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Probability of Equal Mating in Polymix Pollinations of Loblolly Pine (Pinus taeda L.)

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Summary

The assumption that each pollen parent has an equal probability of mating is the basis for using polymix pollinations to estimate general combining abilities. If the above assumption is true, then any particular ovule has an equal chance of being fertilized by any particular pollen in the polymix providing that an equal number of viable pollen grains of each pollen are used in the polymix and that gametic selection is not taking place. Pollinations with a polymix consisting of nine pollens were performed on four clones. Electrophoresis techniques were used to resolve allozymes at 14 isozyme loci.

Deviations from probability of equal mating by each pollen parent in the polymix crosses were tested in two ways: by examining the allozyme frequencies at individual loci and by attempting to identify the male parent of each seed produced.

Of the 56 allozyme frequencies examined only one was significantly different from the expectation. This is actually fewer than would be expected on the basis of equal probability of mating.

The distribution of male parents in the polymix crosses was also consistent with the equal probability of mating hypothesis.

On the basis of these results it was concluded that general combining ability and other statistics produced from polymix crosses are valid with regard to the equal probability of mating assumption.

Key words: allozymes, isozymes, polycross, Hardy-Weinberg.

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Zusammenfassung

Die Annahme, daß jeder Pollen die gleiche Wahrscheinlichkeit hat, als Pollenspender an Kreuzungen beteiligt zu sein, ist die Basis für die Nutzung von Polymix-Bestäubungen zur Schätzung der generellen Kombinationseignung.

Falls die o. a. Annahme zutrifft, hat jede einzelne Eizelle die gleiche Chance von jedem einzelnen Pollen des Pollenmix' befruchtet zu werden, vorausgesetzt, daß im Pollenmix die gleiche Anzahl keimfähiger Pollenkörner eines jeden Pollens enthalten ist, und daß keine Gametenselektion stattfindet. Vier Klone wurden mit einem Pollenmix aus neun verschiedenen Pollen bestäubt. Die Elektrophorese-Technik wird benutzt, um die Allozyme an 14 Isoenzym-Loci zu bestimmen.

Abweichungen von der Wahrscheinlichkeit einer gleichen Beteiligung eines jeden Pollenelters an den Polymix-Kreuzungen wurden auf zwei Arten getestet: Durch die Untersuchung der Allozymfrequenzen an individuellen Loci und durch den Versuch, den Pollenelter eines jeden einzelnen produzierten Samenkornes zu identifizieren.

Von den 56 untersuchten Allozymfrequenzen zeigte nur eine einzige eine signifikante Abweichung von der Erwartung. Diese ist geringer als aufgrund der gleichen Kreuzungswahrscheinlichkeit erwartet wurde.

Die Verteilung der männlichen Eltern stimmte in den Polymix-Nachkommen mit der Paarungshypothese überein.

Auf der Basis dieser Resultate wird gefolgert, daß die generelle Kombinationseignung und andere aus Polymix-Kreuzungen abgeleitete Statistiken hinsichtlich gleicher Paarungswahrscheinlichkeit richtig sind.

Introduction

When polymix matings are combined in a complementary mating design with concurrent half-diallel matings, an elegant system for evaluating family performance and producing advanced generation selections can be developed (van Buijtenen, 1984). The progeny tests produced by the polymix matings are used to estimate general combining abilities (GCA), which are employed as criteria for roguing and as a basis for making advanced generation selections.

The assumption upon which the GCA estimates obtained from polymix progeny tests are based, is that any particular ovule has an equal chance of being fertilized by any particular pollen in the polymix. This is true under the provision that an equal number of viable pollen grains of each pollen are used in the polymix and that gametic selection is not taking place. Preferential mating would cause the GCA estimates to be inaccurate, resulting in deviations from the expected genetic gain.

The use of allozymes to estimate population parameters has been documented in a review by Mitton (1983). Moran and Griffin (1986), working with radiata pine, concluded that an unequal contribution of pollen occurred in polymix and single crosses involving only one female parent and several combinations of four pollen parents. Their discussion focused on gametic selection and pollen competitiveness as the possible cause of unequalness. However, Wiselogel (1985), found no indication of selection in single and polymix crosses at the gametic or zygotic level using four female and nine pollen parents. Neither, was there evidence of unequal pollen fecundity of pollens in the polymix. A regression of mean seeds per cone produced by the individual crosses of each pollen in the polymix to the number of times each pollen was observed in the polymix with each female parent produced an R^2 of zero and a non-significant f-statistic.

The objective of this study was to test the assumption that each pollen has an equal probability of mating in polymix matings of loblolly pine. Two methods were used to test this assumption: (1) Allozyme frequencies were determined for each isozyme locus in the pollen parent population and compared with the observed allozyme frequencies in the embryos contributed to by the pollen parents and (2) the pollen parents were determined for all seed and their distribution was compared to that expected under the random mating assumption using a chi-square test.

