



Asynchrone Flowering in Self-incompatible Annuals

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Presentation of pollen and stigmas at different times by individuals of a population is likely to exert a profound influence on its genetic structure. We have analysed the changes undergone in (1) asynchrony and (2) single locus heterozygosity, under the irruption of self-incompatible variants in a population of random-mating hermaphroditic annuals. Equations relating genotypic frequencies with time-dependent gamete availability parameters were obtained. These were run in a numerical example over 20 generations, starting from a mixed population showing different degrees of asynchrony depending on the mode of inheritance of this trait. Five cases were analysed, differing in the degree of dominance. Self-incompatibility starts to be expressed in the first generation. Dominance for early- and late-flowering times was negatively associated with asynchrony, due to the existence of self-incompatible variants. A higher degree of potential genetic variability was observed in the locus controlling pollen availability than in the one controlling ovules in advanced generations under this reproductive system. © 2000 Annals of Botany Company

Key words: Dichogamy, asynchronous flowering, self-incompatibility, genetic model.

INTRODUCTION

One of the most important factors involved in the transmission of information in ecosystems is sexual reproduction. In flowering plants, this mechanism encompasses a great number of both morphological and behavioural variants (Richards, 1994). Among the latter, we are especially interested in flowering asynchrony, i.e. the presentation of pollen and stigmas at different times by individuals of a population during a given reproductive episode. Asynchrony includes both the coexistence of early- and late-flowering adichogamous individuals, and dichogamy in its monomorphic and dimorphic variants (Lloyd and Webb, 1986). By single reproductive episode we mean the period during which all individuals of a population deliver and receive pollen without any reproductive activity in the progeny (the latter will be reproductively active in the next episode, and then without the participation of the parental generation). We have constructed a genetic model accounting for asynchrony (Medan and Bartoloni, 1998) in random mating populations. In this paper the question of asynchronous flowering in the presence of self-incompatibility (SI) is addressed. We develop a digenic multiallelic model with a pleiotropic effect (Griffiths *et al.*, 1997) affecting both flowering time and gametophytic SI. Self-incompatibility is a well known, genetically-based mechanism (Griffiths *et al.*, 1997; de Nettancourt, 1997) which avoids inbreeding in populations that may otherwise suffer depression due to

self-fertilization or matings between closely related individuals (Falconer and Mackay, 1996). Thus, SI is a cohesion-reinforcing process (Brooks and Wiley, 1988) and we will study the interplay of the two features—asynchrony and SI.

The outcome of some interactions between asynchrony and SI are easy to envisage. To give an extreme example, in a population with hermaphroditic self-compatible individuals flowering in a fully asynchronous way (i.e. one in which the individual flowering periods do not overlap at all), an incoming self-incompatible variant will have no chance of survival because it will be unable to either deliver its pollen to, or receive pollen from, other individuals in the population. After initial exploratory analysis it became clear to us that our original model (with two diallelic loci) (Medan and Bartoloni, 1998) would not account completely for the expression of SI. Therefore, we developed a multiallelic model.

MODELS AND METHODS

We are ultimately interested in steady state structures, i.e. the goals toward which the system will tend (Crow and Kimura, 1970). Given the character of the genetic outcome (i.e. independence of initial conditions, with the exception of trivial structures of course) and in order to standardize the different cases of inheritance, we began with population structures in which all genotypes had the same frequency. Thus, the model departs from a situation in which many genotypes coexist in the population. Then, from the second generation on, SI variants appear and so we can analyse the dynamics of asynchronous phenotypes under the influence of SI.

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We will study asynchrony through a trait with a lesser level of complexity: flowering time. Variations in flowering asynchrony emerge from variations in flowering times.

Genetic control of pollen and ovule availability

We considered a genic locus with three alleles (A_1 , A_2 and A_3)—and therefore with six genotypes (A_1A_1 , A_1A_2 , A_2A_2 , A_1A_3 , A_2A_3 and A_3A_3)—controlling pollen availability. Plants with genotype A_1A_1 have a phenotype for pollen availability per unit time represented by the function $h_1(t)$ which is a continuous function of time (measured on an arbitrary scale). Similarly, the functions $h_2(t)$, $h_3(t)$, $h_4(t)$, $h_5(t)$ and $h_6(t)$ represent pollen availability at time t corresponding to the A_1A_2 , A_1A_3 , A_2A_2 , A_2A_3 and A_3A_3 individuals, respectively. The same considerations hold with respect to ovule availability. A triallelic diploid locus (B_1 , B_2 and B_3) accounts for the availability of ovules through the continuous functions $g_1(t)$, $g_2(t)$, $g_3(t)$, $g_4(t)$, $g_5(t)$ and $g_6(t)$ corresponding, respectively, to the genotypes B_1B_1 , B_1B_2 , B_1B_3 , B_2B_2 , B_2B_3 and B_3B_3 .

Genetic control of SI

A pleiotropic effect is assumed for both loci in addition to gamete availability: they express information about gametophytic SI, the combination of an A_iB_j pollen grain and an A_kB_l/A_kB_1 ($i, j, k, l = 1, 2, 3$) stigma leading to an incompatibility reaction. The assumption of a pleiotropic effect implies a strong restriction. The main reason for invoking such an effect is to analyse the interplay of two evolutionarily important processes: self-incompatibility and asynchrony. If, as may be the case, SI were controlled by another independent locus, there would be no genetic association between these two phenomena: the genotypic arrays would evolve independently and would also reach steady states of their own. For example, if an S_i series controls the SI system then only heterozygotes will remain and, along with them (and independently), the complete array of genotypes corresponding to each case of flowering time (loci A and B).

By assuming a pleiotropic effect we are generating a trade-off situation (a conflict between two opposing processes) worthy of being analysed from an evolutionary point of view for both traits (SI and asynchrony) that seem to counteract each other, one reinforcing cohesion (SI) and the other decreasing it (asynchrony).

We are, furthermore, assuming that there are no differences in viability assignable to the loci A and B and, as stated above, no overlapping generations.

Notation of genotypes and their frequencies

In order to use a complete and simple notation we have first denoted the genotypes corresponding to each locus with the symbols shown in Table 1. Hence, the compound genotypes (i.e. genotypes considering both loci) will be denoted with a symbol containing the non-zero subindexes

TABLE 1. Genotypic symbols

Genotype	Symbol	Genotype	Symbol
A_1A_1	S_{10}	B_1B_1	S_{01}
A_1A_2	S_{20}	B_1B_2	S_{02}
A_1A_3	S_{30}	B_1B_3	S_{03}
A_2A_2	S_{40}	B_2B_2	S_{04}
A_2A_3	S_{50}	B_2B_3	S_{05}
A_3A_3	S_{60}	B_3B_3	S_{06}

corresponding to the simple genotypes that enter in their formulation. For example, the genotype A_1B_2/A_1B_3 will be denoted as S_{15} (the subindex 1 corresponding to genotype A_1A_1 and the subindex 5, to genotype B_2B_3). With respect to the double heterozygotes, which have two linkage phases (Spiess, 1989) a third subindex will be joined (1 or 2) to distinguish them. The symbols shown in Table 2 will be employed for double heterozygotes.

The absolute number and probability corresponding to genotype S_{ij} in generation n (G_n) will be denoted as $N_{ij}^{(n)}$ and $P_{ij}^{(n)}$, respectively, and, in the case of double heterozygotes,

$$P_{ij1}^{(n)} + P_{ij2}^{(n)} = P_{ij}^{(n)}.$$

Simple genotypic frequencies are denoted as:

$$P_{.j}^{(n)} = \sum_{i=1}^6 P_{ij}^{(n)} \quad \text{and} \quad P_{i.}^{(n)} = \sum_{j=1}^6 P_{ij}^{(n)}$$

and the absolute frequencies will be:

$$N_{.j}^{(n)} = \sum_{i=1}^6 N_{ij}^{(n)} \quad \text{and} \quad N_{i.}^{(n)} = \sum_{j=1}^6 N_{ij}^{(n)}$$

For example, $N_{.1}^{(n)}$ is the absolute frequency of genotype B_1B_1 in G_n and $P_{.1}^{(n)}$ its relative frequency. Finally, r stands for the *recombination frequency* (Spiess, 1989). In the case of unlinked loci (independent segregation) r equals 0.5.

Pollen availability functions

As mentioned above, $h_i(t)$ represents the amount of pollen made available at time t by an S_{10} plant. Likewise $\int_0^{T_0} h_i(t) dt = H_i(T_0)$ represents the overall amount of pollen presented by an S_{10} plant during the whole reproductive episode (T_0). The relative frequencies of A_1 , A_2 and A_3 pollen grains at time t are, respectively:

$$p_p^{(n)}(t) = \frac{P_{1.}^{(n)} h_1(t) + \frac{1}{2} P_{2.}^{(n)} h_2(t) + \frac{1}{2} P_{3.}^{(n)} h_3(t)}{\sum_{i=1}^6 P_{i.}^{(n)} h_i(t)}$$

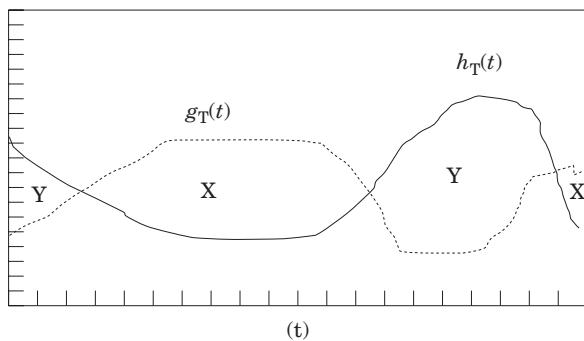
$$q_p^{(n)}(t) = \frac{P_{4.}^{(n)} h_4(t) + \frac{1}{2} P_{2.}^{(n)} h_2(t) + \frac{1}{2} P_{5.}^{(n)} h_5(t)}{\sum_{i=1}^6 P_{i.}^{(n)} h_i(t)}$$

$$r_p^{(n)}(t) = \frac{P_{6.}^{(n)} h_6(t) + \frac{1}{2} P_{3.}^{(n)} h_3(t) + \frac{1}{2} P_{5.}^{(n)} h_5(t)}{\sum_{i=1}^6 P_{i.}^{(n)} h_i(t)}$$

where $p_p^{(n)}(t) + q_p^{(n)}(t) + r_p^{(n)}(t) = 1$.

