

Evolutionary role of gametophytic selection in the domestication of *Pennisetum typhoides* (pearl millet): a two-locus asymmetrical model*

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Gametophytic competition, demonstrated in pearl millet, has been shown to promote homogametic fertilization, especially in the case of wild/cultivated pollen mixtures. Therefore, gametophytic selection can reduce interbreeding between the two forms of pearl millet. A theoretical two-locus asymmetrical model was built in order to evaluate the potential role of pollen competition in the control of gene flow between wild and cultivated pearl millet populations in sympatry. Pollen selection coefficients, estimated in a previous experiment, were input in this model. It was shown that the wild/cultivated hybrid percentage in the cultivated field can be strongly reduced in the presence of strong gametophytic selection. The hybrid percentages obtained from this model were very similar to those observed in natural conditions with pollen migration rates from wild populations ranging between 10 and 40 per cent according to the selective pollen coefficient. It may be concluded from this that pollen competition can contribute to the continuing phenotypic integrity of cultivated forms even when there is an abundance of wild forms adjacent to the field. However, in most cases, an initial divergence between wild and cultivated populations at the homogamy locus, is required for pollen competition to reduce hybridization. This requirement makes it doubtful whether this aspect of reproductive isolation between wild and cultivated forms was involved in domestication.

Keywords: domestication, pearl millet, pollen competition, theoretical modelling.

Introduction

Pearl millet (*Pennisetum typhoides*) is a diploid cereal originating in the Sahel, a region of Africa (Harlan, 1971). Its protogynous flowering habit and abundance of pollen during the flowering period promote outcrossing. Archaeological evidence has shown that this species was already domesticated 3000 years ago in Mauritania (Amblard & Pernès, 1989). Wild forms of pearl millet were then abundant in this area. Now, wild populations belonging to the taxon *Pennisetum violaceum* ($2n = 2x = 14$) are often sympatric with cultivated forms in areas where traditional agricultural systems still exist. Post-zygotic reproductive barriers do not exist between these two forms (Rey-Herme, 1982) so that hybrids (N'douls in the Ouolof language) are found

in cultivated fields. Nevertheless, the percentage of hybrids is low enough that peasants continue to cultivate pearl millet. Thus, domestication of this allogamous cereal can be considered as a successful evolutionary experiment in maintaining divergence of phenotypic structure between wild and cultivated forms, even in areas where wild and field populations are adjacent.

What are the mechanisms underlying this success? Cereal domestication is clearly a case of disruptive selection acting upon different sympatric taxa. For preferentially outcrossing species, this disruptive selection cannot alone explain how the phenotypic structure of cultivated populations can be maintained, especially when there is an abundant pollen flow from wild populations (Laredo & Pernès, 1988).

The establishment of reproductive isolation between adjacent populations connected by gene flow can indirectly be favoured by disruptive selection

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(Dobzhansky, 1940). In other words, speciation could occur in sympatry without any previous allopatric evolution. The basic idea behind this hypothesis is that a gene which reduces gene flow between locally well adapted adjacent populations, will have an advantage because it leads to a lower percentage of less well adapted hybrids. Theoretical studies by Caisse & Antonovics (1978) have shown that phenotypic homogamy due to differential flowering time can lead to the establishment of a prezygotic barrier between populations in sympatry. Moreover, Stam (1983) has shown that such a reproductive isolation between closely adjacent populations, due to homogamy, can be established even without disruptive selection, simply through non-random pollen migration with respect to flowering time. Genetic variability for flowering time is frequent in plant populations. Isolation of adjacent populations, due to differences in flowering time, has been observed to be produced by natural selection in populations of grasses (*Agrostis tenuis* and *Anthoxanthum odoratum*) which grow in mining areas (McNeilly & Antonovics, 1968).

Gametophytic selection is also a factor that contributes to the divergence of populations through homogametic fertilization. Male gametophyte selection due to pollen competition in the style has been demonstrated on pearl millet (Sarr *et al.*, 1988). Pollen selection also exists in other species (see Marshall & Ellstrand, 1986 for a synthesis). Haplo-diploid genetic interactions (pollen-pistil) contribute to determining the fitness of each pollen grain (Sarr *et al.*, 1988; Robert *et al.*, 1989). Such pollen competition promotes homogametic fertilization in pearl millet, as shown by Robert *et al.* (1991) in wild/cultivated pollen competition experiments as well as in analyses of wild/cultivated backcross progenies (Joly-Ichenhauser & Sarr, 1985).

In this paper, we study, by a theoretical model, the role of homogamy due to pollen competition in the domestication of pearl millet, especially in the case of sympatric evolution between wild and cultivated forms.

Model description

General conditions

We modelled adjacent wild and cultivated populations in Africa, as described by Laredo & Pernès (1988). We also took into account the traditional agricultural techniques for pearl millet. Six fundamental assumptions were then made.

1 Farmers harvest only plants with a cultivated phenotype. A fraction of the seed collected is put aside for seeding the following year. Selective pressure is

thus applied to female gametes. Only plants with a cultivated phenotype contribute female gametes to the next generation. All the plants that grew in the field had the same fitness and contributed, to the same extent, to the pollen pool. Farmers therefore only control the transmission of the desirable phenotype through the female.

