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Pollen competitive ability in maize: within population variability and response to selection

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Summary. Male gametophytic selection can play a special role in the evolution of higher plant populations. The main assumption – gametophytic-sporophytic gene expression of a large portion of a plant's genes – has been proven by a number of studies. Population analyses have revealed a large amount of variability for male gametophytic fitness. However, the data available do not prove that at least a portion of this variability is due to post-meiotic gene expression. This paper reports the analysis of a synthetic population of maize based on a gametophytic selection experiment, carried out according to a recurrent scheme. After two cycles of selection, the response was evaluated for gametophytic and sporophytic traits. A parameter representing pollen viability and time to germination, although showing a large amount of genetic variability, was not affected by gametophytic selection, indicating that this variability is largely sporophytically controlled. Pollen tube growth rate was significantly affected by gametophytic selection: 21.6% of the genetical variability was released by selection. Correlated response for sporophytic traits was observed for mean kernel weight: 15.67% of the variability was released. The results are a direct demonstration that pollen competitive ability due to pollen tube growth rate and kernel development are controlled, to a considerable extent, by genes expressed in both tissues. They also indicate that gametophytic selection in higher plants can produce a higher evolution rate than sporophytic selection; it can thus serve to regulate the amount of genetic variability in the populations by removing a large amount of the genetic load produced by recombination.

Key words: Maize pollen – Male gametophytic selection – Pollen competitive ability – Gametophytic fitness variability

Introduction

Evolution of higher plant populations can be produced by selection factors acting during all stages of sporophytic and gametophytic generations (Harding 1975). Because of the large number of pollen grains produced by each individual plant and the competition of several pollen tubes in the same style, selection is expected to be more effective on the male gametophyte than on the female counterpart. Male gametophytic fitness arises from paternal plant traits (pollen grain yield per plant, shedding time and duration) and from pollen grain traits (competitive ability within the anthers, viability, germination time, tube growth rate, selective fertilization) (Pfahler 1975).

The evolutionary importance of the phenomenon has been discussed by Darwin (1877), Jones (1928) and Haldane (1932), and more recently by Heslop-Harrison (1979). On the assumption that pollen trait variability is at least in part gametophytically controlled and because of the haploid condition, it has been proposed that male gametophytic selection may play a special role in the evolution of higher plants in nature (Mulcahy 1979; Ottaviano and Sari-Gorla 1979; Pfahler 1983; Lee 1984) and in cultivated fields (Ottaviano and Mulcahy 1986) and may be used to develop more efficient methods of selection for plant breeding (Ottaviano et al. 1980, 1982; Mulcahy 1983; Zamir 1983).

This idea is supported by evidence of considerable gametophytic gene expression and a large amount of sporophytic-gametophytic genetic overlap (i.e. a large proportion of genes expressed in both phases of the life cycle). Tanksley et al. (1981) in tomato and Sari-Gorla et al. (1986) in maize have shown that a large proportion (0.60 and 0.72, respectively) of a plant's structural genes coding for isozymes in the sporophyte are also expressed

in the pollen. Willing and Mascarenhas (1984) in *Tradescantia* and Mascarenhas et al. (1984) in maize found that about 20,000 mRNA sequences are present in mature pollen grains and that the genetic overlap is 0.60 (60% of the genes express in both sporophyte and gametophyte). Protein synthesis by a large number of mRNA's has been demonstrated in the germinating pollen of *Tradescantia* (Mascarenhas and Mermelstein 1981). Finally, on the basis of distortions from Mendelian segregation, it was shown that of 32 different genes controlling endosperm development in maize, 21 (66%) are also expressed in the male gametophytic phase, affecting pollen development within the anther and/or pollen function (germination time, tube growth rate) (Ottaviano et al. 1988).

Diverse experimental results have demonstrated the effect of male gametophytic selection on the sporophytic generation. Positive response to gametophytic selection has been obtained for specific selective factors, such as tolerance of low temperature in *Lycopersicon* (Zamir et al. 1981, 1982; Zamir and Vallejos 1983), of salinity in *Solanum* (Sacher et al. 1983) and of heavy metals in *Silene dioica* and *Mimulus guttatus* (Searcy and Mulcahy 1985a, 1985b).

Differences in pollen competitive ability between inbred lines (Jones 1928; Sari-Gorla et al. 1975) and between F_1 hybrids (Pfahler 1967; Ottaviano et al. 1983) have been shown in maize. In the same species, correlation between pollen competitive ability and sporophytic growth and vigor has been reported by Mulcahy (1971, 1974) and Ottaviano et al. (1980), although a gametophytic control of the character has not been proven. Response to gametophytic selection for pollen competitive ability and positive correlated response for sporophytic traits has been detected in an open-pollinated population of maize (Ottaviano et al. 1982), although it was not possible to give a clear-cut demonstration of selection acting only on gametophytic genetic variability. Ter-Avanesian (1978) in cotton, wheat and *Vigna sinensis*, McKenna and Mulcahy (1983) in *Dianthus*, Mulcahy et al. (1975) in *Petunia*, and Schlichting et al. (1987) in *Lotus corniculatus* and *Cucurbita pepo* have proven that selection applied to pollen competitive ability affects the sporophytic generation for traits that are an expression of plant growth and vigour and that the characters are controlled by genes expressed both in the gametophytic and the sporophytic phases.