TABLE 2. Double heterozygous genotypic symbols

Genotype	Symbol	Genotype	Symbol
A ₁ B ₁ /A ₁ B ₁	S ₂₂₁	A ₁ B ₂ /A ₂ B ₁	S ₂₂₂
A ₁ B ₁ /A ₂ B ₃	S ₂₃₁	A ₁ B ₃ /A ₂ B ₁	S ₂₃₂
A ₁ B ₂ /A ₂ B ₃	S ₂₅₁	A ₁ B ₃ /A ₂ B ₂	S ₂₅₂
A ₁ B ₁ /A ₃ B ₂	S ₃₂₁	A ₁ B ₂ /A ₃ B ₁	S ₃₂₂
A ₁ B ₁ /A ₃ B ₃	S ₃₃₁	A ₁ B ₃ /A ₃ B ₁	S ₃₃₂
A ₁ B ₂ /A ₃ B ₃	S ₃₅₁	A ₁ B ₃ /A ₃ B ₂	S ₃₅₂
A ₂ B ₁ /A ₃ B ₂	S ₅₂₁	A ₂ B ₂ /A ₃ B ₁	S ₅₂₂
A ₂ B ₁ /A ₃ B ₃	S ₅₃₁	A ₂ B ₃ /A ₃ B ₁	S ₅₃₂
A ₂ B ₂ /A ₃ B ₃	S ₅₅₁	A ₂ B ₃ /A ₃ B ₂	S ₅₅₂

FIG. 1. Representation of $g_T(t)$ and $h_T(t)$.

Ovule availability functions

As in the case of pollen, $g_i(t)$ represents the amount of ovules available in S_{0i} plants at time t . And $\int_0^{T_0} g_i(t) dt = G_i(T_0)$ represents the overall amount of ovules produced by an S_{0i} plant during the whole reproductive episode (T_0). The frequencies of each kind of ovule are:

$$p_O^{(n)}(t) = \frac{P_{.1}^{(n)} g_1(t) + \frac{1}{2} P_{.2}^{(n)} g_2(t) + \frac{1}{2} P_{.3}^{(n)} g_3(t)}{\sum_{j=1}^6 P_{.j}^{(n)} g_j(t)}$$

$$q_O^{(n)}(t) = \frac{P_{.4}^{(n)} g_4(t) + \frac{1}{2} P_{.2}^{(n)} g_2(t) + \frac{1}{2} P_{.5}^{(n)} g_5(t)}{\sum_{j=1}^6 P_{.j}^{(n)} g_j(t)}$$

$$r_O^{(n)}(t) = \frac{P_{.6}^{(n)} g_6(t) + \frac{1}{2} P_{.5}^{(n)} g_5(t) + \frac{1}{2} P_{.3}^{(n)} g_3(t)}{\sum_{j=1}^6 P_{.j}^{(n)} g_j(t)}$$

where $p_O^{(n)}(t) + q_O^{(n)}(t) + r_O^{(n)}(t) = 1$.

The overall amounts of both types of gametes at time t , are:

$$h_T^{(n)}(t) = \sum_{i=1}^6 N_{i.}^{(n)} h_i(t) \text{ and } g_T^{(n)}(t) = \sum_{j=1}^6 N_{.j}^{(n)} g_j(t)$$

Two heuristic curves are shown in Fig. 1. There are zones (X) in which $g_T^{(n)}(t) > h_T^{(n)}(t)$ and others (Y) in which $g_T^{(n)}(t) < h_T^{(n)}(t)$.

During the X periods ovules exceed pollen grains, while

during the Y periods pollen exceeds ovules. These excesses represent lost ovules or lost pollen, since pollinations cannot take place i.e. there can be no offspring. Thus, in order to obtain the overall number of descendants corresponding to a given genotype at time t , we have to multiply their frequency (obtained by random fecundation of gametes) by the term:

$$\pi_T^{(n)}(t) = \min [h_T^{(n)}(t); g_T^{(n)}(t)]$$

Once we have obtained the total number of descendants corresponding to each genotype in G_{i+1} , say K , we calculate the final relative frequency corresponding to genotype x_j as:

$$\frac{\int_{Ch} h_T^{(n+1)}(t) f^{(n+1)}(x_j)(t) dt + \int_{Cg} g_T^{(n+1)}(t) f^{(n+1)}(x_j)(t) dt}{K} = \frac{K_j}{K}$$

where Ch and Cg are the integration intervals in which $g_T^{(n)}(t) < h_T^{(n)}(t)$ and $g_T^{(n)}(t) > h_T^{(n)}(t)$, respectively, $K = \sum_{j=1}^{10} K_j = N_{..}^{(n+1)}$ represents the total number of individuals in G_{i+1} and $f^{(n+1)}(x_j)$ is the frequency of genotype x_j .

Compound gamete production

At time t , the amount of each of the nine types of pollen grains ($A_1B_1, A_1B_2, A_1B_3, A_2B_1, A_2B_2, A_2B_3, A_3B_1, A_2B_2$ and A_3B_3) presented by each plant depends upon the genotype of the generating plant, considering both genes simultaneously and assuming they are linked at an arbitrary (but fixed) distance of r recombination units in coupling phase (Crow and Kimura, 1970). We have the following cases:

(1) *Double homozygotes*. If the genotype of the generating plant is S_{ij} , a single gamete type will be produced which will have the same chromosomal array as the gene-rating plant. The number of gametes produced will be equal to $h_i(t)$.

Hence, the gamete frequency will be $\frac{N_{ij}^{(n)} h_i(t)}{h_T^{(n)}(t)}$. For example,

S_{44} , i.e. A_2B_2/A_2B_2 produces only A_2B_2 gametes with a number equal to $h_2(t)$.

(2) *Simple homozygotes* (simple heterozygotes). If the generating plant is S_{ij} , then $h_i(t)/2$ of the gametes will be genetically equal to one of the two homologues in the generating plant chromosomes and the other half of $h_i(t)$, equal to the other homologue. The frequency of each type of gamete will be $\frac{N_{ij}^{(n)} h_i(t)}{2h_T^{(n)}(t)}$. For example, S_{54} (A_2B_2/A_3B_2)

presents $h_5(t)/2$ A_2B_2 pollen grains and $h_5(t)/2$ A_3B_2 .

(3) *Double heterozygotes*. If the generating plant is S_{ij1} , then there will be $\frac{1-r}{2} h_i(t)$ parental pollen grains of each class and $\frac{r}{2} h_i(t)$ of each recombinant class, and *vice versa* for S_{ij2} . The frequency of each parental gamete will be $\frac{N_{ij1}^{(n)} h_i(t) (1-r)}{2h_T^{(n)}(t)}$, and for each recombinant gamete $\frac{N_{ij1}^{(n)} h_i(t) r}{2h_T^{(n)}(t)}$,

and *vice versa* for S_{ij2} . For example, S_{551} will produce

$\frac{1-r}{2}h_5(t)$ A₂B₂ pollen grains, $\frac{1-r}{2}h_5(t)$ of the A₃B₃ class, $\frac{r}{2}h_5(t)$ of the A₂B₃ type and $\frac{r}{2}h_5(t)$ of the A₃B₂ class.

With respect to the ovules, the same expressions hold except that the functions are $g_j(t)$ instead of $h_i(t)$, i.e. they are associated with the second subindex (j) of the genotype symbol (S_{ij}). For example, S₅₂₁ (A₂B₁/A₃B₂) will present $\frac{1-r}{2}g_2(t)$ A₂B₁ ovules, $\frac{1-r}{2}g_2(t)$ A₃B₂ ovules, $\frac{r}{2}g_2(t)$ A₂B₂

ovules and $\frac{r}{2}g_2(t)$ A₃B₁ ovules.

These frequencies are shown in the Appendix. The functions presented are the frequencies of pollen and ovules generated by meiosis. During the fecundation process—as can be seen in the expressions corresponding to genotypic frequencies—the factors entering the product of gametic frequencies are somewhat different because of the conditionality imposed by SI. Under these conditions, the frequency of the genotype A_iB_j/A_kB_m in G_{n+1} will not be the simple sum of frequency products (correspondingly normalized—see Appendix):

$$f_p^{(n)}(A_iB_j)(t)f_o^{(n)}(A_kB_m)(t) + f_p^{(n)}(A_kB_m)(t)f_o^{(n)}(A_iB_j)(t)$$

but:

$$\begin{aligned} & f_p^{(n)}(A_iB_j)(t)\{f_o^{(n)}(A_kB_m)(t)/\text{stigma not } A_iB_j\} \\ & + f_p^{(n)}(A_kB_m)(t)\{f_o^{(n)}(A_iB_j)(t)/\text{stigma not } A_kB_m\} \end{aligned}$$

the second factor in each term indicating the condition imposed by gametophytic SI on the stigma diploid genotype (it must not contain an allelic array equal to that contained in the pollen grain).

Fecundation under SI

Some of the genotypic frequencies arising under random mating, except for the conditions imposed by self-incompatibility, are presented in the Appendix. There are 45 possible genotypes (taking account of the linkage phase). For this reason, only some are presented in the Appendix.

NUMERICAL EXAMPLE

We have constructed a numerical application employing simple polynomial expressions representing the functions $h_i(t)$ and $g_i(t)$. In this application, for the sake of simplicity, a genotype is considered *synchronous* if its pollen and ovule availability functions at least partially overlap with each other; if the curves do not overlap at all, the genotype is said to be *asynchronous*. We have considered variations in certain properties of the functions defining times (such as range and location) of the curve. Six different situations have been analysed.

(A) All functions have the same range on the time axis and the same value of $H_i(T_0)$ and $G_i(T_0)$ (see Introduction), differing only in their location on the time axis. There are three subcases: (A1) asynchrony without dominance for location where a function of ovule availability, $g_i(t)$, occupies the same range as the function $h_i(t)$ with the same subindex.

