Theor Appl Genet (1999) 98: 62–68

A. Tenkouano · J. H. Crouch · H. K. Crouch
D. Vuylsteke · R. Ortiz

Comparison of DNA marker and pedigree-based methods of genetic analysis of plantain and banana (*Musa* spp.) clones. I. estimation of genetic relationships

Received: 29 October 1997 / Accepted: 14 July 1998

Abstract Traditional approaches to the breeding of *Musa* crops are highly demanding in terms of both time and space. However, the application of molecular genetic analysis may dramatically improve breeding efficiency. The objectives of the present study were to compare pedigree and DNA marker methods of estimating genetic relationships across and within generations among diploid, triploid and tetraploid accessions of plantain and banana. Pedigree-based estimates of parent-offspring relationships were substantially different from those obtained from molecular data. The marker-based contribution of triploid maternal accessions to their diploid offspring was greater than expected from published models of meiosis in *Musa*. Conversely, the maternal contribution to tetraploid offspring was less than expected. Pedigree-based similarity was smallest for clones with no common parent and greatest for full-sibs. There was no association between marker-based similarity and pedigree relationships. While DNA markers may provide a more accurate description of genetic relatedness, this study suggests that pedigree-based analysis may prove useful for the selection of prospective parental combinations in *Musa* breeding.

IITA Journal Article no. 97/101/JA

Communicated by H. C. Becker

A. Tenkouano (✉)[1] · J. H. Crouch[2]
H. K. Crouch · D. Vuylsteke · R. Ortiz[3]
Plantain and Banana Improvement Program,
International Institute of Tropical Agriculture, P.M.B. 5320,
Oyo Road, Ibadan, Nigeria.
E-mail: IITAOnne@Satmail.bt.com.

Present addresses:
[1] IITA c/o L. W. Lambourn and Co., Carolyn House, 26 Dingwall Road, Croydon CR9 3EE, England
[2] Elsoms Seeds Ltd., Spalding, Lincolnshire, PE11 1QG, England, UK
[3] The Royal Veterinary and Agricultural University (KVL), Department of Agricultural Sciences, 40 Thorvaldsensvej, DK-1871 Frederiksberg C, Copenhagen, Denmark

Key words *Musa* breeding · Pedigree analysis · SSRLP relationships · Identity in state · $4x - 2x$ crosses

Introduction

Identifying parental combinations that would produce populations with a high level of genetic variation, and individuals with a high agronomic performance, has been a challenge to plant breeders for decades. Progress in breeding for increasingly high-yielding *Musa* hybrids depends on the ability to detect and access genes and gene combinations most likely to produce enhanced heterosis. This, in turn, requires effective selection of prospective male and female parents. Panter and Allen (1995) suggested that the use of genetic relationships among individuals would increase the accuracy of predicting hybrid performance.

Genetic relationships among parents may be estimated from pedigree data using Malécot's (1948) coefficient of co-ancestry. The coefficient of co-ancestry is the probability of two alleles at a locus being identical by descent. However, the probability of two alleles being identical in state is more relevant to breeding since it has more direct implications for the amount of genetic variance among progeny (Helms et al. 1997) and the subsequent efficiency of selection. Furthermore, pedigree information may not be available because of confidentiality in commercial breeding programs (Bernardo et al. 1996) or lack of adequate historical records (Ajmone-Marsan et al. 1992).

Following recent developments in DNA marker technology (Staub and Serquen 1996; Saghai Maroof et al. 1997), genetic relationships may be estimated as the probability of allelic identity in state using DNA marker polymorphisms. DNA marker systems based on the polymerase chain reaction (PCR) are particularly suited to applications in plant breeding

(Rafalski and Tingey 1993; Rafalski et al. 1995). Among these systems, simple sequence repeat length polymorphisms (SSRLPs) have proven particularly useful in many species (Powell et al. 1996) including *Musa* (Kaemmer et al. 1997; Crouch et al. 1998 b).

The objectives of the present study were to compare pedigree-based and DNA marker-based methods for estimating: (1) the contribution of parents to progeny from interspecific crosses between triploid and diploid *Musa* accessions, and (2) the genetic relationships among some tetraploid and diploid clones derived from these crosses.

Materials and methods

Plant materials

Three triploid plantain landraces (*Musa* spp., AAB group) from West Africa were used as maternal genotypes, and two diploid banana accessions (AA) from South-East Asia were used as paternal genotypes, in this study. The AAB accessions were 'Bobby Tannap' (BT), 'Obino l'Ewai' (OL) and a somaclonal mutant of 'Agbagba' (FR) which exhibits a "French" type of bunch. The AA accessions were *M. acuminata* subsp. *burmanicoides* 'Calcutta 4' (C4) and *M. acuminata* subsp. *malaccensis* 'Pisang lilin' (PL). Five tetraploid and five diploid AAB × AA progenies (Vuylsteke et al. 1993; Vuylsteke and Ortiz 1995) were retained for this study. The 4*x* clones were 1658-4 (OL × PL), 2796-5 (BT × PL), 4698-1 (OL × C4), 6930-1 (OL × C4), and 7002-1 (OL × C4) and the 2*x* clones were 1297-3 (FR × C4), 1448-1 (OL × C4), 2829-62 (BT × C4), 4281-2 (BT × C4) and 4400-8 (BT × C4). Plants of these genotypes were grown under field conditions at the IITA High Rainfall Station, Onne, Nigeria, and used for the isolation of DNA for SSRLP analysis as described previously (Crouch et al. 1998 a).