All these studies prove the efficiency of gametophytic selection acting on the variability controlled by genes expressed in the postmeiotic phase of the male gametophyte. However, evaluation of the weight of the phenomenon as a factor that can regulate the genetical structure and evolution of plant populations calls for knowledge of the amount of genetic variability of the gametophytic fitness component caused by post-meiotic gene expression, and of the proportion of this variability expressed in the sporophytic population.

Population analyses for sporophytic and gametophytic fitness variability have been made for *Phaseolus lunatus*, barley, *Clarkia* and maize (Harding and Tucker 1969; Vasek and Harding 1976; Clegg et al. 1978). In some instances the variability of the male gametophytic fitness parameter is comparable to the net variability in fitness. However, these studies do not discriminate between sporophytic versus gametophytic genetic control of important components of gametophytic fitness, such as pollen viability, pollen competition within the anther and pollen tube competition within the style.

The present paper reports the results of a gametophytic selection experiment based on two cycles of recurrent selection. This analysis of selected populations and of the derived families provides the first account of the amount of genetic variability of pollen competitive ability and of the proportion of this due to post-meiotic gene expression. It also confirms that selection acting on this component produces correlated response in the sporophytic generation.

Materials and methods

Selection procedure

A maize population (BSLE) randomly intercrossed for several generations was the basic material used for this study. Gametophytic and sporophytic traits were measured on families obtained by gametophytic selection. Our procedure for applying gametophytic selection takes advantage of the special structure of the maize ear. At pollination time, the length of the silks increases from apex flowers to basal flowers, where it can reach a length of 20 cm or more. Therefore, when several pollen tubes are competing within the same silk, the intensity of gametophytic selection increases from the apex to the base of the ear. Consequently, kernels at the base of the ear are recovered after more intense gametophytic selection, while those at the apex are recovered after less intense selection. Factors other than pollen competition in the same silk, such as tube capability to reach basal ovules or inhibition of some types of pollen by others, have been excluded (Jones 1928; Mulcahy 1971). If pollen from a single plant is used for pollination, any differences between progeny from apical or basal seed are due to gametophytic selection, derived from genetic variability expressed at the postmeiotic phase.

This type of selection was applied according to a recurrent selection scheme in order to obtain a "base" population (progeny from basal seed of the ear produced under high gametophytic selection intensity) and an "apex" population (progeny from apical seeds, produced under low selection intensity). In 1979 about 100 plants of the BSLE population were selfed and 12 fully fertilized ears were chosen at random. From each of these ears 2 samples of 40 kernels were taken: 1 from the apex and 1 from the base. The remaining kernels were discarded. In 1980 two groups of 12 S_1 families were grown: 1 from the apex and 1 from the base kernels. In each group all F_1 combinations (66) were produced; for each combination 3 plants of both parental S_1 families were used to produce 3 F_1 ears; pollen from a single parental plant was used only once to pollinate a single ear of the

other parent. The two populations thus produced will hereafter be referred to as the "apex" and "base" populations. In 1981 a balanced sample of each, consisting of 5 kernels of each of the $66 \times 3 = 198$ ears, was sown to start a second cycle of selection, which was completed in 1983. The kernel sample of the "apex" population was formed by kernels from the top of each ear, that of the "base" population by kernels from the base.

According to this procedure, within-plant male gametophytic selection was applied in four stages, two in selfing and two in intercrossing. In all stages of this work, plants were chosen completely at random to avoid sporophytic selection effects. Response to selection was evaluated on the basis of 60 S_2 families (30 from the "apex" and 30 from the "base" population).

The pollen competitive ability of each S_2 line was evaluated by means of the pollen mixture technique: equal amounts of pollen from a selected line and from a standard inbred (W22) carrying genes for colored aleurone (all the S_2 have uncolored aleurone), were mixed and used to pollinate ears of an unrelated F_1 hybrid (A632 × Mo17). The resulting ears were divided into five segments of equal length (eight kernels) and scored for kernel color. For each family about three fully fertilized ears were obtained and the overall experiment was repeated in two randomized blocks.

Correlated responses for sporophytic traits (50 kernel weight: 50 KW; kernel number per row: KNR; row number: RN) were evaluated on the basis of 160 (80 apex and 80 base) full-sib families in a standard field trial. A full-sib crossing design was adopted to avoid inbreeding effect on the sporophytic traits.

Statistics

Frequencies of uncolored kernels per segment of the ears obtained by mixed pollination technique allowed estimation of two gametophytic parameters. One is the proportion of uncolored kernels at the apex of the ear (p_1); it represents the relative competitive ability of the line due to pollen viability and germinability. The second parameter is the coefficient of linear regression of the proportion of uncolored kernels on ear segments ($b_{p/s}$), representing the component of gametophytic competitive ability due to pollen tube growth rate.