2 The oldest agricultural systems in Sahel involve rotation and fallows, so there is no continuity of gene flow from cultivated fields to wild populations. The genetic consequences, for wild populations, of gene flow from domesticated forms, were therefore assumed to be very minor. We only studied the evolution of the genetic structure in the cultivated fields. We also assumed the population to be of infinite size. This model is thus a deterministic asymmetrical model.

3 The cultivated or wild phenotype alternatives were assumed to be under the control of a biallelic locus *C/S*. Plants *CC* had the cultivated phenotype and plants *SS* had the wild phenotype. Heterozygotes *CS* had an intermediate phenotype (N'douls). The validity of this hypothesis is justified in the discussion.

4 Each generation, pollen migrates from pure wild populations to the field under cultivation. Migrant pollen has therefore only the *S* genotype. Pollen distribution over the field was homogenous and only *CC* and *CS* plants grew in the field. This assumption is based on the use of the rotation of crops and fallows so that only plants sown by the farmer grew in the field.

5 Self-fertilization was assumed to be almost nil as a consequence of an absolute protogyny.

6 Pollen competitive ability was assumed to have Mendelian inheritance with a biallelic locus *A/B*. Pollen-pistil interactions led to preferential homogametic fertilizations: in *AA* styles, *A* pollen was more competitive than *B* pollen. In *BB* styles, *B* pollen was more competitive than *A* pollen. In *AB* styles, the pollens *A* and *B* had the same competitive ability. This locus was named the 'homogamy locus'. The relative fitnesses of pollens *A* and *B* in *AA* styles were 1 and $1 - s$ respectively, where s was the gametophytic selection coefficient. In *BB* styles, these relative fitnesses became $1 - s$ and 1 respectively. Thus, gametophytic selection was symmetrical.

The gametophytic selection coefficients used in this model were estimated from experimental data on wild and cultivated pollen competition (Robert *et al.*, 1991). These estimates ranged between 0.3 and 0.7.

The other parameters of this model were: r , the genetic recombination rate between the 'domestication' locus and the 'homogamy' locus; m , the pollen migration rate from wild populations to the field; and p_m , the frequency of allele *A* in the migrant pollen. p_m was taken as a constant parameter because wild popula-

tions adjacent to the different field locations were assumed to be at equilibrium for the homogamy locus.

Analytical approach

The following five variables are required to describe the evolution of the allelic frequencies at the two loci through generations.

p the frequency of the A allele in the total pollen (migrant pollen + pollen produced by the plants in the field).

u the frequency of the C allele in the total pollen (migrant pollen + pollen produced by the plants in the field).

D the gametic disequilibrium between the two loci in the total pollen.

g_1 the frequency of AA genotypes among plants with a cultivated phenotype (CC genotypes).

g_3 the frequency of BB genotypes among plants with a cultivated phenotype (CC genotypes).

The five basic recurrence equations of this model are given in the annex. It appeared very complex to derive the analytical solutions to this algebraic system so we only studied the results of simulation runs obtained from a microcomputer program written in BASIC. However, the effect of gametophytic competition on the variation in the frequency of A allele between the capture of pollen by CC stigmas to fertilization stage, can be estimated by one parameter, $d(p)$.

If w_{aa} and w_{bb} are the mean pollen relative fitnesses in AA styles and BB styles, respectively, we obtain the following relations.

$$w_{aa} = 1 - s(1 - p)$$

$$w_{bb} = 1 - sp$$

$$d(p) = sp(1 - p)(g_1/w_{aa} - g_3/w_{bb}), \text{ (see proof 1 in annex).}$$

If $d(p)$ is positive then A is globally favoured during pollen competition on CC plants. If $d(p)$ is negative then B is favoured at the pollen stage. If $d(p) = 0$, there is no change in A allele frequency due to homogamy. $d(p) = 0$ under the following conditions.

- 1 $s = 0$, meaning that no gametophytic selection occurs during reproduction.
- 2 $p = 0$ or $p = 1$, therefore only one allele at the homogamy locus is present in the population. These conditions correspond to the stable equilibria found by Moore (1979) in a one-locus mass-action homogamy model.
- 3 $g_1/w_{aa} - g_3/w_{bb} = 0$, which is equivalent to $g_1/g_3 = w_{aa}/w_{bb}$, i.e. the ratio of AA pistil frequency/ BB pistil frequency is equal to the ratio of the mean pollen relative fitness on these pistils.

It can also be shown that the variation in the frequency of C during reproduction is equal to $d(u) = Dd(p)/p(1 - p)$: proof 2 in the Appendix. As expected, the frequency of C during reproduction changes only if the 'domestication' locus and the 'homogamy' locus are in gametic disequilibrium.

Two stable equilibria, at most, were found in each of the simulation runs, according to the initial frequencies. These two equilibria correspond to those determined by Moore (1979), i.e. the less frequent allele decreases until its total elimination. However, in this model, pollen migration from wild populations maintains polymorphism.

