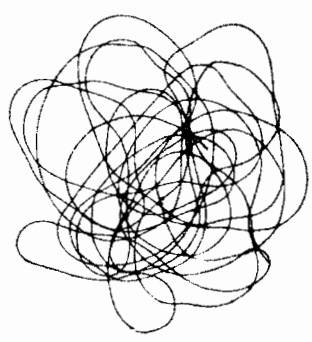


J. PERNES

**EVOLUTION IN SEXUAL  
AND ASEXUAL POPULATIONS  
THE APOMIXIS MODEL**



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Laboratoire de Génétique

EVOLUTION IN SEXUAL AND ASEXUAL POPULATIONS :  
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## Summary

Evolution in sexual and asexual populations is studied from the biologically concrete situation of apomixis. Settlement of a gene allowing the development of unreduced embryo sacs is established, when all selective pressures are missing. Sexual and absolute apomict populations are compared from studying substitutional load, time length of substitution and average load by generation. Sexuality does not appear advantageous, except at the beginning of a dominant substitution. In that case average substitution load is smaller in sexual than apomict populations. Discussion of evolutionary advantage of sexuality shows the necessity of protective barrier to **provent** invading sexual population by apomict genes. In natural populations of Panicum maximum this protective barrier could be the polyploidy level .

Evolution in sexual and asexual populations :  
the apomixis model

by J. PERNES

Several papers have been dealing with advantageous sexuality versus asexuality (R.A. FISHER (1930, 1958), MULLER (1954) J.F. CROW and L. KIMURA (1965, 1969), J.M. SMITH (1968, 1971), I. ESHEL and M.W. FELDMAN (1970), I. ESHEL (1971)). They did not acquire any complete agreement. In natural conditions, sexuality and asexuality can coexist in higher plants. It seems useful to study what happens then, from the point of view of population genetics. Our work has been stimulated by HARLAN and col's studies on apomixis in BOTRIOCHLOA-DICHANTIUM, and our personal analysis on apomict complex of MAXIMAE (Panicum maximum)

In the species Panicum maximum, some genotypes are entirely sexual, the others are facultative apomicts. Seed formation in apomict plants results from an embryo sac development without reduction and fertilization. Pollinator only stimulates the embryo development, but there is no caryomixy. Male gamete formation is always regular, every pollen is reduced and functional.

We shall demonstrate that without any selective advantage, apomixis if it is genetically determined, will rule out sexuality in a population where sexual and apomict genotypes initially coexist.

In an other paper (J. PERNES, 1970) we established some generalizations of the Hardy-Weinberg law and fundamental theorem of natural selection, when reproductive system is facultative apomixis. Evolution of apomict populations is not very different from panmictic ones, apomixis works just as a generalized linkage. In the present paper we shall continue this analysis by comparing the cost of natural selection in an absolute apomict population and a panmictic population, when identical phenotypic substitutions occur.

In Panicum maximum and Botriochloa apomixis and sexuality can occur at the tetraploid level, diploids are only sexual. To simplify the mathematical arguments we shall analyse this genetical situation at the diploid level, we think that dealing this will not weaken qualitative result of our demonstrations.

An other biological simplification is to suppose that apomixis can be the result of intervention of only one allele at a locus. Experimental data of HARLAN J.R., BROOKS M.H., BORGAONKAR D.S., DE WET J.M.J. (1964) and BURTON G.W. and FORBES I. (1960) agree with that hypothesis, but with Panicum it is certainly not true and new results on BOTRIOCHLOA show that it is not so easy (D'CRUZ R. and REDDY P.S. (1971)). The unique fact we are sure in Panicum is that we can obtain apomict hybrids by fertilizing a sexual tetraploid by and apomict tetraploid. Nevertheless we shall examine one gene models, first to analyse diffusion of an apomixis gene in a previous sexual population, second to compare substitution loads in sexual and asexual populations.

I. Substitution, without selection, of an allele which allows unreduced embryo sac development.

A. Dominant apomixis.

We consider an infinite population at one locus A. AA and Aa genotypes are facultative apomicts; let  $k$  be the reduction ratio, i. e. mother plant the phenotype of which is A gives offsprings as a result of sexual reproduction ( oosphere reduction and fertilization ) with a probability of  $k$  and offsprings by an apomict way ( noosphere reduction, no fertilization ) with a probability of  $(1-k)$ ; a a genotype is entirely sexual.

When sexual reproduction occurs,  $f$  percent oosphere are self fertilized, and  $(1-f)$  are randomly fertilized by the whole population.

