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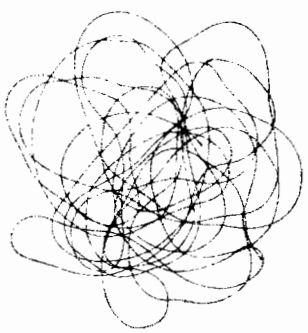
BREEDING

PANICUM MAXIMUM Jacq.



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ABSTRACT

Sexual diploid and tetraploid Panicum maximum are investigated for their genetical yielding abilities. They are compared to different productive apomict Panicum known in our Ivory Coast collection. A 5 parents diallel cross allow to analyse combining abilities of diploid plants. Apomict and sexual hybrids coming from sexual tetraploid x apomict tetraploid crosses might appear as improved varieties. A Plant breeding program concerning Panicum maximum and other apomict grasses is suggested. An important point to scrutiny is the off-type rate of new apomict hybrids.

Additional index words : Apomixis, Guinea grass, Hybrid, diploid, tetraploidization, diallel cross, combining abilities.

BREEDING *Panicum maximum* Jacq.

by

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Panicum maximum is the main species of the maximae agamic complex. *Panicum infestum* and *Panicum trichocladum* are two other components of this complex. The organization of this complex was studied by D. COMBES (1972) and J. PERNES (1972 a). Primitive diploid sexual types of true *Panicum maximum* were found out natural populations in East Africa prospections (1967, 1969, D. COMBES and J. PERNES (1970)). New dihaploids arose from one spontaneous apomict interspecific hybrid (*Panicum maximum* x *Panicum infestum*) (J. PERNES (1971, 1972 a, 1972 b), D. COMBES (1972)).

Apomixis in *Panicum maximum* is well known since/from WARMKE results (1954) and BOGDAN (1963), yet a breeding programm of this plant could not start whithout sexual plants. The major part of forage interesting variability is stored in tetraploid apomict plants. Thus tetraploid sexual plants could allow to combine this frozen gene pool.

There are two ways of raising sexuality up to tetraploid level. The first one is by means of colchicine treatment of sexual diploid. All the tetraploid plants we got are sexual, and hybrids between them are sexual too. The second way is by means of selecting for sexuality through successive off-type generations in apomict plants. Sexual rate increased from 2 % to about 70 % through off springs of a *Panicum maximum* x *Panicum infestum* hybrid (COMBES (1972), PERNES (1971, 1972 a). SMITH (1972) obtained sexual off-types following this latter way. He succeeded in doing this as soon as the first off-type generation. However he did not control embryo sacs and his word sexuality means enzymatic variability in offsprings.

From immediate point of view it does not matter whether thay are true sexual plants or high sexual rated apomict plants. However this can be of consequence in a long term breeding program because of spontaneous evolutive decrease of sexual rate in apomicts (J. PERNES 1970). Even recessive apomict genes concealed in true sexual plants induce sexuality to disappear gradually from population (J. PERNES 1970).

We consider three main problems in dealing with Panicum maximum breeding program:

1. apomict heritability analysis,
2. measure of genetic variability and forage value of sexual gene pool
3. combining abilities of sexual and apomict tetraploid plants, and genetic studies of apomict plants by way of hybridisation with sexual plants.

Here we give some results concerning problem nomber 2. Other papers in preparation will deal with the remaining questions.

Material and Methods

1. Forage value and productivity of sexual plants and first tetraploid hybrid plants.

20 different diploid sexual clones were prospected in East Africa 5 years ago. 5 of them were tetraploidized through colchicine treatment of lateral buds. Thus we can compare isogenic clones at diploid and tetraploid levels. We are aiming at knowing whether after a breeding program on the diploid level we can store the improvement by picking up and tetraploidizing the best plants. We give results in experiment number 1.

Experiments number 2 and 3 compare diploid and tetraploid sexual plants to the best apomicts.

