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Genetic variability of Brazilian Indian landraces of *Arachis hypogaea* L.

F.O. Freitas, M.C. Moretzsohn and J.F.M. Valls

Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, Brasil

Corresponding author: F.O. Freitas
E-mail: fabiof@cenargen.embrapa.br

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ABSTRACT. The Kayabi Indians who inhabit the Xingu Indigenous Park, located in West Central Brazil, have grown and managed peanuts for a long time. A great number of landraces are being maintained by these tribes and some of this germplasm has morphological traits that exceed the variation described in the taxonomic literature. Here, we analyzed the genetic variability of these landraces using a set of microsatellite markers. The analysis showed that, in general, the indigenous samples grouped according to the villages where they were collected. The microsatellite markers used in the present study detected high levels of genetic variation. Similarity groups, genetically distant from each other, were formed, allowing a more efficient use of the existing genetic variability. The present study also showed that these materials can extend the genetic variability available for peanut-breeding programs. Additionally, the microsatellite markers revealed a large dissimilarity among germplasm accessions representing *Arachis hypogaea* varieties so far included in the same subspecies *fastigiata* (*aequatoriana* + *peruviana vs fastigiata* + *vulgaris*), a subject that deserves further investigation. Finally, the Xingu Indigenous Park proved to be an important center of diversity for peanut.

Key words: Groundnut, Peanut, Microsatellites, Simple sequence repeat, Genetic relationships

INTRODUCTION

The genus *Arachis* L., family Fabaceae, is native to South America. Central Brazil is its probable center of origin, in a region extending from the southwest of Mato Grosso do Sul State (and the adjacent border of Paraguay) to the south of Goiás (Valls, 2000). The genus contains 80 described species, assembled into nine taxonomic sections (Krapovickas and Gregory, 1994; Valls and Simpson, 2005).

Cultivated peanut (*A. hypogaea* L.) is an allotetraploid (2n = 4x = 40 chromosomes) with an AABB genome formula. It is believed that peanut originated through the crossing of two distinct diploid species (2n = 20 chromosomes), one with an A genome and the other with a B genome. This cross must have been followed by spontaneous duplication of chromosomes, at least in some tissues of the sterile diploid hybrid, which restored hybrid fertility (Halward et al., 1991; Young et al., 1996). The resulting tetraploid plant has been selected and grown in diverse regions of South America for more than 5000 years, and spread worldwide by the time of the European discovery of the New World, or even before that, following pre-Columbian navigation routes in the Pacific Ocean (Krapovickas, 1998).

The exact place where this species originated and the diploid species that crossed to give rise to the first peanut plant have been a subject of debate (Krapovickas and Gregory, 1994; Kochert et al., 1996; Raina and Mukai, 1999; Raina et al., 2001), but the most recent information favors the combination of *A. duranensis* Krapov. & W.C. Greg., carrying the A genome, and *A. ipaënsis* Krapov., W.C. Greg. & C.E. Simpson, as the B genome parent. This is very well illustrated with fluorescent *in situ* hybridization studies by Seijo et al. (2004), and the sequence of events was recently reconstructed by Fávero et al. (2006), who crossed the two species, artificially doubling the chromosomes of the sterile hybrid, and successfully crossed the amphidiploid with representatives of all six botanical varieties of *A. hypogaea*, obtaining fertile progenies. However, it is still not well established if this was via a unique domestication event or if the crossing and duplication occurred more than once, at different locations and in distinct periods, and perhaps involving distinct diploid species (Simpson et al., 2001).