Table I summarizes gamete formation of different genotypes.

Table I : gamete formation probability with (1-k) facultative apomixis and f self fertilization when sexual, dominant apomixis

| gamete<br>genotype | male gamete   |               |       | female gamete |    |               |               |
|--------------------|---------------|---------------|-------|---------------|----|---------------|---------------|
|                    | A             | a             | AA    | Aa            | aa | A             | a             |
| AA                 | 1             | 0             | (1-k) | 0             | 0  | k             | 0             |
| Aa                 | $\frac{1}{2}$ | $\frac{1}{2}$ | 0     | (1-k)         | 0  | $\frac{k}{2}$ | $\frac{k}{2}$ |
| aa                 | 0             | 1             | 0     | 0             | 0  | 0             | 1             |

Let  $P_n$ ,  $2Q_n$ ,  $R_n$  the genotype frequency of AA, Aa, aa respectively at the  $n^{\text{th}}$  generation. Frequencies at  $(n+1)^{\text{th}}$  generation are :

$$P_{n+1} = (1-k)P_n + \underbrace{kfP_n + \frac{kf}{2} Q_n}_{\text{self fertilization of AA and Aa}} + k(1-f)(P_n + Q_n)^2$$

apomixis                  self fertilization                  random pollination  
of AA and Aa

$$2Q_{n+1} = 2(1-k)Q_n + kfQ_n + k(1-f)(P_n + Q_n)(R_n + Q_n) + [k(1-f)Q_n + (1-f)R_n](P_n + Q_n)$$

$$R_{n+1} = fR_n + (1-f)(R_n + kQ_n)(R_n + Q_n).$$

A gene frequency at  $(n+1)^{\text{th}}$  generation is :

$$(1) \quad P_{n+1} + Q_{n+1} = (P_n + Q_n) \left( 1 + \frac{(1-k)(1-f)}{2} R_n \right).$$

Let us examine expression number (1). If  $k \neq 1$  and  $f \neq 1$ , A gene frequency is always increasing until  $R_n = 0$ . Apomixis eliminates sexuality.

If  $k = 1$  no apomixis, A gene frequency does not move (classical result !).

If  $k = 0$ , absolute apomixis, and  $f = 0$ ,  
 $P_{n+1} = P_n$ , AA frequency is constant, and only Aa frequency increases. Allele a does not vanish but genotype aa does.

If  $f = 1$ , self fertilization (strictly autogamous plant), apomixis cannot settle in the population. It is well know, STEBBINS (1950), that self fertilization and apomixis are incompatible; apomict ancestors are allogamous.

When apomixis is facultative, at equilibrium, population is homogeneous with genotype AA; when apomixis is absolute, and if A occurs first by mutation, at equilibrium, population is homogeneous with genotype Aa.

B. Recessive apomixis.

Preceding hypothesis concerning reproductive process are unchanged, but genotypes SS and Ss are entirely sexual, self fertilization probability is  $f$ ; ss genotype is facultative apomict, the reduction ratio of which is  $k$ .

Table II gives the gamete formation probabilities.

Table II : gamete formation probability with  $(1-k)$  facultative apomixis,  $f$  self fertization when sexual, recessive apomixis.

| gamete<br>genotype | male gamete " |               | female gamete |    |         |               |               |  |
|--------------------|---------------|---------------|---------------|----|---------|---------------|---------------|--|
|                    | S             | s             | SS            | Ss | ss      | S             | s             |  |
| SS                 | 1             | 0             | 0             | 0  | 0       | 1             | 0             |  |
| Ss                 | $\frac{1}{2}$ | $\frac{1}{2}$ | 0             | 0  | 0       | $\frac{1}{2}$ | $\frac{1}{2}$ |  |
| ss                 | 0             | 1             | 0             | 0  | $(1-k)$ |               | k             |  |

Let  $P_n$ ,  $2Q_n$ ,  $R_n$  frequencies of SS, Ss, ss genotypes respectively at the  $n^{\text{th}}$  generation. At the  $(n+1)^{\text{th}}$  generation, frequencies are :

$$P_{n+1} = f P_n + (1-f)(P_n+Q_n)^2 + \frac{f}{2} Q_n$$

self fertili-
random fertiliza-
self fertilitiza-  
zation of SS
tion
tion of Ss

$$2Q_{n+1} = fQ_n + (1-f)(P_n+Q_n)(Q_n+R_n) + (1-f)(Q_n+kR_n)(P_n+Q_n)$$

self ferti-
pollinisation of S
pollinisation of  
lization of
oosphere
s oosphere  
Ss
by S pollen
by S pollen

$$R_{n+1} = (1-k)R_n + kf R_n + \frac{f}{2} Q_n + (1-f)(Q_n+R_n)(Q_n+kR_n)$$

apomixis
self ferti-
self ferti-
pollination of s  
zation
lization
oosphere by s  
ss
Ss
pollen

