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INCOMPATIBILITY ALLELES; CHARACTERISTICS OF A 1-LOCUS SYSTEM

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INCOMPATIBILITY ALLELES; CHARACTERISTICS OF A 1-LOCUS SYSTEM.

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ABSTRACT

The 1-locus incompatibility system that is usually assumed to be present in the red clover is investigated. The allele fluctuations from one generation to the other are demonstrated.

A mathematical state model is deduced for arbitrary numbers of alleles in the population, and its steady state behaviour and stability is discussed. The eigenvalues of the linearized models as well as simulations show that the large systems react slowly on disturbances, while the three allele system oscillates around its equilibrium.

INTRODUCTION

Nature has created several different methods for flowers to prevent self-fertility, that is to prevent offspring from pollen and eggs of the same plant. One of the most effective ways to achieve this uses a specific hereditary factor. This factor is given by the molecular structure of the so called S-locus, a certain segment of the chromosomes, and it is in one of a number of different states, called allelic states.

Two chromosomes with different molecular structure of the S-locus, i.e. with the hereditary factor in different states, are said to have different S-alleles. The possible states are labelled S_1-allele, S_2-allele up to S_n-allele, where n is the number of different alleles.

In most cells of a plant the chromosomes appear in pairs, except in pollen and eggcells, where they are single and half as many. Thus the actual pair of chromosomes in a cell has two alleles, say S_1 and S_2, and the plant is called S_{12}-plant. Pollen from a S_{12}-plant, containing either a S_1-allele or a S_2-allele, is called S_1-pollen or S_2-pollen and likewise for the eggs. A plant from S_1-pollen and S_2-eggs is identical to one from S_2-pollen and S_1-egg, so the notation S_{12} is consistent.

The pistil contains normal cells which have two S-alleles. Pollen with its S-allele identical to any of these will interact with the pistil in such a way that fertilization cannot take place. All other pollen can fertilize the eggs of that pistil.

Thus all self-fertilization is impossible! As many plants have identical alleles, some cross-fertilization will be prevented too.

The system for such incompatibility is called a multi-allelic 1-locus system with gametophytic determination of the pollen specificities, where the S-alleles have an independent fenotypic effect.

An example of such a system is the red clover (Trifolium pratense L.), which has many, maybe more than 30, different S-alleles. There exists also 2-loci systems, for instance in some grasses [2].

The model usually assumed for the allele fluctuations from one generation to another in a population with 1-locus incompatibility, is in this paper described in mathematical terms. Some characteristics of low order systems are discussed. The steady state behaviour and the stability is analysed, and the equations are linearized. This gives interesting characteristics concerning stability and sensitivity of a large system, verified by simulation of the nonlinear system.

THE MODEL

Introduce the notation S_{ij} for the quotient between the number of s_{ij}-plants and the total number of plants of the population. Since S_{ij}- and S_{ji}-plants are identical in respect to incompatibility, the numbers S_{ij} will only be used for $i<j$. Notice the characteristics:

$$0 \leqslant S_{ij} \leqslant 1$$

$$\sum_{\substack{i,j \\ i<j}} S_{ij} = 1$$

The system for reproduction determines the evolution of the population, i.e. how the numbers S_{ij} change generation after generation. If the number of different alleles in the population is n, then the $n(n-1)/2$ numbers S_{ij} constitute the state of the system. The different $S_{ij}(t+1)$:s could be expressed as functions of the $S_{ij}(t)$:s:

$$S_{ij}(t+1) = \sum_{k=1}^{i-1} \frac{1}{2} S_{ki}(t) \, p_j/(p_{tot}-p_k-p_i) + \sum_{\substack{k=i+1 \\ k\neq j}}^{n} \frac{1}{2} S_{ik}(t)p_j/$$

$$(p_{tot}-p_i-p_k) + \sum_{\substack{k=1 \\ k\neq i}}^{j-1} \frac{1}{2} S_{kj}(t) \, p_i/(p_{tot}-p_k-p_j) + \sum_{k=j+1}^{n} \frac{1}{2} S_{jk}(t) \cdot$$

$$\cdot p_i/(p_{tot}-p_j-p_k) \qquad \begin{array}{l} j = 2,\ldots, n \\ i < j \end{array} \qquad (1)$$

where p_i is the proportion of S_i-pollen.