The data are binomial proportions, and the number of observations for each estimated proportion, although very high (about 240), is not constant. Thus, normality of distribution and homogeneity of error variances cannot be assumed.

A normalization of the distribution was obtained by a transformation of the data into linear components of the regression between segments. The observed proportions vector p was linearly transformed, by means of an operator matrix A, into a vector $F = Ap$, according to Grizzle et al. (1969). The A matrix, which specifies additive operations, was used to generate linear functions of the observed proportion vector p. The rows of matrix A correspond to the orthogonal polynomial coefficients that define the linear component; thus the analysis of the F variable refers only to the linear component variability. It is important to note that the elements of vector F are derived from a large number of observations (about 1200) and consequently have an approximate normal distribution (Kock et al. 1977).

The Analysis of Variance model for a randomized complete block design is:

$$F = 1\,\mu + X'_B\,\beta + X'_T\,\tau + e$$

where X'_B is the design matrix for blocks and X'_T is the design matrix for treatments; β represents block effects and τ is the vector of effects representing the linear component.

Taking into account the non-homogeneity of the variances, the linear model was fitted to the data obtained as $F = Ap$ by means of weighted least square analysis. Since the suitable matrix of weights for p is:

$$V_P^{-1} = W_P, \quad \text{where} \quad w_{ij} = n_i/p_i q_i,$$

for F it becomes $V_F^{-1} = [AV_P A']^{-1} = W_F$.

The model is now:

$$\tilde{F} = W_F^{1/2} F = W_F^{1/2}\, 1\,\mu + \tilde{X}_B \beta + \tilde{X}_T \tau + \tilde{e}$$

where:

$$\tilde{X}_B = W_F^{1/2} X'_B \quad , \quad \tilde{X}_T = W_F^{1/2} X'_T$$

with $E(\tilde{e}) = 0$ and $V(\tilde{e}) = I$.

The treatment sum of squares, adjusted for block effects, was obtained according to Pearce (1983) and partitioned into two components: Between Groups (apex versus base population) and Between Families (within populations). The χ^2 criterion was used for both goodness of fit test and for treatment effects (Grizzle et al. 1969).

The expectation for the sum of squares was obtained by the general procedure for expectation of quadratic form (Rao 1973). The computing procedure corresponds to that adopted in the SAS System (GLM Procedure; Goodnight and Speed 1978), and this program was therefore used for MS and variance coefficient evaluation.

The resulting E (MS) Table is:

Source	MS	Expected mean squares
Between groups	GMS	$1 + \mathrm{tr}\{u_0 (u'_0 \tilde{C}^- u_0)^{-1} u'_0\}\,\sigma^2_{F(G)} + 2\,t\,(u'_0 \tilde{C}^- u_0)^1\, t'\,\sigma^2_G$
Between families	F(G) MS	$1 + (a-2)^{-1}\{\tilde{C} - u_0 (u'_0 \tilde{C}^- u_0)^{-1} u'_0\}\sigma^2_{F(G)}$
Error	EMS	1

where:
u_0 is the vector of between-groups contrast; $\tilde{C}^-$ is any generalized inverse of the coefficient matrix of the "reduced" normal equations for treatments, and the expectation for the Error MS is 1, because of the transformation $\tilde{F} = W^{1/2}F$.

The same weighted analysis was performed on the proportions of uncolored kernels in the first segment (p_1); however, in this case no transformation of the original variable was applied.

The proportion of genetic variability between families (h^2_F) can be obtained as:

$$h^2_F = \frac{\sigma^2_G + \sigma^2_{F(G)}}{\sigma^2_G + \sigma^2_{F(G)} + \sigma^2_e}$$

and its component solely due to gametophytic control as:

$$h^2_G = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_{F(G)} + \sigma^2_e}.$$

Standard Errors of variance components were obtained according to the procedure given by Searle (1971) for balanced data. Therefore, these estimates are to be considered approximate values. The expected mean squares, the proportion of genetic variability between families and the standard errors for sporophytic traits were computed by standard methods (Becker 1975).

Results

Table 1 shows the mean values and range of variation of the gametophytic traits of the S_2 lines obtained by selfing plants taken at random from the population produced at high gametophytic selection intensity (base) and of the S_2's from the population obtained at low selection intensity (apex). The quantity p_1 (proportion of uncolored kernels at the apex of the ears of the single-cross hybrid) is the proportion of kernels from ovules fertilized by pollen of the S_2 lines in competition with the pollen of the standard. It represents relative gametophytic competitive ability at the first stage of the pollen function, the components of which are the viability, size and germination time of the pollen grains and the tube growth rate at this very early stage of tube development. Analysis of the size (diameter) and viability, evaluated by staining technique (Heslop-Harrison and Heslop-Harrison 1970) did not reveal significant differences between lines. Therefore, the variability in p_1 can be referred to germination time and/or to the early stage of tube growth. Although the character shows a very large and significant between-family variability (analysis of variance, not reported here), a difference between apex and base populations was not detected and the mean values of both populations were very close to the expectation of 50%. The heritability of the character based on the between-family variance component was 0.89 (SE = 0.27).