Experiment number 4 comares one of the best apomicts (K 187 B), two diploids (D1 and D2), ten hybrids obtained from cross pollinating K 189 T (sexual tetraploid) with apomict plants, G 23 (P_4, P_6, T_1, T_2, T_3, T_4, T_5, T_6) and 267 (T_7, T_8, T_9, T_{10}) respectively.

These four trials are complete block designs. In trials number 1 and 4, plants are 1m x 1m spaced, each elementary plot is a 9 meters row. Plants are clonal multipication by cuttings.

Trial number 2 is a true forage trial, with 60 square meters plots; plants are 0,4m x 0,4m spaced and clonal multiplication is settled by cuttings.

Trial number 3 is hand-sown, on 0,5m spaced rows with a density of 4 kg seeds by hectar, elementary plots aera is 16 square meters, with eight rows in each plot.

2. Combining abilities of diploid sexual plants.

Experiment number 5is a 5 x 5 diallel cross between 5 primitive diploids (T_{35}, T_{40}, T_{41}, T_{44}, K 189 A), with neither self-fertilized lines nor reciprocal crosses. Because of high level of self-incompatibility in sexual Panicum maximum cross-pollination occurs without emasculation. In the field it is a 6 complete blocks design, $\frac{5 \times 4}{2}$ plots per block, 8 plants per block, one meter spaced. Uniform borders between plots are rows of the apomict variety (K 211). Each plant comes from a seed and is measured, every character is measured on 6 x 10 x 8 = 480 plants).

Experiment number 6 analyses general combining ability of the 20 primitive diploids through a polycross trial; seeds are issued from open-pollination fo 20 randomized repetitions of diploid plants. In the field it is a 3 complete blocks design, plots are 20 square meters aera of 0,5m x 0,5m spaced plants, every plant comes from seeds.

3. Characters measured.

Several characters are measured. They are :

- date of heading d
- fresh weight M.V.
- percent dry matter % M.S.
- total dry matter M.S.T.

On an average tetraploidy induces reduction of characters. Moreover tetraploids flower later than diploids. There is no variation in number of tillers.

A full knowledge of tetraploidy effect on genotypes is acquired after glancing at the classification by dendrogram (fig.1). All the characters above studied are included in it. We used proximity indice described in J. PERNES and al. (1970). Isogenic lines are quite neighsbor. Fig. 2 gives the graph of a principal component analysis with last internode and inflorescence characters. It shows significative variety x polyploidy interaction effect. Polyploidy moves the representative points of varieties in any direction but not too far.

2. Comparing 4 diploid clones to K 187B one of the best apomict clones.

K 187B yields, in the field, 50 tons/ha/year dry matter. Results were obtained in a 20 ha plot, with irrigation and controled pasture, at BOUAKE (I.E.M.V.T.), IVORY COAST. This trial began 4 years ago, data above mentionned are a 3 years average.

Data from experiment number 2 come from ADIOPODOUME (IVORY COAST) in a less sunny place, without irrigation. In an other Adiopodoumé trial without irrigation, K 187 B was the best apomict clone with regard to fresh weight.

Tables III and IV give mean values and variance analysis respectively.

Diploids are analogous to K 187B concerning yielding ability. They have a better forage quality (higher percent dry matter and higher F/T ratio).

3. Comparing, by seedling, sexual tetraploid offspring to the best apomict clones.

Sexual tetraploids are two reciprocal crosses offsprings of T44T x K 189 AT (T 44 TO and K 189 AT.O, respectively from the name of maternal parent). K 187B seeds were not available at the settlement time. In other Adiopodoumé (IVORY COAST) Forage experiment, K 211 variety gave better total dry matter values than K 187B. Trial number 3 is irrigated.