Generation of PCR primers and microsatellite amplification

An accession of *M. acuminata* subsp. *malaccensis* was used for generating a genomic library (Jarret et al. 1994). Clones from this library which contained microsatellites were sequenced and primers were designed from flanking regions, as described previously (Crouch et al. 1998 a), to generate microsatellite markers with Ma prefixes. Primer sequences for additional microsatellite markers with the prefix STMS were kindly supplied by Prof. Gunter Kahl (University Frankfurt) from the sequence of genomic clones isolated from the same *M. acuminata* subsp. *malaccensis* accession as above. Finally, microsatellite markers with the prefix CIR were generated by designing primers from *Musa* sequences obtained from screening the GenBank database (http://www.ncbi.nlm.nih.gov). Primers were synthesized by MWG-Biotech (Germany).

The PCR samples consisted of 25 ng of template DNA, 1.2 μM each of forward and reverse primers, 10 mM tris-HCl (pH 9), 2.5 mM Mg^{2+}, 0.2 mM of each dNTP and 1 unit of *Taq* polymerase (Appligene) in a reaction volume of 15 μl. Reaction components were initially denatured for 4 min at 94°C followed by 30 amplification cycles, each consisting of 1 min denaturation at 94°C, 1 min annealing at the primer melting temperature (specific for each primer, see Table 1, Kaemmer et al. 1997; Crouch et al. 1998 a), and a 45-s extension at 72°C. Amplifications were carried out using a Perkin Elmer thermal cycler model 9600. PCR products were separated electrophoretically using 1.5% w/v Nusieve GTG (FMC) + 1.5% w/v Metaphor (FMC) + 0.5% Multipurpose (Appligene) agarose gels containing 0.3 μg/ml of ethidium bromide, in 1 × TBE buffer at 5 V/cm for approximately 4 h. SSRLP bands were visualized and photographed using UV illumination. The following primers generated amplification products when pre-screening the parental genotypes: Ma 1-16, Ma 1-17, Ma 1-19, Ma 1-24, Ma 1-27, Ma 2-7, Ma 2-10, Ma 3-48, Ma 3-90, Ma 3-139, Ma CIR 38a, Ma CIR 276, Ma CIR 631a, STMS 7, STMS 8, STMS 14, and STMS 15. The sequence of forward and reverse primers with STMS and CIR prefixes has been reported elsewhere (Kaemmer et al. 1997) while the sequences of primer pairs with Ma prefixes, excluding those described previously (Crouch et al. 1998 a), are listed in Table 1.

Estimating genetic relationships

Genetic relationships of the clones were estimated using DNA marker polymorphism and pedigree information. DNA marker polymorphism was assessed using simple sequence length polymorphism as described above. A total of 70 primers were pre-screened across diploid and triploid parental genotypes, of which 17 generated reliable and easily scored polymorphic amplification patterns and were used in this study. These primers detected 70 polymorphic loci across parental and progeny genotypes, of which 45 were polymorphic among the diploid and tetraploid hybrid progeny. Using a program run within the Genstat software (Payne et al. 1989), the frequency of co-migrating PCR amplification products in pair-wise comparisons of genotypes was used to calculate Jaccard's (1908) similarity coefficients among the genotypes as follows:

$$_{M}S_{ij} = N_{ij}/(N_{ii} + N_{ij} + N_{jj}),$$

where $_{M}S_{ij}$ is the DNA marker similarity index between the ith and jth genotype, N_{ij} is the number of bands present in both genotypes, N_{ii} is the number of bands present in the ith genotype but lacking in the jth genotype, and N_{jj} is the number of bands lacking in the ith genotype but present in the jth genotype.

Indices developed for the analysis of data from co-dominant marker systems (i.e. Nei and Li 1979) were not used as, in practice, the co-dominant nature of microsatellite markers is largely lost when analyzing polyploid *Musa* germplasm. Thus, allele frequencies and population statistics cannot be calculated and, therefore, the use of indices developed for co-dominant data are not appropriate (Karp et al. 1997). The loss of co-dominant information results from the difficulty of reliably defining allelic relationships due to the high multiplex nature of assays of such material. This is likely to be a consequence of the low level of differentiation between A and B genomes and the high level of locus duplication in both genomes.

