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by Kanti M. Rawal

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NATURAL HYBRIDIZATION AMONG WILD, WEEDY AND CULTIVATED *VIGNA UNGUICULATA* (L.) WALP.

KANTI M. RAWAL

International Institute of Tropical Agriculture, Ibadan, Nigeria

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SUMMARY

As is the case with many cultivated species, *Vigna unguiculata* (L.) WALP. has a wild form growing in secondary forests and derived savannahs and a companion weed form adapted to disturbed habitats such as roadside ditches and fields. Evidence of introgressive hybridization between weedy and cultivated forms has been presented. The zone of extensive natural hybridization corresponds to the cultivation area in northern Nigeria and Niger and may well extend to Upper Volta and Senegal. The pattern of distribution of wild and weedy forms, the extent of introgression and ethnobotanical evidence strongly suggest West Africa as the center of domestication for *V. unguiculata*.

INTRODUCTION

The cowpea, *Vigna unguiculata* (L.) WALP is an important grain legume crop in tropical and sub-tropical areas. In 1971, West Africa procuded more than 85% of the total world cowpea production (RACHIE & ROBERTS, 1974). The cowpea is cultivated commercially in Senegal, Mali, Upper Volta, Niger and Nigeria (north of 8° N latitude).

VERDCOURT (1970) recognized five subspecies of *V. unguiculata*, of which the subspecies *sesquipedalis*, *unguiculata* and *cylindrica* are cultivated, whereas the subspecies *dekindtiana* and *mensensis* are spontaneous. In this paper the morphology of wild and weedy forms is described and evidence of introgressive hybridization between them and the cultivars is presented. For the purpose of this paper *weed* is used to denote plants adapted to habitats disturbed by human activities. *Wild* means plants that thrive well in relatively undisturbed habitats and are neither cultivated nor encouraged by human disturbance (HARLAN, 1970; HARLAN & DE WET, 1965).

MATERIALS AND METHODS

Systematic field collection of cultivated grain legumes and related species was initiated in 1970. During October, November and December of 1971, 1972 and 1973 the author travelled about 38,000 km making collections in Nigeria and Niger. Detailed field observations on the habitat and other relevant characteristics of materials under study were made and geographic locations were recorded as precisely as possible. Herbarium specimens were studied at Kew, British Museum, Paris, Nairobi, Bombay and Ibadan herbaria.

The accessions were grown in uniform nurseries both at the University of Ibadan and at the International Institute of Tropical Agriculture, Ibadan (latitude 7°30′ N)

and detailed notes taken and measurements made on several parameters. Data collected in this study included: average length and width of teminal leaflet, average length of raceme, average number of flowers per raceme, shape of the teminal leaflet, orientation of pods, pod colour and texture, dehiscence of pods and patterns of pigmentation of flowers and seeds.

For terminal leaflet length and width the average of five healthy leaves on ten plants of each accession was considered. Leaflet measurements are variable, but under uniform nursery conditions the differences are so large that highly significant values were obtained. The length of raceme was measured from the base to the tip of racemes and an average of ten such observations per plant on ten plants of each accession was considered. Other characters such as the coarseness of dry pod walls, size and vigour of plant, terminal leaflet shape and orientation of pods on peduncle were scored subjectively from living materials and wherever appropriate, from herbarium specimens. The distribution was established by combining information from field studies, herbarium specimens and the living materials.

VARIATION IN CULTIVARS

The morphological variability in the cultivated forms of *V. unguiculata* is enormous. Growth habit ranges from determinate, erect, non-branching types to indeterminate, prostrate or climbing and profusely branching forms. Length of pod varies from 10 cm to more than 110 cm. The 100 seed weight varies from 18 g to more than 34 g. Detailed information regarding various botanical and agronomic characters of 3,789 cultivars from the World Cowpea Germ Plasm Collection is reported by PORTER et al. (1975). The wide variation in seed coat colours and patterns of pigmentation were genetically analysed by FRANCKOWIAK & BAKTER (1975a, 1975b).

