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Isozyme polymorphism within section reticulatae of genus *Vigna* (Tribe Phaseoleae: Fabaceae)

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Abstract

An electrophoretic comparison of variation at 30 isozyme loci was performed for 45 accessions from genus *Vigna*, section reticulatae. Within the section level, these results fitted the nomenclature used. Within *V. reticulata*, variability was organized geographically and the West African weedy *V. reticulata* genetically was different from West African wild *V. reticulata*. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: *Vigna*; Phaseoleae; Fabaceae; Isozyme polymorphism; Genetic distance

1. Introduction

Vigna Savi (Fabaceae: Phaseoleae) is a pantropical genus which is comprised of 82 species (Maréchal et al., 1978). Two of these are economically important in Africa: the cowpea, *V. unguiculata* (L.) Walp.; and the bambara groundnut, *V. subterranea* (L.) Verdc. The latter species were first domesticated in Africa, where both are encountered as wild plants.

The last comprehensive taxonomic studies of *Vigna* or its parts are those of Verdcourt (1970) and Maréchal et al. (1978). Verdcourt focussed primarily on the taxa represented in Eastern Africa (*sensu* Kew). Maréchal et al., however, presented an overview of the Phaseolastrae Baudet & Maréchal, and were mainly interested in the delimitation of *Vigna* vis-a-vis *Phaseolus* L. They confirmed most of the work of

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Verdcourt (1970) and proposed the transfer of section Leptospron (Benth.) Maréchal et al. from *Phaseolus* to *Vigna*. So treated, the genus *Vigna* included 7 subgenera and 17 sections (Maréchal, 1982).

Recent cpDNA data (Vaillancourt et al., 1993a; Delgado-Salinas et al., 1993), however, suggests some modifications, addressing in particular the separation of the new world *Vigna* from the rest of the genus. The Old World species of *Vigna* are split into several groups: subgenus Haydonia (R.Wilczek) Verdc., subgenus Ceratotropis (Piper) Verdc., the yellow and blue flowered species of subgenus Vigna, and a group including the subgenus Plectrotropis (Schum.) Bak. and the pink or purple flowered species of subgenus Vigna. *V. unguiculata*, *V. vexillata* (L.) A.Rich., *V. reticulata* Hook.f., *V. frutescens* and *V. membranacea* A.Rich. belong to this latter group.

The *Vigna unguiculata* gene pool includes several perennial subspecies which are rather distant, as well as an annual subspecies *unguiculata*, the latter including both cultivated forms (var. *unguiculata*) and wild forms (var. *spontanea* [Schweinf.] Pasquet) (Pasquet, 1993a). This classification, however, is obscured by introgression between wild and cultivated cowpeas, and the existence of a crop-weed complex, at least in the West African sahelian savannas.

In such a context, it is interesting to study closely related species which do not include cultivated forms in Africa, especially *V. reticulata* as weedy forms from this species are commonly encountered in fields in the West African Savanna.

Vigna reticulata belongs to reticulatae Verdc. This section, which is well characterized by parallel tertiary nerves in leaflets, includes half a dozen species, three of which (i.e. *V. reticulata*, *V. wittei* Bak.f. and *V. dolomitica* R.Wilczeck) are available in living collections.

2. Materials and methods

2.1. Plant material

The 45 accessions used in this study are presented in Table 1. They included 39 *V. reticulata* accessions, 5 *V. wittei* accessions from Zaïre and 1 *V. dolomitica* accession, which is an endemic species from cupriferous soils from the Mine de l'Etoile in southern Zaïre. Among the 39 *V. reticulata* accessions, 23 originated from Cameroon and were collected by the second author. These 23 accessions were representative of the entire range distribution of the species in this country, covering the Mandara mountains in the northern savannas to hills surrounding Yaoundé in the southern rain forest. A few of these Cameroon accessions (i.e. V 11, V 79) displayed large seed size and were collected in or near cultivated fields.

