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Genetic relatedness in open-pollinated families of two leguminous tree species, *Robinia pseudoacacia* L. and *Gleditsia triacanthos* L.

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Summary. When conducting tree breeding experiments, geneticists often assume that individuals from open-pollinated families are halfsibs. The reliability of this assumption was tested using data from enzyme electrophoresis to estimate the genetic relatedness among progeny within 22 open-pollinated families of *Robinia pseudoacacia* L. (black locust) and 34 open-pollinated families of *Gleditsia triacanthos* L. (honey locust) from natural stands. An algorithm employing population estimates of fixation indices, pollen allele frequencies, and selfing rates was used to calculate the mean expected number of alleles in common across loci under assumptions of either full-sib (i.e., a single pollen parent) or half-sib (i.e., random mating) relationships. For each open-pollinated family, the average coefficient of relationship among progeny was calculated by linear interpolation from the observed number of alleles in common. For most families of both species, coefficients were significantly higher than 0.25 (half-sib relation), but were significantly lower than 0.50 (full-sib relation). These results suggest that the assumption of a half-sib relationship among progeny of open-pollinated families is violated for these tree species. More critical to the estimation of heritabilities and the prediction of genetic gains was the observation that estimates of the coefficient of relationship varied widely among open-pollinated families (for *R. pseudoacacia* $r_0 = 0.20-0.43$, mean $= 0.34$; for *G. triacanthos* $r_0 = 0.29-0.55$, mean $= 0.36$).

Key words: Allozymes – Coefficient of relationship – Heritability estimates – *Gleditsia triacanthos* – *Robinia pseudoacacia*

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Introduction

When estimating additive genetic variance and the heritability of traits, geneticists often assume a half-sib relationship among progeny within open-pollinated families. This assumption is met only if each progeny is sired by a different male parent and if all male parents are unrelated. The genetic correlation, or coefficient of relationship, among progeny in this case is 0.25, indicating that the progeny have ¼ of their genes in common. Any degree of correlated mating, mating among relatives, or self-fertilization will cause an increase in the coefficient of relationship. If all progeny are sired by a single pollen donor, then all progeny are full sibs and have an average genetic correlation of 0.50. Any such violations of the half-sib assumption will result in overestimations of additive genetic variance, heritability and, subsequently, genetic gains (Falconer 1981).

For several reasons, genetic relatedness coefficients within families of open-pollinated forest trees might be expected to be greater than 0.25 (Namkoong 1966). First, selfing is common for most monoecious or hermaphroditic species (Mitton 1983; Schemske and Lande 1985). Second, extensive vegetative reproduction or limited pollen and propagule dispersion may cause genetic substructuring and the formation of family groups within populations (Rohlf and Schnell 1971; Turner et al. 1982; Hamrick and Loveless 1986). If mating is most frequent among nearest neighbors, then genetic relatedness among progeny will be increased in structured populations. Brown et al. (1989) have pointed out that in entomophilous species, in particular, the combination of pollinator behavior and genetic substructuring may create a hierarchy of correlated matings within inflorescences and individual trees. Third, the number of potential pollen donors in a

population may be so small that correlated matings are unavoidable.

Estimates of genetic correlations within open-pollinated progeny arrays have been attempted for only a single population of the tree species *Gleditsia triacanthos* (Schnabel 1988). In that study, the pedigree of adult trees in a portion of the population was reconstructed based on a genetic analysis of paternity and an estimate of the adult age structure. This pedigree was coupled with a paternity analysis of seeds to estimate minimum and maximum coefficients of relationship among progeny of several families. Average minimum estimates varied from 0.26 to 0.30, whereas maximum estimates ranged from 0.30 to 0.36. Although consistent with prior knowledge of gene flow patterns and spatial genetic structuring in the population, the accuracy of these estimates suffers from the inability to uniquely identify the paternal parent for each seed. More important, because of the requirement for population sizes, sufficient genetic variability, and large financial limitations, paternity analyses will be impractical for many tree species.

Clearly, the assumption of half-sib families should be evaluated for other species of forest trees. In particular, a statistical technique is needed that estimates the general level of genetic relatedness and its variability on a species level. In this study, we introduce such a technique and use it to estimate genetic correlations among progeny in 22 open-pollinated families of *Robinia pseudoacacia* (black locust) sampled throughout its natural range (eastern USA), and 34 open-pollinated families of *G. triacanthos* (honey locust) from three populations in northeastern Kansas, USA. This technique allows us to statistically test each open-pollinated family for deviations from half- and full-sibship. For each *G. triacanthos* population, comparisons of genetic correlations are made within and between two seed collection years. Comparisons are also made among populations in the same year of seed collection.