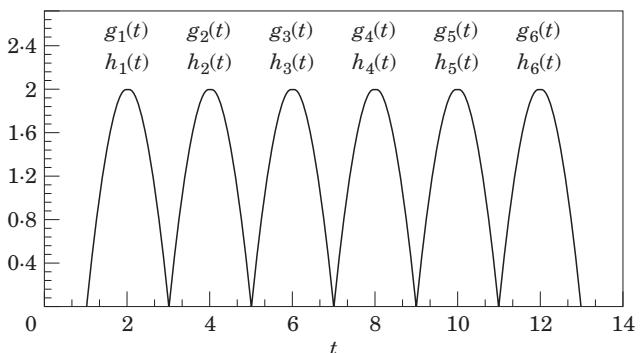


FIG. 2. Flowering time functions corresponding to case A1.

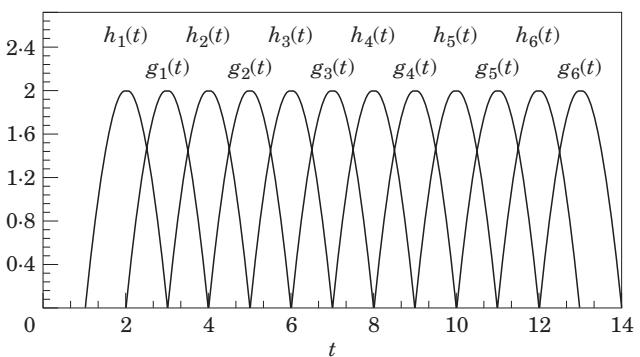


FIG. 3. Flowering time functions corresponding to case A2.

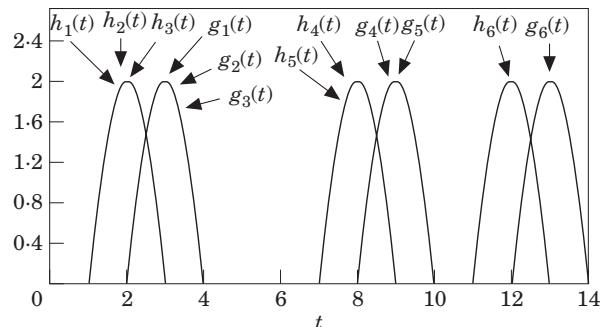


FIG. 4. Flowering time functions corresponding to case A31.

For example, $g_3(t) = h_3(t)$. Six out of the 36 genotypes are fully synchronous, i.e. adychogamous. Furthermore, the functions corresponding to heterozygotes are located between the homozygote ones, not showing dominance (Fig. 2). (A2) Asynchrony without dominance for location, where both functions, $h_i(t)$ and $g_i(t)$, are consecutive and equally spaced along the time axis with a little lag for the functions $g_i(t)$ (Fig. 3). The $g_i(t)$ series of polynomials begin half a range after $h_i(t)$ as seen in the figures. Each polynomial lies exactly between its neighbours showing no dominance. There are no fully synchronous genotypes, i.e. all of them show dichogamy (Fig. 3). (A3) Asynchrony with dominance for location. All genotypes are dichogamous. This, in turn, includes two subsubcases: (A31) complete dominance in the same direction for both pollen and ovule availability functions, the order of dominance among the alleles being A₁ > A₂ > A₃ and B₁ > B₂ > B₃ (Fig. 4). (A32) Complete

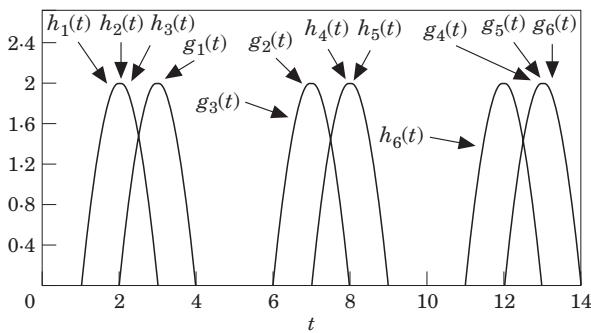


FIG. 5. Flowering time functions corresponding to case A32.

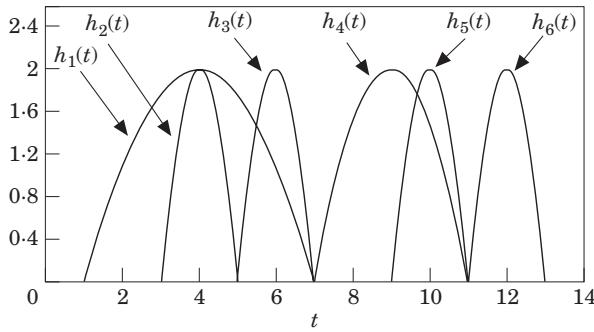


FIG. 6A. Pollen availability functions corresponding to case B1.

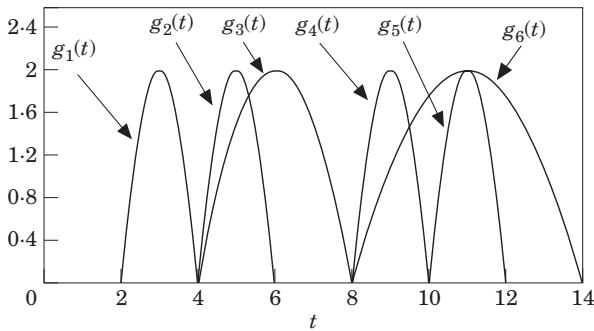


FIG. 6B. Ovule availability functions corresponding to case B1.

dominance in the opposite direction, the order of dominance among the alleles being $A_1 > A_2 > A_3$ and $B_3 > B_2 > B_1$ (Fig. 5).

(B) The functions differ in their time range and total amounts of gametes— $H_i(T_0)$ and $G_i(T_0)$ —showing dominance in opposite directions for pollen and ovules, pollen donors dominating the early stages of the flowering period. There are two subcases: (B1) genotypes with short ranges are dominant (Fig. 6A and B); and (B2) genotypes with long ranges are dominant (Fig. 7).

The functions utilized in the illustration are the following:

Case A1

$h_1(t) = -2t^2 + 8t - 6$, $h_2(t) = -2t^2 + 16t - 30$, $h_3(t) = -2t^2 + 24t - 70$, $h_4(t) = -2t^2 + 32t - 126$, $h_5(t) = -2t^2 + 40t - 198$,

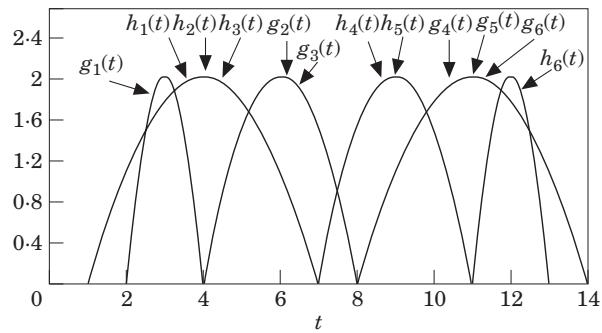


FIG. 7. Flowering time functions corresponding to case B2.

$$h_6(t) = -2t^2 + 48t - 286 \text{ and } g_1(t) = h_1(t), g_2(t) = h_2(t), \dots, g_6(t) = h_6(t)$$

Case A2

Functions $h_i(t)$ are the same as in A1, while $g_i(t)$ are as follows: $g_1(t) = -2t^2 + 12t - 16$, $g_2(t) = -2t^2 + 20t - 48$, $g_3(t) = -2t^2 + 28t - 96$, $g_4(t) = -2t^2 + 36t - 160$, $g_5(t) = -2t^2 + 44t - 240$ and $g_6(t) = -2t^2 + 52t - 336$

Case A31

The polynomials are similar to those above but there are horizontal ‘slides’: $h_1(t) = h_2(t) = h_3(t) = -2t^2 + 8t - 6$, $h_4(t) = h_5(t) = -2t^2 + 32t - 126$, $g_1(t) = g_2(t) = g_3(t) = -2t^2 + 12t - 16$, $g_4(t) = g_5(t) = -2t^2 + 36t - 160$

Case A32

The $h_i(t)$ functions are the same as in A31, but those for $g_i(t)$ are: $g_4(t) = g_5(t) = g_6(t) = -2t^2 + 52t - 336$ and $g_2(t) = g_3(t) = -2t^2 + 28t - 96$

Case B1

There are changes in the polynomial ranges: $h_1(t) = -\frac{2}{9}t^2 + \frac{16}{9}t - \frac{14}{9}$, $h_2(t) = -\frac{1}{2}t^2 + 5t - \frac{21}{2}$, $h_3(t) = -2t^2 + 24t - 70$, $h_4(t) = -\frac{1}{2}t^2 + 9t - \frac{77}{2}$, $h_5(t) = -2t^2 + 40t - 198$, $h_6(t) = -2t^2 + 48t - 286$, $g_1(t) = -2t^2 + 12t - 16$, $g_2(t) = -2t^2 + 20t - 48$, $g_3(t) = -\frac{1}{2}t^2 + 6t - 16$, $g_4(t) = -2t^2 + 36t - 160$, $g_5(t) = -\frac{1}{2}t^2 + 10t - 48$ and $g_6(t) = -\frac{2}{9}t^2 + \frac{44}{9}t - \frac{224}{9}$

Case B2 (Fig. 6)

$h_1(t) = h_2(t) = h_3(t) = -\frac{2}{9}t^2 + \frac{16}{9}t - \frac{14}{9}$, $h_4(t) = h_5(t) = -\frac{1}{2}t^2 + 9t - \frac{77}{2}$, $h_6(t) = -2t^2 + 48t - 286$, $g_1(t) = -2t^2 + 12t - 16$, $g_2(t) = g_3(t) = -\frac{1}{2}t^2 + 6t - 16$, $g_4(t) = g_5(t) = g_6(t) = -\frac{2}{9}t^2 + \frac{44}{9}t - \frac{224}{9}$.

