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Parental contribution and coefficient of coancestry among maize inbreds: pedigree, RFLP, and SSR data

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Abstract The genetic relationship between inbreds *i* and *j* can be estimated from pedigree or from molecular marker data. The objectives of this study were to: (1) determine whether pedigree, restriction fragment length polymorphism (RFLP), and simple sequence repeat (SSR) data give similar estimates of parental contribution and coefficient of coancestry (f_{ij}) among a set of maize (*Zea mays* L.) inbreds, and (2) compare the usefulness of RFLP and SSR markers for estimating genetic relationship. We studied 13 maize inbreds with known pedigrees. The inbreds were genotyped using 124 RFLP and 195 SSR markers. For each type of marker, parental contributions were estimated from marker similarity among an inbred and both of its parents, and were subsequently used to estimate f_{ij}. Estimates of parental contribution differed significantly ($\alpha<0.05$) between pedigree data and either type of marker, but not between the marker systems. The RFLP estimates of parental contribution failed to sum to 1.0, reflecting a higher frequency of non-parental bands with RFLP than with SSR markers. The f_{ij} estimated from pedigree, RFLP, and SSR data were highly correlated (r=0.87–0.97), although significant differences were found among the three sets of f_{ij} estimates. We concluded that pedigree and marker data often lead to different estimates of parental contribution and f_{ij}, and that SSR markers are superior to RFLP markers for estimating genetic relationship. A relevant question is whether or not the inbreds previously genotyped with an older marker system (e.g., RFLP) need to be re-analyzed with a newer marker system (e.g., SSR) for the purpose of estimating genetic relationship. Such re-analysis seems unnecessary if data for the same type of marker are available for a given inbred and both of its parents.

Key words Genetic relationship · Maize · Pedigree · RFLP · SSR

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Introduction

Knowledge of genetic relationships in crops is useful for germplasm organization (Dudley 1994), varietal protection (Hunter 1989), and genetic evaluation (Bernardo 1996). The coefficient of coancestry (f_{ij}, Falconer and Mackay 1996, pp 85–89) is the classic measure of genetic relationship between inbreds *i* and *j*. The f_{ij} coefficient is the probability that, at a given locus, *i* and *j* have alleles that are identical by descent, i.e., copies of the same ancestral allele.

Suppose *i* is a recombinant inbred derived from the cross between inbreds *a* and *b*, and inbred *j* is not a descendant of *i*. The coefficient of coancestry between *i* and *j* depends on: (1) the coefficients of coancestry between *a* and *j* and between *b* and *j*, and (2) the parental contribution to inbred progeny, i.e., the proportion of the genome obtained by *i* from *a* and from *b*. In calculating f_{if} from pedigree records, the parental contributions are assumed equal to their expected values. For example, expected parental contributions are 0.50 for an F_2-derived inbred and either parent, and 0.75 for a BC_1-derived inbred and the recurrent parent. Deviations between observed and expected parental contribution have

been found in maize (*Zea mays* L.), indicating that f_{ij} estimated from pedigrees may not accurately measure genetic relationship (Bernardo et al. 1997). These deviations were probably due to intense selection for yield and other agronomic traits, and genetic drift during inbred development (Hallauer 1990).

Molecular markers provide a direct sampling of the genome and may therefore account for the effects of selection and drift on f_{ij} (Melchinger et al. 1991). Two factors, however, complicate the estimation of f_{ij} from marker data. First, marker similarity (S_{ij}) is not a direct measure of f_{ij}. Marker similarity is measured as the proportion of marker bands common to *i* and *j*. To estimate genetic relationship, S_{ij} needs to be partitioned into the proportions of marker bands that are identical by descent (i.e., marker-based f_{ij}) and of marker bands that are alike in state but not identical by descent (θ_{ij}) (Lynch 1988). Pairs of unrelated inbreds often differ in their values of θ_{ij}. The S_{ij} value is an unbiased estimate of f_{ij} only if θ_{ij} is equal to zero of if the non-zero θ_{ij} can be estimated for each pair of inbreds. Second, the value of θ_{ij} and, consequently, S_{ij} for the same pair of inbreds may differ among types of markers. Restriction fragment length polymorphisms (RFLPs) have been a useful marker system, but simple sequence repeats (SSRs) have become the marker system of choice in maize (Smith et al. 1997). In a study involving 58 maize inbreds, Smith et al. (1997) found a correlation of 0.85 between values of S_{ij} calculated from RFLP and SSR data. Comparisons have not been made, however, between RFLP and SSR estimates of f_{ij} in maize.