Results from simulations

The runs were carried out using a program written in BASIC on a microcomputer. The pollen migration rate, m , was varied by 0.05 steps and the other parameters of the model were varied by 0.1 steps, as follows: m from 0 to 0.5; r from 0 (meaning complete linkage between the two loci) to 0.5 (genetic independence between the two loci); s from 0.3 to 0.7 (values estimated from experimental work). The value $s = 0$ (no gametophytic selection) was also used as a control.

This model is a mass-action type model because it assumes that homogamy operates on all the individuals of the population and not only on a constant fraction in the population. Moore (1979) has already shown that the most frequent allele has an automatic advantage in a mass-action homogamy system, unless strong selection directly favours the heterozygotes at this locus. This last assumption is not in our model. Thus, the only stable equilibrium for wild populations is the loss of the less frequent allele. However, for a two-allelic locus, an unstable equilibrium is reached when the frequencies of the two alleles are equal to 0.5 (Moore, 1979). In standard runs, p_m was thus set at 0.

The initial hybrid percentage was 0 for all runs (i.e. there were only CC plants in the field). The initial linkage disequilibrium in the field was also 0. If A_1 is the initial frequency of the A allele in the field, the initial value of D (linkage disequilibrium in the total pollen) is then $m(1 - m)(A_1 - p_m)$.

$A_1 - p_m$ is a measure of the initial divergence between the wild population and the field at the homogamy locus. The effect of gametophytic selection on hybrid percentage obviously depends on the amount of difference between the field and the wild population for the A allele frequency at the homogamy locus. The higher this difference is, the stronger the effect of this selection on the fitness of the S pollen grains on CC plants. In a first step, we analysed the evolution of the frequency differences between the two populations for the homogamy locus.

Analysis of the evolution of the frequency differences for the homogamy locus

Table 1 gives the minimum rate of initial divergence between the two populations required for the populations to have frequency differences which persist at equilibrium, when $p_m=0$ and for different pairs of r and s values. When $p_m=0.5$, divergence at the homogamy locus at equilibrium is obtained even with a very low initial divergence (data not shown). Table 1 shows that the higher the migration rate is, the smaller the initial divergence required for differences to persist at equilibrium, except when $r=0.5$ and $s=0.3$. How can this unexpected result be explained?

Figure 1 shows the evolution of the frequency of A in the field when $A_1=0.4$, for two values of m and r , with $s=0.3$. When $r=0$ (full curve), it can be seen that the frequency of A in the field increases after a few generations for $m=0.5$ in spite of the massive flow of pollen B from wild populations. Figure 3 shows that this increase in the frequency of A occurs in spite of the negative $d(p)$ at the beginning, i.e. that A remains unfavoured at pollen level. The reason is the selective pressure exerted by farmers choosing the most desirable plants. The elimination of female S gametes by this selection has effects on the B alleles of the homogamy locus because a positive gametic disequilibrium exists between the two loci in the runs (Fig. 2). It can be seen that this gametic disequilibrium is higher for $m=0.5$ as early as the first generation and is maintained at a high value. Thus, this indirect selection on the homogamy locus in favour of A is stronger in the first generation than the effect of both gametophytic selection and migration when $m=0.5$ but not when $m=0.1$. The initial disadvantage of A at pollen level is also lower when $m=0.5$ than when $m=0.1$ (Fig. 3). For $m=0.5$, A is favoured at a pollen level as early as the tenth generation $d(p)>0$. From this moment, homogamy and selection by farmers act together in the same direction for a rapid increase in the frequency of A in the

field. This kind of synergy is due to the maintenance of strong gametic disequilibrium when $r=0$.

When $r=0.5$ (dashed curves) the results are very different because if $m>0.1$ no ultimate divergence between the two populations occurs, whatever the initial frequency of A (Table 1), as illustrated for $A_1=0.4$ by Fig. 1 (dashed lines). This is explained by the conjunction of the following two mechanisms: an initial selective disadvantage of A during pollen competition as shown by the negative initial $d(p)$ (Fig. 3) and a quick decrease in gametic disequilibrium between the two loci due to the high value of the recombination rate (Fig. 2). The A allele is thus less favoured by farmer selection and for a shorter period. This result shows that the interaction between the initial frequencies in the field and the parameters m , r and s strongly influences both the dynamics of frequency evolution and the determination of the final equilibrium. For example, it can be seen in Fig. 4 that for a fixed initial situation (here $A_1=0.5$), if $r<0.2$ the final equilibrium is divergence between the two popu-

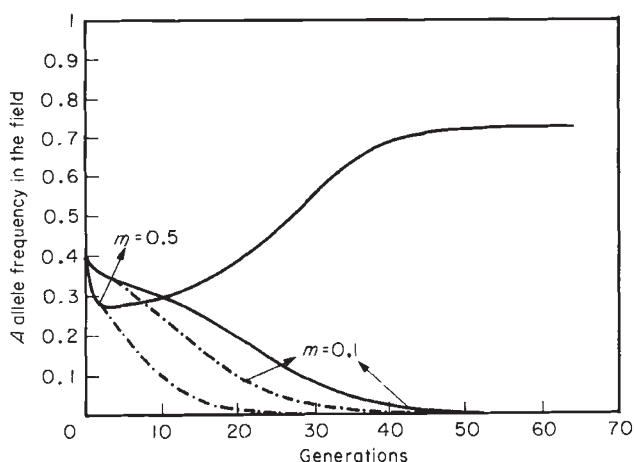


Fig. 1. Evolution of A allele frequency when $A_1=0.4$; $p_m=0$; $s=0.3$ and $r=0$ (—) or $r=0.5$ (---).

