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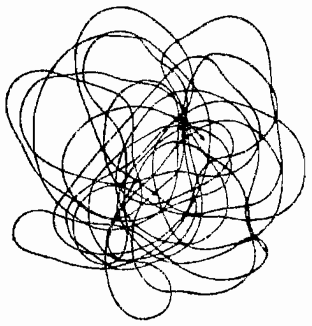
GENETIC ANALYSIS OF SEXUAL AND APOMICT *Panicum maximum*



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SUMMARY

Sexual diploid *Panicum maximum* are as good forage producers as the best tetraploid apomict plants. Colchicine treatments of sexual diploid plants give sexual tetraploid plants. We obtained hybrids by crossing sexual tetraploid mother with apomict father. Hybrid are either sexual or apomict. If they are sexual self Fertilization of them gives mainly sexual progenies, but some are apomict. The off-type rate of natural apomict plants is around 3 per cent; this rate is around 35 per cent in the apomict hybrids progenies of sexual x apomict crosses — Quantitative genetics of *Panicum maximum* began with a 5 x 5 diallel analysis of sexual diploid plants. High heritability occurs with the following characters: number of tillers, leaf length and leaf breadth, days to heading, virus (streak) sensitivity. General combining abilities are generaly more important than specific combinging abilities; specific combining abilities appear significative with inflorescence lengths and number of tillers — New hybrids with better forage quality and higher productivity are obtained by cross breeding tetraploid sexual plants and apomict plants.

Genetic Analysis of Sexual and Apomict Panicum maximum Jacq.

by J. PERNÈS
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Although Panicum maximum is named "guinea grass", its origin center is likely in East Africa. In KENYA and TANZANIA, we found different other species from the "maximae" group. They are Panicum infestum and Panicum trichocladum. Some natural occuring phenotypes look like interspecific hybrids between P. maximum and P. infestum or P. trichocladum respectively. The "maximae" complex is an agamic one, plants are generaly facultative apomict and their chromosome number is 2n = 32. We found out natural populations with 2n = 16 chromosomes plants, each of them were sexual (D. COMBES and J. PERNES (1970)).

A general scheme, describing the evolutive system of "maximae" complex, was suggested in J. PERNES (1972). The diploid sexual gene pool allows intensive recombination. The variability, thus created, can be put into the apomict tetraploid pool. This process is mainly two phasis compounded : first tetraploidization which maintains sexuality, second, hybridization between female sexual tetraploid and male apomict tetraploid which gives apomict as well as sexual hybrids.

Facultative apomixis allows a great efficiency to selective pressures and stores, without disjonction, the exceptional occurence of interspecies hybrids.

This up and down balance between sexual and apomict plants appeals to plant breeder imagination. However this comes up questions which must be solved before choosing a breeding program.

1. How are the sexual gene pools organised ?
2. Can the genetic variability freely flows from apomict pool into induced sexual tetraploid pool ? Must we look for bridge genotypes when we want to combine phenotypically distant plants ? Is there any reproductive and/or developmental barrier between genotypes which are far from each other ?

3. What can we say about variations of apomixis expression through various genetic environments ?

We can hardly answer these by separated experiments; all these problems are tight bound together.

This communication will sum up results about apomixis genetic mecanism and quantitative genetic analysis of sexual plants.

I. Data about Panicum maximum apomixis .

Facultative apomixis can be described by using three different parameters.

1. The observation of an apomict offspring family shows two kinds of plants: a) plants which look like the mother plant and to each other, b) plants with new phenotypes neither identical to the mother plant nor to each other; these latter plants are called off-types. The percent of off-type plants is the off-type rate (H.T.), WARMKE (1954), BOGDAN (1963), COMBES (1972).

2. The chromosome number analysis of the off-type plants sbows two kinds of plants: a) plants which have the mother plant chromosome number, b) plants which have not the same chromosome number as the mother plant. These latter plants mainly come from un reduced embryo sacs. The percent of a. plants among the whole offspring family is called the sexual rate (α)

It can be seen from the definition that sexual rate $\leqslant$ off-type rate ($\alpha \leqslant$ H.T.)

