Euphytica **120:** 143–157, 2001.

Traditional management of cassava morphological and genetic diversity by the Makushi Amerindians (Guyana, South America): Perspectives for on-farm conservation of crop genetic resources

Marianne Elias[1]*, Doyle McKey[1], Olivier Panaud[2], Marie Charlotte Anstett[1] & Thierry Robert[2]
[1]*Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France;* [2]*Laboratoire Evolution et Systématique, bâtiment 360, Université Paris-Sud, 91405 Orsay cedex, France; (*author for correspondence)*

Key words: cassava, genetic resources, management, *Manihot esculenta*, morphological diversity, traditional agroecosystem

Summary

In this paper we present original data on morphological and genetic diversity of cassava managed by the Makushi Amerindians from Guyana. Although they propagate cassava exclusively vegetatively by means of stem cuttings, many Amerindian farmers also use and multiply volunteer plants grown from seeds produced by sexual reproduction. Morphological characters were recorded for 29 varieties cultivated by the Makushi and two populations of plants originating from volunteer cassava seedlings. Genetic characterisation with AFLP markers was available for 21 of the examined varieties. The morphological and agronomic characters were highly variable among varieties. Every variety could be differentiated from any other one, except for one pair of varieties. However, high intra-varietal variability existed, which might lead to confusions between phenotypically similar varieties by the Makushi. Seedlings were on average different from the pool of the varieties studied, but 67% were found to resemble closely enough one of the varieties to be liable to be assigned to it. Confusion between very similar varieties, as well as assignment of seedlings to a variety, should generate genetic variability within varieties, which was detected with AFLP markers. As in other sites in Amazonia, there was only a weak correlation between inter-varietal distances assessed with molecular and with morphological markers, suggesting that diversification of morphological characters has taken place repeatedly and independently across the Amazonian range of the crop. Diversifying selection, exchanges of varieties between farmers, and incorporation of sexually produced volunteer plants are key mechanisms responsible for the high diversity observed. Strategies of conservation of genetic resources should take these dynamic processes into account.

Introduction

Most attempts to conserve diversity of crop plants concern their incorporation in *ex situ* collections. The limitations of this approach are now widely recognised, motivating the search for alternative strategies of conservation of genetic resources such as on-farm strategies, which allow evolutionary forces to shape the pattern of diversity. Indeed, in traditional agroecosystems crop diversity is usually high (see Brush, 1995 for a review) and dynamic evolutionary processes are usually operating, including both human and natural selection (Salick, 1995). Development of on-farm conservation strategies requires (1) characterising crop diversity and (2) documenting the processes (cultural and ecological) that affect gene flow, which are thereby responsible for the observed patterns of diversity.

In management of genetic resources, the variety is often considered to be the unit of conservation. In the case of traditional farming systems, the concept of variety can encompass very diverse genetic entities subject to evolution. Two main factors contribute to such a situation. First, traditional naming and classi-

fication systems are often based on traits that are perceived subjectively, thereby subject to inter-individual variations in their use or interpretation. Confusion between varieties or use of different names for the same entity can occur. Second, different varieties often coexist within a single field, which could promote gene flow between varieties through hybridisation. Existence of gene flow also raises the question of mechanisms responsible for maintenance of the phenotypic distinctiveness of varieties. Determining the relationship between basic units in traditional classification systems, on the one hand, and the structure of genetic variability in traditional farming systems, on the other, is thus essential to define genetic entities that will be used as targets for efforts of conservation of genetic resources. Such an approach requires an analysis of both agro-morphological characters, used in local classification and under human-driven selective pressures, and neutral molecular markers, which reflect the history of varieties and gene flow among them.

In this paper we study the example of traditional cultivation of cassava (*Manihot esculenta* Crantz, Euphorbiaceae) by the Makushi Amerindians of Region IX of Guyana. Region IX, which is the largest of the 10 administrative regions of Guyana, is located in the south-western part of the country, and shares a border with Brazil. Vegetation includes forest and savannah. In terms of total production, cassava is the fourth most important starch crop grown in the world. The genus *Manihot* is neotropical (Rogers & Appan, 1973), but cassava is now cultivated in all tropical regions, where it is grown for its starchy tuberous roots. Cassava is vegetatively propagated by means of stem cuttings, obtained during the harvest, when the entire plant is pulled out. 'Bitter' varieties, the roots of which are characterised by high cyanide content and are toxic, require detoxification before consumption (Dufour, 1995), whereas sweet varieties, characterised by low cyanide content, are eaten safely without detoxification, after simply being boiled or roasted. In Amazonia, bitter cassava is the staple crop for most indigenous and mixed groups (McKey & Beckerman, 1993), including the Makushi. The Makushi practice slash-and-burn agriculture, in which a field cleared in forest or old fallow is cultivated for two or three years, and then left fallow for five to more than 10 years (sometimes up to 30 years). Bitter cassava is the only crop planted in the fields, but different varieties are mixed in the same field. Farmers often exchange varieties, both within a village and with relatives in other villages. Moreover, they sometimes incorporate into the harvest and into propagation material volunteer cassavas grown from seeds, the product of sexual reproduction. Such volunteer plants (hereafter referred to as seedlings) are found in new fields cleared in old fallows, because they come from seeds produced during the former cultivation period, that remained dormant in a soil seed bank during fallow (Elias & McKey, 2000).

Morphological and agronomic characters were recorded for 29 varieties of cassava grown by the Makushi in a single village and for two populations of plants originating from seedlings. We present here an analysis of the diversity based on these characters. Twenty-one of these varieties had been previously characterised with AFLP markers (Elias et al., 2000), and we used these molecular data to compare the pattern of diversity at the morphological and molecular levels. We also examined cultural and natural factors, especially the role of sexual reproduction, that may act on the origin and maintenance of diversity.

Material and methods

Study site

Most of the field work was conducted in Rewa, a Makushi community of 30 households on the Rupununi River in Guyana. At least 76 varieties of bitter cassava and two of sweet cassava are cultivated in Rewa (Elias et al., 2000). By 'variety', we mean what farmers recognise as units of selection. Each variety is given a single denomination by a farmer, and often the name for a given variety is agreed upon by all farmers. Some varieties that share part of their name are differentiated by additional qualifications, e.g., short and tall types of 'caiman stick'. Other Makushi villages in the same region were also visited, to confirm that cultivation practices were similar.

Cultivation practices

Interviews, questionnaires, observations and participatory observations were conducted, in order to understand cultivation practices (Elias et al., 2001).

Morphological diversity

Experimental design

On a plot made available to us by Rewa villagers, we planted a common garden experiment to compare phenotypic traits of different varieties. The common