Pedigree information was used to estimate the percentage contribution of each parental clone to the tetraploid and diploid progeny (Graham et al. 1996), and genetic similarity indices were derived from the absolute distance (Gregorius 1984) of the clones using the following formula:

$$_{P}S_{ij} = 1 - (\Sigma_{k}|\lambda_{ik} - \lambda_{jk}|)/\Delta_{P},$$

where $_{P}S_{ij}$ is the similarity index between the ith and jth progeny, λ_{ik} and λ_{jk} are the expected percentage contributions of the kth

Table 1 Sequence and annealing temperature of previously unpublished *Musa* SSRLP primers generating amplification products in this study

Clone no.	Primer sequence (5′ to 3′)	Annealing temp (°C)
Ma 1-19	ATTGGGCAGGCATCAAGTAC GCAATGGTGCTACCCACC	60
Ma 2-10	GGGTTCCGTGAAGATTGATT TGGACAACTGACGACCATAAT	60

parental clone to the ith and jth progeny, Δ_P is the maximum value observed for $\Sigma_k|\lambda_{ik} - \lambda_{jk}|$, i.e. 0.50 for pairs with no common parents. The contribution of the kth founding clone was ignored when $\lambda_{ik} = \lambda_{jk} = 0$. Expected percentage contributions were determined based on current models of segregation in triploid × diploid crosses in *Musa* (Ortiz and Vuylsteke 1994).

A variant of this method was to use the percentage contributions estimated from DNA marker data. In this case, the formula employed was:

$$_{PM}S_{ij} = 1 - (\Sigma_k|\gamma_{ik} - \gamma_{jk}|)/\Delta_{PM},$$

where $_{PM}S_{ij}$ is the similarity index between the ith and jth progeny, γ_{ik} and γ_{jk} are the estimated percentage contributions of the kth parental clone to the ith and jth progeny, Δ_{PM} is the maximum value for $\Sigma_k|\gamma_{ik} - \gamma_{jk}|$, i.e. 0.50 as above. Likewise, the contribution of the kth parental clone was ignored when $\gamma_{ik} = \gamma_{jk} = 0$.

Pedigree data were also used to calculate Wright's coefficient of additive relationship among genotypes, defined as the genetic correlation among relatives assuming all the phenotypic variances were additive genetic (Fisher 1918; Falconer and Mackay 1996).

In practice, the coefficient of additive relationship between two individuals X and Y is the weighted average of the relationship between X and the parents of Y (and vice versa), i.e.:

$$\varphi_{XY} = c_{Y(m)} \cdot \varphi_{XY(m)} + c_{Y(p)} \cdot \varphi_{XY(p)}$$
$$= c_{X(m)} \cdot \varphi_{X.(m)Y} + c_{X(p)} \cdot \varphi_{X(p)Y},$$

where φ_{XY} is the coefficient of additive relationship between X and Y, X(m) and X(p) are respectively the maternal and paternal parents of X with corresponding contributions of $c_{X(m)}$ and $c_{X(p)}$ to the genome of X, Y(m) and Y(p) are respectively the maternal and paternal parents of Y with corresponding contributions of $c_{Y(m)}$ and $c_{Y(p)}$ to the genome of Y, $\varphi_{XY(m)}$ is the coefficient of relationship between X and the female parent of Y, $\varphi_{XY(p)}$ is the coefficient of relationship between X and the male parent of Y, $\varphi_{X(m)Y}$ is the coefficient of relationship between Y and the female parent of X, $\varphi_{X(p)Y}$ is the coefficient of relationship between Y and the male parent of X.

The calculation of additive relationship coefficients was carried out using tabular analysis as described by Bernardo et al. (1996), based on the expected or marker-based contribution of parental clones to their offspring. Additive relationship coefficients between the ith and jth progeny were denoted as $_{P}\varphi_{ij}$ when based on expected parental contributions, or $_{PM}\varphi_{ij}$ when based on DNA marker estimates of parental contribution to their progeny.

Trisomic segregation of phenotypes has been observed in offspring derived from the triploid parental clones used in this study (Ortiz and Vuylsteke 1994), reflecting the heterozygous nature of these clones. Similarly, segregation was observed in F_1 progenies from crosses between the diploid parental accessions for several morphological traits which were monomorphic in the parents (PBIP 1995), also reflecting the heterozygous nature of the diploid parents. Hence, the average probability of two alleles being identical at any locus in the parental accessions was taken as 1/k, where k is the number of chromosome sets (ploidy level) of the accessions.

Results and discussion

Parental contribution to offspring

Pedigree-based estimates of the contribution of parents to their offspring were substantially different from DNA marker-based estimates, except for clone 1297-3 (Table 2). This suggests that parental contributions are not generally equal to their expected values. The marker-based estimates of the maternal contribution were greater than expected for diploid offspring, but less than expected for tetraploid offspring. The reverse was true for the paternal contribution. The discrepancy between theoretical and estimated contributions to tetraploid offspring was greatest when Calcutta 4 was the male parent (Table 2). Whether the observed differences were statistically significant could not be tested due to the lack of appropriate statistical tools (Bernardo et al. 1996).

