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CULTIVATED COWPEA (*VIGNA UNGUICULATA*): GENETIC ORGANIZATION AND DOMESTICATION

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Abstract

Cowpea gene pool organization is discussed on the basis of morphological and isoenzymatic data. A hypothesis for a single domestication of cowpea in North-East Africa is presented.

Introduction

When dealing with cultivated cowpea *Vigna unguiculata* (L.) Walp., two problems arise. On the one hand, the organization of the cultivated part of the gene pool, on the other hand, the links between cultivated and wild forms, with the formulation of hypotheses for domestication(s)

Two cowpea concepts may be used as a basis for research.

Firstly, that of Piper (1912, Verdcourt 1970, Ng 1990), this being the CG (Cultivar Group) Unguiculata — CG Biflora (subsp. *cylindrica* (L.) Van Eseltine) — CG Sesquipedalis trilogy (Westphal 1974, Maréchal & al. 1978), with a CG Textilis added, equivalent to var. *textilis* A.Chev. This classification has often been difficult to apply: while CG Sesquipedalis is very distinct, CG Biflora can hardly be distinguished from CG Unguiculata. Steele (1972) recognized the inadequacy of this system for African plants, and proposed another new and fairly complicated key, which took into consideration the extra characters of photosensitivity and the texture of the integument of the seeds.

Secondly, that of Chevalier (1944) who took into account the following subdivisions for West Tropical Africa:

- subsp. *oleraceus* (Schumach.) A.Chev. (twining plants from Guinean areas),
- subsp. *lubia* (Forssk.) A.Chev. (trailing plants from Sudano-Sahelian savannas)
 - var. *campestris* A.Chev. (plants with smooth seeds),
 - var. *melanophthalmus* (DC.) A.Chev. (plants with wrinkled seeds),
 - var. *textilis* (plants cultivated for the fibres of their long peduncles).

This classification lends itself well to Steele's results, by contrasting photosensitive cultivars (subsp. *lubia*) and photoindependents (subsp. *oleraceus*) on the one hand, and smooth seeded cultivars (var. *campestris*) and cultivars with wrinkled seeds (var. *melanophthalmus*) on the other.

The genetic organization of cultivated cowpeas

Morphological data

More than five hundred accessions (including 38 from CG Textilis) were studied using 23 quantitative characters and 5 qualitative characters. Two qualitative and two

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quantitative characters enabled the attribution of the accessions studied to the following different groups :

- photosensitivity and smooth seeds : CG Biflora (Asian and African plants, = var. *campestris*).
- photosensitivity and wrinkled seeds : CG Melanophthalma from var. *melanophthalmus*.
- photoindependence and short or medium-length pods : CG Unguiculata [= subsp. *oleraceus* sensu A.Chev.; the type specimen of *Dolichos oleraceus* DC. belongs to *Vigna adenantha* (Hepper 1976)]. The neotype of *Vigna unguiculata* (Westphal 8682 (WAG,K,P)), belongs to this group.
- photoindependence and long, fleshy pods : CG Sesquipedalis.
- long peduncle : CG Textilis.

The analysis of data from 13 of the variables is shown in Figure 1. The variables relative to the dimensions of the different organs make up factor 1 with the dehiscence of the pods. They contrast evolved cultivars on the left and more primitive cultivars and wild forms on the right. In a further interesting distinction, the number of ovules clearly separates the CG Unguiculata — CG Sesquipedalis group (15–24 ovules per pod) from the CG Biflora-CG Melanophthalma group (10–17) and, with photosensitivity, makes up factor 2. The correlation between ovule numbers and photosensitivity is marked : 0.725. The exceptions are essentially CG Textilis cultivars. CG Textilis appears here to be particularly heterogenous.

The isozyme diversity

191 cultivated accessions were studied using 20 enzymes, which showed 36 putative loci, among which only 13 displayed variability.