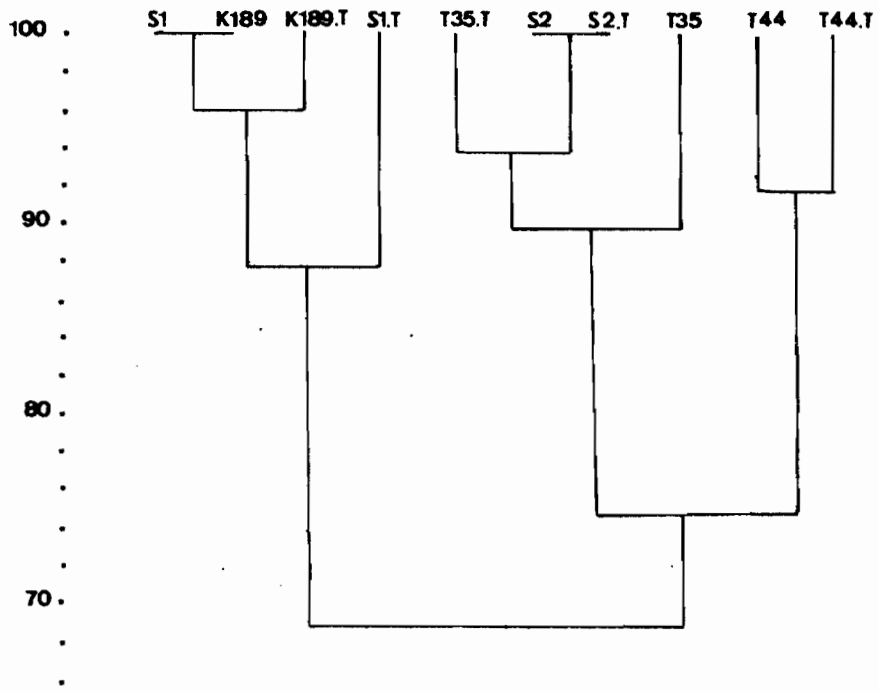

Fig.1 Dendrogram classification (proximity indice) of sexual diploid and tetraploid clones.
T after variety number means tetraploid.