This great diversity in various morphological characters has led to the confusion and lack of agreement regarding the taxonomy among geneticists, agronomists, horticulturists and taxonomists dealing with the cowpeas. VERDCOURT (1970), utilizing published cytological and genetical information suggested that the three cultivated members of the group could not be regarded as distinct species. His key to the infraspecific variants of *V. unguiculata* is based primarily on the ratio of calyx-lobe length to the calyx tube length. The subspecies *dekindtiana*, *sesquipedalis*, *unguiculata* and *cylindrica* possess calyx-lobes mostly shorter than the tube (2.5-5 mm long) whereas the subspecies *mensensis* has calyx-lobes longer than the tube (0.5-1.4 cm long). Our observations during the detailed morphological study of the wild, weedy and cultivated cowpeas from the World Cowpea Germplasm Collection at IITA, comprising of more than 7,000 accessions indicate continuous variation in the calyx-lobe length ranging from 2 mm to 16 mm. This variation was observed across the subspecies of cultivated and spontaneous taxa.

Hybrids among these taxa are easy to make, they are fully fertile and show Mendelian inheritance for the characters that distinguish them (MACKIE, 1946; ROY & RICHHARIA, 1948; BRITTINGHAM, 1950; SEN & BHOWAL, 1960; FAWOLE, 1973). According to PIPER (1912) a complete series of intergrades between all the cultivated taxa exist in respect to many characters of taxonomic significance.

The cultivars from Nigeria and Niger are predominantly indeterminate, prostrate

and photosensitive, flowering sparsely under long day conditions. The terminal leaflets are usually globose or subglobose but subhastate shape is also observed. The peduncles are 20 to 50 cm long with raceme axis rarely more than 1.5 cm long. The flowers are subtended on short pedicels and the standard petal of the flower is 1.0 to 1.5 cm long and 1.5 to 2.5 cm wide with variable pattern of pink-mauve pigmentation on the standard petal and the wings. The patterns of pigmentation observed on open flowers are described in detail by PORTER et al. (1975). The flowers open in the morning, by the ventral uplifting of the standard petal just prior to or at anthesis, and close by mid-morning.

The raceme appears to be restricted in development in the sense that not more than three pods are borne on one peduncle. The pods are oriented horizontal or pendant to the raceme axis. They are usually linear but curved and coiled pods are also observed. The pattern of pigmentation varies from no pigment to solidly pigmented with purple tip, coloured valves, coloured sutures and splashes of pigment all over the pod. Pod size varies from 12 cm to 50 cm in length. The texture of dry pods is usually smooth although papery, leathery and slightly coarse pods are not uncommon. The variation in seed coat colour and eye pattern is enormous and more than 90% of existing variability in the world germplasm of cowpeas is found in Nigeria (FRANCKOWIAK, personal communication). The texture of the seed coat is predominantly rough or wrinkled.

DESCRIPTION AND DISTRIBUTION OF THE WILD FORM

The wild form grows in the secondary forests and woodland savannahs of the humid and subhumid tropical areas of Africa, south of the Sahara. The distribution of this form in Nigeria is presented in Fig. 1. The plants are climbing perennials. They are photosensitive and will not commence flowering under long day conditions (14 hours or more of daylight). However, once the flowering is initiated and the moisture supply is adequate the plants continue to produce flowers throughout the year. The accessions from Lagos State, Ikenne and Ijebu Ode in the Western State and Agenebode in the Midwest State of Nigeria were collected from near swamps or ponds and were observed flowering throughout the year. Profuse flowering, however, takes place under short day conditions (11.5 hours or less of daylight).

The leaves are minutely scabrous on the upper surface and bluish green in colour with very distinct inverted V shaped, greenish yellow or white marks connecting both margins of the three leaflets. These marks are usually associated with the light green blotch at the leaflet bases. However, in some accessions these light green blotches are observed without the inverted V marks. In some accessions the white, waxy deposit is also noticed along the midribs of the leaflets. In rare instances all three types of marks are observed together. The stipules at the base of petioles are up to 10 mm long and 8 mm wide, cordate and appendaged with a conspicuous spur.

The peduncles are 30 to 50 cm long, solitary and axillary. The apex of the peduncle terminates into a raceme 30 to 50 mm long bearing 10 to 25 flowers that develop and mature slowly over a period of 3 to 4 months. The flowers are almost sessile, conspicuously large (20 to 30 mm long) and with solid mauve pigment all over the standard petal and the wings. They are aromatic with a strong, pleasant fragrance. The calyx