Table 1. Varieties for which morphological and agronomic characters (this study), and AFLP genetic markers (Elias et al., 2000) were characterised

code in this study	Makushi name	English name	sample size in this study	sample size for AFLP based genetic characterisation (codes used in Elias et al., 2000)
2	ainis pîye	Inez stick	30	
5	amuru pîye (= isman pîye)	thick stick (= Isman stick)	46	5 (E25)
6	anra pîye	crane stick	26	5 (E6)
7	fatpoi pîye	Fat Boy stick	38	4 (E7)
8	kraiwa pîye	Brazilian stick	30	
12	eti pîye	Eddie stick	33	3 (E12)
14	kaima pîye (= eri pîye)	pumpkin stick (= Ely stick)	26	8 (E14, E18)
17	sona pîye	Johna stick	17	5 (E17)
19	kasiri pîye	kasiri stick	26	4 (E19)
21	kini'pîye	dry stick	32	5 (E21)
22	kuraatuma pîye (short)	caiman stick (short)	30	5 (E22)
23	kurarî pîye	corral stick	28	4 (E23)
24	kuraswa pîye	Crash Water stick	30	
26	paranakîrî pîye itakon ye (= naman pîye)	white man stick cousin (= Naman stick)	32	8 (E26, E34)
31	mai pîye	bitter stick	22	
36	paakaima ye	buffalo stick	32	
39	pîrîkwa pîye	bird stick	30	5 (E39)
40	paranakîrî pîye	white man stick	30	4 (E40)
43	sapîrî pîye	fine fish stick	25	4 (E23)
47	siment pîye	cement stick	30	3 (E47)
48	supra pîye	cutlass stick	16	4 (E48)
49	tarekaya pîmoi pîye	water turtle egg stick	74	4 (E49)
54	wo' ye	drink stick	31	
57	siwal pîye (= uwi pîye)	Sea Wall stick (= farine stick)	32	3 (E53)
58	kana (brown stem)	sweet cassava (brown stem)	17	5 (E58)
59	kuraatuma pîye (tall)	caiman stick (tall)	30	
60	reni pîye	Renie stick	32	5 (E41)
112	zacari pîye	Zaccharie stick	20	5 (E45)
118	kana (white stick)	sweet cassava (white stem)	38	
A	population of seedlings in the first field		35	
N	population of seedlings in the second field		35	

garden was constituted of 15 blocks. In each block, we prepared 35 hoed mounds, for each of 35 varieties (including two sweet varieties) selected for this experiment and representative of the phenotypic and agronomic diversity of the varieties cultivated in the village. In each mound, we planted three cuttings of the same variety. We followed Makushi practices in preparation of mounds and planting. Cuttings were donated by Makushi farmers, and the location of the varieties within each plot was randomised using a random number generator program. When the plants were eight months old, identity of each variety was checked with a Makushi assistant. Because of problems of synonymy and homonymy, misclassification was found for some plants, and we had to exclude 6 varieties from the analysis, keeping 27 bitter and both sweet varieties (Table 1). For all of these, 14 morphological characters that are important for the identification of varieties by farmers and four agronomic traits were recorded on two individuals per mound, eight months

Table 2. Morphological and agronomic characters used to characterise 29 cassava varieties and 70 seedlings

	characters	description	measured on seedlings
morphological characters	nbstem	number of stems produced by the initial cuttings	no
	basdiam	basal diameter of the largest stem	yes
	ram	degree of ramification (number of orders of branching)	yes
	nblobe	number of lobes per leaf	yes
	arealobe	length × width of the middle lobe (indicator of the area of the leaf)	yes
	ratiolobe	width/length of the middle lobe (indicator of the shape of the leaf)	yes
	petiolg	length of the petiole	yes
	yglcol	colour of young leaves	yes
	petiocol	colour of the petiole	yes
	stemcol	colour of the stem	yes
	rootcol	external colour of the root	no
	peelcol	colour of the inner peel of the root	no
	pulpcol	colour of the pulp of the root	no
	nbroot	number of roots	no
agronomic characters	wroot	total weight of the roots (production)	no
	drymat	percentage of dry matter in the roots	no
	nbinflo	total number of inflorescences (including old ones) counted on the plant	no
	mf	multiplication factor, i.e., number of usable cuttings obtained from the plant	no

after planting (Table 2). Colour of the pulp of the root was considered as a morphological variable, although it is also an important trait under human diversifying selection (Elias et al., 2001). Colours varied continuously in the different organs from deep colours (i.e., purplish colours) to light colours (i.e., green, grey, white, or brown for the inner peel) and were recorded semi-quantitatively, from the lightest to the deepest for petiole, young leaves, stem and pulp, and from the deepest to the lightest for roots and for the inner peel. To estimate the multiplication factor, we asked an assistant to cut the stems into cuttings, as she would do if preparing them to plant in her farm. A subset of the morphological characters (Table 2) was used to characterise two populations of seedlings originating from two fields belonging to two different farmers (Table 1). Recording the other characters (mainly characters of the roots) of these plants would have required their destruction, and we did not want to impose this on owners of the field. Both fields had been cultivated for two years (two crops), and then left fallow for five years.

Statistical analysis

Univariate analysis. Analysis of variance was performed, and correlations between variables were examined using procedures GLM and CORR, respectively, of the SAS program (SAS, 1996). Correlations were calculated using the mean values of variables for each variety. For the analysis of variance both 'block' and 'variety' variables were specified as random variables. The Tukey-Kramer test (Sokal & Rohlf, 1985), appropriate when classes have different size, was used to compare means of characters among varieties.

Multivariate analysis. In order to describe the structure of morphological diversity, and to view the diversity of the seedlings compared to that of the varieties, principal component analysis in which seedlings were plotted as supplementary individuals was performed on the 29 varieties using the subset of morphological variables (program XLSTAT 4.3, 1999). Discriminant analyses were performed with STATISTICA software 5.1 (1997). A first discriminant analysis was conducted with all morphological characters on the 29 varieties to assess the possibility of confusions between varieties and to test the relative importance of morphological variables in discrimination of the vari-

Table 3. Means ($\bar{x}$) and coefficient of variations (v = $\sigma/\bar{x}$, σ being the standard deviation) of 14 morphological characters and 4 agronomic traits

