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Genotyping and assessment of genetic relationships in elite polycross breeding cultivars of sweet potato in Taiwan based on SAMPL polymorphisms

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Abstract. Selective amplification of microsatellite polymorphic loci (SAMPL) markers was used to analyze the genetic relationships between 22 elite cultivars of sweet potato [*Ipomoea batatas* (L.) Lam.] used in polycross breeding in Taiwan. These elite cultivars included varieties introduced from China and Japan and landraces from Taiwan as well as cultivars derived either from hybrid or polycross breeding programs. Among 12 SAMPL primer pairs tested, 7 amplified 19 loci while the other 5 SAMPL primer pairs gave ambiguous banding profiles. Fifty-five alleles were amplified in total. The unweighted pair group method with arithmetic mean (UPGMA) and principal coordinate analysis (PCA) of SAMPL data suggest that Taiwan landraces are distantly related to Chinese and Japanese cultivars after many years of independent selection and may have originated from Java and Brahman. Polycross derived cultivars are closely related to different landraces. Employment of SAMPL markers is efficient compared to other molecular marker methods, such as random amplified polymorphic DNA (RAPD) and simple sequence repeat (SSR), in assessing the genetic relationships of sweet potato cultivars used in the polycross breeding program in Taiwan.

Keywords: Genetic relationships; Polycross; SAMPL; Sweet potato.

Introduction

Information on germplasm diversity and genetic relationships among elite breeding lines is critical in crop improvement. Sweet potato (2n=6X=90) (Ozias-Akins and Jarret, 1994) is the seventh most-important crop in the world and a major source of food and nutrition in developing countries (International Potato Center, 1996). Sweet potato in Taiwan was first introduced from Java and Brahman as early as the 17th century during Dutch colonization. Afterwards, the Japanese introduced sweet potato materials from Japan, the USA, China, and also from Java and Brahman. Other sweet potatoes were introduced after World War II mainly from China, Japan, and the USA. The breeding of sweet potatoes is mostly through hybrid or polycross breeding. Pre-screening of cross-compatibility is necessary, but time consuming, for the success of hybrid breeding. Jones (1965) proposed a polycross breeding scheme in which 20-30 parental lines are planted in an isolated plot and subjected to open pollination by insects and mass selection to eliminate the pre-screening of cross-compatibility. The polycross strategy has been used in Taiwan to generate many elite sweet potato cultivars such as high yield, high β-carotene, and high protein cultivars. Despite common failure in positive identification of parental lines using morphological markers that are subject to change due to environmental factors and cultural practices (Bernatzky and Tanksley, 1989), polycross breeding has been the major breeding program practiced in Taiwan since 1966. Since then, sweet potatoes of China and Japan and landraces in addition to hybrid- and polycross-derived cultivars have dominated the polycross breeding parental lines in Taiwan.

In sweet potato, random amplified polymorphic DNA (RAPD) has been used in cultivar fingerprinting (Connolly et al., 1994; Hwang et al., 1999), estimation of genetic diversity (Sagredo et al., 1998; Zhang et al., 1998), genome mapping (Ukoskit and Thompson, 1997), and locating a root-knot nematode resistance gene (Ukoskit et al., 1997). Although open pollination by insects and mass selection are practiced in polycross breeding programs, the breeding efficiency is low. In recent years it has become well recognized that PCR-based DNA markers make powerful tools for genetic analysis and for breeding programs because of their simplicity and ease of handling. Primers designed to flank simple sequence repeats (SSRs) loci were developed (Jarret and Bowen, 1994) and used to genotype sweet potato cultivars (Hwang et al., 2002). However, Buteler et al. (1999) reported that in sweet potato, inser-

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tions/deletions and base substitutions occurred in the microsatellite flanking regions, meaning SSR markers may not be appropriate for the study of genetic relationships among sweet potato polycross breeding lines.

Amplification fragment length polymorphism (AFLP) analysis was developed as a PCR-based method for detecting differences in restriction fragments (Vos et al., 1995). Selectively amplification of microsatellite polymorphic loci (SAMPL) analysis (Witsenboer et al., 1997) extends AFLP technology to include amplification of microsatellite loci and might be useful in identifying positive parental lines used in polycross breeding. By combining the advantages of SSR and AFLP, the genetic relationships of core cultivars used in polycross breeding can be obtained, and breeding efficiency can be improved.