3. In a plant, the observation of the ovaries shows two kinds of embryo sacs 4 nuclei embryo sacs and 8 nuclei sacs, (WARMKE (1954), COMBES (1972)). By eight nuclei embyo sac rate (S) we mean the following ratio :

$$S = \frac{\text{number of ovaries with only one embryo sac, this one being a 8 nuclei embryo sac}}{\text{number of observed ovaries.}}$$

We do not know whether every 8- nuclei embryo sac is a reduced one, but what we can say is that every apomict plant shows some 4- nuclei embryo sac. We shall call "sexual" a plant which never has 4- nuclei embryo sac and which shows character recombinations in its offspring plants.

Apomixis parameters values from different plants.

Let us consider two kinds of plants. First, plants we shall call, " "natural occuring plants" which are coming from spontaneous populations through successive either vegetative or apomict multiplications. Second, plants we shall call "synthetised apomicts", which are coming from either successive off-types generations or hybridization between sexual and apomict tetraploid plants.

Table I gives different off-types rates recorded from literature and personal observations. We must match the great homogeneity of natural apomict against variation which occurs in synthetised apomicts. Let us note SMITH (1972) observations which show that the off-type rate could raise to or nearly to 100 percent, according to he has got either true sexual plants or high off-types rated plants.

Embryo sacs observations are more tedious, therefore they are less numerous. Moreover, various methods are used. The best method is by phase contrast observation described in J.M. HERR (1971). Table II gives some 8-nuclei embryo sacs rate (S).

The high values of S in T 19 36,5 and T 19 36,5 offsprings are to be matched against their high H.T. values. However there is not a simple relation between H.T. and S. HARLAN and al. (1964) find similar results in DICHANTHIUM-BOTRICHLOA complex.

Cross breeding T 19 36,5 with sexual tetraploids can increase S. Apomict plants issued from families K 189.TxG3 and P2 x 57 have a S value near the over all mean of natural apomicts. P2 x 57 is a three way hybrid (K 189.T x G23) sexual x 57 (∿ G3) apomict. S from P2 x 57 is significatively smaller than S from K 189.T x G3.

The H.T. rate is under genetic control; this occurs from the analysis of T19 successive offsprings. The S rate is also under genetic control (from family differences between P2 x 57 and K 189.T x G23 and from increasing S in T19 36,5 x T 35.T).

There are apomict plants having a very high S and high H.T. They look like sexual plants and can be used as female parents.

Inheritance of giving only 8- nuclei embryo sacs as single sacs.

Sexual diploid plants gave only 100 percent S values. Tetraploid plants obtained by colchicine treatment of buds on diploid plants are also sexual and 100 % S valued. Comparing the number of seeds produced under the same environmental conditions through self-pollination and cross pollination shows that diploid and tetraploid sexual plants are hightly self sterile plants. Crosses result from open-pollination in isolated pollinating plots of a sexual plant T surrounded by a clonal multiplication of an apomict. Plants without father characteristics are exceptional in offsprings thus obtained. They can be easily eliminated from a genetic analysis.

Because of emasculating difficulties, hybrid offsprings here analysed came from controled pollination (isolated plots and or two inflorescences in a bag) without anther elimination.

4- nuclei embryo sacs were looked for in hybrids from sexual female x apomict male and apomict female x sexual male. The second way cross uses T19 36,5 a high off-types rated apomict. Results are given in TABLE III.

These data show that either apomixis or sexuality can be conveied by male gamet (sexual x apomict crosses and apomict x sexual crosses respectively).

All these results agree with a 1:1 ratio ; a 3:1 ratio is ruled out. In apomict x apomict crosses we never find a sexual plant; SMITH (1972) has got 4 % plants among off-type plants which could be sexual. We are waiting for complementary results before propounding an interpretation.