Variety	nbstem		basdiam		branching		nblobe		arealobe		ratiolobe		petiolg		yglcol		petiocol	
	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v
2	1.73	0.46	15.04	0.15	1.70	0.62	4.83	0.29	30.63	0.29	0.18	0.33	13.61	0.25	1.77	0.46	5.87	0.06
5	2.30	0.40	14.90	0.14	1.74	0.66	4.25	0.20	41.86	0.17	0.32	0.31	13.49	0.26	1.26	0.35	4.83	0.15
6	1.75	0.49	17.64	0.16	2.42	0.42	3.79	0.28	27.71	0.21	0.22	0.55	9.78	0.21	3.31	0.19	5.15	0.10
7	1.71	0.40	17.68	0.20	3.32	0.27	2.96	0.40	37.36	0.36	0.32	0.34	9.44	0.33	2.47	0.38	4.24	0.29
8	1.40	0.40	17.83	0.15	3.73	0.23	2.87	0.47	37.44	0.26	0.33	0.33	8.37	0.39	2.67	0.41	3.47	0.40
12	2.18	0.45	19.21	0.20	3.00	0.25	4.67	0.22	21.57	0.24	0.17	0.65	10.16	0.21	1.94	0.12	3.33	0.32
14	1.81	0.41	19.62	0.18	3.73	0.30	3.50	0.41	24.64	0.29	0.26	0.50	7.92	0.35	4.19	0.21	5.62	0.09
17	2.41	0.36	16.59	0.16	3.00	0.29	3.74	0.38	18.62	0.59	0.14	0.79	9.88	0.36	4.18	0.26	5.06	0.11
19	1.92	0.36	14.00	0.21	2.15	0.61	4.15	0.40	27.22	0.34	0.14	0.36	11.73	0.39	3.15	0.28	1.08	0.25
21	2.06	0.37	16.05	0.14	3.09	0.15	4.48	0.25	15.86	0.25	0.09	0.44	8.91	0.28	2.25	0.47	1.31	0.36
22	1.53	0.41	16.28	0.14	2.67	0.34	4.23	0.34	37.46	0.19	0.26	0.31	12.48	0.38	1.33	0.36	1.47	0.35
23	3.07	0.41	17.30	0.13	1.75	0.74	5.45	0.29	28.34	0.27	0.11	0.27	13.99	0.27	3.50	0.21	1.14	0.32
24	1.70	0.41	19.23	0.14	2.17	0.59	4.12	0.50	42.24	0.29	0.27	0.22	9.93	0.51	1.27	0.35	1.40	0.36
26	1.63	0.40	18.22	0.17	2.44	0.45	2.84	0.43	52.25	0.19	0.36	0.31	9.10	0.45	1.53	0.54	3.63	0.36
31	1.41	0.42	17.11	0.22	3.32	0.27	2.21	0.41	39.32	0.24	0.41	0.22	8.78	0.31	2.82	0.37	5.00	0.00
36	1.84	0.39	17.31	0.10	2.94	0.21	2.77	0.47	38.54	0.27	0.42	0.29	9.03	0.48	4.63	0.11	4.13	0.29
39	2.10	0.53	15.67	0.16	2.53	0.37	3.82	0.23	33.77	0.36	0.24	0.42	10.43	0.24	4.43	0.19	1.47	0.56
40	1.60	0.35	17.82	0.18	3.70	0.16	1.28	0.54	41.91	0.32	0.41	0.12	5.60	0.32	2.47	0.26	1.40	0.36
43	2.16	0.42	16.44	0.22	2.88	0.35	3.92	0.46	20.75	0.32	0.18	0.44	8.83	0.40	1.48	0.34	1.28	0.48
47	1.93	0.41	17.98	0.17	3.13	0.31	3.92	0.47	35.58	0.26	0.27	0.41	11.33	0.35	2.67	0.36	4.07	0.28
48	1.56	0.40	20.03	0.18	2.69	0.40	3.47	0.51	47.53	0.25	0.31	0.29	11.34	0.37	1.75	0.26	1.00	0.00
49	2.04	0.40	15.37	0.17	3.64	0.22	1.41	0.62	35.37	0.32	0.44	0.20	5.58	0.46	2.68	0.25	1.11	0.28
54	1.77	0.50	17.24	0.18	2.74	0.28	3.63	0.31	27.57	0.30	0.20	0.30	10.29	0.48	1.77	0.32	4.61	0.24
57	1.53	0.47	16.97	0.19	2.81	0.31	3.36	0.20	14.94	0.36	0.10	0.20	7.04	0.35	2.53	0.29	5.38	0.25
58	2.12	0.44	13.50	0.25	1.18	0.75	3.94	0.35	43.60	0.23	0.29	0.21	11.68	0.41	3.06	0.41	1.18	0.33
59	1.67	0.43	17.22	0.12	2.37	0.28	4.02	0.26	33.85	0.26	0.29	0.14	10.94	0.27	1.40	0.36	1.40	0.36
60	1.81	0.33	17.91	0.19	0.94	1.57	5.66	0.34	49.73	0.23	0.28	0.07	17.76	0.34	2.00	0.36	5.25	0.11
112	3.25	0.30	15.95	0.18	0.00	–	6.58	0.12	40.77	0.15	0.15	0.13	19.84	0.11	2.00	0.40	1.00	0.00
118	3.00	0.42	14.25	0.15	2.19	0.57	3.70	0.47	46.72	0.27	0.34	0.15	11.14	0.49	2.05	0.20	5.90	0.05

eties. A matrix of Mahalanobis distances (Dagnélie, 1975) between varieties was produced. A second discriminant analysis was performed with the subset of morphological characters adding seedlings as supplementary individuals, to simulate and test possibilities of incorporation of seedlings in the varieties.

Comparison of genetic and morphological distances between varieties

Two combinations of AFLP primers (EcoRI + AAC × MseI + GTA, and EcoRI + ACG × MseI + GGT) were used to characterise the genetic diversity of 21 of the 29 varieties studied (Elias et al., 2000; and see Table 1), generating 85 bands, of which 66 where polymorphic over the sample. We computed Nei & Li (1979) distances between individuals, and constructed an unrooted neighbour-joining dendrogram using the PHYLIP program (Felsenstein, 1993). Chakraborty & Jin (1993) distances between varieties were also computed using the POPULATION 1.2 sofware (Langella, 2000). A Mantel test (Mantel, 1967) was performed to compare genetic and morphological distance matrices using the GENETIX program (Belkhir et al., 2000).

Results and discussion

Mean values of characters for each variety

Means ($\bar{x}$) and coefficients of variation (v) of morphological and agronomic characters for each variety are

Table 3. Continued

Variety	stemcol		rootcol		peelcol		pulpcol		nbroot		wroot		drymat		fertility		mf	
	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v
2	4.80	0.09	1.07	0.23	3.13	0.11	1.13	0.31	4.93	0.34	717.73	0.44	38.30	0.10	2.80	1.84	9.00	0.30
5	1.09	0.27	1.87	0.18	3.57	0.14	3.70	0.15	6.13	0.43	871.76	0.44	38.56	0.05	0.63	3.29	10.65	0.42
6	1.77	0.60	2.00	0.00	3.54	0.14	2.08	0.23	5.72	0.31	688.20	0.51	38.34	0.04	14.04	0.61	8.50	0.39
7	4.90	0.09	1.00	0.00	3.47	0.15	2.79	0.22	4.87	0.44	950.66	0.55	37.30	0.10	17.03	0.67	10.45	0.51
8	3.00	0.00	1.00	0.00	3.33	0.14	2.67	0.27	3.93	0.60	712.67	0.52	37.70	0.09	15.00	0.49	8.33	0.46
12	1.88	0.18	1.49	0.34	3.52	0.14	3.12	0.16	6.30	0.39	887.42	0.61	38.86	0.05	10.97	1.24	18.64	0.49
14	1.65	0.38	1.23	0.35	2.00	0.00	4.58	0.11	6.92	0.49	1217.50	0.63	33.39	0.13	14.31	0.82	12.39	0.40
17	1.88	0.49	1.47	0.35	3.59	0.14	3.88	0.09	4.12	0.50	550.00	0.45	32.14	0.11	22.94	0.38	14.12	0.38
19	5.00	0.00	1.04	0.19	1.23	0.67	1.15	0.47	3.58	0.52	536.15	0.74	40.00	0.08	2.92	1.74	8.81	0.34
21	4.31	0.22	1.00	0.00	3.38	0.14	2.56	0.39	3.72	0.49	689.22	0.51	39.45	0.11	12.72	0.64	11.31	0.41
22	3.00	0.00	1.00	0.00	3.13	0.11	1.40	0.58	4.33	0.51	603.17	0.44	34.88	0.15	10.07	1.06	5.67	0.41
23	4.79	0.16	1.00	0.00	3.36	0.15	3.64	0.17	4.68	0.48	1067.68	0.47	36.11	0.29	9.73	1.09	15.18	0.46
24	4.00	0.26	1.00	0.00	3.47	0.15	4.07	0.06	3.70	0.59	993.03	0.56	36.20	0.16	12.07	0.82	13.33	0.35
26	1.38	0.36	1.88	0.18	3.50	0.15	2.94	0.15	4.91	0.49	921.09	0.60	39.08	0.08	0.38	3.05	10.94	0.44
31	1.00	0.00	1.91	0.15	3.55	0.14	3.09	0.30	4.10	0.54	738.18	0.59	35.06	0.08	16.50	0.65	9.66	0.61
36	4.75	0.12	1.00	0.00	3.19	0.17	2.44	0.25	4.66	0.42	856.25	0.42	38.42	0.08	13.59	0.69	10.66	0.42
39	1.00	0.00	1.93	0.13	3.27	0.14	1.07	0.23	5.13	0.39	436.33	0.50	36.85	0.20	10.07	0.61	9.70	0.76
40	1.47	0.35	1.73	0.26	3.47	0.18	3.67	0.17	4.10	0.30	834.17	0.50	38.07	0.09	20.96	0.37	10.50	0.74
43	1.32	0.48	1.76	0.25	3.20	0.13	2.24	0.42	4.44	0.45	583.40	0.44	36.61	0.15	12.48	0.80	9.84	0.36
47	4.86	0.11	1.00	0.00	3.40	0.18	2.13	0.30	6.30	0.27	1077.50	0.39	36.36	0.09	19.32	0.73	11.37	0.43
48	4.63	0.16	1.00	0.00	3.38	0.15	1.50	0.35	4.56	0.39	1064.69	0.66	38.52	0.09	15.31	0.78	13.00	0.48
49	2.05	0.32	1.87	0.18	3.92	0.07	4.92	0.07	3.93	0.60	716.76	0.67	31.86	0.08	14.74	0.59	10.45	0.61
54	4.81	0.11	1.00	0.00	3.67	0.17	3.07	0.22	5.00	0.44	956.45	0.42	38.42	0.06	11.77	0.82	13.55	0.50
57	1.27	0.62	1.94	0.13	2.00	0.00	5.00	0.00	3.72	0.57	634.38	0.74	37.44	0.08	13.88	0.69	8.91	0.57
58	2.73	0.32	1.00	0.00	3.29	0.22	1.00	0.00	1.94	0.95	192.77	1.06	35.65	0.09	4.94	1.17	7.35	0.67
59	3.00	0.00	1.07	0.23	3.27	0.14	1.20	0.34	4.17	0.38	675.00	0.49	38.95	0.13	3.60	1.86	8.83	0.46
60	1.00	0.00	2.00	0.00	3.69	0.16	2.25	0.25	5.34	0.37	665.00	0.42	41.42	0.11	2.78	1.94	11.63	0.36
112	4.67	0.10	1.10	0.28	3.00	0.00	2.90	0.19	7.35	0.42	926.25	0.88	36.62	0.09	0.00	–	14.40	0.76
118	1.06	0.22	1.00	0.00	2.00	0.00	1.00	0.00	2.74	0.79	286.08	0.74	37.05	0.12	6.61	1.14	11.71	0.52