S gene frequency becomes at the  $(n+1)^{\text{th}}$  generation :

$$(2) \quad P_{n+1} + Q_{n+1} = (P_n + Q_n) \left( 1 - \frac{(1-f)(1-k)}{2} R_n \right)$$

Let us examine expression number (2). If  $k \neq 1$  and  $f \neq 1$ ,  $P_n + Q_n$  always decreases, and S allele will be ruled out. At the beginning of the substitution  $R_n$  is nearly 1 in (1) expression and nearly 0 in (2) expression. Substitution begins slower in the recessive apomixis case than in the dominant apomixis case. Equilibrium is realized when the whole population is homogeneous with genotype ss. When  $f = 1$ , apomixis substitution cannot start.

### C. Additive reduction ratio modifiers.

Let us suppose the population is entirely a facultative apomict one, but it is polymorph at the modifier locus K.



Genotype  $K_1 K_1$  is a facultative apomict, with a reduction ratio of  $k - \alpha$

Genotype  $K_1 K_2$  is a facultative apomict, with a reduction ratio of  $k$

Genotype  $K_2 K_2$  is a facultative apomict with, a reduction ratio of  $k + \alpha$ .

Thus  $\alpha$  effect at the  $K$  locus is of an additive type. We suppose random pollination of oösphere when it is reduced.

Table III gives the gamete formation probabilities.

Table III : gamete formation probability with  $(1-k)$  facultative apomixis, random mating when sexual modification of reduction ratio.

| gamete<br>genotype | male gamete   |               | female gamete |           |              |               |               |  |
|--------------------|---------------|---------------|---------------|-----------|--------------|---------------|---------------|--|
|                    | $K_1$         | $K_2$         | $K_1 K_1$     | $K_1 K_2$ | $K_2 K_2$    | $K_1$         | $K_2$         |  |
| $K_1 K_1$          | 1             | 0             | $1-k+\alpha$  | 0         | 0            | $k-\alpha$    | 0             |  |
| $K_1 K_2$          | $\frac{1}{2}$ | $\frac{1}{2}$ | 0             | $1-k$     | 0            | $\frac{k}{2}$ | $\frac{k}{2}$ |  |
| $K_2 K_2$          | 0             | 1             | 0             | 0         | $1-k-\alpha$ | 0             | $k+\alpha$    |  |

Let  $P_n, 2Q_n, R_n$  be the  $n^{\text{th}}$  generation genotype frequencies of  $K_1 K_1, K_1 K_2, K_2 K_2$  respectively; at the  $(n+1)^{\text{th}}$  generation, these frequencies are :

$$P_{n+1} = 1 - (k-\alpha)P_n + k(P_n+Q_n)^2 - \alpha P_n (P_n+Q_n)$$

$$2Q_{n+1} = (1-k)Q_n + 2k(Q_n+R_n)(P_n+Q_n) + \alpha R_n(P_n+Q_n) - \alpha P_n(Q_n+R_n)$$

$$R_{n+1} = 1 - (k+\alpha)R_n + k(Q_n+R_n)^2 + \alpha R_n(Q_n+R_n)$$

$K_1$  allele frequency at the  $(n+1)^{th}$  generation is :

$$P_{n+1} = P_{n+1} + Q_{n+1} = P_n + Q_n + \frac{\alpha}{2} \left[ (P_n + Q_n)(R_n + P_n) + P_n \right]$$

$$(3) \quad P_{n+1} - P_n = \Delta P = \frac{\alpha}{2} \left[ (2 P_n + Q_n) - 2 (P_n + Q_n)^2 \right].$$

Let us examine expression number (3).