$$P_i = p_i(t) = \sum_{k=1}^{i-1} \frac{1}{2} S_{ki}(t) + \sum_{k=i+1}^{n} \frac{1}{2} S_{ik}(t)$$

and

$$P_{tot} = \sum_{i=1}^{n} P_i = 1$$

Regard the first term of (1); Half of the number of eggs produced by S_{ki}-plants are S_i-eggs, which together with S_j-pollen form new S_{ij}-plants. However, these S_i-eggs can be fertilized by any pollen except S_k-pollen and S_i-pollen, so just the part $p_j/(p_{tot}-p_k-p_i)$ of the S_i-eggs will mature to new S_{ij}-plants. The rest of the terms are formed similarily. It is thus also assumed that if x % of the plants carry a S_i-allele, x % of the pollen will too. Furthermore all types of pollen have the same chance to performe fertilization.

It can usually be assumed that pollen exists in excess, so that the variable that limits the next generation is the number of eggs. This means that the terms for the S_i-eggs from all S_{ki}-plants and the S_j-eggs from all S_{kj}-plants could be added as in eq (1).

This assumption may be wrong. If, in actual practice, there is a shortage of inseets, this can cause a deficiency of pollen. Thus in the other extreme there are eggs in excess and termes from the pollen could be added.

Both these models could be simulated on a digital computer

5.

(See below and [1]), and the differences are small. The system with eggs in excess is somewhat slower than the one with pollen in excess.

Probably a real system will be somewhat in between. As the differences are small, the model with abundance of pollen could be representative.

Once the primary model is formulated, it is easy to structure the effects of a change in an assumption or of an added restriciton, such as pollen with a certain allele being more vital [1].

The system described by (1) is complicated. It is non-linear. The right hand side contains multiplications as well as divisions of state variables. The number of terms increases with the number of alleles. The time behaviour is difficult to realize from the equations. In order to get some insight, the two systems of lowest order are presented.

For a 3-allele system, the equation (1) is very simple

$$
\begin{cases}
S_{12}(t+1) = 1/2\, S_{13}(t) + 1/2\, S_{23}(t) \\
S_{13}(t+1) = 1/2\, S_{12}(t) + 1/2\, S_{23}(t) \\
S_{23}(t+1) = 1/2\, S_{12}(t) + 1/2\, S_{13}(t)
\end{cases}
$$

or using matrix notion

$$
S(t+1) = \begin{bmatrix} 0 & 1/2 & 1/2 \\ 1/2 & 0 & 1/2 \\ 1/2 & 1/2 & 0 \end{bmatrix} S(t)
$$

This system is linear and oscillates around the mean value (=1/3) as shown in Fig.1. The plant frequencies always approach 1/3, which is an equilibirum with global stability.
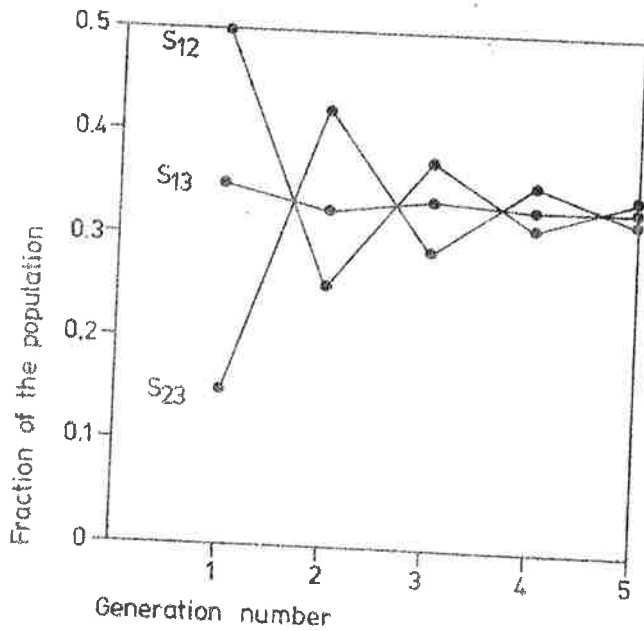
Fig 1. - Simulation of a 3-allele population.