The separation between the two morphophysiological groups is not very clear. 64 accessions, made up from all the cultigroups, show the same pattern. What is more, all of the cultivar groups have the same most common alleles for each isozyme. The analysis of isoenzymatic data, however, brings a third group to light (Fig. 2):

- CG Unguiculata with alleles got2-110 and fle3-104
- West African CG Biflora and CG Melanophthalma with alleles amp3-103
- Ethiopian CG Biflora with alleles gpd-105, enp-105 and fle3-104

CG Textilis still appears very heterogenous.

Discussion

Cultivated cowpea can be split up into two groups, well characterized by their ovule numbers and their photosensitivity, with fairly primitive and fairly evolved forms in each group. These two morphophysiological groups are, however, difficult to distinguish isoenzymatically, as are those of sorghum (Ollitrault 1989) and pearl millet (Tostain & Marchais 1989). We are still far from the examples of double domestication where there is a clear isozymatic distinction between groups, as in *Phaseolus vulgaris* (Singh & al. 1991) or rice (Second 1985). This leads us to consider that there has been only a single domestication of cowpea.

CG Biflora from Ethiopia and CG Textilis have in common alleles encountered nowhere else among cultivated accessions. Ethiopian CG Biflora also shows isoenzymatic similarities to CG Unguiculata, which might place it at a watershed between the two divergent paths (CG Unguiculata-CG Sesquipedalis and CG Biflora-CG Melanophthalma).