Previously, we used SSR markers in determining genetic relationships between elite sweet potato cultivars and found that polycross-derived cultivars originated from various sources (Hwang et al., 2002). However, the results of principal coordinate analysis (PCA) using SSR markers did not support the result of the UPGMA (unweighted pair-group method with arithmetric average) analysis. The discrepancy between UPGMA and PCA in SSR assay suggested that SSR markers are probably not efficient in sweet potato genotyping. In this paper, we examine the SAMPL markers as a remedy to the insertions/deletions and base substitutions inherent in microsatellite flanking regions (Buteler et al., 1999). Therefore, the objective of this investigation was to further analyze by SAMPL analysis the genetic relationships of elite cultivars to be used in polycross breeding in Taiwan.

Materials and Methods

Plant Materials

Cuttings of 22 sweet potato cultivars were kindly provided by the Chiayi Agricultural Research Institute, and seeds of *Ipomoea triloba*, provided by Dr. Hsin-Fu Yen (National Science Museum, Taichung, Taiwan), were planted in the greenhouse. *Ipomoea triloba* was used as an outgroup. Two cultivars were from China, four from Japan, two derived from hybrid breeding, six derived from polycross breeding, and eight were landraces (Table 1). Tainung 67 was derived from a hybrid cross between Nunglin 18 and Nancy Hall, Nunglin 18 being Japanese material. Tainung 57 was derived from a cross between Tainung 27 and Nancy Hall. Nancy Hall, introduced from the USA, was the paternal parent for both Tainung 67 and Tainung 57. Although Taoyuan-2 was classified as a polycross-derived cultivar, it is possibly a clonal variant of the landrace Yongtsai (Liang Li, sweet potato breeder and former director of Chiayi Agricultural Research Institute, personal communication). Chinese Hsusu 18 was derived from a cross between Nancy Hall and Japanese Okinawa 100 (paternal parent). Chinese Litzhsian was derived from a cross between Okinawa 100 and Nancy Hall (paternal parent).

DNA Extraction

Three separate DNA extractions were made for each cultivar. Plant tissue was ground separately into powder in liquid nitrogen for the extraction of genomic DNA based on a modified CTAB procedure (Doyle and Doyle, 1990).

Table 1. Name, origin, and classification of 22 sweet potato cultivars.

Cultivar number	Cultivar name	Country of origin	Symbol	Characteristics	Pedigrees
1	Changhua	Taiwan	◆	Virus-resistant	
2	Hualien PF-1	Taiwan	◆		
3	Hualien PF-2	Taiwan	◆		
4	Kingmen	Taiwan	◆		
5	Penhu RF	Taiwan	◆	High yield	
6	Red flesh	Taiwan	◆	High yield	
7	Yangmingshan PF	Taiwan	◆		
8	Yongtsai	Taiwan	◆	Leafy vegetable	
9	Tainung 57	Taiwan	✖	High vitamin A	Tainung 27 X Nancy Hall
10	Tainung 67	Taiwan	✖	Better starch digestibility	Nunglin 18 X Centennial
11	Tainung 65	Taiwan	■	High protein	
12	Tainung 66	Taiwan	■	Yield stability	
13	Tainung 68	Taiwan	■	High starch	
14	Tainung 70	Taiwan	■	High b-carotene	
15	Tainung 71	Taiwan	■	High yield	
16	Taoyuan-2	Taiwan	■	Leafy vegetable	
17	Hsusu 18	China	●		Nancy Hall X Okinawa 100
18	Litzhsian	China	●		Okinawa 100 X Nancy Hall
19	Okinawa 100	Japan	⊡		
20	Siemen 1	Japan	⊡		
21	Beniazuma	Japan	⊡		
22	Satsumahikari	Japan	⊡		
23	*Ipomoea triloba*			Wild sweet potato	

Symbol representation: Landrace (◆), Hybrid (✖), Polycross (■), Chinese materials (●), and Japanese materials (⊡).

Table 2. Sequences of primers and adaptor used.