For a 4-allele system, the equation (1) is quite different

$$S_{12}(t+1) = \frac{1}{2}S_{13} \, [S_{12}+S_{23}+S_{24}]/[S_{12}+S_{14} + S_{23}+2S_{24}+S_{34}]+$$

$$+ \frac{1}{2}S_{14} \, [S_{12}+S_{23}+S_{24}]/[S_{12}+S_{13}+2S_{23}+S_{24}+S_{34}]+$$

$$+ \frac{1}{2}S_{23} \, [S_{12}+S_{13}+S_{14}]/[S_{12}+S_{13}+2S_{14}+S_{24}+S_{34}]+$$

$$+ \frac{1}{2}S_{24} \, [S_{12}+S_{13}+S_{14}]/[S_{12}+2S_{13}+S_{14}+S_{23}+S_{34}]$$

and analogously for the other allele combinations. This
system is nonlinear, and it usually does not oscillate. When
simulated on a computer the plant frequencies always approached
1/6, which is a stable equilibrium, probably the only equili-
brium.

EQUILIBRIA

Since the alleles are assumed to be equal, there should be an equilibrium

$$S_{12} = S_{13} = \ldots \ldots S_{n-1,n} = 1/N$$

where n is the number of alleles, and $N = n(n-1)/2$ is the number of different plants.

It is easily shown that this is the only steady state solution to the 3-allele system: From (1)

$$S_{12} = (S_{13} + S_{23})/2 \qquad \text{(a)}$$

$$S_{13} = (S_{12} + S_{23})/2 \qquad \text{(b)}$$

$$S_{23} = (S_{12} + S_{13})/2 \qquad \text{(c)}$$

(a) and (b) give

$$S_{13} = \frac{1}{4} S_{13} + \frac{3}{4} S_{23}$$

or equivalently

$$S_{13} = S_{23}$$

and again using (a)

$$S_{12} = S_{13} \; (= S_{23})$$

which also satisfies (c)

That $S_{ij} = 1/N$ is an equilibrium (probably the only one), could be proven for all n:

$$S_{ij}(t) = \frac{2}{n(n-1)} \qquad \forall i,j$$

$$P_i(t) = 1/n \qquad \forall i$$

Thus, according to (1), $S_{ij}(t+1)$ is a sum of $2(n-2)$ equal terms

$$S_{ij}(t+1) = 2(n-2)\frac{1}{2} \frac{2}{n(n-1)} \frac{1/n}{1-1/n-1/n} = \frac{2}{n(n-1)} = S_{ij}(t)$$

STABILITY

In the 3-allele system $S_{ij} = 1/3$ is an equilibrium with global stability.

$$S(t+1) = \begin{bmatrix} 0 & 1/2 & 1/2 \\ 1/2 & 0 & 1/2 \\ 1/2 & 1/2 & 0 \end{bmatrix} S(t)$$

or when deviations from the equilibrium are considered

$$\Delta S = \begin{bmatrix} S_{12} \\ S_{13} \\ S_{23} \end{bmatrix} - \begin{bmatrix} 1/3 \\ 1/3 \\ 1/3 \end{bmatrix}$$

$$\Delta S(t+1) = \begin{bmatrix} 0 & 1/2 & 1/2 \\ 1/2 & 0 & 1/2 \\ 1/2 & 1/2 & 0 \end{bmatrix} \Delta S(t) = \Phi \Delta S(t)$$

The eigenvalues of Φ are $\lambda = 1$, $-1/2$ and $-1/2$, and the eigenvectors are $[1\ 1\ 1]^T$, connected to $\lambda = 1$ and $[a\ b\ c]^T$, $a+b+c=0$, connected to $\lambda = -1/2$.