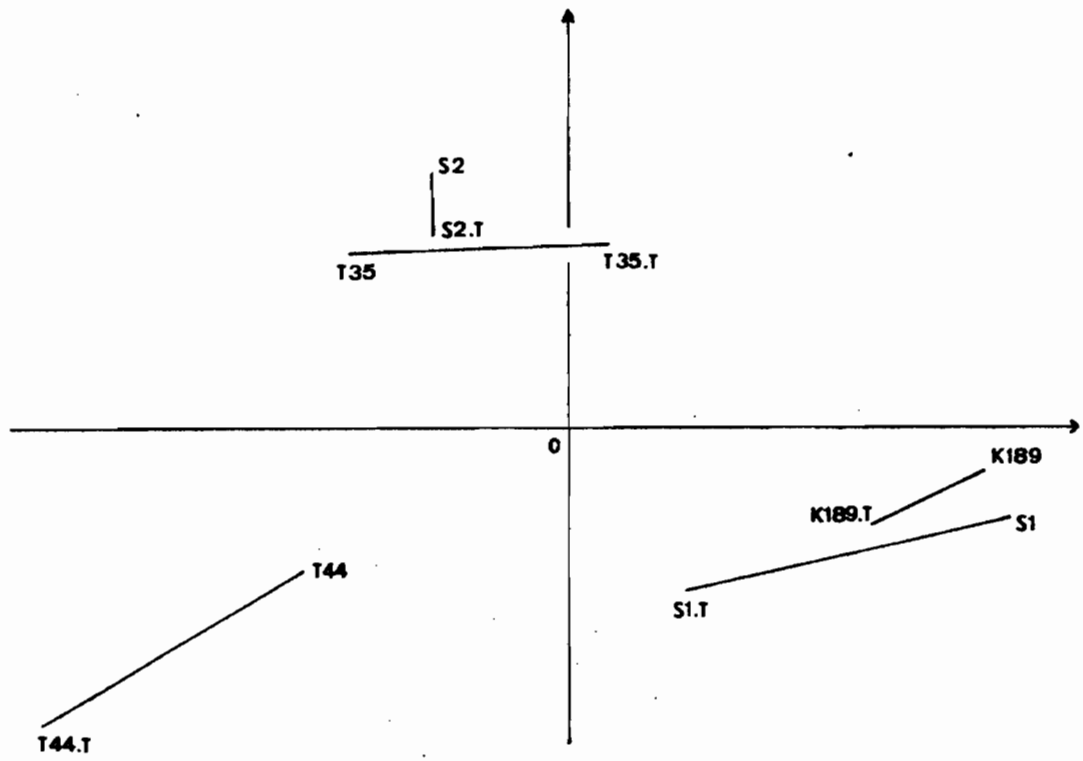

Fig.2 Two main principal components graph.
Description of sexual diploid and tetraploid clones.
T after variety number means tetraploid.
Continuous line brings together isogenic (diploid–tetraploid) varieties.

First component : $\frac{3}{4}(n+F+L_i)+L+\frac{1}{25}II$

Second component : $\frac{1}{4}n+\frac{2}{5}(F-L_i)-\frac{1}{4}L+II$

Tables V and VI give mean values and variance analysis respectively.

Both sexual tetraploid hybrid offsprings have high productivity and a high forage value just about those of the best apomict plants.

4. Comparing new tetraploid (Sexual x apomict)hybrids to K 187 B .

Hybrids come from open-pollination of sexual tetraploid K 189 AT with apomict plant (either 267 or G 23), in isolated plots. Offsprings coming from sexual K 189 AT are sown in small pots and then planted in the field, 1m x 1m spaced. Good looking plants were chosen and multiplied by cuttings. P_4, P_6, T_1, to T_6 clones are full sibs from K 189 AT x G 23 cross. T_7, T_8, T_9, T_{10}, clones are fullsibs from K 189 AT x 267. D_1 and D_2 clones are clones coming from an open pollination of sexual diploid K 189. A_1, A_2, A_3, A_4, clones are full sibs from apomict seed offsprings of K 187 B.

Table VII and VIII give mean values and variance analysis respectively.

T2 and P4 hybrids are more productive (total dry matter) than K 187B,with a higher number of tillers and better percent dry mater.

T8, P6, D1, have a Good production and an improved forage quality.

P4, P6, T_8, T_{10} hybrids are apomict tetraploids

T_2, T_6, T_4, T_9 hybrids are sexual tetraploids (SAVIDAN personal communication).

5. Diallel crosses between sexual diploids.

GRIFFING (1956) variance analysis is used to test and estimate general and specific combining ability variances. Variance analysis results and variance estimations are given in Table IX. Intraclass correlations $h = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_S + \sigma^2_e}$ and $h' = \frac{\sigma^2_G + \sigma^2_S}{\sigma^2_G + \sigma^2_S + \sigma^2_e}$ are analogous to heritabilities ("sensu stricto" and "sensu lato" respectively).

There is a great variability within family (between full sibs). Thus it is liable that diploid sexual Panicum maximum are hightly heterozygous. In spite of a great genotypic residual within family variance high combining abilities mean squares show a strong heritability for some characters.

Let us note the high heritability (h and h') values for the number of tillers, date of heading (d), leaf characters, l.l. (last leaf width), F (last leaf length), G (last leaf length) and virus (streak) sensibility.

Figure 3 shows a principal component analysis from variance between-crosses matrix concerning some high h-valued characters (l.l., F, G, t_1 , d). T_{41}, T_{35}, T_{44}, having highest general combining abilities lead definitely their hybrids to specific positions in the graph. On the other hand T40 and K 189 are neutral (central position on the graph and low general combining ability).

Table X gives general combining ability values. From productivity, forage quality, number of tillers and virus resistance the most interesting family is T_{35} x T_{44} . The worst parent is T_{41} .

