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Effects of the *ms10* gene, polygenes and their interaction on pistil and anther-cone lengths in tomato flowers

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Pistil and anther-cone lengths (PL and AL) are important traits in tomato hybrid seed production with the use of male-sterile flowers and in fruit production of fertile plants under high temperature. The effects of the male sterility gene *ms10*, polygenes, and their interaction on tomato PL and AL and on the difference between them (DIF) were studied in two experimental populations, each obtained from a different cross and comprised of F_3 families derived from selfed heterozygous (*Ms10/ms10*) F_2 plants. Data were analysed using a mixed model for a single gene, polygenes, and their interaction. The presence of the *ms10* gene resulted in AL and PL that were shorter by 2.5 (± 0.1) mm and 1.2 (± 0.1) mm, respectively, in male-sterile flowers than in male-fertile ones. Thus DIF was greater by 1.3 (± 0.1) mm in male-sterile flowers than in male-fertile flowers. 'Main polygenic variance' was found in all three traits. The variance due to interaction between polygenes and the *ms10* gene, even when significant, was always smaller than the variance due to polygenes alone, or to environment. Emasculation of the *ms10* male-sterile parent appears to be unavoidable for the efficient production of hybrid seeds.

Keywords: anther-cone, male sterility, *ms10*, pistil, single gene × polygene interaction, tomato.

Introduction

Male sterility, which in tomato is controlled by a single recessive gene, reduces the cost of hybrid seed production by eliminating the need to emasculate the female parent prior to anthesis (Rick & Robinson, 1951; Lapushner & Frankel, 1967; Scott *et al.*, 1980; Yordanov, 1983; Stevens & Rick, 1986).

Pistil and anther-cone lengths (PL and AL) are highly important characteristics of the female flower in the production of tomato hybrid seeds. An exserted pistil in the male-sterile flower facilitates efficient hand pollination, whereas stigma inserted within the anther-cone necessitate removal of the anther-cone prior to pollination (Philouze, 1969; Scott *et al.*, 1980). On the other hand, self-pollination of the hybrid plants, necessary for yield production, requires a pistil that is shorter than the anther-cone. Exserted pistils in tomato have been associated with poor fruit set, which is often enhanced by high temperatures (Philouze, 1969; Levy *et al.*, 1978; Scott *et al.*, 1980).

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PL and AL have been described as quantitative traits with continuous distributions (Scott *et al.*, 1980). AL was found to be controlled by a few polygenes, with complete dominance of the longer cone (Georgiev & Atanassova, 1980). Hanna (1980) found partial dominance of short styles and 73 per cent heritability of style length. Significant variance in both general and specific combining abilities was found for PL and AL in an 8 × 8 diallel experiment (Atanassova, 1978).

The difference (DIF) between PL and AL is controlled by two to 20 polygenes, the number depending on the genotype and experimental conditions, with partial dominance of the exserted pistil. A dominance coefficient of 0.76 towards an exserted pistil has been reported (Currence, 1944; Ruttencutter & George, 1975; Scott *et al.*, 1980). Other experiments have found 34 and 43 per cent heritability of the exserted pistil length (Rick & Dempsey, 1969; Levy *et al.*, 1978).

The single gene, *ms10*, which controls male sterility in tomato, is widely used in hybrid seed production (Philouze, 1970, 1974; Yordanov, 1983). This gene also causes shortening of the pistil and the anther-cone.

A mixed model incorporating the effects of a single gene, polygenes, and the interaction between them was proposed by Elkind & Cahaner (1986). Components of the model are estimated by the use of an experimental design composed of F_3 families derived from selfed F_2 plants heterozygous for the single gene in question. The purpose of the present work was to use this experimental design to estimate the effects of the *ms10* gene, polygenes, and their interaction on PL and AL and their DIF.

Materials and methods

Experimental populations

Four parental lines were used, two with male-fertile flowers (P_1 and P_2) and two with male-sterile flowers (P_3 and P_4). The male-sterile lines also carried the anthocyanin-absent allele *aa*, which is closely linked (1.7 ± 1.1 cM) to the *ms10* gene (Philouze, 1974). The parental lines were in an F_5 generation with determinate growth habit (*sp/sp*). The P_3 and P_4 lines were derived from self-pollinated heterozygous (*Ms10/ms10*) plants, and thus included all three *ms10* genotypes.

