

BIOLOGY AND NATURAL POPULATIONS
OF Panicum maximum Jacq.

J. PERNÈS

D. COMBES

R. RENÉ-CHAUME

Y. SAVIDAN



OFFICE DE LA RECHERCHE SCIENTIFIQUE ET TECHNIQUE OUTRE-MER

CENTRE D'ADIPODOUMÉ - CÔTE D'IVOIRE

B. N. 20 - ARIJAN



Novembre 1973

Summary

This paper analysed the heredity of apomixis in Panicum maximum, and the genetic structures of some ^{of} its populations. Natural tetraploid plants were facultative apomict (sexual rate about 3%). Exceptional diploid sexual plants occurred in central populations. Hybridizations between tetraploid sexual plants and tetraploid apomict plants gave $\frac{1}{2}$ sexual hybrids and $\frac{1}{2}$ apomict hybrids. The sexual rate measured either by the off type rate or by the reduced embryo sac rate is partially under genetic control.

The natural populations of apomict plants were of a very simple structure if they were marginal, and quite similar to populations of allogamous plants if they were in the central area. The populations of diploid plants and tetraploid apomict plants in the central area shew the same continuous and allogamous variability type.

The genetic analysis of diploid plants and of tetraploid hybrids between sexual tetraploid and apomict tetraploid plants demonstrated that there was a continuity of genomes from sexual diploid to apomict tetraploid plants although there was a clear cut separation between sexual and apomict natural plants because of the ploidy level.

Finally the following questions are asked : why were sexual tetraploid in natural populations so rare that we never found one ? Why were the sexual rate of natural apomict plants so low and so homogeneous although it could be variable ? Why looked the central apomict populations like the central sexual populations although the reproductive mode was so different ?

Biology and natural populations of Panicum maximum Jacq.

by

J. PERNES
D. COMBES
R. RENE-CHAUME
Y. SAVIDAN

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

The phenotype of these latter plants could not be distinguished by external examination from the phenotype of the surrounding tetraploid plants.

We shall try to analyse the genetic determinisms of apomixis versus sexuality. We shall examine also the relations between sexual and apomict genoms as they appear through natural populations and experimental hybrids.

A - Reproductive mode

I. Facultative apomixis in natural Panicum maximum

Natural Panicum (excepted diploids) gave their seeds by facultative apomixis. This reproductive mode can be described either through the direct observation of the offsprings of a plant, or through the analysis of the formation of the embryo sacs.

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.).

The table I gives different H.T. values which were observed by WARMKE (1954), BOGDAN (1963), COMBES (1972), PERNES and COMBES (1970)

Table I : off-type rates (H.T.) observed in natural varieties of Panicum maximum

variety	authors	number of observed off springs	H.T. (%)
common guinea	WARMKE	1,365	4.7
-	WARMKE	1,106	2.6
- (267)	PERNES-COMBES	551	4.0
gramalote	WARMKE	1,103	1.3
type II	PERNES-COMBES	291	3.1
309*	PERNES-COMBES	220	1.4
T 19* *	COMBES	1,008	3.9
T 25	COMBES	103	5.0
mean value of 9 varieties	BOGDAN	520	1.2

* 309 is similar to Gramalote variety and G3, 57 and G23 varieties which will be extensively used in the following experiments

* * T 19 is a putative natural interspecific hybrid between P.maximum and P.infestum.

In apomict plants, the observation of the ovaries shew two kinds of embryo sacs 4 nuclei embryo sacs and 8 nuclei sacs, (WARMKE (1954), COMBES (1972)). By eight nuclei embryo sac rate (s) we mean the following ratio :

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

WARMKE counted once 16 chromosoms in cells from a 8 nuclei embryo sacs, and counted several times 32 chromosomes in cells from a 4 nuclei embryo sac. 4 nuclei embryo sac have got only one polar nucleus and no antipodial cells ; the 4 cells were all together in the same part of the embryo sac. Different technics could be used for the embryo sac studies. WARM KE(1954) COMBES (1972) used cuts. Faster and safer observations could be done now with the HERR'S technic (1971) (squash and phase contrast microscopy). Because of no direct relation between H.T and S some authors doubted if every 8 nuclei embryo sac was a reduced one. However we shall show later there could be a simultaneous increasing of both rates.

Diploid sexual plants had always only one embryo sac per ovary and this sac was a 8 nuclei one. Apomict plants had very often several embryo sacs per ovary. We do not know whether every 8 - nuclei embryo sac is a reduced one, but what we can say is that every apomict plant shew some 4 - nuclei embryo sac. We shall call " sexual " a plant which never had 4 - nuclei embryo sac and which shew character recombinations in its offspring plants.

The table II gives the S rates observed in natural apomict plants.

II - Sexual Panicum maximum and their hybrids with the apomict plants.

The sexual diploid ($2n = 16$) plants were very un-common ; they formed natural populations in East Africa among tetraploid apomict populations (See part B).

We obtained tetraploid plants from sexual diploid plants by colchicin treatment either of seeds (S_1T and S_2T came from seeds of the self pollinated diploid K189 T) or of buds (T34T, T 35 T, T 44 T, K 189 T). Tetraploid plants thus obtained have got only ovaries with only one 8 nuclei embryo sac. Their heterogeneous offsprings confirmed that they were sexual.

Variety	authors	number of observed ovaries	S (%)
Common guinea	WARMKE(1954)cuts	111	27.9
-	COMBES(1972)cuts	40	25.0
-	SAVIDAN (this paper)(squash)	155	22.6
gramalote	WARMKE	57	0
G 3*	SAVIDAN	119	0.8 ⁺
K 85	COMBES	16	12.5
K 76	SAVIDAN	123	12.2
K 133	SAVIDAN	119	3.4
K 77* *	SAVIDAN	145	7.6
P. infestum	SAVIDAN	116	2.6
G 23	SAVIDAN	133	4.5
K 211	SAVIDAN	112	1.8
Trichoglume			
G 41	SAVIDAN	76	26.3
average on six varieties	JAVIER(1970)	387	36.2

Table II : frequency of ovaries having 8 nuclei embryo sac as single sac.