Cultivated Cowpea: Genetic Organization and Domestication

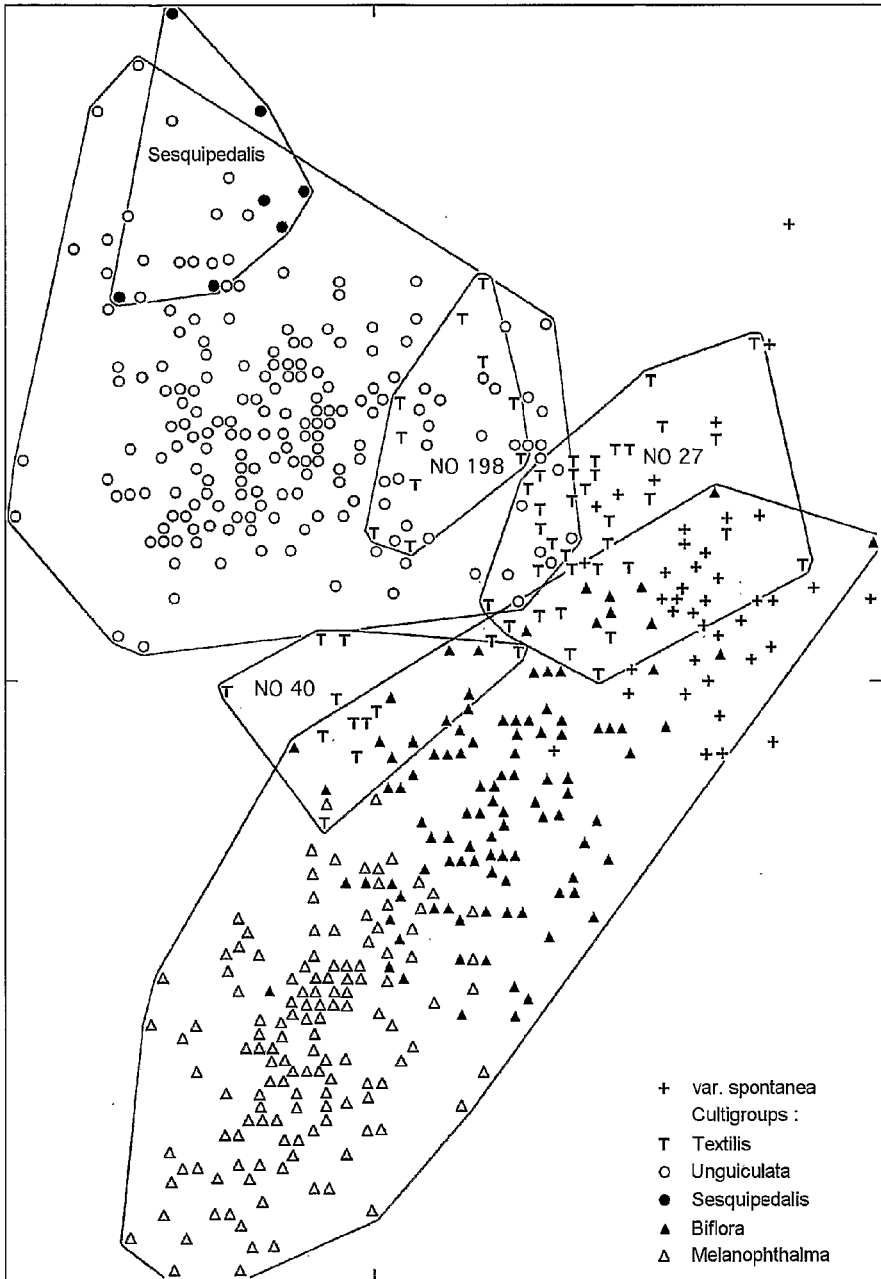


FIG. 1. Principal components analysis of morphological data. 'NO 27', 'NO 40' and 'NO 198' are three cultivars from CG Textilis.

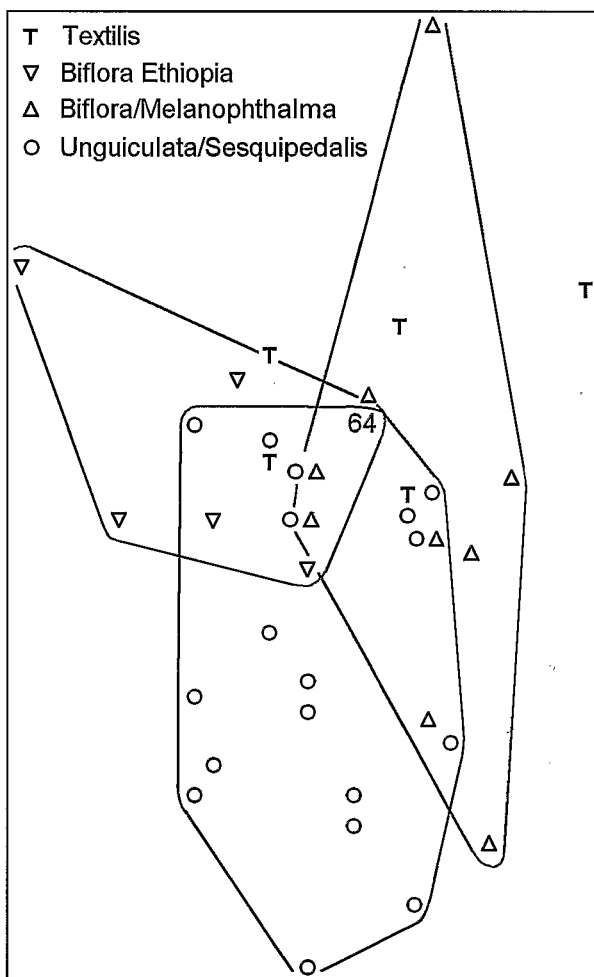


FIG. 2. Isozyme diversity. Principal components analysis of Nei's distances table. '64' is the most common pattern.

This could confirm the antagonism between a possible first period, when cowpea was grown for its fibre (of which only scattered relics remain), and a more recent period, when cowpea started to be grown for its seeds, and when only two evolutionary paths developed. The poor overall diversity does not rule out the initial wild stock being the same, nor that CG Biflora developed from CG Textilis.

There then followed the divergence between West African CG Biflora and CG Unguiculata (or Asian CG Biflora, but this latter group has not yet been studied isoenzymatically). Finally, there was the emergence of CG Melanophthalma from West African CG Biflora and CG Sesquipedalis from CG Unguiculata.

