

WILD COWPEA (*VIGNA UNGUICULATA*) EVOLUTION

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Abstract

A new hypothesis of wild cowpea evolution is proposed, based on morphological and biogeographic data, isozyme and breeding system studies.

Introduction

Cowpea, *Vigna unguiculata* (L.) Walp., is one of the major pulses in the semi arid and humid tropics. Verdcourt (1970) and Maréchal & al. (1978) classified *Vigna unguiculata* into *V. unguiculata* subsp. *unguiculata* (which included the cultivated forms), and half a dozen wild taxa (Tab. I).

Until recently, this infraspecific classification was accepted (Ng 1990), but it does not cover all situations (Lush 1979, Ng 1990: 20).

In order to understand the gene pool organisation of *V. unguiculata*, a living collection of more than 150 wild accessions was studied, focusing on morphology, isozyme diversity and breeding systems.

Morphology

Thirty five morphological characters were observed, among them several not previously noted, i.e., rootstock swelling, primary leaf shape, life-span, inflorescence rachis, flower scent, colour patterns and appendages of the standard petal, keel shape, number of ovules, and seed size.

Analysis of the morphological data leads to ten clusters. They correspond to geographically characterised groups, which can be traced through herbarium material (Fig. 1), and are ranked as subspecies (Pasquet 1993a & 1993b) (Tab. 2). The word "mensensis" is now excluded, as *Vigna mensensis* Schweinf. is synonymous with *V. membranacea*. Subsp. *dekindtiana* is now reduced to the perennial taxon from the Huilla Hills (Angola) and, as suggested by Lush (1979), the cultivated taxon is reduced to varietal rank, along with annuals, within subsp. *unguiculata* (Pasquet 1993a). Weeden's team recently confirmed this status for the cultivated plants using cpDNA data (Vaillancourt & Weeden 1992).

In the morphological analysis, there are two levels. First, vegetative characters separate the subspecies which will be called out/inbreds (Fig 1B). All these taxa display strong morphological features such as pubescence, seed size or leaf shape.

Secondly, floral characters separate the subspecies which will be called outcrossers (Fig. 1A). These latter subspecies cannot be separated through vegetative characters.

Geographically, all the outcrossing subspecies (and the outcrossing parts of the out/inbreds) are restricted to Guinean or highland areas. Out/inbreds cover larger and drier areas with a more or less coastal distribution. *Vigna monantha* Thulin is not well-known, but could belong to this latter group.



TABLE 1. Recent *Vigna unguiculata* infraspecific classifications

Verdcourt 1970	Maréchal & al. 1978	Pasquet 1993a-1993b	
subsp. <i>protracta</i> <i>V. angustifoliolata</i>	subsp. <i>dekindtiana</i> var. <i>protracta</i> subsp. <i>stenophylla</i> }	subsp. <i>stenophylla</i>	} perennial gene pool
<i>V. tenuis</i> <i>V. pubescens</i>	subsp. <i>tenuis</i> subsp. <i>dekindtiana</i> var. <i>pubescens</i>	subsp. <i>tenuis</i> subsp. <i>pubescens</i>	
subsp. <i>momensis</i>	subsp. <i>dekindtiana</i> var. <i>momensis</i>	{ subsp. <i>letouzeyi</i> subsp. <i>burundiensis</i> subsp. <i>paawekia</i>	
subsp. <i>dekindtiana</i> <i>V. brachycalyx</i>	subsp. <i>dekindtiana</i> var. <i>dekindtiana</i>	{ subsp. <i>baoulensis</i> subsp. <i>alba</i> subsp. <i>dekindtiana</i>	
subsp. <i>unguiculata</i> subsp. <i>cylindrica</i> subsp. <i>sesquipedalis</i> }	subsp. <i>unguiculata</i> var. <i>unguiculata</i>	subsp. <i>unguiculata</i> var. <i>spontanea</i>	wild/weedy annuals
		subsp. <i>unguiculata</i>	cultivated gene pool

Isozyme Diversity

Accessions were also screened by starch gel protein electrophoresis for a total of 20 enzymes (ADH, MDH, SDH, IDH, FDH, GDH, GPD, PGD, D1A, GR, GOT, PGM, EST, FLE, β GLU, ENP, LAP, PGI, MPI, CAT), which showed 35 putative loci products suitable for further analysis.

Nei's distance UPGMA analysis produces clusters fairly similar to those of the morphological analysis (Fig. 2). With the exception of subsp. *pubescens*, perennial subspecies are strongly separated by high Nei's distances.