* variety similar to GRAMALOTE

** putative natural interspecific hybrid between P. maximum and P. Infestum.

+ we found eight nuclei embryo sacs in ovaries with more than 1 embryo-sac (28,8 nuclei embryo sacs among 249 observed sacs).

Because the pollen coming from apomict plants was efficient we studied hybrids between sexual tetraploid females and apomict males. The table III gives the number of hybrid plants which were apomict and sexual respectively

sexual female	apomict male	number of apomict hybrids	number of sexual hybrids
K 189T	267	1	1
K 189T	G 23	4	5
K 189T	G 3	14	14
S1 T	G 3	3	4
T 44T	57 (~ G3)	3	3
P ₂ (sexual hybrid)	57	40	34
apomict female	sexual male		
T 19, 36-5	P ₂	5	4

Table III : number of sexual and apomict hybrids coming from crosses between sexual and apomict tetraploid plants. Results came from embryo sac analysis.

A sexual hybrid (P₂) coming from the K 189T x G 23 cross was also used as the female parent. An apomict plant T 19, 36,5 coming from a selection (through off-type generations) for a high off-type rate was used as a female, the sexual hybrid P₂ was the male parent.

At last, a sexual hybrid offspring from the P₂ x 57 cross was freely open pollinated by its full-sibs (half of them were sexual, half of them apomict and randomly distributed). The progenies coming from this open pollination gave 12 apomict plants, 35 sexual plants (i.e. $\frac{1}{4}$, $\frac{3}{4}$).

Every result is in a good agreement with a $\frac{1}{2}$, $\frac{1}{2}$ disjunction in the offsprings of the (sexual apomict) crosses. We could interpret results coming from open pollination in the following way. Half of the pollens were issued from sexual plants and shew no disjunction, half of the pollens were issued from apomict hybrids and shew disjunction ($\frac{1}{2}$, $\frac{1}{2}$) for sexual versus apomict genetic determinisms.

It did not look like as if sexual hybrids kept a memory of its apomict origin, concerning this disjunction.

III - Variations of H.T. and S. in apomict plants.

The table I shew the homogeneous values of H.T. (between 1% and 5%) in natural apomict plants ; the table II shew S values all below 40%.

These results were non longer true when we considered either some apomict plants coming from off-types, or apomict hybrids coming from (sexual x apomict) crosses. The table IV gives various H.T. values so obtained.

The highest off-type rate was obtained when observed off-springs came from isolating plots where T 19, 36,5 was pollinated by sexual tetraploids of a quite different phenotype. We found two kinds of off types : first those we used to find from self pollination or from open pollination with the same phenotypes, second hybrid off-types. Results are given in table V.

variety	number of observed plants	H.T. %
hexaploid off-types	138	13.9
H ₁ from commonguinea		
H ₈	238	19.6
off-types from T 19		
37,1	84	4.0
35,9	98	19.0
36,5	104	44.0
36,10	90	38.0
off-types from 8,10	100	44.6
T19, 36-5 7,8	100	46.8
10,2	100	24.0
5,10	100	13.0
off-types from T19, 36-5, 8-10 and T19, 36-5, 7-8	160	40.6
apomict hybrids coming from		
K189T x G23 cross P ₃	140	29.3
P ₄	150	24.7
P ₆	206	37.1
P2x57 and K189T x 63	1966	5.8

Table IV : off-type rates coming from either apomict off-types or apomict hybrids after either self-pollination or open pollination by full sib plants.

pollinator	number of observed plants	H.T. total	off-type rate of same type plants	hybride off-type rate
K189 T	216	56.9	30.1	26.8
P 2	101	66.3	25.7	40.6
T35 T	176	61.4	37.5	23.9
S2 T	206	54.4	25.7	28.6

Table V : off-type rates of T 19,36-5 when pollinated, in isolated plots, by 4 different sexual tetraploid plants.

Thus the off-type rate was under genetic control (increasing and perpetuating through successive generations of off-types) and depended on pollinators. It was high enough (30%) in the first generation of apomict hybrids.

The S rate was studied in different off-types and hybrids. These values are given in table VI.

variety	number of observed ovaries	S %
T19, 36-5	275	77.5
apomict hybrids issued as off-types of T19,36-5 pollinated by sexual tetraploid plants		
T19, 36,5 x T35 T	30	96.7
T19, 36-5 x P2 (1)	35	74.3
- (2)	29	72.4
apomict hybrids from sexual x apomict crosses		
K 189 T x 267	14	28.6
K 189 T x G 3	224	23.2
P2 x 57 (3way hybrid)	744	16.4
(P2 x57) x(P ₂ x57)' full-sib cross sexual apomict	273	10.6

Table VI : rate of ovaries with 8 nuclei embryo sac as

The increasing of H.T. in T19, 36-5 came with an increasing of S. In hybrid off-types of T19, 36-5, S was still high and increased near 100 %. This latter plant is still a facultative apomict one but we need a numerous analysis to detect its apomixis. On the contrary S values in apomict hybrids were not higher to those of natural apomicts. It looked like if S decreased as the number of back-crossing on apomict parent (G 3 or 57) increased (last part of table VI). G 3 or 57 (Gramalote varieties) had very small s rate (table II).*

There could be some relation between H.T. and S but this could be dimed because plants with equal S gave different H.T. depending on their off-type viabilities. Apomict hybrids (because of hybridity) could express better their potentiel off-type rate which could be near S.

B - Structures of naturel populations.