Sequence name	Sequence	Annealing temperature
SSR primers		
Ib2/30 F	5´-ACGCATAAGGGTATTGGTGAAG-3´	65-60°C
Ib2/30 R	5´-ACGGAGGATGGTTCAGGTG-3´	
Ib2/42 F	5´-GCGGAACGGACGAGAAAA-3´	65-60°C
Ib2/42 R	5´-ATGGCAGAGTGAAAATGGAACA-3´	
Ib2/55 F	5´-CGTCCATGCTAAAGGTGTCAA-3´	65°C
Ib2/55 R	5´-ATAGGGGATTGTGCGTAATTTG-3´	
Ib3/24 F	5´-TTTGGCATGGGCCTGTATT-3´	65-60°C
Ib3/24 R	5´-GTTCTTCTGCACTGCCTGATTC-3´	
Ib3/28 F	5´-TCGCCTTTCTCTTTGCACC-3´	65°C
Ib3/28 R	5´-CCCCTCTCTTCTACAACCCTTC-3´	
Ib3/31 F	5´-TTCCCTTTCCTTTCCTTCCC-3´	62°C
Ib3/31 R	5´-ACCCCAAATCCCAACTCCA-3´	
AFLP adaptor and primer		
*Eco*RI	5´-CTCGTAGACTGCGTACA-3´	
	3´-CATCTGACGCATGTTTAA-5´	
*Eco*RI primer	5´-GACTGCGTACAAATTCG-3´	

Ground leaf material (300 mg) was placed in 5 ml of extraction buffer (2% CTAB, 0.1 M Tris-HCl (pH 8.0), 0.2 M EDTA, 1.4 M NaCl, 1% N-lauroylsarcosine, 1% SDS, 2% β-mercaptoethanol). The homogenate was incubated at 65°C for 30 min, followed by another extraction with the addition of 50 µg/ml protease K in the extraction buffer and incubated at 55°C for 30 min, followed by an equal volume extraction with chloroform:isoamylalcohol (24:1) and centrifuged for 20 min at 12,800 *g*. The aqueous phase was transferred to a fresh centrifuge tube. Genomic DNA was precipitated with a two-thirds volume of absolute alcohol. Following centrifugation at 12,800 *g* for 10 min, the alcohol was removed, and the DNA pellet was rinsed twice with 75% (v/v) ethanol. The pellet was dried and resuspended in 200 µl TE buffer (pH 8.0) and placed at 4°C. DNA concentration was determined using GeneQuant II RNA/DNA Calculator (Amersham Pharmacia Biotech). The DNAs from three plants of the same cultivar were bulked for the subsequent analysis.

SAMPL Amplification

The selective amplification of microsatellite polymorphic loci method was modified from the strategy of AFLP (Vos et al., 1995), described in Witsenboer et al. (1997). Genomic DNA (300 ng) was first cut with 5 U of *Eco*RI restriction enzyme and then ligated to *Eco*RI adaptor. The *Eco*RI fragments were then subjected to PCR pre-amplification with the annealing of *Eco*RI and SSR primers (Table 2). The pre-amplification mix consisted of 0.1 µM SSR primer, 0.15 µM AFLP primer, 0.25 U *Taq* polymerase, 0.5 µg/µl RNase, and 0.1 µM dNTPs in a reaction buffer (500 mM KCl, 15 mM $MgCl_2$, 100 mM Tris-HCl, pH 9.0). The final volume was 10 µl. The PCR program for pre-amplification was 20 cycles of 30 sec at 94°C, 1 min at 56°C, and 1 min at 72°C. The PCR of the pre-amplification was carried out using a Robocycler GRADIENT 96 temperature cycler (Stratagene). An aliquot of the PCR product (1 µl) was then subjected to a second round of PCR amplification with Cy5 labeled AFLP *Eco*RI primer and SSR primer (Table 2). The second round of PCR reaction was conducted on a DNA Programmable Thermal Cycler (MJ Research). Step 1 of the PCR program was at 94°C for 3 min. Step 2 was 12 cycles of 30 sec at 94°C, 30 sec at 65°C with 0.5°C touchdown per cycle, and 1 min at 72°C. Step 3 was 30 sec at 94°C, 30 sec at 56°C, and 1 min at 72°C for 23 cycles. The last step was 5 min at 72°C. PCR products were separated on an 8% ReproGel High Resolution (Amersham Pharmacia Biotech), using Cy5 labeled 50-500 bp size ladder (Amercham Pharmacia Biotech). Electrophoresis was conducted on an ALF Express II DNA Analysis System, and the DNA fragments were recorded by ALFwin Fragment Analysis 1.01 software (Amercham Pharmacia Biotech).