Each case starts as a rather idealized population in which

TABLE 3. Genotypic and phenotypic neg-entropy of the system at G_0 , G_{20} and percentage of change

Case	$H_{g(0)}$	$H_{g(20)}$	$A_g(\%)$	$H_{p(0)}$	$H_{p(20)}$	$A_p(\%)$
A1	5.170	4.531	-12.36	0.650	0.727	+11.85
A2	5.170	4.458	-13.77	0.888	0.977	+10.02
A31	5.170	4.448	-13.97	0.964	0.986	+2.28
A32	5.170	3.296	-36.25	0.852	0.996	+16.90
B1	5.170	4.219	-18.39	0.998	0.995	-0.30
B2	5.170	4.394	-15.01	0.964	0.861	-10.68

all the genotypes are present at the same frequency, 1/36 (double heterozygotes with half their frequencies for each linkage phase and $r = 0.5$). In all cases the model was run over 20 generations.

RESULTS

From the assumption of 45 possible genotypes, we analysed the changes undergone in (1) asynchrony and (2) single locus heterozygosity over time. Overall, the irruption of SI

TABLE 4. Frequency of asynchronous phenotypes over 20 generations for each type of expression

Generation	A1	A2	A31	A32	B1	B2
0	0.83	0.69	0.61	0.72	0.53	0.39
1	0.76	0.61	0.42	0.71	0.45	0.31
2	0.78	0.60	0.44	0.64	0.46	0.30
3	0.80	0.60	0.43	0.59	0.46	0.30
4	0.80	0.59	0.43	0.58	0.46	0.29
5	0.80	0.59	0.43	0.56	0.46	0.29
6	0.80	0.59	0.43	0.55	0.46	0.28
7	0.80	0.59	0.43	0.55	0.46	0.28
8	0.80	0.59	0.43	0.54	0.46	0.28
9	0.80	0.59	0.43	0.54	0.46	0.28
10	0.80	0.59	0.43	0.54	0.46	0.28
11	0.80	0.59	0.43	0.54	0.46	0.28
12	0.80	0.59	0.43	0.54	0.46	0.28
13	0.80	0.59	0.43	0.54	0.46	0.28
14	0.80	0.59	0.43	0.54	0.46	0.28
15	0.80	0.59	0.43	0.54	0.46	0.28
16	0.80	0.59	0.43	0.53	0.46	0.28
17	0.80	0.59	0.43	0.53	0.46	0.28
18	0.80	0.59	0.43	0.53	0.46	0.28
19	0.80	0.59	0.43	0.53	0.46	0.28
20	0.80	0.59	0.43	0.53	0.46	0.28

TABLE 5. Genotypic frequencies in initial generations and in the final one, and types of flowering times corresponding to case A1

Genotype	G_0	G_1	G_2	G_3	...	G_{20}	Flowering time
$A_1A_1B_1B_1$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
$A_1A_1B_1B_2$	0.0278	0.0309	0.0158	0.0154	...	0.0150	Asynchronous
$A_1A_1B_2B_2$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
$A_1A_1B_1B_3$	0.0278	0.0309	0.0158	0.0154	...	0.0150	Asynchronous
$A_1A_1B_2B_3$	0.0278	0.0123	0.0279	0.0271	...	0.0270	Asynchronous
$A_1A_1B_3B_3$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
$A_1A_2B_1B_1$	0.0278	0.0324	0.0354	0.0285	...	0.0284	Asynchronous
$A_1A_2B_1B_2$	0.0278	0.0801	0.0732	0.0679	...	0.0676	Synchronous
$A_1A_2B_2B_2$	0.0278	0.0324	0.0354	0.0285	...	0.0284	Asynchronous
$A_1A_2B_1B_3$	0.0278	0.0524	0.0559	0.0647	...	0.0652	Asynchronous
$A_1A_2B_2B_3$	0.0278	0.0524	0.0559	0.0647	...	0.0652	Asynchronous
$A_1A_2B_3B_3$	0.0278	0.0093	0.0177	0.0211	...	0.0216	Asynchronous
$A_2A_2B_1B_1$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
$A_2A_2B_1B_2$	0.0278	0.0309	0.0158	0.0154	...	0.0150	Asynchronous
$A_2A_2B_2B_2$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
$A_2A_2B_1B_3$	0.0278	0.0324	0.0354	0.0285	...	0.0284	Asynchronous
$A_2A_2B_2B_3$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
$A_2A_3B_1B_1$	0.0278	0.0324	0.0354	0.0285	...	0.0284	Asynchronous
$A_2A_3B_1B_2$	0.0278	0.0524	0.0559	0.0647	...	0.0652	Asynchronous
$A_2A_3B_2B_2$	0.0278	0.0123	0.0279	0.0271	...	0.0270	Asynchronous
$A_2A_3B_1B_3$	0.0278	0.0324	0.0354	0.0285	...	0.0284	Asynchronous
$A_2A_3B_2B_3$	0.0278	0.0093	0.0177	0.0211	...	0.0216	Asynchronous
$A_2A_3B_3B_3$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
$A_3A_3B_1B_1$	0.0278	0.0324	0.0354	0.0285	...	0.0284	Asynchronous
$A_3A_3B_1B_2$	0.0278	0.0123	0.0279	0.0271	...	0.0270	Asynchronous
$A_3A_3B_2B_2$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
$A_3A_3B_1B_3$	0.0278	0.0309	0.0158	0.0154	...	0.0150	Asynchronous
$A_3A_3B_2B_3$	0.0278	0.0309	0.0158	0.0154	...	0.0150	Asynchronous
$A_3A_3B_3B_3$	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous

TABLE 6. Genotypic frequencies in initial generations and in the final one, and types of flowering times corresponding to case A2

Genotype	G ₀	G ₁	G ₂	G ₃	...	G ₂₀	Flowering time
A ₁ A ₁ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₁ A ₁ B ₁ B ₂	0.0278	0.0238	0.0052	0.0069	...	0.0092	Asynchronous
A ₁ A ₁ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₁ B ₁ B ₃	0.0278	0.0272	0.0235	0.0170	...	0.0210	Asynchronous
A ₁ A ₁ B ₂ B ₃	0.0278	0.0102	0.0244	0.0188	...	0.0245	Asynchronous
A ₁ A ₁ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₂ B ₁ B ₁	0.0278	0.0357	0.0346	0.0279	...	0.0326	Synchronous
A ₁ A ₂ B ₁ B ₂	0.0278	0.0766	0.0771	0.0741	...	0.0830	Synchronous
A ₁ A ₂ B ₂ B ₂	0.0278	0.0255	0.0356	0.0375	...	0.0420	Asynchronous
A ₁ A ₂ B ₁ B ₃	0.0278	0.0562	0.0471	0.0428	...	0.0410	Asynchronous
A ₁ A ₂ B ₂ B ₃	0.0278	0.0460	0.0552	0.0526	...	0.0467	Asynchronous
A ₁ A ₂ B ₃ B ₃	0.0278	0.0102	0.0064	0.0082	...	0.0054	Asynchronous
A ₂ A ₂ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₂ A ₂ B ₁ B ₂	0.0278	0.0374	0.0213	0.0230	...	0.0162	Asynchronous
A ₂ A ₂ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₂ A ₂ B ₁ B ₃	0.0278	0.0136	0.0203	0.0188	...	0.0137	Synchronous
A ₂ A ₂ B ₂ B ₃	0.0278	0.0306	0.0222	0.0195	...	0.0139	Asynchronous
A ₂ A ₂ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₃ B ₁ B ₁	0.0278	0.0281	0.0316	0.0310	...	0.0394	Asynchronous
A ₁ A ₃ B ₁ B ₂	0.0278	0.0596	0.0708	0.0822	...	0.0990	Synchronous
A ₁ A ₃ B ₂ B ₂	0.0278	0.0204	0.0326	0.0412	...	0.0465	Asynchronous
A ₁ A ₃ B ₁ B ₃	0.0278	0.0646	0.0524	0.0531	...	0.0573	Synchronous
A ₁ A ₃ B ₂ B ₃	0.0278	0.0528	0.0573	0.0619	...	0.0628	Asynchronous
A ₁ A ₃ B ₃ B ₃	0.0278	0.0230	0.0106	0.0133	...	0.0095	Asynchronous
A ₂ A ₃ B ₁ B ₁	0.0278	0.0179	0.0225	0.0208	...	0.0256	Asynchronous
A ₂ A ₃ B ₁ B ₂	0.0278	0.0680	0.0806	0.0848	...	0.0838	Asynchronous
A ₂ A ₃ B ₂ B ₂	0.0278	0.0357	0.0426	0.0460	...	0.0454	Synchronous
A ₂ A ₃ B ₁ B ₃	0.0278	0.0562	0.0533	0.0517	...	0.0426	Asynchronous
A ₂ A ₃ B ₂ B ₃	0.0278	0.0782	0.0791	0.0731	...	0.0557	Synchronous
A ₂ A ₃ B ₃ B ₃	0.0278	0.0281	0.0190	0.0168	...	0.0096	Asynchronous
A ₃ A ₃ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₂	0.0278	0.0204	0.0239	0.0282	...	0.0250	Asynchronous
A ₃ A ₃ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₃	0.0278	0.0272	0.0279	0.0271	...	0.0250	Asynchronous
A ₃ A ₃ B ₂ B ₃	0.0278	0.0272	0.0219	0.0215	...	0.0238	Synchronous
A ₃ A ₃ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous

variants in G₁ decreases the frequency of asynchronous phenotypes (Table 4), although not with the same intensity. Cases A31 and A32 (dominance for location but not for range) show the greatest differences between G₀ and G₂₀ with asynchronous phenotypes decreasing from 61 to 43 % in A31 and from 72 to 53 % in A32. The existence of dominance for range results in smaller differences between G₀ and G₂₀ with asynchronous phenotypes decreasing from 53 to 43 % in B1 and 39 to 28 % in B2.

