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Reduction in seed size in crosses between wild and cultivated cowpeas

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SIMILAR to many cultivated species of plants, the origin and evolution of the cowpea, *Vigna unguiculata* (L.) Walp., conforms to the model proposed by Harlan[1–3]. The wild progenitor grows in the secondary forests and woodland savannahs of the humid and the sub-humid regions of Africa south of the Sahara. The plants belonging to the wild form are perennial climbers with distinct marks on leaflets; large, aromatic flowers; and black, dehiscent pods. The colonizer weed form is widely adapted to the sites of natural disturbance along the margins of streams and lakes in lowland tropical Africa. This predominantly annual creeper and prolific seeder is semiwild and difficult to distinguish from the wild form by external morphology alone. The companion weed of the cultivated *V. unguiculata* is exclusively an annual plant with variable growth habit ranging from erect and semierect to prostrate and climbing types. The plants belonging to the companion weed form hybridize freely with the cultivars and a complete series of intergrades between them has been observed in Northern Nigeria and Niger[5].

In this paper the reduction in seed weight of F_1 seeds obtained by crossing the wild form and various elite cultivars is reported with a view to elucidating the mechanism of evolutionary divergence at an infraspecific level in *V. unguiculata*.

Materials and Methods

The following accessions from the World Cowpea Germplasm Collection maintained at the International Institute of Tropical Agriculture, Ibadan, were used in this investigation:

Accession no.	Variety and source of collection
TVu 161	Early Ramshorn, USA
TVu 1760	Texas Cream, USA
TVu 4552	IFH 44-5, Ile-Ife, Nigeria
TVu 4569	IFH 144-1, Ile-Ife, Nigeria
TVx 819-IE	Ile-Ife, Nigeria
TVx 883-3D	Ile-Ife, Nigeria
TVu 4036	Wild, 15 miles NW of Agenebode, Mid-Western State, Nigeria
TVu 4581	Wild, Erin-Ijesha, Western State, Nigeria.

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The crosses were made by hand emasculation and pollination according to the technique described by Rachie et al.[4].

The average single seed weight of the parents used in crosses was calculated after weighing three lots of 100 seeds each. The average single weight of the F_1 seeds was calculated after weighing all the seeds harvested from each cross. All seeds were dried under uniform conditions for 72 hours to about 13 percent moisture. The percent reduction in seed weight was calculated as follows:

$$\frac{(\text{Parent seed weight}) - (F_1 \text{ seed weight})}{\text{Parent seed weight}} \times 100.$$

Results and Discussion

Under natural conditions the wild form sets a lower number of seeds per plant per year than the colonizer and companion weed forms. The plants belonging to the wild form appeared to be obligately outcrossing. Upon close examination of the reproductive parts it was observed that the stamens were 2 mm shorter than the receptive stigma and, in spite of abundant pollen, self fertilization was impossible. Under greenhouse conditions the rate of flower abscission was high and attempts to use the two accessions belonging to the wild form as female parents failed. Both accessions, TVu 4036 and TVu 4581 shed abundant amounts of pollen. Hand crossing using these accessions as male parents was highly successful.

In the Cowpea Improvement Program at the University of Ife, Ile-Ife, Grain Legume Improvement Program at the IITA, Ibadan and during the biosystematic studies on *Vigna* at the University of Ibadan, more than 4,500 crosses involving the cultivars and wild and weedy forms of *Vigna unguiculata* were made. A reduction in F_1 seed weight was not noted in any of the crosses among the various cultivated and companion weed forms of *V. unguiculata*, even though in certain crosses among cultivars lethal combinations have been identified by Saunders[6] and by the authors.

The average single weed weight of each of the parents reported in this study and the F_1 hybrids are listed in Table 1. The seeds were shrivelled with shrunken and often collapsed cotyledonous tissue. In every cross involving the two wild accessions, TVu 4036 and TVu 4581, the seed weight of F_1 hybrids was reduced significantly. The effects of the reduction in seed weight were evident as the seeds were subsequently grown. The seedlings of the hybrids were weak and infested with disease and insect pests. Had they not been protected by insecticides, they would not have reached maturity. The plants were also susceptible to viruses and produced only a very small number of F_2 seeds.

Crosses involving the wild accessions and those belonging to the colonizer weed form were not similarly affected. However, the crosses between the wild and companion weed form showed varying degrees of reduction in hybrid seedling vigor (Rawal, unpublished).

The cotyledons of cowpeas are perispermous and the reduction in their development in crosses involving the wild form indicates genic disharmony between the parents. Among a large number of crosses, the reduction in seed weight was observed only in crosses involving only wild accessions and elite cultivars. Moreover, this reduction was consistent, suggesting the presence of barriers to gene exchange between various forms of *V. unguiculata*. Although the magnitude of these genetic barriers is rather small, they are suggestive of evolutionary divergence at an infraspecific level. As Wright[7,8] has pointed out, the most efficient population structure for rapid evolutionary divergence consists of a large population divided into several partially isolated subpopulations. The cultivated forms of *V. unguiculata* evolved predominately in the semiarid tropics, whereas the wild form is restricted to the sub-humid and humid areas. Hence, the wild form is spatially and ecologically isolated from the cultivated ones, and the colonizer and companion weed forms provide a bridge between the two diverse forms.

Rawal[5] proposed that the domesticated races of *V. unguiculata* were derived primarily from the colonizer weed and not from the perennial climber of the forest areas. The evidence presented in this paper supports that contention. Under artificial selection the cultivated forms have evolved either by directional selection or disruptive selection, whereas the wild form has been subjected to natural selection, which has a stabilizing action. Under these circumstances the accumulation of mutations directed by human interference would lead to the evolutionary divergence between the cultivated and the wild forms. In this case we have a documented example of a genetic barrier developing between the two forms.

Summary

The cultivated *Vigna unguiculata* (L.) Walp. has a wild form growing in secondary forests and derived savannahs and a companion weed form adapted to disturbed habitats. Although crosses between the wild and the cultivated forms can be made when the wild form is used as the male parent, there is significant reduction in F_1 seed weight. The evolutionary implications of this phenomenon are discussed with reference to gene exchange barriers between the wild and the cultivated forms.

Table I. Average seed weights for the F_1 and parental lines used in crosses between cultivated and wild forms of *V. unguiculata*

Parents	No. F_1 seeds	F_1 seed weight (g/seed)	♀ parent seed weight (g/seed)	Seed reduction (%)
TVu 4036 (♂)				
× TVu 161	26	0.109	0.160	31.9
× TVu 1760	8	0.100	0.186	46.2
× TVu 4552	41	0.155	0.215	27.9
× TVu 4569	45	0.096	0.225	57.3
× TVx 819-1E	16	0.041	0.160	74.4
× TVx 883-3D	6	0.104	0.180	42.2
TVu 4581 (♂)				
× TVu 161	27	0.083	0.160	48.1
× TVu 1760	10	0.102	0.186	45.2
× TVu 4552	36	0.143	0.215	33.5
× TVu 4569	40	0.103	0.225	54.2
× TVu 819-1E	13	0.069	0.160	56.9
× TVx 883-3D	6	0.095	0.180	47.2

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