From the Department of Agronomy, Iowa State University, Ames. Dr. Jones is currently at the USDA-ARS Forage and Range Research Laboratory, Utah State University, Logan. Contribution of the Department of Agronomy, Iowa State University. Journal Paper No. J-12523 of the Iowa Agriculture and Home Economics Experimental Station, Ames, Iowa. Project No. 2569. Address reprint requests to Dr. Jones, USDA-ARS Forage and Range Research Laboratory, Utah State University, Logan, UT 84322.

References

1. Ambastha, H. N. S. Cytological investigations in *Phalaris.* Genetica 28:64-98, 1956.

2. Anderson, D. E. Taxonomy and distribution of the genus *Phalaris.* Iowa State J. Sci. 36:1-96, 1961.

3. Busbice, T. H., R. R. Hill, Jr., and H. L. Carnahan. Genetics and breeding procedures. In Alfalfa science and technology (C. H. Hanson, ed.). Agronomy 15:283-318, 1972.

4. Hanson, A. A., and H. D. Hill. The occurrence of aneuploidy in *Phalaris* spp. Bull. Torrey Bot. Club 80: 16-20, 1953.

5. Knowles, R. P. Feasibility of production of commercial hybrids in reed canarygrass, *Phalaris arundinacea* L., using a yellow-seeded mutant. Can. J. Plant Sci. 66: 111-116, 1986.

6. Marum, P., A. W. Hovin, and G. C. Marten. Inheritance of three groups of indole alkaloids in reed canarygrass. Crop Sci. 19:539-544, 1979.

7. McWilliam, J. R., and C. J. Shepherd. The nature and genetic control of a red anthocyanin pigment in the root meristems of *Phalaris.* Aust. J. Biol. Sci. 17:601-608, 1964.

8. Mehra, P. N., and M. L. Sharma. Cytological studies in some central and eastern Himalayan grasses. III. The Agrostideae, Aveneae, Brachypodieae, Bromeae, Festuceae, Phalarideae and Triticeae. Cytologia 40:441-452, 1975.

9. Stanford, E. H. Tetrasomic inheritance in alfalfa. Agron. J. 43:222-225, 1951.

10. Starling, J. L. Cytogenetic study of interspecific hybrids between *Phalaris arundinacea* and *P. tuberosa.* Crop Sci. 1:107-111, 1961.

11. Strickberger, M. W. Genetics, 2nd ed. Macmillan, New York, 1976.

12. Tarkowski, C. Investigations of meiosis and fertility in grasses with free or isolated flowering. Plant Breed. Abstr. 35:254, 1965.

13. Woods, D. L., and K. W. Clark. Genetic control and seasonal variation of some alkaloids in reed canarygrass. Can. J. Plant Sci. 51:323-329, 1971.

Genetics and Histology of a Corky-Stem Mutant in Pigeonpea

K. B. Saxena, I. S. Dundas, D. G. Faris, and S. C. Gupta

A mutant pigeonpea (*Cajanus cajan* (L.) Millsp.) characterized by cork formation on its stems and branches was identified and designated as "corky-stem." The inheritance of this trait was studied in the F_1, F_2, and BC_1F_1 (mutant × F_1) generations of two crosses. The results suggest that the corky-stem character is governed by one recessive allele and one dominant allele, designated *sm* and *Ck*, respectively. The dominant form of the *sm* allele completely masked the expression of the *Ck* allele, resulting in a smooth stem surface. Cork formation was attributed to the development of a periderm layer which is normally absent in the pigeonpea stem.

The stem surface of cultivated pigeonpea (*Cajanus cajan* (L.) Millsp.) remains smooth and green throughout its life owing to the absence of the corky bark characteristic of many woody perennials. A true breeding mutant characterized by dry, rough, brown-colored bark with irregular cracks on its stem and branches was identified among self-pollinated progeny of the pigeonpea accession ICP 3940 at ICRISAT. Apart from its abnormal stem surface, this mutant had reduced height, few branches, and low pod set. This is the first report of such an abnormality in pigeonpea and we are unaware of a similar character in other grain legume crops. This note reports the inheritance and histology of this character.

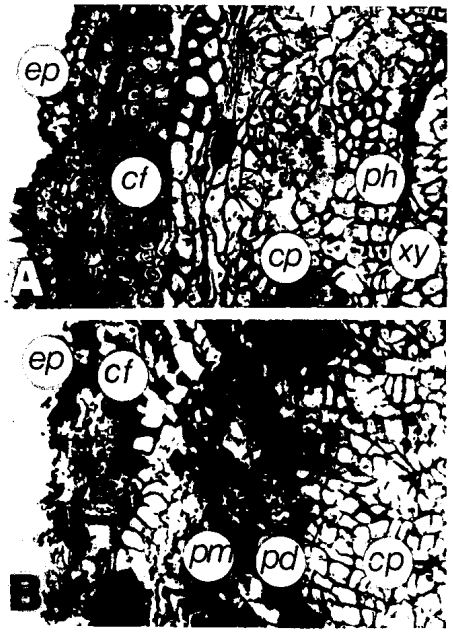

Figure 1. Portions of cross sections of normal smooth (A) and corky-stem mutant (B) of pigeonpea. Note the development of a periderm in the mutant type. cf, cortical fibers; cp, cortical parenchyma; ep, epidermis; pd, phelloderm; ph, phloem; pm, phellem; xy, xylem (×180).