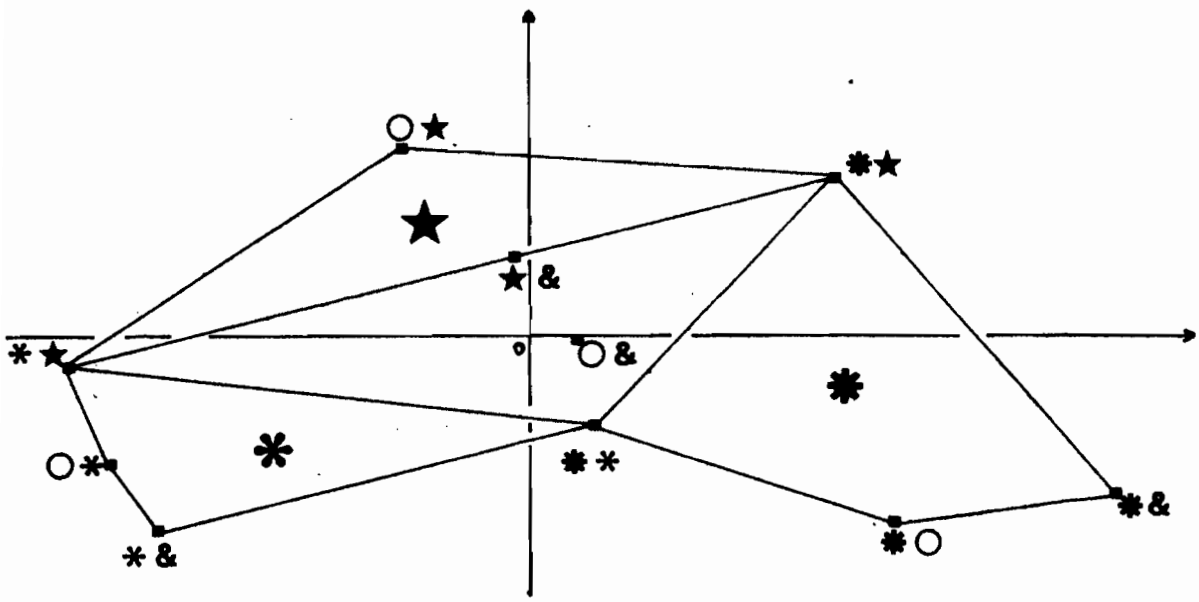

Fig.3 Two main principal components graph.

Dots representative of hybrids are two parent symbols composed

✱ T 35 ○ T40 ✱T41 ★T44 & K189

T35, T41, T44 parents (only one symbol) are located at the barycenter of their hybrids. First component : $(H+G+F)+\frac{2}{3}d-t_1$

Second component : $t+d-\frac{1}{4}F-\frac{2}{3}(G+H)$

6. Polycross analysis of general combining abilities of diploids.

Tables XI and XII give mean values and variance analysis. High yielding diploid offsprings T_{26} and T_{27} have got a very bad forage quality.

The reason why we mention these quite partial results is they show the variability range of diploids sampled in the diallel cross versus the whole range of 20 primitive diploids.

In another paper the analysis of seed germination will be described with details. These results show a significative genetic variability and a clear-cut environmental effect.

DISCUSSION

Before choosing a breeding programm we need to know

1. genetic potentialities of primitive gene pool
2. responses to different stresses (inbreeding, hybrization, polyploïdisation)
3. heritabilities of characters.

Here we must add

4. genetic determinism of reproductive system (apomixis versus sexuality).

This paper is the first one as far as we konw to give answers to questions about breeding Panicum maximum.

1. Sexual gene pool is, on the average, as good as apomict gene pool. We mean to say that sexuality does not seem to be bound to disadvantageous forage abilities. Quite on the contrary, better sexual hybrids can be issued from mixing up sexual and apomict gene pools.

2. There is a huge variability stored in apomict plants; but it is frozen. On the other hand diploid variability is quite tiny, but it is not frozen. Up to now we cannot increase diploid variability with genes coming from apomict pool. Dihaploid plants are uncommon and sterile, although having unreduced embryo sac (D. COMBES (1972)), J. PERNES (1972b)). Therefore we think it is easier to create a new sexual variability at the tetraploid level.