Expected contributions of triploid and diploid parental clones to the progeny under study were based on earlier reports of modified megasporogenesis leading to the production of 2n gametes in triploid parents (Ortiz and Vuylsteke 1994). However, the discrepancy

Table 2 Pedigree relationships of diploid and tetraploid *Musa* clones, expected and DNA marker-based estimates of parental contributions to progeny

Clones	Parents[a]		Expected contribution		Marker-based contribution	
	Female	Male	Female	Male	Female	Male
Diploid clones						
1297-3	FR	C4	0.500	0.500	0.500	0.500
1448-1	OL	C4	0.500	0.500	0.550	0.450
2829-62	BT	C4	0.500	0.500	0.516	0.484
4281-2	BT	C4	0.500	0.500	0.549	0.451
4400-8	BT	C4	0.500	0.500	0.580	0.420
Tetraploid clones						
1658-4	OL	PL	0.750[b]	0.250	0.733	0.267
2796-5	BT	PL	0.750	0.250	0.738	0.262
4698-1	OL	C4	0.750	0.250	0.568	0.432
6930-1	OL	C4	0.750	0.250	0.656	0.344
7002-1	OL	C4	0.750	0.250	0.669	0.331

[a] Parental genotypes are triploid (AAB) West African plantain landraces Obino l'Ewai (OL), Bobby Tannap (BT) and a somaclonal French reversion mutant of Agbagba (FR), and South East Asian diploid (AA) accessions Calcutta 4 (C4) and Pisang lilin (PL)

[b] Based on the assumption of 2n egg formation in triploid female parents resulting from second-division restitution (Ortiz and Vuylsteke 1994)

between expected and observed parent-offspring relationships may arise from genetic recombination during the formation of 2n gametes (Crouch et al. 1998 a).

Genetic relationships among 4*x* and 2*x* clones

Coefficients of similarity among tetraploid and diploid clones were estimated using five different combinations of SSRLP data and pedigree relationships. Dendrograms derived from the similarity indices were rather dissimilar, since each method resulted in a different clustering pattern of the clones (Figs. 1–5).

As expected, methods based on both SSRLP data and absolute distance methods assigned a value of one for the relationships between a hybrid and itself ($_{M}S_{ii} = {}_{M}S_{jj} = {}_{P}S_{ii} = {}_{P}S_{jj} = {}_{PM}S_{ii} = {}_{PM}S_{jj} = 1$). In contrast, the coefficients of additive relationships based on the expected parental contribution to progeny were small for tetraploid ($_{P}\varphi_{ii} = 0.219$) and diploid clones

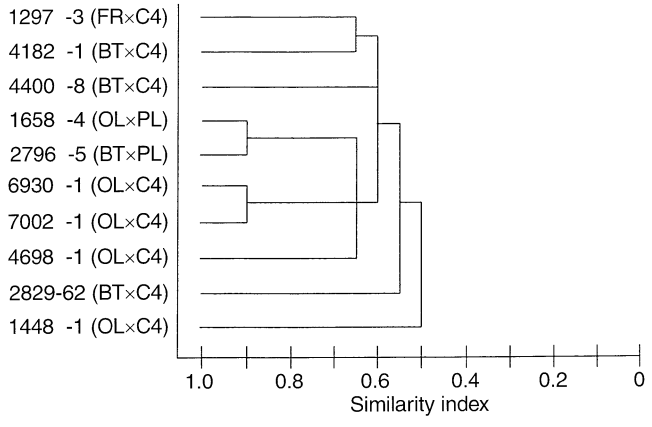

Fig. 1 Dendrogram of tetraploid and diploid *Musa* clones based on SSRLP data. Parentage of clones is indicated in parentheses

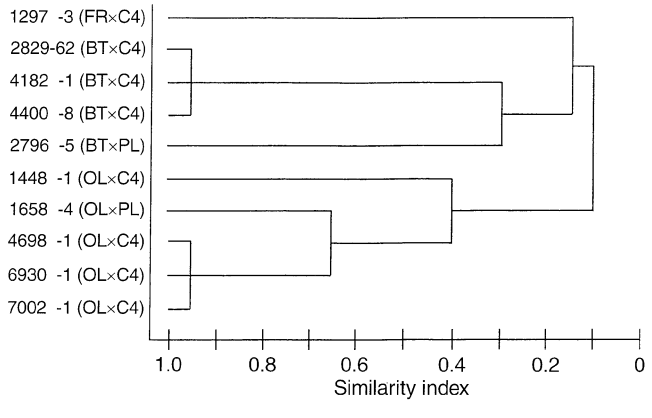

Fig. 2 Dendrogram of tetraploid and diploid *Musa* clones based on genealogical distance calculated from pedigree information. Parentage of clones is indicated in parentheses