given in Table 3. Considering the values of the coefficients of variation, all agronomic characters except percentage of dry matter in roots were highly variable within variety (e.g., for weight of the roots [wroot], v had an average value of 0.565, ranging from 0.388 to 1.055), as were size variables (except basal diameter). Conversely, colour variables, which in our enquiries appeared as the most salient characters used by farmers to identify their varieties, did not display high variability within variety (e.g., for colour of the petiole [petiocol] v had an average value of 0.244, ranging from 0 to 0.558).

Analysis of variance between the varieties for 14 morphological and 4 agronomic characters

The 'variety' factor was highly significant for all characters (Table 4), as expected for characters involved in variety identification by the farmers, and characters that are targets of farmer selection. The 'block' factor was also significant for some variables, especially basal diameter (basdiam), multiplication factor (mf), length of the petiole (petiolg) and area of the central lobe (aeralobe), which are size variables. Colour variables of the root did not display much variability among blocks. However, for colour of the stem (stemcol) and of the petiole, a significant effect of blocks was detected. There was a significant interaction between blocks and varieties for all characters.

Table 4. Results of analysis of variance among the 29 varieties, for the 14 morphological and 4 agronomic characters. Significance of values of F: NS = non significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

variables	variety		block		variety block*	
	F	df1, df2	F	df1, df2	F	df1, df2
nbstem	7.28***	28, 367	0.72 NS	14, 383	0.62*	341, 495
basdiam	8.76***	28, 361	7.46***	14, 374	1.54***	340, 495
ram	16.43***	28, 358	1.40 NS	14, 368	1.86***	341, 496
petiocol	83.18***	28, 344	2.04*	14, 346	11.29***	342, 498
nblobe	17.65***	28, 358	1.91*	14, 368	2.01***	342, 498
arealobe	26.12***	28, 367	4.38***	14, 381	1.40***	340, 489
ratiolobe	29.36***	28, 371	2.62*	14, 384	1.29***	340, 488
petiolg	18.00***	28, 363	4.18***	14, 375	1.50***	340, 394
yglcol	26.40***	28, 341	3.99***	14, 343	9.56***	338, 490
stemcol	118.23***	28, 340	3.12***	14, 343	5.93***	335, 491
rootcol	39.54***	28, 343	1.58 NS	14, 345	9.65***	340, 494
peelcol	23.74***	28, 342	1.23 NS	14, 344	9.76***	339, 493
pulpcol	70.52***	28, 341	1.72 NS	14, 343	12.26***	339, 493
nbroot	7.15***	28, 368	2.97***	14, 384	1.24**	341, 596
wroot	6.75***	28, 364	1.99*	14, 378	1.48***	342, 497
drymat	6.66***	28, 343	2.68***	14, 357	1.59***	334, 58
nbinflo	10.16***	28, 355	0.95 NS	14, 363	1.50***	338, 386
mf	4.40***	28, 360	5.16***	14, 370	1.84***	342, 498

Some salient characters were thus highly variable in a heterogeneous environment, and this might cause confusion between varieties.

A Tukey-Kramer test on means of the characters shows that all pairs of varieties can be differentiated by at least one morphological character (data not shown), except for varieties 22 and 59, for which no significant difference was found for both morphological and agronomic characters. Varieties that differed by a small number of characters (e.g. varieties 7 and 47, one character; varieties 7 and 54, three characters) are often confused by farmers. Variety 112 differed for at least 7 characters from any other variety.

Correlation between morphological and agronomic characters recorded for 29 varieties

Several groups of morphological and agronomic characters were correlated (Table 5). Colour of the stem and external colour of the root covaried, perhaps because the same pigmentation pathway is responsible for both colourations. Several size variables and architectural parameters covaried, and this could be explained taking into account the architecture of cassava, a succession of modules with terminal sexuality and di- or tri-chotomous ramifications. Extent of ramification (ram) appeared to be negatively correlated with number of stems produced by a cutting (nbstem which depends in fact on the capacity of the plant to reiterate). This could be due to selection for optimising exploitation of aerial space, whole-crown photosynthesis and thereby yield. Negative correlations between degree of ramification, on the one hand, and length of petiole and number of lobes (nblobe, i.e., size of leaves), on the other, reflect the fact that the greater the degree of ramification, the smaller the diameters of the terminal internodes and the smaller the leaves (Hallé et al., 1978; Brouat et al., 1998).

Concerning agronomic characters, yield of roots (wroot) increased with production of above-ground parts (basdiam), and with number of roots (nbroots). As expected, the multiplication factor increased with the numbers and diameters of stems (nbstem and basdiam, respectively). Number of inflorescences (nbinflo) is determined by the extent of ramification, and was thus correlated with all variables affected by branching. It also decreased with percentage of dry matter in roots (drymat), which is consistent with the observation that starch stored in roots is used for flowering (N. Morante, personal communication).