Different results were obtained for the quantitiy $b_{p/s}$ (coefficient of linear regression of the proportion of uncolored kernels on ear segments), representing relative pollen competitive ability of the S_2 lines due to pollen tube growth rate (Table 1; Fig. 1). The character shows a very large amount of variability; moreover, the differences between the two populations (groups) were significant, indicating that the gametophytic competitive ability of the population obtained at high selection intensity (base) is higher than that obtained at low intensity. Quantitative estimates of the proportion of the variance due to populations and family (within population) are obtained by means of the weighted analysis of variance in Table 2. The proportion of the genetical variance obtained by pooling between population and between family (within population) components was $h^2_F = 0.88$ (SE = 0.22), while the proportion accounting only for between populations difference was $h^2_G = 0.19$, representing 21.6% of the total genetic variability. The former value is an estimate of the between-family heritability of the character, the latter an estimate of the genetical variability released under the pressure of within-plant gametophytic selection.

Table 3 shows the results obtained for sporophytic characters studied on full-sib families produced by intercrossing plants taken at random within each of the two populations (base and apex). All the characters revealed

Table 1. Gametophytic traits of S_2 lines evaluated on the basis of the proportions of fertilization of the S_2 pollen (uncolored kernels) produced by mixed pollinations of F_1 (Mo17 × A632) hybrid ears. p_1 is the proportion of uncolored kernels at the apex of the ear; $b_{p/s}$ is the coefficient of linear regression of the proportion of uncolored kernels on ear segments

	p_1		$b_{p/s}$	
	mean	range	mean	range
Base population	49.27	14.79 75.12	0.31	−5.34 5.58
Apex population	51.88	9.02 92.08	−1.24	−8.50 2.66
Differences	−2.61 ns		1.55 **	

Table 2. Analysis of variance of $b_{p/s}$ (regression coefficient of uncolored kernels proportion on ear segments) of S_2 line pollen in mixed pollinations

Source	SS	DF	χ^2	Expected mean squares	σ^2	SE
G	103.41	1	**	$1+1.82\,\sigma^2_{F(G)}+54.58\,\sigma^2_G$	1.68	1.55
F(G)	812.98	58	**	$1+2.20\,\sigma^2_{F(G)}$	5.92	1.16
Error	1.82	58	ns	1	1	0.01

ns: not significant
** $P < 0.01$

Table 3. Sporophytic values of full-sib populations

	50 KW		KNR		RN	
	mean	range	mean	range	mean	range
Base population	15.67	11.96 19.02	46.00	39.91 51.70	15.60	13.20 18.10
Apex population	14.53	11.22 17.88	46.80	38.70 52.00	16.3	13.70 19.30
Differences	1.14*		−0.80 ns		−0.07 ns	
h^2_F	0.58 ± 0.09		0.53 ± 0.08		0.57 ± 0.10	

Table 4. Analysis of variance of 50 KW values of full-sib populations

Source	DF	MS	EMS	σ^2	SE
Blocks	2	8.12			
Groups	1	157.14 **	$\sigma^2_e+3\,\sigma^2_{F(G)}+240\,\sigma^2_e$	0.62	0.53
Full-sib families (within groups)	158	7.48 **	$\sigma^2_e+3\,\sigma^2_{F(G)}$	1.95	0.28
Error	318	1.647	σ^2_e	1.65	0.13

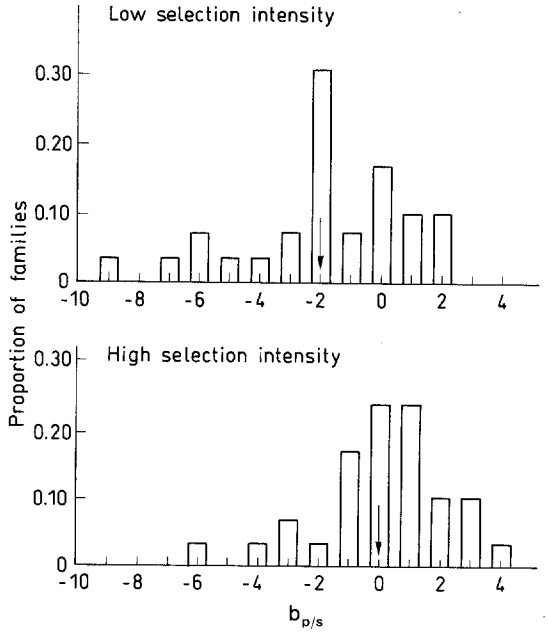

Fig. 1. Gametophytic competitive ability ($b_{p/s}$) of 60 S_2 families from populations produced by gametophytic selection. $b_{p/s}$ is the coefficient of regression estimating competitive ability due to tube growth rate