Our objectives in this study were to: (1) determine whether pedigree, RFLP, and SSR data give similar estimates of parental contribution and coefficient of coancestry among a set of maize inbreds, and (2) compare the usefulness of RFLP and SSR markers for estimating genetic relationship.

Materials and methods

Maize inbreds

We studied a set of 13 public maize inbreds with known pedigrees (see Table 1). The founder inbreds B37, B73, and GE440 were assumed unrelated, and were the progenitors of the ten other inbreds. B37 and B73 were derived from Iowa Stiff Stalk Synthetic, a population from which one of the parents of most, if not all, maize single crosses grown in the central U.S. Corn Belt has been derived. GE440 was derived from Hastings Prolific. The inbred seed used in this study was obtained either directly from the institute or university that developed the inbred, from the U.S. Department of Agriculture North Center Regional Plant Introduction Station (Ames, Iowa), or from stocks that had been maintained in long-term cold storage at Purdue University. Pedigree and SSR data were available for all 13 inbreds. The RFLP data were available only for B73, H84, H123, Va95, Va96, Va97, and Va98.

RFLP and SSR analysis

Leaf tips were harvested from 30 seedlings of each of the 13 inbreds. The DNA was extracted using a CTAB procedure (Saghai-Maroof et al. 1984). The RFLP analysis was performed by PE AgGen (Salt Lake City, Utah) using procedures described by Helentjaris et al. (1985). The 13 inbreds were first screened with 191 probes and with *Eco*RI as the restriction enzyme. We examined the RFLP markers for their polymorphism, clarity of bands, and simplicity of banding patterns. A final set of 124 RFLP markers were selected for estimating parental contribution and f_{ij}.

The 13 inbreds were initially screened with 206 SSR primer pairs, of which 189 were *bmc* primers [developed jointly by Brookhaven National Laboratory (New York, USA), PE AgGen, and a consortium of 15 private companies] and 17 were *phi* primers (developed by Pioneer Hi-Bred International, Johnston, Iowa). We examined the SSR markers for their polymorphism and selected a final set of 195 polymorphic SSR markers for estimating parental contribution and f_{ij}. In the SSR analysis, the primer pairs were labeled with one of three phosphoramidite fluorescent dyes (6-FAM, VIC, NED). The PCR cocktail consisted of 10 µl each of forward and reverse primer (20 pmol/µl) and 475 µl of True Allele™ PCR premix (PE Applied Biosystems). The True Allele™ PCR premix contained an optimized mixture of Ampli*Taq* GoldT™ DNA polymerase, buffer, magnesium chloride, and dNTPs. An ABI Prism™ 877 Integrated Thermal Cycler prepared and amplified 384 single-plex reactions: ninety six wells for each of four primers pairs, with each well containing 4.6 µl of cocktail and 0.4 µl of sample DNA (10 ng at 25 ng/µl). The PCR procedure comprised: (1) an initial hold at 95°C for 10 min; (2) 10 cycles at 94°C for 30 s, 55°C for 30 s, and 72°C for 60 s; (3) 20 cycles at 89°C for 30 s, 55°C for 30 s, and 72°C for 60 s; and (4) a final hold at 72°C for 10 min. Samples containing 1.0 µl of PCR product and 2.0 µl of loading cocktail (350 µl of GS400HD ROX size standard, 100 µl of blue dextran, 450 µl of deionized formamide and 100 µl of odd or even lane standards in the ratio 7:2:9:2) were heated at 95°C for 5 min, then loaded onto 5% Long Ranger™ denaturing polyacrylamide gels. The DNA samples were electrophoresed at 200 W for 2.5 h on an ABI Prism™ 377 DNA Sequencer equipped with ABI Prism™ 377-96 Collection software (v. 2.5 ABI Prism™ 377-96 Collection). The DNA fragments were sized automatically and assigned to specific alleles based on binning a range of sizes (±0.5 bp), as determined by Genotyper software using the local Southern algorithm (Elder and Southern 1987).