Arachis hypogaea is classified, based on the presence or absence of flowers on the main axis, into two subspecies, *hypogaea* and *fastigiata* Waldron. These two subspecies were further classified into six botanical varieties, based on morphology and growth habits. The subspecies *hypogaea* was divided into two botanical varieties, *hypogaea* and *hirsuta* Köhler, while subsp. *fastigiata* was divided into the varieties *fastigiata*, *vulgaris* Harz, *aequatoriana* Krapov. & W.C. Greg. and *peruviana* Krapov. & W.C. Greg. (Krapovickas and Gregory, 1994). However, even these cited authors have hypothesized that more than two diploid species could have been involved in the origin of the peanut, considering the differences detected on the satellited chromosomes between the two subspecies. This hypothesis becomes more likely from the analysis of germplasm accessions collected in the Xingu Indigenous Park (Parque Indígena do Xingu) and surroundings, which have morphological traits, especially in the pods, exceeding the variation described (Freitas and Valls, 2001).

The Xingu Indigenous Park, located in the north-northeastern part of Mato Grosso State in Brazil (Figure 1), was officially created on April 14, 1961, covering an area of almost 30,000 km^2 (Novaes, 1985). It is located in a transition area between the savanna biome to the south, and the Amazon Forest to the north. This region was first visited and documented in 1884 by Karl von den Steinen, who described some cultural aspects and the geographic

location of several indigenous tribes (Steinen, 1942). Many of these tribes still live in this area, such as the Kamaiurá, Suiá, Yawalapiti, and Waurá, but others were transferred to there after the official creation of the Park, such as the Kayabi (Villas Boas and Villas Boas, 1976; Ferreira, 1994). Nowadays, more than 4000 Indians from 14 different ethnic groups, belonging to six linguistic families live in the Park, which is evidence of the great cultural diversity that exists in that area.

Figure 1. Map of Brazil and its states. The detail in the center, in the State of Mato Grosso (MT), shows the location of the Xingu Indigenous Park, where most of the samples were collected.

The Kayabi Indians belong to the Tupi linguistic family, and originally occupied the region located in the northwest of Mato Grosso State and southwest of Pará State, but gradually migrated eastward to the Park during the last four decades. Fourteen tribes (or villages) of the Kayabi Indians are still living in the Park. These Indians have grown and managed peanut for a long time, and this plant is one of the most important for this people, both as a food and culturally. As a consequence, a great number of landraces are being managed and maintained by this tribe (Figure 2).

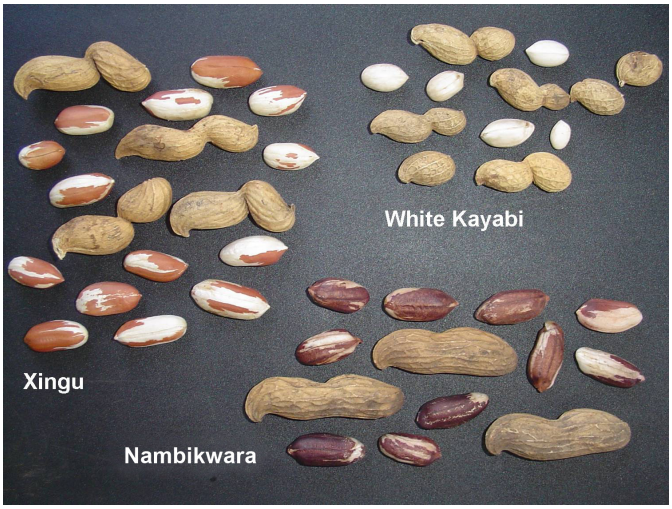

Figure 2. The three main peanut landrace types managed by the Kayabi Indians.

The objectives of the present study were to analyze the genetic variability of peanut samples collected in two Kayabi villages in the Xingu Indigenous Park and to compare it to the six described varieties of *A. hypogaea*.

