

# Genetics and Utilization of Apomixis for the Improvement of Guineagrass (*Panicum maximum* Jacq.)

Y.H. SAVIDAN

Office de la Recherche Scientifique et Technique,  
Outre-Mer (ORSTOM), Abidjan, Ivory Coast

## Summary

Natural polymorphism in guineagrass (*Panicum maximum* Jacq.) has been stabilized in tetraploid biotypes by apomixis. Sexual diploids were found in East African populations. Our objective was to determine whether apomixis could be related with a simple genetic background and manipulated in an improvement program.

Apomicts of guineagrass are characterized by a 4-nucleate embryo sac structure, and this trait was used in genetical analyses to differentiate apomictic from sexual hybrids. Progeny tests were also conducted as controls. Ten different types of progenies were analyzed: tetraploid sexual (from colchicine treatment of diploids) × apomictic F<sub>1</sub> hybrids; selfed and backcrossed progenies of sexual F<sub>1</sub> hybrids; three-way hybrids combining information from one sexual and two different apomicts; selfed and backcrossed progenies of sexual three-way; sib-mating progenies (crosses between sexual hybrids or sex × apo combinations); test-crossed progenies; and selfed progenies of facultative apomicts.

All the data fit with a single gene model for the inheritance of apomixis, in which the sexual diploids would have the genotype aa, and the apomictic tetraploids the genotype Aaaa. Apomixis is dominant.

Apomixis in *Panicum maximum* is often facultative, but with a low percentage of residual sexuality. Eighty natural apomicts and 80 apomictic hybrids were compared to show that this rate of sexuality remains low following hybridization.

According to these cytogenetical and embryological studies, along with other data from plant evolution studies, an improvement scheme was drawn up and successfully tested. From each cross combination one-half of the hybrids are apomicts that can be immediately propagated by means of seeds if they are found to be promising.

We have conclusively demonstrated that apomixis could be simply inherited in guineagrass and thus easily manipulated in an improvement program. Different hybrids adapted to the humid tropical lowlands of West Africa have been selected. The conservation of a large germ plasm of guineagrass and related species has also been realized.

KEY WORDS: guineagrass, *Panicum maximum*, apomixis, embryo sac analysis, crop improvement.

## INTRODUCTION

In early 1969, 500 accessions of *Panicum maximum* (guineagrass) were established in the south of Ivory Coast, following the exploration, by Combes and Pernès (1970), of natural populations in East Africa (Kenya and Tanzania). Twenty-two sexual diploids ( $2n = 16$ ) were found in this material. Nearly all of the other plants were tetraploids ( $2n = 32$ ), reproducing by apomixis.

This discovery of sexuality has led us to the consideration of new breeding procedures for guineagrass. Many genes heretofore unavailable to the plant breeder could potentially be released and promising new types created by hybridization.

Preliminary studies showed that hybridization between sexual and apomictic plants gives rise to sexual as well as

to apomictic hybrids (Combes 1972, Savidan 1978, 1980). Our major objectives were to study the inheritance of apomixis and sexuality in *Panicum* and thus to determine whether these modes of reproduction could be easily manipulated in an improvement program.

## METHODS

Since genetical analyses require a large number of progenies, cytological methods were preferred, although small progeny tests were periodically used as controls. A microscopic technique, using phase contrast, appeared to be especially rapid and convenient. It was made possible by the fact that apomixis and sexuality are closely related, with two different embryo sac structures in *Panicum maximum* as well as in most grasses of the *Panicoideae* sub-family. Sexual biotypes contain only 8-nucleate embryo sacs. Apospory is characterized by a 4-nucleate structure. In our material, apospory appeared to be linked with parthenogenesis so that the observation of some 4-nucleate

The author's current address is G.P.D.P., Centre National de la Recherche Scientifique, 91190 Gif sur Yvette, France.