Materials and methods

Seed collections and electrophoresis

Seeds were collected from 22 trees of *R. pseudoacacia*, representing 11 seed sources located throughout its natural range (Fig. 1). Each seed source consisted of a circular area with a radius of approximately 10 km. Within sources, seeds were sampled from single maternal trees in each of one to four stands separated by distances ranging from 0.1 to several kilometers. This sampling scheme was employed to assure that seed collections were from separate clones. Although they probably cannot be considered as interbreeding units, collections from each seed source were treated as a single population for the purpose of estimating fixation indices, selfing rates, and pollen allele frequencies. From each progeny group, 48 randomly selected seedlings were assayed for eight enzyme systems encoded by 16 polymorphic loci [fluorescent esterase (FE-1), α-galactosidase (αGAL-1), isocitrate dehydrogenase (IDH-1), leucine minopeptidase (LAP-2), malate

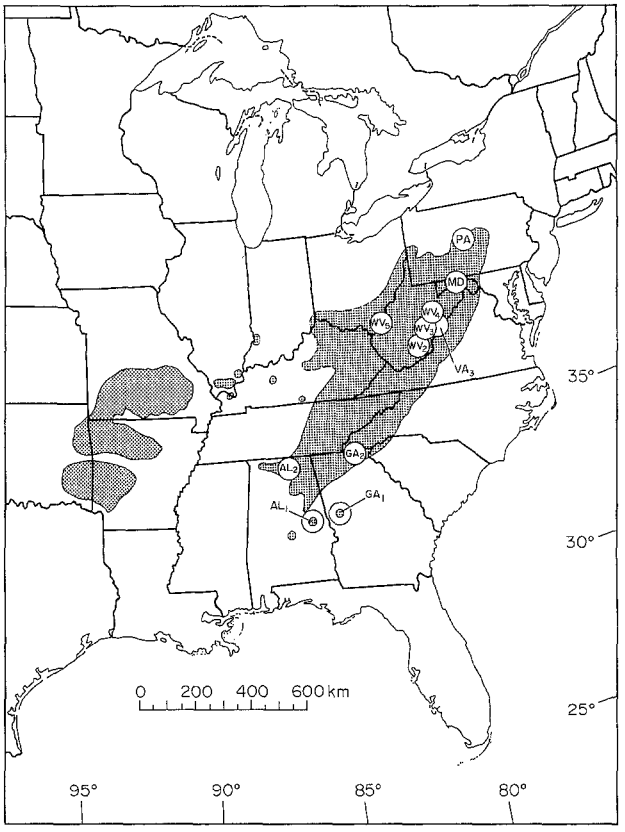

Fig. 1. Natural range (shaded area) and location of the 11 seed sources of *R. pseudoacacia*

dehydrogenase (MDH-1, MDH-2, MDH-3), phosphoglucomutase (PGM-1, PGM-2, PGM-3), 6-phosphogluconate dehydrogenase (6PDGH-1, 6PDGH-2, 6PDGH-3, 6PDGH-5), and shikimate dehydrogenase (SKDH-1, SKDH-2)]. Details of seed germination and electrophoretic procedures are described in Surles et al. (1989). For each allozyme locus, pollen allele frequencies were estimated by first inferring the maternal genotype from genotypes in the progeny array, then excluding the maternal allele from the genotype of each progeny, and calculating frequencies of the residual paternal alleles. The ambiguous cases of identical heterozygous genotypes for mother and progeny were handled by randomly assigning one maternal allele to half of those progeny and the other maternal allele to the remaining half. Selfing rates (Surles et al. 1990) were estimated on a seed-source basis using the multilocus model of Ritland and Jain (1981). Due to the low number of sample (maternal) trees per seed source, fixation indices were calculated using progeny data.