The value $\lambda=1$ is an implication of $\sum_{i<j} S_{ij}$ being constant, equal to one.

The evolution of the state is thus in fact restricted to a subspace of dimension N-1, but it is favorable not to solve this dependence. It makes the expression (1) simpler and more symmetric.

Since the other two eigenvalues are within the unitcircle the 3-allele system is stable, and the negative sign of them shows

the oscillatory behaviour.

The global stability has not been shown for the nonlinear systems with 4 or more alleles, but some calculations can be done.

LINEARIZATION

In order to find out if $S_{ij} = 1/N$ is a stable solution of (1), small changes are considered and the equation linearized around the equilibrium.

$$\Delta S_{12}(t+1) \quad \alpha_{12}\Delta S_{12}(t) + \alpha_{13}\Delta S_{13}(t) + \ldots + \alpha_{n-1,n} \Delta S_{n-1,n}(t)$$

where

$$\alpha_{12} = \frac{n-3}{(n-1)(n-2)}$$

$$(2)$$

$$\alpha_{13} = \frac{(n-2)^2-(n-3)}{(n-1)(n-2)^2} = \alpha_{14} = \ldots = \alpha_{1n} = \alpha_{23} = \ldots = \alpha_{2n} \quad (3)$$

$$\alpha_{34} = -\frac{2(n-3)}{(n-1)(n-2)^2} = \alpha_{35} = \ldots = \alpha_{3n} = \ldots = \alpha_{n-1,n} \quad (4)$$

$\Delta S_{13}(t+1)$, $\Delta S_{14}(t+1)$ and so on could be expressed by the same factors α, but permuted. Thus

$$\Delta S(t+1) = \phi \; \Delta S(t)$$

The matrix ϕ is symmetric and contains the three different elements α_{12}, α_{13} and α_{34} spread out in a regular pattern. The matrix for the 4-allele system is shown as an example. The expressions (2) - (4) give with n = 4

$$\alpha_{12} = 1/6$$

$$\alpha_{13} = 1/4$$
$$\alpha_{34} = -1/6$$

and the pattern is

$$\Phi = \begin{pmatrix} \frac{1}{6} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \frac{-1}{6} \\[6pt] \frac{1}{4} & \frac{1}{6} & \frac{1}{4} & \frac{1}{4} & \frac{-1}{6} & \frac{1}{4} \\[6pt] \frac{1}{4} & \frac{1}{4} & \frac{1}{6} & \frac{-1}{6} & \frac{1}{4} & \frac{1}{4} \\[6pt] \frac{1}{4} & \frac{1}{4} & \frac{-1}{6} & \frac{1}{6} & \frac{1}{4} & \frac{1}{4} \\[6pt] \frac{1}{4} & \frac{-1}{6} & \frac{1}{4} & \frac{1}{4} & \frac{1}{6} & \frac{1}{4} \\[6pt] \frac{-1}{6} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \frac{1}{6} \end{pmatrix}$$

The eigenvalues of Φ have been computed for some different number of alleles in the populations:

$n = 3$	1			$-\frac{1}{2}$	$-\frac{1}{2}$
$n = 4$	1	$\frac{1}{3}$ $\frac{1}{3}$ $\frac{1}{3}$		$-\frac{1}{2}$ $-\frac{1}{2}$	
$n = 5$	1	$\underbrace{\frac{7}{12} \quad \frac{7}{12} \dots}_{4}$		$\underbrace{-\frac{1}{3} \quad -\frac{1}{3} \dots}_{5}$	
$n = 6$	1	$\underbrace{\frac{\prime}{10} \quad \frac{\prime}{10} \dots}_{5}$		$\underbrace{-\frac{1}{4} \quad -\frac{1}{4} \dots}_{9}$	
$n = 8$	1	$\underbrace{\frac{17}{21} \quad \frac{17}{21} \dots}_{7}$		$\underbrace{-\frac{1}{6} \quad -\frac{1}{6} \dots}_{20}$	

Because the eigenvalues are inside the unitcircle the steady state solution of all these systems are stable.