MATERIAL AND METHODS

Plant material

Thirty samples of ethnovarieties obtained in 1999 from two Kayabi villages (Guarujá and Ilha Grande) located in the Xingu Indigenous Park, in Mato Grosso State, were included in the present study (Table 1). This set of samples does not necessarily represent the whole peanut diversity presently existing, nor does it mean that all the peanut types ever cultivated by the two families (villages) were included. Moreover, 12 additional accessions of *A. hypogaea* were included, which comprised 1 or 2 from each of the six described peanut varieties plus one accession collected in the surroundings of the Xingu Indigenous Park in 1990 (accession V 12549). Finally, samples of five wild *Arachis* species were analyzed: *A. monticola* Krapov. & Rigoni, *A. ipaënsis*, *A. duranensis*, *A. stenosperma* Krapov. & W.C. Greg., and *A. villosa* Benth. These 17 samples were obtained from the *Arachis* germplasm collection maintained by Embrapa Recursos Genéticos e Biotecnologia - CENARGEN, in Brasília, DF, Brazil (Table 1).

DNA isolation and microsatellite loci assay

Total genomic DNA was extracted from young leaves according to the protocol described by Grattapaglia and Sederoff (1994), with some modifications, that is, proteinase K (20 mg/mL) was added to the extraction buffer and an additional step of polysaccharide precipitation with 1.2 M NaCl was included.

Polymerase chain reaction of simple sequence repeat (SSR) loci was performed in 13-µL volumes, containing 1X polymerase chain reaction buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl,

Table 1. *Arachis* spp accessions analyzed in the present study. Numbers in parentheses, after some *Arachis hypogaea* accession numbers, correspond to codes included in the dendrogram (Figure 4).

Species/subspecies/variety (type)	Collection site	Accession number	Accession code (BRA)
Arachis hypogaea subsp. *hypogaea* var. *hypogaea*	Pará, Brazil	Pd 3324 (HH1)	029807
A. hypogaea subsp. *hypogaea* var. *hypogaea*	Tocantins, Brazil	V 13009 (HH2)	030015
A. hypogaea subsp. *hypogaea* var. *hypogaea*	Aldeia Kayabi Ilha Grande*	Of 120	040657
A. hypogaea subsp. *hypogaea* var. *hirsuta*	Pichincha, Ecuador	Mf 1538 (HHi)	037397
A. hypogaea subsp. *fastigiata* var. *aequatoriana*	Morona, Ecuador	Mf 1640 (FA1)	037427
A. hypogaea subsp. *fastigiata* var. *aequatoriana*	Sucurubios, Ecuador	Mf 1678 (FA2)	037435
A. hypogaea subsp. *fastigiata* var. *fastigiata*	Tocantins, Brazil	V 12896 (FF1)	029858
A. hypogaea subsp. *fastigiata* var. *fastigiata*	Minas Gerais, Brazil	Pd 2656 (FF2)	023876
A. hypogaea subsp. *fastigiata* var. *peruviana*	Pastaza, Ecuador	Mf 1560 (FP1)	037401
A. hypogaea subsp. *fastigiata* var. *peruviana*	Yurimaguas, Peru	Sv 429 (FP2)	033065
A. hypogaea subsp. *fastigiata* var. *vulgaris*	Rivera, Uruguay	FT 85273 (FV1)	036200
*A. hypogaea*subsp. *fastigiata* var. *vulgaris*	Rivera, Uruguay	FT 85062 (FV2)	027251
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Guarujá	Of 103	037605
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Guarujá	Of 113	037702
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Guarujá	Of 114	033711
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Ilha Grande	Of 117	039357
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Ilha Grande	Of 119	039373
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Ilha Grande	Of 123	040673
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Ilha Grande	Of 125	040690
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Ilha Grande	Of 128	040711
A. hypogaea ("Nambikwara" type)	Aldeia Kayabi Ilha Grande	Of 129	040720
A. hypogaea ("Xingu/Nambikwara" intermediate)	Aldeia Kayabi Guarujá	Of 104	037613
A. hypogaea ("Xingu/Nambikwara" intermediate)	Aldeia Kayabi Ilha Grande	Of 115	039331
A. hypogaea ("Xingu/Nambikwara" intermediate)	Aldeia Kayabi Ilha Grande	Of 118	039365
A. hypogaea ("Xingu" type)	Aldeia Kayabi Guarujá	Of 105	037621
A. hypogaea ("Xingu" type)	Aldeia Kayabi Guarujá	Of 106	037630
A. hypogaea ("Xingu" type)	Aldeia Kayabi Guarujá	Of 107	037648
A. hypogaea ("Xingu" type)	Aldeia Kayabi Guarujá	Of 108	037656
A. hypogaea ("Xingu" type)	Aldeia Kayabi Guarujá	Of 109	037664
A. hypogaea ("Xingu" type)	Aldeia Kayabi Guarujá	Of 110	037672
A. hypogaea ("Xingu" type)	Aldeia Kayabi Guarujá	Of 111	037681
A. hypogaea ("Xingu" type)	Aldeia Kayabi Ilha Grande	Of 116	039349
A. hypogaea ("Xingu" type)	Aldeia Kayabi Ilha Grande	Of 121	039462
A. hypogaea ("Xingu" type)	Aldeia Kayabi Ilha Grande	Of 122	040665
A. hypogaea ("Xingu" type)	Aldeia Kayabi Ilha Grande	Of 124	040681
A. hypogaea ("Xingu" type)	Aldeia Kayabi Ilha Grande	Of 126	039471
A. hypogaea ("Xingu" type)	Aldeia Kayabi Ilha Grande	Of 127	040703
A. hypogaea ("Xingu" type)	Aldeia Kayabi Ilha Grande	Of 130	040738
A. hypogaea ("Xingu" type)	Mato Grosso, Brazil	V 12549 (Xingu)	030716
A. hypogaea ("White Kayabi" type)	Aldeia Kayabi Guarujá*	Of 101	037583
A. hypogaea ("White Kayabi" type)	Aldeia Kayabi Guarujá	Of 102	037591
A. hypogaea ("White Kayabi" type)	Aldeia Kayabi Guarujá	Of 112	037690
A. duranensis	Salta, Argentina	V 14167	036200
A. ipaënsis	Tarija, Bolívia	K 30076	036234
A. monticola	Jujuy, Argentina	V 14165	036188
A. stenosperma	Mato Grosso, Brazil	V 12575	030767
A. villosa	Artigas, Uruguay	V 12812	030813