Gleditsia triacanthos seeds were collected over two seasons in each of three populations in northeastern Kansas. Two populations (abbreviated here as NAS and RBT) were located within the University of Kansas Ecological Reserves and the third (WCS) was located on the West Campus of the University of Kansas in Lawrence/KS. Each site contained 100–300 reproductive individuals and several hundred non-reproductive seedlings and saplings within areas of 1–2 hectares [detailed descriptions of these sites can be found in Schnabel (1988)]. Only those trees from which greater than 20 seeds could be collected were used in the analysis. The maximum number of seeds used from any one tree was 48. All seedlings were assayed for 13 enzyme systems, which provided data for 18 polymorphic al-

Table 1. Frequencies of progeny from half-sib matings in a three-allele system. The maternal genotype self-fertilizes with probability $s=1-t$. Pollen allele frequencies are denoted by θ_i and the fixation index by F

Mating type	Offspring					
	A_1A_1	A_1A_2	A_1A_3	A_2A_2	A_2A_3	A_3A_3
$A_1A_1(♀)\times A_1A_1(♂)$	tP_{11}	–	–	–	–	–
$A_1A_1(♀)\times A_1A_2(♂)$	$\frac{1}{2}tP_{12}$	$\frac{1}{2}tP_{12}$	–	–	–	–
$A_1A_1(♀)\times A_1A_3(♂)$	$\frac{1}{2}tP_{13}$	–	$\frac{1}{2}tP_{13}$	–	–	–
$A_1A_1(♀)\times A_2A_2(♂)$	–	tP_{22}	–	–	–	–
$A_1A_1(♀)\times A_2A_3(♂)$	–	$\frac{1}{2}tP_{23}$	$\frac{1}{2}tP_{23}$	–	–	–
$A_1A_1(♀)\times A_3A_3(♂)$	–	–	tP_{33}	–	–	–
$A_1A_1(♀)$ selfs	s	–	–	–	–	–
$A_1A_2(♀)\times A_1A_1(♂)$	$\frac{1}{2}tP_{11}$	$\frac{1}{2}tP_{11}$	–	–	–	–
$A_1A_2(♀)\times A_1A_2(♂)$	$\frac{1}{4}tP_{12}$	$\frac{1}{2}tP_{12}$	–	$\frac{1}{4}tP_{12}$	–	–
$A_1A_2(♀)\times A_1A_3(♂)$	$\frac{1}{4}tP_{13}$	$\frac{1}{4}tP_{13}$	$\frac{1}{4}tP_{13}$	–	$\frac{1}{4}tP_{13}$	–
$A_1A_2(♀)\times A_2A_2(♂)$	–	$\frac{1}{2}tP_{22}$	–	$\frac{1}{2}tP_{22}$	–	–
$A_1A_2(♀)\times A_2A_3(♂)$	–	$\frac{1}{4}tP_{23}$	$\frac{1}{4}tP_{23}$	$\frac{1}{4}tP_{23}$	$\frac{1}{4}tP_{23}$	–
$A_1A_2(♀)\times A_3A_3(♂)$	–	–	$\frac{1}{2}tP_{33}$	–	$\frac{1}{2}tP_{33}$	–
$A_1A_2(♀)$ selfs	$\frac{1}{4}s$	$\frac{1}{2}s$	–	$\frac{1}{4}s$	–	–
⋮			⋮			⋮

$P_{ii}\equiv\theta_i^2+\theta_i(1-\theta_i)F$
$P_{ij}\equiv 2\theta_i\theta_j(1-F)$

Table 2. Frequencies of matings together with the expected number of alleles in common in a full-sib mating system with inbreeding. The maternal genotype selfs with probability $s=1-t$. There are n offspring in each family. The pollen allele frequencies are denoted by θ_i, and the fixation index by F

Mating type	Expected no. of alleles in common	Frequency
$A_1A_1(♀)\times A_1A_1(♂)$	2	$t[\theta_1^2+\theta_1(1-\theta_1)F]$
$A_1A_1(♀)\times A_1A_2(♂)$	A	$2t\theta_1\theta_2(1-F)$
$A_1A_1(♀)\times A_1A_3(♂)$	A	$2t\theta_1\theta_3(1-F)$
$A_1A_1(♀)\times A_2A_2(♂)$	2	$t[\theta_2^2+\theta_2(1-\theta_2)F]$
$A_1A_1(♀)\times A_2A_3(♂)$	A	$2t\theta_2\theta_3(1-F)$
$A_1A_1(♀)\times A_3A_3(♂)$	2	$t[\theta_1^2+\theta_1(1-\theta_1)F]$
$A_1A_1(♀)$ selfs	2	s
$A_1A_2(♀)\times A_1A_1(♂)$	A	$t[\theta_1^2+\theta_1(1-\theta_1)F]$
$A_1A_2(♀)\times A_1A_2(♂)$	B	$2t\theta_1\theta_2(1-F)$
$A_1A_2(♀)\times A_1A_3(♂)$	C	$2t\theta_1\theta_3(1-F)$
$A_1A_2(♀)\times A_2A_2(♂)$	A	$t[\theta_2^2+\theta_2(1-\theta_2)F]$
$A_1A_2(♀)\times A_2A_3(♂)$	C	$2t\theta_2\theta_3(1-F)$
$A_1A_2(♀)\times A_3A_3(♂)$	A	$t[\theta_3^2+\theta_3(1-\theta_3)F]$
$A_1A_2(♀)$ selfs	B	s
⋮	⋮	⋮