Table 1 Minimum amount of initial divergence at the homogamy locus required for frequency differences to persist between populations at equilibrium when $p_m=0$ and for different pairs of r and s values

	m									
	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50
$r=0, s=0.3$	0.48	0.47	0.45	0.43	0.42	0.41	0.40	0.39	0.37	0.36
$r=0, s=0.7$	0.45	0.41	0.37	0.35	0.33	0.31	0.29	0.27	0.26	0.25
$r=0.5, s=0.3$	0.54	0.58	0.64	*	*	*	*	*	*	*
$r=0.5, s=0.7$	0.47	0.44	0.42	0.41	0.39	0.38	0.37	0.37	0.36	0.36

*No difference between populations in frequency at the homogamy locus whatever the amount of initial divergence.

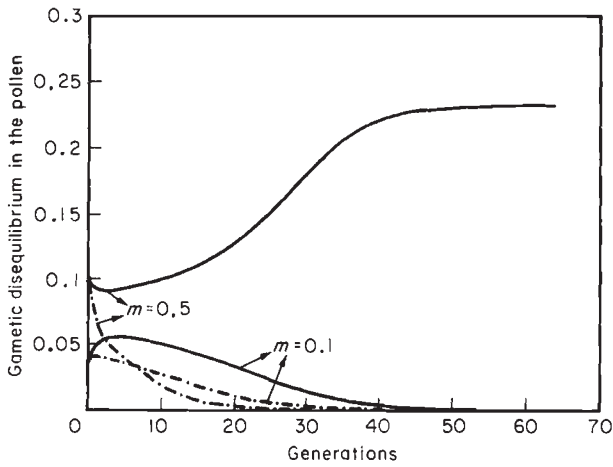


Fig. 2. Evolution of gametic disequilibrium in the pollen when $A_1 = 0.4$; $p_m = 0$; $s = 0.3$ and $r = 0$ (—) or $r = 0.5$ (---).

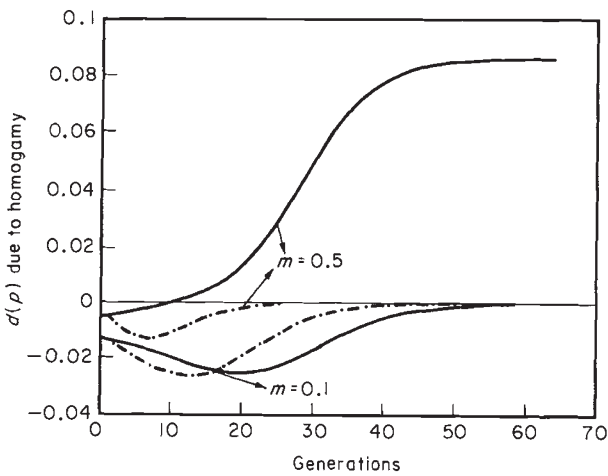


Fig. 3. Evolution of $d(p)$ due to homogamy when $A_1 = 0.4$; $p_m = 0$; $s = 0.3$ and $r = 0$ (—) or $r = 0.5$ (---).

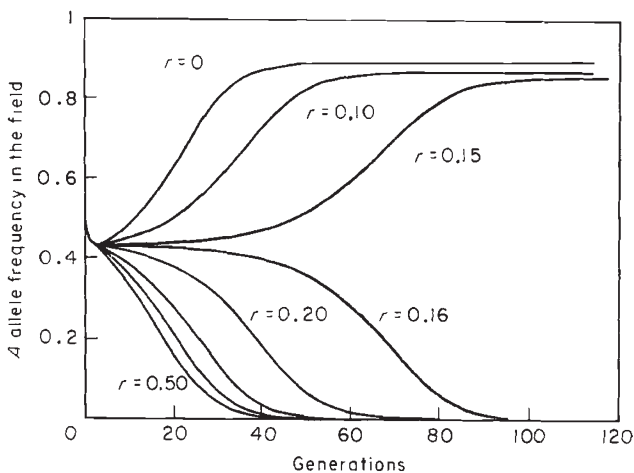


Fig. 4. Evolution of A allele frequency for different r values when $A_1 = 0.5$; $p_m = 0$; $s = 0.3$ and $m = 0.2$.

lations whereas if $r > 0.2$ no divergence is observed for the homogamy locus.

Hybrid percentage in the field at equilibrium: effects of the biological parameters

As shown in Fig. 5, m strongly influences the hybrid percentage at equilibrium. The values observed in natural conditions are close to those obtained in these runs when m is about 10 per cent without pollen selection. Pollen migration rates between cultivated fields and adjacent wild populations of pearl millet have never been estimated. However, it is likely that this rate is more than 10 per cent when large wild populations grow in the neighbourhood of the field populations. These conditions are probably similar to those at the beginning of pearl millet domestication (Amblard & Pernès, 1989).

