self	Neighbor	Dist.	Long Dist.	Mix	O.P.	R[1]	2B[2]
I	1	3.21	12.54	27.75	27.06	23.58	51.04	.136	8.0
	2	2.08	17.27	23.59	35.55	40.76	46.72	.051	11.9
	3	2.16	38.15	37.91	37.17	31.57	54.03	.069	10.7
	4	4.28	25.03	27.37	34.58	35.72	25.53	.120	8.5
	5	1.11	31.45	36.36	55.08	28.54	54.26	.039	13.0
	Mean:	2.57	24.89	30.60	37.89	32.04	46.32	.083	10.4
Subpopulation mean =			28.11						
II	1	.28	11.85	18.96	29.50	36.86	22.84	.008	19.3
	2	.11	14.67	14.34	12.76	13.22	27.23	.008	19.3
	3	1.21	18.88	23.50	12.46	3.13	65.97	.387	3.8
	4	7.63	25.75	21.47	23.64	16.21	51.97	.471	3.0
	5	.54	24.70	19.55	19.14	12.69	35.52	.043	12.6
	Mean:	1.95	19.17	19.56	19.50	16.42	40.71	.183	11.6
Subpopulation mean =			19.15						
III	1	.14	15.74	11.22	16.67	9.00	39.63	.016	16.5
	2	.76	7.78	11.42	16.54	13.71	43.29	.055	11.6
	3	.55	10.41	13.19	7.01	10.21	42.66	.054	11.7
	4	.38	6.85	12.24	8.53	26.01	18.71	.015	16.8
	5	2.65	11.88	9.00	17.38	18.67	29.03	.142	7.8
	Mean:	.90	10.53	11.41	15.23	15.57	34.66	.056	12.9
Subpopulation mean =			13.72						
IV	1	2.43	22.80	26.72	29.57	45.37	51.03	.054	11.7
	2	.53	7.97	5.90	8.11	3.51	14.13	.151	7.6
	3	.91	8.56	5.66	3.27	-	-	-	-
	4	.00	16.37	7.08	7.37	5.63	-	.000	-
	5	1.63	35.20	31.41	32.24	34.29	27.36	.048	12.1
	Mean:	.92	18.18	15.35	16.11	22.20	30.84	.050	10.5
Subpopulation mean =			15.09						
Overall		1.63	18.37	19.05	21.61	21.51	38.94	.068	10.8
Mean Separation[3]		A	B	B	B	B	C		

[1] R = relative self-fertility,

$$\frac{\text{Percent full seed from selfing}}{\text{Percent full seed from outcrossing (polymix)}}$$

[2] Lethal equivalents per zygote.

[3] Mean separation by cluster analysis.

Germination of sound seed averaged 89.4% over all pollinations and ranged from 80.8 to 91.4% (*Table 3*). Seeds resulting from self-pollination and open-pollination had lower germination (80.8 and 84.3%, respectively) than seeds from the unrelated polymix pollinations (90.1%). Excluding the self- and open-pollinations there were no significant differences in germination among the types of pollination.

Seedling survival averaged 75.1% for all pollinations. Survival of seedlings derived from self-pollination was significantly lower (63.2%) than survival of seedlings from all other pollination types (*Table 3*). The data do not suggest a relationship between survival and distance between parents.

Average seedling height after five months in the greenhouse and at the end of the second growing season in the nursery was 38.0 and 83.5 cm, respectively. Differences in seedling height between subpopulations were small and ranged from 36.9 to 40.4 cm in the greenhouse and from 83.0 to 87.8 cm in the nursery. Progenies from self-pollinations were significantly slower growing than those from other pollination types (*Table 5*). Seedling height after five months in the greenhouse was not related to distance between parents. However, after two growing seasons in the nursery there was an indication that seedling height was positively related to distance between parents (*Table 5*).

Table 5. — Mean heights of seedlings in greenhouse and nursery by type of cross.

Cross type	Heights of seedlings in Greenhouse (cm)	Heights of seedlings in Nursery (cm)
Self-pollination	34.6	72.0
Neighbor	38.5	85.2
Distant Males	38.7	86.0
Long Distant Males	38.4	86.5
Pollen Mix	38.4	87.6
Open Pollination	39.0	86.1
Mean	38.0	84.5

Table 6. — Variance components of greenhouse and nursery heights for disconnected diallel cross.

Variance components		Greenhouse Value	Greenhouse VC %	Nursery Value	Nursery VC %
Subpopulations	(σ^2_p)	0.22	0.22	0.99	0.30
GCA	(σ^2_g)	1.07	1.05	3.04	0.92
SCA	(σ^2_s)	3.62	3.55	26.11	7.87
Maternal	(σ^2_m)	-0.08	0.00	-1.51	0.00
Reciprocal	(σ^2_r)	3.04	2.98	18.61	5.61
Error	(σ^2_e)	93.93	92.20	283.10	85.30
Total		101.88	100.00	331.85	100.00

Table 7. — Variance components of greenhouse and nursery heights for disconnected factorial cross, combined over distant and long distant males.