$A=[(3/2)n-2]/(n-1)$
$B=[(5/4)n-2]/(n-1)$
$C=[(9/8)n-2]/(n-1)$

lozyme loci [acid phosphatase (ACP), diaphorase (DIA), fluorescent esterase (FE-1, FE-2), glutamate-oxaloacetate transaminase (GOT-2, GOT-3), isocitrate dehydrogenase (IDH-1), leucine aminopeptidase (LAP-1, LAP-2), malic enzyme (ME), malate dehydrogenase (MDH), phosphoglucoisomerase (PGI-2), phosphoglucomutase (PGM-1, PGM-2), 6-phosphogluconate dehydrogenase (6PDGH-1, 6PDGH-2), shikimate dehydrogenase (SKDH-1), triosephosphate isomerase (TPI)]. Seed germination and electrophoretic procedures are presented in Schnabel (1988).

Pollen allele frequencies and outcrossing rates were estimated as described for *R. pseudoacacia*, except that maternal genotypes were unambiguously known for all loci and families. Fixation indices were calculated for each locus using observed and Hardy-Weinberg expected population heterozygosities.

Data analysis

Given the maternal genotypes, the expected number of alleles in common (NAC) based on half-sib and full-sib matings was calculated from the pollen allele frequencies $[\Theta_i]$ at each locus, the fixation index (F), and selfing rate (s) of the parent population. The expected numbers of alleles in common under these two mating systems were compared with the mean number of alleles in common observed in each progeny array.

Define n to be the size of each progeny array and n_k as the sample size at the k^{th} locus. Then the mean number of alleles in common observed at the k^{th} locus is:

$$\text{NAC}_k=1/n_k\sum_{i}^{nk}\sum_{j}^{nk}\text{NAC}(g(i,k),g(j,k)) \tag{1}$$

where $\text{NAC}(g(i,k),g(j,k))$ is the number of alleles in common between genotypes $g(i,k)$ and $g(j,k)$. The indices i and j represent the i^{th} and j^{th} individuals in the sample of size n_k at the k^{th} locus.

More formally, we have:

$\text{NAC}(g(i,k),g(j,k))=2$, individuals i and j share both alleles;
$=1$, individuals i and j share one allele;
$=0$, individuals i and j share no alleles.

The mean number of alleles in common across all loci is then:

$$\text{NAC}=1/N\sum_{k}^{K}\sum_{i}^{nk}\sum_{j}^{nk}\text{NAC}(g(i,k),g(j,k)) \tag{2}$$

where $N=\sum_{k}^{nk}$.

Table 3. Selfing rates, mean expected and observed number of alleles in common (NAC), and coefficients of relationship (r_0) for 22 open-pollinated families of *Robinia pseudoacacia*. Family designations give the abbreviation of the state in which the collection was made, the seed-source number within each state (arabic numbers), and the family within seed sources (lowercase letters). Observed and expected NAC values that do not differ significantly ($\alpha = 0.05$) are presented in boldface type