Materials and Methods

In the spring of 1982, four clones were successfully pollinated with a polymix consisting of equal volumes of nine pollens used in the Texas Forest Service "good mix"; 5—30, 7—34, 11—45, 12—8, 14—20, 15—39, S1PT10, S6PT2, and S6PT3. The clones used as female parents were chosen on the basis of flower production and their unrelatedness to each other and the pollen parents. All the female clones, BA1—2, BA3F10—20, S2PT12, and S3PT7, are located at the Arthur Temple Research Area near Fastrill, Texas. Pollen viability, determined by counting germinated pollen grains on an agar nutrient media, indicated that no significant differences existed among pollen parents.

Seed handling and preparation procedures follow those described by Conkle *et al.* (1982), except for stratification which followed the procedure described by Barnett (1976). Starch gel electrophoresis techniques followed those described by Jech and Wheeler (1984), and the enzyme nomenclature was modeled after that of Yeh and Layton (1979).

Each pollen parent's allozyme phenotype was derived from a sample of 10 megagametophytes produced by that pollen parent. The allozyme phenotype of the male gamete contributed by a pollen parent to an embryo was determined by electrophoretic analysis of the seed's megagametophyte and its corresponding embryo. The megagametophyte consists of haploid tissue representing the gametic contribution of the female parent, thus, the gametic contribution of the pollen parent could be deduced by comparing the allozymes of the embryo with the megagametophyte.

Goodness-of-fit chi-square tests were performed for the allozyme frequency data for each locus and on the number of matings contributed to each pollen parent on the basis of the observed male gametes. A sample of 80 seeds was used from the BA3F10—20, S2PT12, and S3PT7 polymix matings and of 39 seeds from the BA1—2 polymix mating. The null hypothesis tested for the allozyme frequency data was Ho : $p_0 = p_1$, where p_0 is the allozyme frequencies for the polymix and p_1 is the allozyme frequency of the pollen parent contribution in the progeny. The allozyme frequencies of the pollen parents in the polymix were used as the expected, p_0 because under the equal probability of mating assumption each pollen parent would contribute equally to the progeny population.

The most widely accepted method employed to test Mendelian segregation, is the goodness-of-fit chi-square test:

$$X_i^2 = \sum_{j=1}^{n} \left(\frac{(f_{1ij} - f_{2ij})^2}{f_{1ij}} \right)$$

where

f_{1ij} = the frequency of the jth allozyme at the ith isozyme locus in the pollen parent population and

Table 1. — The isozymes assayed, their abbreviations, and number of allozymes observed.

Isozymes	Abbreviation	E.C.[1]	# allozymes observed
Aconitase	Aco	3.1.3.2	3
Glucose-6-phosphate dehydrogenase	G6pd	1.1.1.49	2
Glutamate dehydrogenase	Gdh	1.4.1.2	2
Glycerate-2-dehydrogenase	G2dh	1.1.1.29	2
Malate dehydrogenase 2	Mdh 2	1.1.1.37	2
Malate dehydrogenase 3	Mdh 3	1.1.1.37	2
Malic enzyme	Me	1.1.1.40	2
Phosphoglucomutase	Pgm	2.7.5.1	2
6-Phosphogluconate dehydrogenase 1	6pgd 1	1.1.1.44	2
6-phosphogluconate dehydrogenase 2	6pgd 2	1.1.1.44	2
Phosphoglucose isomerase 1	Pgi 1	5.3.1.9	2
Phosphoglucose isomerase 2	Pgi 2	5.3.1.9	2
Phosphomannose isomerase	Pmi	5.3.1.8	2
Shikimate dehydrogenase	Skdh	1.1.1.25	3

¹) Enzyme commission designations.

Table 2. — The nine pollen parent's multilocus alozyme phenotypes and the number of possible gametes that can be produced by each pollen parent, based on their allozyme phenotypes.

Isozymes	Pollen Parents								
	5-30	7-34	11-45	12-8	14-20	15-39	S1PT10	S6PT2	S6PT3
Aco	1/2	2/2	1/3	2/2	1/2	2/2	2/2	2/2	2/3
G6pd	1/1	1/1	1/1	1/1	1/1	1/3	1/1	1/1	1/1
Gdh	1/1	1/1	1/1	1/1	1/2	1/1	1/2	1/2	1/1
G2dh	1/2	2/2	2/2	1/2	1/1	1/1	1/2	1/2	1/1
Mdh 2	1/1	1/1	1/2	1/1	1/1	1/1	1/1	1/1	1/1
Mdh 3	1/2	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/2
Me	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/1	1/2
Pgm	1/1	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1
6Pgd 1	1/2	1/1	1/2	1/2	1/2	1/2	1/1	2/2	2/2
6Pgd 2	3/3	3/3	1/3	3/3	3/3	3/3	3/3	3/3	1/3
Pgi 1	1/2	1/1	1/1	1/2	1/2	2/2	1/2	1/1	1/2
Pgi 2	1/1	2/2	1/2	1/2	1/2	2/2	2/2	1/1	2/2
Pmi	1/1	2/2	1/2	1/1	1/2	1/1	1/1	1/1	1/1
Skdh	1/5	1/1	2/5	1/1	1/2	1/1	1/1	1/1	2/5
No. of unique Gametes	128	8	256	32	256	8	16	4	64