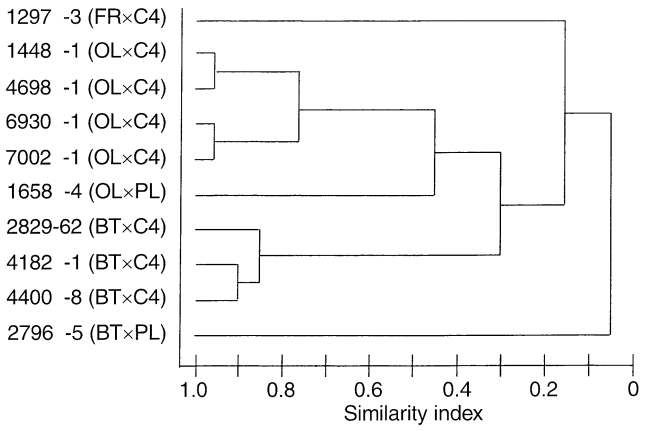

Fig. 3 Dendrogram of tetraploid and diploid *Musa* clones based on genealogical distance calculated from a combination of pedigree and SSRLP data. Parentage of clones is indicated in parentheses

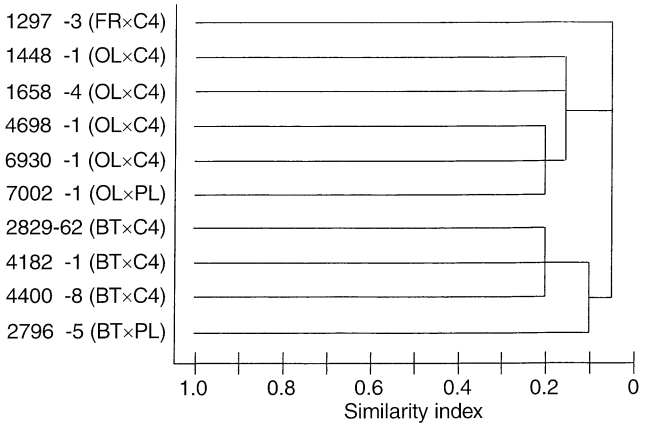

Fig. 4 Dendrogram of tetraploid and diploid *Musa* clones based on coefficients of additive relationships calculated from pedigree data. Parentage of clones is indicated in parentheses

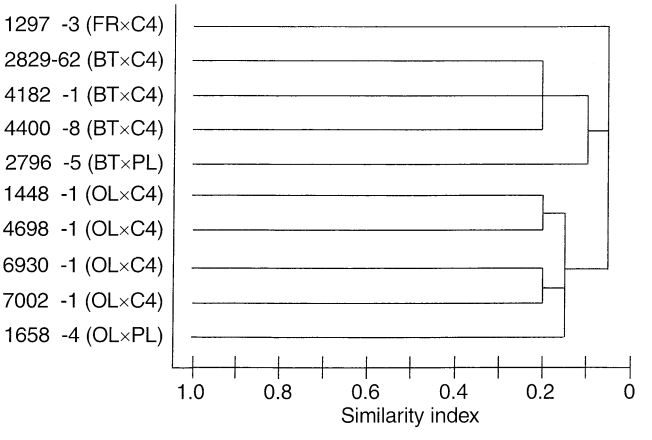

Fig. 5 Dendrogram of tetraploid and diploid *Musa* clones based on their coefficients of additive relationships calculated from a combination of pedigree and SSRLP data. Parentage of clones is indicated in parentheses

($_{P}\varphi_{jj} = 0.208$). When the parental contribution was estimated with SSRLP data, the coefficients of additive relationships ($_{PM}\varphi_{ii}$, $_{PM}\varphi_{jj}$) ranged from 0.200 to 0.208 for the diploid clones and from 0.202 to 0.216 for the tetraploid clones (Table 3). This more accurately reflects the heterozygous nature of the clones.

The pedigree-based similarity indices ($_{P}S_{ij}$, $_{P}\varphi_{ij}$) were smaller than those calculated solely from SSRLP data ($_{M}S_{ij}$) for all $4x - 2x$ pairs. When marker data was combined with pedigree information to calculate similarity coefficients ($_{PM}S_{ij}$, $_{PM}\varphi_{ij}$), the values obtained were also greater than those derived from pedigree data alone (Table 4). This results from the fact that pedigree data exclude genetic similarity due to alleles alike in state but not identical by descent. Thus, pedigree data alone did not capture the extent of genetic similarity between hybrid genotypes. Furthermore, the assumption of genetic unrelatedness of the parental genotypes based solely on their diverse geographical origin may be incorrect. The generation of higher coefficients of genetic relationships when using molecular data as opposed to pedigree data has also been reported in maize (Bernardo et al. 1996) and strawberry (Graham et al. 1996).