*Both Kayabi villages (Guarujá and Ilha Grande) located in the Parque Indígena do Xingu (Xingu Indigenous Park), Mato Grosso State, Brazil.

1.5 mM $MgCl_2$), 0.2 mM of each dNTP, 1 unit *Taq* DNA polymerase, 2.5 µg/µL (1.3 µL) purified BSA, 3.5 pmol of each primer, and 10 ng genomic DNA. Amplifications were performed using a PTC-100 (MJ Research) thermal cycler, with the following conditions: 94°C for 5 min (1 cycle),

94°C for 1 min, 55-66°C for 1 min, 72°C for 1 min (30 cycles), and 72°C for 7 min (1 cycle). Each primer pair had an optimum annealing temperature. Amplified fragments were separated on 5% denaturing polyacrylamide gels stained with silver nitrate (Creste et al., 2001). Fragment sizes were estimated by comparison with a 10-bp DNA ladder standard (Gibco/BRL, MD).

Thirteen polymorphic SSR markers published for peanut were included in the analysis: Ah4-20, Ah4-24, Ah4-26, Ah6-125, and Lec-1 (Hopkins et al., 1999), PM3, PM36, and PM50 (He et al., 2003), Ah-041, Ah-193, and Ah-558 (Moretzsohn et al., 2004), Ah26 and Ah51 (Gimenes et al., 2007).

Data analysis

Genetic relationships among the 47 accessions were evaluated using the 13 SSR markers. Each band was treated as a unique character and scored as present (1) or absent (0). The data matrix was used to calculate the Jaccard (1908) similarity coefficient. Dendrograms were constructed using the unweighted pair-group method analysis. These analyses were performed using NTSYS-pc software, version 2.02 (Rohlf, 2000).