Table 5. Correlations between mean values of morphological and agronomic variables. Only significant values for Pearson's r are shown (r: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$)

basdiam	ram	petiocol	nblobe	arealobe	ratiolobe	petiolg	yglcol	stemcol	rootcol	peelcol	pulpcol	nbroot	wroot	drymat	nbinflo	mf	
–0.39*	–0.524**	–	0.541**	–	–	0.501**	–	–	–	–	–	–	–	–	–	0.489**	nbstem
	0.379*	–	–	–	–	–	–	–	–	–	–	0.421*	0.741***	–	0.423*	0.437*	basdiam
		–	–0.78***	–	–	–0.882***	–	–	–	–	–	–	–	–	0.771***	–	ram
			–	–	–	–	–	–	–	–	–	–	–	–	–	–	petiocol
				–	–0.688***	0.869***	–	–	–	–	–	–	–	–	–0.564**	–	nblobe
					0.704***	–	–	–	–	–	–	–	–	–	–	–	arealobe
						–	–	–	–	–	–	–	–	–	–	–	ratiolobe
							–	–	–	–	–0.376*	–	–	–	–	–	petiolg
								–	–	–	–	–	–	–	0.397*	–	yglcol
									0.797***	–	–	–	–	–	–	–	stemcol
										–	–	–	–	–	–	–	rootcol
											–	–	–	–	–	–	peelcol
												–	–	–0.411*	0.376*	–	pulpcol
													0.652***	–	–	0.425*	nbroot
														–	–	0.505**	wroot
															–0.457*	–	drymat
																–	nbinflo

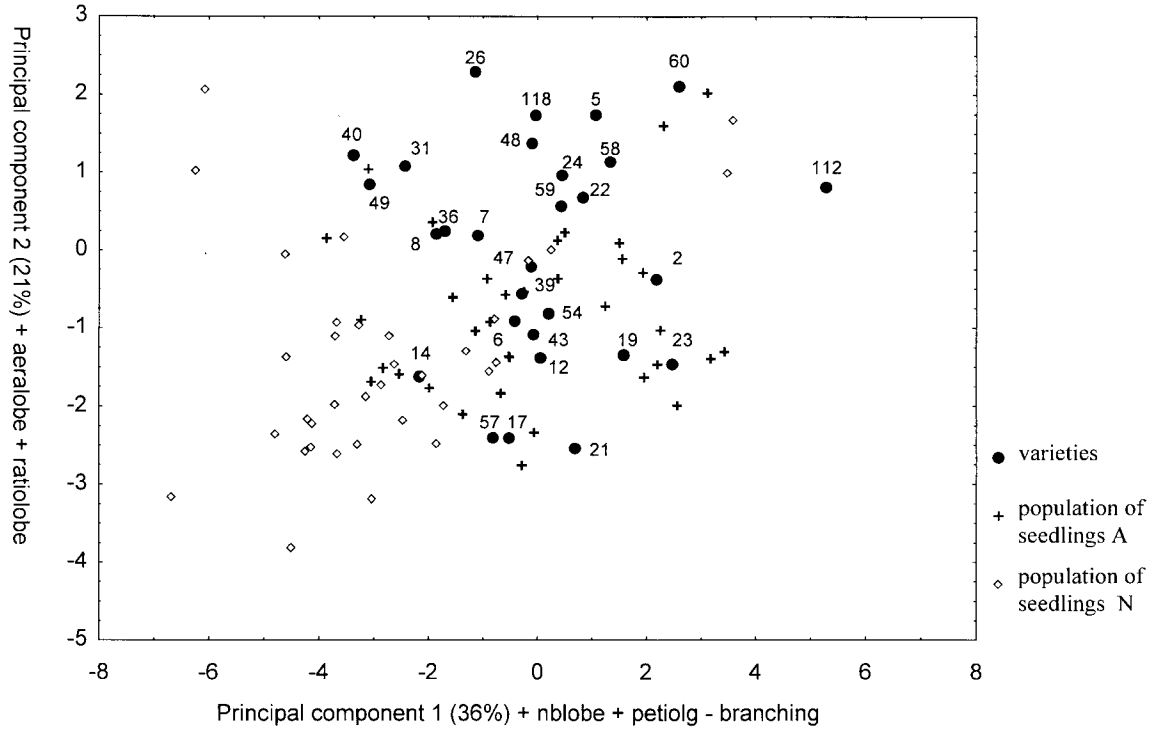

Figure 1. Principal components analysis performed on the 29 varieties (principal components 1 and 2). Percentage of variance explained is indicated under each component, as well as the variables that are most strongly correlated with the principal components (correlation coefficient is in parentheses). Seedlings were specified as supplementary individuals.

Varieties with coloured roots (high carotene content) had lower percentage of dry matter than varieties with white roots. Finally, agronomic traits were in general weakly correlated with traits used in the varietal classification.

Principal components analysis

Figure 1 shows the 29 varieties and the seedlings plotted on principal components 1 and 2 of a principal components analysis performed on the mean values of the 29 varieties (these axes accounted for 36% and 21% of the variance, respectively). Number of lobes, length of petiole and degree of ramification were highly associated with principal component 1, while area and ratio of the lobe were correlated with principal component 2. Colour of the stem and colour of the petiole were correlated with principal component 3 (14% of the total variance). Some pairs of varieties are very close (e.g. 22 and 59; 40, 49 and 31; 36 and 8). Variety 112 was distinctive and isolated from all others.

Most seedlings were far from the mean values for any of the varieties, especially for population N. Seedlings of population N were significantly more branched than the varieties (two-tailed t-test: $t = 4.88$, df = 64, $p < 10^{-4}$), and had darker young leaves ($t = 6.59$, df = 69, $p < 10^{-4}$). For seedlings of population A, the colour of the stem was different from that of the varieties ($t = -2.65$, df = 64, $p = 0.010$). Seedlings of population A were also slightly less branched, and had smaller leaves than the varieties ($t = -2.59$, df = 65, $p = 0.012$ for ram, $t = -5.05$, df = 66, $p < 10^{-4}$ for arealobe, and $t = -2.78$, df = 66, $p = 0.007$ for petiolg). These differences suggest that distinctive phenotypes, relative to recognised varieties, might be produced by sexual reproduction. The differences could be attributed to the origin of each population of seedlings. They might have been produced by crosses within or between varieties that are morphologically distinct from the sample of 29 varieties examined in this study. Alternatively, these differences may reflect the fact that some varieties are more likely to produce seeds than others. Degree of ramification, for instance, is highly correlated with

fertility in cassava because of architectural constraints. Highly fertile, therefore highly branched varieties are expected to contribute more to sexual reproduction. If this trait is heritable, seedlings are expected to be highly branched, as in population N. However, we cannot discard the possibility that the differences observed reflect environmental variation (seedlings did not grow under the same conditions as the varieties), especially for size variables. Indeed, inspection of the data showed that at the time of measurement, seedlings of population A were smaller than the other plants, which may account for their reduced ramification and smaller leaves. Unfortunately, we do not have data concerning tuber characteristics, especially yield and pulp colour, for seedlings. Both criteria are the most important, if not the only ones, for the decision whether or not to multiply a seedling.

However, some seedlings were morphologically very close to one or more recognised varieties. The variables used in the analysis are variables that are important in the local taxonomy, and one can hypothesise that some of these seedlings could be assigned to recognised varieties. Figure 1 suggests that some varieties are more likely candidates for absorbing such incorporation of seedlings than are others.

A discriminant analysis was performed, in order to test on the basis of these traits the strength of the local varietal taxonomy and the possibility and potential frequency of assignment of seedlings to the varieties studied here.

Discriminant analysis

Table 6 summarises the results of the first discriminant analysis. The discrimination was very high (Wilks λ varied between 1.88 E^{-5} and 1.04 E^{-4}). All variables contributed significantly to the discrimination model. The most discriminant characters were the colour of the stem, the colour of the petiole and the colour of the pulp (pulpcol), which is not surprising because colours of above ground parts are salient characters for identification, and colour of the pulp is under strong diversifying selection.