This would make north-eastern Africa an excellent potential centre of domestication. The ethnobotanical (Pasquet & Fotso 1994) and linguistic (Pasquet

unpublished data) studies carried out in Cameroon indicate that cowpea is more closely linked with Tchadic speakers than with Adamawa or Benoue-Congo speakers. In the same way, CG *Textilis* could be linked to some Nilo-Saharan speakers. Both of these linguistic groups locate domestication around North-East Africa.

Relations between cultivated and wild cowpea

The progenitor of cultivated cowpea

Cultivated accessions are genetically similar to wild annuals (Nei's distance median is 0.154) and subsp. *pubescens* (Nei's distance median is 0.202), but half a dozen loci distinctly separate cultivated accessions from subsp. *pubescens* (Fig. 3). This proximity justifies the classification of wild annuals (var. *spontanea*) and cultivated cowpea (var. *unguiculata*) under subsp. *unguiculata*, as Lush suggested (1979). Var. *spontanea* constitutes the most likely progenitor of cultivated cowpea.

The bottleneck

The bottleneck between wild and cultivated cowpeas seems great. Its importance is lessened if one considers that perennials could be treated as distinct species according to their genetic distances. With legumes of neighbouring genera, the variability observed in the wild forms (Schinkel & Gepts 1989, Koenig & Gepts 1989, Potter & Doyle 1992) corresponds to that observed in the var. *spontanea* alone. So, if one takes subsp. *unguiculata* only, the bottleneck is less impressive. It is nevertheless a fact that the variability of cultivated forms alone is poor compared to related legumes or to all cultivated plants (Doebley 1989).

This pronounced bottleneck is a second reason for proposing a single cowpea domestication.

Discrepancy between wild and cultivated cowpeas

There is an isoenzymatic shift between wild and cultivated forms, as two loci clearly separate them. Nei's distances between wild and cultivated are greater than the distances between cultivated forms and the distances between wild forms themselves (Fig. 3). Furthermore, this gap is confirmed in the Vaillancourt & Weeden cpDNA study (1992).

Such discrepancies are fairly rare in cultivated plants (Doebley 1989), but not without precedent. A similar situation can be found with both sorghum (Ollitrault & al. 1989, Aldrich & al. 1992) and pearl millet (Tostain 1992). The comparison with the studies carried out in sorghum is particularly interesting. As in our research, the discrepancy observed between wild and cultivated forms is above all a phenomenon of the western and southern zones, and authors have used this as the basis of their main argument in the formulation of hypotheses for sorghum domestication in Northeast Africa. The northeast of Africa, from where sorghum originated, could, therefore, also be the area where its traditionally-associated legume — cowpea — originated. Vaillancourt & Weeden (1992) have suggested Nigeria as a centre for domestication, but their analysis was based on only 32 cultivars. Only two cpDNA patterns were observed. One was found nowhere among the 26 wild accessions studied and the other in two Nigerian accessions, NI 951 and NI 991. But the morphology of these two accessions would indicate that they could be weedy types resulting from hybridization between wild and cultivated plants. Both cultivated form patterns could exist among wild forms in an area, such as northeast Africa, which has been sampled very little or not at all.