Pedigree-based genetic similarity should be smallest for hybrids that have no common parent and greatest for those with identical female and male parents. The tetraploid hybrid 1658-4 (Obino l'Ewai × Pisang lilin) had no parent in common with the diploid hybrids 2829-62 (Bobby Tannap × Calcutta 4), 4281-2 (Bobby Tannap × Calcutta 4) and 4400-8 (Bobby Tannap × Calcutta 4). There was also an absence of common parents between the tetraploid hybrid 2796-5 (Bobby Tannap × Pisang lilin) and the diploid hybrids 1297-3 (Agbagba French Reversion × Calcutta 4) and 1448-1 (Obino l'Ewai × Calcutta 4). Pedigree-based similarity coefficients were zero ($_{P}S_{ij} = {}_{PM}S_{ij} = {}_{P}\varphi_{ij} = {}_{PM}\varphi_{ij} = 0$) for all these $4x - 2x$ pairs, except for the pair (1658-4, 2829-62) which had a non-zero $_{PM}S_{ij}$ ($_{PM}S_{ij} = 0.872$) (Table 4). The tetraploid clones 4698-1, 6930-1 and 7002-1, and the diploid clone 1448-1 had identical pedigrees (Obino l'Ewai × Calcutta 4). As expected, similarity coefficients were greatest for pair-wise comparisons between these three $4x$ hybrids and the $2x$ hybrid (Table 4).

In contrast, the DNA marker-based similarity coefficient between $4x$ and $2x$ hybrids was highest for the maternal half-sibs 1658-4 and 1448-1 ($_{M}S_{ij} = 0.733$). The most dissimilar pairs were 2796-5, 1297-3 ($_{M}S_{ij} = 0.404$), which had no common parents, and 2796-5, 2829-62 ($_{M}S_{ij} = 0.396$), which were maternal half-sibs. Finally, the full-sib pairs (4698-1, 1448-1), (6930-1, 1448-1) and (7002-1, 1448-1) had $_{M}S_{ij}$ values of 0.611, 0.694 and 0.604, respectively (Table 4).

Lack of agreement between DNA marker and pedigree estimates of genetic relationships is not unprecedented. Graham et al. (1996) reported similar observations and attributed the discrepancy between pedigree and DNA marker similarity coefficients in strawberry to incorrect naming of the parental clones, suggesting that some clones were given different names while they were in fact the same or very similar genetically. Conversely, differences between co-ancestry coefficients and RAPD-based similarity estimates in soybean were attributed to the fact that the former indicates the proportion of alleles that are identical by descent while the latter indicates the proportion of alleles that are identical in state in predominantly non-coding regions (Helms et al. 1997).

Pedigree-based methods cannot estimate the proportion of alleles that are identical in state given that they are not identical by descent. For this reason, DNA marker data may provide a more accurate measure of genetic similarity. However, DNA markers may

Table 3 Estimated probability of allelic identity (inbreeding) of diploid and tetraploid *Musa* clones based on DNA marker polymorphism and pedigree information

Clones[a]	DNA marker similarity ($_{M}S_{ii}$)	Absolute similarity[b]		Additive relationships[b]	
		Expected ($_{P}S_{ii}$)	Estimated ($_{PM}S_{ii}$)	Expected ($_{P}\varphi_{ii}$)	Estimated ($_{PM}\varphi_{ii}$)
1297-3 [FR × C4]	1	1	1	0.208	0.208
1448-1 [OL × C4]	1	1	1	0.208	0.202
2829-62 [BT × C4]	1	1	1	0.208	0.206
4281-2 [BT × C4]	1	1	1	0.208	0.202
4400-8 [BT × C4]	1	1	1	0.208	0.200
1658-4 [OL × PL]	1	1	1	0.219	0.215
2796-5 [BT × PL]	1	1	1	0.219	0.216
4698-1 [OL × C4]	1	1	1	0.219	0.202
6930-1 [OL × C4]	1	1	1	0.219	0.202
7002-1 [OL × C4]	1	1	1	0.219	0.204

[a] Pedigrees of clones are given in brackets: parents are triploid (AAB) West African landraces Obino l'Ewai (OL), Bobby Tannap (BT) and a somaclonal French reversion mutant of Agbagba (FR), and South East Asian diploid (AA) accessions Calcutta 4 (C4) and Pisang lilin (PL)

[b] Expected parental contribution to progeny based on a genetic model for segregation in triploid × diploid crosses in *Musa* (Ortiz and Vuylsteke 1994). Estimated contribution based on 70 SSRLP alleles

Table 4 Estimates of similarity coefficients among diploid and tetraploid *Musa* clones based on DNA marker polymorphism and pedigree information