Thus, the transformations undergone by the genetic structures do not have the same magnitude at the phenotypic level compared to the genotypic level. In order to assess the degree of transformation at both levels we calculated the value of neg-entropy (Brillouin, 1960) at G₀ and G₂₀ in each case, and then the percentage of change in that measure. The measures employed are defined as:

$$H_{g(k)} = - \sum_{i=1}^6 \sum_{j=1}^6 P_{ij}^{(k)} \log_2 P_{ij}^{(k)} \quad \text{and}$$

$$H_{p(k)} = -f^{(k)}(A) \log_2 f^{(k)}(A) - f^{(k)}(S) \log_2 f^{(k)}(S)$$

where H_{g(k)} stands for the genotypic entropy at G_k, H_{p(k)} for

phenotypic entropy at G_k, f^(k)(A) for the frequency of asynchronous phenotypes at G_k and f^(k)(S) for the frequency of synchronous phenotypes. The figures obtained are presented in Table 3. The percentage of change at the phenotypic level is lower (much lower in some cases) than that at the genotypic level. In case B1, for example, asynchrony seems to remain undisturbed (-0.30 %) while a great deal of change at the genotypic level has taken place. While genotypic structures have organized around some genotypes in G₂₀ [$\Delta_g(\%)$ is negative in all cases], phenotypic structures, on the other hand, have become more disorganized [$\Delta_p(\%)$ positive] or at least are less organized than genotypic ones [$\Delta_p(\%)$ negative in cases B₁ and B₂].

We will now consider these properties in particular.

Asynchrony

In Tables 4–10, we have presented, for brevity, only the first four plus the last generations because most of the transformations in genetic structure take place in the first generations. Asynchrony appears as the most stable feature over time. Except for case A32 [in which there is 25 %

TABLE 7. Genotypic frequencies in initial generations and in the final one, and types of flowering times corresponding to case A31

Genotype	G ₀	G ₁	G ₂	G ₃	...	G ₂₀	Flowering time
A ₁ A ₁ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₁ A ₁ B ₁ B ₂	0.0278	0.0380	0.0394	0.0404	...	0.0422	Synchronous
A ₁ A ₁ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₁ B ₁ B ₃	0.0278	0.0380	0.0379	0.0389	...	0.0412	Synchronous
A ₁ A ₁ B ₂ B ₃	0.0278	0.0253	0.0429	0.0438	...	0.0473	Asynchronous
A ₁ A ₁ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₂ B ₁ B ₁	0.0278	0.0475	0.0496	0.0498	...	0.0492	Synchronous
A ₁ A ₂ B ₁ B ₂	0.0278	0.0902	0.0911	0.0936	...	0.0931	Synchronous
A ₁ A ₂ B ₂ B ₂	0.0278	0.0261	0.0221	0.0214	...	0.0207	Asynchronous
A ₁ A ₂ B ₁ B ₃	0.0278	0.0776	0.0781	0.0823	...	0.0841	Synchronous
A ₁ A ₂ B ₂ B ₃	0.0278	0.0538	0.0589	0.0595	...	0.0606	Asynchronous
A ₁ A ₂ B ₃ B ₃	0.0278	0.0166	0.0146	0.0158	...	0.0162	Asynchronous
A ₂ A ₂ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₂ A ₂ B ₁ B ₂	0.0278	0.0285	0.0208	0.0210	...	0.0194	Asynchronous
A ₂ A ₂ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₂ A ₂ B ₁ B ₃	0.0278	0.0158	0.0165	0.0167	...	0.0161	Asynchronous
A ₂ A ₂ B ₂ B ₃	0.0278	0.0190	0.0158	0.0140	...	0.0136	Synchronous
A ₂ A ₂ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₃ B ₁ B ₁	0.0278	0.0475	0.0459	0.0461	...	0.0457	Synchronous
A ₁ A ₃ B ₁ B ₂	0.0278	0.0776	0.0774	0.0811	...	0.0809	Synchronous
A ₁ A ₃ B ₂ B ₂	0.0278	0.0166	0.0174	0.0176	...	0.0172	Asynchronous
A ₁ A ₃ B ₁ B ₃	0.0278	0.0776	0.0707	0.0723	...	0.0735	Synchronous
A ₁ A ₃ B ₂ B ₃	0.0278	0.0432	0.0497	0.0492	...	0.0502	Asynchronous
A ₁ A ₃ B ₃ B ₃	0.0278	0.0166	0.0133	0.0133	...	0.0135	Asynchronous
A ₂ A ₃ B ₁ B ₁	0.0278	0.0190	0.0334	0.0300	...	0.0304	Asynchronous
A ₂ A ₃ B ₁ B ₂	0.0278	0.0538	0.0553	0.0541	...	0.0517	Asynchronous
A ₂ A ₃ B ₂ B ₂	0.0278	0.0237	0.0175	0.0150	...	0.0140	Synchronous
A ₂ A ₃ B ₁ B ₃	0.0278	0.0412	0.0460	0.0442	...	0.0436	Asynchronous
A ₂ A ₃ B ₂ B ₃	0.0278	0.0462	0.0372	0.0327	...	0.0308	Synchronous
A ₂ A ₃ B ₃ B ₃	0.0278	0.0142	0.0114	0.0101	...	0.0099	Asynchronous
A ₃ A ₃ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₂	0.0278	0.0158	0.0136	0.0146	...	0.0136	Asynchronous
A ₃ A ₃ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₃	0.0278	0.0158	0.0120	0.0122	...	0.0115	Asynchronous
A ₃ A ₃ B ₂ B ₃	0.0278	0.0148	0.0113	0.0101	...	0.0098	Asynchronous
A ₃ A ₃ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous

variation from G₀ to G₂₀ (Table 8)], asynchrony remains constant over time in spite of underlying genotypic variation. The most asynchronous system is A1 with a tendency to stabilize at a high level over time [more than 80 % of asynchronous individuals (Table 4)]; the least asynchronous system is B2 with a tendency to stabilize in 28 % of individuals flowering asynchronously (Table 10). The other scores are intermediate, with A2 approx. 60 % (Table 6), A31 approx. 43 % (Table 7), A32 approx. 53 % (Table 8) (with some steep variation during the first four generations) and B1 around 46 % (Table 9). Dominance for flowering times (both in range and location) is negatively associated with asynchrony, and asynchrony drops off over time even when the initial frequency of asynchronous phenotypes is high (as in case A32).

Single locus genotypic frequencies and variability

All the cases start with 50 % heterozygosity in each locus with zero variance (all the genotypes have the same frequency, 1/6). Due to the mechanism of SI, heterozygosity tends to increase in all systems, but the increase varies between cases and loci.

In cases A1 and A2, locus A heterozygosity reaches 83 %; locus B, however, reaches 77 % and stabilizes at that value in A1 and at 74 % in A2. In the case of A31 both loci behave similarly reaching 78 % in G₄–G₅ and remaining at that value over time.

When dominance changes direction with respect to ovule availability (case A32), locus B becomes more heterozygous than locus A. In G₂, heterozygosity increases in both loci (78 %). Then, locus A decreases monotonically with its degree of heterozygosity remaining at 60 %. Locus B, instead, increases, stabilizing at 88 % over time.

In cases B1 and B2, gene A heterozygosity stabilizes at 71 % and 76 %, respectively. Gene B increases monotonically, stabilizing at 83 % in B1 and 80 % in B2.

With respect to genetic variability at each locus, we have computed the coefficients of variation of genotypic frequencies in each generation, including the six genotypes for each locus in the calculation.

In all the cases considered here, locus B is less variable than locus A. The greatest degree of variability in locus A is found in system A32 because of the relatively high frequency of genotype A₂A₃: the coefficient stabilizes at 136 % after G₁₂. The other cases are less variable with

TABLE 8. Genotypic frequencies in initial generations and in the final one, and types of flowering times corresponding to case A32

Genotype	G ₀	G ₁	G ₂	G ₃	...	G ₂₀	Flowering time
A ₁ A ₁ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₁ B ₁ B ₂	0.0278	0.0160	0.0015	0.0003	...	0.0000	Asynchronous
A ₁ A ₁ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₁ B ₁ B ₃	0.0278	0.0098	0.0012	0.0002	...	0.0000	Asynchronous
A ₁ A ₁ B ₂ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₁ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₁ A ₂ B ₁ B ₁	0.0278	0.0229	0.0157	0.0078	...	0.0004	Asynchronous
A ₁ A ₂ B ₁ B ₂	0.0278	0.0375	0.0313	0.0144	...	0.0007	Asynchronous
A ₁ A ₂ B ₂ B ₂	0.0278	0.0048	0.0107	0.0041	...	0.0000	Asynchronous
A ₁ A ₂ B ₁ B ₃	0.0278	0.0233	0.0277	0.0138	...	0.0007	Asynchronous
A ₁ A ₂ B ₂ B ₃	0.0278	0.0102	0.0132	0.0122	...	0.0006	Asynchronous
A ₁ A ₂ B ₃ B ₃	0.0278	0.0029	0.0073	0.0036	...	0.0000	Synchronous
A ₂ A ₂ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₂ A ₂ B ₁ B ₂	0.0278	0.0128	0.0105	0.0123	...	0.0182	Asynchronous
A ₂ A ₂ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₂ A ₂ B ₁ B ₃	0.0278	0.0068	0.0128	0.0122	...	0.0182	Asynchronous
A ₂ A ₂ B ₂ B ₃	0.0278	0.0102	0.0229	0.0241	...	0.0365	Synchronous
A ₂ A ₂ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₃ B ₁ B ₁	0.0278	0.0219	0.0083	0.0046	...	0.0000	Asynchronous
A ₁ A ₃ B ₁ B ₂	0.0278	0.0791	0.0484	0.0329	...	0.0008	Asynchronous
A ₁ A ₃ B ₂ B ₂	0.0278	0.0358	0.0091	0.0113	...	0.0000	Asynchronous
A ₁ A ₃ B ₁ B ₃	0.0278	0.0651	0.0450	0.0293	...	0.0008	Asynchronous
A ₁ A ₃ B ₂ B ₃	0.0278	0.0858	0.0492	0.0325	...	0.0004	Asynchronous
A ₁ A ₃ B ₃ B ₃	0.0278	0.0339	0.0058	0.0095	...	0.0000	Synchronous
A ₂ A ₃ B ₁ B ₁	0.0278	0.0232	0.0338	0.0410	...	0.0471	Asynchronous
A ₂ A ₃ B ₁ B ₂	0.0278	0.0846	0.1078	0.1310	...	0.1646	Asynchronous
A ₂ A ₃ B ₂ B ₂	0.0278	0.0406	0.0306	0.0401	...	0.0376	Synchronous
A ₂ A ₃ B ₁ B ₃	0.0278	0.0688	0.0988	0.1236	...	0.1646	Asynchronous
A ₂ A ₃ B ₂ B ₃	0.0278	0.0960	0.1048	0.1276	...	0.1570	Synchronous
A ₂ A ₃ B ₃ B ₃	0.0278	0.0368	0.0229	0.0371	...	0.0376	Asynchronous
A ₃ A ₃ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₃ A ₃ B ₁ B ₂	0.0278	0.0563	0.0907	0.1058	...	0.1165	Synchronous
A ₃ A ₃ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₃	0.0278	0.0504	0.0903	0.1001	...	0.1165	Synchronous
A ₃ A ₃ B ₂ B ₃	0.0278	0.0645	0.0892	0.0684	...	0.0851	Asynchronous
A ₃ A ₃ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous

coefficients below 74 %. Locus B is less variable, with the highest degree of variability again in case A32 (76%), the other cases being slightly less variable (case B2 is the least variable with 64% variation).