The higher r is and the lower s is, the stronger the effect of m on the hybrid percentage. The strong effect of m on the hybrid percentage shows that isolation by distance between fields and wild populations could have been an important factor in the success of pearl millet domestication, as noted by Laredo & Pernès (1988).

s also has an important effect on hybrid percentage as shown in Fig. 6. When wild populations and the cultivated field populations diverge at equilibrium for the homogamy locus, pollen competition decreases the hybrid percentage. When $s = 0.7$, the values obtained for $m = 0.1$ and $m = 0.2$ are 3.8 and 8.4 (for $r = 0$) and 5.3 and 11.6 (for $r = 0.5$), respectively, which are much lower than the values for $s = 0$ (18.3 and 33.3, respectively). Figure 5 shows that for $s = 0.7$ and $r = 0$, there are only 20 per cent hybrids (a percentage frequently observed in natural conditions) when the pollen migration rate is 40 per cent, whereas 10 per cent of migrant

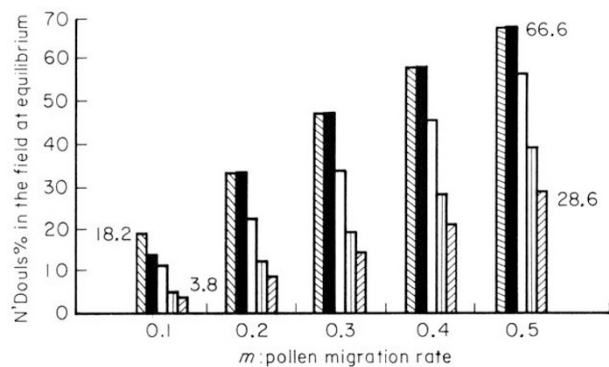


Fig. 5. Effect of m on the hybrid percentage in the field when $p_m = 0$. (■) $s = 0$; (■) $s = 0.3$, $r = 0.5$; (□) $s = 0.3$, $r = 0$; (▨) $s = 0.7$, $r = 0.5$; (⊞) $s = 0.7$, $r = 0$.

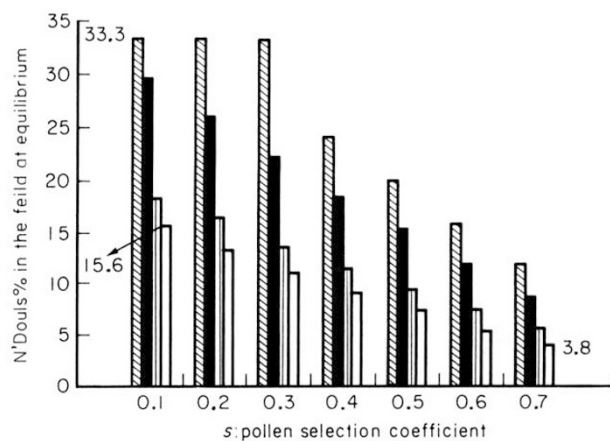


Fig. 6. Effect of s on the hybrid percentage in the field when $p_m = 0$. (▨) $m = 0.2$, $r = 0.5$; (■) $m = 0.2$, $r = 0$; (▩) $m = 0.1$, $r = 0.5$; (□) $m = 0.1$, $r = 0$.

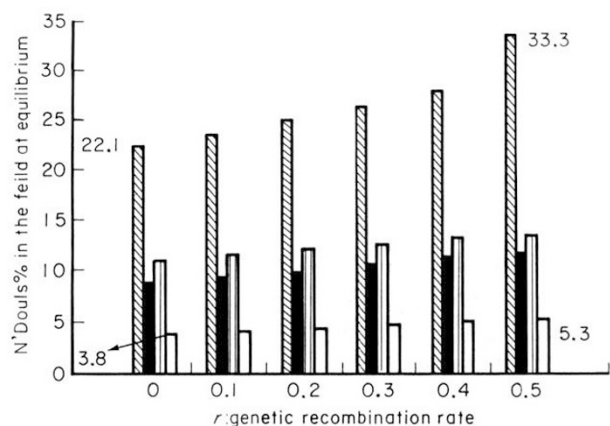


Fig. 7. Effect of r on the hybrid percentage in the field when $p_m = 0$. (▨) $m = 0.2$, $s = 0.3$; (■) $m = 0.2$, $s = 0.7$; (▩) $m = 0.1$, $s = 0.3$; (□) $m = 0.1$, $s = 0.7$.

pollen grains is enough to obtain 20 per cent of hybrids in the absence of pollen competition. The lowest value of gametophytic selection coefficients estimated from wild/cultivated pollen mixture experiments (Robert *et al.*, 1991) was 0.3. Figure 6 shows that this value of s is enough to decrease by one-third the hybrid percentage (10.9 per cent for $s = 0.3$, $m = 0.1$ and $r = 0$, and 18.2 per cent for $s = 0$ with $m = 0.1$).