Variance components		Greenhouse height Value	Greenhouse height VC %	Nursery height Value	Nursery height VC %
Subpopulations (S),	σ^2_p	-0.12	0.0	-14.64	0.0
Females (F),	σ^2_F	1.99	3.41	13.46	3.92
Males (M),	σ^2_M	1.96	3.35	5.61	1.64
F x M,	σ^2_{FM}	2.09	3.58	26.95	7.85
Replicate x S,	σ^2_{RS}	1.73	2.96	18.92	5.51
Error	σ^2_e	50.66	86.70	278.32	81.08
Total		58.43	100.00	343.26	100.00

Variance components for early seedling development are presented in *Tables 6* and *7*. Genetic-environmental error accounts for most of the variation at the end of the greenhouse stage and, to a lesser degree, at the end of the nursery stage.

In the disconnected diallel, specific combining ability (SCA) variance is the largest genetic source of variance at the greenhouse (3.55%) and nursery (7.87%) stages, whereas general combining ability (GCA) variance is only about 1% at both stages. Variance components for reciprocal effects are also important, accounting for 2.98 and 5.61% of total variance at the greenhouse and nursery stages, repectively. Variance due to maternal effects is negligible and variance due to subpopulations is small for both the greenhouse and nursery materials.

Female by male interaction variance is the largest source of genetic variance among families tested by the disconnected factorial analysis. Among these materials variance due to subpopulations is negligible. The magnitude of genetic sources of variance, i.e., σ^2_F, σ^2_M and σ^2_{FM}, are similar (about 3.5%) at the greenhouse stage but change during the nursery stage so that variance attributable to female parents is more than twice that due to male parents.

Discussion

Genetic Load

On average, the proportion of empty seeds resulting from selfpollination is 98%, which is about 1.3 times higher than that from unrelated mix pollinations. Similar increases in the proportion of empty seeds following self-pollination have been reported for many coniferous species (Mergen *et al.*, 1965; Franklin, 1971; Koski, 1971; Sorensen, 1971; Coles and Fowler, 1976) and are generally attributed to the increased frequency of deleterious genes in a homozygous condition.

Estimates of genetic load for individual trees ranged from 3.0 to 19.3 and averaged 10.8 embryonic lethal equivalent per zygote. These estimates are based on the assumption of one embryo per ovule. Polyembryony, although not studied in tamarack, is common in conifers. Thus, these estimates must be considered as minimum estimates. Although there are ways of estimating embryonic lethals based on multiple fertilizations (Bramlett and Popham, 1971), Sorensen (1971) considers estimates based on a single fertilization per ovule to be most reasonable because they offset a tendency to overestimate embryonic lethals at high levels of inbreeding, i.e., selfing.

Tamarack progenies from self-pollination had lower germination and survival than progenies from out-crossings. However, the effects of selfing on germination and survival are small compared to the effect on percent full seed. This is in agreement with results from studies with other conifers in which genetic load is expressed prior to seed maturity (Sarvas, 1968; Koski, 1973).

Coefficients of Relationship

In this study, the relationship among trees is measured in terms of Wright's (1922) coefficient of relationship *(r)*, which is twice Malecot's (1948) coefficient of parentage assuming that parents are not inbred. Coefficients of relationship are estimated from the percent sound seed data presented in *Table 3*. A two-point regression equation, in which r for self-pollination is 1 and r for unrelated mix-pollination is 0, was solved using observed percent sound seed to provide estimates of r. The coefficients of relationship decreased as the distance between parents increased. The coefficient among neighboring trees, those growing within an average of 22 m of each other, is .167. Coefficients for parents separated by an average of 59 and 135 m are .115 and zero, respectively. These estimates are lower than those reported by Coles and Fowler (1976) for two stands of white spruce, *(Picea glauca* (Moench) Voss), in which the coefficients were $r = 0.23$ and 0.30 for trees separated from each other by less than 100 m. Morgenstern's (1972) estimate of $r = 0.16$ for stands of black spruce in southern Ontario is more comparable to the results reported here.

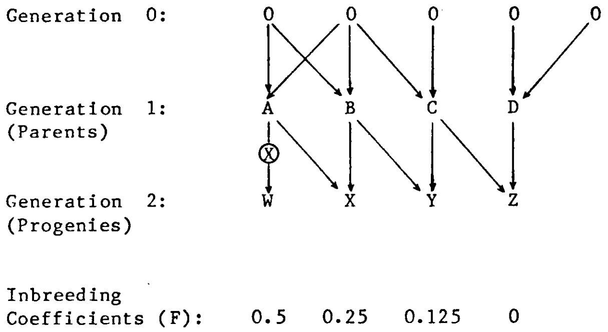

Figure 1. — Neighboring inbreeding model under a simplified assumption: No inbreeding is assumed in generation 1, i.e., A and B family relationships are established in generation 1, i.e., A and B are full-sibs, B and C are half-sibs, and D is not related. Mating of individuals in generation 1 produces inbred progenies: W, A, and Y are inbred by selfing, full-sibbing, and half-sibbing, respectively, and Z is non-inbred.