DISCUSSION AND CONCLUSIONS

Our simulation has shown stable genetic structures (Jacquard, 1978) with respect to asynchrony. Over 20 generations under the same reproductive conditions (open pollination, gametophytic SI, no overlapping generations), all the systems modelled reached steady state equilibria (Crow and Kimura, 1970). Thus, if reproductive behaviour is under genetic control (as may, very reasonably, be argued) (Pors and Werner, 1989), even with simple genetic models such as the one employed here, real situations in which SI and asynchrony are found together may be simulated and explored.

The existence of SI makes the occurrence of a proportion of synchronous phenotypes in the population necessary (otherwise, the population risks extinction). The cohesive power of SI (Brooks and Wiley, 1988) can be seen in the

depressor effect that the introduction of SI phenotypes has on the level of asynchrony (Tables 3 and 4). However, considering the values in Table 3, it may be noted that the impact of the encroaching SI variants is much less intense at the phenotypic than at the genotypic level.

It must be stressed that we are not considering genetic differences with respect to viability, i.e. we are assuming that selection does not operate. We are trying to explain the existence of completely (and not completely) asynchronous phenotypes as a by-product of reproductive behaviour only. Clearly, differences in viability may favour asynchronous variants, even in the absence of SI, but this should exert a stronger influence on the system that must be explained (and demonstrated in real experiments). So, a model without selective differential pressure (such as the one presented here) has weaker assumptions. We have constructed systems with different degrees of asynchrony only assuming various modes of gene expression for this trait.

Dominance in opposite directions with respect to flowering time (dominance of early variants in locus A and late variants in locus B) is negatively associated with asynchrony, even in the case of disrupting dominance as in

TABLE 9. Genotypic frequencies in initial generations and in the final one, and types of flowering times corresponding to case B1

Genotype	G ₀	G ₁	G ₂	G ₃	...	G ₂₀	Flowering time
A ₁ A ₁ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₁ A ₁ B ₁ B ₂	0.0278	0.0132	0.0051	0.0025	...	0.0030	Synchronous
A ₁ A ₁ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₁ B ₁ B ₃	0.0278	0.0120	0.0050	0.0026	...	0.0033	Synchronous
A ₁ A ₁ B ₂ B ₃	0.0278	0.0150	0.0099	0.0051	...	0.0063	Asynchronous
A ₁ A ₁ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₂ B ₁ B ₁	0.0278	0.0189	0.0113	0.0084	...	0.0170	Synchronous
A ₁ A ₂ B ₁ B ₂	0.0278	0.0633	0.0521	0.0486	...	0.0652	Synchronous
A ₁ A ₂ B ₂ B ₂	0.0278	0.0320	0.0215	0.0211	...	0.0210	Asynchronous
A ₁ A ₂ B ₁ B ₃	0.0278	0.0701	0.0609	0.0583	...	0.0717	Synchronous
A ₁ A ₂ B ₂ B ₃	0.0278	0.0855	0.0789	0.0714	...	0.0692	Asynchronous
A ₁ A ₂ B ₃ B ₃	0.0278	0.0377	0.0306	0.0307	...	0.0251	Asynchronous
A ₂ A ₂ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₂ A ₂ B ₁ B ₂	0.0278	0.0364	0.0558	0.0666	...	0.0878	Asynchronous
A ₂ A ₂ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₂ A ₂ B ₁ B ₃	0.0278	0.0421	0.0645	0.0782	...	0.0961	Synchronous
A ₂ A ₂ B ₂ B ₃	0.0278	0.0486	0.0526	0.0526	...	0.0564	Synchronous
A ₂ A ₂ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₁ A ₃ B ₁ B ₁	0.0278	0.0167	0.0064	0.0041	...	0.0065	Asynchronous
A ₁ A ₃ B ₁ B ₂	0.0278	0.0338	0.0218	0.0169	...	0.0182	Synchronous
A ₁ A ₃ B ₂ B ₂	0.0278	0.0115	0.0150	0.0128	...	0.0109	Asynchronous
A ₁ A ₃ B ₁ B ₃	0.0278	0.0469	0.0286	0.0226	...	0.0219	Synchronous
A ₁ A ₃ B ₂ B ₃	0.0278	0.0422	0.0473	0.0398	...	0.0301	Asynchronous
A ₁ A ₃ B ₃ B ₃	0.0278	0.0221	0.0255	0.0209	...	0.0152	Asynchronous
A ₂ A ₃ B ₁ B ₁	0.0278	0.0054	0.0043	0.0025	...	0.0034	Asynchronous
A ₂ A ₃ B ₁ B ₂	0.0278	0.0500	0.0590	0.0679	...	0.0731	Asynchronous
A ₂ A ₃ B ₂ B ₂	0.0278	0.0331	0.0372	0.0379	...	0.0309	Synchronous
A ₂ A ₃ B ₁ B ₃	0.0278	0.0688	0.0759	0.0868	...	0.0854	Asynchronous
A ₂ A ₃ B ₂ B ₃	0.0278	0.0978	0.1281	0.1350	...	0.1057	Synchronous
A ₂ A ₃ B ₃ B ₃	0.0278	0.0477	0.0561	0.0558	...	0.0399	Synchronous
A ₃ A ₃ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₂	0.0278	0.0093	0.0123	0.0130	...	0.0106	Asynchronous
A ₃ A ₃ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₃	0.0278	0.0205	0.0179	0.0192	...	0.0145	Asynchronous
A ₃ A ₃ B ₂ B ₃	0.0278	0.0197	0.0164	0.0190	...	0.0114	Synchronous
A ₃ A ₃ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous

cases A32 and B2 in this study. This fact has an interesting evolutionary implication: selection, in general, is more efficient in the absence of dominance for fitness (Spiess, 1989) because it can operate on heterozygotes. Therefore, if these genotypes for flowering time were associated with Darwinian fitness, we would assume that synchrony would be more easily altered, i.e. asynchrony is a trait that would have a high degree of adaptedness, and the pressure of SI towards higher cohesion (although decreasing the level of asynchrony) would not prevent this. This fact makes asynchrony an important character for the stable evolution of the population. We have analysed a further case (not presented here) in which the degree of dominance in opposite directions was even higher: alleles A₁ and A₂ were equally dominant over A₃ (A₁ = A₂ > A₃), and B₃ = B₂ > B₁, for locus B. Under these conditions, the degree of asynchrony dropped more than in case B2, the least asynchronous case analysed here.

Heterozygosity

In cases A1 and A2 there are higher degrees of potential

genetic variability (heterozygosity) for pollen availability (locus A) than for ovules (locus B); when there is dominance (both for location and range), the degree of potential variability switches to ovules, although the differences between the with-dominance and the without-dominance cases are not high. There seems to be no clear association between asynchrony and degree of actual genetic variability (measured by the coefficient of variation of genotypic frequencies). Therefore, bearing in mind that selection is more efficient under no-dominance (see preceding paragraph), presumably most of the evolutionary resources with respect to asynchrony will be transferred to pollen. In other words, it is *siring* the trait that will probably adapt more rapidly—at least under the boundary conditions assumed in this model. It would be worth investigating if this is generally the case in nature.

Asynchrony could be studied in actual annual populations of known phenological behaviour to search for genetic variants. Obviously, a more complex genetic basis could be found than the one assumed here (for example, given a greater number of alleles per locus the degree of asynchrony would be higher). In fact, the frequency of asynchronous

TABLE 10. Genotypic frequencies in initial generations and in the final one, and types of flowering times corresponding to case B2