II. Problems suggested by the occurence of high off-type rated apomict plants.

1. Mean forage value of a facultative apomict offspring;.

Let us consider 4 full sib plants coming K 189.T x G23 (sexual x apomict cross). P_2 is sexual, P_3, P_4, P_6 are apomict. Offspring obtained by open pollination from each plant are studied for their dry matter yield. Thay were 1 m x 1 m spaced in the field, off-types were counted. Every plant is weighted. TABLE IV gives mean values of off-type and non off-type plants and the expected productions per hectare per year.

Because of bad values of numerous off-type plants there is a great loss of productivity. A vegetative multiplication of P_3, P_4, P_6, instead of an apomict seedling, could yield 30 percent more per hectare per year, if there was no major competition between plants.

Thus, from a breeding program point of view, the off-type rate is a parameter with great pratical value. It matters to know whether we could decrease a such high rate obtained after sexual x apomict hybridization.

2. Consequences of confounding high off-type rated apomict plants and true sexual plants.

Let us consider populations where sexual and apomict plants are mixed and could freely inter pollinate, for they have the same chromosomes number. In PERNES (1970) we showed that the spontaneous evolution will drive the initial population to one which is only apomict plants compounded. Sexuality is ruled out although there were no difference between fitnesses of sexual and apomict plants.

Let us consider now a population entirely apomict plants compounded. However there is a genetic variability for the off-types rates. Although selective pressures were missing, the population should be driven to an homogeneous off-type rate, the smallest being chosen.

Thus we cannot maintain a high sexuality level in freely evolving population of apomict plants. If we want do deal with a self-maintained sexual gene pool, we must be sure of putting in to it no apomict plant. Sometimes it can be awfully difficult to warrant it, for instance with high either S or H.T. ratio.

We have to protect seriously sexuality when we have got it.

3. Sexuality protection by mean of diploid plants.

Every tetraploid natural population is apomict. Sexuality can occur at the tetraploid level but we never find a natural sexual tetraploid. On the other hand natural diploid plants are sexual plants. However dihaploid plants are known among T19, 36,5 off-types. They have 4- nuclei embryo sac (therefore apomict) but they are sterile. DE WET and HARLAN (1970) acquired sexual, fertile dihaploid plants from BOTRIACHLOA-DICUANTIUM complex and 4- nuclei embryo sac sterile plants. It could be there was something wrong with apomixis at the diploid level.

Let us imagine there is a no completely sterile apomict dihaploid. Must sexuality disappear ? We do not think so because of small selective value of dihaploids and we can show which selective disadvantage is required to rule out apomixis from the population. PERNES (1970) results deal with no sexual selective advantage, that can be the case at the tetraploid level. Here we shall give a disadvantage to apomixis because of dihaploidy.

Let us consider the following quite particular situation (TABLE V) (this is the most favorouble situation for apomixis). Genotype frequencies in the next generation are

$$P_{n+1} = k \; P'_{n+1} = P_n \; (1-s)$$

$$2Q_{n+1} = k \times 2\,Q'_{n+1} = 2Q_n \; (1-s) + R_n \; (P_n + Q_n) \; (1-s)$$

$$R_{n+1} = k \; R'_{n+1} = R_n \; (Q_n + R_n)$$

with $K = 1 - s \left[1 - R_n \; (R_n + Q_n) \right]$.

The equilibrium value $R_\infty = R$ is solution of

$$R \left(1 - s \left[1 - R(R + Q) \right] \right) = (R + Q)R \qquad (1).$$

Let us study the case when $P = 0$, because of no AA gentotype in the first generation. Then $2Q + R = 1$, and (1) equation becomes :

$$R \; (1-R) \; \left(\frac{1}{s} \; (1-2s) - R\right) = 0. \qquad (2).$$

There are three equilibrium points, stabilities of which we have to analyse. It is easier to begin with

$$R''' = \frac{1}{s} \; (1-2s).$$

R''' is a genotype frequency if $\frac{1}{3} \leqslant s \leqslant \frac{1}{2}$. $R''' = R' = 1$ with $s = \frac{1}{3}$, $R''' = R'' = 0$ if $s = \frac{1}{2}$.