The accessions X and NI were from the IPGRI base collection of Phaseolinae maintained at the National Botanic Garden of Belgium, in Meise. The accessions MT were collected by Mithen and are now duplicated in Meise. The accessions V were from the ORSTOM collection which is now being duplicated in Meise. Each accession consisted of one to three autogamous lines, and were maintained as such, each of these lines originating from one seed of the original stock.

Table 1
Accessions studied. BDI: Burundi; CIV: Ivory Coast; CMR: Cameroon; HVO: Burkina Faso; KEN: Kenya; NGA: Nigeria; TZA: Tanzania; UGA: Uganda; ZAR: Zaire; ZMB; Zambia; ZWE: Zimbabwe

Accession	Country	Latitude and longitude	Locality	Other accession number
Vigna reticulata				
V 11	CMR	10 16 N 14 39 E	Kolara	–
V 12	CMR	10 28 N 13 38 E	Kila	–
V 24	CMR	10 41 N 13 36 E	Roumzou	–
V 33	CMR	10 36 N 13 59 E	Goudoul	–
V 40	CMR	6 42 N 12 36 E	Djombi	–
V 43	CMR	7 20 N 13 13 E	Mbibol	–
V 69	CMR	–	Bilassora	NI 1343
V 73	CMR	6 20 N 13 33 E	Dir	–
V 79	CMR	8 23 N 14 19 E	Kourouk	–
V 88	CMR	7 39 N 14 18 E	Ambarang	–
V 89	CMR	7 39 N 14 18 E	Ambarang	–
V 93	CMR	7 57 N 14 42 E	Ndok	NI 1338
V 99	CMR	10 53 N 14 07 E	Mada	–
V 113	CMR	8 22 N 13 12 E	Béré – > col	–
V 116	CMR	4 30 N 11 15 E	km 3 Yambassa – > Yaoundé	–
V 123	CMR	4 57 N 13 53 E	km 11 Mbomba – > Bertoua	–
V 128	CMR	3 54 N 11 28 E	Bikanga	NI 1341
V 130	CMR	10 12 N 13 40 E	Nivé	–
V 167	CIV	–	Lamto	–
V 172	HVO	–	–	–
V 209	CMR	7 17 N 13 17 E	km 1 Likok – > Ngaoundéré	–
V 213	CMR	8 57 N 13 25 E	km 3 Mayo Douké – > Boumedjé	–
V 214	CMR	7 33 N 13 34 E	–	–
V 221	CMR	–	km 7 SO Martap, Anam	–
V 236	CMR	–	Mayo Lopé	–
V 281	ZAR	0 33 N 25 13 E	Kisangani	–
V 282	UGA	0 21 N 32 35 E	Kyadondo, Kanyanya West	–
MT 24	ZWE	16 45 S 31 05 E	–	NI 1453
MT 64	ZWE	20 15 S 32 50 E	–	–
MT 101	ZWE	18 24 S 32 55 E	–	–
NI 174	CIV	–	–	–
NI 424	ZMB	13 09 S 28 24 E	Luanshya	–
NI 441	ZAR	6 45 S 23 57 E	km 9 S Gandajika	–
NI 445	ZAR	–	M'Passu, 12 km S Gandajika	–
NI 480	BDI	–	Gitega	–
NI 1035	KEN	–	km 5 S Ukanda – > Ramisi	–
NI 1038	NGA	–	Tsawuni near Kano	–
NI 1051	KEN	4 34 S 39 24 E	Ramisi Sugar Factory	–
NI 1168	TZA	–	–	–
NI 1317	BDI	4 01 S 30 01 E	Bukemba, km 4 S Gihofi	–
Vigna dolomitica				
V 283	ZAR	11 38 S 27 35 E	Mine de l'Etoile	–
Vigna wittei				
NI 193	ZAR	–	near Kinshasa	–
NI 238	ZAR	6 45 S 23 57 E	INEAC Gandajika	–
NI 290	ZAR	6 45 S 23 57 E	INEAC Gandajika	–
NI 442	ZAR	6 45 S 23 57 E	Tshingomba	–

2.2. Procedure

Seeds were set out on water to imbibe for 24 hours and then ground. The gels were prepared as described by Second and Trouslot (1980). The histidine/citrate system at pH 6.0 was used for all enzymes. The gel mixture contained 14% starch. The enzyme systems and the reference for staining procedures which were used are indicated in Table 2. AMP was stained with leucine-β-naphtylamide (Amp2 and Amp3) or alanine-β-naphtylamide (Amp2 and Amp4), FLE and βGAL with derivatives of 4-methyl-umbelliferyl compounds.