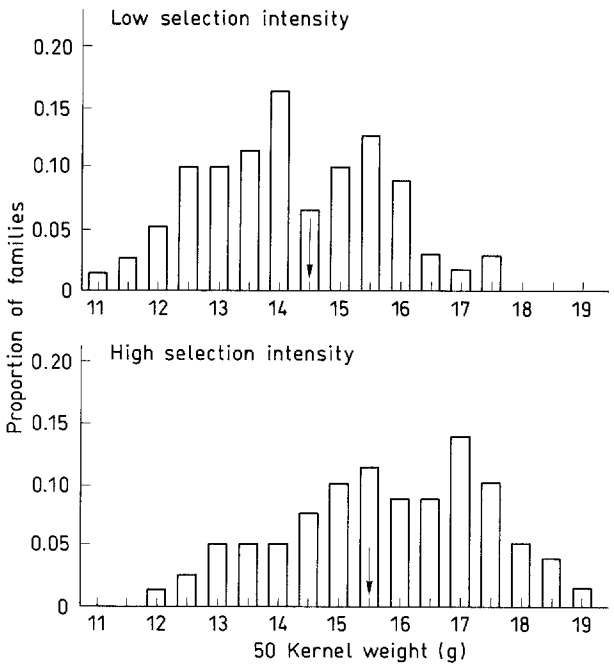

Fig. 2. Fifty kernel weight of 160 full-sib families from populations produced by gametophytic selection

a large amount of genetical variability, but only for mean kernel weight (50 KW) was the difference between base and apex populations significant: the mean value of this character is greater in the population obtained at higher selection intensity (Fig. 2). The analysis of variance in Table 4 allows for estimation of the proportion of the between-family genetical variability of the character ($h^2_F = 0.60$) and that accounting for the between group (base vs apex) difference ($h^2_G = 0.16$). The latter value represents 24.27% of the genetical variability, which can be interpreted as the proportion of the genetical variance released as correlated response to gametophytic selection.

Discussion

This study shows that maize populations contain a large amount of genetic variability controlling important components of pollen competitive ability. It also provides information with regard to the sporophytic and gametophytic control of this variability. Relative pollen germination time and tube growth in the early stage were not affected by within-plant gametophytic selection. On the other hand, gametophytic competitive ability due to pollen tube growth in later stages was significantly affected: a portion of the genetical variability of the character is released by within-plant selection. This response to selection is a direct demonstration that pollen tube growth rate is also controlled by genes expressed during the gametophytic phase. The proportion of genetical variability accounting for response to selection (between-groups component in the Analysis of Variance) probably represents an underestimate of genetical variability due to post-meiotic gene expression. For a character showing quantitative variability, further response to selection is generally found (Falconer 1961).

These results confirm that competitive ability in the early stage of the pollen function is largely controlled by the sporophytic tissues (Ottaviano et al. 1982), which can modulate the amount of storage material contained in pollen grains and supporting the first stage of pollen tube growth. Later on, the gametophyte changes from autotrophic to auxotrophic development (Heslop-Harrison et al. 1984), where the growth rate is largely controlled by pollen style interaction and by genes of the gametophyte specifically connected with pollen tube growth. This interpretation does not mean that pollen development within the anthers is only sporophytically controlled. Effects of post-meiotic gene expression on pollen viability and pollen size have been detected in cases of deleterious mutations of the endosperm showing pleiotropic effect on male gametophyte development (Ottaviano et al. 1988). Sporophytic control of the early stage of pollen competitive ability can also explain the results obtained by Yamada and Murakami (1983), showing the superior-

ity (heterosis effect) of the pollen produced by hybrid combinations in comparison with that of the inbred parents. These authors did not discriminate between the two components of competitive ability, and this superiority could be due to the effect of the sporophyte-controlled component.

The correlated response detected for mean kernel weight indicates that genes expressed at the gametophytic phase controlling pollen tube growth rate are also expressed during endosperm development. An alternative hypothesis could be based on the linkage between genes acting on the two different tissues. However, since the original population was randomly mated for several generations, the effect of linkage disequilibrium is likely to be minimum on the S_2 line population, which was obtained at random for all sporophytic traits. On the other hand, genes expressed in both the gametophytic phase and in the endosperm are well described in maize. These genes are involved in the control of starch metabolism, such as *waxy* (Brink and MacGillvrary 1924) or *amylose extender* (Moore and Creech 1972) and of endosperm development, as *defective endosperm* factors (Ottaviano et al. 1988). Moreover, positive correlations between pollen competitive ability and kernel weight have been detected in a number of studies in maize (Mulcahy 1971; Mulcahy et al. 1978; Ottaviano et al. 1980; Yamada and Murakami 1983). Genes controlling basic metabolic processes such as energy production, starch metabolism and wall synthesis, which are important for both kernel development and pollen tube growth, can be hypothesized as contributing to the genetic overlap. This idea is also supported by the fact that most enzymes involved in these metabolic pathways are found in pollen (Brewbaker 1971; Dickinson et al. 1973; Heslop-Harrison et al. 1973; Mascarenhas 1975) and by isozyme analysis showing post-meiotic gene expression and sporophytic-gametophytic genetic overlap (Tanksley et al. 1981; Sari-Gorla et al. 1986).