Male-sterile plants of P_3 and P_4 were used to prepare the F_1 hybrids. Self-pollination of the F_2 plants heterozygous for *ms10* from the crosses $P_1 \times P_3$ and $P_2 \times P_4$ produced the experimental F_3 populations, 1 and 2, respectively. Offspring of F_2 plants heterozygous for the *ms10* gene formed an F_3 family. The F_3 populations 1 and 2 were composed of 20 and 27 families, respectively.

Experimental procedures

The experiment was conducted using a split-plot design in two randomized blocks, with one main plot for each family per block. Within each main plot (family), plants with the same *ms10* genotype were grouped into the same sub-plot. Each family consisted of about 33 plants.

Identification of the *ms10* genotype in F_2 and F_3 male-sterile plants was according to sterile phenotype. In the male-fertile plants, *ms10* genotype was determined in young seedlings using the tight linkage between *aa* and *ms10* genes (Philouze, 1974), and also by progeny testing in the field. One-week-old, dark-room-grown (25°C) seedlings from each male-fertile plant were exposed to intense light for 24 h, and then scored for green and purple colour.

PL and AL of flowers at anthesis were measured in six flowers per plant. The lengths were measured from the base of the ovary to the top of the stigma or stamens, and DIF was obtained by subtraction of AL from PL.

Data analysis

PL, AL and their DIF were analysed according to the mixed model for a single gene, polygenes and their interaction, in a split-plot design (Elkind & Cahaner, 1986):

$$Y_{ijlk} = \mu + F_j + B_l + (FB)_{jl} + \beta_i + (\beta F)_{ij} + (\beta B)_{il} + W_{ijlk} \quad (1)$$

where Y_{ijlk} is the trait mean of flowers from plant k with the *ms10* genotype i of family j, grown in block l; μ is the general mean; F_j is the effect of family j, $j = 1 \ldots f$ (f = number of families), each family being a randomly sampled combination of polygenes; B_l is the effect of block l ($l = 1$ or 2); $(FB)_{jl}$ is the family by block interaction; β_i is the effect of the *ms10* genotype i, with three possible genotypes; $(\beta F)_{ij}$ is the *ms10* by family (polygenes) interaction; $(\beta B)_{il}$ is the *ms10* by block interaction; W_{ijlk} is the 'residual' effect of plant k within the *ms10* genotype i, family j and block l, $k = 1 \ldots k$ (k is the number of plants in every combination of family j, *ms10* genotype i, and block l). μ and β_i were considered 'fixed' effects, while the rest of the effects were 'random'. The variance between the families represents variance between polygenes.

Variance was analysed by the restricted maximum likelihood method, with program 3V of the BMDP (Dixon *et al.*, 1985). Hypothesis testing was accomplished by calculation of the difference, distributed as chi-square with one degree of freedom (Dixon *et al.*, 1985), between $-2 \times \log$ of maximum likelihood of the complete model and that of a model in which the tested component was absent.

Heterogeneity of the slopes of the three *ms10* genotype means within families over family means was analysed by using joint regression analysis (Elkind & Cahaner, 1986). The family means and the mean of each *ms10* genotype in every family were the 'least-square means' (Sokal & Rohlf, 1981). The null hypothesis of homogeneous slopes was tested by the use of the following model:

$$Y_{ij} = \mu + \beta_i + Y_{\cdot j} + b_i(Y_{\cdot j}) + W_{ij} \quad (2)$$

where Y_{ij} is the trait mean of plants with the *ms10* genotype i from family j; μ is the general mean; β_i is the effect of the *ms10* genotype i; $Y_{\cdot j}$ is the mean of family j; b_i is the regression coefficient of the mean *ms10* genotype i within families over family means, and W_{ij} is the error term. Y_{ij} was weighted by the inverse of its standard error. Slope heterogeneity was also observed in 'single gene/family' plots (Elkind & Cahaner, 1986) in which Y_{ij} is plotted against $Y_{\cdot j}$. The

means of the *ms10* genotypes were 'least-square means' (SAS, 1985).