For each enzymatic system, the presumed loci were numbered by increasing distance from the anode, and the numeration was the same as in *V. unguiculata* (Pasquet, 1993b). For each isozyme, the most common allele was designated as 100 and the other allozymes were measured in millimetres relative to that standard. This procedure was the same as utilized by Koenig and Gepts with *Phaseolus vulgaris* L. (1989).

The data from the enzymatic analysis allowed calculation of Nei's distances (1972). The UPGMA (Sneath and Sokal, 1973) was computed using the BIOSYS software version 1.7.

Table 2
Enzyme systems studied

Enzyme system	Number of loci scored	Staining procedure
Alcool dehydrogenase (ADH) 1.1.1.1	2	Second and Trouslot (1980)
Formate dehydrogenase (FDH) 1.2.1.2.	1	Wendel and Weeden (1989)
Malate dehydrogenase (MDH) 1.1.1.37	4	Second and Trouslot (1980)
Shikimate dehydrogenase (SDH) 1.1.1.25	1	Second and Trouslot (1980)
Malic enzyme (ME) 1.1.1.40	1	Wendel and Weeden (1989)
Isocitrate dehydrogenase (IDH) 1.1.1.42	2	Second and Trouslot (1980)
Phosphogluconate dehydrogenase (PGD) 1.1.1.43	2	Second and Trouslot (1980)
Glucose-6-phosphate dehydrogenase (G6PD) 1.1.1.49	1	Vallejos (1983)
Glutamate dehydrogenase (GDH) 1.4.1.2	1	Second and Trouslot (1980)
NADH diaphorase (DIA) 1.6.2.2	1	Harris and Hopkinson (1976)
Superoxyde dismutase (SOD) 1.15.1.1	1	Wendel and Weeden (1989)
Phosphoglucomutase (PGM) 2.7.5.1	2	Second and Trouslot (1980)
Esterase (EST) 3.1.1.1	1	Second and Trouslot (1980)
Fluorescent esterase (FLE) 3.1.1.2	1	Harris and Hopkinson (1976)
β-Galactosidase (βGAL) 3.2.1.23	1	Vallejos (1983)
Endopeptidase (ENP) 3.4.-.-.	1	Cardy et al. (1980)
Aminopeptidase (AMP) 3.4.11.1	3	Second and Trouslot (1980)
Phosphoglucose isomerase (PGI) 5.3.1.9	3	Second and Trouslot (1980)
Mannose phosphate isomerase (MPI) 5.3.1.8	1	Harris and Hopkinson (1976)

3. Results and discussion

3.1. Isozyme patterns

The 19 enzyme systems enabled the scoring of 30 loci. Isozyme patterns were very close to those observed in *V. unguiculata* (Pasquet, 1993b; Vaillancourt et al., 1993b) and *V. vexillata* (Garba and Pasquet, unpublished data).

FDH, ME, GDH, βGAL, EP and MPI appeared as unique bands; whereas Sdh and G6pd were expressed as double bands.

As observed previously for *V. vexillata* (Garba and Pasquet, unpublished data), DIA yielded many more bands in these species than in *V. unguiculata* (Pasquet, 1993b). However, because most bands were poorly stained, only the strong slow band (Dia2) was scored. Dia2 also showed menadione reductase activity. Similarily, SOD was expressed as one strong band, Sod2, while Sod1 and Sod3 were poorly stained and not scored. Seed extracts had a single βEst band (Est3). A very faint fast αEst band was observed but not scored. FLE had two bands, but the fast one was barely discernable and the slow one (Fle3) was the only one scored.