Chromosomal locations of the 124 RFLP and 195 SSR markers were determined from a consensus linkage map created by J. Romero-Severson from five mapping populations (http://www.agron.missouri-edu:80/cgi-bin/sybgw_mdb/mdb3/Reference/145837). There were 18 RFLP markers on chromosome I, 12 on II, 11 on III, 13 on IV, 14 on V, 14 on VI, 9 on VII, 13 on VIII, 6 on IX, and 12 on X. Similarly, there were 22 SSR markers on chromosome I, 32 on II, 29 on III, 14 on IV, 12 on V, 12 on VI, 14 on VII, 16 on VIII, 15 on IX, and 13 on X. Two RFLP markers and 16 SSR markers had unknown or duplicate chromosomal locations.

Data analysis

The parental contribution of inbred *a* to inbred *i* was denoted λ_a, whereas the parental contributin on inbred *b* to inbred *i* was denoted λ_b. For pedigree data, the values of λ_a and λ_b were equal to those expected from Mendelian segregation. For RFLP or SSR data, the parental contributions were estimated from the marker similarity among *a*, *b*, and *i*. Simple matching coefficients (Sneath and Sokal 1973) were used to estimate marker similarity among inbreds. A band will be similar between *a* and *i* if (1) the band is common to *a* and *b* and is transmitted to *i* through either parent, or (2) the band is unique to *a* and is transmitted directly to *i*. Thus, the expectatation of the marker similarity between *a* and *i* is $S_{ai}=(\lambda_a+\lambda_b)S_{ab}+\lambda_a(1-S_{ab})$, where S_{ab} is the marker similarity between the parental inbreds. This equation reduces to $S_{ai}=\lambda_a+\lambda_b S_{ab}$. Similarly, the expectation of the marker similarity between *b* and *i* is $S_{bi}=\lambda_b+\lambda_a S_{ab}$. We then estimated the parental contributions as:

$$\lambda_a=(S_{ai}-S_{bi}S_{ab})/[1-(S_{ab})^2]$$

and

$$\lambda_b=(S_{bi}-S_{ai}S_{ab})/[1-(S_{ab})^2].$$

Table 1 Maize inbreds, parents, and parental contributions (λ_a and λ_b) estimated from pedigree, RFLP, and SSR data. Inbreds were derived from the founder inbreds B37, B73, and GE440

Inbred	Parents (*a*, *b*)	Parental contributions estimates from:					
		Pedigree data		124 RFLP markers		195 SSR markers	
		λ_a	λ_b	λ_a	λ_b	λ_a	λ_b
H84	B37, GE440	0.50	0.50			0.68*	0.31*
H93	B37, GE440	0.97	0.03			0.79*	0.20*
H123	B73, H84	0.75	0.25	0.63*	0.28	0.65	0.35
Lo903	B73, B37	0.75	0.25			0.77	0.23
Lo904	B73, B37	0.75	0.25			0.72	0.27
Lo916	B73, B37	0.50	0.50			0.42*	0.57*
Va95	B73, H84	0.75	0.25	0.64*	0.28	0.64	0.36
Va96	B73, H84	0.75	0.25	0.68	0.26	0.58*	0.41*
Va97	B73, H84	0.50	0.50	0.45	0.50	0.56	0.44
Va98	B73, H84	0.50	0.50	0.48	0.46	0.55	0.44

* Significantly different (α<0.05) from the pedigree estimate of parental contribution. None of the RFLP estimates of λ_a and λ_b differed significantly from the SSR estimates of λ_a and λ_b

We used three different sets of λ_a and λ_b estimates (i.e., pedigree, RFLP, and SSR) in calculating f_{ij} among the inbreds. A tabular analysis procedure (Emik and Terrill 1949) was used for systematically calculating f_{ij}. The inbreds were first sorted from oldest to newest, so that an inbred was listed before any of its progeny. Starting from the oldest inbred, the coefficient of coancestry between *i* and *j* was calculated as:

$$f_{ij}=\lambda_a f_{aj}+\lambda_b f_{bj},$$

where f_{aj} was the coefficient of coancestry between *a* and *j*, and f_{bj} was the coefficient of coancestry between *b* and *j*.