Data Collection and Analysis

Each SAMPL fragment was treated as a unit character and scored as binary codes (1/0=+/-). Similarity matrices were constructed from the binary data with Jaccard's coefficients (Jaccard, 1908). Jaccard's similarity=*Nab*/*Na*+*Nb*, where *Nab* represents the number of fragments shared by line a and b, *Na* the amplified fragments in sample a, and *Nb* the amplified fragments in sample b. Dendrograms were generated with the UPGMA algorithm as described by Sneath and Sokal (1973). PCA (Gower 1966) was also used to graphically display genetic relationships. All statistical analyses were performed by NTSYS-pc, Version 2.0 (Exeter Software, Setauket, NY).

Results and Discussion

Levels of SAMPL Polymorphisms

Six pairs of SSR primers (12 SSR primers) were used in combination with the *Eco*RI primer to genotype sweet potato cultivars (Table 3). Among 12 SAMPL primer pairs, 7 amplified 19 loci while the other 5 SAMPL primer pairs gave ambiguous banding profiles and were thus excluded from further analysis. Fifty-five alleles were obtained for

Table 3. Number of loci, number of alleles, number of polymorphic bands, and percent polymorphism, produced by SAMPL markers.

Primer pairs	No. of loci	No. of alleles	No. of polymorphic bands	% Polymorphism
Ib2/42 F	1	5	4	80.0
Ib2/42R	4	11	10	90.9
Ib2/55F	2	5	4	80.0
Ib2/28 F	2	4	3	75.0
Ib2/28R	4	13	11	84.6
Ib3/31F	3	8	7	87.5
Ib3/31R	3	9	8	88.9
Total	19	55	47	
Average	2.7	7.9	6.7	85.5

19 amplified loci (Table 3). Of the 55 alleles amplified for 23 genotypes, 47 were polymorphic, and 8 were monomorphic. The percentages of polymorphism for SAMPL analysis ranged from 75.0% to 90.9% and averaged 85.5%. On average, there were 2.7 polymorphic loci, 7.9 alleles, and 6.7 polymorphic alleles per SAMPL primer pairs. Two SAMPL primer pairs produced 4 loci (AFLP+Ib2/42R and AFLP+Ib3/28R), but AFLP+ Ib2/42F generated only single locus markers.

Pejic et al. (1998) reported that AFLP fingerprinting revealed less polymorphism but a much higher number of amplified bands in comparison with RFLP, RAPD, and SSR molecular markers. However, previous researchers found that SSR generated more bands that were polymorphic compared to RFLP, RAPD, and AFLP. The method of SAMPL adopted the advantages of both SSR and AFLP, and produced not only highly polymorphic bands but also a higher number of alleles amplified (Witsenboer et al., 1997). In this study, SAMPL using seven combinations of primer pairs produced 2.4, 2.5, and 2.6 fold increases in the number of loci, number of alleles, and number of polymorphic bands amplified, respectively, compared to previous SSR assays using the same set of sweet potato materials (Hwang et al., 2002). Both the SAMPL assay in this study and the previous SSR study found high levels of polymorphism in elite polycross breeding lines in Taiwan.

Genetic Similarity Among Sweet Potato Cultivars

The frequency of pair-wise similarity coefficients for SAMPL analysis is shown in Figure 1. SAMPL-based Jaccard's coefficient ranged from 0.469 to 0.950, with a mean of 0.691. These results are similar to those of Huang and Sun (2000), who used inter-simple sequence repeats (ISSR) to analyze five sweet potato cultivars and found them to have an average similarity coefficient of 0.658, which was consistent with RAPD data (Connolly et al., 1994). Most SAMPL similarity coefficients ranged from 0.600 to 0.740, accounting for 70.1% of the total frequency of pair-wise similarity coefficients in this study. It is likely that the large genome size, allopolyploidy, and heterozygosity of sweet potato affect the level of polymorphism. Moreover, genetic diversity is maintained for the self-incompatibility and vegetative reproduction present in this