Genotype	G ₀	G ₁	G ₂	G ₃	...	G ₂₀	Flowering time
A ₁ A ₁ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₁ A ₁ B ₁ B ₂	0.0278	0.0092	0.0065	0.0049	...	0.0038	Synchronous
A ₁ A ₁ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₁ B ₁ B ₃	0.0278	0.0092	0.0065	0.0049	...	0.0038	Synchronous
A ₁ A ₁ B ₂ B ₃	0.0278	0.0137	0.0130	0.0098	...	0.0075	Asynchronous
A ₁ A ₁ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₁ A ₂ B ₁ B ₁	0.0278	0.0155	0.0129	0.0109	...	0.0112	Synchronous
A ₁ A ₂ B ₁ B ₂	0.0278	0.0500	0.0345	0.0402	...	0.0382	Synchronous
A ₁ A ₂ B ₂ B ₂	0.0278	0.0254	0.0224	0.0219	...	0.0194	Asynchronous
A ₁ A ₂ B ₁ B ₃	0.0278	0.0500	0.0345	0.0402	...	0.0382	Synchronous
A ₁ A ₂ B ₂ B ₃	0.0278	0.0634	0.0626	0.0594	...	0.0520	Asynchronous
A ₁ A ₂ B ₃ B ₃	0.0278	0.0254	0.0224	0.0219	...	0.0194	Asynchronous
A ₂ A ₂ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₂ A ₂ B ₁ B ₂	0.0278	0.0276	0.0283	0.0309	...	0.0330	Synchronous
A ₂ A ₂ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₂ A ₂ B ₁ B ₃	0.0278	0.0276	0.0283	0.0309	...	0.0330	Synchronous
A ₂ A ₂ B ₂ B ₃	0.0278	0.0373	0.0346	0.0359	...	0.0348	Synchronous
A ₂ A ₂ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₁ A ₃ B ₁ B ₁	0.0278	0.0152	0.0130	0.0112	...	0.0121	Synchronous
A ₁ A ₃ B ₁ B ₂	0.0278	0.0509	0.0452	0.0427	...	0.0429	Synchronous
A ₁ A ₃ B ₂ B ₂	0.0278	0.0262	0.0230	0.0227	...	0.0206	Asynchronous
A ₁ A ₃ B ₁ B ₃	0.0278	0.0509	0.0452	0.0427	...	0.0429	Synchronous
A ₁ A ₃ B ₂ B ₃	0.0278	0.0656	0.0650	0.0622	...	0.0566	Asynchronous
A ₁ A ₃ B ₃ B ₃	0.0278	0.0262	0.0230	0.0227	...	0.0206	Asynchronous
A ₂ A ₃ B ₁ B ₁	0.0278	0.0066	0.0086	0.0071	...	0.0075	Asynchronous
A ₂ A ₃ B ₁ B ₂	0.0278	0.0619	0.0689	0.0738	...	0.0817	Synchronous
A ₂ A ₃ B ₂ B ₂	0.0278	0.0413	0.0442	0.0442	...	0.0432	Synchronous
A ₂ A ₃ B ₁ B ₃	0.0278	0.0619	0.0689	0.0738	...	0.0817	Synchronous
A ₂ A ₃ B ₂ B ₃	0.0278	0.1016	0.1280	0.1336	...	0.1326	Synchronous
A ₂ A ₃ B ₃ B ₃	0.0278	0.0413	0.0442	0.0442	...	0.0432	Synchronous
A ₃ A ₃ B ₁ B ₁	0.0278	0.0000	0.0000	0.0000	...	0.0000	Asynchronous
A ₃ A ₃ B ₁ B ₂	0.0278	0.0278	0.0308	0.0346	...	0.0403	Asynchronous
A ₃ A ₃ B ₂ B ₂	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous
A ₃ A ₃ B ₁ B ₃	0.0278	0.0278	0.0308	0.0346	...	0.0403	Asynchronous
A ₃ A ₃ B ₂ B ₃	0.0278	0.0387	0.0368	0.0386	...	0.0397	Synchronous
A ₃ A ₃ B ₃ B ₃	0.0278	0.0000	0.0000	0.0000	...	0.0000	Synchronous

phenotypes in situations such as in case A1—complete asynchrony for some genotypes—will be, with n alleles per locus, $\frac{n^2+n-2}{n^2+n}$ allowing for a wider genetic basis supporting the flowering behaviour. Thus, greater degrees of stable asynchrony may be found in nature.

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APPENDIX

Frequencies of pollen and ovules generated by meiosis

For the sake of brevity in the following expressions, $P_{ij}^{(n)}$ will be written simply as P_{ij} .
Pollen

$$f_p^{(n)}(A_1B_1)(t) = \left\{ \begin{array}{l} [(2P_{11} + P_{12} + P_{13})h_1(t) + (P_{21} + [P_{221} + P_{231}][1-r] + [P_{222} + P_{232}]r)h_2(t)] \\ + (P_{31} + [P_{321} + P_{331}][1-r] + [P_{322} + P_{332}]r)h_3(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_1B_2)(t) = \left\{ \begin{array}{l} [(2P_{14} + P_{12} + P_{15})h_1(t) + (P_{24} + [P_{221} + P_{252}][1-r] + [P_{222} + P_{251}]r)h_2(t)] \\ + (P_{34} + [P_{322} + P_{351}][1-r] + [P_{321} + P_{352}]r)h_3(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_1B_3)(t) = \left\{ \begin{array}{l} [(2P_{16} + P_{13} + P_{15})h_1(t) + (P_{26} + [P_{231} + P_{251}][1-r] + [P_{232} + P_{252}]r)h_2(t)] \\ + (P_{36} + [P_{331} + P_{351}]r + [P_{332} + P_{352}]r)[1-r]h_3(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_2B_1)(t) = \left\{ \begin{array}{l} [(2P_{41} + P_{42} + P_{43})h_4(t) + (P_{51} + [P_{521} + P_{531}][1-r] + [P_{522} + P_{532}]r)h_5(t)] \\ + (P_{21} + [P_{221} + P_{231}]r + [P_{222} + P_{232}][1-r])h_2(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_2B_2)(t) = \left\{ \begin{array}{l} [(2P_{44} + P_{42} + P_{45})h_4(t) + (P_{24} + [P_{221} + P_{252}][1-r] + [P_{222} + P_{251}]r)h_2(t)] \\ + (P_{54} + [P_{521} + P_{552}]r + [P_{522} + P_{551}][1-r])h_5(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_2B_3)(t) = \left\{ \begin{array}{l} [(2P_{46} + P_{43} + P_{45})h_4(t) + (P_{26} + [P_{231} + P_{251}][1-r] + [P_{232} + P_{252}]r)h_2(t)] \\ + (P_{56} + [P_{531} + P_{551}]r + [P_{532} + P_{552}]r)[1-r]h_5(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_3B_1)(t) = \left\{ \begin{array}{l} [(2P_{61} + P_{62} + P_{63})h_6(t) + (P_{31} + [P_{321} + P_{331}]r + [P_{322} + P_{332}]r)[1-r]h_3(t)] \\ + (P_{51} + [P_{521} + P_{531}]r + [P_{522} + P_{532}]r)[1-r]h_5(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_3B_2)(t) = \left\{ \begin{array}{l} [(2P_{64} + P_{62} + P_{65})h_6(t) + (P_{34} + [P_{321} + P_{352}][1-r] + [P_{322} + P_{351}]r)h_3(t)] \\ + (P_{54} + [P_{521} + P_{552}][1-r] + [P_{522} + P_{551}]r)h_5(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

$$f_p^{(n)}(A_3B_3)(t) = \left\{ \begin{array}{l} [(2P_{66} + P_{65} + P_{63})h_6(t) + (P_{36} + [P_{331} + P_{351}][1-r] + [P_{332} + P_{352}]r)h_3(t)] \\ + (P_{56} + [P_{531} + P_{551}][1-r] + [P_{532} + P_{552}]r)h_5(t) \end{array} \right\} \frac{N^{(n)}}{2h_T^{(n)}(t)}$$

Ovules

$$f_o^{(n)}(A_1B_1)(t) = \left\{ \begin{array}{l} [(2P_{11} + P_{21} + P_{31})g_1(t) + (P_{12} + [P_{221} + P_{321}][1-r] + [P_{222} + P_{322}]r)g_2(t)] \\ + (P_{13} + [P_{231} + P_{331}][1-r] + [P_{232} + P_{332}]r)g_3(t) \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}$$

$$f_o^{(n)}(A_1B_2)(t) = \left\{ \begin{array}{l} [(2P_{14} + P_{24} + P_{34})g_4(t) + (P_{12} + [P_{222} + P_{322}][1-r] + [P_{221} + P_{321}]r)g_2(t)] \\ + (P_{15} + [P_{251} + P_{351}][1-r] + [P_{252} + P_{352}]r)g_5(t) \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}$$

$$f_o^{(n)}(A_1B_3)(t) = \left\{ \begin{array}{l} [(2P_{16} + P_{26} + P_{36})g_6(t) + (P_{15} + [P_{252} + P_{352}][1-r] + [P_{251} + P_{351}]r)g_5(t)] \\ + (P_{13} + [P_{232} + P_{332}][1-r] + [P_{231} + P_{331}]r)g_3(t) \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}$$

$$f_o^{(n)}(A_2B_1)(t) = \left\{ \begin{array}{l} [(2P_{41} + P_{21} + P_{51})g_1(t) + (P_{42} + [P_{222} + P_{521}][1-r] + [P_{221} + P_{522}]r)g_2(t)] \\ + (P_{43} + [P_{232} + P_{531}][1-r] + [P_{231} + P_{532}]r)g_3(t) \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}$$

$$f_o^{(n)}(A_2B_2)(t) = \left\{ \begin{array}{l} [(2P_{44} + P_{24} + P_{54})g_4(t) + (P_{42} + [P_{221} + P_{522}][1-r] + [P_{222} + P_{521}]r)g_2(t)] \\ + (P_{45} + [P_{252} + P_{551}][1-r] + [P_{251} + P_{552}]r)g_5(t) \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}$$

$$f_o^{(n)}(A_2B_3)(t) = \left\{ \begin{array}{l} [(2P_{46} + P_{26} + P_{56})g_6(t) + (P_{45} + [P_{251} + P_{552}][1-r] + [P_{252} + P_{551}]r)g_5(t)] \\ + (P_{43} + [P_{231} + P_{532}][1-r] + [P_{232} + P_{531}]r)g_3(t) \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}$$

$$f_o^{(n)}(A_3B_1)(t) = \left\{ \begin{array}{l} [(2P_{61} + P_{51} + P_{31})g_1(t) + (P_{62} + [P_{322} + P_{522}][1-r] + [P_{321} + P_{521}]r)g_2(t)] \\ + (P_{63} + [P_{332} + P_{532}][1-r] + [P_{331} + P_{531}]r)g_3(t) \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}$$

$$f_{\text{O}}^{(n)}(A_3B_2)(t) = \left[\begin{array}{l} \left[(2P_{64} + P_{54} + P_{34})g_4(t) + (P_{62} + [P_{321} + P_{521}][1-r] + [P_{322} + P_{522}]r)g_2(t) \right] \frac{N_{..}^{(n)}}{2g_{\text{T}}^{(n)}(t)} \\ + (P_{65} + [P_{352} + P_{552}][1-r] + [P_{351} + P_{551}]r)g_5(t) \end{array} \right]$$

$$f_{\text{O}}^{(n)}(A_3B_3)(t) = \left[\begin{array}{l} \left[(2P_{66} + P_{56} + P_{36})g_6(t) + (P_{65} + [P_{551} + P_{351}][1-r] + [P_{552} + P_{352}]r)g_5(t) \right] \frac{N_{..}^{(n)}}{2g_{\text{T}}^{(n)}(t)} \\ + (P_{63} + [P_{331} + P_{531}][1-r] + [P_{332} + P_{532}]r)g_3(t) \end{array} \right]$$

