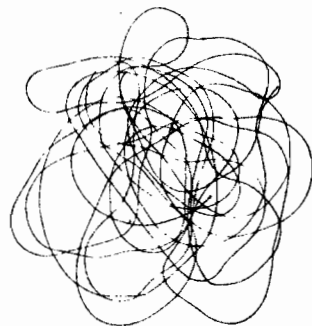


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POPULATION GENETICS MODELS OF APOMIXIS



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Summary

Some population genetics models are analysed to explain how a genetically controlled apomixis could be spread into sexual populations. Genetic structures of facultative and absolute apomict populations are described, and some mechanisms explaining stable polymorphisms are suggested.

These results are parallelized with the observed results elsewhere reported.

populations variabilities are analogous to those we should expect from allogamous populations. This was so clear cut that these populations helped us to find out stations with sexual diploid plants. Could population models explain that facultative apomixis maintained an allogamous type of variability ? Could absolute apomixis explain stable simple polymorphisms ?

We expect that the analysis of these various situations can lead to a comparative study of evolutionary characteristics of sexuality and apomixis.

We shall analyse successively :

I - Replacement of sexuality by apomixis

A. Internal evolution of populations

- A.1. Substitution without selection of an allele which allows unreduced embryo sac development.
- A.2. Additive reduction ratio modifiers
- A.3. Absolute apomixis under dominant allele control, apomixis is selected against

B. Group selection and adaptive values of the apomict process.

- B.1. Substitution loads in apomict and panmictic populations.
- B.2. Extinction function in sexual and apomict mixed populations.

II. Polymorphisms with apomict reproduction

A. Competition and absolute apomixis

B. Population structures with facultative apomixis

HAROHY-WEINBERG law and variations of gene frequencies under selection.

Thus α 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 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	0	0	$k-\alpha$	0	0
$K_1 K_2$	$\frac{1}{2}$	$\frac{1}{2}$	0	$1-k$	0	0	0	$\frac{k}{2}$	$\frac{k}{2}$	0
$K_2 K_2$	0	1	0	0	$1-k-\alpha$	0	0	0	0	$k + \alpha$

Let P_n , $2Q_n$, R_n be the n^{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 $(n+1)^{\text{th}}$ generation is :

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

$$(3) \quad p_{n+1} - p_n = \Delta p = \frac{\alpha}{2} [(2P_n+Q_n) - 2(P_n + Q_n)^2]$$

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

$$P_n = \theta_{11,n} p^2, \quad Q_n = \theta_{12,n} p q.$$

$\theta_{ij,n}$ is a non panmictic equilibrium correction index for the $K_i K_j$ genotype frequency at the n^{th} generation.

(3) expression becomes

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

If $\frac{1-\theta_{11}}{\theta_{12}} > \frac{q}{2p}$, Δp decreases. In PERNES (1970) we showed that in facultative apomixis Hardy-Weinberg law is asymptotically true, thus ^{the} decreasing ^{of} p can be transitory. After a first decrease, p increases when every θ_{ij} comes nearer 1. Hence we can conclude that K_2 allele will ultimately disappear. Thus the sexual rate of apomixis will always decrease.

A.3. Absolute apomixis under dominant allele control, apomixis is selected against.

Preceding results dealt with no sexual selective advantage, that can be the case at the tetraploid level. Here we shall give a disadvantage to apomixis because of dihaploidy (for instance)

Let us consider the following quite particular situation (Table III) this is the most favorable situa-

TABLE III

Fitnesses and genotype frequencies when absolute apomixis is dominant

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

Table IV

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

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

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

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

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

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

B. Group selection and adaptive values of apomict process.

B.1. 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 panmictif 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 is under the control of a dominant allele, second the advantageous phenotype is under the control of a recessive allele.

Dominant phenotype advantageous

Starting frequencies are given in table V.

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

genotype	phenotype	starting phenotypic frequencies	genotype frequencies	selective values
AA	A	P ₀	p ₀ ²	1 + s
Aa	A		2p ₀ q ₀	1 + s
aa	a	1 - P ₀	q ₀ ²	1

When absolute apomixis, phenotype frequencies at the nth generations are given by :

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

and if n_A is the number of generations necessary to go from P₀ to P_n,

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

Let P₀ = 1 - q₀² = p₀ (1 + q₀) and P_n = p_n (1 + q_n) the measure by panmictic equivalent gene frequencies, we can write

$$(6) \quad n_A = \frac{1}{\text{Log}(1+s)} \left(\text{Log} \frac{P_n}{(1-p_n)^2} - \text{Log} \frac{P_0}{(1-p_0)^2} + \text{Log} \frac{2-p_n}{2-p_0} \right)$$

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

$$p_1 - p_0 = \Delta p \approx sp_0q_0^2, \text{ and } n_p \text{ is :}$$

$$(7) n_p = \frac{1}{s} \left[\text{Log} \frac{p_n}{p_0} - \text{Log} \frac{1-p_n}{1-p_0} + \frac{1}{2} \left(\frac{1}{1-p_n} - \frac{1}{1-p_0} \right) \right]$$

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

$$(8) n_p - n_A = \frac{1}{s} \left[\frac{q_0 - q_n}{2q_n q_0} + \text{Log} \frac{q_n}{1+q_n} - \text{Log} \frac{q_0}{1+q_0} \right]$$

Thus $n_p > n_A$, 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 $s : 10^{-3}$, $p_0 = 10^{-1}$, $p_n = 1-10^{-1}$, $n_p - n_A \approx 2.85 \cdot 10^3$ generations and $n_A \approx 6.93 \cdot 10^3$.