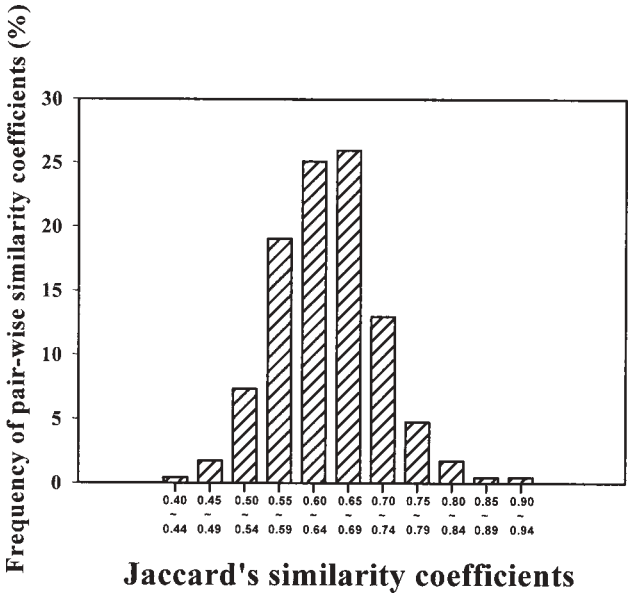

Figure 1. Frequency distribution of pair-wise SAMPL based similarity estimates among 22 polycross breeding lines of sweet potato.

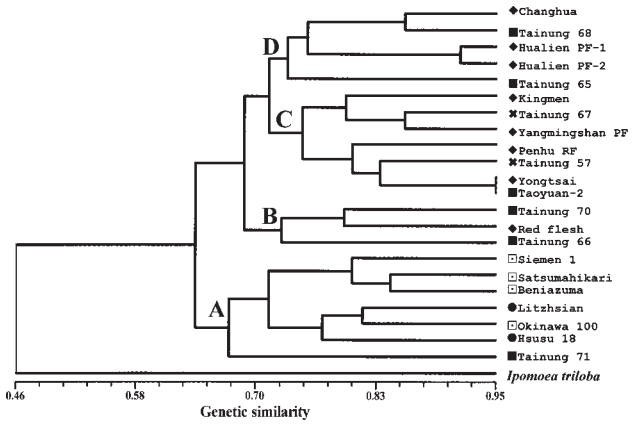

Figure 2. UPGMA based dendrogram of polycross breeding lines generated from SAMPL markers. The numerical scale indicates genetic similarity. Polycross breeding line numbers correspond to Table 1. The symbols for polycross breeding lines are Landrace (◆), Hybrid (✖), Polycross (■), Chinese materials (●), and Japanese materials (⊡).

species. It was reported by He et al. (1995) that high levels of polymorphism among sweet potato plants are fixed through vegetative reproduction and maintained through high levels of gene flow because of the self-incompatibility of this plant. The wide range of genetic variation in the elite polycross breeding cultivars used in Taiwan likely lowers polycross breeding efficiency, especially when parental cultivars are cross incompatible.

Genetic Relationships Among Sweet Potato Cultivars

Similarity matrices based on Jaccard's similarity coefficient were used to perform UPGMA analysis to generate a dendrogram (Figure 2). PCA for SAMPL data supports their UPGMA clustering (Figure 3). The first and second principal coordinates comprised 20.8 and 11.9% of the total variation, respectively. Both UPGMA and PCA analysis showed clear genetic relationships between the 22 sweet potato polycross breeding lines used.

Four major clusters were found by UPGMA analysis with Jaccard's coefficients of 0.644, 0.694, and 0.719. Both UPGMA and PCA clearly separated Chinese and Japanese germplasms from Taiwan landraces, hybrids, and polycross derived cultivars, except Tainung 71. Chinese and Japanese materials were grouped into two separate sub-clusters within cluster A. Okinawa 100, a Japanese cultivar, was grouped into a sub-cluster of cluster A because it is either the paternal or maternal parent of Chinese Shusu 18 and Litzhsian. Okinawa 100, developed by the Okinawa Agricultural Experimental Station in 1934, was introduced into China in 1941 and introduced into Taiwan in 1948. Chinese Litzhsian and Shusu 18 were derived from a cross between Okinawa 100 and Nancy Hall. Another sub-cluster of cluster A has three Japanese cultivars (Siemen-1, Satsumahikari, and Beniazuma). Except for Tainung 71, hybrid and polycross derived cultivars were grouped together with various Taiwan landraces. Tainung 71, a polycross derived cultivar, is closely related to Chinese and Japanese materials. Hualien PF-1, Huanlien PF-2, Changhua, Tainung 68, and Tainung 65 were grouped into cluster D. Kingmen, Taiung 67, and Yangmingshan PF were grouped into one of the two sub-cluster of cluster C. Another sister sub-cluster of cluster C contains Penhu RF, Tainung 57, Yongtsai, and Taoyuan-2. Cluster B consists of Tainung 70, Redflesh, and Tainung 66. Therefore, the results of SAMPL analysis appear appropriate in defining the genetic relationships of the cultivars used in polycross breeding. These results suggest that most landraces in Taiwan might not be cross compatible with Chinese or Japanese germplasms after many years of independent evolution and selection.