Clones[a]		DNA marker similarity ($_{M}S_{ij}$)	Absolute similarity[b]		Additive relationships[c]	
Female (4*x*)	Male (2*x*)		Expected ($_{P}S_{ij}$)	Estimated ($_{PM}S_{ij}$)	Expected ($_{P}\varphi_{ij}$)	Estimated ($_{PM}\varphi_{ij}$)
1658-4 [OL × PL]	1297-3 [FR × C4]	0.689	0.000	0.000	0.000	0.000
	1448-1 [OL × C4]	0.733	0.334	0.400	0.125	0.134
	2829-62 [BT × C4]	0.571	0.000	0.872	0.000	0.000
	4281-2 [BT × C4]	0.596	0.000	0.000	0.000	0.000
	4400-8 [BT × C4]	0.531	0.000	0.000	0.000	0.000
2796-5 [BT × PL]	1297-3 [FR × C4]	0.404	0.000	0.000	0.000	0.000
	1448-1[OL × C4]	0.447	0.000	0.000	0.000	0.000
	2829-62 [BT × C4]	0.396	0.334	0.000	0.125	0.127
	4281-2 [BT × C4]	0.413	0.334	0.398	0.125	0.135
	4400-8 [BT × C4]	0.444	0.334	0.440	0.125	0.143
4698-1 [OL × C4]	1297-3 [FR × C4]	0.604	0.000	0.242	0.063	0.109
	1448-1[OL × C4]	0.611	0.500	0.964	0.187	0.202
	2829-62 [BT × C4]	0.564	0.000	0.242	0.063	0.105
	4281-2 [BT × C4]	0.500	0.000	0.242	0.063	0.098
	4400-8 [BT × C4]	0.527	0.000	0.226	0.063	0.091
6930-1 [OL × C4]	1297-3 [FR × C4]	0.653	0.000	0.184	0.063	0.086
	1448-1[OL × C4]	0.694	0.500	0.788	0.187	0.198
	2829-62 [BT × C4]	0.577	0.000	0.126	0.063	0.083
	4281-2 [BT × C4]	0.667	0.000	0.126	0.063	0.078
	4400-8 [BT × C4]	0.702	0.000	0.126	0.063	0.072
7002-1 [OL × C4]	1297-3 [FR × C4]	0.537	0.000	0.108	0.063	0.083
	1448-1 [OL × C4]	0.604	0.500	0.762	0.187	0.197
	2829-62 [BT × C4]	0.647	0.000	0.108	0.063	0.080
	4281-2 [BT × C4]	0.708	0.000	0.108	0.063	0.075
	4400-8 [BT × C4]	0.673	0.000	0.108	0.063	0.070

[a] Pedigrees of clones are given in brackets: parents are triploid (AAB) West African landraces Obino l'Ewai (OL), Bobby Tannap (BT) and a somaclonal French reversion mutant of Agbagba (FR), and South East Asian diploid (AA) accessions Calcutta 4 (C4) and Pisang lilin (PL)
[b] Expected contribution based on a genetic model for segregation in triploid × diploid crosses in *Musa* (Ortiz and Vuylsteke 1994). Estimated contribution based on 70 SSRLP alleles
[c] Expected values based on the assumption that tetraploid and diploid clones contribute two chromosomes and one chromosome, respectively, to their progeny. Estimated values are based on 70 SSRLP alleles

overestimate kinship relationships. Bernardo et al. (1996) have developed a method that allows for partitioning of the proportion of alleles common to two genotypes into those that have identical origin and those that are identical in state, but not by descent, based on a joint pedigree and DNA marker analysis.

Bernardo et al. (1996) also found the coefficient of co-ancestry derived from pedigree data to be smaller than that derived from RFLP data for maize inbreds, although the correlation between pedigree and marker estimates was high (0.89**). A lower but significant correlation ($r = 0.27$**) was reported by Cox et al. (1985) for co-ancestry coefficients estimated from pedigree data and similarity coefficients based on gliadin storage-protein electrophoretic patterns in wheat.

The Spearman rank correlation was calculated among the five methods used for estimating genetic relationships in this study. The correlations between DNA marker-based and pedigree-based estimates were not significant. On the other hand, positive correlations among pedigree-based methods ranged from $r = 0.568$ ($P = 0.0031$) for absolute distance methods to $r = 0.940$ ($P = 0.0001$) for additive relationships methods (Table 5).

The positive correlation coefficient between pedigree-based estimates of similarity suggests that the parental contribution to offspring may be assumed to be equal to their expectations, which would facilitate the determination of genetic relationships from pedigree data. The correlation between absolute similarity coefficients and additive relationship coefficients ranged from 0.647 to 0.845, suggesting that either approach would be satisfactory. However, absolute similarity based on differences of the parental contribution to progeny is easier to calculate and, unlike the additive relationship method, does not require tabular analysis. Knowledge of the parents is required but no assumptions need be made concerning their actual contribution to their offspring.