If $R_n < R'''$ then $R_{n+1} < R_n$; if $R_n > R'''$ then $R_{n+1} > R_n$. Thus R''' is an unstable equilibrium point. Table VI gives the different stability situations according to s values.

If $s \leqslant \frac{1}{3}$, the selective disadvantage of apomict genotypes is not enough to rule out apomixis, and sexuality will disappear.

If $\frac{1}{3} < s < \frac{1}{2}$ either elimination or fixation will depend on depend on initial frequency of apomict genotypes; if Ro $< \frac{1}{s}$ (1-2s), apomixis will be fixed; if $R_0 > \frac{1}{s}$ (1-2s) apomixis will be eliminated.

If $s \geqslant \frac{1}{2}$, there is a too heavy slective disadvantage to allow apomixis to establish in the population.

Thus s values are high enough and a population can pay the apomixis acquiring with a quite heavy load. However the selective disadvantage which forbids apomixis fixation is easily reached for observed dihaploid plants.

We think that diploidy is a good protection of sexuality and it is the best level to store it.

III. Genetic analysis of sexual gene pool .

1. Comparing sexual and apomict variabilities.

In an apomict offspring, phenotypic variability comes from off-types genetic variability and environmental variations. The off-type analysis allow to separate the proper variation of non off-type plants.

Table VII compares the variabilities of sexual plant offsprings to non off-type and off-type offsprings from apomict plants. Three characters were chosen, G (last-leaf sheath length and l_i (inflorescence branching length) because of their small environmental variance, M.V. (fresh matter weight) because of its large environmental variance.

As expected σ^2 sexual $>$ σ^2 non.off-type and σ^2 off-type $>$ σ^2non.off-type. However σ^2 sexual $>$ σ^2off-type as there was some selective pressure which gives a particular homogeneity among off-types.

Offsprings coming from a sexual tetragenic (P2) are not more variable then offsprings coming from a sexual duplex tetraploid K 189T).

Let us note that COMBES (1972) shows that the diploid variability is larger than tetraploid duplex variability.

We must conclude that sexuality plays through active recombination more than through offsprings variabilities. The main advantage of apomixis is not homogeneity but ability to maintain a good hybrid without disjonction. Needless to say that advantage decreases when off-type rate increases (see table IV).

2. Diploid diallel crosses analysis.

We shall not repeat here the genetic results publisheb in RÉNÉ-CHAUME and al. (1973). In that present communication we are comparing results coming from two diallel crosses, concerning seeds germination and number of tillers. We are also interested in dry matter yielding.

The first diallel cross is a 5 parents diallele cross $(\frac{5 \times 4}{2}$ hybrids); the second diallel cross is a 4 x 4 complete one .

Two genotypes are in both experiments (T35 and T41). We want to show the range of values which can be expressed in the diploid sexual gene pool.

Table VIII gives the genetic variances reckoned with GRIFFING (1956) diallel analysis of variance. Table IV gives mean values and mean general combining ability effects.

Seed germination

It is well known there is a Panicum seed dormancy. We can partly escape this dormancy by eliminating seed lemma. However the whole inhibition is not released and it occurs that isolated embryos have a better germination than seeds, even without lemma.

Characters ① and ② are concernig hybrid seeds which were just harvested. Character ① measures something about germinative faculty because of releasing of the main part of inhibition. There is a large genetic variability, entirely built with specific combining ability. The mean value of germination rate is 51,2 % and specific combining ability range is (+9,0 % ; -14,5 %).

Character ② measures seed germination, inhibition factor included because of entire seeds. The main part of genetic variation depends on general combining abilities. More over there is a significative maternal effect. Table IX shows that genetic variation is responsable of about a 25 % variation around the avevage germination value.

Genetic variation concerning character ③ is smoother than that of character ①. It leads to an ordering of hybrids identical to character ① . However, pollinators are entirely unknown, and genetic differences are smooth because of bad definition of embryo and endosperm genotypes.

Thus, three is an interesting genetic variability we can use to improve the seed germination.

