

# EXPECTED AND ACHIEVED RESPONSES TO SELECTION FOR STEM THICKNESS IN THE GENERATIONS $F_2$ AND $F_2\text{Syn}_3$ OF THE SEMIEXOTIC MAIZE POPULATION Mo17 x La Posta

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Received November 20, 2001

**ABSTRACT** - Selection in  $F_2$  vs selection in advanced generations of  $F_2$  random mating ( $F_2\text{Syn}_n$ ) differ in degree of linkage disequilibrium in the initial population and in time required for the obtainment of this population. Expected and realized responses to mass selection on stalk thickness were compared when selection was applied to  $F_2$  and  $F_2\text{Syn}_3$  populations. Four successive generations of random mating were performed on material obtained from crossing the adapted inbred of maize Mo17 with the exotic population Across 8443 La Posta. In the second and fifth generations ( $F_2$  and  $F_2\text{Syn}_3$ ) the genetic variance of the traits stem thickness, days to pollen shedding, and grain yield was studied by means of a family analysis. A 5% selection pressure for increased stem thickness was applied simultaneously in both  $F_2$  and  $F_2\text{Syn}_3$  to obtain two selected populations ( $F_{2s}$  and  $F_{2\text{Syn}_3s}$ ). Analysis of the genetic structure and comparison of the expected and realized responses to selection indicated that there are no appreciable changes in genetic structure between  $F_2$  and  $F_2\text{Syn}_3$  of the semiexotic for stem thickness or days to pollen shedding. However, differences in grain yield were found between the two populations, apparently due to linkage disequilibrium in  $F_2$ , with groups in repulsion phase. In both generations, no differences were seen between the expected and realized responses to selection for stem diameter. Likewise, the correlated response to selection in days to pollen shedding occurred as predicted. A significant correlated response in grain yield with selection for stem thickness was estimated in  $F_2\text{Syn}_3$ . Therefore, to breed for grain yield directly or indirectly through stem diameter in this semiexotic population, several generations of intermating are needed to reach linkage equilibrium. In the present study, four were sufficient.

**KEY WORDS:** Genetic structure; Stem diameter; Semiexotic population; Yield; Linkage equilibrium.

## INTRODUCTION

Maize breeders have shown interest in germplasm of tropical or subtropical origin, also known as exotic germplasm (HALLAUER, 1978), because it is a major source of genetic variability (GOODMAN and BROWN, 1988; RAGOT *et al.*, 1995, GOUESNARD *et al.*, 1996). The possibility of including exotic germplasm in maize adapted to temperate climates to broaden its genetic base and develop superior inbreds has been studied from the mid-twentieth century (BRUCE and LINDSTROM, 1954; KRAMER and ULLSTRUP, 1959) to the present (OYERVIDES-GARCÍA *et al.*, 1985; MUNGOMA and POLLAK, 1988; BOSCH *et al.*, 1994; HAMEED *et al.*, 1994; HOLLAND *et al.*, 1996; SELIG *et al.*, 1999; BIASUTTI *et al.*, 2000). The main difficulty arising from this breeding strategy is the time needed, and it is commonly considered a long-term way of improvement in temperate areas like the Corn Belt (HALLAUER, 1990; HOLLAND *et al.*, 1996).

Currently, the first problem to be overcome is the adaptation of the exotic germplasm to a given area, mainly in order to correct the response to the new photoperiod (HALLAUER, 1978). To shorten this adaptation process it may be convenient to cross the exotic material with an adapted inbred or variety and to use the resulting semiexotic population as the starting point for the breeding program (ALBRECHT and DUDLEY, 1987a, 1987b; BOSCH *et al.*, 1994; CASAÑAS *et al.*, 1994; HOLLAND *et al.*, 1996). The presence of adapted germplasm can also enhance the heterotic response when the semiexotic lines derived are crossed with adapted lines to produce hybrids. To save time in such a program, it is very important to evaluate the expected response to selection that will be found in the  $F_2$  and successive random mating generations ( $F_2\text{Syn}_n$ ) of the semiexotic population, as linkage could interfere in the process. In practice, a minimum number (one or two) of gen-

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erations of intermating is used in most recurrent selection programs. HALLAUER and MIRANDA (1988) and LAITER (1965, 1966a, 1966b) examined the effects of linkage on the limits of selection and concluded that reduction in total response was minor unless the recombination probability among loci was less than 0.1. Although according to HANSON (1959) four generations of intermating may be sufficient to reach linkage equilibrium, semiexotic populations have enough particularities to make previous studies advisable to establish in which generation it is most convenient to start with selection.