Suppose realized the panmictic equilibrium frequencies for  $P_n$ ,  $Q_n$  and  $R_n$ , let

$$P_n = p^2$$

$$2Q_n = 2pq$$

$$R_n = q^2,$$

then

$$\Delta P = \frac{\alpha}{2} pq,$$

always positive until  $q = 0$ . With the panmictic genotype frequencies the highest reduction rate allele ( $K_2$ ) vanishes. If panmictic equilibrium genotype frequencies are not realized, let

$$P_n = \theta_{11;n} p_n^2, \quad Q_n = \theta_{12;n} p_n q_n.$$

$\theta_{ij;n}$  is non panmictic equilibrium correction index for the  $K_i K_j$  genotype frequency at the  $n^{th}$  generation. (3) expression becomes

$$\Delta P = \frac{\alpha}{2} p \left[ 2p(\theta_{11}-1) + \theta_{12} q \right].$$

If  $\frac{\theta_{11}-1}{\theta_{12}} > \frac{q}{2p}$ ,  $p$  decreases. In PERNES (1970) we showed

that in facultative apomixis Hardy-Weinberg law is asymptotically true, thus decreasing  $p$  can be transitory. After a first decrease,  $p$  increases when every  $\theta_{ij}$  comes nearer 1. Hence we can conclude that  $K_2$  allele will ultimately disappear.

Thus we can say that when there is no selective pressure, sexuality will disappear always, or be reduced. Apomixis, by itself, eliminates/<sup>sexuality</sup>. In natural populations we never find sexual tetraploid even near natural sexual diploid populations. From some genotypes we succeed in selecting artificially an increase of reduction ratio; thus there was a potential variability in the natural population, but natural populations reduction ratio was maintained at its lowest value. Therefore there is no natural tendency to impose sexuality when it can be, and our models agree with that, there is no spontaneous advantage to sexuality. To rule out apomixis one must give a selective advantage to sexuality, but how can this be accomplished. This does not in fact result from an analysis of selective response in facultative apomict population we studied in PERNES (1970). We shall try to solve this problem by studying some particular cases of substitution load in absolute apomict and panmictic populations.

## II. Substitution loads in apomict and panmictic populations.

Substitutions of advantageous phenotypes occur by gene substitution when population is panmictic and by straight phenotypic substitution if absolute apomict. Comparison must be done at the level of phenotypic frequencies. We shall speak of equivalent gene frequencies with apomict populations, that is to say gene frequencies which should account of equal observed phenotypic frequencies in a panmictic population but these are not true gene frequencies.

We intend to estimate first, total substitution loads for a given phenotypic substitution, second the time length which is necessary to achieve a particular change of phenotypic frequencies, and third by mean of the ratio  $\frac{\text{total substitution load}}{\text{time length}}$ , the average substitution load in a generation. This last expression will be a good measure for mean decrease of reproductive value which is imposed, at every generation, to a population which undertakes the phenotypic substitution.

Two situations will be analysed, first the advantageous phenotype under the control of a dominant allele, second the advantageous phenotype under the control of a recessive allele.

A. Dominant phenotype advantageous.

Starting frequencies are given in table IV.

Table IV : initial phenotype frequencies, and selective values, for the dominant case.

| genotype | phenotype | starting phenotypic frequencies | genotype frequencies           | selective values |
|----------|-----------|---------------------------------|--------------------------------|------------------|
| AA       | A         | P <sub>0</sub>                  | p <sub>0</sub> <sup>2</sup>    | 1 + s            |
| Aa       | A         |                                 | 2p <sub>0</sub> q <sub>0</sub> | 1 + s            |
| aa       | a         | 1-P <sub>0</sub>                | q <sub>0</sub> <sup>2</sup>    | 1                |

When absolute apomixis, phenotype frequencies at the n<sup>th</sup> generations are given by :

$$\frac{P_n}{1-P_n} = (1+s)^n \frac{P_0}{1-P_0},$$

and if n<sub>A</sub> is the number of generations necessary to go from P<sub>0</sub> to P<sub>n</sub>,

$$n_A = \frac{1}{\text{Log}(1+s)} \left( \text{Log} \frac{P_n}{1-P_n} - \text{Log} \frac{P_0}{1-P_0} \right)$$

Let P<sub>0</sub> = 1 - q<sub>0</sub><sup>2</sup> = p<sub>0</sub>(1+q<sub>0</sub>) and P<sub>n</sub> = p<sub>n</sub>(1+q<sub>n</sub>) the measure by panmictic equivalent gene frequencies, we can write

$$(4) \quad n_A = \frac{1}{\text{Log}(1+s)} \left[ \text{Log} \frac{P_n}{(1-P_n)^2} - \text{Log} \frac{P_0}{(1-p_0)^2} + \text{Log} \frac{2-P_n}{2-p_0} \right]$$