RESULTS AND DISCUSSION

Genetic similarities among accessions were estimated by the presence or absence of bands in 42 accessions of *A. hypogaea* and five accessions of *Arachis* section *Arachis* wild species, using 13 SSR primer pairs. An example of an SSR amplification pattern obtained with marker Ah4-26 on polyacrylamide gel is shown in Figure 3. Among the 42 *A. hypogaea* accessions, the average Jaccard similarity value was 0.647. The lowest value (0.375) was observed between accessions FT 85062 (*fastigiata* var. *vulgaris*) and Mf 1560 (*fastigiata* var. *peruviana*). Only one pair of accessions could not be differentiated using these primers and showed a similarity value equal to 1.000 (Of 115 and Of 118). Considering the wild species, *A. monticola* showed high similarity to *A. hypogaea* accessions. *A. ipaënsis* showed no common alleles with both *A. duranensis* and

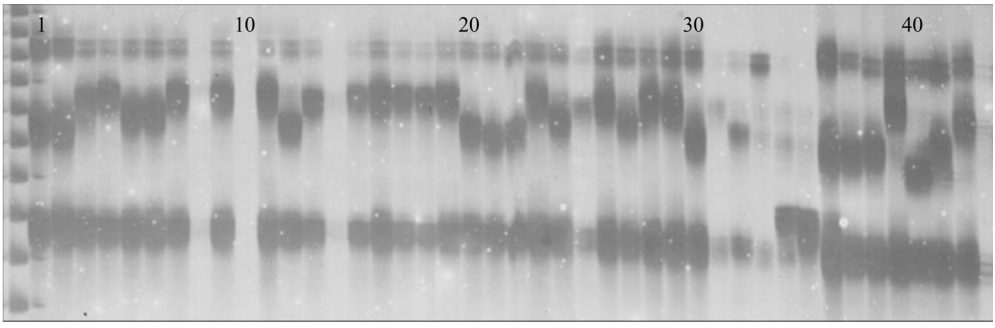

Figure 3. Polymorphism in *Arachis* species obtained with simple sequence repeat marker Ah4-26 visualized on a silver-stained denaturing 5% polyacrylamide gel. The first 30 lanes are samples from the Xingu Park followed by *Arachis magna* (not included in the analysis), *A. monticola*, *A. ipaënsis*, *A. villosa*, *A. stenosperma*, *fastigiata/vulgaris*1 (FT 85273), *fastigiata/vulgaris*2 (FT 85062), *hypogaea/hypogaea*1 (Pd 3324), *fastigiata/peruviana*1 (Mf 1560), *fastigiata/aequatoriana*1 (Mf 1640), *fastigiata/aequatoriana*2 (Mf 1678), *fastigiata/fastigiata*1 (V 12896), *fastigiata/fastigiata*2 (Pd 2656), *hypogaea/hirsuta*, *A. duranensis*, *A. hypogaea* ("Xingu" type - V 12549), *hypogaea/hypogaea*2 (V 13009), *fastigiata/peruviana*2 (Sv 429). A 10-bp ladder was loaded on the left side of the *Arachis* lanes.

A. *stenosperma*, with similarity values equal to zero. Comparing the relationships between *A*. *hypogaea* accessions and the diploid species, the highest similarity value (0.412) was observed between Of 111 from the Xingu Indigenous Park and the *A*. *duranensis* accession.

An unweighted pair-group method analysis dendrogram based on Jaccard's similarity was constructed for the 47 section *Arachis* accessions (Figure 4). The *A*. *monticola* accession grouped with the *A*. *hypogaea* accessions, and it could not be separated from the cultivated species using the 13 SSR markers. The four diploid species formed a separate group. *A*. *duranensis* followed by *A*. *ipaënsis* showed the highest similarity values as compared to the *A*. *hypogaea* group. Considering only the *A*. *hypogaea* and *A*. *monticola* accessions, four main groups were evident. Group I contained the two *fastigiata/peruviana* accessions, the two *fastigiata/aequatoriana*, and 11 accessions collected in the Xingu Park. Eight of the indigenous accessions of this group have thin and smooth fruit shell and the pod constricted in the middle, which can be easily broken into two segments. For practical reasons, they are differentiated as the "Xingu" type in Table 1. The three additional local landraces have a hard shell and a densely reticulated pod, and only white seeds. This less frequent type is differentiated as the "White Kayabi" in Table 1. Within this group, four minor groups were formed, separating samples collected in the two different villages. Group I-a was composed of five accessions from Guarujá tribe (Of 101, Of 102 and Of 112 - the three representatives of the "White Kayabi" type, plus Of 105 and Of 106, of the "Xingu" type) and one