The natural populations of Panicum maximum were either small isolates of some thousand square meters, or linear colonies of several kilometers along to roads and rivers, or actual large savannahs. In the marginal area of East Africa and in other African countries where Panicum could be more recently introduced, populations looked like only one clone compounded. Sometimes several quite different clones could be counted, but they were not very numerous (never more than 10). On the contrary, in the central area, a more confused variability appeared, built with numerous different, but not well distinguished, phenotypes. All, but one, of the 275 plants that we sampled in East Africa were apomict tetraploid (HT \neq 3%). The excepted plant (N° K 189) was a sexual diploid one. Thus, with the same reproductive mode quite different structures of variabilities were associated.

In order to obtain an objective, clear cut representation of these different structures, we shall exhibit different classifications of phenotypes sampled in a definite area. We used different algorithms of classification* and different series of measures (quantitative characters) and notations (qualitative characters).

* The different schemes of classification were derived from methods described in SOKAL and SNEATH (1959)'s book.

○ MARALAL

○ RUMURUTI

○ THOMSON'S FALLS

KENYA

Mt

* MGWAKAETHE

○ NAIROBI

KENYA
+ + + + +
TANZANIA

KILIMANDJARO

USAMBARA Mt

KOROGWE

* TANGA

ZANZIBAR

MOROGORO

* BAGAMOYO (T25, T26)

○ DARESSALAAM

T19

EAST AFRICA MAP

Every observation came from either vegetative multiplication or apomict seedlings of the sampled plants ; all of them were in the same environment at the same time. If we obtained the same classification of a set of plants through different algorithms and different series of observations, that meant that the observed phenotypes are well defined entities. On the contrary, if we could not have stable groups that meant that the characters could be indefinitely distributed among various phenotypes and that the associations of phenotypes were depending on recombinations of the various observed characters.

I - Homogeneity and discontinuity of the marginal populations, continuous heterogeneity of the central populations.

The case of maralal populations shew that the same structure could be read as well from a series of measures (12 quantitative characters, (fig.1) as from a series of 50 different qualitative characters (fig.2). THOMSON'S FALLS and MARALAL are two countries distant of about 200 kilometers from each other. Populations were sampled between these two points.

In MGWAKAETHE area a polymorphic population was observed. There were only about 5 well different phenotypes. One of them was a P.infestum, an other one looked like an interspecific hybrid between P.infestum and an other P.maximum phenotype (we called this last hybrid C type ; T19 coming from an other area was a C type too). The same sets of phenotypes were identified through the different classifications shown in figures 3,4 and 5.

In KOROGWE area, where we fortuitously* found out the diploid plant (N°K189), the classifications lost their well defined structures and their reliabilities (fig.6 and 7). The nodal method which ought to allow closed groups of phenotypes completely failed in showing such a structure.

II - Organization of the diploid and tetraploid variabilities in the central populations.

A more detailed prospection allowed us to study the variability of diploid plants in the central populations of KOROGWE. We did it by referring either to tetraploid plants coming from.

* We said fortuitously because nothing in its phenotype shew it was so different with its surrounding tetraploid plants.