On average, 83% of the individuals of each variety were classified by the analysis in their original variety. While all individuals of varieties 2, 24 and 118 and more than 80% of individuals in 13 other varieties were 'correctly' classified by the analysis, in varieties 7 and 47, only 50% and 48% of individuals, respectively, were classified in their original variety. All 9 misclassified individuals of variety 59 were a posteriori classified in variety 22, and 8 out of 10 misclassified individuals of variety 22 were classified in variety 59. To a lesser extent, a similar situation was observed with varieties 7 and 54, and 7 and 47. Indeed, intra-varietal phenotypic variation due to environmental factors (block effect) and their interaction with genotypes for traits involved in the classification of the varieties, leads to overlapping of some varieties. These varieties have a greater probability of being confused, which was confirmed in the field (unpublished data). Other studies (Boster, 1985) also accounted for confusions of morphologically close varieties. Varieties 22 and 59 are said by farmers to be identical for all traits except size, hence their name ('caiman stick tall type' and 'caiman stick small type'). No farmer had both types. Many farmers were not able to distinguish them in the field or disagreed with each other, which led us to wonder whether they really were two genetically distinct varieties.

Confusions between close varieties can happen either when one farmer acquires cuttings from another one (exchanges), or even in the farmer's own field, when he or she selects the plants that will provide cuttings to be planted in the next field. Because such a

Table 6. Results of the discriminant analysis. For each variable, Wilks λ measures the discriminative power of the general model excluding the variable (λ = 0 if the discrimination is perfect and λ = 1 if there is no discrimination at all). Partial Wilks λ measures the contribution of each variable to the discrimination power of the general model (ratio λ after the variable has been added to the model / λ before the variable has been added to the model). All values of F were highly significant (*** = $p < 0.001$)

variables	Wilks λ	Partial Wilks λ	F associated to partial wilks λ (df: 28,786)
nbstem	1.96E-05	0.846	5.104***
basdiam	2.06E-05	0.804	6.828***
ram	2.19E-05	0.757	9.027***
nblobe	1.88E-05	0.880	3.810***
arealobe	2.23E-05	0.744	9.637***
ratiolobe	2.53E-05	0.657	14.686***
petiolg	2.00E-05	0.831	5.728***
yglcol	4.23E-05	0.392	43.536***
petiocol	1.04E-04	0.160	147.255***
stemcol	7.71E-05	0.215	102.444***
rootcol	3.11E-05	0.533	24.578***
peelcol	3.84E-05	0.432	36.956***
pulpcol	8.03E-05	0.207	107.854***
nbroot	2.03E-05	0.817	6.303***

confusion results in an individual from one variety being considered to belong to another one, this could be assimilated to a 'migration' event from the first variety towards the second.

Genetic structure and intra-varietal genetic polymorphism in 21 varieties assessed with AFLP markers

A neighbour-joining dendrogram constructed on a matrix of inter-individual Nei and Li distances is shown in Figure 2 (data were not available for varieties 2, 8, 24, 31, 36, 54, 59 and 118).

Varieties 5, 19, 22, 39 and 60 were monomorphic, i.e. all individuals of each of them had the same AFLP band pattern. Varieties 14, 17, 23, 40, 48, 49, 57 and 58 were polymorphic, but for each of them the individuals clustered in the dendrogram. In particular, for varieties 23 and 48, differences in AFLP band pattern concerned only one band, and such slight differences could be attributed to somatic mutations. The 8 remaining varieties, and variety 7 in particular, were polymorphic and their individuals were dispersed in the dendrogram. Intra-varietal genetic variability therefore exists and the proportion of polymorphic varieties is very high, in spite of the probably strong bottleneck affecting each variety (at least at the within-field level). This bottleneck occurs because of the very low number of individuals that genetically contribute, through cuttings, to the next generation. It is noticeable that with one exception (variety 22, but see the discussion concerning this variety in the previous section), monomorphic varieties and those almost monomorphic (23 and 48) had on average a high proportion (88%) of correctly classified individuals in the discriminant analysis. These varieties can therefore be seen as phenotypically and genotypically homogeneous. The number of individuals analysed per variety is however too small to state that these varieties are really monoclonal.

Intra-varietal variability can be attributed to confusions between genetically different plants that share most of their morphological characters (see above). Varieties displaying more intra-varietal morphological variability are more liable to incorporate new genotypes, thereby further increasing their intra-varietal genetic variability. For the same reason, morphologically homogeneous varieties are expected to show less genetic variability. Intra-varietal genetic variability was also detected among farmers in Brazil (Second et al., 1997; Sambatti et al., 2001) and in Malawi (Mkumbira et al., in prep.).

Comparison of genetic and morphological diversity

A Mantel test showed that distances between varieties computed on morphological and genetic data were significantly correlated (r = 0.283, $p < 0.01$), but the correlation was rather weak. Similarly weak correlation between genetic and morphological characters for cassava within a single locality has been found in other studies (Carvalho et al., 1998). In cassava, neutral molecular markers show geographic structure (Santos-Mühlen, personal communication), whereas morphological characters are very diverse within sites, but relatively homogeneous from one part of Amazonia to another. Neutral molecular markers reflect the history of diffusion of cassava across Amazonia. In the case of strictly vegetatively propagated plants, one should expect morphological characters to reflect the same evolutionary pattern as these molecular markers. Diversifying selection on morphological characters (Boster, 1985) that may have taken place repeatedly and independently across the Amazonian range, on the one hand, and recombination between selected genes and neutral loci due to occurrence of sexual reproduction, on the other, may explain the weak correlation we found between these two matrices of distance.

Assignment of seedlings to varieties

Seedlings that are multiplied by farmers can be considered by them either as a new variety, or be incorporated into a variety with which they share most of their morphological features. On the basis of morphological data, we tested whether each seedling could be incorporated into one of the 29 varieties studied. The assignment procedure was the following: if the Mahalanobis distance (computed during the discriminant analysis) from a seedling to a variety (centroid) was within the 95% confidence interval of the distances of all individuals of this variety to the centroid, we assigned the seedling to this variety. When a seedling could be assigned to several varieties, the variety for which the distance between the centroid and the seedling was the shortest was chosen.

Results are summarised in Figure 3. In our simulation 26% of the seedlings of population A and 46% of those of population N were not assigned to any variety. Some varieties, such as 14 or 6, are more likely candidates to incorporate seedlings. These varieties have large 95% confidence intervals, and have characters