f_{2ij} = the frequency of the jth allozyme at the ith isozyme locus in the progeny population with (number of classes) — 1 — (the number of parameters estimated from the data) degrees of freedom (Hartl, 1980).

The null hypothesis $H_0 : E=O$ tested the difference between the expected (E) number of matings of each pollen in the polymix assuming equal probability of mating with those observed, O. The determination of parentage was performed by multilocus allozyme phenotypes. Each pollen parent was expected to contribute equally to the progeny population, so the expected number was calculated by dividing the number of seeds sampled by the number of pollen parents. In the cases where a pollen contribution could not be traced back to an individual pollen parent in the polymix each pollen parent which could have possibly contributed the gamete was given equal credit, i.e. if 5—30 and 7—34 both could have contributed a gamete which fertilized a sample seed each would receive 1/2 credit for the mating.

Results and Discussion

Seed Collection

The four polymix crosses produced sufficient numbers of seed for electrophoretic analysis. Only BA1—2 × polymix did not produce the desired 80 seed; however, the 39 seed germinated from the cross were enough to obtain information on allozyme segregation.

Isozymes

Of the 14 screened isozymes all were polymorphic (*Table 1*). The key for interpreting the zymograms observed for these isozymes is presented in *Figure 1*. Their inheritance and characteristics are discussed in detail by Wiselogel (1985). These polymorphic isozyme loci were used to determine multilocus allozyme phenotypes of the pollen parents (*Table 2*), the female parent allozyme contribution to the seed, and the allozyme phenotypes of the pollen that fertilized the seed. Observed pollen and allozyme frequencies were obtained from the pollen data.

Allozyme Frequency

Of the 56 allozyme frequency chi-squares performed, only the Pmi locus in BA1—2 produced allozyme frequencies that varied significantly, at the .05 level, from those expected under equal probability mating. If none of the isozyme loci are in linkage disequilibrium, then five out of every 100 chi-squares performed should be significant by chance³).

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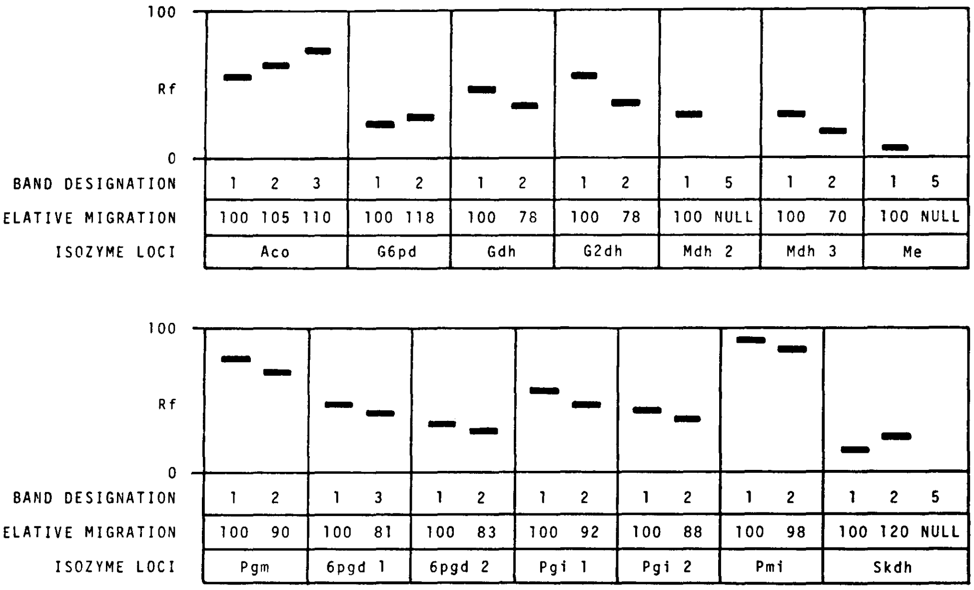
³) No linkage was deducted among the 14 loci in an analysis conducted recently.