When inbreeding in the preceeding generation is assumed to be zero, the inbreeding coefficient of a progeny is half the coefficient of relationship, i. e., $F = 0.05\ r$. Under this simplifying assumption, average inbreeding coefficients for the progenies of neighbor and distant crosses are .084 and .058, respectively, and those of long-distant crosses are zero. Using the model presented in *Figure 1*, for example this level of inbreeding among neighboring trees could occur if 66.8 and 33.2% of the matings are half-sibs and unrelated, respectively. However, other proportions of related, or unrelated, matings are quite possible. Similarly when the average distance between parents is increased to 59 m, the level of inbreeding found in this study could result from 46.0% half-sib mating and 54.0% unrelated matings.

Variance Components

The prime purpose for estimating variance components is to provide information on covariances of relatives, and, if they are derived from a random mating population, the covariances can readily be translated into additive and dominance genetic variances. Difficulty in interpreting variance components in this study arises because of relatedness within the study population, necessitating a modified interpretation compared to one that assumes panmixia. Further investigations such as those of Hinkelmann (1969 and 1971) are required to obtain accurate estimates of additive and dominance genetic variances.

A breeding program directly applying these variance components thus fosters some reservation. Despite the shortcomings in interpreting variance components when the parents are partially inbred, they can be useful in comparing different kinds of genetic effects. Interpretation of variance components in this study was similar to that of Cockerham (1963). General combining ability variance, σ^2_g, *(Table 6)* is the average effects of parents and is interpreted as additive effects. The interaction variance, σ^2_s; is the variation in the reciprocal sums after σ^2_g is subtracted, and is interpreted as non-additive effects. The variance component for material effects, σ^2_m, is the average material effect of each parent, and the variance component for reciprocal effect, σ^2_r, is the variation in the reciprocal differences not ascribable to σ^2_m.

Variance among subpopulations is small in this study, and consequently, the data have been pooled for the four subpopulations. SCA variance in the disconnected dialled analysis is high compared to that of GCA variance, especially for nursery height. This suggests relatively high non-additive gene action, although relatedness among the parents may cause an over-estimation. The reason for the relatively large reciprocal effect and the absence of maternal effects is more nebulous. It is possible that some non-genetic factor such as low temperature during the later stages of sporogenesis has resulted in differential selection within males but has had no measurable effect on females.

In the disconnected factorial analysis the largest source of genetic variance is the interaction between females and males and again suggests that non-additive variance is relatively important. Assuming that non-additive effects will continue to be the most important source of genetic variance throughout the life of tamarack, breeding programs should utilize non-additive variance.

During the early stages of seedling growth, maternal and cultural effects may mask genetic effects. In this study, percent of genetic components for seedling height increased with seedling age when compared with total variance. The genetic components, as determined by the disconnected diallel analysis ($\sigma^2_{p} + \sigma^2_{g} + \sigma^2_{s} + \sigma^2_{m} + \sigma^2_{r}$), increased from 7.8 to 14.7% for greenhouse and nursery measurements, respectively. Similarily, the increase in genetic components for the disconnected factorial analysis ($\sigma^2_{p} + \sigma^2_{F} + \sigma^2_{M} + \sigma^2_{FM}$) from greenhouse to nursery was from 10.3 to 13.4% of the total variance.

Implications

Inbreeding in tamarack, as in most other coniferous species, results in an increase in the proportion of empty seeds produced and in reduced germination, survival, and growth. In the mass-production phase of any tamarack improvement program, matings between related trees should be minimized. In a program based on selection of phenotypically superior trees in natural stands, the selected trees should be separated by a minimum of 100 m.

To date, the study reported here has not provided any information on the genetic control of quality characters such as stem form, branching habit or wood quality in this species. The study does, however, suggest that non-additive genetic variance must be considered if growth rate of this species is to be effectively improved. To capture the non-additive components of genetic variance it will be necessary to identify individuals which have high specific combining ability and to use them to mass produce improved progenies. Vegetative propagation of superior genotypes is an effective means of capturing the additive and non-additive components of variance. Vegetative propagation also provides a means of overcoming the low seed set typical of tamarack (USDA Forest Service, 1974) and other larches (Ekberg *et al.*, 1968; Hall, 1979). It is possible that the mass production of cuttings from juvenile materials as decribed by Armson *et al.* (1980) could be used effectively as a method to mass produce genetically improved tamarack.

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