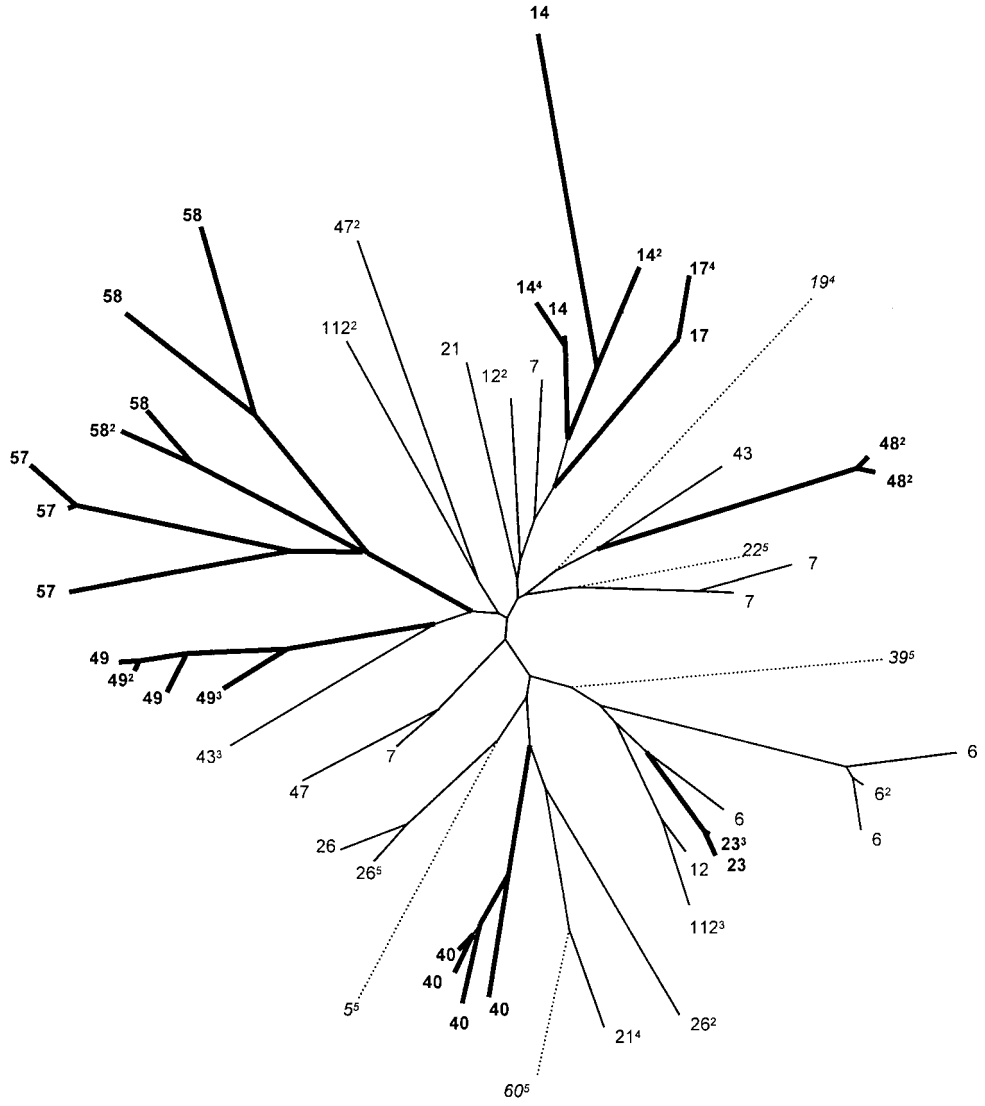

Figure 2. Unrooted Neighbour-Joining dendrogram constructed from a Nei and Li distance matrix computed with AFLP data on 21 varieties (101 individuals). Each individual is represented by the code of the variety to which it belongs. Exponent number following the variety code indicates the number of individuals at the end of the branch (i.e., individuals having the same AFLP patterns). Monomorphic varieties are presented in italics and their branches with dashed lines, and polymorphic varieties with individuals clustering together are represented in bold characters with bold branches.

that are rare among the varieties but that are more frequent in seedlings, such as high degree of ramification or purple young leaves.

Although we lack data on the behaviour of the farmers pertaining to incorporation of seedlings, the study of which would require careful survey over several years, scarce observations in the field showed that most seedlings were named after the name of a variety with which they shared morphological characters (e.g., a seedling resembling ‘bird stick’ will be named ‘bird stick seedling’, ‘bird stick cousin’, or ‘bird stick brother-in-law’). We suspect that the suffixes ‘seedling’ ‘cousin’ or ‘brother-in-law’ often disappear after a few generations of planting. In three cases we observed a farmer who found a seedling very similar to a recognised variety to assign the seedling directly to the variety.

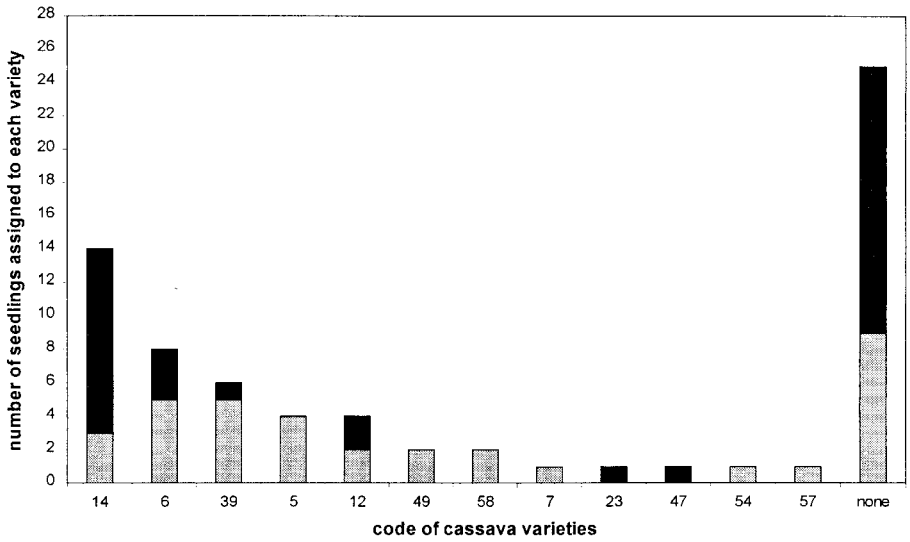

Figure 3. Number of seedlings of each field that were assigned to each variety in the discriminant analysis. Populations A and N are represented with grey and black colours, respectively.

More data on the frequency of multiplication of seedlings and of their incorporation into varieties are needed. Also, genetic consequences of incorporations must be assessed by studying molecular polymorphism in populations of seedlings. Since genetic composition is not strongly correlated with morphological structure in this collection of varieties, the seedlings incorporated into a variety are not expected to be genetically close. The use of co-dominant markers such as microsatellites could be useful in determining the genetic relationships between varieties and seedlings.

Conclusion

Local classification, cultivation practices and structure of diversity

Our results show a good agreement of local classification with the structure of morphological diversity. Some morphological traits appear more salient than others, e.g. colour variables, especially colour of the stem, of the petiole and of the pulp of the root. Colour variables are those that show the least intra-varietal variability. In the field, colour variables seem to play an important role in assessment of similarity, as they do for other Amazonian cassava cultivators (Boster, 1985).

However, possibilities of confusion exist, because some varieties overlap, and differ significantly only for a few traits. For this reason, misidentification of individuals is probably responsible for 'gene flow' between varieties that have very similar phenotypes. Moreover, seedlings that have a combination of morphological variables close to that of a variety are likely to be deliberately or unconsciously assigned to this variety, thereby introducing a new genotype into the variety. These two factors should increase intra-varietal genetic variability, which was detected using AFLP markers. This explanation for intra-varietal diversity is also supported by the absence of strong correlation between inter-varietal genetic and morphological distances. A new individual assigned to a variety on the basis of phenotypic similarity is therefore not expected to be genetically close to the variety.

Cultivation practices are responsible for the observed patterns of diversity. First, Makushi farmers exert a diversifying, rather than directional selection on morphological and agronomic characters. Even low-yielding varieties are not systematically discarded, and are instead kept at low frequencies. The Makushi are eager to acquire new varieties through exchanges or from seedlings (leading eventually to incorporation of new genotypes into a recognised variety). Second, in a traditional agroecosystem, human selection strongly interacts with natural selection. Differential mortality rate or yield between varieties may be partially due to differential responses to herbivores, diseases or climatic pressures. Cultural and ecological factors also play an important role in cassava sexual reproduction (Elias & McKey, 2000).