We used three approaches in comparing the pedigree, RFLP, and SSR estimates of f_{ij}. First, we calculated simple correlation coefficients between f_{ij} estimated from the three types of data. Pairs of unrelated inbreds (i.e., with zero f_{ij}) were excluded from the correlation analysis. Second, we compared the sum of λ_a and λ_b for RFLP and for SSR markers. The procedure for calculating λ_a and λ_b from RFLP or SSR data did not impose the constraint of $(\lambda_a+\lambda_b)=1.0$. The sum of the estimated parental contributions therefore served as a useful criterion for comparing the two types of markers. Third, we performed *z*-tests (α=0.05) on the difference in λ_a, λ_b, and f_{ij} estimated from pedigree, RFLP, and SSR data. The approximate standard errors of λ_a, λ_b, and f_{ij} were obtained by bootstrapping. In this procedure, we first partitioned the RFLP and SSR markers into linkage groups, i.e., ten in maize. The two RFLP markers and 16 SSR markers with unknown chromosomal locations were excluded from the analysis. We estimated λ_a, λ_b, and f_{ij} for each linkage group and assumed that the ten estimates of each parameter were independently and identically distributed. From the ten estimates of each parameter, we obtained 10 000 bootstrap samples and calculated the standard error of λ_a, λ_b, and f_{ij}.

Results and discussion

Parental contribution to progeny

The pedigree estimates of parental contribution to progeny were $\lambda_a=\lambda_b=0.50$ for the four F_2-derived inbreds (H84, Lo916, Va97, and Va98), $\lambda_b=0.75$ and $\lambda_b=0.25$ for the five BC_1-derived inbreds (H123, Lo903, Lo904, Va95, and Va96), and $\lambda_a=0.97$ and $\lambda_b=0.03$ for H93, a BC_4-derived inbred (Table 1). Among the five inbreds with RFLP data, differences between the RFLP and pedigree estimates of parental contribution were significant for H123 and Va95. Among BC_1-derived inbreds, the RFLP estimates of λ_a ranged from 0.63 to 0.68, and were lower than the pedigree estimate of λ_a=0.75. Among the F_2-derived inbreds, the values of λ_a or λ_b ranged from 0.45 to 0.50.

Differences between the SSR and pedigree estimates of parental contribution were significant for H84, H93, Lo916, and Va96 (Table 1). Differences between SSR and pedigree estimates of λ_a were largest (0.18) for H84 and H93. Among the BC_1-derived inbreds, SSR estimates of the recurrent parent contribution ranged from 0.58 to 0.77. In terms of parental contribution, the F_2-derived inbred H84 (λ_a=0.68, λ_b=0.31) was similar to BC_1-derived inbreds. Bernardo (1996) considered the probability of fixation of an allele with selection, and found that the following ranges of λ_a and λ_b were likely: (1) 0.26 to 0.74 for an F_2-derived inbred and either of its parents; (2) 0.53 to 0.91 for a BC_1-derived inbred and the recurrent parent; and (3) 0.09 to 0.47 for a BC_1-derived inbred and the donor parent. The SSR estimates of λ_a and λ_b in this study were within these expected ranges for F_2- and BC_1-derived progeny.

Differences between pedigree and marker estimates of parental contribution suggested that selection, drift, or both selection and drift, were present during the development of the inbreds. Pedigree and marker data therefore lead to different estimates of genetic relationship among inbreds. None of the differences were significant between SSR and RFLP estimates of parental contribution. But the results indicated that SSR markers were superior to RFLP markers in estimating parental contribution, and consequently f_{ij}, among inbreds. We expect that the sum of λ_a and λ_b should equal 1.0, but the procedure we used for estimating parental contribution did not constrain the λ_a and λ_b estimates to sum to 1.0. The estimates of λ_a and λ_b failed to sum to 1.0 because some of the marker bands in the progeny inbred could not be traced to either of its parents, i.e., were non-parental bands. For SSR data, the sum of the λ_a and λ_b estimates ranged from 0.99

Table 2 Coefficient of coancestry estimated from pedigree data (above diagonal) and from 195 SSR markers (below diagonal)

