





## ABSTRACT

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### GENETIC CONTROL OF FACULTATIVE APOMIXIS AND APPLICATION IN BREEDING *PANICUM MAXIMUM*

A diallel cross realized between eight sexual tetraploids and eight facultative apomicts of *Panicum maximum* gave tetraploid hybrids that segregate in a 1:1 ratio between sexual and apomictic plants. Selfed, backcrosses and further progenies led to specify the simple genetic control of apomixis in this species. Apomictic hybrids are either facultative or obligate, and this characteristic looks to be under a more complex genetic determinism. Two, three and four ways hybrids with good forage productivity emphasize the efficiency of using facultative apomixis in a breeding programme for this tropical grass. That probably should also successfully be done with other plants of the *Panicoidae* subfamily.

The *Panicum maximum* agamic complex has its center of diversity in East Africa. It includes mostly tetraploid types which are facultative apomicts. Some small natural populations with diploid number of chromosomes were found in Kenya. They were shown to be entirely sexual (1).

A lot of theoretical investigations have been conducted on this biological material during the last decade, in such fields as numerical taxonomy, quantitative and population genetics, cytogenetics (2 to 6). They have led to a good knowledge of the structural organization and evolution of natural variability. An evolutionary scheme has been proposed (7) that is in agreement with the diploid-tetraploid-haploid cycle previously presented by DE WET (8) for the *Bothriochloa-Dichanthium* complex, after which an improvement programme was built and successfully tested (9).

Four years ago, crosses were attempted between eight sexual tetraploids and eight natural apomicts (Table 1). Among these sexual genitors, five were issued from colchicine treatment of diploids, while the other three were F1 hybrids from previous sexual x apomictic crosses. The eight apomicts were chosen to

2n =	16	24	32°	48	64	sum
F1	1	4	77	32	3	117
R1	1	0	205	13	2	221

reproduction :            sexual            S & A            apomictic

TABLE 1. Chromosome numbers in F1 (sex x apo) and R1 (F1 crossed by another apomict) with modes of reproduction.

° including aneuploids with 30, 31 or 33 chromosomes.

represent - as well as it was possible with only eight plants - the main divisions of our classification of the variability encountered within the complex (10). Quite distant plants were crossed in this way, but fertile hybrids were obtained from



	APO	SEX
T34.T x apo	4	2
T35.T x apo	1	0
T44.T x apo	6	3
K189.T x apo	34	37
S1.T x apo	4	5
S2.T x apo	23	15
sum	72	62

TABLE 2. Modes of reproduction of F1 hybrids.

### F2 generation

Within F2 generation, plants we shall examine result of selfing, backcrossing and recrossing of F1 by a new apomict (which we have called R1 hybrids).

### Selfed-progenies

122 plants sprung from self-fertilization were analysed. Table 3 shows that 121 are sexual, only one being apomictic.

	APO	SEX
(K189.T x G3) 1	0	18
(K189.T x K4) 1	0	29
(K189.T x K26) 1	0	46
(K189.T x K26) 2	0	21
(S2.T x C1) 1	0	5
(S2.T x C1) 2	1	2
sum	1	121

TABLE 3. Modes of reproduction in selfed progenies of sexual x apomictic F1 hybrids.

### Backcrosses

A skew appeared in the backcrosses (Table 4) : while our natural sexual diploids and the artificial sexual tetraploids were shown to reproduce mostly by outcrossing, the rate of autocompatibility greatly increased in further sexual progenies. Combining numbers of seeds produced comparatively from

self-fertilization and from backcrosses, with morphological and cytological observations, it is clearly demonstrated that a sexual outcrossing F1 hybrid give many more apomictic than sexual plants in its backcrosses progenies.

	APO	SEX	sum
(K189.T x K4)1	1	39	40
(K189.T x K26)1	9	42	51
(S2.T x C1)1	11	10	21
(K189.T x G3)2	12	2	14
(K189.T x G3)3	23	2	25

TABLE 4. Modes of reproduction in backcrosses progenies of sexual x apomictic F1 hybrids.