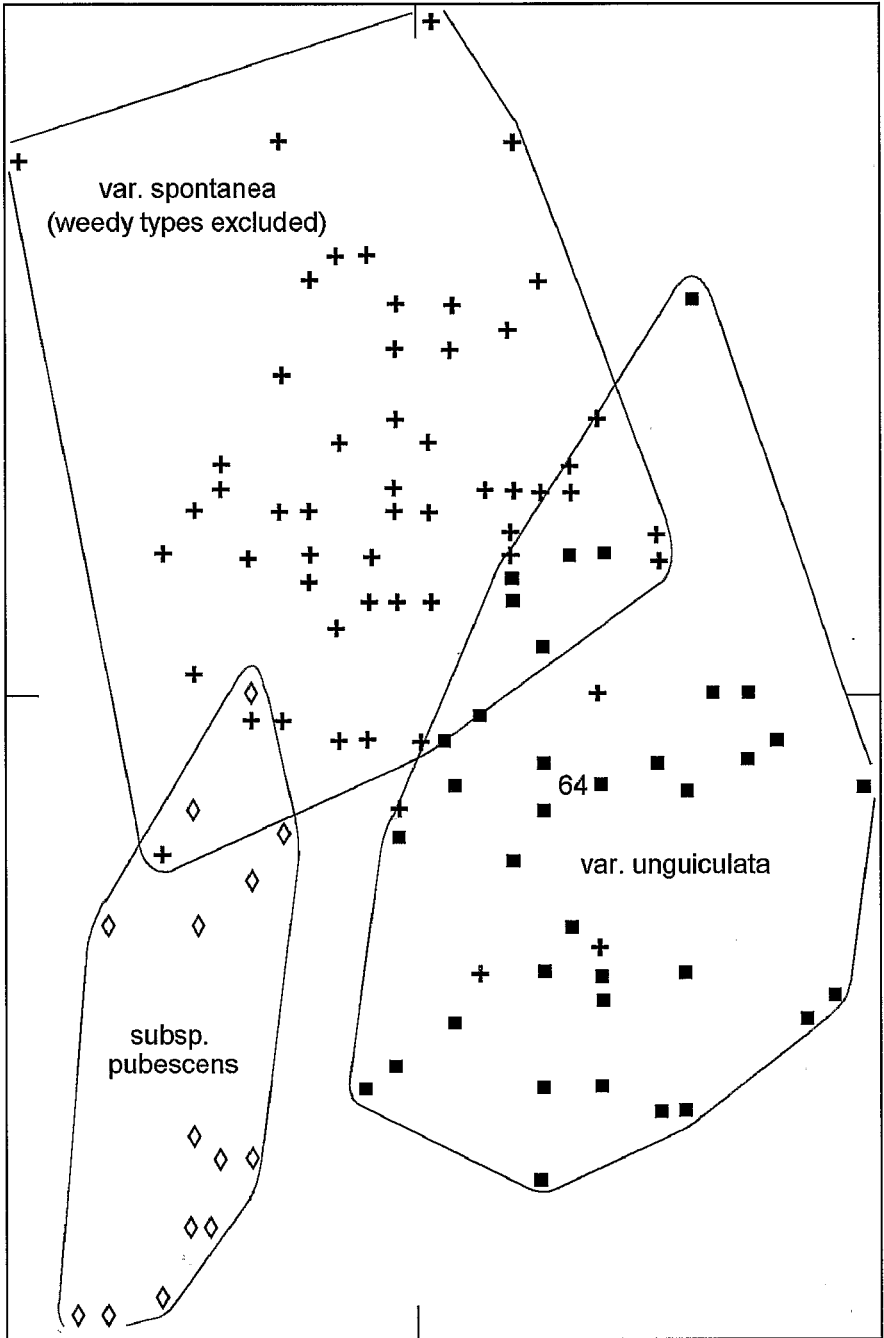


FIG. 3. Subsp. *pubescens*, wild annuals and cultivated cowpeas. Principal components analysis of Nei's distances table. '64' is the most common pattern.

Now the evolutionary scheme of cultivated cowpea has become clearer, and there are many reasons for proposing a hypothesis of unique domestication in Northeast Africa. However, the shift between wild and cultivated forms still needs to be explained, and the real progenitor among var. *spontanea* still needs to be found.