As discussed above, the effect of r on hybrid percentage can be important because r acts together with s and m to determine whether divergence at the homogamy locus between field and wild populations is obtained at equilibrium. For example, it can be seen on Fig. 7 that the difference in the hybrid percentage for $r = 0.4$ and $r = 0.5$ when $m = 0.2$ is 5.6 per cent. This strong value is explained by the persistence of allelic

frequency differences between the two populations at equilibrium when $r = 0.4$ but not when $r = 0.5$. On the other hand, the same difference is observed between $r = 0$ and $r = 0.4$, the field and the wild population being divergent at the homogamy locus in both cases. This shows that when the variation of r does not change the equilibrium state of the field at the homogamy locus, i.e. divergence or no divergence with the wild population, the effect on the hybrid percentage is weak.

Dynamics of hybrid frequency evolution

A major requirement for gametophytic selection to have an important influence on the domestication process is that the reduced hybrid percentage should be reached quickly in time spans consistent with those of domestication. Table 2 indicates the number of generations necessary for a hybrid percentage to reach equilibrium. In the runs, equilibrium was defined as being reached when the hybrid frequency change over 10 generations was less than 0.0005. Each equilibrium obtained in the different runs was checked by a comparison between the equilibrium frequencies and the frequencies obtained 300 generations later, to avoid pseudo-equilibria. These results were obtained with an initial hybrid frequency equal to 0 and initial A frequency equal to 0.5 or 1. In fact, these two values correspond to the extrema for the time taken to reach equilibrium.

When $A_1 = 1$, in most cases, the equilibrium is quickly reached, between 5 and 50 generations. The stronger s and the smaller r are, the lower the number of generations before equilibrium is reached. However, the effects of m , r and s do not seem important in comparison with the effect of the initial frequency of $A(A_1)$.

When A_1 was 0.5 the time required to reach the equilibrium was longer, between 15 and 85 generations. Nevertheless, note that the equilibrium conditions defined here are very stringent. Since equilibrium is reached in an asymptotic way, as can be seen in Fig. 8, the system almost always comes close to equilibrium very quickly. For example, when $s = 0.1$, it can be seen in Fig. 8 that hybrid frequency at equilibrium (33.3 per cent) is approached in about 20 generations, although the value obtained by the test described above was 80 generations (Table 2).

Discussion

In this model we assume that only one locus controls the cultivated/wild phenotype. Genetic studies on pearl millet have shown that one gene controls shedding

Table 2 Number of generations required to reach the N'Douls percentage value at equilibrium as a function of s

$p_m = 0$ s	$A_1 = 1$				$A_1 = 0.5$			
	$m = 0.1$ $r = 0$	$m = 0.1$ $r = 0.5$	$m = 0.2$ $r = 0$	$m = 0.2$ $r = 0.5$	$m = 0.1$ $r = 0$	$m = 0.1$ $r = 0.5$	$m = 0.2$ $r = 0$	$m = 0.2$ $r = 0.5$
0	10	10*	10	10*	10	10*	10	10*
0.1	10	80*	10	40*	180	80*	155	60*
0.2	10	45	10	55*	85	70*	80	55*
0.3	10	25	10	170*	60	50*	55	40*
0.4	5	15	5	30	45	30*	40	30*
0.5	5	10	5	20	35	60*	30	55*
0.6	5	10	5	10	30	35	25	35
0.7	5	10	5	10	25	30	20	25

* A frequency = 0 at equilibrium.

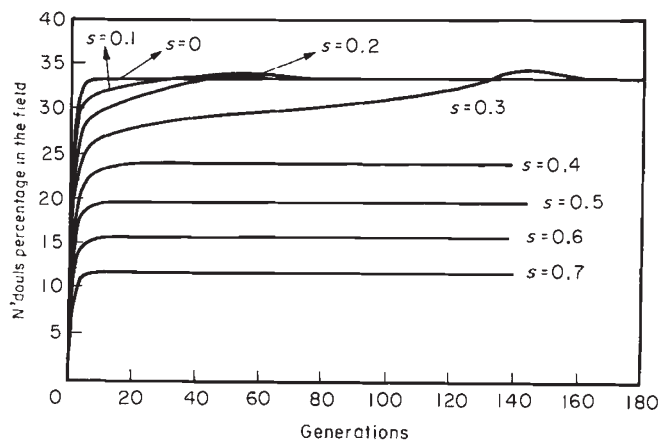


Fig. 8. Evolution of the N'Douls percentage for different s values when $A_1 = 1$; $p_m = 0$; $r = 0.5$ and $m = 0.2$.

ability (Joly-Ichenhauser, 1984). It has been suggested that this character was the first to be selected during the process of cereal domestication (Harlan, 1975). Thus, it is at least plausible that a single gene initially determined the difference between cultivated and wild phenotypes for pearl millet as well as for maize.