Inbred	B37	B73	GE440	H84	H93	H123	Lo903	Lo904	Lo916	Va95	Va96	Va97	Va98
B37		0	0	0.50	0.97	0.13	0.25	0.25	0.50	0.13	0.13	0.25	0.25
B73	0		0	0	0	0.75	0.75	0.75	0.50	0.75	0.75	0.50	0.50
GE440	0	0		0.50	0.03	0.13	0	0	0	0.13	0.13	0.25	0.25
H84	0.68*	0	0.31		0.50	0.25	0.13	0.13	0.25	0.25	0.25	0.50	0.50
H93	0.79*	0	0.20*	0.60*		0.13	0.24	0.24	0.48	0.13	0.13	0.25	0.25
H123	0.24*	0.65	0.11	0.35	0.21*		0.59	0.59	0.44	0.63	0.63	0.50	0.50
Lo903	0.23	0.77	0	0.15	0.18	0.55		0.63	0.50	0.59	0.59	0.44	0.44
Lo904	0.27	0.72	0	0.18*	0.21	0.53	0.62		0.50	0.59	0.59	0.44	0.44
Lo916	0.57	0.43*	0	0.39*	0.45	0.41	0.46*	0.46		0.44	0.44	0.38	0.38
Va95	0.24*	0.64	0.11	0.36	0.21*	0.54*	0.55	0.53	0.41		0.63	0.50	0.50
Va96	0.28*	0.59*	0.13	0.41*	0.25*	0.52*	0.51	0.50*	0.41	0.52*		0.50	0.50
Va97	0.30	0.56	0.14*	0.44	0.26	0.51	0.50	0.48	0.41	0.51	0.51		0.50
Va98	0.30	0.55	0.14*	0.44	0.27	0.51	0.49	0.48	0.41	0.51	0.51	0.50	

* SSR estimate was significantly different ($\alpha<0.05$) from the pedigree estimate of the coefficient of coancestry

to 1.0 (Table 1). Among the five inbreds with RFLP data, the sum of the λ_a and λ_b estimates ranged from 0.91 for H123 to 0.95 forVa97. Smith et al. (1997) likewise found a higher frequency of non-parental bands among RFLP markers (0.04) than among SSR markers (0.02).

The reasons for the higher frequency of non-parental bands with RFLP than with SSR markers are unclear. Smith et al.(1997) gave several possible reasons for the existence of non-parental bands. First, residual heterozygosity may be present in the parental inbreds. A problem with marker analysis of inbreds and their parents is that DNA samples are taken from plants grown from remnant seed stocks. Ideally, DNA samples should be taken from the actual plants used to make the original cross from which an inbred was developed. Residual heterozygosity may therefore cause marker genotypes to differ between remnant seed stocks and the actual plants used to make the cross. Second, contamination by stray pollen may have occurred during inbred development. Third, seed stocks of inbreds may have changed genetically over time by mutation, contamination by stray pollen, or physical mixing with seed from another inbred. But in this study, the same seed stocks were used to extract DNA for both the RFLP and SSR analysis. The above reasons therefore explain why non-parental bands may be present, but do not explain why the frequency of non-parental bands was higher with RFLP than with SSR markers. Perhaps the superiority of SSR over RFLP markers in this study was partly due to the method used for scoring each type of marker. Scoring of SSR bands was done in an automated system whereas scoring of RFLP bands was performed manually. The scoring of RFLP bands from autorads was proofread twice, but whether or not faint bands are consistently scored affects the repeatability of RFLP data (J. Romero-Severson, unpublished data). We also speculate, without any firm evidence, whether RFLP markers are biologically more prone to non-parental bands than SSR markers. A restriction fragment comprises a long segment of DNA (4000–20000 base pairs), and changes in the restriction site due to (1) recombination or (2) insertion or deletion events due to transposon activity, are certainly possible. On the other hand, SSR fragments comprise only 80–300 bp, but small changes in base pair number are possible due to slippage of the DNA polymerase during replication (Levinson and Gutman 1987).