#### Recrossing of F1 hybrids

Sexual F1 hybrids were crossed by a new (second) apomict (Table 5). Among the 279 R1 hybrids obtained, one half is apomictic - 135 plants - and the other is sexual (144) as it was observed for F1 hybrids.

	APO	SEX
P2 x apo'	56	56
IS3 x apo'	32	42
IS4 x apo'	47	46
sum	135	144

TABLE 5. Modes of reproduction of R1 hybrids (sex x apo x apo')

#### F3 generation

Our F3 material is composed of selfed and backcrossed progenies of R1 hybrids. From selfing, the 56 plants observed were all sexual. In the backcrosses (Table 6), the same observations as in previous backcrosses can be made. When autocompatibility is low, apomictic and sexual products seem to segregate in a 3 to 1 ratio.

	APO	SEX	sum
(IS4 x T25)1	3	38	41
(P2 x C1)1	12	8	20
(IS4 x T25)2	36	16	52

TABLE 6. Modes of reproduction in backcrosses progenies of R1 hybrids .

### Discussion

Suming these results, which come from analysis of 855 hybrids, a simple monogenic determinism can be proposed for inheritance of apomixis.  $A^+$  would be the wild allele, while  $A^-$  would induce unreduced embryo-sac formation. Artificial sexual tetraploids would be  $A^+ A^+ A^+ A^+$ , and natural apomicts  $A^+ A^- A^- A^-$ . If backcrosses of sexual F1 hybrids can give a majority of apomictic plants in such a model, the structure of these sexual F1 hybrids has to be heterozygote. This does not agree with data from self-fertilization in which apomixis is quite absent.

Differences in pollen competitiveness, as observed by NOGLER (13) in *Ranunculus*, can perhaps be considered. We observed a significant difference between the fertility of backcrossed and selfed seeds. So both gametophytic and sporophytic selections can be argued for the absence of apomixis in selfed progenies. Several new crosses will be undertaken this year to test these different hypotheses.

Gametophytic apomixis of *Panicum maximum* is facultative. As it has been often said that this was a barrier to farming utilization, we also studied the rate of sexuality of natural and hybrid apomicts. In our collection, which comprises more than five hundred natural apomictic accessions, a polymorphism can be observed for this rate of sexuality. At the cytological level, natural apomicts showed to have from 1 to 27 per cent of ovules with a single sexual embryo-sac. In the field, we observe only 1 to 5 per cent of off-type plants in non-competitive conditions. This difference is due largely to selection : off-types are plants with a low vigour because of their selfed origin in plants that reproduce by outcrossing when sexuality appears. In farming conditions, all off-types are eliminated.



71 apomictic hybrids of our 8 x 8 diallel cross were examined for this characteristic. One hundred ovules were observed for each of them. The large majority of these apomicts seems to be obligate or nearly obligate. Only two hybrids showed a high degree of sexuality that really exclude farming utilization. And in these latter cases, sister plants could be found that were obligate apomicts.

While apomixis looks like a presence-absence characteristic with a simple genetic determinism, the rate of sexuality in apomicts seems to have a much more complex inheritance. It has already been showed within several apomictic species that it can be greatly conditioned by environmental variations such as day length (14 to 19). It does not constitute a barrier to farming utilization of facultative apomicts of *Panicum maximum*. In this species, apomictic hybrids which combine informations from a sexual and one, two or three different apomictic genitors were successfully tested in farming conditions. Our improvement programme yielded a great increase of productivity as early as the first hybrid generation.

The same is to be expected from other apomictic grasses, i.e. almost all tropical forage grasses. Data on biology and evolution already available in these plants emphasizes a great homology of function. Even if details are different, a research programme such as that realized within the *Panicum* agamic complex could be successfully engaged with each of these *Gramineae* (20).

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