This asymmetrical model shows that homogamy due to pollen competition in pearl millet could greatly reduce the percentage of wild/cultivated hybrids in fields that receive a substantial quantity of pollen from adjacent wild populations. The real observed percentage of hybrids in traditional agricultural systems are very close to those obtained by simulation with a pollen migration rate ranging between 20 and 40 per cent, according to the allelic frequencies at the homogamy locus in the wild population. The large

decrease in the percentage of intermediate phenotypes due to pollen selection does not require any genetic linkage between the homogamy locus and the 'domestication' locus. Nevertheless, the synergy between the two selective pressures can be maintained more easily when the two loci are closely linked. This explains why, in some cases, different values of the parameter r lead to very different equilibrium values. Moreover, the increase in the time span to reach the equilibrium observed when gametophytic selection occurs is very small. In most cases, the equilibrium value of the hybrid percentage is reached in a few generations, which suggests that domestication of pearl millet was initiated very quickly, as noted by Laredo & Pernès (1988).

The real effect of gametophytic selection on the domestication process, especially when it is weak, is difficult to estimate because the initial conditions have a great influence on the equilibrium. One of the most stringent requirements for a final positive effect is the existence of an initial divergence, albeit low, between the wild and the cultivated populations. This condition could have been caused by various circumstances, such as migration of seed stocks. When this condition is met, preservation of the phenotypic integrity of a cultivated form is easier when gametophytic selection occurs, because it decreases the frequency of crosses between the two forms. A similar situation could occur in the case of maize because it has been shown that pollen competition *Gal* genes have a higher frequency in adjacent populations of maize and teosinte than in isolated populations (Bianchi & Lorenzoni, 1975).

Simulations of adjacent wild and cultivated populations suggest that the first steps in domestication are

easier for autogamous species because self-fertilization limits the gene flow from spontaneous to cultivated populations (Laredo & Pernès, 1988). Domestication of allogamous cereals therefore needs isolation (especially by distance) between wild and cultivated forms of the same species. Nevertheless, note that the percentages of hybrids we obtained in our model with strong gametophytic selection ($s = 0.7$) are very close to those obtained by Laredo & Pernès (1988) with a self-fertilization rate equal to 50 per cent. Thus, the control of gene flow between wild and cultivated pearl millet by strong pollen competition is as efficient in maintaining the phenotypic structure of the cultivated form as a mixed-mating system with a high self-fertilization rate. In this model, we assumed that no self-fertilization occurred. Self-fertilization can occur, however, in pearl millet populations (Sarr, 1987). Estimations of self-fertilization rates on experimental populations vary between 2.1 and 21.7 per cent (M. Sandmeier, personal communication). It seems likely, therefore, that gametophytic competition and self-fertilization together reduce gene flow between wild and cultivated pearl millet populations in natural conditions.

Hypotheses about other biological mechanisms have been put forward to explain the dynamics of domestication for outcrossing cereals in areas where related wild forms are numerous. In pearl millet, as well as in maize, the genes that encode for the spikelet structure of the cultivated form are tightly linked (Galinat, 1978; Rey-Herme, 1982; Joly-Ichenhauser, 1984). This genetic structure limits recombination between these loci, thus increasing the frequency of cultivated phenotypes in the backcrosses which spontaneously occur between hybrids and plants with a cultivated phenotype. This could favour domestication of pearl millet and maize (Pernès, 1986).

Phenological barriers between cultivated and related wild forms due to variability in the flowering period have also been shown in pearl millet (Belliard & Pernès, 1977) and in maize (Wilkes, 1977). Stam (1983) has shown that a non-random pollen migration between two sub-populations, consecutive to a shift in the flowering period due to environmental effects, can lead to the establishment of a reproductive barrier. This phenomenon occurs if there is a genetic variability for the flowering period in the two sub-populations but no initial divergence is required.

Studies on the domestication of pearl millet have tried to evaluate its genetic consequences in cultivated populations but its consequences for natural populations have been neglected. In rice, hybrids between cultivated form and its related weed red rice (*O. sativa* L.) are found in weedy populations (Langevin *et al.*, 1990). The incidences and the effects of reciprocal

gene flow on the two forms of pearl millet must therefore be evaluated.

The study of the reproductive organization of pearl millet shows that a preferential outcrossing mating system with homogamy due to pollen competition, associated with tight linkage between genes of the domestication syndrome, would permit introgression of wild genes into cultivated populations without any alteration of their phenotypic integrity. In fact, recombination, in a broad sense, between wild and cultivated genomes is influenced by the mating system of these forms and its evolution during the domestication. Understanding this evolution could therefore lead to a better control of this recombination and thus to an efficient management of wild genetic resources, especially for dynamic conservation.

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Appendix

The following five equations are the basic recurrence equations system of the model. They give the relationships between two successive generations for each variable, (*n*) and (*n* + 1) being the generation index. As a matter of clarity, we used *w_{aa}* and *w_{bb}*, the mean relative fitnesses of pollen on *AA* and *BB* styles, respectively, in the expression of the recurrence equations. We also used *g₂*, the *AB* female frequency. We have the following relationships, whatever *n*.