When panmixis, evolution of gene frequencies are obtained by classical way (EWENS, 1968, for instance) :

$$p_1 - p_0 = \Delta p \simeq sp_0 q_0^2, \text{ and } n_p \text{ is :}$$

$$(5) \quad n_p = \frac{1}{s} \left[ \text{Log} \frac{p_n}{p_0} - \text{Log} \frac{1-p_n}{1-p_0} + \frac{1}{2} \left( \frac{1}{1-p_n} - \frac{1}{1-p_0} \right) \right]$$

Comparing  $n_A$  and  $n_p$ , when  $s$  small ( $\text{Log}(1+s) \simeq s$ ),

$$(6) \quad n_p - n_A = \frac{1}{s} \left[ \frac{q_0 - q_n}{2q_n q_0} + \text{Log} \frac{q_n}{1+q_n} - \text{Log} \frac{q_0}{1+q_0} \right]$$

$n_p > n_A$ , substitution is very much slower in panmixis than in apomixis; a allele can be stored in apomixis not in panmixis. A numerical example gives : with  $s = 10^{-3}$ ,  $p_0 = 10^{-1}$ ,  $p_n = 1-10^{-1}$ ,  $n_p - n_A \simeq 2,85.10^3$  generations and  $n_A \simeq 6,93.10^3$ .

Let us reckon now substitution loads.

When absolute apomixis, continuous time approximation gives the following expression for time variation of phenotypic frequencies :

$$\frac{dP}{dt} = sP(1-P).$$

In time interval  $(t, t + dt)$ , differential genetic deaths of [a] is :

$$(1-P)s dt,$$

and the total load, from  $P_0$  to  $P_n$  is :

$$L_A(P_0, P_n) = \int_0^n [1-P(t)] s dt$$

$$L_A(P_0, P_n) = \int_{P_0}^{P_n} \frac{dP}{P}$$

$$L_A(P_0, P_n) = \text{Log} P_n - \text{Log} P_0.$$

By using equivalent gene frequencies

$$(7) \quad L_A (P_o, P_n) = \text{Log} \frac{P_n}{P_o} + \text{Log} \frac{2 - P_n}{2 - P_o} .$$

When panmixis,

$$\frac{dp}{dt} = spq^2, \text{ and (EWENS (1968),}$$

$$(8) \quad L_p (p_o, p_n) = \text{Log} p_n - \text{Log} p_o$$

When  $p_n = 1$  and  $p_o$  small  $L_p - L_A \simeq \text{Log} 2$ . Substitutional load is smaller in apomixis than panmixis. The preceding numerical example gives

$$L_A = 1,52$$

$$L_p = 2,20 .$$

The  $\frac{L_A}{n_A}$  and  $\frac{L_p}{n_p}$  ratios are very similar,  $\frac{L_A}{n_A} \simeq 2,20 \cdot 10^{-4}$ ,

$$\frac{L_p}{n_p} = 2,25 \cdot 10^{-4} .$$

Let us compare now expressions for  $L'_A = \frac{L_A}{n_A}$  and

$L'_p = \frac{L_p}{n_p}$ . By using expressions (4) and (7), and (5) and (8)

respectively,

$$n_A = \frac{1}{s} (L_A - 2 \text{Log} \frac{1 - P_n}{1 - P_o})$$

$$n_p = \frac{1}{s} \left( L_p - \text{Log} \frac{1 - P_n}{1 - P_o} + \frac{1}{2} \frac{P_n - P_o}{(1 - P_n)(1 - P_o)} \right) ;$$

then

$$L'_A = \frac{L_A}{n_A} = \frac{s L_A}{L_A - 2 \text{Log} \frac{1 - P_n}{1 - P_o}} ,$$

and 
$$L'_p = \frac{-L_p}{n_p} = \frac{sL_p}{L_p - \text{Log} \frac{1-p_n}{1-p_0} + \frac{1}{2} \frac{p_n-p_0}{(1-p_n)(1-p_0)}}$$

Therefore,

(9) 
$$L'_p - L'_A = ks,$$

where 
$$k = \frac{1}{1 - \frac{2}{L_A} \log \frac{1-p_n}{1-p_0}} - \frac{1}{1 - \frac{1}{L_p} \text{Log} \frac{1-p_n}{1-p_0} + \frac{1}{2L_p} \frac{p_n-p_0}{(1-p_n)(1-p_0)}}$$

$$k = \frac{N}{C}, \text{ where } C \text{ is always } > 0 \text{ and}$$

$$N = \left[ \frac{1}{L_p} - \frac{1}{L_A} \right] \text{Log} \frac{1-p_n}{1-p_0} - \frac{1}{L_A} \text{Log} \frac{1-p_n}{1-p_0} - \frac{1}{2L_p} \frac{p_n-p_0}{(1-p_n)(1-p_0)}.$$

We are interested in knowing if N (and k), is positive or negative.