Family	Selfing rate[a]	No. of alleles in common (NAC)			r_0 (±95% L)
		Expected half-sib	Observed (95% L)[b]	Expected full-sib	
AL1a	0.26	**1.573**	**1.601** (1.571, 1.631)	1.638	0.35 (±0.11)
AL1b	0.26	1.556	1.626 (1.590, 1.646)	1.692	0.37 (±0.06)
AL2a	0.28	1.583	1.625 (1.604, 1.663)	1.750	0.31 (±0.03)
AL2b	0.28	1.496	1.605 (1.577, 1.633)	1.652	0.42 (±0.04)
AL2c	0.28	**1.544**	**1.518** (1.496, 1.540)	1.719	0.21 (±0.03)
AL2d	0.28	1.496	1.605 (1.576, 1.633)	1.644	0.43 (±0.04)
GA1	0.18	**1.554**	**1.568** (1.525, 1.575)	1.747	0.24 (±0.03)
GA2a	0.34	1.586	1.654 (1.621, 1.687)	1.759	0.34 (±0.04)
GA2b	0.34	**1.602**	**1.568** (1.534, 1.602)	1.765	0.20 (±0.05)
GA2c	0.34	**1.627**	**1.644** (1.613, 1.675)	1.780	0.27 (±0.05)
GA2d	0.34	1.582	1.662 (1.636, 1.688)	1.717	0.39 (±0.05)
VA3a	0.16	1.556	1.670 (1.639, 1.701)	1.730	0.41 (±0.04)
VA3b	0.16	1.539	1.574 (1.554, 1.593)	1.705	0.30 (±0.03)
MD1a	0.13	1.475	1.577 (1.542, 1.613)	1.653	0.39 (±0.05)
MD1b	0.13	1.505	1.604 (1.581, 1.628)	1.667	0.40 (±0.03)
WV2	0.09	1.588	1.744 (1.717, 1.771)	1.797	0.43 (±0.03)
WV3	0.00	1.533	1.583 (1.557, 1.609)	1.713	0.32 (±0.03)
WV4	0.16	1.499	1.578 (1.544, 1.611)	1.660	0.37 (±0.05)
WV5a	0.19	1.523	1.616 (1.590, 1.641)	1.711	0.37 (±0.03)
WV5b	0.19	1.530	1.586 (1.562, 1.610)	1.745	0.31 (±0.02)
WV5c	0.19	1.539	1.595 (1.566, 1.623)	1.745	0.31 (±0.03)
PA1	0.00	1.434	1.542 (1.512, 1.571)	1.593	0.41 (±0.04)
Mean		1.542	1.608 (1.588, 1.628)	1.708	0.34 (±0.03)

[a] Surles et al. 1990
[b] 95% confidence limit

The expected value of this statistic under half-sib mating can be estimated from a table similar to Table 1 (smaller or larger depending on the number of alleles). Estimates of pollen allele frequencies, fixation index, and selfing rate of the k^{th} locus were obtained by the method of Ritland and Jain (1981). These values can be substituted into Table 1. Multiplying each entry in Table 1 by the sample size n_k and taking the integer part of each expectation yields an expected progeny array. These expected progeny arrays for each locus and maternal genotype can be substituted into Eqs. (1) and (2) to obtain the NAC_{HS}.

The expected value of this statistic under full-sib mating can be computed from a table similar to Table 2. Given one of six possible fathers in the three-allele case, one can compute the expected number of alleles in common for a family of size n. These are the constants 2, A, B, or C in Table 2, depending on the mating type. The expected number of alleles in common at the k^{th} locus, NAC_{FSk}, is then the sum of products of columns B and C.

Standard errors on the mean number of alleles in common (NAC_k) were computed by bootstrap resampling of progeny from each family. Resampling of n_k progeny with replacement was performed from each progeny array based on the collection of n_k multilocus genotypes (and not on a locus-by-locus basis).

Coefficients of relationship were calculated by interpolation for each family from the relationship of the mean observed NAC for the family to the NAC values expected for full and half sibs in that family. We assumed that the relationship between the NAC value and the coefficient of relationship was linear. Thus, for family ALla of *R. pseudoacacia*, the expected half- and full-sib NAC values were 1.533 and 1.638, while the observed value was 1.601 (Table 3). The observed NAC is closer to the half-sib expected value (0.028) than to the full-sib expected value (0.037), producing a coefficient of relationship of 0.36 for this family.

Results

For *R. pseudoacacia*, the overall mean expected number of alleles in common (NAC) assuming half-sib and full-sib mating were $NAC_{HS} = 1.542$ and $NAC_{FS} = 1.708$, and varied considerably among families (Table 3). The NAC_{HS} values ranged from 1.434 in family PA1 to 1.627 in family GA2c, whereas NAC_{FS} values ranged from 1.593 in family PA1 to 1.797 for WV2. Observed values (NAC_{OBS}) were

Table 4. Sample sizes, mean expected and observed number of alleles in common (NAC), and coefficients of relationship (r_0) for 34 open-pollinated families from three populations of *Gleditsia triacanthos*. Observed and expected NAC values that do not significantly differ are presented in boldface type