16 AVRIL 1985

C. R. S. T. O. M. Fonds Documentaire

N° : 17310, ex 1

Cote : B

Table 1. Segregation for modes of reproduction in ten different cross combinations.

| Cross combinations                  | No. plants observed |        |           | Theoretical ratio expected | Chi <sup>2</sup> |
|-------------------------------------|---------------------|--------|-----------|----------------------------|------------------|
|                                     | total               | sexual | apomictic |                            |                  |
| 1. F1 hybrids (S1xA1)               | 133                 | 62     | 71        | 1:1                        | .48              |
| 2. F1 sexual selfed                 | 126                 | 126    | 0         | 1:0                        | 0                |
| 3. F1 sexual backcrossed (S1xA1xA1) | 26                  | 12     | 14        | 1:1                        | —                |
| 4. Three-way hybrids (S1xA1xA2)     | 279                 | 144    | 135       | 1:1                        | .23              |
| 5. Three-way sex selfed             | 57                  | 57     | 0         | 1:0                        | 0                |
| 6. Three-way sex backcrossed by A2  | 113                 | 60     | 53        | 1:1                        | .32              |
| 7. Sib mating (SxS)                 | 82                  | 82     | 0         | 1:0                        | 0                |
| 8. Sib mating (SxA)                 | 60                  | 34     | 26        | 1:1                        | 1.06             |
| 9. Test cross S1 × apom. hybrid     | 23                  | 10     | 13        | 1:1                        | —                |
| 10. Apo × apo                       | 71                  | 18     | 53        | 1:3                        | 0                |

Chi<sup>2</sup> are indicated when N>30.

embryo sacs could be considered to be sufficient proof of an apomictic behavior.

Cytological and embryological techniques have already been described in previous papers (Herr 1971, Savidan 1975). All cross combinations were made between tetraploids, using the high self sterility of the sexual progenitors. The 970 plants reported in Table 1 are tetraploid. The 10 progenies studied were the F<sub>1</sub> progeny from a sexual × apomictic cross (1), the selfed progeny of sexual F<sub>1</sub> hybrids (2), the backcross progeny of the same sexual F<sub>1</sub> hybrids (3). Some of these sexual F<sub>1</sub> hybrids were crossed with a second apomict (A2) to give the so-called three-way hybrids (4). Sexual plants from this progeny were selfed (5), backcrossed with A2 (6), or crossed with other hybrids from the same progeny (7 and 8). Some apomictic hybrids were crossed with the original sexual progenitor S<sub>1</sub> (9). Finally, using a facultative apomict with 40% off-types in progeny tests, apomictic × apomictic crosses were made (10). The segregation reported for this cross combination was observed among the off-types.

## RESULTS

Modes of reproduction appeared to segregate in our progenies (Table 1) according to the following rules: sexual × sexual hybrids (or sexual selfed) are always sexual; sexual × apomictic hybrids segregate in a 1:1 ratio; apomictic × apomictic hybrids segregate in a 1:3 ratio (apomictic hybrids are 3 times more numerous).

Apomixis in *Panicum maximum* is often facultative, and the possibility of using such a reproductive process in plant breeding is sometimes questioned. The sexual potential of 80 apomictic hybrids was compared to that of 80 natural apomicts (Table 2). Obligate apomixis was observed in 21 hybrids, and many others were nearly obligate.

## DISCUSSION

All the segregations we observed fit perfectly into a single gene model for the inheritance of apomixis in *Panicum maximum*. In such a model, sexual diploids would

Table 2. Distributions of percentage sexuality in natural and hybrid apomicts of guinea-grass (*Panicum maximum*).

|                         | No. plants with percentage sexuality* of |      |       |       |       |       |       |       |       |       |
|-------------------------|--|------|-------|-------|-------|-------|-------|-------|-------|-------|
|                         | 0  | 0-10 | 10-20 | 20-30 | 30-40 | 40-50 | 50-60 | 60-70 | 70-80 | 80-90 |
| Natural apomicts (N=80) | 10                                       | 54   | 6     | 4     | 4     | 1     | —     | 1     | —     | —     |
| Hybrid apomicts (N=80)  | 21                                       | 49   | 5     | 1     | 1     | —     | 1     | —     | 1     | 1     |

\*Sexuality: percentage ovules with a single 8-nucleate embryo sac (100 ovules observed/plant).

have the genotype aa and the tetraploids arising from colchicine treatment of these diploids the genotype Aaaa. The 1:1 ratios observed in all sexual × apomictic progenies could be explained by an Aaaa genotype for apomicts. Thus, apomixis of guineagrass is dominant over sexuality.

