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TWO OUTCROSSING MECHANISMS IN COWPEAS, *VIGNA UNGUICULATA* (L.) WALP

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SUMMARY

Several types of outcrossing mechanisms in cowpeas are observed in breeding plots at IITA. Two of these have been studied. One is genetic male sterility controlled by the simple recessive conditions of a gene designated as ms_2 ms_2. The other is mechanical male sterility involving petals constricted in such a way as to provide an opening for stigma and style to emerge at an early, pre-receptive stage of development; while simultaneously restricting stamen development. It is also inherited as a recessive character with the gene symbol designation of *Cp* – as normal and *cp cp* as constricted petal. The flower structure is unique and is easily recognized in large populations. Because fruit set is extremely poor it appears less promising than the genetic male sterility at present.

INTRODUCTION

Development of population improvement breeding schemes in self pollinated crops has stimulated the search for male sterility and other outcrossing mechanisms to facilitate gene flow in the recombination cycle of recurrent selection procedures. Procedures for population improvement in crops are described by SPRAGUE (1967), while specific schemes for recurrent selection in self pollinated crops utilizing genetic male sterility are proposed by DUVICK (1966), and described for sorghum by DOGGETT & EBERHART (1968) and DOGGETT (1972) and for soybeans by BRIM & STUBER (1973). Other schemes with hand crossing in the recombination phase are proposed by COMPTON (1968) and JENSEN (1970).

It is obvious that recurrent selection can be effectively applied in self-pollinated species but the methodology can be highly variable depending on improvement objectives, facilities available, rate of generation advance, mating habits and ease of genetic manipulation of the species worked with.

Availability of outcrossing mechanisms could be important in recurrent selection schemes for accelerating the rate of controlled gene recombination. However, these mechanisms way be more effective in plants with wind-dispersed pollen than in species dependent on insects for outcrossing, because insect control is often essential especially in tropical regions. Perhaps because of their non-entomophilous pollination habits male sterility and other outcrossing mechanisms have been developed and used more extensively in Graminaceous species. Various forms of outcrossing mechanisms exist for dicotyledonous crop species, like cotton (MEYER, 1969) and soybeans (STEWART & WENTZ, 1926; HADLEY & STARNES, 1964; BRIM & YOUNG, 1971). Some of these may have limited usefulness because of unpredictability of the mechanisms. Some forms of sterility are influenced by environmental conditions (CAVINESS & FAGALA, 1973).

Genetic male sterility controlled by a single recessive gene in cowpeas is reported in the variety Poona (SEN & BHOWAL, 1962). Male sterile plants were observed to be more vigorous with floral parts smaller than normal for that variety. The anthers failed to develop and were much smaller in size and whitish or dull yellow in color. They did not shed pollen even when fully developed nor were fruits produced unless hand crossed with pollen from fertile plants. A study of microsporogenesis in the anthers of both fertile and sterile segregants showed the archesporium to be formed as usual. A single archesporial cell was found in each lobe of the anther but pollen mother cells degenerated at the early prophase stage and growth ceased. In many cells of the sporogenous tissue from sterile plants, nuclei appeared to be poorly differentiated at all stages of development. Although the early stages of prophase were normal, meiotic activity ceased before diakinesis. The proposed gene symbols are *Ms* (fertility) and *ms* (male sterility) for this character.

SEARCH FOR OUTCROSSING MECHANISMS

A systematic search for male sterility was begun in 1971 at IITA. Several million cowpea plants were scrutinized for outcrossing mechanisms with the most intensive search made within a large planting of the erect, determinate, short-duration cultivar, Prima, developed by Federal Ministry of Agriculture at Moor Plantation, Ibadan.

The best time to look for sterility and other outcrossing mechanisms is during senescence. The steriles, without sufficient sinks (fruits) for the assimilates produced, tend to continue vegetative growth and remain green. Moreover, they continue flowering thereby facilitating the scrutiny of floral organs for malformation. From 1971 to 1973 several steriles were identified but many were totally sterile (both male and female) or partially sterile plants, which were highly influenced by environmental conditions. In other cases gross chromosomal aberrations or unidentified diseases may have been involved. However, two Prima plants identified during the first season, 1972, appeared promising and several cuttings were obtained and propagated in the greenhouse for further study. Repeatedly propagated single plant cuttings were continued from the original plants in order to cross them onto other genetic backgrounds.

STRUCTURAL DESCRIPTION

Two outcrossing mechanisms, one of which is conventional genetic male sterility, were obtained in the cultivar Prima. These were transferred to different genetic backgrounds and studied for their inheritance and possible utility in breeding systems. They occurred in an estimated population of 200,000 plants and are described in sections that follow.

Genetic male sterility. This is similar to the sterility described by SEN & BHOWAL (1962). The anthers are small, poorly formed and do not produce viable pollen (Fig. 1). Outwardly the flower development is identical with that of fertile plants. However, without hand or insect pollination they do not produce fruits, but remain green and continue growing and flowering as long as conditions remain favorable (in studies

Fig. 1. Normal (left) and male sterile (right) flowers of cowpea with petals removed.

at IITA). Crossing is carried out without emasculation and results in much higher fruit setting than with crossing to normal fertiles. The F_1 proved fertile and the F_2 segregated in the ratio 3F : 1S (Table 1).

Constricted petal. This is a structural anomaly of the corolla resulting from constricted petals to form a subconical inflorescence in such a way that a tubular opening is formed through which the female organs, stigma and style, emerge (Fig. 2). The filaments are impeded in development and the stamens are folded back on themselves (Fig. 3). Pollination of the stigma is physically not possible. The anthers dehisce normally, and the pollen is viable.