Population	Family	No. of alleles in common (NAC)			r_0 (±95% L)
		Expected half-sib	Observed (95% L)	Expected full-sib	
NAS 1985	45	1.510	1.558 (1.532, 1.586)	1.607	0.37 (±0.06)
	46	**1.581**	**1.602** (1.571, 1.633)	1.677	0.30 (±0.08)
	166	1.568	1.620 (1.584, 1.655)	1.676	0.37 (±0.08)
	167	1.565	1.617 (1.587, 1.648)	1.679	0.36 (±0.06)
Mean		1.556	1.599	1.660	0.35
NAS 1986	103	1.566	1.605 (1.587, 1.622)	1.674	0.34 (±0.04)
	166	1.588	1.629 (1.607, 1.650)	1.697	0.34 (±0.05)
	176	1.588	1.624 (1.601, 1.650)	1.697	0.33 (±0.05)
	182	**1.560**	**1.588** (1.556, 1.610)	1.667	0.31 (±0.07)
	188	1.572	1.621 (1.591, 1.651)	1.670	0.37 (±0.07)
	198	1.557	1.583 (1.562, 1.603)	1.671	0.30 (±0.04)
	323	1.602	1.650 (1.628, 1.673)	1.717	0.35 (±0.04)
Mean		1.576	1.614	1.686	0.33
RBT 1983	1	1.591	1.641 (1.621, 1.660)	1.730	0.33 (±0.03)
	2	1.637	1.807 (1.787, 1.826)	1.778	0.55 (±0.04)
	3	1.581	1.660 (1.636, 1.685)	1.709	0.40 (±0.04)
	4	1.584	**1.716** (1.677, 1.755)	**1.710**	0.51 (±0.07)
	5	1.595	1.652 (1.618, 1.686)	1.729	0.35 (±0.06)
	6	1.581	1.643 (1.615, 1.671)	1.709	0.37 (±0.05)
	7	1.548	1.633 (1.608, 1,659)	1.664	0.43 (±0.05)
	8	1.578	1.641 (1.612, 1,671)	1.709	0.37 (±0.05)
	9	1.593	1.628 (1.601, 1.656)	1.731	0.31 (±0.04)
	10	1.572	1.601 (1.577, 1.624)	1.704	0.30 (±0.04)
Mean		1.586	1.662	1.717	0.39
RBT 1985	3	1.540	1.627 (1.601, 1.654)	1.658	0.43 (±0.05)
	203	1.596	1.654 (1.617, 1.689)	1.720	0.36 (±0.07)
	449	1.560	1.597 (1.570, 1.623)	1.676	0.32 (±0.05)
	724	**1.597**	**1.618** (1.571, 1.665)	1.714	0.29 (±0.10)
	725	1.460	1.525 (1.495, 1.555)	1.562	0.40 (±0.07)
Mean		1.541	1.597	1.656	0.36
WCS 1985	70	1.545	1.609 (1.586, 1.632)	1.653	0.39 (±0.05)
	76	1.559	1.617 (1.584, 1.632)	1.668	0.38 (±0.07)
	162	**1.566**	**1.596** (1.565, 1.627)	1.677	0.31 (±0.06)
	179	**1.596**	**1.626** (1.594, 1.659)	1.719	0.31 (±0.06)
	247	1.575	1.640 (1.608, 1.673)	1.678	0.40 (±0.07)
Mean		1.569	1.618	1.680	0.36
WCS 1986	70	1.519	**1.626** (1.607, 1.646)	**1.645**	0.46 (±0.03)
	212	1.583	1.635 (1.611, 1.659)	1.716	0.34 (±0.04)
	248	1.571	1.627 (1.602, 1.651)	1.714	0.34 (±0.04)
Mean		1.558	1.629	1.692	0.38
Overall mean		1.570	1.627 (1.599, 1.654)	1.688	0.36 (±0.02)

generally intermediate between the NAC_{HS} and NAC_{FS} values. The overall mean NAC_{OBS} (1.608) was significantly different from both the expected half-sib and full-sib values.

Coefficients of relationship (r_0) were calculated from NAC values by linear interpolation. The range of estimates was large (0.20–0.43), but the average of 0.34 ± 0.03 was intermediate between the expected half- and full-sib values (Table 3). The value of r_0 was significantly less than 0.50 in all families, and was significantly greater than the expected half-sib value in 17 families. Of those families in which the observed number of alleles in common was significantly different from both expected half-sib and full-sib values, only six families had observed relatedness closer to the full-sib level than to the half-sib level.