Materials and Methods

Self-pollinated progeny of the mutant plant were crossed to two early maturing cultivars, UPAS 120 (cross 1) and ICPL 87 (cross 2), in November 1983. Part of the seed from both crosses was sown in April 1984 in a greenhouse for generation advance and also to make testcrosses with the corky-stem parent. During September 1984, the F_1, F_2, and BC_1F_1 seeds were grown together with the parents in the field, and plant counts were made to study the inheritance of the corky-stem character.

To study the histology of the mutant, stem portions of both normal and corky-stem plants collected from a range of stem ages were fixed in Randolph's solution and embedded in a paraffin-wax according to Johansen's tertiary-butyl alcohol dehydration schedule.[1] Sections 15 to 20 μm thick were stained in safranin and fast green, mounted in Canada balsam, and observed under a microscope (×180).

Results and Discussion

The corky-stem plants grown both in the greenhouse and in the field showed no differences in the expression of the character. The F_1 progenies of both crosses had smooth stems (Table 1). In the F_2 generation of cross 1, 186 of 1,066 plants had corky-stems whereas in the second cross, 125 of 735 plants had corky-stems. Chi-square tests indicted that the segregation in the F_2 progenies fitted the expected ratio of 13 smooth:3 corky-stem (Table 1). These observations indicate the presence

Table 1. Segregation for smooth- and corky-stem in two crosses of pigeonpea

Cross/generation	Smooth (normal)	Corky (mutant)	Expected ratio	*P*
Cross 1: UPAS 120 × mutant				
F_1	44	0	—	—
F_2	880	186	13:3	0.25-0.30
Mutant × F_1	20	15	1:1	0.40-0.50
Cross 2: ICPL 87 × mutant				
F_1	14	0	—	—
F_2	610	125	13:3	0.20-0.25
Mutant × F_1	35	31	1:1	0.60-0.70
F_3[a]	25	87	1:3	0.50-0.60
BC_1F_2[a]	24	59	1:3	0.40-0.45

[a] Pooled data from segregating corky-stem progenies.

of epistasis in the expression of corky-stem. The testcross progenies of both cross 1 and 2 fit the expected ratio of 1 smooth:1 corky-stem (Table 1).

Segregation patterns in F_2 and testcross progenies of the two crosses suggest that the corky-stem character in pigeonpea is governed by two loci, one with a recessive allele designated *smsm*, and the other with a dominant, designated *CkCk*. For the development of the corky-stem character, the presence of the *Ck* allele in either the homozygous or heterozygous condition is essential. However, its expression is masked when the *Sm* allele is present. Thus, considering the segregation in the F_2 and BC_1F_1 generations, the expected genotypes of the corky-stem and both smooth-stem parents used in the initial crosses should be *smsm CkCk* and *SmSm ckck*, respectively.

Although it was not tested in this study, the genotype of the parent line ICP 3940 was probably *sm sm ck ck* which by our postulate would appear normal. If this is the case then corky-stem plants in ICP 3940 would arise from natural outcrosses with other normal lines such as those used for the crosses reported here. Another less likely possibility is that the genotype of ICP 3940 was *Sm Sm Ck Ck* and that the corky-stem plants arose from a mutation of *Sm* allele to the recessive *sm*. Finally, an even less probable postulate is that ICP 3940 had the genotype *sm sm Ck Ck* and that the corky-stem plants arose from a double mutant to give the *Sm Sm ck ck* genotype.

Genetic testing of segregation patterns in the F_3 and BC_1F_2 generations was restricted to the progenies of corky-stem plants from the cross 2. On the basis of a two-gene epistatic model developed on the F_2 and BC_1F_1 generations some corky-stem plants should have been *sm sm Ck ck* genotype, which on selfing, would yield plants of both stem types. Low population sizes did not allow appropriate analyses of segregation patterns within and among the progenies. However, the pooled data from seven segregating F_3 progenies gave 87 corky-stem and 25 normal plants. This fits the expected ratio of 3:1 (Table 1). Five corky-stem BC_1F_2 progenies gave 59 corky-stem and 24 normal segregants which also fits the expected ratio of 3:1 (Table 1). These results confirm the genetic system proposed for this stem character.

Microtome sections of smooth and corky-stems showed clear differences in the development of the outer stem layers (Figure 1A and B). A periderm layer, common to many woody species, is not formed in the normal pigeonpea stem. The exovascular region is normally composed of an epidermal layer, and several cortical layers of chlorenchyma, fibers, and parenchyma cells (Figure 1A).

By contrast, the corky-stem mutant develops a prominent periderm section in the stem, interior to the cortical fiber band (Figure 1B). This periderm is composed of three sections: a) the phellem (outermost), of 30 to 40 layers of dead, flattened, suberized cork cells; b) the phellogen, a single layer of cambial cells; and c) the phelloderm (innermost), of 5 to 6 layers of large cells with deeply staining cytoplasm, adjacent to the cortical parenchyma (Figure 1B).

The observations suggest that the corky-stem character is controlled by two genes with epistatic effect, of which one is recessive and the other dominant. The morphological difference between the two types of stem, smooth and corky, can be linked to the development of a secondary cambial layer in the cortex of the corky-stem mutant.

From the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India. Submitted as journal article no. 631 by ICRISAT. Address reprint requests to Dr. Saxena, International Crops Research Institute for the Semi-Arid Tropics, Patancheru P.O. 502 324, A.P., India.

Reference

1. Johansen, D. A. Plant microtechnique. McGraw-Hill, New York, 1940, 523.