In maize at least nine different loci, referred to as *gametophytic factors,* have been detected (Nelson 1952; Schwartz 1960; Bianchi and Lorenzoni 1975). All these loci show gametophytic expression and the mutant alleles *(Ga)* confer high competitive ability to the pollen, due to the increased pollen tube growth rate (House and Nelson 1958). Because of the positive interaction between pollen and style carrying the same *Ga* alleles, these genes favour assortative mating. Although the population analyzed in our study did not show the presence of such gametophytic factors – in mixed pollination they would reduce the fertilization due to the standard line (colored kernels) to a value close to zero – this does not mean that these loci were not involved: it is possible that various recessive isoalleles, having minor phenotypical effects, exist in the population and their segregation would produce the typical pattern of a quantitative character. Indeed, this type of variability favouring self-fertilization was found by Jones (1928) by analysis of several inbred lines in mixed pollination. Although this control of the breeding system is not found in all cases (Pfahler 1965), it has been confirmed by Ottaviano et al. (1983) in an experiment including inbred and F_1 hybrids and by Johnson and Mulcahy (1978) who showed that competitive ability of the pollen in the style of the same plant is enhanced through successive generations of selfing. Moreover Paterniani (1969), selecting for reproductive isolation between two populations of maize, found a positive response in part due to a mechanism that favours fertilization by pollen produced within the population or prevents growth of pollen from another population. In the interpretation of the results of the experiment reported in this paper, the effects of genes producing this type of variability are likely to play a minor role. In fact, effects of *Ga* alleles on sporophytic traits, other than silk control of tube growth of *Ga* and *ga* pollen, have not been reported.

Gametophytic selection and gametophytic competitive ability evaluation have been carried out at high pollination density, with hundreds of male gametophytes in competition within the same silk. In standard corn field pollination density is lower: Kisselbach (1949) estimated that about 13 pollen grains land on an individual silk; Sadras et al. (1985) had a very similar average value (12 pollen grains) and found that the proportion of silks without pollen was close to zero. Therefore gametophytic selection, although at lower intensity, is operating in normal corn fields.

The special features of the male gametophytic phase (haploid state and large population size) and the gametophytic-sporophytic expression of genes controlling both gametophytic fitness components and important sporophytic traits support the idea that gametophytic selection is a factor regulating the population structure and evolution rate. First, gametophytic selection can be considered an important mechanism regulating the amount of genetic variability in a population. In fact, natural selection acts on quantitative traits controlled by complex gene combinations; for these characters the large amount of genetic load produced by genetic recombination can be removed by gametophytic selection at a cost (loss of pollen genotypes) compatible with the size of the male gametophytic population. In this sense, gametophytic selection is a more efficient mechanism than those provided by chromosomal rearrangements, such as inversions, which eliminate the product of recombination in both male and female gamete populations. Secondly, the haploid state allows attainment of a much higher evolution rate than sporophytic selection and it is maximized when sporophytic and gametophytic selection act in the same direction, i.e. when the two types of selection are positively correlated (Pfahler 1983). In fact, the large amount of genetic load produced to attain

a high evolutionary rate (Haldane 1957) would easily be supported if it were removed in the pre-zygotic stage from the male gametophytic generation. Finally, considering crop plants, gametophytic selection can be used as a tool in breeding programs. Although little research has been carried out in this field, several interesting results have been obtained. They concern single genes and complex genetical characters: environmental stress resistance, resistance to heavy metals and phytotoxins (for reviews see Zamir 1983; Ottaviano and Mulcahy 1986).

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References

Beker WA (1975) Manual of quantitative genetics. Washington State University Press, Pullman

Bianchi A, Lorenzoni C (1975) Gametophytic factors in *Zea mays*. In: Mulcahy DL (ed) Gamete competition in plants and animals. North Holland, Amsterdam, pp 257–263

Brewbaker HL (1971) Pollen enzymes and isoenzymes. In: Heslop-Harrison J (ed) Pollen development and physiology. Butterworth, London, pp 156–170

Brink RA, MacGillvrary JH (1924) Segregation of the *waxy* character in maize pollen and differential development of the male gametophyte. Am J Bot 11:465–469

Clegg MT, Kahler AL, Allard RW (1978) Estimation of life cycle component of selection in an experimental plant population. Genetics 89:765–792

Darwin C (1877) The different forms of flowers on plants of the same species. Appleton, New York

Dickinson DB, Hopper JE, Davies MD (1973) A study of pollen enzymes involved in sugar nucleotide formation. In: Loewus F (ed) Biogenesis of plant cell wall polysaccharides. Academic Press, New York, pp 29–48

Falconer DS (1961) Introduction to quantitative genetics. Oliver and Boyd, Edinburgh London

Goodnight JH, Speed FM (1978) Computing expected mean squares. SAS Institute, Cary NC

Grizzle JE, Starmer CF, Kock GG (1969) Analysis of categorical data by linear models. Biometrics 25:489–504