1. From  $p_0$  fixed, when  $p_n \rightarrow 1$ ,  $N \rightarrow -\infty$  with  $\frac{1}{1-p_n}$  and  $C \rightarrow +\infty$  with  $\frac{1}{1-p_n} \text{Log} (1-p_n)$ . Thus  $L'_p - L'_A$  vanishes when fixation is attained; on the overall substitution  $L'_p$  is slightly smaller than  $L'_A$ .

the

2. At/beginning of the substitution, when  $p_0$  and  $p_n$  are small and not very different, let  $p_n = \alpha p_0$  and  $= 1 + \epsilon$ . Then,

from (8) 
$$L_p = \text{Log} \frac{p_n}{p_0} \sim \epsilon$$
 and from (7)

$$L_A = \text{Log} \frac{p_n}{p_0} + \text{Log} \frac{2-p_n}{2-p_0} \sim \epsilon.$$

from (5) ,  $n_p \sim \frac{1}{s} (\xi + \frac{1}{2} p_0)$  and from (4)  $n_A \sim \frac{1}{s}$  .

Then,

$$L'_A \sim s$$

$$L'_p \sim \frac{2s}{2 - p_0}$$

$$(10) \quad L'_p - L'_A \sim - \frac{sp_0}{2 - p_0} \sim - \frac{1}{2} p_0 s.$$

At the beginning of the substitution the average substitution load by generation is smaller in panmixis than in apomixis.

We have to conclude that substitution is quicker and globally less costly in apomixis than panmixis. Loads per generation are quite similar, but starting a substitution is less impeding with panmictic populations.

#### B. Recessive phenotype advantageous.

In the same way, starting from table V characteristics, we obtain the following results.

Table V : initial phenotype and genotype frequencies, and selective values for the recessive case.

| genotype | Phenotype | phenotypic frequency | genotypic frequency | selective value |
|----------|-----------|----------------------|---------------------|-----------------|
| AA       | A         | } $1 - P_0$          | $q_0^2$             | 1               |
| Aa       | A         |                      | $2p_0q_0$           | 1               |
| aa       | a         | $P_0$                | $p_0^2$             | $1 + s$         |



a. time length substitution.

With apomixis, it is exactly the same result, after modifying notation :

$$(11) \quad n_A \simeq 2 \operatorname{Log} \frac{p_n}{p_o} - \operatorname{Log} \frac{1-p_n}{1-p_o} - \operatorname{Log} \frac{1+p_n}{1+p_o}, \text{ when } s \text{ small.}$$

With panmixis, classical result (EWENS 1968) gives

$$(12) \quad n_p = \frac{1}{s} \left[ \operatorname{Log} \frac{p_n}{p_o} - \operatorname{Log} \frac{1-p_n}{1-p_o} - \left( \frac{1}{p_n} - \frac{1}{p_o} \right) \right].$$

Comparing  $n_A$  and  $n_p$  gives, when  $s$  small,

$$(13) \quad n_p - n_A \simeq \frac{1}{s} \left[ \operatorname{Log} \frac{p_o(1+p_o)}{p_n(1+p_n)} + \frac{p_n - p_o}{p_o p_n} \right].$$

Expression (13) is always positive. Time length substitution is always higher with panmixis. For a complete substitution,  $p_n \rightarrow 1$ , and  $p_o$  small enough to confound  $\operatorname{Log}(1+p_o)$  with  $p_o$ ,

$$n_p - n_A \simeq \frac{1}{s} \left( \frac{1}{p_o} + p_o^{-1} + \operatorname{Log} \frac{p_o}{2} \right),$$

that is

$$(14) \quad n_p - n_A \simeq \frac{1}{p_o s}.$$

The smaller are the values  $p_o$  and  $s$ , the higher is  $n_p - n_A$ . A numerical example, with the same value as mentioned above ( $s = 10^{-3}$ ;  $p_o = 0,10$ ;  $p_n = 0,90$ ) gives  $n_p - n_A \simeq 6,16 \cdot 10^3$ ,  $n_A \simeq 5,05 \cdot 10^3$  generations.

b. substitutional load .