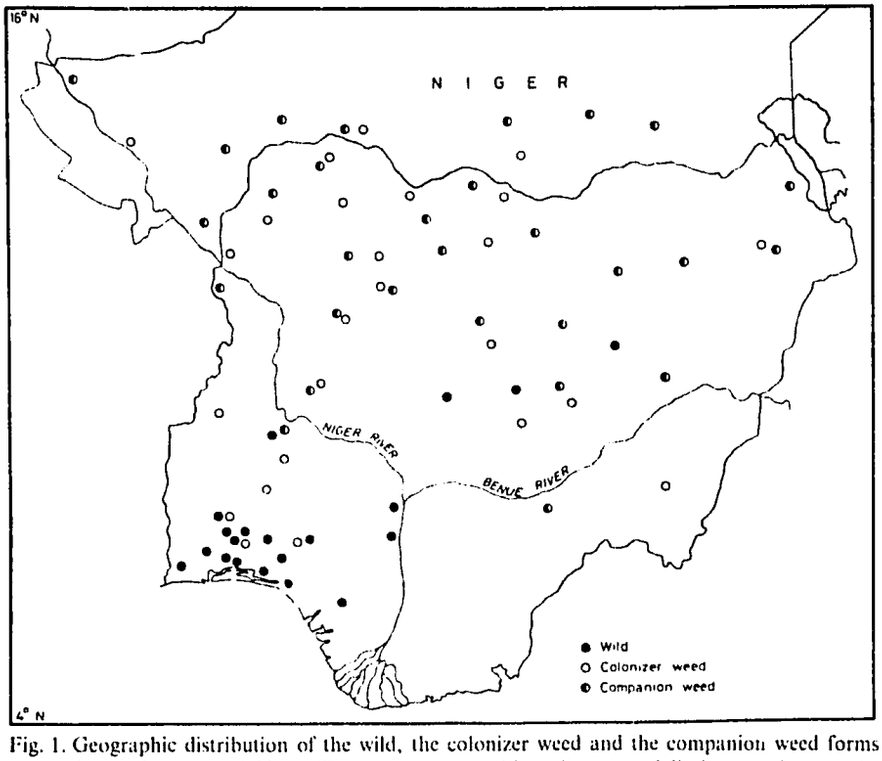

Fig. 1. Geographic distribution of the wild, the colonizer weed and the companion weed forms of *V. unguiculata* in Nigeria and Niger. The cowpeas are cultivated commercially in areas between latitudes 8° N and 15° N.

lobes are usually shorter than or equal in length to the calyx tube, however in the accessions from Erin-Ijesha and Ijebu-Igbo (Western State, Nigeria) the calyx lobes were found to be 1.5 to 2 times longer than the calyx tube. The flowers remain open for most of the day under high humidity conditions and anthesis appears to be delayed at least 4 to 5 hours after the flowers open. Under greenhouse conditions the rate of flower abscission in the wild form is high.

The pods are 5 to 10 cm long, linear and green in colour turning black upon maturity. The pod walls are coarse, scabrous and sand-papery in texture. The pods are oriented parallel to the raceme axis. Upon maturity they dehisce along the sutures with the spiral twisting of the valves. The seeds are smooth and self-coloured with black spots and mottling on tan background. The seeds are 3 to 5 mm long and 1 to 1.5 mm wide with 100 seed weight around 1 to 3 g. The seeds are dormant for at least 8 months and at room temperature remain viable for 3 to 4 years. Under uniform conditions, the wild form produced less seeds per plant per year than the colonizer and companion weed forms.

DISTRIBUTION AND DESCRIPTION OF THE WEED FORM

The weed form appears to be distributed all over the continental Africa and Malagasy. The numerous herbarium collections of this form include specimens from Nigeria, Niger, Upper Volta, Ghana, Ivory Coast, Sierra Leone, Senegal, Togo, Dahomey, Cameroon, Zaire, Congo, Sudan, Ethiopia, Kenya, Uganda, Tanzania, Sout Africa, Rhodesia and Angola.

The weedy plants thrive well in the disturbed habitats such as the fields and the road sides. There appear to be two races of the weedy *V. unguiculata*. The weed race of subhumid and humid areas in Nigeria (Fig. 1) grows along margins of water collections and the roadside and is difficult to distinguish from the wild form by external morphology alone. PIPER's description (1913) of the wild prototype of the cowpeas could refer to this weed form as well. This race is well adapted to naturally disturbed habitats in high rainfall areas, is photosensitive and usually grows prostrate. It is annual in growth habit and is a prolific seeder. The seeds are dormant for only 5 to 6 months and although the seeds germinate during the first rains (March-April in Southern Nigeria) the flowering takes place only around August. There is inconspicuous or no interaction between this race and the cultivated cowpeas. The gene exchange between this race and the wild form is not easily detectable. The flowers are the same size as the wild form. They are solidly pigmented as in the wild form but occasionally mutants devoid of any pigment on flowers are observed. The seed type is identical with that of the wild form and in only two accessions have seeds with solid tan colouration without mottling and black spots been observed.