ADH occurred in the form of a heterodimer from two loci, Adh1 and Adh2. The fast monomer stained strongly, as it did in *V. vexillata* (Garba and Pasquet, unpublished data) and contrary to that in *V. unguiculata* (Vaillancourt et al., 1993b). MDH presents four isozymes. The isozyme closest to the anode, Mdh1, appeared as a weak band, followed by the heterodimer formed by Mdh2 and Mdh3. Mdh4, a strongly stained band, did not migrate far from the cathode, as in *V. unguiculata* (Pasquet, 1993b) and *V. vexillata* (Garba and Pasquet, unpublished data), and contrary to the blue- and yellow-flowered *Vigna* (Pasquet and Vanderborght, unpublished data). IDH had two isozymes with the stronger-stained isozyme (Idh2) closer to the cathode. Both PGD and PGM also had two isozymes and the PGM isozyme closer to the anode stained stronger. For AMP, Amp2, which cleaved both alanine- and leucine-β-naphtylamide showed greater staining. The substrate for Amp3 and Amp4 were leucine-β-naphtylamide and alanine-β-naphtylamide respectively. Pgi1 was supposed to be chloroplastic, as it is in cowpea (Vaillancourt et al., 1993b), while Pgi2 and Pgi3 formed as heterodimers. As in *V. unguiculata* (Pasquet, 1993b) and *V. vexillata* (Garba and Pasquet, unpublished data), and opposite to most blue- and yellow-flowered *Vigna* (Pasquet and Vanderborght, unpublished data), the fast monomer (Pgi2) stained stronger.

3.2. Interspecific relationships

Table 3 presents Nei's distances observed within and between each species. In this Table and in the UPGMA cluster phenogram based on Nei's distances (Fig. 1), the three species were clearly separated by high distances, much higher than those encountered within species. These interspecific distances were higher than those calculated between cowpea perennial subspecies (Pasquet, 1993b). *Vigna wittei* was characterized by exclusive alleles in 4 loci, *V. dolomitica* in 3 loci, *V. reticulata* in

Table 3
Nei's distances between accessions (minimum, average and maximum) from same or different species. For each group, the number of accessions studied is given in brackets

	V. reticulata (40)	*V. wittei* (4)	*V. dolomitica* (1)
V. reticulata	0.035 0.264 0.555		
V. wittei	0.477 0.752 0.969	0.081 0.205 0.323	
V. dolomitica	0.405 0.606 0.824	0.738 0.764 0.785	–

1 locus; the most common alleles in *V. wittei* were not encountered in the other species for 7 loci, in *V. reticulata* for 4 and in *V. dolomitica* for 3 (Table 4).

In reticulatae, results of isozyme polymorphism fitted the formal nomenclature proposed by previous workers (Verdcourt, 1970; Maréchal et al., 1978), which does not appear to be the case in *V. luteola* (Jacq.) Benth. – *V. marina* (Burm.) Merrill – *V. oblongifolia* A.Rich. (Pasquet and Vanderborght, unpublished data), *V. membranacea* – *V. frutescens* (Pasquet and Vanderborght, unpublished data), *V. vexillata* – *V. lobatifolia* Bak. (Garba and Pasquet, unpublished data). The inclusion of the three species in the same section is also confirmed by the higher Nei's genetic distances (between 0.91 and 0.95, using 26 loci from 16 enzyme systems) calculated by Vaillancourt and Weeden (1993) between *V. reticulata*, *V. vexillata*, and *V. unguiculata*.

3.3. *Polymorphism within V. reticulata*

Genetic diversity in *V. reticulata* (Table 4) was similar to that found in *V. vexillata* (Garba and Pasquet, unpublished data), but lower than in *V. unguiculata* (Pasquet, 1993b). The UPGMA diagram (Fig. 1) showed four groups: group 1 (from V 12 to NI 174) included mainly accessions from West African lowlands savannas; group 2 (from NI 1035 to NI 445, and MT 24) included accessions from East Africa; group 3 (from V 43 B to V 282) included most of the accessions from Cameroonian Adamawa highlands and accessions from Central Africa; and group 4 (from V 179 to V 172) included the weedy *V. reticulata* accessions which have the largest seed sizes.