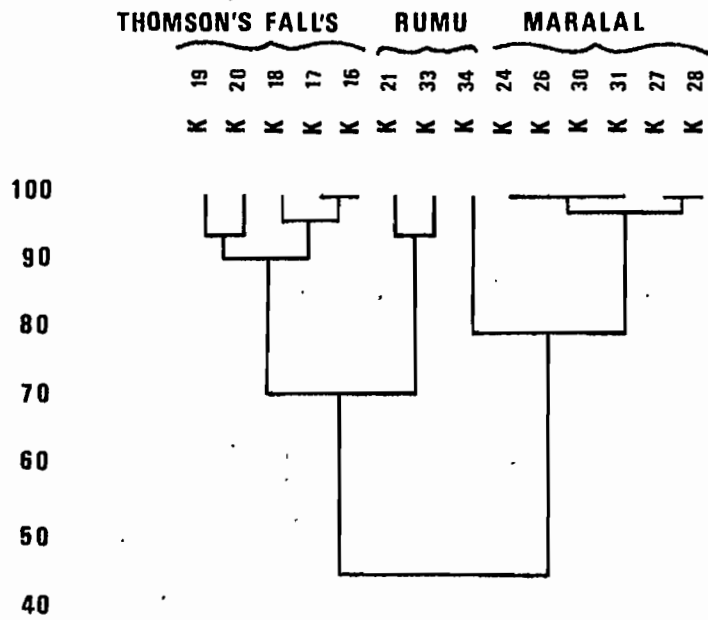


Fig.1

quantitative characters

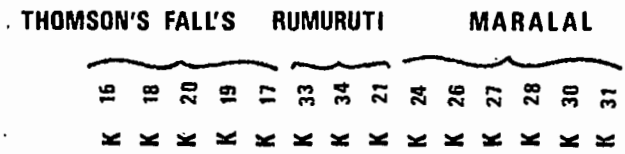


Fig.2

qualitative characters

DENDROGRAM OF THE PHENOTYPES FROM MARALAL THOMSON'S FALL'S

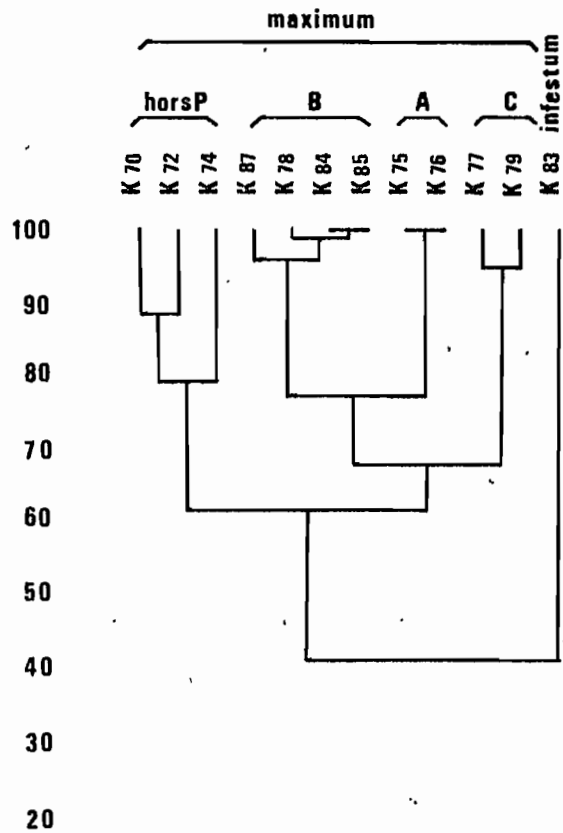


Fig. 3

Two series of quantitative characters

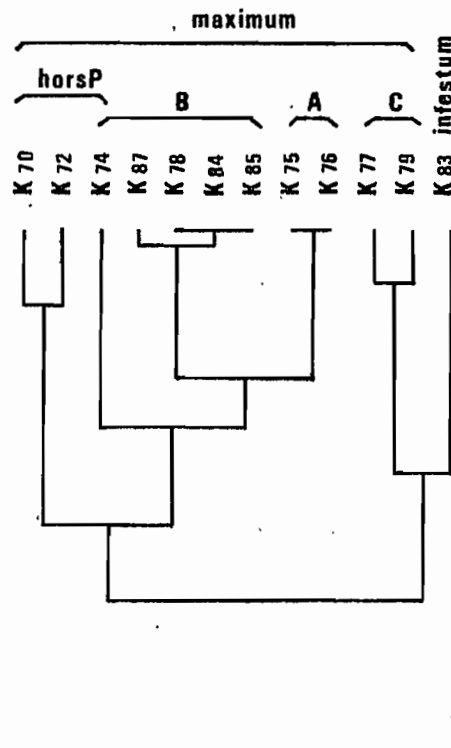


Fig. 4

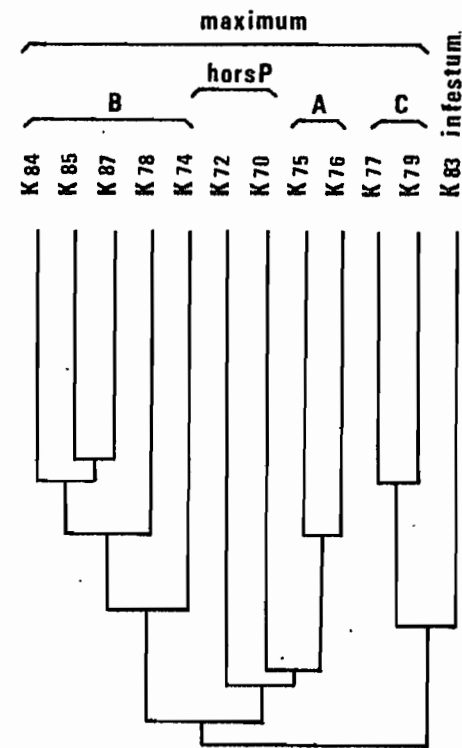


Fig. 5

qualitative characters

DENDROGRAM ANALYSIS OF THE M'GWAKAETHE POPULATION

hors P: plants used as witnesses in other comparisons. They came from populations surrounding MGWAKAETHE
 A,B,C: indices for the different categories of phenotypes



Fig. 6

Quantitative characters

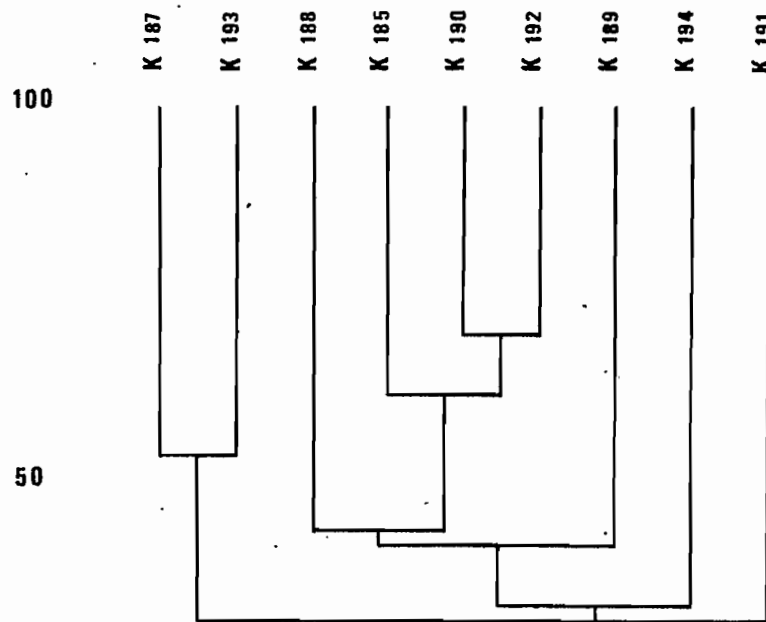


Fig. 7

Qualitative characters

KOROGWE AREA

NO CLOSED GROUP RESULTS FROM THESE CLASSIFICATIONS WHICH LOOK DIFFERENT
 THE DIPLOID K 189 WAS NOT ISOLATED

the same area or from plants situated a bit out of there. The figure N°8, using the nodal method of classification shew how were expressed the different variabilities.

Both T26 and T25 plants came from a population(BAGAMOYO) which were very far from the central area. In that population, these two very similar phenotypes were associated, although they were diploid and tetraploid respectively. The table VII gives the distances between and within groups obtained from observations of 50 different qualitative characters. In this table we arbitrarily put together(group IV)the 3 tetraploids which were sampled out of the KOROGWE area ; in fact the analysis isolated each of them.

	group I diploids coming from KOROGWE- VUGIRI	group II tetraploids coming from KOROGWE-VUGIRI	group III plants from BAGAMOYO	group IV tetraploids out of KOROGWE area but not too far
group I	0.234	0.427	0.465	0.471
group II		0.278	0.581	0.456
group III			0.125	0.453
group IV				0.400

Table VII : within and between group distances in nodal analysis of diploid and tetraploid populations from KOROGWE.