After modifying notations, the result of part A becomes

$$(15) \quad L_A (P_o, P_n) = 2 (\text{Log } P_n - \text{Log } P_o) .$$

If substitution is achieved,  $P_n = p_n = 1$ ,

$$L_A (P_o, 1) = -2 \text{Log } p_o$$

With panmixis, classical result (EWENS, 1968) gives

$$(16) \quad L_p (p_o, p_n) = (\text{Log } p_n - \text{Log } p_o) - \frac{1}{p_n} + \frac{1}{p_o}$$

When substitution is achieved,

$$L_p (p_o, 1) = \frac{1}{p_o} - \text{Log } p_o .$$

Comparing (15) and (16) , we find

$$L_p - L_A = \frac{P_n - P_o}{P_o P_n} + \text{Log } \frac{P_o}{P_n} .$$

When  $p_n \rightarrow 1$  ,

$$L_p - L_A = \frac{1}{p_o} - p_o + \text{Log } p_o ;$$

if  $p_o$  is small,

$$L_p - L_A \approx \frac{1}{p_o} .$$

The preceding numerical example gives :

$$L_A = 4,4$$

$$L_p = 11,1$$

$$\frac{L_A}{n_A} \approx 8,8 \cdot 10^{-4}$$

$$\frac{L_p}{n_p} \approx 10,0 \cdot 10^{-4} .$$

c. average substitution load .

From (11) and (15) expression and (12) and (16) respectively,

$$L_A = \frac{L_A}{n_A} = \frac{sL_A}{L_A - \text{Log} \frac{1-p_n}{1-p_o}}$$

$$L'_p = \frac{L_p}{n_p} = \frac{sL_p}{L_p - \text{Log} \frac{1-p_n}{1-p_o}} ,$$

then

$$L'_p - L'_A = s \left[ \frac{1}{1 - \frac{1}{L_p} \text{Log} \frac{1-p_n}{1-p_o}} - \frac{1}{1 - \frac{1}{L_A} \text{Log} \frac{1-p_n}{1-p_o}} \right]$$

$$L'_p - L'_A = ks .$$

We are interested in the sign  $k$  , when  $s$  is small versus 1.

$$k = \frac{N}{C} , \text{ with } C > 0 \text{ and}$$

$$N = \left[ \frac{1}{L_p} - \frac{1}{L_A} \right] \text{Log} \frac{1-p_n}{1-p_o} - \frac{1}{L_A} \text{Log} \frac{1+p_n}{1+p_o} .$$

-  $p_o$  fixed and  $p_n \rightarrow 1$ ,  $N > 0$  average substitutional load is higher in panmixis

-  $p_n$  fixed and  $p_o \rightarrow 0$ ,  $N \rightarrow 0$  ; there is no difference for the average reckoned all over the whole substitution range

-  $p_n$  and  $p_o$  small and not very different, let  $p_n = \alpha p_o$  ,  $\alpha = 1 + \epsilon$  . We find

$$L'_p - L'_A \approx - p_o^2 s .$$

Recessive case initial economy of genetic death of panmixis is less pronounced than dominant case. At the end of the substitution, apomixis is less costly by generation. Qualitative conclusions are comparable with dominant situation: apomict substitution is quicker than panmictic one, its total load is lighter, and there is no excess average load substitution by generation.

### III. Discussion.

J.M. SMITH (1966) gave some counter example to the analysis of CROW and KIMURA (1965), which showed that the speed of evolution is not always high in sexual versus asexual populations. Here,

we show that there is no advantage of sexuality from the point of view of substitution load. When selective pressures are missing, apomixis rules out sexuality. All these results are quite paradoxal because no doubt sexuality seems an evolutionary advantage.

All arguments have been focussed on substitution efficiency and the speed of evolution, and that was probably a trap. Sexual advantage is not immediate, it appears first in ensuring perennality to its populations. In fact, natural populations are submitted to variable environments. Environments undertake two kinds of variations: determinist and random. Sexual population responses are slow and, by generation, less costly at the beginning of substitutions. Thus there is a more important delay in sexual response to variation than in apomictic response. Apomict populations waste their reproductive value by following randomly fluctuating environments, sexual populations do not so much. Consequently, with an equal decrease of reproductive capacity, sexual population can bear more mutation load or can pay its population homeostasis by accepting some segregational load. Thus in this respect we agree with ESHEL and FELDMANN (1970), "the chief evolutionary advantage of a sexual (and, here, diploid) system is not to ensure the population a faster rate of adaptation (as is often believed) but rather, quite the opposite, to curb too rapid genetic response to irregular and temporal environmental changes".