Nei's distances between accessions from the same and different groups are presented in Table 5. Distances within groups, were slightly lower than distances between groups while all the distances between groups are broadly equivalent. Within *V. reticulata* groups and within subspecies of *V. unguiculata* (Pasquet, 1993b), genetic distances are of the same order. However, between *V. reticulata* groups distances are

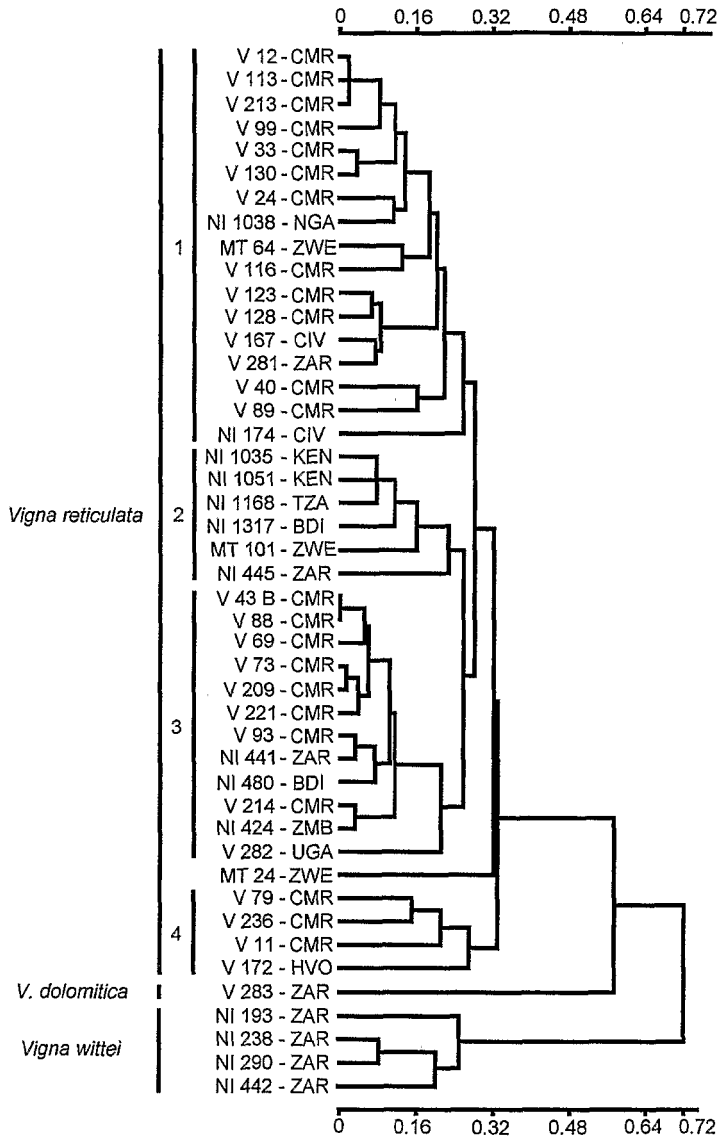

Fig. 1. Dendrogram (UPGMA) based on Nei's distance values calculated from isozyme data.

much smaller than between subspecies of *V. unguiculata*. With the exception of Gdh-105 (which characterized group 3), no allele was exclusive of either *V. reticulata* group. However, there were some differences in the most common alleles: Sdh-96 was largely identified in group 1, Amp4-105, Pgi3-100 and Mpi-87 in group 2, Est3-107,

Table 4
Allelic frequencies, mean gene diversity index (H), proportion of polymorphic loci (L), and number of alleles at polymorphic loci (A). For each group, the number of accessions studied is given in brackets