The four identified groups were approximately equidistant (fig.8). They were :

- Group I : the set of diploids from KOROGWE-VUGIRI, sampled in three different stations.
- Group II : the set of tetraploids sampled in two stations among the three where the diploids came from.
- Group III : both plants from BAGAMOYO (one diploid, one tetraploid)
- Group IV : this was not a closed group. These 3 plants came from one populations and they were distant of only a few meters from each of them, the environment seemed

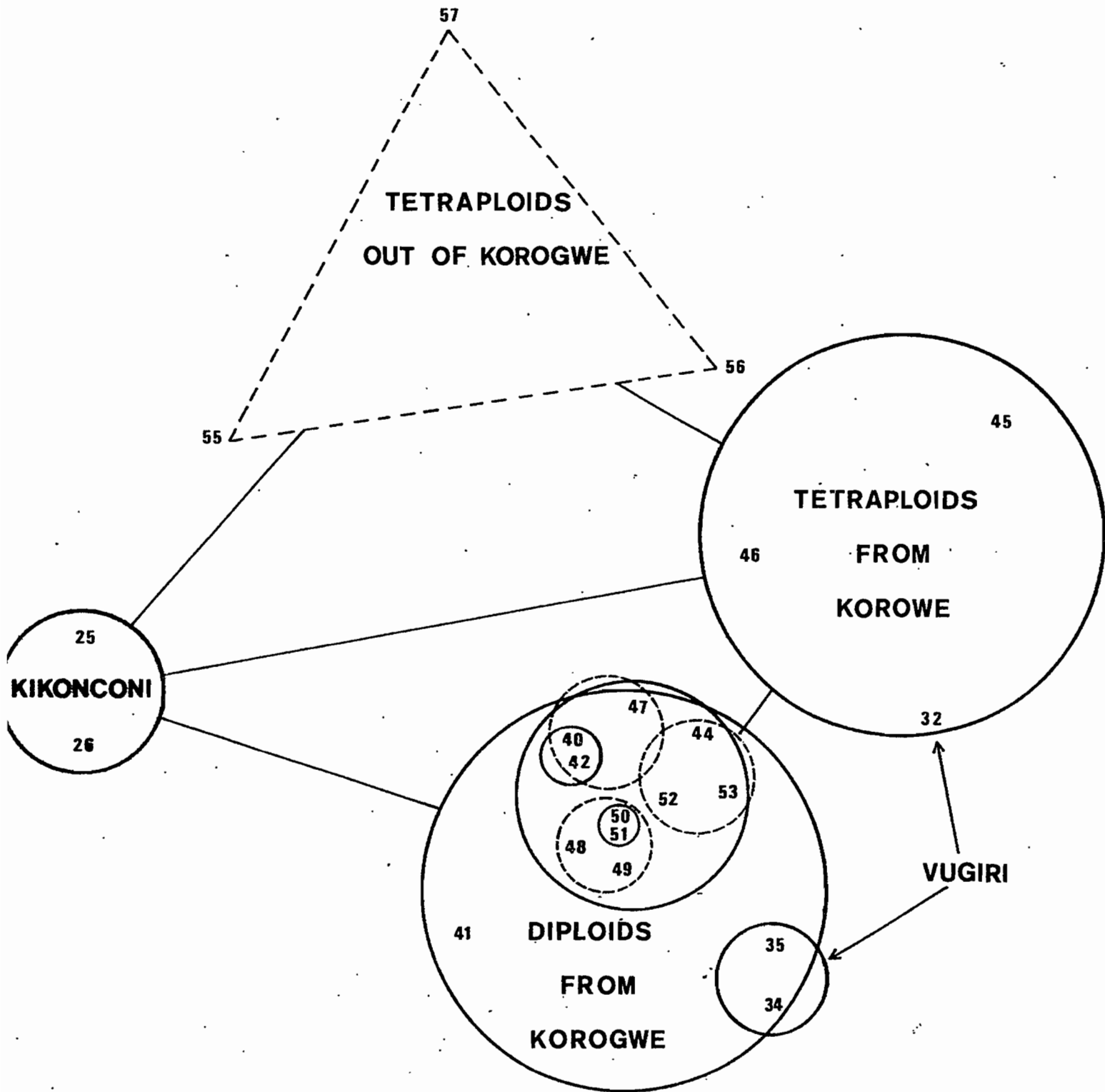


Fig. 8

NODAL ANALYSIS OF DIPLOID AND TETRAPLOID POPULATIONS FROM KOROGWE

highly homogeneous. This population was not very far from KOROGWE center (about 40 km), but it was clearly out of this area.

The within group distances gave the following evidences.

1. The group III was highly homogeneous, although there were two ploidy levels. Both plants came from a marsh, this was an exceptional environment for the P.maximum in East Africa.

2. The diploid and tetraploid coming from KOROGWE-VUGIRI (the same environments) shew a similar variability.

3. The group IV was heterogeneous, with three different phenotypes. They exhibited a large differentiation higher than those of diploids and tetraploids from KOROGWE. However the geographical area occupied by the plants in this group IV was very small and very much more homogeneous than KOROGWE-VUGIRI area.

Generally speaking, the classification of these phenotypes was well definite, in good agreement with the geographical and biological characteristics. Let us note the following facts :

1. The variability of sexual diploids was clear but maintained into a well established type.
2. The variability of apomict tetraploids from the same area was similar and of a same size.
3. The population out of the diploid area was compounded with very different plants.

The integrated variability of the diploid population was such that we should expect from a sexual population in a varied environment. The variability of the neighbor tetraploids slightly differed from that of diploids, but it kept the same structure.