3. Diploids and digenic tetraploid coming from colchicine treatment of diploids are quite similar and the main part of characters expression is unchanged. Thus we can easily imagine the features of a digenic tetraploid when its original diploid is known. These new tetraploids are always sexual, and cross breeding among them leads to good sexual forage plants. They are nearly complete self sterile plants.

4. Therefore there is no problem to cross breed them by apomict plants which are pollinator parents. By this way we acquired improved hybrids and incrased sexual tetraploid gene pool as well as apomict gene pool.

5. Genetic combining abilities were measured in diploid gene pool and heritabilities were estimated. There is an efficient response to selection for characters such as the number of tillers, virus resistance, date of heading, leaf width and leaf length. As a matter of fact, sexual x apomict tetraploid hybrid features suggest it is true with the same characters at tetraploid level. A definitive analysis is undertaken in our lab. We think that Panicum must be improved by successive crosses of high yielding sexual tetraploid plants with several apomict plants picked up from particular high heritable qualities. The breeding scheme can be :

A first hybrid generation is issued from sexual x apomict number 1 crosses. Good sexual hybrids (SA_1) are chosen, and a second hybrid generation (three way hybrids, (SA_1) x apomict number 2), can be tested in field trials. As soon as good apomict hybrids came into sight they have to be scanned for their off-type rate (New apomict hybrids reach as high an off-type rate as 35 percent). If they get high off-type rate they are ruled out as commercial seeds.

Thus, the major problem is to know how we can decrease off-type rates of apomict plants. We need to have a definite knowledge of apomixis versus sexual genetical determinism. We prepare a paper about this point.

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TABLE I : Variance analysis of experiment 1.

** 1 % singificative F

* 5 % singificative F

TABLE II : Polyploidy mean effect when significative.

TABLE III : Mean values on 24 cuts in experiment 2. One cut every six weeks. Weight (MV and MST) in tons/ha/year.

- 5 % significative difference with K 187 B (lower than K 187 B)

+ 5 % singificative difference with K 187 B (higher than 187 B).

TABLE IV : Variance analysis of experiment 2.

** 1 % significative F.

TABLE V : Mean values in experiment 3 (6 cuts, one cut every 4 weeks) Weight (M.V. and M.S.T.) in tons/ha/year.

TABLE VI : Variance analysis of experiment 3.

** 1 % significative F.

TABLE VII : Mean values in experiment 4 (7 cuts, one cut every four weeks) Weight (M.V and M.S.T.) in tons/ha/year.

TABLE IX : Variance analysis of experiment (diallel cross) (every value is multiplied by a 10^3 factor excepted h and h').

* 5 % significative F.

** 1 % significative F.

+ degree of freedom are 2 and 210 for block and residual effect respectively.

] residual effect degree of freedom is 45

‡ t_1 number of tillers one month after field planting

t_2 number of tillers started after the first cut.

§ because of definite variance estimations, date were log transformed after adding mean value.

‖ n is $\sqrt{n}$ transformed .

++ measured by averaging coded values from 0 (no symptom) to 5 (strongly depressed).

TABLE VIII : Variance analysis of experiment 4.

** 1 % significative F.

TABLE X : General combining ability values in experiment 5.

TABLE XI : Mean values in experiment 6 (second cut result) Weight in tons/ha/year *

* We do not intend to say that it could be the true productivity on a several years trial.

TABLE XII : Variance analysis of experiment 6 (polycross design).

transformation used is Arc sin.

TABLE I

Variance analysis of experiment 1.