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References

- Aldrich, P.R., Doebley, J., Schertz, K.F. and Stec, A. (1992). Patterns of allozyme variation in cultivated and wild *Sorghum bicolor*. *Theor. Appl. Genet.* **85**: 451–460.
- Chevalier, A. (1944). La Doliqne de Chine en Afrique. *Rev. Bot. Appl. Agric. Trop.* **24**: 128–152.
- Doebley, J. (1989). Isozymic evidence and the evolution of crop plants. In D.E. Soltis & P.S. Soltis (editors). *Isozymes in plant biology*, pp. 165–191. Chapman and Hall, London.
- Hepper, F.N. (1976). The West African herbaria of Isert and Thonning. Bentham-Moxon Trust, Kew.
- Koenig, R. and Gepts, P. (1989). Allozyme diversity in wild *Phaseolus vulgaris*: further evidence for two major centers of genetic diversity. *Theor. Appl. Genet.* **78**: 809–817.
- Lush, W.M. (1979). Floral morphology of wild and cultivated cowpeas. *Econ. Bot.* **33**: 442–447.
- Maréchal, R., Masherpa, J.M. and Stainier, F. (1978). Etude taxonomique d'un groupe complexe d'espèces des genres *Phaseolus* et *Vigna* (*Papilionaceae*) sur la base de données morphologiques et polliniques, traitées par l'analyse informatique. *Boissiera* **28**: 1–273.
- Ng, N.Q. (1990). Recent developments in cowpea germplasm collection, conservation, evaluation and research at the genetic resources unit, IITA. In N.Q. Ng & L.M. Monti (editors). *Cowpea genetic resources*, pp. 13–28. IITA, Ibadan.
- Ollitrault, P., Arnaud, M. and Chanterau, J. (1989). Polymorphisme enzymatique des sorghos. II. Organisation génétique et évolutive des sorghos cultivés. *Agron. Trop.* **44**: 211–222.
- Pasquet, R.S. & Fotso, M. (1994). Répartition des cultivars de niébé (*Vigna unguiculata* (L.) Walp.) du Cameroun: influence du milieu et des facteurs humains. *J. Agr. Trop. Bot. Appl.* **36**: 93–143.
- Piper, C.V. (1912). Agricultural varieties of the cowpea and immediately related species. USDA. Bureau of Plant Industry, Bulletin No. 229. Washington, Government Printing Office: 1–160.
- Potter, D. and Doyle, J.J. (1992). Origins of the african yam bean (*Sphenostylis stenocarpa*, *Leguminosae*): evidence from morphology, isozymes, chloroplast DNA, and linguistics. *Econ. Bot.* **46**: 276–292.
- Schinkel, C. and Gepts, P. (1989). Allozyme variability in the Tepary Bean, *Phaseolus acutifolius* A. Gray. *Plant Breed.* **102**: 182–195.
- Second, G. (1985). Evolutionary relationships in the *Sativa* group of *Oryza* based on isozyme data. *Génét. Sél. Evol.* **17**: 89–114.
- Singh, S.P., Nodari, R. and Gepts, P. (1991). Genetic diversity in cultivated common bean: 1. Allozymes. *Crop Sci.* **31**: 19–23.

Advances in Legume Systematics 8: Legumes of Economic Importance

- Steele, W.M. (1972). Cowpeas in Nigeria. Ph. D. Thesis. University of Reading. UK.
- Tostain, S. and Marchais, L., (1989). Enzyme diversity in pearl millet (*Pennisetum glaucum*). 2. Africa and India. *Theor. Appl. Genet.* **77**: 634-640.
- Tostain, S. (1992). Enzyme diversity in pearl millet (*Pennisetum glaucum*). 3. Wild millet. *Theor. Appl. Genet.* **83**: 733-742.
- Vaillancourt, R.E. and Weeden, N.F. (1992). Chloroplast DNA polymorphism suggests Nigerian center of domestication for the cowpea, *Vigna unguiculata* (*Leguminosae*). *Amer. J. Bot.* **79**: 1194-1199.
- Verdcourt, B. (1970). Studies in the *Leguminosae-Papilionoideae* for the Flora of Tropical East Africa. IV. *Kew Bull.* **24**: 507-569.
- Westphal, E. (1974). Pulses in Ethiopia: their taxonomy and agricultural significance, Agricultural Research Reports 815. Centre for Agricultural Publishing and documentation, Wageningen.