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 :

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

By using equivalent gene frequencies

$$(9) L_A (P_0, P_n) = \text{Log} \frac{p_n}{p_0} + \text{Log} \frac{2-p_n}{2-p_0} .$$

When panmixis,

$$(10) L_p (p_0, p_n) = \text{Log} p_n - \text{Log} p_0 \text{ EWENS (1968)}$$

When $p_n = 1$ and p_0 small, $L_p - L_A \approx \text{Log} 2$. Substitutional load is smaller in apomixis than in 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, $\frac{L_A}{n_A} \approx 2.20 \cdot 10^{-4}$
 $\frac{L_p}{n_p} = 2.25 \cdot 10^{-4}$

Let us compare now expressions for $L'_A = \frac{L_A}{n_A}$ and $L'_p = \frac{L_p}{n_p}$ after calculations, we find

$$(11) \quad L'_p - L'_A = ks,$$

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

Let us write:

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

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

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 $\frac{1}{1-p_n} \log(1-p_n)$. Thus $L'_p - L'_A$ vanishes when fixation is attained; on the overall substitution L'_p is slightly smaller than L'_A .

2. At the beginning of the substitution, when p_0 and p_n are small and not very different, let

$$p_n = (1 + \epsilon) p_0.$$

$$\text{Then, } L_p = \log \frac{p_n}{p_0} \sim \epsilon \text{ and}$$

$$L_A = \log \frac{p_n}{p_0} + \log \frac{2-p_n}{2-p_0} \sim \epsilon$$

$$n_p \sim \frac{\epsilon}{s} \left(1 + \frac{1}{2} p_0 \right) \text{ and } n_A \sim \frac{1}{s}.$$

Then,

$$L'_A \approx s$$

$$L'_p \approx \frac{2s}{2+p_0}$$

$$(12) \quad L'_p - L'_A \sim -\frac{sp_0}{2+p_0} \sim -\frac{1}{2} p_0 s.$$

The smaller are the values p_0 and s , the higher is $n_p - n_A$. A numerical example, with the same value as mentioned above ($s = 10^{-3}$; $p_0 = 0.10$; $p_n = 0.90$) gives $n_p - n_A \sim 6.16 \cdot 10^3$, $n_A \sim 5.05 \cdot 10^3$ generations.

b. substitutional load.

$$L_p - L_A = \frac{p_n - p_0}{p_0 p_n} + \text{Log} \frac{p_0}{p_n}.$$

When $p_n \rightarrow 1$,

$$L_p - L_A = \frac{1}{p_0} - p_0 + \text{Log} p_0 ;$$

if p_0 is small,

$$L_p - L_A \approx \frac{1}{p_0} .$$

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.

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

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

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

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

- p_n fixed and $p_0 \rightarrow 0$, $N \rightarrow 0$; there is no difference for the average reckoned all over the whole substitution range.

- p_n and p_0 small and not very different, let

$$p_n = \alpha p_0, \quad \alpha = 1 + \epsilon. \quad \text{We find}$$

$$L'_p - L'_A \approx -p_0^2 s.$$

Recessive case initial economy of genetic death of panmixis is less pronounced than dominant case. 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.

B.2. Extinction function in sexual and apomict-mixed populations

We want to look for the relation between the reproductive mode and the probability of extinction of a finite population. We suppose that the environment is submitted to exceptional abrupt variations. The acquiring of an extinction function is the first phase to study the stationary distributions which result from the balance between internal selection (elimination of sexuality) and group selection (extinction of populations which were too highly apomict).

A recent paper, BOORMAN and LEVITT (1973) shew the importance of sigmoid shaped extinction function. We shall observe here such functions when we consider mixed populations having sexual plants and apomict plants both together, at the same ploidy level.

Let us suppose the environment is submitted to an abrupt variation. Only a percent of individuals survive after this environment change occurred. The more variable a population is, the higher the percent of surviving individuals.

The higher the percent of sexual plants in a mixed population is, the higher the variability can be.

Let us reckon the frequencies of genotypes A and B, P' and Q' respectively, at the next generation :

$$P' = [(P^2 + kPQ) S_A i_{AA} + (1-k) PQ S_A i_{AB}] \times \frac{1}{\bar{\omega}} = \frac{\omega_A P}{\bar{\omega}}$$

$$Q' = [(Q^2 + kPQ) S_B i_{BB} + (1-k) PQ S_B i_{AB}] \times \frac{1}{\bar{\omega}} = \frac{\omega_B Q}{\bar{\omega}}$$

$\bar{\omega}$ is the mean fitness of the population ($\bar{\omega} = \bar{\omega}_A P + \bar{\omega}_B Q$).