A more general problem when selecting for grain yield is the low heritability of this trait (HALLAUER and MIRANDA, 1988), and the difficulty of an improvement process based only on yield (yield is a trait measured after flowering, so the selected plants cannot be crossed), makes indirect selection strongly recommended when possible. Among traits with a reasonable heritability and good additive genetic correlation with yield, stem diameter appears to be a useful one, both in adapted maize, where it has been successfully used to drag increased ear yield (CASAÑAS *et al.*, 1998) and in semiexotic maize (MAS *et al.*, 1998). In the latter study, recurrent selection to improve the population Mo17 x Across 8443 La Posta itself or for its combining ability with the B73 inbred appeared to be a promising strategy in the development of hybrids for mild Mediterranean areas.

In this context we conducted several experiments in order to: i) analyse the genetic structure and expected response to selection for the semiexotic population of maize Mo17 x Across 8443 La Posta in  $F_2$  and  $F_2\text{Syn}_3$  (obtained from  $F_2$ , after three successive generations of random mating), ii) compare the expected and achieved responses to selection, together with the correlated variations in earliness and grain yield after a generation of selection in  $F_2$  and  $F_2\text{Syn}_3$  for thickness of the stem diameter.

## MATERIAL AND METHODS

### Germplasm

The exotic population Across 8443 La Posta was provided by the International Maize and Wheat Improvement Centre (CIMMYT). Across 8443 La Posta was obtained from population 43 Across 8443 La Posta, a tropical late dent Tuxpeño synthetic composed of 16 inbred lines, after four cycles of family selection for yield and ear height based on the International Progeny Test Trials conducted by CIMMYT (CIMMYT, 1984; PANDEY *et al.*, 1986).

### Family analysis

In order to obtain the semiexotic Mo17 x Across 8443 La

Posta ( $F_1$ ), one hundred randomly chosen plants of the exotic population were crossed to the inbred line Mo17. The  $F_2$  population was obtained by intercrossing a set of two hundred  $F_1$  plants. Three subsequent generations of random mating were carried out to develop the  $F_2\text{Syn}_3$  population.

To generate half and full-sib families, randomly chosen  $F_2$  plants (MAS *et al.*, 1998) were used as male parents and crossed to six female parents of the same population; the same was done within the  $F_2\text{Syn}_3$  population. After harvesting, three ears with adequate seed set, representing a cross with a particular male plant, were randomly chosen to constitute a single male group (half-sib family). A total of 50 such half-sib groups were obtained giving 150 full-sib families for the study of genetic variances and correlations. These families were grown in N.E. Spain, between 41° and 42°N, with a mild Mediterranean climate, at a density of 62,500 plants/ha. Irrigation was available with a minimum water supply of 30 mm per week. In each trial 12 plants per full-sib family were studied throughout three blocks (four randomly distributed plants per block).  $F_2$  offspring were studied at a single location (MAS *et al.*, 1998) in a two year trial (the same full-sib families were used each year), and  $F_2\text{Syn}_3$  offspring were studied in a single year in a three-location trial.

All experimental data were recorded for individual plants. Before harvest the following traits were considered: the thinnest diameter in the central part of the first elongated internode of the stem in mm, days to pollen shedding, and grain yield in g of dry matter per plant.

The methods used in this study were based on assumptions of the nested mating design (North Carolina Design D) from COMSTOCK and ROBINSON (1948): random mating, regular diploid behaviour, no reciprocal effects, no linkage disequilibrium, and no epistasis. Linkage disequilibrium might affect estimates of genetic variances and correlations. Furthering knowledge on this point is one of the aims of this study.

The estimates of the components of variance were computed using the VARCOMP procedure (method Restricted-Maximum Likelihood, REML) of the SAS program (SAS INSTITUTE, 1990; SAS INSTITUTE, 1997) following the linear model:

$$x_{ijklr} = \mu + y_i + b_{j(i)} + m_k + f_{l(k)} + (ym)_{ik} + (yf)_{il(k)} + e_{ijklr}$$

where  $x_{ijklr}$  is the observed value of the individual plant with  $k$  male parent and  $l(k)$  female parent in the  $j(i)$  block during the  $i$  year of study in  $F_2$  progenies or  $i$  location of study in the  $F_2\text{Syn}_3$  progenies;  $\mu$  is the overall mean;  $y$ ,  $b$ ,  $m$ , and  $f$  refer to the sources of variation (year in  $F_2$  and location in  $F_2\text{Syn}_3$ , blocks, males and females);  $e_{ijklr}$  is the error associated with observation  $ijklr$ . Effects of all sources of variation were considered at random. Their asymptotic standard errors were computed by taking the square root of the estimated asymptotic covariances of the components of variance.

Estimates of  $\sigma^2_M$  and  $\sigma^2_P$  were used to estimate additive genetic variances ( $\sigma^2_A = 4\sigma^2_M$ ), dominance variances ( $\sigma^2_D = 4(\sigma^2_P - \sigma^2_M)$ ) and their interactions with environments. Narrow-sense heritability was estimated as  $h^2 = \sigma^2_A / \sigma^2_P$ , where  $\sigma^2_P$  is the total phenotypic variance estimated on an individual basis. The asymptotic standard errors of genetic variances and heritabilities were computed according to the d method (RAO, 1973) using the asymptotic covariance matrix of the components of variance, and components of variance, estimated using the REML-method according to the lineal model above described.