The negative eigenvalues corresponding to oscillating terms become less accentuated as n increases, while the growing positive eigenvalues indicate that the distrubances only very slowly penetrates a large system. The overshoots, typical for a 3-allele population, occur in a 4-allele system for the special case when the allele frequencies are almost equal but the plant frequencies differ. The start

$$\begin{cases} S_{12} = S_{34} = 0.5 \\ S_{13} = S_{14} = S_{23} = S_{24} = 0 \end{cases}$$
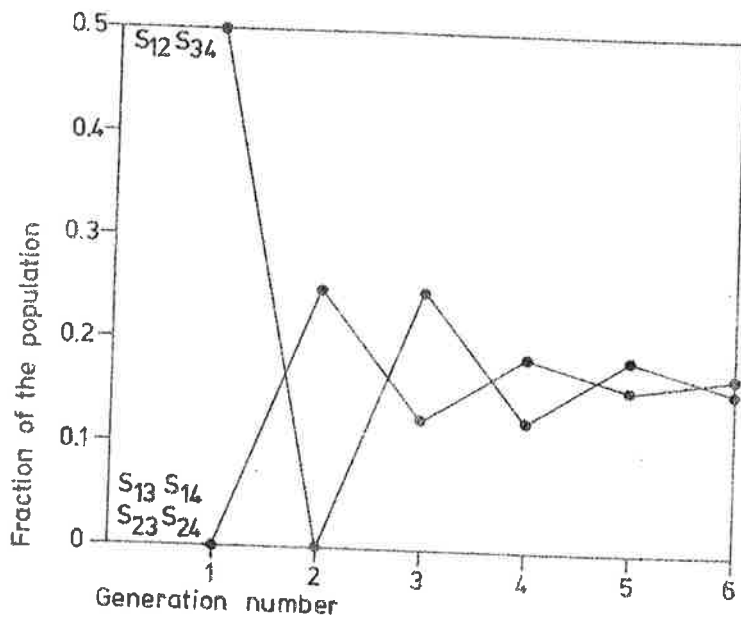
of eq (1) gives the fluctuations in Fig. 2.

Fig 2. - A special starting value giving an oscillating 4- allele population.

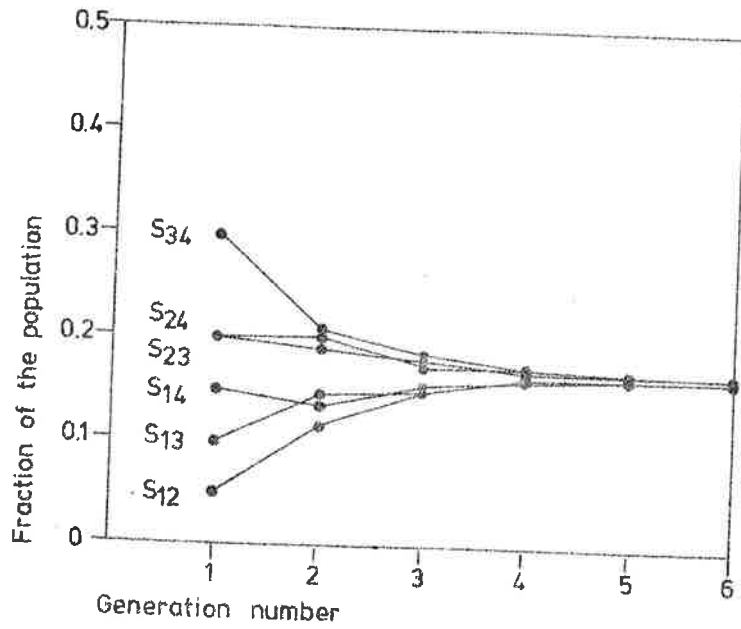For larger systems, overshoots are rare, as shown by the simulations in Fig 3 and Fig 4.