Number of tillers

This character has major consequences concerning forage quality. We are looking for numerous thin tillers.

Results ③,④ and ⑤ are in complete agreement. There is a great genetic variability. General and specific combining abilities explain a variation of about 25 % of the average number of tillers.

Total dry matter

This character is mainly under general combining ability control and this can allow for an about 15 % yielding improvenant. This is satisfying because of the reduced gene pool we used in this diallel cross experiment.

Thus for characters of economical interest we can see that even in a such limited gene pool there are well defined sources of genetic improvement. These are encouraging results and we can hope good combinations by using sexual x apomict hybrids.

Concluding remarks.

The general features of a breeding program concerning Panicum improvement can be outlined (see PERNES and al.(1973)). We think that difficulties ought not occur from genetic determinisms of characters to improve, but from genetic determinism of opomixis and off-types rates. Because of neither straight nor simple relations between S and H.T rates it is still difficult to definitely know how to be master of apomixis and sexuality.

TABLE I

off-types rate in "natural" and "synthetised" apomicts (H.T. and α)

natural apomicts	H.T	α	n
common guinea (∼ 267)(1)	4.7 2.6		1,365 1,106
GRAMALOTE (1)	1.3		1,103
mean of 9 varieties(2)	1.2		520
common guinea (267)(3)	4.0	2.9	551
II type(3)		3.1	291
309(3) (G23)		1.4	220
C type(4) (maximum x infestum) T 19	3.9	1.4	1,008
T25 (Bagamoyo)	5.0		103

Synthetised apomicts	H.T	n
off-types from 267(3)		
H29(5)	3.0	67
H11(5)	2.5	80
H9 (5)	7.9	38
H10(6)	3.5	86
H1 (7)	13.9	138
H8 (7)	19.6	238
off-types from T19(4)		
37,1	4.0	84
39,6	8.0	73
35,9	19.0	98
35,6	38.0	98
36,5	44.0	104
36,10	38.0	90

Synthetised apomicts	H.T	α	n
off-types from T19 36,5			
8,10	44.6		100
7,8	46.8		100
7,10	45.1		100
10,2	24.0		100
10,3	20.0		100
5,10	13.0		100
mean of third generation from T19 36,5; 8,10 and T19 36,5; 7,10	40.6		170
T 19 36,5 (8)	60.3	36.2	121
apomict hybrids issued from K 189 T x G23 cross			
P_3	29.3		140
P_4	24.7		150
P_6	37.1		205

Note: the off-types rates are measured from self-fertilization or open-pollination in a field homogeneously planted with the variety under study, excepted off-springs labeled(8).

(1) from WARMKE (1954)
(2) from BOGDAN (1963)
(3) from PERNES and COMBES (1970)
(4) from COMBES (1972)

(5) 32 chromosomes
(6) 36 chromosomes
(7) 48 chromosomes
(8) freely pollinated by sexual tetraploids

T 19 36,5 gives dihaploid off-types (26 now recorded)

They are sterile plants but they have 4 nuclei embryo sacs.

H.T.	off-types rate
α	sexual rate
n	number of plants observed

TABLE II

S ratio (percent 8-nuclei embryo sacs as single sacs) in "natural and "synthetised" apomict

"natural" apomict	S (%)	n	"synthetised" apomict	S (%)	n
common guinea$^{(1)}$	27,9	111	C types		
gramalote(1)	0	57	T 19 36,5$^{(3)}$	77,5	275
common guinea(2) 267	25,0	40	T 19 36,5 x T 35T$^{(3)}$	96,7	30
K85$^{(2)}$	12,5	16	(T 19 36,5 x P_2)1$^{(3)}$	74,3	35
K76$^{(2)}$	16,7	12	(T 19 36,5 x P_2)2$^{(3)}$	72,4	29
K133$^{(2)}$	0	12	K 189T x G23$^{(3)}$	23,2	224
Panicum infestum$^{(2)}$ (K83)	41,2	17	P_2 x 57$^{(3)}$	16,4	744
C type$^{(2)}$ (infestum x maximum)	53,3	15			

(1)	from WARMKE (1954)	section cutting observations
(2)	from COMBES (1972)	-
(3)	from SAVIDAN (1973)	phase contrast observations
n	number of ovaries observed	

T 19 36,5 x T 35 T is an apomict hybrid offspring coming from pollination of T19 36,5 with the sexual tetraploid T 35 T

(T 19 36,5 x P_2)1 and (T 19 36,5 x P_2)2 are two full sibs coming from pollination of T 19 36,5 with the sexual tetraploid P_2 .