Allele		*V. wittei* (4)	*V. dolomitica* (1)	*V. reticulata* (40)	Group 1 (17)	Group 2 (7)	Group 3 (12)	Group 4 (4)
Adh1	104	0	0	0.025	0	0.142	0	0
	100	1	1	0.975	1	0.857	1	1
Adh2	105	0	1	0	0	0	0	0
	100	1	0	1	1	1	1	1
Fdh	108	0.625	0	0	0	0	0	0
	104	0.125	1	0.037	0.029	0	0.083	0
	100	0	0	0.912	0.853	0.8	0.917	1
	96	0	0	0.050	0.058	0.2	0	0
Mdh1	107	1	0	0	0	0	0	0
	100	0	1	1	1	1	1	1
Mdh2	100	1	1	1	1	1	1	1
Mdh3	100	1	1	1	1	1	1	1
Mdh4	100	1	1	1	1	1	1	1
Sdh	104	0.875	0	0	0	0	0	0
	100	0	0	0.637	0.176	1	1	0.875
	96	0.125	1	0.337	0.764	0	0	0.125
	92	0	0	0.025	0.059	0	0	0
Me	100	1	0	0.975	1	1	1	0.750
	95	0	0	0.025	0	0	0	0.250
	90	0	1	0	0	0	0	0
Idh1	108	0	1	0.025	0	0.143	0	0
	100	1	0	0.687	0.588	0.857	0.708	0.750
	92	0	0	0.287	0.411	0	0.291	0.250
Idh2	100	1	1	1	1	1	1	1
Pgd1	100	0.5	1	1	1	1	1	1
	95	0.5	0	0	0	0	0	0
Pgd2	100	1	1	1	1	1	1	1
G6pd	100	0	0	0.875	1	0.857	1	0
	96	0	1	0.125	0	0.143	0	1
	92	1	0	0	0	0	0	0
Gdh	105	0	1	0.3	0	0	1	0
	100	1	0	0.7	1	1	0	1
Dia2	110	0.75	0	0	0	0	0	0
	100	0	1	1	1	1	1	1
	96	0.25	0	0	0	0	0	0
Sod2	100	1	1	0.975	1	1	1	0.750
	98	0	0	0.025	0	0	0	0.250
Pgm1	100	0	0.5	1	1	1	1	1
	96	1	0.5	0	0	0	0	0
Pgm2	104	0	0	0.025	0	0	0.083	0
	102	0	0	0.025	0.059	0	0	0
	100	1	1	0.925	0.941	0.857	0.917	1
	96	0	0	0.025	0	0.143	0	0

—continued

Table 4—*continued*

Allele		*V. wittei* (4)	*V. dolomitica* (1)	*V. reticulata* (40)	Group 1 (17)	Group 2 (7)	Group 3 (12)	Group 4 (4)
Est3	115	1	1	0	0	0	0	0
	112	0	0	0.025	0.059	0	0	0
	110	0	0	0.025	0	0	0	0.250
	107	0	0	0.325	0.059	0.143	0.917	0
	105	0	0	0.225	0.353	0	0	0.750
	100	0	0	0.375	0.470	0.857	0.083	0
	90	0	0	0.025	0.059	0	0	0
Fle3	106	0	0	0.025	0	0.143	0	0
	102	0	0	0.175	0.235	0	0	0.750
	100	0	1	0.800	0.764	0.857	1	0.250
	98	1	0	0	0	0	0	0
βGal	104	0	1	0.025	0	0	0.083	0
	102	1	0	0.100	0.118	0.143	0.167	0
	100	0	0	0.725	0.824	0.571	0.666	0.750
	98	0	0	0.125	0.058	0.143	0.083	0.250
	96	0	0	0.025	0	0.143	0	0
Enp	104	0.25	0	0	0	0	0	0
	102	0.75	0	0.137	0.235	0.071	0	0
	100	0	1	0.837	0.706	0.928	1	1
	98	0	0	0.025	0.058	0	0	0
Amp2	102	0.625	0	0.075	0	0.143	0	0.500
	100	0.375	1	0.925	1	0.857	1	0.500
Amp3	108	0	1	0.150	0	0.143	0.417	0
	104	0.125	0	0.200	0.353	0	0	0.500
	100	0	0	0.625	0.588	0.857	0.583	0.500
	98	0.875	0	0	0	0	0	0
	96	0	0	0.062	0.059	0	0	0
Amp4	105	0	0	0.187	0.118	0.643	0	0.250
	102	0.75	0.5	0.012	0	0.071	0	0
	100	0.25	0.5	0.425	0.294	0.214	0.875	0
	98	0	0	0.350	0.588	0	0.083	0.750
	96	0	0	0.025	0	0.071	0.042	0
Pgi1	100	1	1	1	1	1	1	1
Pgi2	100	0.25	0	0.975	1	0.857	1	1
	95	0.50	1	0.025	0	0.143	0	0
	93	0.25	0	0	0	0	0	0
Pgi3	110	0	0	0.050	0	0	0.083	0.250
	105	1	1	0.462	0.529	0.214	0.500	0.50
	100	0	0	0.487	0.470	0.785	0.417	0.250
Mpi	120	0	1	0	0	0	0	0
	103	0	0	0.025	0	0.143	0	0
	100	0.250	0	0.487	0.912	0	0	1
	94	0.125	0	0	0	0	0	0
	90	0	0	0.312	0.029	0	1	0
	87	0.625	0	0.150	0	0.857	0	0
	80	0	0	0.025	0.059	0	0	0
	H	0.143	0.033	0.212	0.158	0.146	0.089	0.149
	L	0.333	0.067	0.633	0.400	0.500	0.267	0.366
	A	2.20	2.00	3.21	2.75	2.27	2.50	2.09