Haldane JB (1932) The cause of evolution. Harper and Row, New York

Haldane JB (1957) The cost of natural selection. J Genet 55:511–524

Harding J (1975) Models for gamete competition and self fertilization as components of natural selection in populations of higher plants. In: Mulcahy DL (ed) Gamete competition in plants and animals. North-Holland, Amsterdam, pp 243–255

Harding J, Tucker CL (1969) Quantitative studies on mating system. II. Method for the estimation of male gametophytic selective values and differential outcrossing rates. Evolution 23:85–95

Heslop-Harrison J (1979) The forgotten generation: some thoughts on the genetics and physiology of Angiosperm gametophytes. In: Davies DR, Hopwood DA (eds) The plant genome. 4th Innes Symp, Norwich, pp 1–14

Heslop-Harrison J, Heslop-Harrison Y (1970) Evaluation of pollen viability by enzymatically induced fluorescence; intracellular hydrolysis of fluoroscein diacetate. Stain Techn 45:115–120

Heslop-Harrison J, Heslop-Harrison Y, Knox RB, Howlett B (1973) Pollen wall proteins: gametophytic and sporophytic fraction in pollen wall of Malvaceae. Ann Bot 37:403–412

Heslop-Harrison Y, Reger BJ, Heslop-Harrison J (1984) The pollen-stigma interaction in the grasses. 6. The stigma ("silk") of *Zea mays* L. as host to the pollens of *Sorghum bicolor* L. (Moench) and *Pennisetum americanum* L. (Leeke). Acta Bot Neerl 227:205–227

House RL, Nelson OE (1958) Tracer study of pollen-tube growth in cross-sterile maize. J Hered 49:18–21

Johnson CM, Mulcahy DL (1978) Male gametophyte in maize. 2. Pollen vigour in inbred plants. Theor Appl Genet 51:211–215

Jones DF (1928) Selective fertilization. University of Chicago Press, Chicago

Kiesselbach TA (1949) The structure and reproduction of corn. University of Nebraska, Lincoln

Kock GG, Landis JR, Freeman JL, Freeman DH, Lehnen RG (1977) A general methodology for the analysis of experiments with repeated measurement of categorical data. Biometrics 33:133–158

Lee TD (1984) Patterns of fruit maturation: a gametophyte competition hypothesis. Am Nat 123:427–432

Mascarenhas JP (1975) The biochemistry of angiosperm pollen development. Bot Rev 41:259–314

Mascarenhas JP, Mermelstein J (1981) Messenger RNAs: their utilization and degradation during pollen germination and tube growth. Acta Soc Bot Pol 50:13–20

Mascarenhas NT, Bashe D, Eisenberg A, Willing RP, Xiao CM, Mascarenhas JP (1984) Messenger RNA in corn pollen and protein synthesis during germination and pollen tube growth. Theor Appl Genet 68:323–326

McKenna M, Mulcahy DL (1983) Ecological aspects of gametophytic competition in *Dianthus chinensis*. In: Mulcahy DL, Ottaviano E (eds) Pollen: biology and implications in plant breeding. Elsevier, New York, pp 414–424

Moore CW, Creech RG (1972) Genetic fine structure analysis of *amylose-extender* locus in *Zea mays* L. Genetics 70:611–619

Mulcahy DL (1971) A correlation between gametophytic and sporophytic characteristics in *Zea mays* L. Science 171:1155–1156

Mulcahy DL (1974) Correlation between speed of pollen tube growth and seedling weight in *Zea mays* L. Nature 249:491–492

Mulcahy DL (1979) The rise of the Angiosperms: a genecological factor. Science 206:20–23

Mulcahy DL (1983) Manipulation of gametophytic population. In: Lange W, Zeven AC, Hogenboom NG (eds) Efficiency in plant breeding. Proc 10th EUCARPIA Congr, Pudoc, Wageningen, pp 167–179

Mulcahy DL, Mulcahy GB, Ottaviano E (1975) Sporophytic expression of gametophytic competition in *Petunia hybrida*. In: Mulcahy DL (ed) Gamete competition in plants and animals. North Holland, Amsterdam, pp 227–232

Mulcahy DL, Mulcahy GB, Ottaviano E (1978) Further evidence that gametophytic selection modifies the genetic quality of the sporophyte. Soc Bot Fr Actual Bot 1–2:57–60

Nelson OE (1952) Non reciprocal cross sterility in maize. Genetics 37:101–124

Ottaviano E, Mulcahy DL (1986) Gametophytic selection as a factor of crop plant evolution. In: Barigozzi C (ed) The origin and domestication of cultivated plants. Elsevier, Amsterdam, pp 101–120

Ottaviano E, Sari-Gorla M (1979) Genetic variability of male gametophyte in maize. Pollen genotype and pollen-style interaction. In: Israeli-Italian Joint Meeting Genet Breed Crop Plants. Monogr Genet Agraria IV, Roma, pp 89–106

Ottaviano E, Sari-Gorla M, Mulcahy DL (1980) Pollen tube growth rate in *Zea mays:* implications for genetic improvement of crops. Science 210:437–438