Responses to selection ( $R$ ) per unit of applied intensity ( $i$ ) were computed according to the expression  $R_i = h^2 \sigma_P$  (FALCONER, 1989).

Following the same linear model and using the GLM procedure of the SAS program (SAS INSTITUTE, 1990; SAS INSTITUTE, 1997) with RANDOM and MANOVA options, multiple analysis of variance was computed to obtain cross-mean products and additive covariances needed to obtain additive genetic correlations ( $r_A$ ).

Correlated response to selection in the trait  $y$  ( $CR_{y_i}$ ) per unit of applied intensity of selection in the trait  $x$  ( $i$ ) was computed according to the expression  $CR_{y_i} = h_x r_A \sigma_{Ay}$  (FALCONER, 1989), where  $h_x$  is the square root of the heritability of the  $x$  trait,  $r_A$  the additive genetic correlation between the involved traits, and  $\sigma_{Ay}$  the square root of the additive genetic variance of the trait  $y$ .

#### Selection in Mo17xAcross 8443 La Posta $F_2$ and $F_2Syn_3$ generations

Two thousand competitive plants of Mo17xAcross 8443 La Posta  $F_2$  and  $F_2Syn_3$  generations, with an effective density of 62,500 plants/ha, were used in each selection process. The smallest diameter of the central part of the first elongated internode of each plant was measured when the earliest plants shed pollen. The female inflorescences of the 100 plants with greatest diameter were covered before silking. When silks were receptive on 15 plants, pollination was performed by collecting the pollen of all selected plants, mixing it together, and using it to pollinate all the receptive plants. This process was repeated every two days until all 100 selected plants were pollinated. The applied selection pressure of 5% corresponds to a selection intensity of  $i=2.06$  (FALCONER, 1989), as normal distributions were assessed in our populations. Kernels were removed from the cobs of the resulting ears and mixed together to produce the seeds for the comparative trial. All generations of selection were carried out in N.E. Spain, between 41° and 42° N, with a mild Mediterranean climate in 1999. Irrigation was available with a minimum water supply of 30 mm per week.

The comparative study of Mo17xAcross 8443 La Posta,  $F_2$ ,  $F_2Syn_3$ ,  $F_2$  selected ( $F_{2s}$ ) and  $F_2Syn_3$  selected ( $F_{2Syn_3s}$ ) populations was performed from July through October 2000, under irrigation at three different locations, all in N.E. Spain. An experi-

mental design of randomised blocks with six replications was used at each location. Each block consisted of four rows (one for each population). Each row (plot) consisted of 34 competitive plants (density 62,500 pl/ha).

The following traits were recorded:

- Stem diameter in millimetres. The thinnest diameter in the central part of the first elongated internode of the stem, recorded plant by plant.
- Days to flowering. Recorded as the number of days from planting to 50% of plants in a plot shedding pollen.
- Grain yield per plant (in g). Ears were harvested long after the appearance of the black layer.

Data were analysed according to the linear model,

$$x_{ijkl} = \mu + g_i + l_j + b_{k(i)} + gl_j + e_{l(ijk)}$$

where,

$g_i$  = population effect

$l_j$  = location effect

$b_{k(i)}$  = block effect within location

$e_{l(ijk)}$  = residual effect (plot within generation, block and location).

Calculations were performed using the GLM procedure of the SAS statistical package (SAS INSTITUTE, 1990; SAS INSTITUTE, 1997).

## RESULTS AND DISCUSSION

In generation  $F_2$  the variances owing to environmental factors (year and block) were not significant for any trait, and neither were the interactions of these factors with the male and female effects (Table 1). The male and female effects were, however, significantly different from zero for all traits except male in the trait grain yield (Table 1).

TABLE 1 - Estimates of variance components of year ( $\sigma^2_Y$ ) or location ( $\sigma^2_L$ ), bloc ( $\sigma^2_B$ ), male ( $\sigma^2_M$ ), female ( $\sigma^2_F$ ), year or location  $\times$  male ( $\sigma^2_{YM}$  or  $\sigma^2_{LM}$ ), and year or location  $\times$  female ( $\sigma^2_{YF}$  or  $\sigma^2_{LF}$ ) in  $F_2$  and  $F_2Syn_3$ , and their asymptotic standard errors.