Characters séries 1	Mean square variety effect	mean square polyploidy effect	mean square variety x polyploidy interaction effect	residual mean square
degree of freedom	4	1	4	45
M V	7,773**	31,828**	9,224**	1,239
% M S	2,835	0,028	4,366*	1,446
M S T	0,426**	1,542**	0,528**	0,064
Characters series 2 (inflorescence)				
degree of freedom	4	1	4	360
L_i	1275,414**	3,780	259,056**	54,918
l_i	590,998**	22,080	40,695	21,969
F	985,824**	86,058	276,780**	97,732
l.l.	500,649**	189,343**	53,337	27,472
G	470,778**	26,124	29,610	18,833
L	3629,682**	637,812*	322,056**	149,140
n	58,842**	2,268	12,642**	3,343

** 1 % significative F * 5 % significative F

TABLE II

Polyploidy mean effect when significative

Characters	mean of diploids	mean of tetraploids
M.V.	61,3 t/ha	46,7 t/ha
M.S.T.	14,2 t/ha	11,0 t/ha
l.l.	1,92 cm	1,79 cm
L	111,1 cm	108,6 cm

TABLE III

mean values on 24 cuts in experiment 2. one cut every six weeks. Weight (MV and MST) in tons/ha/year.

clones / Characters	Sexual diploids				Apomict tetraploid K 187 B
	T 34	T 44	T 52	T 54	
M V	104.8^{-}	101.9^{-}	95.5^{-}	94.8^{-}	117.8
% M S	23.8^{+}	21.4^{+}	20.8^{+}	21.1^{+}	19.3
M S T	23.9^{+}	20.9	19.3^{-}	19.3^{-}	21.8
F/T ratio	0.901^{+}	0.894^{+}	0.848^{+}	0.909^{+}	0.796

\- 5 % significative difference with K 187B(lower than K 187 B)

\+ 5 % significative difference with K 187 B (higher than 187 B)

TABLE IV

Variance analysis of experiment 2

mean square	clonal effect	block effect	residual variance
degree of freedom	4	2	8
M.V.	62 933**	34 862**	3 427
% M.S.	7.885**	3.075**	0.263
M.S.T.	2 695.7**	275.9	119.1
F/T ratio	0.00676**	0.00009	0.00009

** 1 % significative F.

TABLE V

Mean values in experiment 3 (6 cuts, one cut every 4 weeks)

Weight (M.V. and M.S.T.) in tons/ha/year

varieties / Characters	sexual tetraploid		apomict					
	K 189 A To	T 44 To	267	K 220	K 196	89	K 204	K 211
M.V.	258	240	246	234	232	231	228	203
% M.S.	19.7	19.3	19.7	20.9	20.7	18.1	20.0	22.0
M.S.T.	50	45	48	47	47	42	45	46

TABLE VI

Variance analysis of experiment 3

Mean square values	variety effect	block effect	residual effect	5 % mean variety least square deviation
degree of freedom	7	3	21	21
M.V.	634.5**	28.6	138.6	17.32
% M.S.	5.399**	2.157**	0.232	0.71
M.S.T.	14.60**	12.32	4.73	3.20

** 1 % significative F.

TABLE IX

variance analysis of experiment (diallel cross)

(every value is multiplied by a 10^3 factor excepted h and h')

	mean square cross effect	mean square block effect	mean square G.C.A.	mean square S.C.A.	residual mean square σ^2_e	AGC variance σ^2_G	ASC variance σ^2_S	h	h'
egree of reedom	9	5	4	5	420				
.V. §	81**	132**	131**	41**	22	3.46	2.26	0.125	0.206
M.S.*	11650**	75430**	18950**	5810	3750	965	490	0.185	0.280
.S.T.+ §	80**	98**	149**	25	22	8.06	0.71	0.262	0.285
1 + §	422**	82	686**	212**	40	220.51	204.8	0.253	0.506
2 ‡ §	663**	306**	1136**	284*	96	33.02	22.38	0.218	0.366
	127350**	144190**	262460**	19250	15360	844.44	463.10	0.331	0.351
§	1407**	2671**	1765**	1120	563	38.16	66.31	0.057	0.166
i §	25**	5	31**	21**	4	0.86	2.02	0.125	0.419
-i §	26**	11**	32**	21**	4	0.89	2.02	0.129	0.421
§	225.17**	38.56	440.11**	53.22	24.47	13.19	3.42	0.321	0.404
.l. §	329.74**	340.51**	701.69**	32.18	24.67	21.49	0.89	0.457	0.476
§	37.00**	3.13	71.07**	9.73**	2.53	2.18	0.86	0.391	0.545
§	33**	19**	55**	15**	6	1.56	1.07	0.180	0.305
n ‖	348.90**	136.00	500.00**	228.00	92.16	12.95	16.17	0.107	0.240
virus] ++ sensi-bility	371**	250**	653**	145**	48	134.44	80.83	0.511	0.818