Coefficient of coancestry

Pedigree estimates of f_{ij} ranged from zero for eight pairs of inbreds, to 0.97 between B37 and H93 (Table 2). Among the seven inbreds with RFLP data, pedigree estimates of f_{ij} ranged from zero between B73 and H84, to 0.75 between B73 and H123, Va95, or Va96. The corresponding RFLP estimates of f_{ij} ranged from zero between B73 and H84, to 0.68 between B73 and Va96 (Table 3). Among the related inbreds with RFLP data, the mean f_{ij} estimated from pedigree data was 0.52. In contrast, the mean f_{ij} estimated from RFLP data were 0.46. The lower mean f_{ij} with RFLP than with pedigree data was due to the failure of RFLP estimates of λ_a and λ_b to sum to 1. The correlation between the pedigree and RFLP estimates of f_{ij} was 0.972 ($\alpha<0.05$), indicating a strong linear association between these two measures of genetic relationships across a moderate range of f_{ij} values. Despite this strong linear correlation, differences between pedigree

Table 3 Coefficient of coancestry estimated from 124 RFLP markers

Inbred	H84	H123	Va95	Va96	Va97	Va98
B73	0	0.63*	0.64*	0.68	0.46	0.48
H84		0.29	0.28	0.26	0.50	0.46
H123			0.49*	0.51*	0.43*, †	0.43*, †
Va95				0.51*	0.43*	0.44*, †
Va96					0.44	0.45
Va97						0.45*, †

* RFLP estimate was significantly different ($\alpha<0.05$) from the pedigree estimate of the coefficient of coancestry

† RFLP estimate was significantly different ($\alpha<0.05$) from the SSR estimate of the coefficient of coancestry

and RFLP estimates of f_{ij} were significant for 10 out of the 20 pairs of related inbreds with RFLP data (Table 3). The largest difference (0.14) between pedigree and RFLP estimates of f_{ij} was between H123 and Va95. These two inbreds had significant differences between pedigree and RFLP estimates of λ_a, consequently leading to the large deviation between pedigree and RFLP estimates of f_{ij}.

The SSR estimates of f_{ij} ranged from zero for eight pairs of inbreds to 0.79 between B37 and H93 (Table 2). Excluding the zero f_{ij} values, the mean f_{ij} estimated from SSR data was 0.42, which was close to the mean f_{ij} of 0.41 estimated from pedigree data. The correlation between pedigree and SSR estimates of f_{ij} was 0.92 ($\alpha<0.05$). Differences between pedigree and SSR estimates of f_{ij} were significant for 22 out of the 70 pairs of related inbreds. As expected, most of these significant differences involved the four inbreds (H84, H93, Lo916, and Va96) for which the pedigree and SSR estimates of parental contribution were significantly different. The largest difference (0.18) between pedigree and SSR estimates of f_{ij} was between B37 and H84.

Despite the lack of significant differences between RFLP and SSR estimates of parental contribution, significant differences between RFLP and SSR estimates of f_{ij} were found for four (i.e., between H123 and Va97; H123 and Va98; Va95 and Va98; and Va97 and Va98) out of 20 pairs of related inbreds (Table 3). The magnitudes of these significant differences ranged from 0.05 to 0.08. In all four instances, the difference between the pedigree and SSR estimates of f_{ij} was small (0.00–0.01) and was not significant. The correlation between RFLP and SSR estimates of f_{ij} was 0.87 ($\alpha<0.05$), indicating a strong linear association between the estimates of genetic relationship with the two marker systems.

In conclusion, our results indicated that (1) pedigree and marker data often lead to different estimates of parental contribution and coefficient of coancestry, and (2) SSR markers are superior to RFLP markers for estimating genetic relationship. Our results agree with previous findings (Bernardo et al. 1996, 1997) that deviations between observed and expected parental contributions occur among maize inbreds. The lower frequency of non-parental bands was the primary advantage of SSR data over RFLP data. But, in general, both types of markers gave similar estimates of genetic relationship. As newer types of markers are developed, a relevant question is whether or not the inbreds that have been previously genotyped with RFLP markers need to be re-analyzed with the newer type of marker. Our results suggest that, for the purpose of estimating genetic relationship, such re-analysis is unnecessary if data for the same type of marker are available for a given inbred and both of its parents. Parental contributions can then be estimated either with RFLP or SSR markers, and the estimates of parental contribution can be used to estimate f_{ij}. If both RFLP and SSR data are available for an inbred and its parents, then the estimates of parental contribution for each type of marker can be pooled into a single estimate of parental contribution.

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