Coefficients of relationship within the 34 open-pollinated families of *G. triacanthos* were similar to *R. pseudoacacia*, generally intermediate between the expected

half- and full-sib values (Table 4). The overall mean NAC estimate for all three populations was 1.627 which, upon interpolation, yielded an intermediate genetic correlation of $r_0 = 0.36 \pm 0.02$. In five families, estimates of r_0 were not significantly greater than 0.25 (halfsibs); in two other families, r_0 was not significantly different from 0.50 (fullsibs); and in one family (RBT 1983-family 2), r_0 was not significantly greater than 0.50.

With the sampling scheme employed for *G. triacanthos*, it was possible to make comparisons of genetic correlations between years within populations and among populations within the same year. On the whole, population mean r_0 values were similar to one another, varying from 0.33 to 0.39, and estimates for each population differed by only 0.02–0.03 between years. This consistency, however, was not always observed for individual trees. Although progeny from NAS-family 166 and RBT-family 3 had similar coefficients of relationship between years, progeny from WCS-family 70 were intermediate between halfsibs and fullsibs in 1985 ($r_0 = 0.39 \pm 0.05$), but were nearly fullsibs in 1986 ($r_0 = 0.46 \pm 0.03$).

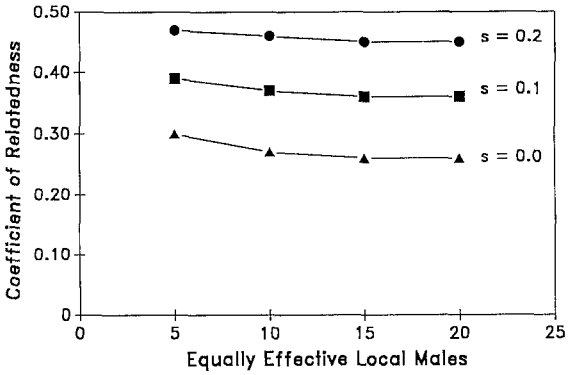

Fig. 2. The effect of the number of individuals contributing pollen on the coefficient of relationship of progeny arrays of individual seed plants. It was assumed that each father contributed equally to the progeny array. The influence of selfing on the coefficient of relationship is also represented

Discussion

The intermediate coefficients of relationship estimated for open-pollinated families of *R. pseudoacacia* and *G. triacanthos* appear to be reasonable, based on knowledge of the natural histories of the two species. Although often occupying similar, early successional habitats, *R. pseudoacacia* and *G. triacanthos* differ significantly in their reproductive biology and population genetic structure. Because the degree of relatedness within families is largely a function of these factors (Squillace 1974), processes generating the coefficients of relationship found in this study are thus most likely not the same for the two species.

Several characteristics of *R. pseudoacacia* populations are of particular importance in explaining why genetic correlations among progeny differ significantly from the expected half-sib level. First, populations are generally founded by few individuals and population sizes often remain small. Stand sizes of *R. pseudoacacia* represented in this study ranged from 1 to 20 individuals (mostly less than ten) and are typical of other stands found throughout the range. Because 20 of more effective fathers are necessary for open-pollinated families to approximate halfsibs (Squillace 1974) (Fig. 2), the potential for half-sib families may not exist in many populations. Furthermore, chances for inbreeding and increased correlation among progeny will be heightened if several individuals in these small populations are related.

Second, genetic correlations among progeny may be increased by self-fertilization (Fig. 2). Although earlier research in Hungary suggested that *R. pseudoacacia* is self-incompatible (Kerezstesi 1980), Surles et al. (1990) found that the probability of outcrossing within the majority of 23 seed sources from the eastern United States was significantly lower than 1.0. An investigation of the relative maturity of anthers and stigmas in a single stand of *R. pseudoacacia* indicated that flowers of this species are protogynous, but that variation in flower maturity within trees provides the opportunity for geitonogamous selfing (Surles et al. 1990).

A third characteristic of *R. pseudoacacia* that simultaneously limits the number of genotypes in the population and increases the chance of geitonogamy is frequent and extensive clonal growth via root sprouting. For example, an electrophoretic study of a *R. pseudoacacia* population near Athens/GA revealed that several hundred indvidual stems were vegetative ramets of only two stumps (distinct genotypes) with little interdigitation of the two genotypes (J. L. Hamrick and S. E. Surles, unpublished data). In another study, genotypes in three populations located in the southern Appalachians were found to be distributed in a "clumped" fashion (B. C. Bongarten, J. L. Hamrick, S. E. Surles, unpublished data). Thus, the number of genetically distinct individuals in populations of *R. pseudoacacia* may often be much smaller than the number of stems. Moreover, if these clonal groups rarely interdigitate, the nearest neighbors for most stems will be genetically identical, further increasing the potential for inbreeding through intraclonal self-fertilization.