* 5 % significative F

** 1 % significative F

\+ degree of freedom are 2 and 210 for block and residual effect respectively

] residual effect degree of freedom is 45

‡ t_1 number of tillers one month after field planting

t_2 number of tillers started after the first cut

§ because of definite variance estimations, data were log transformed after adding mean value

‖ n is $\sqrt{n}$ transformed

++ measured by averaging coded values from 0 (no symptom) to 5 (strongly depressed).

TABLE X

General combining ability values in experiment 5

characters / genotype	M.V	% M S	MST	t_1	t_2	d	I	L	l_i	F	l.l.	L	G	n	virus
T_{35}	0.048	0.339	0.078	-0.092	-0.115	0.626	-0.005	0.020	0.016	0.100	0.099	0.005	0.006	-0.009	-0.00
T_{40}	0.003	-0.661	-0.007	0.083	0.120	0.486	-0.034	-0.003	0.005	-0.015	0.014	0.008	0.017	-0.029	-0.04
T_{41}	-0.039	0.019	-0.054	-0.019	-0.041	-2.351	0.195	-0.019	-0.013	-0.053	-0.109	-0.019	-0.040	0.101	-0.09
T_{44}	-0.017	0.046	-0.019	0.067	0.073	1.459	-0.125	-0.010	-0.020	-0.031	-0.017	-0.022	-0.000	-0.069	-0.16
K 189 A	0.007	-0.244	0.002	-0.038	-0.038	-0.221	-0.031	0.010	0.013	-0.001	0.013	0.028	0.017	0.005	0.31

TABLE XI

Mean values in experiment 6 (second cut result)

weight in tons/ha/year *

	K189 A	K189 B	T_{26}	T_{27}	T_{33}	T_{34}	T_{35}	T_{40}	T_{41}	T_{42}	T_{43}	T_{44}	T_{47}	T_{48}	T_{49}	T_{50}	T_{51}	T_{52}	T_{53}	T_{54}
M.V.	264	237	348	334	215	253	270	270	217	243	227	247	195	246	250	266	227	240	229	240
% M.S.	16.8	17.5	16.0	14.8	16.5	16.8	17.3	18.2	17.1	18.0	18.3	17.2	18.2	18.4	17.9	17.2	18.5	17.0	17.4	17.4
M.S.T.	43.9	42.0	55.4	49.7	35.6	42.3	46.4	49.0	36.9	44.0	41.4	43.7	35.1	45.3	44.8	45.9	41.4	41.0	39.8	41.8
t	37.3	42.7	54.6	45.8	34.5	30.9	32.1	36.7	36.7	45.0	43.7	36.5	30.4	35.1	39.7	33.0	36.8	27.4	37.4	33.5

* We do not intend to say that it could be the true productivity on a several years trial.

TABLE XII

Variance analysis of experiment 6 (polycross design)

	mean square variety effect	mean square block effect	residual mean square
degree of freedom	19	2	38
M.V.	81.468**	1 134.97**	29.913
% M.S.	2.453**	0.097	0.731
M.S.T.	1.396**	35.808**	0.722
t	120.964**	1207.841**	36.297
percent seed germination one year after harvest	0.071**	0.048**	0.010

transformation used is Arc sin $\sqrt{\ }$