The additive (a) effect of the *ms10* gene was calculated as half of the difference between the two homozygotes, and the dominance (d) effect as the difference between the heterozygotes and the mean of the two homozygotes.

'Net polygenic heritability' (Elkind & Cahaner, 1986), representing heritability in the F_3 generation due to polygenes, independent of the *ms10* gene effect, was calculated according to Cahaner & Hillel (1980) for traits in cases where the additive-dominance model was not rejected by the joint scaling test (data not shown).

Results

In both populations the effect of the *ms10* gene was significant for all three traits. The *Ms10* fertile allele exhibited complete dominance in all three traits, d similar to a (Table 1). The PL and AL of the sterile genotype (*ms10/ms10*) were 1.2 mm and 2.5 mm shorter, respectively, than either of the fertile genotypes (*Ms10/Ms10*, *Ms10/ms10*). Thus, DIF was 1.3 mm greater in sterile than in fertile flowers. This can also be observed in '*ms10*/family' graphs (Fig. 1a–f). The means of the *Ms10/Ms10* and *Ms10/ms10* genotypes within families were greater than those of *ms10/ms10* genotypes for PL and AL, and smaller for DIF. Despite the large differences between the two populations in *ms10* genotype means for the analysed traits, a and d effects of the *ms10* gene were almost identical (Table 1).

Table 1 Mean and standard error (SE) of *ms10* genotypes for pistil length (PL), anther-cone length (AL) and the difference between them (DIF) (0.1 mm) in two independent populations

	PL		AL		DIF	
Variance source	Mean	SE	Mean	SE	Mean	SE
Population 1						
ms10/ms10	73.2	1.3	72.9	2.3	0.3	2.1
Ms10/ms10	85.3	1.2	98.2	2.3	−12.9	2.1
Ms10/Ms10	85.3	1.3	98.4	2.3	−13.1	2.1
a	6.1	0.5	12.7	0.4	−6.7	0.6
d	6.1	0.5	12.5	0.4	−6.5	0.5
Population 2						
ms10/ms10	92.6	0.8	72.2	0.9	20.4	1.2
Ms10/ms10	104.8	0.8	97.2	0.8	7.6	1.2
Ms10/Ms10	104.9	0.8	97.5	0.9	7.5	1.2
a	6.1	0.3	12.7	0.5	−6.5	0.4
d	6.1	0.2	12.4	0.4	−6.4	0.4

a = Additive effect, d = dominance effect.