On the contrary the facultative apomixis worked, out of this area, apparently without storing a memory of an ancient allogamous structure. Here the variability was built with a discrete polymorphism.

Thus we could explain that the samples coming from the neighborhood of KOROGWE were a mixture of numerous individualised phenotypes, not a simple polymorphism like those of the marginal populations. A more detailed analysis of the natural populations of P.maximum could be read in PERNES and COMBES (1970) and PERNES (1972).

The aim of the following analysis is the examination of the genetic characteristics which could allow for the similarities of the variability organisations in central populations (sexual diploid as well as apomict tetraploid).

C - Genetical analysis of sexual and apomict plants

I. The effects of tetraploidisation on phenotypes

The effect of chromosome doubling was studied by comparing the vegetative multiplications of 5 diploids to their isogenic tetraploids obtained by colchicine treatment. The table VIII gives the analysis of variance for 10 characters. Let us add the results concerning two other characters : flowering time is later in tetraploid plants, no difference for the number of tillers.

In the whole the chromosome doubling had very small effects on the phenotypes and we do not need to imagine any secondary adaptation to the environment to explain the similarities between tetraploids and diploids. A graphical representation (fig.8) by mean of principal components analysis shew the small displacements obtained with the most tetraploidisation sensitive characters.

Characters series 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 VIII : analysis of variance of the polyploidy effect and the interaction variety x polyploidy effect.

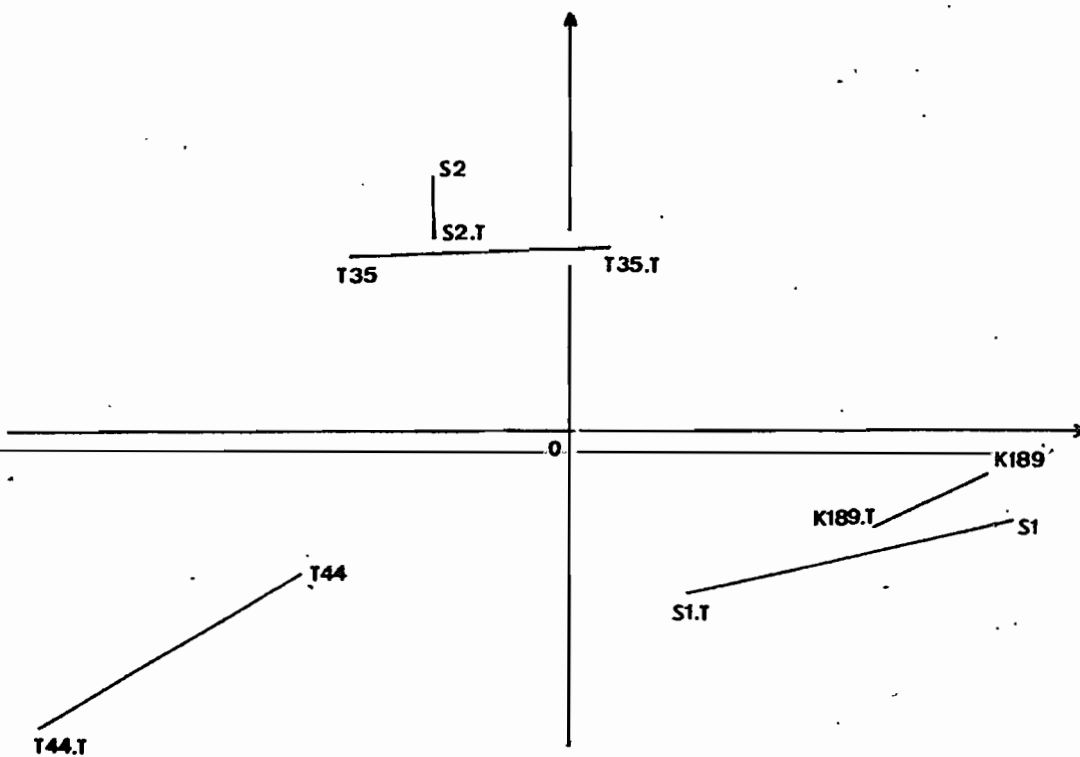


Fig.8 Two main principal components graph.

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

II - Comparison of variabilities of offsprings of sexual tetraploid plants and off-types et apomict hybrids.

The table IX shew, on the average, that the variance of an offspring of an entirely sexual plant was higher than the variance between off-types of an apomict hybrid. This latter variance was higher to that of a strictly apomict offspring (variance between non off type plants). However there could be some exceptions and it often occured that environmental variance was so large that the genetic effect did not appear. The variance between off-types hybrids coming from T19, 36,5 was particularly strong. That could be a consequence of the meeting of genetically very distant genoms.

Thus the apomict hybrids with their high off-types rates (30%) could still yield a fresh variability.

characters	mean of variances of offsprings of sexual hybrids	mean of variances between off types from apomict -hybrids	mean of variances between non off-types from apomict hybrids	mean of variances between off-types from T19, 36.5 non hybrids	hybrids
number of measured plants	300	108	380	20	20
sheath length G	30,19	20,41	10,00	31,05	68,36
inflorescence length l	82,26	41,74	38,66	72,07	204,03
Fresh matterweight M V	161,47	78,94	64,16	31,88	210,58

Table IX : average of variances between sexual and apomict plants for three characters chosen for their different degrees of sensitivity to the environment.