SMITH J.M. (1970) reminds us the long term advantage of sexuality which is the ability of uniting different evolutionary history of populations which met fortuitously each other. Then new gametic types can be built and stabilized in new "linkats" (DEMARLY 1972).

These interpretations do not show any immediate protection of sexuality, and our first analysis demonstrates that there is no spontaneous protective barrier against a genetically determined apomixis. So, must sexuality disappear? Natural populations of Panicum maximum are tetraploid and apomicts, except very rare diploid which are sexual (COMBES and PERNES (1970)). However we can produce (by colchicine treatments for instance) sexual tetraploid. So, sexual tetraploid are biologically possible, but they do not maintain in evolution. We can select some higher sexual rates from off-type plants, offsprings of facultative apomict, but in natural conditions, sexual rate is always at its lower level.

The biological device to protect sexuality seems to induce sterility in diploid plants when they are potentialy (genotypically?) apomicts. Every dihaploid Panicum obtained from tetraploid apomict plants were sterile when they showed unreduced embryo sac. This system explains the actual observations of natural partitioning sexuality and apomixis into two polyploidy levels. But this does not explain how sexuality succeeds first.

An explanation comes perhaps from the following point of view on sexuality, which is a little out of scope of the present paper. According to THOM, R. (1972) the sexual advantage comes from meiosis which allows for "morphogenesis sleep". Meiosis and gamet meeting can be the conditions of cleaning environmental perturbations to begin again a fresh and complete morphogenesis. We can find the same idea in DEMARLY (1972), who thinks that union of genotypically different gamets is needed to avoid complete repression of genes; inbreeding effect could occur from partial repression because kinship of uniting gamets. We have no prove that apomixis which occurs in the same cellular environment than sexuality cannot afford the same "morphogenesis sleep". However, natural apomict populations can adapt precisely and quickly to their environments, and good memory of this adaptation is stored by apomict seeds (J. PERNES and col. 1970). This memory can be afforded by spontaneous gene mutations, but it is not impossible that this can be footprints of morphogenetic differentiations which have not been deleted in apomict seeds because meiosis was missing.

## BIBLIOGRAPHY

- BURTON G.W. & FORBES I. -(1960). The genetics and manipulation of obligate apomixis in common Bahiagrass (Paspalum notatum FLUGGE), Proc. 8<sup>th</sup> Intern. Grassland congress 1, 66.
- COMBES D. & PERNES J. (1970). Variations dans les nombres chromosomiques de Panicum maximum en relation avec le mode de reproduction. C.R. Acad. Sci. PARIS, 270, 782
- CROW J.F. & KIMURA M. (1965). Evolution in sexual and asexual populations. Amer. Nat. 99, 439.
- CROW J.F. & KIMURA M. (1969). Evolution in sexual and asexual populations, a Reply Amer. Nat. 103, 89.
- D'CRUZ R. & REDDY P.S. (1971). Inheritance of apomixis in Dichanthium. Ind. J. of. Gen. and Plant Breeding 31, 3, 451.
- DEMARLY Y. (1972). Regulation et hétérosis. Ann. Am. Plantes.
- ESHEL I. (1971). On evolution in a Population with an Infinite number of Types. Theor. Pop. Biol., 2, 2, 209.
- ESHEL I. & FELDMANN M.F. . On the evolutionary effect of recombination. Theor. Pop. Biol., 1, 88 .
- EWENS W.J. (1968). Population Genetics, Methuen, London.
- FISHER R.A. (1930, 1958). The Genetical Theory of Natural Selection, DOVER, LONDON.
- 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.
- MULLER H.J. (1964). The relation of recombination to mutational advance. Mutation research 1, 2.

- PERNES J. (1970). Etude du mode de reproduction: apomixis facultative du point de vue de la génétique des populations. *Travaux et Documents ORSTOM*, 66 p. PARIS.
- PERNES J., COMBES D., RENE-CHAUME R. (1970). Differentiation des populations naturelles de l'espèce Panicum maximum Jacq. en Côte d'Ivoire, par acquisition de modifications non transmissibles par graines et autoentretenues par multiplication végétative. *C.R. Acad. Sc. Paris*, 270, 1992.
- SMITH J.M. (1968). Evolution in sexual and asexual populations. *Amer. Nat.*, 102, 469.
- SMITH J.M. (1971). What use is sex ? *J. Theor. Biol.* 30, 2, 319.
- STEBBINS G.L. (1950). Variation and evolution in Plants, COLUMBIA University Press, 643 p.
- THOM R. (1972). Statilité structurelle et morphogénèse, 362 p., EDISCIENCE, PARIS.