Ottaviano E, Sari-Gorla M, Pé M (1982) Male gametophytic selection in maize. Theor Appl Genet 63:249–254

Ottaviano E, Sari-Gorla M, Arenari I (1983) Male gametophyte competitive ability in maize. Selection and implications with regard to the breeding system. In: Mulcahy DL, Ottaviano E (eds) Pollen: biology and implications for plant breeding. Elsevier, New York, pp 367–373

Ottaviano E, Petroni D, Pé E (1988) Gametophytic expression of genes controlling endosperm development in maize. Theor Appl Genet 75:252–258

Paterniani E (1969) Selection for reproductive isolation between two populations of maize, *Zea mays* L. Evolution 23:534–547

Pearce SC (1983) The agricultural field experiments. Wiley, New York

Pfahler PL (1965) Fertilization ability of maize pollen grain. 1. Pollen sources. Genetics 52:513–526

Pfahler PL (1967) Fertilization ability of maize pollen grains. 2. Pollen genotype, female sporophyte and pollen storage interactions. Genetics 57:513–521

Pfahler PL (1975) Factors affecting male transmission in maize (*Zea mays* L.). In: Mulcahy DL (ed) Gamete competition in plants and animals. North Holland, Amsterdam, pp 115–124

Pfahler PL (1983) Comparative effectiveness of pollen genotype selection in higher plants. In: Mulcahy DL, Ottaviano E (eds) Pollen: biology and implication for plant breeding, Elsevier, New York, pp 361–366

Rao CR (1973) Linear statistical inference and its applications. Wiley, New York

Sacher R, Mulcahy DL, Staples R (1983) Developmental selection for salt tolerance during self pollination of *Lycopersicon* × *Solanum* F_1 for salt tolerance of F_2. In: Mulcahy DL, Ottaviano E (eds) Pollen: biology and implications for plant breeding. Elsevier, New York, pp 329–334

Sadras VO, Hall AJ, Schlichter TM (1985) Kernel set of the uppermost ear of maize. 1. Quantification of some aspects of floral biology. Maydica 30:37–48

Sari-Gorla M, Ottaviano E, Faini D (1975) Genetic variability of gametophytic growth rate in maize. Theor Appl Genet 46:289–294

Sari-Gorla M, Frova C, Binelli G, Ottaviano E (1986) The extent of gametophytic-sporophytic gene expression in maize. Theor Appl Genet 72:42–47

Schlichting CD, Stephenson AG, Davis LE, Winsor JA (1987) Pollen competition and offspring variance. Evol Trend Plant 1:35–39

Schwartz D (1960) The analysis of a case of cross-sterility in maize. Proc Natl Acad Sci 36:719–724

Searcy KB, Mulcahy DL (1985a) Pollen selection and the gametophytic expression of metal tolerance in *Silene dioica* (Caryophyllaceae) and *Mimulus guttatus* (Scrophulariaceae). Am J Bot 72:1700–1706

Searcy KB, Mulcahy DL (1985b) Pollen tube competition and selection for metal tolerance in *Silene dioica* (Caryophillaceae) and *Mimulus guttatus* (Scrophulariaceae). Am J Bot 72:1695–1699

Searle SR (1971) Linear models. Wiley, New York

Ter-Avanesian DV (1978) The effect of varying the number of pollen grains used in fertilization. Theor Appl Genet 52:77–79

Tanksley SD, Zamir D, Rick CM (1981) Evidence for extensive overlap of sporophytic and gametophytic gene expression in *Lycopersicion esculentum*. Science 213:453–455

Vasek FC, Harding J (1976) Outcrossing in natural populations. 5. Analysis of outcrossing, inbreeding and selection in *Clarkia exilis* and *Clarkia tembloriensis*. Evolution 30:403–411

Willing RP, Mascarenhas JP (1984) Analysis of complexity and diversity of mRNAs from pollen and shoots of *Tradescantia*. Plant Physiol 75:865–868

Yamada M, Murakami K (1983) Superiority in gamete competition of pollen derived from F_1 plant in maize. In: Mulcahy DL, Ottaviano E (eds) Pollen: biology and implications for plant breeding. Elsevier, New York, pp 389–395

Zamir D (1983) Pollen gene expression and selection: applications in plant breeding. In: Tanksley SD, Orton JJ (eds) Isozymes in plant genetics and breeding. Elsevier, Amsterdam, pp 313–330

Zamir D, Vallejos EC (1983) Temperature effects on haploid selection of tomato microspores and pollen grains. In: Mulcahy DL, Ottaviano E (eds) Pollen: Biology and Implication for Plant Breeding. Elsevier, New York, pp 335–341

Zamir D, Tanksley SD, Jones RA (1981) Low temperature effect on selective fertilization by pollen mixture of wild cultivated tomato species. Theor Appl Genet 59:235–238

Zamir D, Tanksley SD, Jones RA (1982) Haploid selection for low temperature tolerance of tomato pollen. Genetics 101:129–137