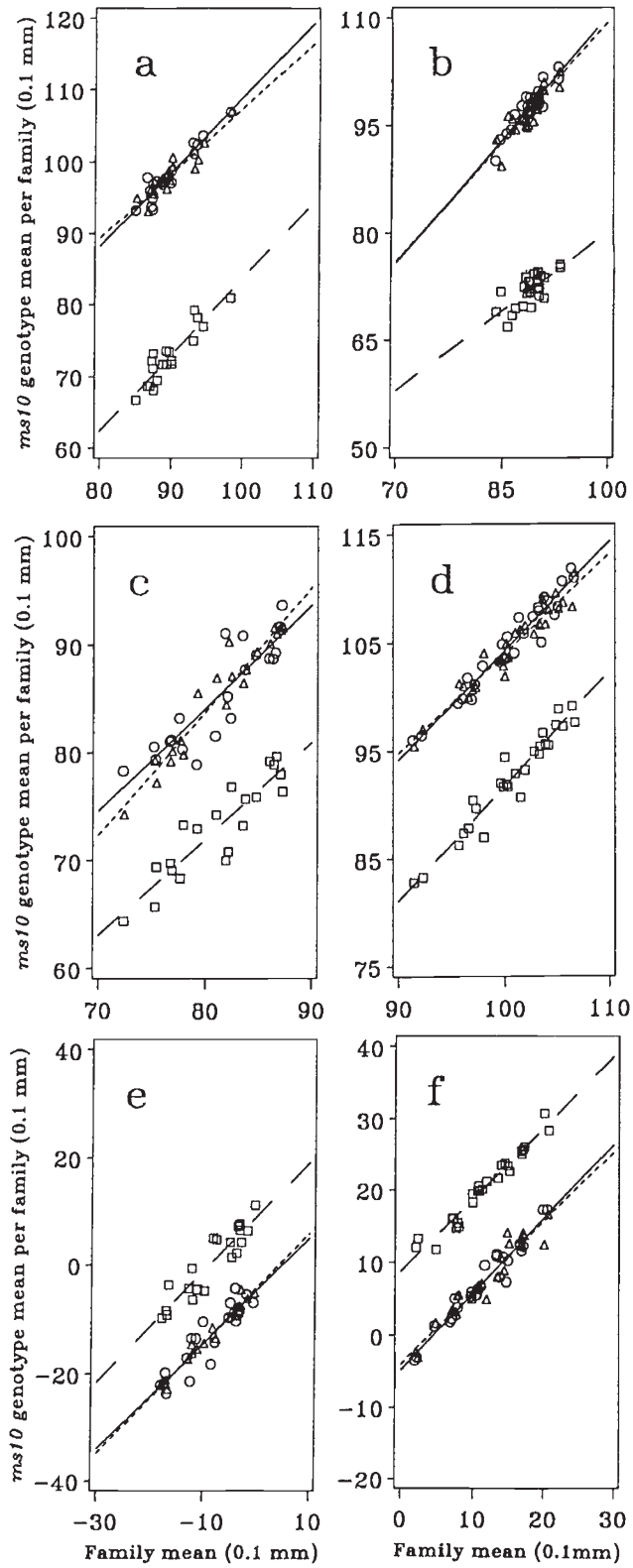

Fig. 1 *ms10* by family plot for anther-cone length (a and b), pistil length (c and d) and the difference between them (e and f) in populations 1 and 2, respectively. Means within each family of the *ms10* gene are *ms10/ms10* □, *Ms10/ms10* △, and *Ms10/Ms10* ○; observed regression lines are — — - - - and ——, respectively.

Table 2 Analysis of variance and estimates of variance components (σ^2), their standard errors (SE) and their chi-square probability (χ^2) for pistil length (PL), anther-cone length (AL) and the difference between them (DIF) (0.1 mm) in an 'F_3-families' experiment using restricted maximum likelihood

	PL			AL			DIF		
Variance source	σ^2	SE	$P(\chi^2)$	σ^2	SE	$P(\chi^2)$	σ^2	SE	$P(\chi^2)$
Population 1									
Between families	19.33	7.1	0.000	8.79	3.6	0.000	30.27	10.8	0.000
Block	0.58	1.0	NS	9.50	13.7	0.015	5.13	7.4	0.023
Family by block	1.48	0.9	0.009	2.67	1.1	0.000	1.36	0.9	0.017
ms10 by family	3.35	1.3	0.000	1.22	0.6	0.001	4.46	1.6	0.000
ms10 by block	0.00	—	NS	0.13	0.3	NS	0.00	—	NS
Residual	19.76	1.2		12.53	0.7		20.03	1.2	
Population 2									
Between families	14.19	4.4	0.000	1.48	1.4	NS	22.64	6.7	0.000
Block	0.00	—	NS	0.81	1.5	NS	0.82	1.4	NS
Family by block	1.69	0.8	0.001	3.76	1.3	0.000	1.15	0.7	0.025
ms10 by family	0.00	—	NS	1.64	0.6	0.000	0.45	0.5	NS
ms10 by block	0.00	—	NS	0.20	0.3	NS	0.17	0.3	NS
Residual	20.24	1.0		12.45	0.6		21.72	1.1	

'Between-families' variance was found to be significant for all traits, except for AL in population 2 (Table 2). This exception is reflected in Fig. 1b, where the range of family means for each of the *ms10* genotypes is smaller than for the other traits. The *ms10* by family interactions were found to be significant for most traits, except for PL and DIF in population 2 (Table 2). The regression lines for the three *ms10* genotypes in each trait were parallel (Fig. 1a–f), and did not differ from one other (Table 3), indicating the absence of multiplicative *ms10* by family interaction. The means of the three *ms10* genotypes within families deviated from these lines in a random fashion.