However, there are several divergences from the morphological analysis. Subsp. *pubescens* can almost be included in var. *spontanea*, whereas it was a major group in the morphological analysis. Subsp. *tenuis* divides into an inland outcrossing cluster and a coastal cluster. Accessions from the latter cluster are mainly inbreds, possibly due to introgression with var. *spontanea*. Subsp. *alba* displays a similar feature since inland inbreeding accessions are included in the var. *spontanea* cluster. In both cases, slight morphological differences exist between these subgroups. It is likely that subsp. *stenophylla* and subsp. *pubescens* show a similar division but too few outcrossing accessions of these subspecies have been studied.

In the same way, the "south" cluster of var. *spontanea* is made up of accessions from Namibia to Zimbabwe, which seem to show introgression with subsp. *tenuis* or subsp. *stenophylla*, just as the rather strong isozyme diversity within the var. *spontanea* cluster is mainly due to introgressions by local perennial subspecies. Most var. *spontanea* accessions, from Senegal to South Africa, are weedy forms, as their isozyme patterns are nearly identical to those of cultivated accessions.

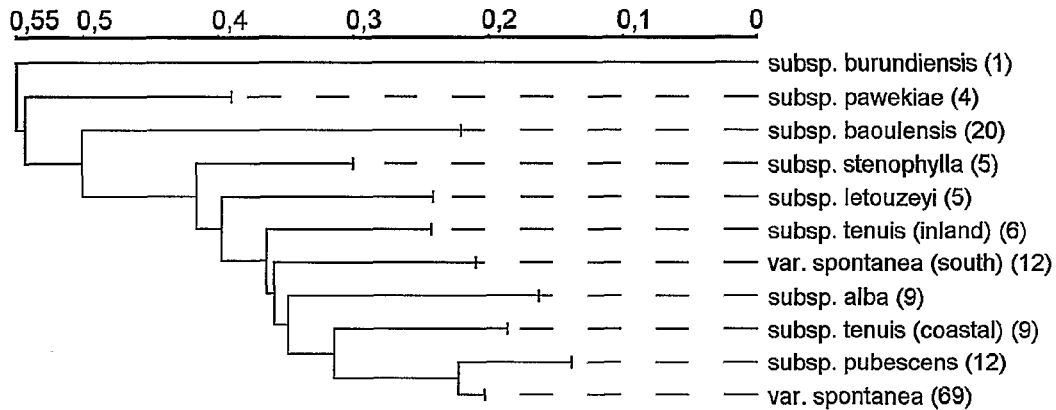


FIG. 2

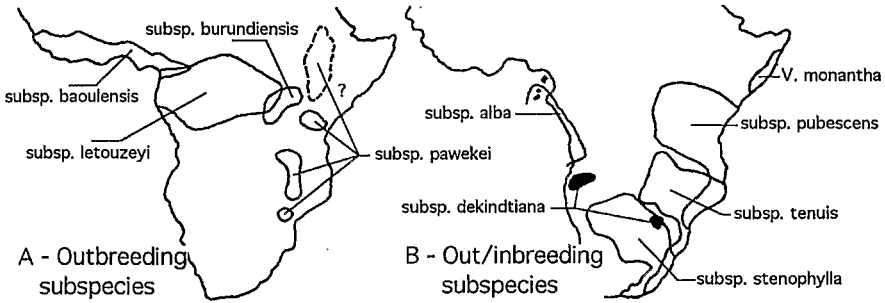


FIG. 1. Geographic distribution of perennial subspecies.

There are also divergences at the accessions level, almost always between var. *spontanea* and perennial subspecies, which probably reflect introgressive hybridizations. This has been proved, for example, by thorough analysis of several lines obtained from different seeds taken from Richards 17805 (K), a var. *spontanea* specimen introgressed by subsp. *pubescens*.

Breeding System

A breeding system study was undertaken, because of the high variability in seed setting observed among accessions. Outcrossing accessions with low pod set (0.00–0.40 pod/flower) were separated from inbreeding accessions, including cultivated cowpeas, which displayed high pod set (0.70–1.00 pod/flower).

Besides several floral differences (Rawal 1975), outcrossing accessions are characterised by the arrangement of their anthers and stigma, which prevents selfing (Lush 1979). This can easily be overcome by hand-pollination or insect tripping, which restore high pod setting. In addition, the accessions display great variability in

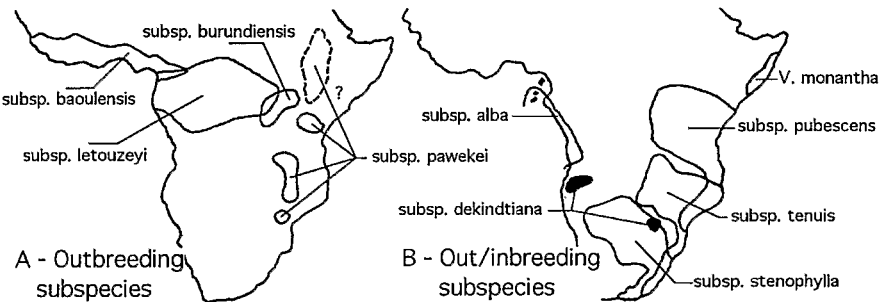


FIG. 2. Simplified schema of UPGMA clustering based on Nei's genetic distances between accessions. The number of accessions in the cluster is in brackets. Clusters not detailed are indicated by dashed lines.