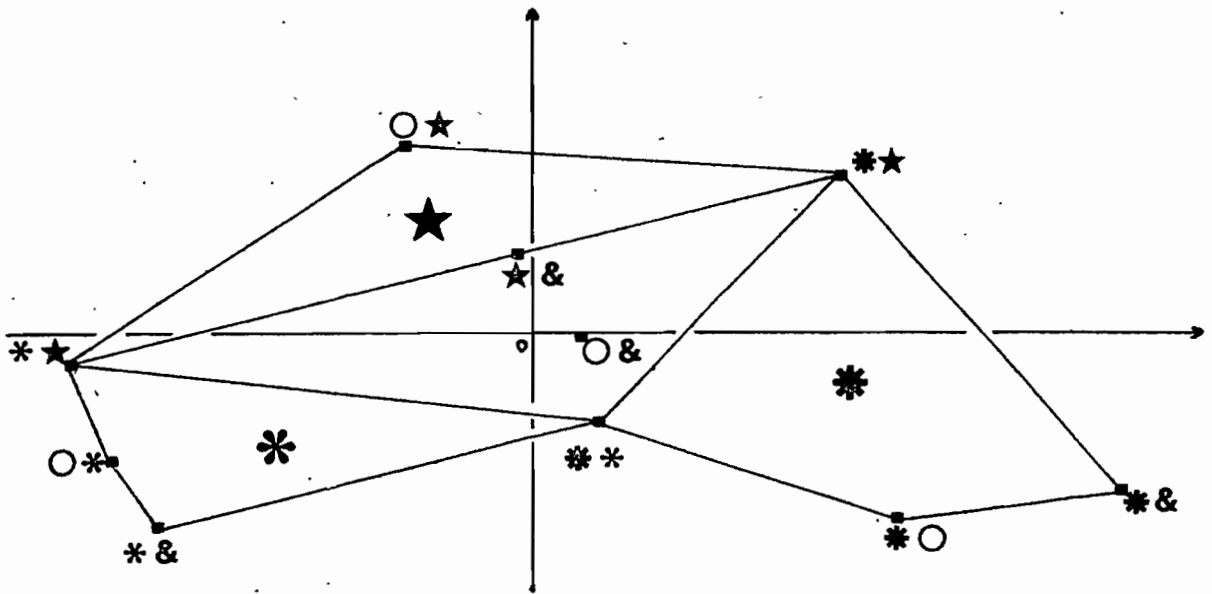


Fig.9 Two main principal components graph.

Dots representative of hybrids are two parent symbols composed

***T35 O T40 *T41 ★T44 &K189**

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

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

III - Genetic organization of diploid plants

This analysis used diallel crosses. This allowed us to measure : general and specific combining abilities for different characters, heritabilities and maternal effects. Some of these results should be compared to the genetic data obtained at the tetraploid level by the way of analysing hybrids between sexual and apomict plants. Two series of diallel crosses were observed the first one with 5 parents without reciprocal crosses and self-fertilization, the second one was a complete 4 x 4 diallel.

There was a high within-family variability, that shew a high heterozygosity of the diploid plants. In spite of this high residual variance we found strong heritabilities and high combining abilities for the following characters : number of tillers, date of heading, leaf characteristics (sheath and leaf sizes), virus sensitivity. The figure 9 shew the distribution of the hybrids in a description by mean of a principal components analysis of the between cross mean square matrix. The characters with high heritability were chosen. The following parents (T41, T35, T44) had high general combining abilities and they shifted the representative points of hybrids towards specific positions on the graph. From the fig.8 we saw that these 3 diploids were a good sample of diploid phenotypic variability. We observed maternal effects for the number of tillers and the seed germination. The sexual diploids gave results like those from an allogamous plant. The variability could be widely available by the plant breeders.

IV - Genetic analysis at the tetraploid level.

Two interesting characteristics were studied. First we compared apomict hybrids to sexual hybrids which were full sibs. This was to analyse if apomixis or sexuality was associated with a decrease of vigor. Two series of fresh weigh analysis did not show any difference.

Second, we analysed several families having the same apomict male parent and different sexual tetraploid female parent (K189T, S₁T, S₂T, T 44T and P2 a sexual hybrid). This was

to see if the meeting of sexual and apomict genoms lead to any disequilibrium or genetic anomaly. We used six randomly chosen plants in every family. The vegetative multiplication of these plants allowed a hierarchal analysis of variance of variations between and within families (table X). Variations within families are very much higher than variations between families. This demonstrated that the heterozygosity, of the parents was the major source of variability. The constant parent regressions; reckoned on family means, indicated there was however a definite between family genetic variation, with every character (table XI). The most particular family was that with P₂ female parent. Because it was a sexual hybrid between K 189 T and G 23 this fact shew the importance of the apomict G 23 which was not coming from KOROGWE. The analysis with several characters, by mean of principal components of between plants matrix put the family means nearby the mid parents.

Thus, there was neither genetic impediment nor functional anomaly when hybridizations between sexual and apomict tetraploids occured. However we did not choose phenotypes which could be to much distant from each other. But, what we wanted to tell was there was not any barrier to the gene flow which could be allowable, at the tetraploid level, to any fundamental structural particularity bound to either apomixis or sexuality.

Origin of variation	degrees of freedom	mean squares for characters				
		G	l.l.	n	li	l
between family	4	1105.0	3.987	180.75**	1688.1**	745.8*
within family	25	472.9 ⁺⁺	2.827 ⁺⁺	29.14 ⁺⁺	410.1 ⁺⁺	268.8 ⁺⁺
residual	870	15.6	0.102	0.95	20.1	11.0

* significant F 4,25 at 5%

++ significant F 25,870 at 1%

** significant F 4,25 at 1%

Table X : variations within and between families in a constant parent regression G3 apomict male parent ; K189T, S1T, S2T, P2; T 44T sexual tetraploid females. Residual variances came from vegetative multiplication of every hybrid.