For PL and the DIF the 'between-families' variance was about half of the total variance, and was similar for the two populations (Table 2). For AL the major sources of variance were 'between-families', blocks, and residual in population 1, and residual in population 2 (Table 2). Variance due to *ms10* by family interaction was about 8 per cent and 0 per cent of the total variance for PL in populations 1 and 2, respectively; the corresponding proportions were 5 per cent and 11 per cent for AL and 7 per cent and 0 per cent for DIF. The estimated residual variance was similar in both populations for all three traits.

The 'net polygenic heritability', based on variance components within and between F_3 families, is the ratio of polygenic variance to total phenotypic variance in the F_3 generation, after removal of the *ms10* effect. The calculated value was 0.62 for PL in population 2. For cases with significant genetic interaction, but of small relative magnitude, the 'net polygenic heritability' values serve as rough estimates only. They were: 0.74 for PL in population 1; 0.62 for AL in population 1, and no genetic variance was found for AL in population 2; for DIF the values were 0.90 and 0.76 in populations 1 and 2, respectively.

Table 3 ANOVA of a joint regression analysis for heterogeneity of the slopes of *ms10* genotypes within family means over family means; sums of squares (SS) and F values for pistil length (PL), anther-cone length (AL) and the difference between them (DIF) (0.1 mm)

	Population 1*			Population 2†		
	SS	F	$P(F)$	SS	F	$P(F)$
PL	16.1	1.7	0.20	4.1	1.3	0.28
AL	2.5	0.5	0.58	9.9	2.0	0.14
DIF	3.4	0.3	0.74	1.3	0.3	0.74

*With 2 and 32 degrees of freedom.
†With 2 and 50 degrees of freedom.

Discussion

The ms10 *gene*

The *ms10* gene reduced both PL and AL in male-sterile flowers relative to fertile ones, with greater reduction in the latter trait, as previously reported (Philouze, 1969, 1973). The DIF was therefore greater in male-sterile than in fertile flowers, which led in population 2 to a relatively more exserted stigma in

male-sterile than in fertile flowers (Fig. 1f), as also reported by Philouze (1974). With other genetic backgrounds, such as families with high DIF in population 1, it can lead to an exserted stigma in male-sterile flowers and an inserted stigma in fertile ones (Fig. 1e). In all three traits, complete dominance of the male-fertile allele was found, in agreement with a previous report (Atanassova & Georgiev, 1986).

Despite the differences in mean PL between the two populations, both additive and dominance effects of *ms10* on the three examined flower traits in the two populations were identical. Similarly, Elkind *et al.* (1990), using the same experimental design, found the additive and dominance effects of the *nor* gene on tomato fruit softness to be identical in two different populations. It is therefore concluded that the 'F_3-families' experimental design facilitates accurate estimation of single gene effects on quantitative traits.

'Main polygenic variance'

The 'between-families' variance component was found to be significant in all cases, except that of AL in population 2. This component reflects polygenes acting in a similar manner (with respect to direction and size) on the three *ms10* genotypes, and is referred to hereafter as 'main polygenic variance'. For example, polygenic combinations that code for long pistils maintain their effect on pistil size in all three *ms10* genotypes. It seems that most of the continuous genetic variance is due to the main polygenic component (Table 2). This suggests that genetic information regarding these flower traits in fertile plants, obtained in other studies (Ruttencutter & George, 1975; Atanassova, 1977; Hanna & Hernandez, 1979; Scott *et al.*, 1980), might apply to male-sterile plants as well. This is true, however, only when the magnitude of the 'between-families' variance is relatively large.