Table 5
Nei's distances between accessions (minimum, average and maximum) from same or different *V. reticulata* groups. For each group, the number of accessions studied is given in brackets

	Group 1 (17)	Group 2 (7)	Group 3 (12)	Group 4 (4)
	0.017			
Group 1	0.175			
	0.325			
	0.143	0.069		
Group 2	0.259	0.185		
	0.380	0.371		
	0.143	0.143	0.000	
Group 3	0.278	0.253	0.101	
	0.457	0.380	0.266	
	0.105	0.182	0.215	0.143
Group 4	0.272	0.319	0.366	0.217
	0.511	0.467	0.531	0.279
	0.457	0.568	0.629	0.568
V. wittei	0.690	0.697	0.759	0.749
	0.916	0.836	0.916	0.908
	0.522	0.522	0.389	0.522
V. dolomitica	0.589	0.624	0.497	0.638
	0.710	0.756	0.557	0.782

Amp4-100 and Mpi-90 in group 3, and G6pd-96, Est3-105, Fle3-102 in group 4 (Table 4).

Obviously, the first three groups (West Africa, East Africa, Central Africa) reflect some geographical differentiation, parallel to that found in the perennial *V. unguiculata* subspecies: subsp. *baoulensis* (A.Chev.) Pasquet in West Africa, subsp. *letouzeyi* Pasquet in Central Africa and subsp. *burundiensis* Pasquet in East Africa (Pasquet, 1993a). This is so even though *V. reticulata* is a savanna plant, while the perennial wild subspecies of *V. unguiculata* are encountered in more humid ecologies.

Compared to the first three *V. reticulata* groups, groups 1 and 4 shared the same geographical areas. However, both of the latter were separated by allelic frequencies at four loci, i.e. Sdh, G6pd, Est3 and Fle3. In group 1, some accessions which displayed group 4 alleles, i.e. V 24 and V 99 also showed slightly larger seeds. Although most accessions studied here came from North Cameroon, a group of weedy *V. reticulata* from West Africa appear adapted to cultivated fields and disturbed areas, and are genetically different and separated from the West African wild *V. reticulata.*

This is of great interest regarding cowpea crop-weed complex, as weedy cowpeas in West Africa are more genetically linked to cultivated taxon than to wild annual taxon (Pasquet, 1994). In such a context, the existence of weedy *V. reticulata* provides an argument for considering that the cowpea has issued from secondary domestication

instead of primary domestication (Blumler, 1992), and overcomes the old debate of cowpea origin between West African or East African cowpea (Vavilov, 1926; Murdock, 1959; Harlan, 1971; Steele, 1972; Vaillancourt and Weeden, 1992). As weedy *V. reticulata*, weedy cowpea could have come from somewhere else and have spread in West Africa through disturbances caused by man's agricultural activity. Cowpeas could have then been domesticated from the weedy forms. This was a hypothesis Chevalier raised in 1944, but arguments for or against it are scarce and make this *V. reticulata* study critical.

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