Table 5 Spearman rank correlation among similarity coefficients derived from different combinations of pedigree and DNA marker data in *Musa*. Numbers in parentheses are *P*-values

Methods	(A)	(B)	(C)	(D)	(E)
(A) DNA markers	1.000	− 0.013 (0.9511)	0.154 (0.4615)	0.136 (0.5162)	− 0.012 (0.9414)
(B) Absolute similarity (expected)		1.000	0.568 (0.0031)	0.845 (0.0001)	0.794 (0.0001)
(C) Absolute similarity (estimated)			1.000	0.647 (0.0005)	0.720 (0.0001)
(D) Additive relationships (expected)				1.000	0.940 (0.0001)
(E) Additive relationships (estimated)					1.000

References

Ajmone-Marsan P, Livini C, Messmer MM, Melchinger AE, Motto M (1992) Cluster analysis of RFLP data from related maize inbred lines of the BSSS and LSC heterotic groups and comparison with pedigree data. Euphytica 60 : 139–148

Bernardo R, Murigneux A, Karaman Z (1996) Marker-based estimates of identity by descent and alikeness in state among maize inbreds. Theor Appl Genet 93 : 262–267

Cox TS, Lookhart GL, Walker DE, Harrell LG, Albers LD, Rodgers DM (1985) Genetic relationships among hard red winter wheat cultivars as evaluated by pedigree analysis and gliadin polyacrylamide-gel electrophoretic patterns. Crop Sci 25 : 1058–1063

Crouch HK, Crouch JH, Jarret RL, Cregan PB, Ortiz R (1998 a) Segregation of microsatellite loci from haploid and diploid gametes in *Musa*. Crop Sci 38 : 211–217

Crouch JH, Vuylsteke D, Ortiz R (1998 b) Perspectives on the application of biotechnology to assist the genetic enhancement of banana and plantain (*Musa* spp.). Electronic J Biotechnol 1: http://www.ejb.org

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edn. Longman, England

Fisher RA (1918) The correlations between relatives on the supposition of Mendelian inheritance. Trans Roy Soc Edin 52 : 399–433

Graham J, McNicol RJ, McNicol JW (1996) A comparison of methods for the estimation of genetic diversity in strawberry cultivars. Theor Appl Genet 93 : 402–406

Gregorius HR (1984) A unique genetic distance. Biometrical J 22 : 13–18

Helms T, Orf J, Vallad G, McClean P (1997) Genetic variance, coefficient of parentage, and genetic distance of six soybean populations. Theor Appl Genet 94 : 20–26

Jaccard P (1908) Nouvelles recherches sur la distribution florale. Bull Soc Vandoise Sci Nat 44 : 223–270

Jarret RL, Bhat KV, Cregan P, Ortiz R, Vuylsteke D (1994) Isolation of microsatellite DNA markers in *Musa*. InfoMusa 3 : 3–4

Kaemmer D, Fischer D, Jarret RL, Baurens F-C, Grapin A, Dambier D, Noyer JL, Lanaud C, Kahl G, Lagoda PJL (1997) Molecular breeding in the genus *Musa*: a strong case for STMS marker technology. Euphytica 96 : 49–63

Karp A, Kresovich S, Bhat KV, Ayad WG, Hodgkin T (1997) Molecular tools in plant genetic resources conservation: a guide to the technologies. IPGRI Tech Bull no. 2. International Plant Genetic Resources Institute, Rome, Italy

Malécot G (1948) Les mathématiques de l'hérédité. Masson et Cie, Paris

Nei M, WH Li (1979). A mathematical model for studying genetic variation in terms of restriction endonucleases. Proc Natl Acad Sci USA 76 : 5259–5273

Ortiz R, Vuylsteke D (1994) Inheritance of black sigatoka disease resistance in plantain-banana (*Musa* spp.) hybrids. Theor Appl Genet 89 : 146–152

Panter DM, Allen FL (1995) Using best linear unbiased predictions to enhance breeding for yield in soybean. II. Selection of superior crosses from a limited number of yield trials. Crop Sci 35 : 405–410

Payne RW, Lane PW, Ainsley AE, Bicknell KE, Digby PGN, Harding SA, Leech PK, Simpsom HR, Todd AD, Verrier PJ, White RP (1989) Genstat 5 reference manual. Oxford University Press, UK

PBIP (1995) Plantain and banana improvement program 1994 annual report. Crop Improvement Division, International Institute of Tropical Agriculture, Nigeria

Powell W, Mackray GC, Provan J (1996) Polymorphism revealed by simple sequence repeats. Trends Plant Sci 1 : 215–222

Rafalski JA, Tingey SV (1993) Genetic diagnostics in plant breeding: RAPDs, microsatellites and machines. Trends Genet 9 : 275–280

Rafalski JA, Morgante M, Powell W, Vogel JM, Tingey SV (1995) Generating and using DNA markers in plants. In: Birren B, Lai E (eds) Non-mammalian genomic analysis: a practical guide. Academic Press, California, USA, pp 75–134

Saghai Maroof MA, Yang GP, Zhang Q, Gravois KA (1997) Correlation between molecular marker distance and hybrid performance in U.S. southern long grain rice. Crop Sci 37 : 145–150

Staub JE, Serquen FC (1996) Genetic markers, map construction, and their application in plant breeding. HortScience 31 : 729–741

Vuylsteke D, Ortiz R (1995) Plantain-derived diploid hybrids (TMP2*x*) with black sigatoka resistance. HortScience 30 : 147–149

Vuylsteke D, Swennen R, Ortiz R (1993) Registration of 14 improved tropical *Musa* plantain hybrids with black sigatoka resistance. HortScience 28 : 957–959