In contrast, the intermediate coefficients of relationship found in 26 of 34 *G. triacanthos* families cannot be explained by small populations, self-fertilization, or clonal growth. Population sizes in *G. triacanthos* are often in the hundreds, and although some root sprouting does occur in this species, large clonal groups are uncommon (A. Schnabel, personal observation). Self-fertilization is also not of great concern, because *G. triacanthos* is mostly dioecious, with rare hermaphroditic individuals occur-

ring in some but not all populations. All seed trees used in this study were strictly female.

An alternative explanation of our results involves correlated matings among relatives in family-structured populations. Although population sizes are large, it is likely that not all males contribute equally to each progeny array (e.g., Bijlsma et al. 1986; Schoen and Stewart 1987). The actual number of males contributing pollen to a progeny array may be small (fewer than 20), especially if near-neighbor matings predominate in the population. Moreover, spatial autocorrelation analyses conducted in the three *G. triacanthos* populations have shown that each is genetically substructured (Schnabel 1988). This result is consistent with predictions based on short-distance seed dispersal (Turner et al. 1982; Hamrick and Loveless 1986). Seed dispersal in *G. triacanthos* is in fact very limited by the size and weight of the pods, and a majority of pods fall near their maternal tree (A. Schnabel, personal observation). Furthermore, seed pods are indehiscent and multiseeded, so several seeds may often be dispersed as a unit and germinate in close proximity to one another. These observations suggest the presence of family groups in the three *G. triacanthos* populations, which would further increase genetic correlations within progeny arrays if pollination events are primarily between nearest neighbors. These hypotheses concerning variation in male mating success and patterns of gene flow are currently under investigation.

Implications for tree breeding

Knowledge of the genetic correlation among family members is essential for efficient genetic selection and prediction of genetic gains in artificial selection programs. Because there are few empirical data to suggest correct genetic correlations, open-pollinated families are often assumed to have correlations similar to half-sib families. In general, narrow-sense heritabilities (h^2) for open-pollinated families are calculated as

$$h_2 = \sigma_F^2 / [(r_0 - r_p)\,\sigma_w^2 + r_0\,\sigma_F^2], \quad (3)$$

where σ_F^2 = variance among families, σ_w^2 = variance within families, r_0 = genetic correlation among family members, r_p = inbreeding coefficient.

When families are assumed to be composed of half-sibs ($r_0 = 0.25$ and $r_p = 0$), the expression in Eq. (1) reduces to

$$h^2 = 4\sigma_F^2 / (\sigma_F^2 + \sigma_w^2). \quad (4)$$

For several quantitative traits measured in open-pollinated trees of *R. pseudoacacia*, the ratio of within-family to among-family variance was 9:1 (Kennedy 1983). When these values are substituted into Eq. (4), h^2 is approximately 0.40. If instead we set $r_0 = 0.34$, heritability decreases to 0.29, indicating that the assumption of half-sib families would cause h^2 to be overestimated by 38%. On the other hand, correlation among maternal and paternal parents will decrease overestimates of heritability. Estimates of inbreeding coefficients from 23 seed sources of *R. pseudoacacia* ranged from -0.005 to 0.177, with a mean of 0.065 (Surles et al. 1989). With $r_p = 0.065$ and $r_0 = 0.34$, the estimate of h^2 becomes 0.36. In this case, assuming that open-pollinated families are composed entirely of halfsibs results in a predicted gain that is inflated by about 11%.

This value of r_0 (0.34) is an average for *R. pseudoacacia*. Within a species, as we have shown, families vary widely in their genetic correlations and inbreeding coefficients. As a result, family and within-family heritabilities will be specific for each family. This well especially affect within-family heritability. In combined selection, even after adjustment of heritabilities on a species level, selection of individuals from families with high genetic correlations well be favored over those with low genetic correlations, and expected gain will be biased upwards. Consequently, combined selection is probably not appropriate within open-pollinated progeny tests for which genetic correlations and inbreeding coefficients are not known for each family. More generally, our results show that comparisons among open-pollinated families cannot be interpreted without empirical knowledge of the mating parameters for each family.

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