T 35 T comes from colchicine treatment of the sexual diploid T35

P_2 is a sexual hybrid issued from K189 T x G23 cross

K 189 T comes from colchicine treatment of the sexual diploid K189

G23 is a~~n~~ natural apomict

K189T x G3 and P_2 x 57 data are an average on 14 and 40 apomict full sibs hybrids respectively

G3 and 57 are two geneticaly identical natural apomicts. It is liable they are analogous to gramalote.

TABLE III

Number of hybrid plants with or without 4. nuclei embryo sacs

Sexual x apomict	plants without 4 nuclei embryo sacs	plants with at least one 4 nuclei embryo sac
K 189 T x G23	2	3
K 189 T x G3	14	14
P2 x 57	34	40
K 189 S,T x G3	4	3
T 44T x 57	3	3
Apomict x sexual T19; 36,5 x P2	4 *	5 **

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* because of possibility of high~~t~~ S valued apomict (table II) some of these plants could be apomict. The number of ovaries observed for these 4 plants are respectively : 89, 28, 25 and 20.

** Two plants have 48 chromosome; their S are 96,7 % (30 ovaries observed), and 72,4 % (35 ovaries observed) respectively.

TABLE IV

Mean dry matter in offsprings from P_2, P_3, P_4, P_6 /.

	off-type plants mean in g.	non off-type plants mean in g.	overall mean value in t/ha/year	expected mean value without off-type plants (t/ha/year)
P_3	95	330	34,4	42,9
P_4	108	315	34,8	40,9
P_6	94	304	29,5	39,5
P_2		235	30,5	

the number of plants observed was given in Table I.

TABLE V

Fitnesses and genotype frequencies when absolute apomixis is dominant

genotype	phenotype	frequency	fitness
AA	apomict	P_n	1-s
Aa	apomict	$2\,Q_n$	1-s
aa	sexual	R_n	1

TABLE VI

Stability of equilibrium according to s values
(selective disadvantage of apomixis)

s	R'' (0)	R''' $\frac{s}{2}(1-2\ s)$	R' (1)
$< \frac{1}{3}$	stable		unstable
$= \frac{1}{3}$	stable $R'' = R'''$		unstable
$\frac{1}{3} < s < \frac{1}{2}$	stable	unstable	stable
$= \frac{1}{2}$	unstable	$R' = R'''$	stable
$> \frac{1}{2}$	unstable		stable

TABLE VII

Mean and Variance of apomict and sexual hybrid offsprings

	Offspring	K189T x G3	P_2 x 57	(K189T x G23)AF P_2	(K189T x G23)AF P_3		(K189T x G23)AF P_4		(K189T x G23)AF P_6		T19 36,5 x (P_2, K189T T35T, S_2T)		
	categories	sexual	sexual	sexual	NHT	HT	NHT	HT	NHT	HT	NHT	H T	
												C	hybrid
log G	observation number	69	90	141	98	37	112	33	123	38	48	20	20
	mean ($x10^2$)	259.1	255.6	257.6	268.4	265.3	265.7	262.0	267.3	263.9	250.3	244.0	253.6
	variance ($x10^4$)	29.10	22.84	35.42	11.11	22.27	6.58	19.35	11.76	19.51	11.24	31.05	68.36
log l_i	observation number	68	90	154	100	37	112	33	123	37	47	20	20
	mean ($x10^2$)	252.8	246.4	241.4	259.0	253.1	250.7	246.3	251.8	246.6	210.4	205.4	226.8
	variance ($x10^4$)	75.81	94.53	77.94	25.41	41.72	18.58	36.83	40.29	46.12	110.41	72.07	204.03
log(M.V + 1,0)	observation number	119	139	123	107	39	114	34	127	74	48	20	33
	mean ($x10^2$)	33.57	34.63	35.579	42.155	18.130	39.641	17.811	40.002	19.76	235.1	127.1	220.1
	variance ($x10^4$)	184.35	88.86	221.40	96.47	96.54	64.12	61.10	49.00	77.86	32.37	31.88	210.58