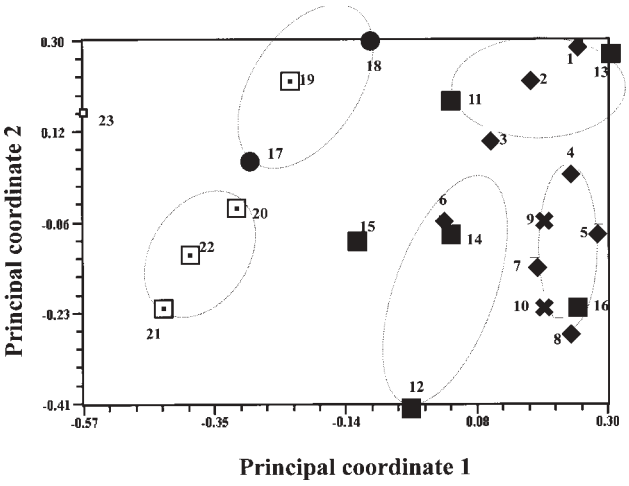

Figure 3. Principal coordinate analysis of 22 sweet potato polycross breeding lines included in this analysis based on SAMPL markers. Polycross breeding line numbers correspond to Table 1. The symbols for polycross breeding lines are Landrace (◆), Hybrid (✖), Polycross (■), Chinese materials (●), and Japanese materials (⊡).

Ipomoea triloba, analyzed by SAMPL, is distantly related to polycross breeding lines (Figure 2). *Ipomoea triloba* was once thought to be the ancestor of cultivated sweet potato (Austin, 1988); however, it is now realized through molecular marker evidence that *Ipomoea trifida* has a much closer genetic relationship with hexaploid sweet potato than *Ipomoea triloba* (Jarret et al., 1992; Huang and Sun, 2000).

In our study, SAMPL was found to be an efficient marker technique for detecting genetic relationships in sweet potato breeding lines and appears superior to microsatellites (Hwang et al., 2002). SSR failed to differentiate the genetic relationships of elite sweet potato cultivars. The SSR failure is probably related to the insertions/deletions and base substitutions in the microsatellite flanking regions as reported by Buteler et al. (1999).

In conclusion, SAMPL markers can be used to efficiently resolve the genetic relationships among polycross parental lines. The ability to resolve better genetic relationships among sweet potato polycross breeding lines may be directly related to the number of loci detected with the SAMPL method. SAMPL probably detected more genetic variation in the microsatellite flanking regions and resulted in better resolution of the genetic relationships among sweet potato polycross breeding lines. Breeders may find SAMPL markers can differentiate different selections of core cultivars for breeding purposes. Also, SAMPL markers may be useful in finding linkages between DNA markers and agronomic traits of interest.

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以 SAMPL 多型性對台灣多向雜交甘藷品種之基因組分型與遺傳關係之解析

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本研究以微衛星多型性基因座選擇性擴增分子標誌 (SAMPL) 分析 22 個台灣多向雜交育種使用之甘藷優良品種之遺傳關係。甘藷優良品種包括來自中國及日本之品種，也有台灣之本地種及經由雜交及多向雜交育種而得之品種。在 12 個 SAMPL 引子對中，有 7 個引子對可擴增出 19 個基因座，另外 5 個引子對所擴增之條待型式模糊不清，不適於進一步分析。擴增出的 19 個基因座總共含有 55 個對偶基因。利用非加權駢對之算術平均數的方法及主座標分析，結果顯示台灣本地種與中國及日本品種有較遠之遺傳關係，此點可能與台灣本地種在經過多年的獨立演化及篩選有關，而很可能的台灣本地種是源自爪哇及婆羅州。再者，多向雜交育成之品種與台灣本地種有較近的遺傳關係，因此利用 SAMPL分子標誌可有效的解析甘藷多向雜交品種之遺傳關係。

關鍵詞：遺傳關係；多向雜交；微衛星多型性基因座選擇性擴增分子標誌；甘藷。