Let be $i_{AB} = i_{AA} + \epsilon = i_{BB} + \epsilon'$, we find

$$\omega_A = S_A (1 + (1-k) \epsilon Q)$$

$$\omega_B = S_B (1 + (1-k) \epsilon' P).$$

Thus, because of competition, selective coefficients of A and B genotypes depend on genotype frequencies.

Let be $S_A = (1 + \alpha) S_B$, α arbitrarily > 0 . There will be an equilibrium of genotype frequencies if $\omega_A = \omega_B$. This will occur with

$$\hat{p} = \frac{\epsilon (1-k)(1+\alpha) + \alpha}{\epsilon (1-k)(1+\alpha) + (1-k)\epsilon'}$$

When ϵ and $\epsilon' > 0$, \hat{p} is a genotype frequency of a stable equilibrium if

$$\alpha < (1-h) \epsilon'$$

When ϵ and $\epsilon' < 0$, the equilibrium is unstable, the population becomes monomorphic. If $0 < \hat{p} < 1$ the genotype which disappears depends on initial frequencies above or below \hat{p}

When $\epsilon > 0$ and $\epsilon' < 0$, A genotype always eliminates B.

When $\epsilon < 0$ and $\epsilon' > 0$ every situation is possible (it depends on relative values of ϵ , ϵ' , and α), even the stable polymorphic equilibrium.

When k increases (more vegetative propagation) stable polymorph equilibrium becomes more and more exceptional. Thus the various simple polymorphisms and series of different monomorph populations could be taken account by competition with absolute apomixis.

B. Population structures with facultative apomixis

Detailed calculations were published elsewhere (PERNES, 1970). We shall give here a quick summary of the main results.

Every genotype is a facultative apomict, with the sexual rate α .

When sexuality works, pollination occurs at random.

In these populations, without selective pressures, genotypic frequencies shift asymptotically to the HARDY-WEINBERG equilibrium values. Under selective pressures, gene frequencies are moved following the approximate law :

$$\Delta p \cong \frac{p_n q_n}{2 \bar{w}} \frac{d\bar{w}_n^*}{dp},$$

where p_n and q_n are the allele frequencies in one locus at the n^{th} generation, \bar{w} is the population mean fitness, \bar{w}_n^* is given by the following expression :

$$\bar{w}_n^* = \bar{w}_{p,n} + (1-\alpha) \bar{w}_{\theta,n}.$$

$\bar{w}_{p,n}$ is the mean fitness of a population whose genotype frequencies are those given by the Hardy-Weinberg law ; $\bar{w}_{\theta,n}$ is a residual mean fitness allowable to departures from panmictic equilibrium.

These results shew that facultative apomict populations are quite similar to allogamous populations. It depends on initial variability. Thus, apomixis is something like a generalized linkage which allows for more damped adaptive response than entirely sexual populations.

Also we can expect important gametic disequilibrium. Those will be strongly settled in this kind of populations. This could be a reason why marginal populations are quickly separated, after migrations in discontinuous phenotypes.

III - Discussion

Did these analysis of apomixis agree with the population structures observed ?

We consider first the generalization of apomixis at the tetraploid level. The models shew how temporary ought to be the sexuality when apomict plants are surrounding. On the contrary, the diploid level can be well protected from acquiring apomixis through dihaploid plants/if selection acts against spontaneous trend of apomixis to increase into sexual populations.

*

By mean of modifier genes of the sexual rate, the overall trend is the decreasing of sexual rate. We saw that a very low rate could be optimal, thus it did not appear there is any room for group selection to increase the sexual rate above the 1% to 5% observed. Neither substitution loads nor extinction functions could lead to drastic external selection to maintain sexuality above the 5% rate ; it could be enough to allow perennality to Panicum maximum.

Second, the observations of natural polymorphisms shew the two kinds of polymorphisms suggested. Simple polymorphism could be maintained through quasi-absolute apomixis after choosing phenotypes either adapted to various niches or with competitive values in good agreement.

We observed allogamous polymorphisms among apomict plants in the neighborhood of diploid populations. The sexual rate allowed the maintenance of initial panmictic like structure. Successive migrations induce progressively the simplification of this polymorphism when going far from the sexual center. The structure nearby the sexual structure could^{be} perpetuated through the occurrence of introgressions from the diploid pool (by pollination of an unreduced diploid oosphere by a reduced diploid pollen).

* This is a general trend of the evolution of modifiers ; they always lead to the structures which induce less variability.

Panicum maximum, and it is liable other apomict grasses, organize their adaptations by mean of both sexual reproduction (diploid level, and perhaps transitory tetraploid level) and asexual reproduction. The facultative apomixis of tetraploid plants allow the progressive transfer of allogamous structures into simple colonizing structures without impeding the survival of the whole group. Only the farthest colonisators might disappear, the central kernel (sexual diploid and apomict tetraploid) allow for the creation of variability and the resistance against the fluctuations of the environment. It was the central tetraploid pool which built the coordinated gametic structures from where the numerous well individualised genotypes underfook the long term migrations.

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