In a normal cowpea flower the papillionaceous corolla opens because of the ventral uplifting of the standard petal just prior to or at anthesis. With the constricted petal the stigma protrudes from the flower from the early stages of development. Because the inflorescence is drastically modified and somewhat conicular in shape this character is distinctive and easily recognized in the field. Because the sterility is mechanical rather than physiological it should be unaffected by environmental conditions.

Table 1. Genetic ratios observed for the inheritance of male sterility' (ms_2 ms_2) and constricted petal (cp cp) at IITA.

Source	Observed ratios			
	normal	ms_2/cp	total	χ^2
Male sterile (F_2)				
a) Greenhouse – 1973	903	277	1180	1.1
b) Field – 1973 F	310	109	419	0.23
Pooled	1213	416	1629	0.25[1]
Heterogeneity				3.10
Constricted petal (F_2)				
b) Greenhouse – 1973	49	11	60	1.42
b) Field – 1973 F	62	21	83	0.00
Pooled	111	32	143	0.52[1]
Heterogeneity				0.90

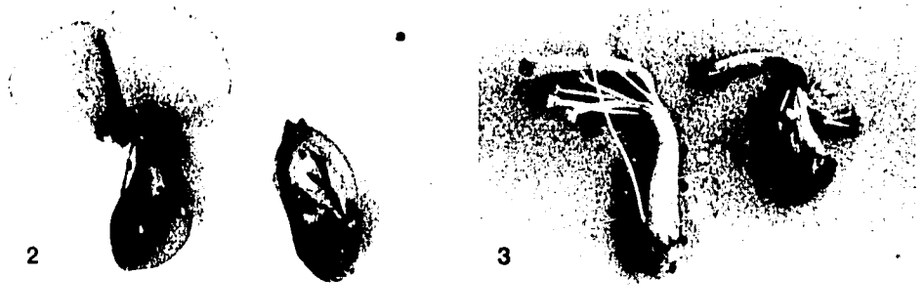

Fig. 2 and 3. Normal (left) and constricted petal (right) flowers of cowpea. Note the folding of stamens but fully developed anthers in constricted petal.

Constricted petal has been transferred to several genetic backgrounds through crossing both as male and female. The F_1 is normal and the F_2 segregates 3N:1Cp (Table 1). The character is difficult to cross using it as a female parent. It appears the stigma and style are exposed for such a long period that they become superficially dessicated and are not receptive to fertilization. Under field conditions during the second season, 1973, where moderate insect control was practiced only five pods were produced on about 300 plants. Studies continue and collaborative investigations in environments with lower populations of harmful insects and more moderate temperatures and humidities are planned.

DISCUSSION AND CONCLUSIONS

This is the second report of genetic male sterility in this species and, until confirmed to be identical with that found in the c.v. Poona (India), it is designated Ms_2. The constricted petal character may be unique in legumes and the gene symbol, *Cp*, is proposed for this character. The condition Ms_2- and *Cp*-confer normality while $ms_2\ ms_2$ and *cp cp* result in genetic sterility and constricted petal, respectively.

Genetic male sterility ($ms_2\ ms_2$) was utilized in development of elite populations at IITA. It was found extraordinarily successful for increasing the rate of hand crossability in this species. Seed set per number of hand crosses between fertiles normally ranges between 10 and 30 percent, and is strongly influenced by genotype, direction of crossing and environmental conditions during the post-pollination period. High temperatures and low humidities during hand crossing markedly reduce pod set. Genetic male sterility ($ms_2\ ms_2$) tends to increase fruiting even when temperatures and humidity are marginal. Moreover, sterile plants appear to set more pods than emasculated fertiles and will often produce as many or more pods as naturally selfed fertile plants. In the Prima genetic background, steriles will frequently produce as many pods per plant as naturally self-fertilized plants.

Constricted petals could offer many advantages in terms of stability, ease of identification and two-way crossability (both as pollinator and seed parent). Unfortunately, the reasons for low seed set are poorly understood. A further problem under field conditions appears to be unattractiveness of the flowers to winged insect pollina-

tors, because of the non-papillionaceous appearance of mature flowers, accompanied by lack of fragrance and the mechanical difficulty in probing nectaries inside the flower. Under both greenhouse and field conditions at Ibadan ants appear to play a role in pod setting in plants with constricted petals, but would probably not contribute significantly either to selfing or crossing in normal fertiles.

Future investigations. Considerably more needs to be learned about these two outcrossing mechanisms particularly about field management to increase the rate of natural outcrossing. Several questions remain unanswered including: 1) environmental conditions optimal for both hand and natural outcrossing, 2) stages of floral development most favorable to cross pollination, 3) most effective insect pollinators and conditions optimal for their activity, 4) the reasons for exceptionally high set in ms_2 ms_2 plants, 5) outcrossing capabilities of these two characters in a broad range of genetic backgrounds, and 6) possibilities of developing lines with closely linked seedling markers to facilitate identifying steriles in the early stages of growth.

Preliminary observations indicate considerable potential for the ms_2 ms_2 form of male sterility in spite of the problem of identification and the possibility of fertility reversion of steriles under some environmental conditions. The constricted petal character requires further investigation to establish whether or not it would have any useful potential. Considering the potential importance of both characters and the possibility of environmental and genetic influences on their expression, seeds of these two stocks in diverse genetic backgrounds will be offered to interested plant scientists for study under their ecological conditions. Simultaneously, advanced populations comprised of elite lines and for specific breeding purposes will be developed at IITA for later distribution and future collaborative investigations.

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