TABLE VII

G23, G3, 57 are apomict plants (their off-type rate are about 3 % and their 8-nuclei embryo sac frequency are about 25 %). It is lianle that G3 and 57 are two different numbers for the same genotype T19, 36,5 is a most sexual rated apomict coming from offspring of an interspecific hybrid. Its 8-nuclei embryo sac frequency is 75 %, its off-type rate when measured after self-fertilization is about 40 %, its off-type rate when measured after open-pollination (without emasculation) is about 65 %.

On the average ranks of variance : σ^2 sexual $>$ σ^2 off-type $>$ σ^2 apomict.

off-type offsprings from P_3, P_4, P_6 respectively are analogous to P offspring coming from self fertilization. However P_2 offsprings are the most variable. Compeition between 4-nuclei ambryo sac in apomict plants could be restrictive to off-type variability. Comparing P_2 x 57 and K189T x G3 offsprings shows that P_2 which is the most heterozygous genotype does not lead to the highest variance.

Comparing the two off-type categories in T19 36,5 shows the importance an variability of hybridization versus self-fertilization. A major source of variability in hybrid offsprings could be a developmental incompatibility because of genetic distance between 719 and sexual types.

TABLE VIII

genetic variances from diallel croses

		mean square gen. comb. ability	mean square spec. comb. ability	mean square maternal ability	mean square spec.maternal ability	σ^2 gen. comb. ability	σ^2 spec.comb. ability	σ^2 maternal
seed germination	1	11.30	375.82^{**}			0	601.9	
	2	142.8^{**}	35.6	52.8^{*}	21.0	95.28	0	27.79
	3	138.5^{**}	45.0			3.32	0	
number of tillers	4	5774.00^{**}	1267.23^{**}			173.24	113.18	
	5	61.44^{**}	149.50^{**}	11.73	4.30	41.92	26.57	0
	6	7397.30^{**}	865.40^{**}			398.62	134.00	
dry matter yield	7	0.0545^{**}	0.0025^{*}			0.00298	0.00034	

* 5 % significative F

** 1 % significative F

1 hybrid seeds without lemma (5 x 5 diallel cross)

2 entire hybrid seeds (4 x 4 diallel cross)

3 entire seeds harvested on hybrid families (5 x 5 diallel cross)

4 before the first cut (5 x 5 diallel cross)

5 before the first cut (4 x 4 diallel cross)

6 average value after cutting (4 cuts, each cut every 4 weeks)

7 a 4 cuts mean (one cut every 4 weeks).

TABLE IX

general combining abilities when significative and maximum and minimum specific combining abilities when significative.

		T_{35}	T_{41}	T_{40}	T_{44}	T_{47}	T_{49}	K 189	max. and min. values of specific combining ability		averal mean
									max.	min.	
% seed germination	2	+7.1	-4.8			+2.8	-5.1				48 %
	3	+1.8	+0.8	-1.6	-2.2			+0.9			42 %
number of tillers	4	-8.7	-1.7	+7.4	+6.3			-3.3	+4.7	-5.3	76
	5	-7.1	+5.3			+3.3	-1.6				50
	6	-12.0	-0.9	+12.8	+7.2			-7.1	+5.9	-8.9	150
dry matter g/plant	7	+48	-16	-7	-18			-7	+12	-10	350

2 , 3, 4, 5 , 6 , 7 number explained at the bottom of Table VIII.

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