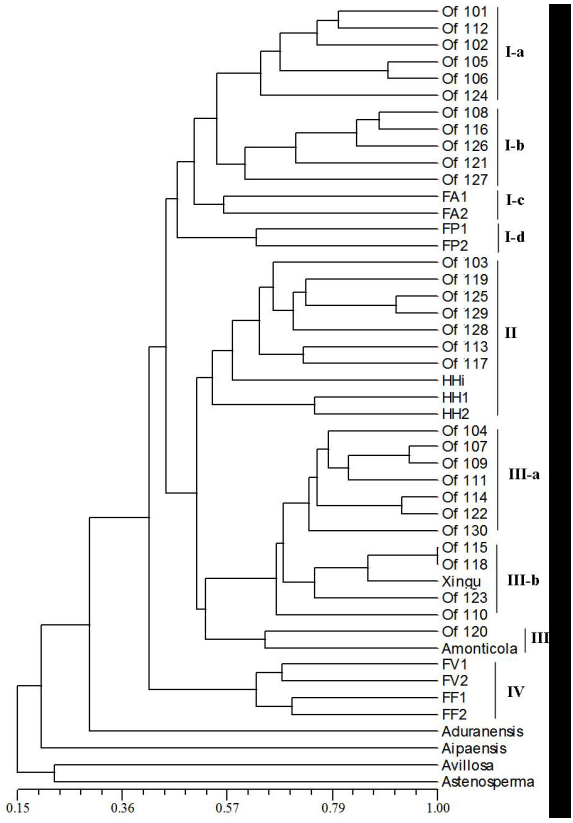

Figure 4. Dendrogram for 42 *Arachis hypogaea* accessions and 5 wild *Arachis* species generated by unweighted pair-group method analysis. Accession numbers and codes are identified in Table 1.

from Ilha Grande (Of 124 - also "Xingu" type) which was the most distant. Group I-b had four accessions from Ilha Grande (Of 116, Of 121, Of 126, and Of 127) and one from Guarujá (Of 108), all of the "Xingu" type. The two *fastigiata/aequatoriana* and the two *fastigiata/peruviana* accessions formed the third and the fourth (I-c and I-d) minor groups, respectively.

Group II contained the two *hypogaea/hypogaea* accessions, the *hypogaea/hirsuta* accession, and seven accessions collected in the Xingu Park, five being from the Ilha Grande tribe and two from Guarujá. Indigenous samples of this group are morphologically distinguished as the "Nambikwara" type, characterized by very large seeds, straight pods with prominent longitudinal ridges, and a thick, hard fruit shell, corresponding to *A. nambyquarae* Hoehne, a taxon presently included in the synonymy of *A. hypogaea* subsp. *hypogaea* var. *hypogaea* (Krapovickas and Gregory, 1994). In fact, their closest association was with the three typical representatives of that subspecies, but including both *hypogaea* and *hirsuta* varieties.