BAND DESIGNATION	1 2 3	1 2	1 2	1 2	1 5	1 2	1 5
RELATIVE MIGRATION	100 105 110	100 118	100 78	100 78	100 NULL	100 70	100 NULL
ISOZYME LOCI	Aco	G6pd	Gdh	G2dh	Mdh 2	Mdh 3	Me

BAND DESIGNATION	1 2	1 3	1 2	1 2	1 2	1 2	1 2 5
RELATIVE MIGRATION	100 90	100 81	100 83	100 92	100 88	100 98	100 120 NULL
ISOZYME LOCI	Pgm	6pgd 1	6pgd 2	Pgi 1	Pgi 2	Pmi	Skdh

Figure 1. — Isozyme zymogram Key.

Table 3. — Observed pollen frequencies with partial credit for gametes which could have been produced by more than one pollen parent.

Pollens	Female Parent			
	BA1-2	BA3F10-20	S2PT12	S3PT7
5-30	5.833 (5)[1]	14.250 (11)	7.834 (6)	16.333 (12)
7-34	4.000 (4)	6.000 (4)	11.000 (9)	5.500 (5)
11-45	8.000 (8)	7.250 (6)	8.000 (7)	6.500 (6)
12-8	4.833 (3)	9.933 (5)	13.750 (8)	13.167 (10)
14-20	7.000 (5)	16.650 (4)	12.250 (9)	11.000 (7)
15-39	2.000 (2)	5.733 (4)	6.416 (4)	7.500 (4)
S1PT10	2.000 (2)	6.433 (2)	6.750 (3)	7.666 (3)
S6PT2	0.834 (0)	7.584 (5)	4.500 (3)	6.334 (3)
S6PT3	4.500 (4)	6.167 (4)	9.500 (7)	6.000 (5)
Total	39.000 (33)	80.000 (65)	80.000 (56)	80.000 (54)

[1]) Number of positively identified pollen gametes.

Taking this into account, having only one significant chi-square test at the .05 level out of 56 indicates that the observed allozyme frequencies do not deviate significantly from the equal probability of mating model. If differential fertilization were occurring and a particular pollen parent contributed a disproportional number of gametes to the polymix mating, all of its isozymes would be expected to be over-represented resulting in significant chi-square values for several loci.

Frequency of fertilizations by pollen parents

The pollens used in this study were not chosen based on unique allozyme phenotypes, thus, several pollen parents could produce gametes which were indistinguishable from each other (*Table 2*). The method used to deal with this problem, discussed in the Materials and Methods section, could have biased the results of the pollen frequency chi-squares in favor of the null hypothesis, equal probability of mating, by causing a more even distribution of pollen contribution than that which actually occurred.

The observed frequencies of fertilization attributed to each pollen parent are given in *Table 3*. No pollen parent was estimated to have fertilized more than 21% of the seed of any female. This was determined by dividing the number of seed produce by a mating with a particular pollen, (*Table 3*) by the total number of seed sampled for that cross. The chi-square test results on these fertilization frequency data supports the conclusions derived from the allozyme frequency chi-square test. None of the four polymix pollinations produced evidence to reject the equal probability of mating hypothesis. None of the fertilization frequency chi-square tests are significant at the .05 level. The allozyme frequency chi-square test results, which are not affected by the aforementioned source of bias support the results of the fertilization frequency chi-square analysis.

When deviations from equal mating occur the GCA of some female parents may be over-or underestimated, because the mixture of male gametes effecting fertilization may contain an excess of superior or inferior genotypes. The situation would be particularly damaging if the overly successful male parents, differed from cross to cross.

The chi-square analyses of this study, indicate that no significant deviation from the equal probability of mating hypothesis occurred in the polymix matings which lends credence to the GCAs and other statistics produced from polymix progeny test data.

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Analysis of Diallel Matings with Missing Values

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Summary

A computer program (called Diallel Analysis by GENSTAT, DAG) is presented to analyse data from half-diallel matings without selfs. The program is flexible, coping with mixed models, varying number of traits and missing values (in the form of both missing trees and missing crosses). The program, based on analysis of variance and regression techniques, is easy to use and provides opportunities to pool sums of squares in the analysis of disconnected half-diallel matings. The output is directed towards generating variance components of particular interest to tree breeding and population genetics.

Key words: Computer program, half-diallel matings, missing values, variance components.

Zusammenfassung

Ein Computerprogramm (bezeichnet als Diallel Analyse mit Hilfe von GENSTAT, DAG) zur Auswertung von Daten aus halb-diallelen Kreuzungen ohne Selbstungen wird vorgestellt. Das Programm ist flexibel und setzt sich mit gemischten Modellen auseinander sowie mit variierenden Zahlen von Merkmalen und fehlenden Daten sowohl durch fehlende Bäume als auch durch fehlende Kreuzungen. Das Programm basiert auf der Varianz- und Regressionsanalyse, ist leicht anwendbar und bietet Möglichkeiten, die

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