Some genotypic frequencies in G_{n+1} under gametophytic SI

Because of the SI mechanism double homozygotes do not exist; thus, at time t :

$$f^{(n+1)}(A_iB_j/A_iB_j)(t) = \pi_{\text{T}}^{(n)}(t)f_{\text{P}}^{(n)}(A_iB_j)(t)\{f_{\text{O}}^{(n)}(A_iB_j)(t)/\text{mother not } A_iB_j/A_iB_j\} = \pi_{\text{T}}^{(n)}(t)f_{\text{P}}^{(n)}(A_iB_j)(t)0 = 0$$

Some of the frequency functions corresponding to simple homozygotes (simple heterozygotes) are:

$$f^{(n+1)}(A_1B_1/A_1B_2)(t) = \pi_{\text{T}}^{(n)}(t) \left[\begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t)\{f_{\text{O}}^{(n)}(A_1B_2)(t)/\text{stigma not } A_1B_1\} \\ + f_{\text{P}}^{(n)}(A_1B_2)(t)\{f_{\text{O}}^{(n)}(A_1B_1)(t)/\text{stigma not } A_1B_2\} \end{array} \right]$$

$$= \pi_{\text{T}}^{(n)}(t) \left\{ \begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t) \left[(2P_{14} + P_{24} + P_{34})g_4(t) + \left(\frac{P_{15} + [P_{251} + P_{351}][1-r]}{[P_{252} + P_{352}]r} \right)g_5(t) \right] \\ + f_{\text{P}}^{(n)}(A_1B_2)(t) \left[(2P_{11} + P_{21} + P_{31})g_1(t) + \left(\frac{P_{13} + [P_{231} + P_{331}][1-r]}{[P_{232} + P_{332}]r} \right)g_3(t) \right] \end{array} \right\} \frac{N_{..}^{(n)}}{2g_{\text{T}}^{(n)}(t)}$$

$$f^{(n+1)}(A_1B_1/A_1B_3)(t) = \pi_{\text{T}}^{(n)}(t) \left[\begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t)\{f_{\text{O}}^{(n)}(A_1B_3)(t)/\text{stigma not } A_1B_1\} \\ + f_{\text{P}}^{(n)}(A_1B_3)(t)\{f_{\text{O}}^{(n)}(A_1B_1)(t)/\text{stigma not } A_1B_3\} \end{array} \right]$$

$$= \pi_{\text{T}}^{(n)}(t) \left\{ \begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t) \left[(2P_{16} + P_{26} + P_{36})g_6(t) + \left(\frac{P_{15} + [P_{252} + P_{352}][1-r]}{[P_{251} + P_{351}]r} \right)g_5(t) \right] \\ + f_{\text{P}}^{(n)}(A_1B_3)(t) \left[(2P_{11} + P_{21} + P_{31})g_1(t) + \left(\frac{P_{12} + [P_{221} + P_{321}][1-r]}{[P_{222} + P_{322}]r} \right)g_2(t) \right] \end{array} \right\} \frac{N_{..}^{(n)}}{2g_{\text{T}}^{(n)}(t)}$$

$$f^{(n+1)}(A_1B_1/A_2B_1)(t) = \pi_{\text{T}}^{(n)}(t) \left[\begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t)\{f_{\text{O}}^{(n)}(A_2B_1)(t)/\text{stigma not } A_1B_1\} \\ + f_{\text{P}}^{(n)}(A_2B_1)(t)\{f_{\text{O}}^{(n)}(A_1B_1)(t)/\text{stigma not } A_2B_1\} \end{array} \right]$$

$$= \pi_{\text{T}}^{(n)}(t) \left\{ \begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t) \left[(2P_{41} + P_{51})g_1(t) + (P_{42} + P_{521}[1-r] + P_{522}r)g_2(t) \right. \\ \left. + (P_{43} + P_{531}[1-r] + P_{532}r)g_3(t) \right] \\ + f_{\text{P}}^{(n)}(A_2B_1)(t) \left[(2P_{11} + P_{31})g_1(t) + (P_{12} + P_{321}[1-r] + P_{322}r)g_2(t) \right. \\ \left. + (P_{13} + P_{331}[1-r] + P_{332}r)g_3(t) \right] \end{array} \right\} \frac{N_{..}^{(n)}}{2g_{\text{T}}^{(n)}(t)}$$

Some functions corresponding to double heterozygotes:

$$f^{(n+1)}(A_1B_1/A_2B_2)(t) = \pi_{\text{T}}^{(n)}(t) \left[\begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t)\{f_{\text{O}}^{(n)}(A_2B_2)(t)/\text{stigma not } A_1B_1\} \\ + f_{\text{P}}^{(n)}(A_2B_2)(t)\{f_{\text{O}}^{(n)}(A_1B_1)(t)/\text{stigma not } A_2B_2\} \end{array} \right]$$

$$= \pi_{\text{T}}^{(n)}(t) \left\{ \begin{array}{l} f_{\text{P}}^{(n)}(A_1B_1)(t) \left[(2P_{44} + P_{24} + P_{54})g_4(t) + (P_{42} + P_{522}[1-r] + P_{521}r)g_2(t) \right. \\ \left. + (P_{45} + [P_{252} + P_{551}][1-r] + [P_{251} + P_{552}]r)g_5(t) \right] \\ + f_{\text{P}}^{(n)}(A_2B_2)(t) \left[(2P_{11} + P_{21} + P_{31})g_1(t) + (P_{12} + P_{321}[1-r] + P_{322}r)g_2(t) \right. \\ \left. + (P_{13} + [P_{231} + P_{331}][1-r] + [P_{232} + P_{332}]r)g_3(t) \right] \end{array} \right\} \frac{N_{..}^{(n)}}{2g_{\text{T}}^{(n)}(t)}$$

$$f^{(n+1)}(A_1B_2/A_2B_1)(t) = \pi_{\text{T}}^{(n)}(t) \left[\begin{array}{l} f_{\text{P}}^{(n)}(A_1B_2)(t)\{f_{\text{O}}^{(n)}(A_2B_1)(t)/\text{stigma not } A_1B_2\} \\ + f_{\text{P}}^{(n)}(A_2B_1)(t)\{f_{\text{O}}^{(n)}(A_1B_2)(t)/\text{stigma not } A_2B_1\} \end{array} \right]$$

$$= \pi_{\text{T}}^{(n)}(t) \left\{ \begin{array}{l} f_{\text{P}}^{(n)}(A_1B_2)(t) \left[(2P_{41} + P_{21} + P_{51})g_1(t) + (P_{42} + P_{521}[1-r] + P_{522}r)g_2(t) \right. \\ \left. + (P_{43} + [P_{232} + P_{531}][1-r] + [P_{231} + P_{532}]r)g_3(t) \right] \\ + f_{\text{P}}^{(n)}(A_2B_1)(t) \left[(2P_{14} + P_{24} + P_{34})g_4(t) + (P_{12} + P_{322}[1-r] + P_{321}r)g_2(t) \right. \\ \left. + (P_{15} + [P_{251} + P_{351}][1-r] + [P_{252} + P_{352}]r)g_5(t) \right] \end{array} \right\} \frac{N_{..}^{(n)}}{2g_{\text{T}}^{(n)}(t)}$$

$$\begin{aligned}
f^{(n+1)}(A_1B_1/A_2B_3)(t) &= \pi_T^{(n)}(t) \left[f_P^{(n)}(A_1B_1)(t) \{f_O^{(n)}(A_2B_3)(t)/\text{stigma not } A_1B_1\} \right. \\
&\quad \left. + f_P^{(n)}(A_2B_3)(t) \{f_O^{(n)}(A_1B_1)(t)/\text{stigma not } A_2B_3\} \right] \\
&= \pi_T^{(n)}(t) \left\{ \begin{array}{l} f_P^{(n)}(A_1B_1)(t) \left[(2P_{46} + P_{26} + P_{56})g_6(t) + (P_{43} + P_{532}[1-r] + P_{531}r)g_3(t) \right. \\ \left. + (P_{45} + [P_{251} + P_{552}][1-r] + [P_{252} + P_{551}]r)g_5(t) \right] \\ + f_P^{(n)}(A_2B_3)(t) \left[(2P_{11} + P_{21} + P_{34})g_1(t) + (P_{13} + P_{331}[1-r] + P_{332}r)g_3(t) \right. \\ \left. + (P_{12} + [P_{221} + P_{321}][1-r] + [P_{222} + P_{322}]r)g_2(t) \right] \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)} \\
f^{(n+1)}(A_1B_3/A_2B_1)(t) &= \pi_T^{(n)}(t) \left[f_P^{(n)}(A_1B_3)(t) \{f_O^{(n)}(A_2B_1)(t)/\text{stigma not } A_1B_3\} \right. \\
&\quad \left. + f_P^{(n)}(A_2B_1)(t) \{f_O^{(n)}(A_1B_3)(t)/\text{stigma not } A_2B_1\} \right] \\
&= \pi_T^{(n)}(t) \left\{ \begin{array}{l} f_P^{(n)}(A_1B_3)(t) \left[(2P_{41} + P_{21} + P_{51})g_1(t) + (P_{43} + P_{531}[1-r] + P_{532}r)g_3(t) \right. \\ \left. + (P_{42} + [P_{222} + P_{521}][1-r] + [P_{221} + P_{522}]r)g_2(t) \right] \\ + f_P^{(n)}(A_2B_1)(t) \left[(2P_{16} + P_{26} + P_{36})g_6(t) + (P_{13} + P_{332}[1-r] + P_{331}r)g_3(t) \right. \\ \left. + (P_{15} + [P_{252} + P_{352}][1-r] + [P_{251} + P_{351}]r)g_5(t) \right] \end{array} \right\} \frac{N^{(n)}}{2g_T^{(n)}(t)}
\end{aligned}$$