Group III was composed of the *A. monticola* accession and 13 accessions from Xingu, including the one collected in 1990, in the surroundings of the Park (V 12459) and identified as Xingu in the dendrogram (Figure 4). Indigenous plants of this group are not as morphologically homogeneous as in groups I and II, and the reasons why they grouped together are not clear. Local landraces included in group III can be mostly assigned to the "Xingu" type, but include three accessions that are morphologically intermediate between the "Nambikwara" and "Xingu" types and a rare accession of the "Nambikwara" type with small pods. However, this result showed that the accessions collected in the Xingu area have expanded the known genetic variability of the cultivated peanut. The indigenous accessions were divided into three minor groups (III-a,b,c). One such minor group (III-c) joined the *A. monticola* accession and one sample from the Xingu Park (Of 120). *A. monticola*, the only tetraploid species in section *Arachis* besides *A. hypogaea*, is considered to be the probable ancestor of the cultivated peanut (Halward et al., 1991; Kochert et al., 1991; Lu and Pickersgill, 1993; Hilu and Stalker, 1995) or eventually a derivative retaining wild characteristics, branched along the evolution of the peanut (Krapovickas and Gregory, 1994). The clustering of *A. monticola* and Of 120 in this group is in agreement with the ethnobotanic information obtained from the Kayabi Indians, who said that this sample was the most antique type of peanut cultivated by them. This peanut is known to the Indians by the name of "peanut of the field", and was grown in their former lands, before their migration to the Park. This result shows the importance of preserving the traditional knowledge of the Indians, which can be very useful in combination with experimental analysis.

The fourth main group (group IV) contained the two *fastigiata/fastigiata* and the two *fastigiata/vulgaris* accessions (Figure 2).

The dendrogram shows that, in general, the indigenous samples grouped according to the villages where they were collected. Although belonging to the same ethnic group (Kayabi), peanut samples maintained by the two villages are genetically differentiated, suggesting that exchange of samples between these two villages has been rare and that they have grown different types of peanut. This fact becomes evident, for example, in group I. In group I-a only one sample of six was from Ilha Grande, while group I-b had four accessions from Ilha Grande and only one from Guarujá. This differentiation can be explained by their life history. Each tribe is, in fact, a family group who inhabited a different region in their original lands, in the northwest of Mato Grosso State and southwest of Pará State. Moreover, Indians from the Ilha Grande

tribe lived far from the other Kayabi villages before their migration to the Xingu Indigenous Park. Thus, traditionally, both villages had maintained political isolation, which resulted in difficulties in the exchange of peanuts between them. This fact has favored the differentiation of types, which was confirmed in the analysis of genetic relationships by the separation of the samples collected in each village. The present analysis also showed that Indians from the two villages have managed a large genetic variability, and that they have used peanuts for a long time, maintaining and expanding the genetic variability of their traditional cultivation.

The SSR markers used in the present study detected high levels of genetic variation. Similarity groups, genetically distant from each other, were formed. The establishment of similarity groups, jointly with morphologic and agronomic data, can be used in the selection and crossing of superior plants, allowing a more efficient use of the existing genetic variability. Studies of molecular characterization of cultivated peanut have rarely included the "Xingu" and "Nambikwara" types, and probably never included the less common "White Kayabi" type. The present study also showed that these materials can extend the genetic variability available for peanut breeding programs. Additionally, the SSR markers revealed a large dissimilarity between germplasm accessions representing *A. hypogaea* varieties so far included in the same subspecies *fastigiata* (*aequatoriana* + *peruviana vs fastigiata* + *vulgaris*), a subject that deserves further investigation. An analysis of the genetic relationships among more than 200 *A. hypogaea* accessions belonging to the six known varieties and including some more accessions collected in Xingu Park is currently underway at Embrapa Recursos Genéticos e Biotecnologia and will probably explain some of the results obtained here.

The Xingu Indigenous Park proved to be an important center of diversity for peanut together with the west of Mato Grosso State, where the Kayabi lived before their migration to the Park. This region is located along the southern border of the Amazon Forest, a region considered to be a domestication area for several plant species, including cassava (*Manihot esculenta* Crantz) (Piperno and Pearsall, 1998; Olsen and Schaal, 2001).

Finally, it can be concluded that the Kayabi Indians have an important material that needs to be maintained and better studied. It must be recognized that eventual economic benefits of any future use of this material under millenary maintenance and management, should no doubt be shared with the Kayabi people.

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