$$w_{aa(n)} = 1 - s[1 - p_{(n)}]; w_{bb(n)} = 1 - sp_{(n)};$$

$$g_{2(n)} = 1 - g_{1(n)} - g_{3(n)}$$

The five recurrence equations are

$$p_{(n+1)} = 0.5(1 - m)[(p_{(n)}(1 + s) + 1 - s)g_{1(n)}/w_{aa(n)} + (1 - s)p_{(n)}g_{3(n)}/w_{bb(n)} + (p_{(n)} + 0.5)g_{2(n)}] + mp_m$$

$$g_{1(n+1)} = \frac{[p_{(n)}u_{(n)} + D_{(n)}][g_{1(n)}/w_{aa(n)} + g_{2(n)}/2]}{u_{(n)} - sD_{(n)}[g_{3(n)}/w_{bb(n)} - g_{1(n)}/w_{aa(n)}]}$$

$$g_{3(n+1)} = \frac{[(1 - p_{(n)})u_{(n)} - D_{(n)}][g_{3(n)}/w_{bb(n)} + g_{2(n)}/2]}{u_{(n)} - sD_{(n)}[g_{3(n)}/w_{bb(n)} - g_{1(n)}/w_{aa(n)}]}$$

$$D_{(n+1)} = 0.5(1 - m)[(p_{(n)}u_{(n)} + D_{(n)})(g_{1(n)}/w_{aa(n)} + g_{3(n)}(1 - s)/w_{bb(n)} + g_{2(n)}) + (1 + g_{1(n)} - g_{3(n)})/2 + r\{[p_{(n)}(1 - u_{(n)}) - D_{(n)}][g_{3(n)}(1 - s)/w_{bb(n)} + g_{2(n)}/2] - [(1 - p_{(n)})(1 - u_{(n)}) + D_{(n)}][g_{1(n)}(1 - s)/w_{aa(n)} + g_{2(n)}/2]\} - p_{(n+1)}u_{(n+1)}$$

$$u_{(n+1)} = 0.5(1 - m)[1 + u_{(n)} - sD_{(n)}(g_{3(n)}/w_{bb(n)} - g_{1(n)}/w_{aa(n)})].$$

Moreover, let *y* be the N'Douls percentage. We have the following recurrence equation between *y_(n+1)* and *y_(n)*.

$$y_{(n+1)} = (1 - m)y_{(n)}/2 + m + sD_{(n)}[g_{3(n)}/w_{bb(n)} - g_{1(n)}/w_{aa(n)}].$$

Proof 1

The successful pollen frequencies on *AA* females are *p/w_{aa}* and *q(1 - s)/w_{aa}* for *A* and *B* pollen, respectively, where *q* = 1 - *p*.

The same reasoning has led to successful pollen frequencies on *BB* females equal to *p(1 - s)/w_{bb}* and *q/w_{bb}* for *A* and *B* pollen respectively. On *AB* females, the successful pollen frequencies for *A* and *B* pollen are *p* and *q* respectively. Overall, the *A* successful pollen frequency is:

$$p' = pg_1/(1 - sq) + pg_2 + p(1 - s)g_3/(1 - sp).$$

Since *g₂* = 1 - *g₁* - *g₃*, we have:

$$p' = g_1(-p + p/w_{aa}) + g_3[-p + p(1 - s)/w_{bb}] + p.$$

$$\text{Thus, } d(p) = p' - p = p[g_1(1 - w_{aa})/w_{aa} + g_3(1 - s - w_{bb})/w_{bb}].$$

Since *w_{aa}* = 1 - *sq* and *w_{bb}* = 1 - *sp* we obtain:

$$d(p) = p[sgg_1/w_{aa} + sg_3(p - 1)/w_{bb}],$$

then *d(p)* = *spq(g₁/w_{aa} - g₃/w_{bb})*.

Proof 2

Let t_1, t_2, t_3 and t_4 be the frequencies in the total pollen cloud of *CA*, *CB*, *SA* and *SB* pollen, respectively.

Let u be the frequency of *C* pollen in the total pollen cloud, $u = t_1 + t_2$;

On *AA* females, the frequencies of successful *C* and *S* pollen are $[t_1 + t_2(1-s)]/w_{aa}$ and $[t_3 + t_4(1-s)]/w_{aa}$ respectively.

On *BB* females, these frequencies are

$[(1-s)t_1 + t_2]/w_{bb}$ and $[(1-s)t_3 + t_4]/w_{bb}$, respectively.

On *AB* females, they are $t_1 + t_2$ and $t_3 + t_4$, respectively.

Overall, the frequency of successful *C* pollen is:

$$u' = [t_1 + t_2(1-s)]g_1/w_{aa} + (t_1 + t_2)g_2 + [(1-s)t_1 + t_2]g_3/w_{bb} \quad (\text{I})$$

Since $p = t_1 + t_3$ and $q = t_2 + t_4$, (I) becomes:

$$g_1[t_1 - t_2 - st_2 - (t_1 + t_2)w_{aa}]/w_{aa} + g_3[t_1 + t_2 - st_1 - (t_1 + t_2)w_{bb}]/w_{bb} + t_1 + t_2 \quad (\text{II})$$

Since $w_{aa} = 1 - sq$ and $w_{bb} = 1 - sp$, and $t_1 t_4 - t_2 t_3 = D$, we have:

$$u' = sg_1 D/w_{aa} - sg_3 D/w_{bb} + u. \quad \text{Then, } d(u) = u' - u = sD(g_1/w_{aa} - g_3/w_{bb}) \text{ or again, } d(u) = d(p)D/pq.$$