The existence of significant genetic interaction affects the relevance of heritability estimates for selection purposes, and such estimates should therefore be viewed with caution. In our study, PL and DIF in population 2 had no significant *ms10* by polygenes interaction. Significant polygenic interaction was detected for DIF by a joint scaling test (data not shown). Therefore, in population 2 the 'net polygenic heritability' could be estimated only for PL, and was 0.62 (calculated from Table 2). This value is similar to the estimate (0.72) reported by Hanna (1980) for fertile plants. Heritability estimates for population 1, in which little interaction was detected for each of the three traits, ranged from 0.6 to 0.9.

Variance due to ms10 *by polygenes interaction*

The *ms10* by families interaction was found to be significant and random in nature for all traits in population 1 and for AL in population 2 (Table 2, Fig. 1). Such an interaction may result from polygenes that have different effects on each *ms10* genotype (Elkind & Cahaner, 1986). This is the first description of such interaction between the *ms10* gene and polygenes for PL and AL. Significant random single-gene by polygenes interaction was found for the *Rht* gene and culm length in spring wheat (Baharav *et al.*, 1992) and for the *nor* gene and tomato fruit softness (Elkind *et al.*, 1990).

For population 1, although *ms10* by families interaction was found significant for all three traits, it contributed a relatively small part of the continuous genetic variance (12–15 per cent, calculated from Table 2). In population 2 the *ms10* by families interaction for AL was similar in magnitude to that in population 1, but it was the major source of continuous genetic variation because the 'main polygenic variance' was very small (Table 2). This might indicate that the polygenes involved in the interactions are independent of those having the main effects.

Despite the relatively small variance due to the *ms10* by polygenes interaction, the 'F_3 family' experiment allowed its detection with a high level of significance. This demonstrates that an experiment of the size used in our experiment (20 families, 670 plants) has a sufficient power of test. Similar conclusions were reached in a computer simulation study (Elkind, unpublished results).

Use of the ms10 *gene in a tomato breeding programme*

Many modern fresh-market tomato varieties are hybrids, and the percentage of hybrid varieties for processing is on the rise. Male sterility greatly reduces the production costs of hybrid seeds (Lapushner & Frankel, 1967; Scott *et al.*, 1980; Yordanov, 1983). An exserted pistil in the male-sterile flower eliminates the need for emasculation prior to pollination, and further reduces production costs. On the other hand, only inserted pistils can ensure good self-pollination and successful fruit set of the hybrid plants cultivated under high temperatures (Levy *et al.*, 1978; Hanna, 1980). Thus the ideal flower type for seed production differs markedly from that of the commercial hybrid plants.

Theoretically this conflict can be solved using one of the following genetic options: (1) a male-sterile gene that codes for long pistil and/or short anther-cone; (2) a polygenic combination that controls exserted pistil in male-sterile flowers and inserted pistil in fertile

flowers; (3) a male-sterile female line with polygenes for exserted pistils and a male line with a polygenic combination producing inserted pistils in the hybrid.

In this study, the effect of the *ms10* gene seems to fulfil the requirements of the first option by reducing AL more than PL. In a certain polygenic combination this will result in stigma exsertion of about 0.6 mm in the male-sterile flower and stigma insertion of about 0.6 mm in a fertile flower (Table 1). However, high temperatures, which cause even greater stigma exsertion (Levy *et al.*, 1978), may lead to exserted stigmas in fertile flowers. The *ms10* gene is therefore insufficient for option (1). Because of the small variance due to the *ms10* by polygenes interaction, the second option is inapplicable given the genetic variation present in this experiment. This option might be useful only if a larger genetic variation for *ms10* by polygenes interaction could be detected and introduced into the breeding material. The third option might be of practical value, since additive polygenic variance was found for the DIF. However, others have reported dominance of exserted pistil (Ruttencutter & George, 1975; Atanassova, 1977; Scott *et al.*, 1980), and in such populations the third option would therefore be inapplicable.

It thus seems that emasculation of the *ms10* male-sterile parent is unavoidable in most cases for hybrid seed production. Possible alternatives to this process are seed production under high temperatures or application of gibberellic acid in order to increase PL (Scott *et al.*, 1980; Yordanov, 1983).

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