TABLE 2. Morphological features of the different subspecies.

subspecies	root	rachis internodes	flower	calyx-lobe	keel twisting	ovule numbers	seed
<i>baoulensis</i>	no rootstock	short, numerous	very large	short	left	high	long/med.
<i>letouzeyi</i>	no rootstock	short, numerous	large	long	right	high	long/med.
<i>burundiensis</i>	no rootstock	short, numerous	large	very long	right	high	medium
<i>pawekiae</i>	root./no root.	short, numerous	med./large	long	left	high	long/med.
<i>dekindtiana</i>	rootstock	short, numerous	large	short/med.	beaked	low	long
<i>stenophylla</i>	rootstock	short, numerous	small/med.	medium	left	low	long
<i>tenuis</i>	rootstock	short, few	small/med.	short	right	low/med.	short/med.
<i>alba</i>	rootstock	short, numerous	medium	short/med.	right	very hi.	very small
<i>pubescens</i>	no rootstock	long, numerous	medium	med./long	right	low/med.	medium
<i>unguiculata</i> var. <i>spontanea</i>	no rootstock	short, num./few	medium	short/med.	right	low/high	medium

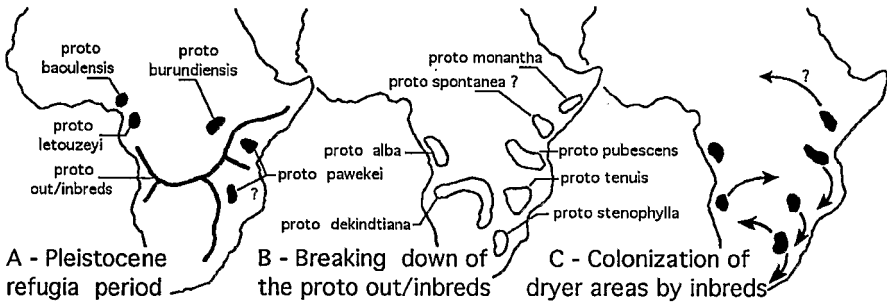


FIG. 3. Schema for the hypothesis of the three step evolution of *Vigna unguiculata*.

the number of pollen grains per anther (200–700 for cultivated and inbreds, 600–1200 for outcrossers), even if the Cruden index (1977) is not greatly modified (2.38–2.64 for cultivated and inbreds, 2.41–2.90 for outcrossers, which accounts for variability between facultative autogamy and facultative xenogamy).

A hypothesis of evolution of *Vigna unguiculata*

Opposition between outbreeding subspecies and out/inbreeding subspecies, and within the second group, opposition between outcrossers and inbreds (through slight divergences in morphological features and isozyme polymorphism), led to presumption of a three-step evolution of the *Vigna unguiculata* complex, which could be explained in the following very simplified manner.

The strong genetic distances between perennial taxa suggest an initial diversification probably dating from well before the Pleistocene, as these taxa require a more “humid” environment (Fig. 3 A). This hypothesis is reinforced by the distribution of these subspecies, and especially by the separation in Cameroon between subsp. *baoulensis* and subsp. *letouzeyi*, a well-known boundary in studies of Pleistocene refugia (Maley 1987). At that time a proto-taxon, adapted to drier (and rather cool) conditions through favourable morphological features (rootstock, pubescence, small leaves...), probably grew over an area spread from the Congo and the Huilla Hills to Ethiopia and the Transvaal through the Congo-Zambesi watershed (Fig. 3 A).

Progressive breaking down of this proto-taxon, through several climatic changes, would successively isolate taxa leading to the present-day out/inbreeding subspecies (Fig. 3 B).

The last event seems to be an evolution from outcrossing to inbreeding, which could have allowed colonization of drier areas (and certainly warmer), as, within the out/inbreds, inbreeders occupy rather drier areas than their outcrossing counterparts (Fig. 3 C).

An ultimate evolution would have resulted in the diffusion of the cultivated cowpea, which made var. *spontanea* fairly common throughout Africa. Var. *spontanea* also has the status of a true subspecies, as some accessions display outbreeding tendencies, and as its outbreeding counterparts must exist. But it is strongly indebted to the cultivated cowpea for its present state as well, although studies of available accessions have not provided an explanation of the relative importance of both phenomena.

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