The plants belonging to the weedy race of semi-arid region in Northern Nigeria and Niger are diverse in growth habit and both the prostrate and climbing types were observed. The prostrate plants were found predominantly along the roadsides and in the cultivated fields. The climbing types were seen in the woodland savannah along the margins of the ponds and in the relatively less disturbed habitats like sugarcane farms, abandoned fields and on hedges.

The plants are annual and prolific seeders. The seeds vary in pigmentation patterns from those of the wild form to those with solid tan, black with tan coloured mottling and solid red colouration. The raceme axis is 30 to 50 mm long and has been observed to bear upto 20 pods. The pods are black, 8 to 10 cm long and dehiscent. The terminal leaflet is subhastate and the leaflets may be with or without the marks seen in the wild form. The flowers are smaller in size than those in the wild form often without the aroma.

Of these, the prostrate race growing along with the cultivated cowpeas appears to hybridize freely with the cultivars (Fig. 2). Our living collection of these introgression types consists of 78 accessions from 29 locations in Nigeria and Niger representing all gradations from the typical weed form to the cultivated types. The area of introgression may well extend into the whole of Guinea Savannah zone of West Africa, where cultivation of cowpeas is most widely practiced. The weedy form in the farmer's fields is similar to the cultivated plants at all stages of growth except for the dehiscence of mature pods. The farmers of Northern Nigeria and Niger realize this and have terms by which to indicate this habit. In Hausa the term *waken beyi beyi* (meaning 'forbidden beans') is used for the semi-wild or weedy forms that

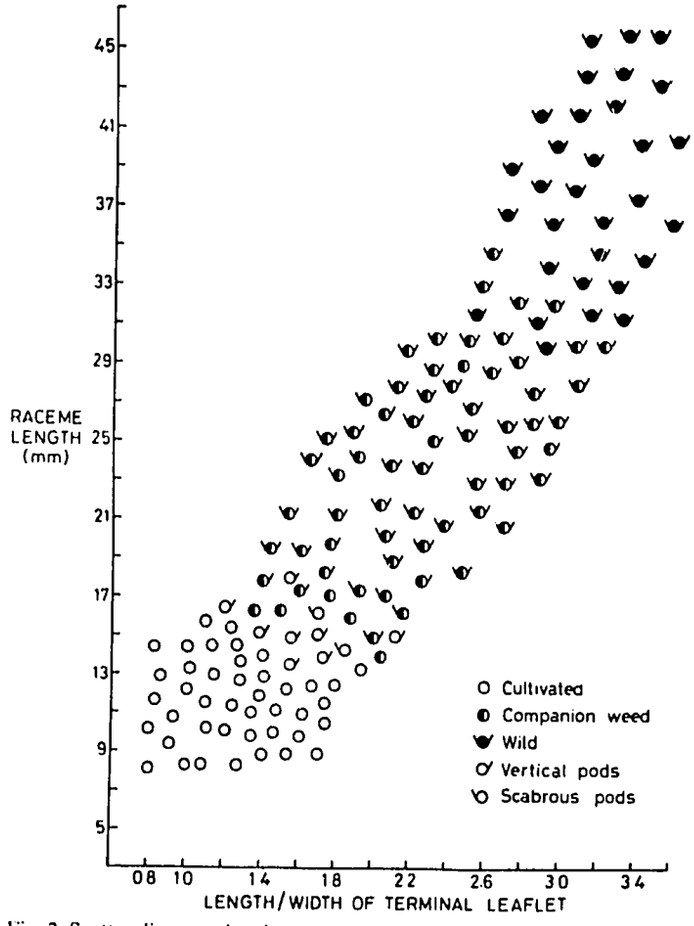

Fig. 2. Scatter diagram showing some morphological characters of the cultivated, weedy and wild forms of *V. unguiculata*.

climb vigorously on hedges or on the stalks of grasses and small trees in the savannah. The seeds of these plants are usually not eaten. However, the author has noted the the use of these seeds in Madarumfa (30 km north-west of Maradi, Niger) as an aphrodisiac and a must for puberty and initiation rites of adolescent males. Madarumfa is located on the fringe of a freshwater lake (about 2 km in diameter). There is an island in the middle of the lake where a large population of the wild form of *V. unguiculata* thrives under human protection. The pods are harvested before they shatter and disperse the seeds. The seeds are soaked and ground to make a paste, which is steamed and consumed with salt by those participating in the ritual. The females are prohibited from eating these seeds since it is believed they would lose fertility if they do so.