Characters	Correlation coefficients	regression coefficients
G	0.985	0.37
l.l.	0.770	0.28
n	0.970	0.65
L_i	0.998	0.46
l	0.989	0.42

Table XI : correlation and regression coefficients of the constant parent regression on family means (5 degrees of freedom)

D - Discussion

Apomixis seemed a source of discontinuity in nature. The observations of marginal populations of Panicum maximum agreed with this opinion. The heredity of apomixis versus sexuality, by the very clear cut disjunctions $\frac{1}{2}$, $\frac{1}{2}$ was in good agreement too. We could admit there was a simple genetic control of the ability to give only ovaries with 8 nuclei embryo sacs as single sac. Even if we had to find other disjunction ratios by using different apomict parents we could expect they ought to be something like simple mendelian ratios in genetics of tetraploids. Such simple determinisms were reported else where in other apomict plants (BURTON and FORBES (1960), HARLAN and al.(1964), READ and BASHAW (1968), TALIAFERO and BASHAW (1966), VOIGT and BASHAW (1972)).

However this discontinuity disappeared with more detailed analysis. The sexual rate (measured either by H.T. or by S) looked variable, although results from natural populations were very regular. This sexual rate was genetically controlled but it depended also on pollinators and it could be sensitive to photoperiod (see KNOX and HESLOP-HARRISON on apomict Andropogonae). Thus the apomixis varied from quasi-absolute to values so small that a potentially apomict plant could be hardly distinguished from a sexual one through the observation of its offsprings.

The discontinuity disappeared also when we studied central populations ; we found the same variability in sexual diploid and apomict tetraploid populations. The analysis of tetraploid hybrids between sexual and apomict plants failed to give evidence of any difference of genetic organisation between sexual and apomict groups. There was not barrier to the free integration of genes coming from apomict plants into the sexual tetraploid plants. The sexual hybrids were not at disadvantage in comparison with apomict hybrids.

Thus there was not any actual break between the sexual and the apomict status ; sexuality was not incompatible with tetraploidy although every natural tetraploids were apomict.*

This biological analysis was useful to propound a plant breeding program of Panicum maximum (PERNES and al.1973). However it asked some unsolved questions. Why every natural tetraploid was apomict ? Why sexual rate of these apomict plants were so uniformly low ? How could the apomixis keep allogamous like polymorphic structure up, in central populations ?

Some tentative answers could be find by studying the evolutionary consequences of apomixis by the way of population genetics models. That was we tried to start in an associated paper (PERNES 1973).

* The contrary could be false : it could there was something wrong with the apomixis at the diploid level, every dihaploid (potentially apomict from embryo sac study) were sterile. DE WET and HARLAN found the same thing in BOTRIOCHLOA-DICHANTHUM.

BIBLIOGRAPHY

- BOGDAN (A.V.) - 1963 - A note on breeding behaviour of Panicum maximum in Kenya. Trop.Agric. 40, 313-314.
- BURTON (G.W.) & FORBES (I.) - 1960 - The genetics and manipulation of obligate apomixis in common Bahiagrass (Paspalum notatum FLUGGE), Proc.8th Intern.Grassland congress 1, 66.
- COMBES (D.) - 1972 - Mode de reproduction et polymorphisme d'un groupe agamique du genre Panicum (graminées) unpublished es-science Doctoral Thesis PARIS ORSAY (France).
- COMBES (D.), PERNES (J.) - 1970 - Variations dans les nombres chromosomiques du Panicum maximum Jacq. en relation avec le mode de reproduction. C.R.Acad.Sci.Paris, 270, 782-785.
- HARLAN (J.R.), BROOKS (M.H.), BORGAOUNKAR (D.S.) DE WET (J.M.S. - 1964 - Nature and Inheritance of apomixis in Botriochloa and Dichanthium. Bot.Gaz.125, 41.
- HERR (J.M.) - 1971 - A new clearing squash technique for the study of ovule development in angiosperm. Amer.J.Bot., vol 58 (8) : 785-790.
- JAVIER (E.Q.) - 1970 - The flowering habits and mode of reproduction of guinea grass (Panicum maximum Jacq.) GRASSL.CONG.PROC. 11, 284-289.
- KNOX R.B.), HESLOP-HARRISON (J.) - Experimental control of aposporous apomixis in a grass of the Andropogonae Bot. Notisher 116, 127-141.
- PERNES (J.) - 1972a - Organisation évolutive agamique du genre Panicum (graminées) es-sciences Doctoral thesis Paris Orsay (France) (sous presse).
- PERNES (J.) - 1973 - Population genetics models of apomixis (in preparation).

- PERNES (J.), COMBES (D.) - 1970 - Incidence des modes de reproduction sur la structure et la différenciation des populations naturelles de Panicum maximum, JACQ., en Côte d'Ivoire. Cahiers de l'O.R.S.T.O.M., 14, 13-24.
- PERNES (J.) COMBES (D.), RENE-CHAUME (R.) - 1970 - Différenciation des populations naturelles de l'espèce Panicum maximum JACQ. en Côte d'Ivoire, par acquisition de modifications non transmissibles par graines et autoentretenuës par multiplication végétative, C.R. Acad.Sc.PARIS, 270, 1992-1995.
- PERNES (J.), RENE-CHAUME (R.), RENE (J.), SAVIDAN (Y.) - 1973 - Schéma d'amélioration génétique des complexes agamiques du type Panicum (proposé aux annales de l'INRA).
- READ (J.C.), BASHAW (E.C.) - The cytology and mode of reproduction of hybrids between sexual buffel grass and apomict birdwood-grass. Agron. Abst. Madison p.19 (Abst.)
- SOKAL (R.R.) SNEATH (P.H.A.) - 1959 - Principles of numerical taxonomy, FREEMAN.
- TALIAFERRO (C.M.), BASHAW (E.C.) - 1966 - Inheritance and control of obligate apomixis in breeding buffel-grass, Pennisetum ciliare. CROP.Sci. 6, 473-476.
- VOIGT (P.W.), BASHAW (E.C.) - 1972 - Apomixis and sexuality in Eragrostis curvulae, CROP Sci. 12, 843-847.
- WARWKE (H.E.) - 1954 - Apomixis in Panicum maximum. Amer.Bot. J. 41, 5-11.