Key to conserving crop diversity is understanding how this diversity is perceived and valued by farmers. Diversifying selection, especially the retention even of varieties that predictably have low yields, at least in current environments, results in the conservation of a pool of genes that may be useful if conditions change. The maintenance of this diversity may thus reduce risks, and minimising risks over the long term may be the function that in evolutionary terms explains why so many groups employ diversifying selection. However, the immediate determinants of this mode of selection are not ecological factors (e.g., local adaptation) but human factors (symbolism, social organisation, etc.) that are subject to very rapid change. Brush (1991) has demonstrated for potato in Andean valleys and for rice in upland regions of Thailand that despite the recent development of modern agricultural techniques and the use of modern varieties, farmers continue to cultivate ancient local landraces. However, in many cases such cultural change is accompanied by erosion of crop genetic diversity (Heywood, 1995). Spread of modern agricultural techniques for cassava cultivation in Amazonia might ineluctably lead to disappearance of some of the mechanisms generating diversity in traditional agro-ecosystems. In particular, the practice of preserving volunteer cassava seedlings in fields, and a fortiori incorporating them in cultivated varieties or creating new varieties, might be lost. This practice has been performed for thousands of years in Amazonia. It is rarely practiced in many parts of Africa, where cassava was introduced in post-Columbian times (but see also Chiwona-Karltun et al. [1998] who document this practice in Malawi), and disappear in some cultural contexts in Amazonia (McKey et al., 2001). On-farm conservation of cassava diversity should take into account the importance of sexual reproduction in the dynamics of diversity of this vegetatively propagated crop.

The role of sexual reproduction in generating diversity is complex. Not only does it directly generate new genotypes, it also influences the way in which genetic diversity is distributed across perceived categories. This effect on perception of diversity can lead to further indirect effects on the dynamics of diversity, because it changes the relation between the phenotypes that are the objects of selection and management, and the genotypes, the durable results of selection.

Acknowledgements

The European Commission (DGVIII, Future of Tropical Forest Peoples Program) and the CNRS (Programme Environnement, Vie et Société, France) provided funds for fieldwork. A grant from the Bureau des Ressources Génétiques (France) supported all genetic analyses. We are grateful to the government of Guyana, especially the Ministry of Amerindian Affairs and the Environmental Protection Agency, for allowing us to carry out our fieldwork in Guyana. We are also grateful to personnel of the Amerindian Research Unit of the University of Guyana and to the National Agronomic Research Institute (Georgetown, Guyana) for their advice and support. We wish to thank Philippe Brabant for his useful advice concerning the experimental design and Bruno Toupance for generating random numbers. We especially thank the Makushi Amerindians of Rewa, for their inestimable contribution to our study, for their useful advice concerning cassava farming and processing, for taking care of the experimental plot, and for their hospitality.

References

Belkhir, K. et al., 2000. GENETIX 4.0, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UPR 9060, Université de Montpellier II, Montpellier (France).

Boster, J.S., 1985. Selection for perceptual distinctiveness: evidence from Aguaruna cultivars of *Manihot esculenta*. Econ Bot 39: 310–25.

Brouat, C., M. Gibernau, L. Amsellem & D. McKey, 1998. Corner's rules revisited: ontogenetic and interspecific patterns in leaf-stem allometry. New Phytol 139: 459–470.

Brush, S.B., 1991. A farmer based approach to conserving crop germplasm. Econ Bot 45: 153–165.

Brush, S.B., 1995. *In situ* conservation of landraces in centers of crop diversity. Crop Sci 35: 346—354.

Carvalho, L.J.C.B., B.A. Schall & W.M.G. Fukuda, 1998. Cassava (*Manihot esculenta* Crantz) phenetic relationships and genetic diversity revealed by morphological descriptors and RAPD markers. Rev Brasil Genét 17: 13.

Chakraborty, R. & L. Jin, 1993. A unified approach to study hypervariable polymorphisms: statistical considerations of determining relatedness and population distances. In: S.D.J. Pena, R. Chakraborty, J.T. Epplen & A.J. Jeffreys (Eds.), DNA Fingerprinting: State of the Science, pp. 153–175. Basel.

Chiwona-Karltun, L., J. Mkumbira, J. Saka, M. Bovin, N.M. Mahungu & H. Rosling, 1998. The importance of being bitter – a quantitative study on cassava cultivar preference in Malawi. Ecol Food Nutr 10: 1–27.

Dagnélie, P., 1975. Analyses Statistiques à Plusieurs Variables. Les Presses Agronomiques de Gembloux, Belgique.

Dufour, D.L., 1995. A closer look at the nutritional implications of bitter cassava use. In L.E. Sponsel (Ed.), Indigenous Peoples and

the Future of Amazonia: An Ecological Anthropology of an Endangered World, pp. 147–165. The University of Arizona Press, Tucson & London.

Elias, M. & D. McKey, 2000. The unmanaged reproductive ecology of domesticated plants in traditional agroecosystems: an example involving cassava and a call for data. Acta Oecol 21: 223–230.

Elias, M., O. Panaud & T. Robert, 2000. Assessment of genetic variability in a traditional cassava (*Manihot esculenta* Crantz) farming system using AFLP markers. Heredity 85: 219–230.

Elias, M., L. Rival & D. McKey, 2001. Perception and management of cassava (*Manihot esculenta* Crantz) diversity among Makushi Amerindians of Guyana (South America). J Ethnobiol (in press).

Felsenstein, J., 1993. PHYLIP. *Phylogeny Inference Package*. version 3.5c. Department of Genetics, University of Washington, Seattle.

Hallé, F., R.A.A. Oldeman & P.B. Tomlinson, 1978. Tropical Trees and Forests. An Architectural Analysis, Berlin, Germany; Heidelberg, Germany and New York, USA. Springer-Verlag.

Heywood, V.H., 1995. Global Biodiversity Assessment. Cambridge University Press, Cambridge.

Langella, O., 2000. Populations 1.0.6, http: //www.cnrs-gif.fr/pge.

Mantel, N., 1967. The detection of disease clustering and generalised regression approach. Cancer Res 27: 209–220.

McKey, D. & S. Beckerman, 1993. Chemical ecology, plant evolution and traditional cassava cultivation systems. In: C.M. Hladik, A. Hladik, H. Pagezy, O.F. Linares, G.J.A. Koppert & A. Froment (Eds.), Tropical Forests, People and Food, pp. 83–112. UNESCO, Paris.

McKey, D., L. Emperaire, M. Elias, F. Pinton, T. Robert, S. Desmoulière & L. Rival, 2001. Gestions locales et dynamiques régionales de la diversité variétale du manioc en Amazonie. Génét Sél Evol (in press).

Nei, M. & W. Li, 1979. Mathematical model for studying genetic variations in terms of restriction endonucleases. Proc Natl Acad Sci USA 76: 5269–5273.

Rogers, D.J. & S.G. Appan, 1973. *Manihot* and *Manihotoides* (Euphorbiaceae). Flora Neotropica 13: 1–272.

Salick, J., 1995. Toward an integration of evolutionary ecology and economic botany: personal perspectives on plant/people interactions. Ann Miss Bot Garden 82: 25–33.

Sambatti, J.B.M., P.S. Martins & A. Ando, 2001. Folk taxonomy and evolutionary dynamics of cassava: a case study in Ubatuba – Brazil. Econ Bot (in press).

SAS, 1996. SAS/STAT User's Guide, Release 6.12. Cary, N.C.: SAS Institute.

Second, G., A.C. Allem, R.A. Mendes, L.J.C.B. Carvalho, L. Emperaire, C. Ingram & C. Colombo, 1997. Molecular marker (AFLP)-based *Manihot* and cassava numerical taxonomy and genetic structure analysis in progress: implications for their dynamic conservation and genetic mapping. Afr J Root Tuber Crops 2: 140–147.

Sokal, R.R. & F.J. Rohlf, 1985. Biometry. New York: W.H. Freeman.

STATISTICA, 1997. Statistica 5.1, StatSoft Inc, http: //www.statsoft.com.

XLSTAT, 1999. Xlstat 4.3, http: //www.xlstat.com.