The terms *waken gizo* (meaning 'grows by itself') and *gayan gayan* (meaning 'the

weedy weed') relate to the weed form that grows along with the cultivated cowpea. The weed form is tolerated because the plants are similar to those cultivated at all stages of growth except that at maturity the dry pods of the weedy plants dehisce and shatter the seeds. The Hausa saying '*ka yi diya ka watsas*' meaning 'you get children only to scatter them' is used of these owing to the dehiscence of pods and scattering of the seeds (DALZIEL, 1937).

Artificial hybrids were made between all the races, subraces and the cultivars. The hybrids were fully fertile and the hybrids between the weed form and the cultivars produced intermediate type plants. Further backcrossing produced a pattern of variation among the derivatives similar to that observed in the introgression products. These plants possess pods with varying degrees of coarseness and brown colour when dry. The dehiscence of pods is controlled by a single dominant gene (RAWAL, unpublished).

PROBABLE ORIGIN OF THE COMPANION WEED

The morphological differences between the wild, weedy and cultivated forms of *V. unguiculata* are summarized in Table 1. Dependent upon the synthesis of information regarding the habit, habitat distribution and interaction among the wild and weed forms of *V. unguiculata* the following hypothesis is proposed to account for the origin of the weed form:

1. The wild form presently confined to subhumid and humid lowland tropical parts of Nigeria and probably Africa is the progenitor of the weed and the cultivated forms of cowpeas.
2. The wild form was at one time distributed in a wider geographical range than its present distribution. The colonizer form presently growing all over the sub-humid and semi-arid region evolved from the wild form.

Table 1. Morphological differences between wild, weedy and cultivated *V. unguiculata*.

Character	Wild	Weedy	Cultivated
growth habit	climbing	prostrate and climbing	erect, prostrate climbing
life span	perennial	annual	annual
terminal leaflet shape	subhastate	subhastate	globose, subglobose
length of raceme	40 mm	30 50 mm	25 mm
flower colour	solid mauve	solid mauve rarely white	solid mauve, intermediate, white
orientation of pods	vertical	vertical	pendant
pod colour pod immature	green	green	green, purple tip, purple sutures, purple valves, solid purple
pod mature	black	black, brown, splashed	cream, brown, splashed
pod dehiscence	shatters	shatters	non-shattering
Eye pattern - seeds	solid	solid	solid to eyeless
Eye colour seeds	mottled with speckles and black spots	variable	variable

3. The natural colonizer was brought under domestication in the sub-humid and semi-arid regions of West-Africa.
4. The interaction between the colonizer and the cultivated plants gave rise to the present day companion weed form observed in the fields, introgressing with the cultivated *V. unguiculata*.

The case of *V. unguiculata* appears to follow Harlan's model closely (HARLAN, 1970). The sequence of the genetic events leading to the evolution of cultivated *V. unguiculata* appears to be from the wild progenitor giving rise to the natural colonizer adapted to naturally disturbed habitats (growing widely in the sub-humid and semi-arid regions), to the present day crop-weed complex. According to HARLAN (1969) the weed races are characteristic of primary centres of the domestication of the crop. Upon examination of the folklore of the peoples of Northern Nigeria, associated with the weedy *V. unguiculata* it appears that the bifurcation into the cultivated and companion weed forms could have occurred at the start of domestication.

From his detailed analysis of the range of morphological variation in the cultivated cowpeas, geographic distribution of related species and crossability studies with various members of the genus *Vigna*, VARIS (1965) concluded that West or Central Africa is the centre of origin for *Vigna unguiculata*. From the evidence reported in this paper, the author supports the findings and conclusions of FARIS (1965) and asserts that West Africa is the centre of the origin of this crop on the grounds that both the wild and weed forms grow in this area, the companion weed is frequently present in the fields, the folklore around the weed form is unique, and the introgressive hybridization between the cultivated and companion weed forms is extensive.

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