Figure 4. - A small amount of a new allele (s_1) entering a population in steady state.
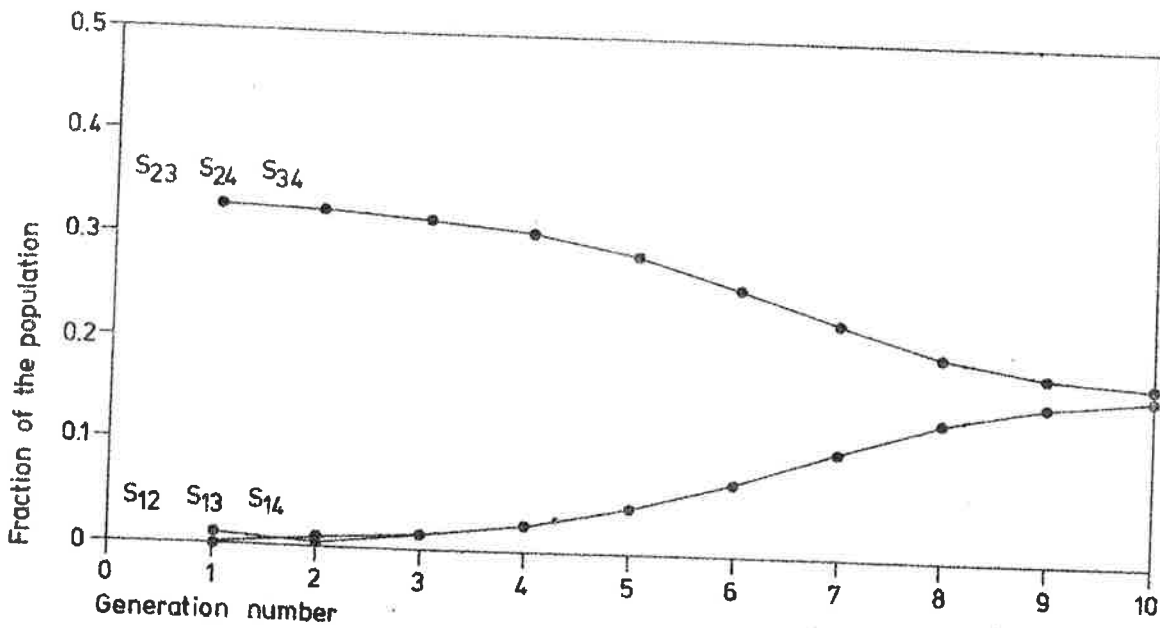

Figure 3. - A normal starting value giving a damped 4-allele population.

CONCLUSIONS

The incompatibility system with one locus and several
possible alleles has been described. The behaviour of
populations with few alleles is not relevent for large
systems. The recovery after a disturbance occurs very
slowly and (without) overshoots. The same happens when a
small amount of a new allele enters a population. The
symmetry and the structure of the system give nice pat-
terns in the linearized systems.

It is difficult to predict the result of a crossing ex-
periment or an elite multiplication, and it would be valu-
able to compute the expected values from a model of the
population. The costs for an experiment and a simulation
differ by several orders of magnitude.

An estimate of the randomness in the system, [1], indicates
that it would be possible to check the model against a field
experiment of a four allele population. Such experiment will
be conducted by Doc. Thore Denward, Balsgård, Sweden. The
starting values will be

$$\begin{cases} S_{12} = S_{13} = S_{14} = 1/3 \\ S_{23} = S_{24} = S_{34} = 0 \end{cases}$$

reaching the equilibrium point $S_{ij} = 1/6$ in the next generation.
A corresponding 3 allele system would behave otherwise with
oscillations:

$$\begin{cases} S_{12} = S_{13} = 1/2 \\ S_{23} = 0 \end{cases}$$

gives in the next generation

$$
\begin{cases}
S_{12} = S_{13} = 1/4 \\
S_{23} = 1/2
\end{cases}
$$

The differencies could also be seen in the allele frequencies.

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