Crosses between apomicts with a high percentage of sexuality gave one-fourth of sexual plants among the off-types, as the model predicted. The fact that true sexuality can arise from apomictic accessions could explain the discovery of sexual tetraploids from South African apomictic introductions, as reported by Smith (1972) and Hanna et al. (1973). Some of these South African introductions in our field nursery showed an especially high percentage of sexuality.

Apomicts collected in East African populations usually exhibit a low potential for sexuality. Our data show that highly apomictic hybrids can be recovered following hybridization between sexual and apomictic accessions, contrary to earlier statements.

Data from cytogenetical studies, along with other data from biological and plant evolution analyses (Combes 1972, Pernès 1972), led us to propose an improvement scheme for *Panicum maximum* that could be used in similar agamic complexes (Pernès et al. 1975). Several series of sexual × apomictic crosses were attempted, following a tetraploidization process using the 2 × × 4 × crosses made in natural mixed populations of Tanzania. These crosses have led to a rapid extension of the sexual tetraploid pool and the regular release of apomictic hybrids. Some of the latter have already been tested in Ivory Coast. About 10 of them exhibited grass productions higher than 30 tons dry matter/ha/yr, with a seed production of 200 to 500 kg/ha. National societies for the development of cattle production in Ivory Coast are now growing several *Panicum maximum* varieties selected by

ORSTOM. The Institute is also engaged in the conservation of a large germ plasm pool including apomictic as well as sexual material.

#### LITERATURE CITED

- Combes, D. 1972. Polymorphisme et modes de reproduction dans la section des *Maximæ* du genre *Panicum* (Graminées) en Afrique. Thesis, Univ. of Paris (France): Mém. ORSTOM 77, Paris (1975).
- Combes, D., and J. Pernès. 1970. Variations dans les nombres chromosomiques du *Panicum maximum* Jacq. en relation avec le mode de reproduction. C.R. Acad. Sci. Paris, sér. D. 270:782-785.
- Hanna, W.W., J.B. Powell, J.C. Millot, and G.W. Burton. 1973. Cytology of obligate sexual plants in *Panicum maximum* Jacq. and their use in controlled hybrids. Crop Sci. 13:695-697.
- Herr, J.M. 1971. A new clearing squash technique for the study of ovule development in angiosperms. Am. J. Bot. 58:785-790.
- Pernès, J. 1972. Organisation évolutive d'un groupe agamique: la section des *Maximæ* du genre *Panicum* (Graminées). Thesis, Univ. of Paris (France): Mém. ORSTOM 75, Paris (1975).
- Pernès, J., R. René-Chaume, J. René, and Y. Savidan. 1975. Schéma d'amélioration génétique des complexes agamiques du type *Panicum*. Cah. ORSTOM, sér. Biol. 10:67-75.
- Savidan, Y. 1975. Hérité de l'apomixie. Contribution à l'étude de l'hérité de l'apomixie sur *Panicum maximum* Jacq. (analyse des sacs embryonnaires). Cah. ORSTOM, sér. Biol. 10:91-95.
- Savidan, Y. 1978. L'apomixie gamétophytique chez les Graminées et son utilisation en amélioration des plantes. Ann. Amélior. Pl. 28:1-9.
- Savidan, Y. 1980. Chromosomal and embryological analyses in sexual × apomictic hybrids of *Panicum maximum* Jacq. Theor. Appl. Genet. 57:153-156.
- Smith, R.L. 1972. Sexual reproduction in *Panicum maximum*. Crop Sci. 12:624-627.

## Preliminary Evaluation of Legume Germ Plasm in the Cerrados of Brazil

D. THOMAS and R.P. DE ANDRADE  
CIAT, Colombia, and EMBRAPA-CPAC, Brazil

### Summary

The cerrados of the west central region of Brazil occupy 180 million ha and are classified as well-drained, tropical savannas. The Brazilian cattle population numbers 110 million, almost 60% of which is found in the cerrados. To improve the nutrition of the grazing animal, attention has been focused on cultivated pasture species, particularly tropical legumes. None of the commercial legume cultivars can be recommended for large areas of the cerrados. Species such as leucaena (*Leucaena leucocephala* [Lam.] de Wit) are not adapted to these acid, infertile soils with a high aluminum content, while *Stylosanthes* Sw. species are highly susceptible to the fungal disease anthracnose (*Colletotrichum gloeosporioides* Penz.).