$F_2$	$\sigma^2_Y$	$\sigma^2_B$	$\sigma^2_M$	$\sigma^2_F$	$\sigma^2_{YM}$	$\sigma^2_{YF}$
Days to pollen shedding	21.055 ±2.22	0.3120 ±0.241	4.524* ±1.28	4.3589* ±0.721	0.0142 ±0.103	0
Stem diameter (mm)	0.9136 ±0.936	0.0500 ±0.046	0.736* ±0.251	1.040* ±0.198	0	0
Grain yield (g/plant)	128.72 ±149.27	50.47 ±40.22	71.93 ±95.09	318.39* ±68.10	44.36 ±32.22	0
$F_2Syn_3$	$\sigma^2_L$	$\sigma^2_B$	$\sigma^2_M$	$\sigma^2_F$	$\sigma^2_{LM}$	$\sigma^2_{LF}$
Days to pollen shedding	0.7250 ±0.613	0.0026 ±0.025	3.6901* ±0.9406	2.0330* ±0.3973	0	0
Stem diameter (mm)	0	0.3517* ±0.1741	0.5283* ±0.1679	0.6200* ±0.1228	0	0.0162 ±0.0577
Grain yield (g/plant)	694.13 ±575.3	0	331.08* ±95.42	137.48* ±63.94	0	37.858 ±55.92

\* Variance component significantly different from zero at  $p \leq 0.05$ .

TABLE 2 - Estimates of additive variances ( $\sigma^2_A$ ), dominance variances ( $\sigma^2_D$ ), narrow-sense heritabilities ( $h^2$ ), expected response to selection ( $R/i$ ) and expected percent increase (%inc) achieved in each trait per unit of applied selection, in  $F_2$  and  $F_2Syn_3$  generations.

$F_2$	$\sigma^2_A$	$\sigma^2_D$	$h^2$	$R/i$	%inc
Days to pollen shedding	18.10* ±5.12*	0	0.69* ±0.18*	3.54* ±0.68	4.44* ±0.85
Stem diameter (mm)	2.94* ±1.01	1.22 ±1.43	0.29* ±0.10	0.926* ±0.20	3.29* ±0.73
Grain yield (g/plant)	287.73 ±236.37	985.86* ±422.27	0.09 ±0.07	5.08 ±6.67	3.68 ±4.84
$F_2Syn_3$	$\sigma^2_A$	$\sigma^2_D$	$h^2$	$R/i$	%inc
Days to pollen shedding	14.76* ±3.76	0	0.78* ±0.16	3.39* ±0.79	4.12* ±0.96
Stem diameter (mm)	2.11* ±0.67	0.37 ±0.92	0.29* ±0.09	0.79* ±0.24	3.20* ±0.99
Grain yield (g/plant)	1324.31* ±381.69	0	0.28* ±0.08	19.15* ±5.47	11.27* ±3.22

\* Variance component significantly different from zero at  $p \leq 0.05$ .

\*  $\sigma^2_A$ ,  $\sigma^2_D$  or  $h^2$  asymptotic standard error.

In generation  $F_2Syn_3$ , the variances due to environmental factors (location and block) were not significant except block for the trait stem diameter, which falls near the limit of significance (Table 1). The interactions of the environmental factors with the male and female effects were not significant, either (Table 1). Male and female effects were significantly different from zero in all traits (Table 1).

#### Genetic structure in $F_2$ and $F_2Syn_3$

Small differences were found between  $F_2$  and  $F_2Syn_3$  for the heritability of stem diameter (Table 2). Similar values for both generations were also estimated for the expected response to selection per unit of applied intensity of selection for this trait (Table 2). Thus it seems that the genetic structure that controls stem thickness has not undergone radical changes between generation  $F_2$  and  $F_2Syn_3$ . The presumed linkage disequilibrium in  $F_2$  is not important and the deviations in the estimates of  $\sigma^2_A$  and  $\sigma^2_D$  caused by it are small, and not significant (Table 2).

The situation for the trait days to flowering is similar. Neither the estimates of  $\sigma^2_A$  and  $\sigma^2_D$ , nor the heritability and the response to selection per unit of applied intensity of selection are significantly different between  $F_2$  and  $F_2Syn_3$  (Table 2).

Grain yield showed no significant additive variance in  $F_2$ , with the one due to dominance being the most important genetic source of variation (31%

of total phenotypic variance). Although not very common (HALLAUER and MIRANDA, 1988), similar situations were reported in adapted germplasm by CASAÑAS *et al.* (1988), GOUESNARD *et al.* (1989) and MALVAR *et al.* (1996). We can suppose that for this trait the Mo17 x Across 8443 La Posta had not reached equilibrium, so that linkage bias would cause underestimations of additive variance and overestimations of dominance variance (HALLAUER and MIRANDA, 1988).

In  $F_2Syn_3$  the additive variance is very high with respect to  $F_2$ , while the dominance equal to 0 (Table 2), with the consequence that heritability and the response to selection per unit of applied intensity of selection are statistically significant.

The results show that three additional generations of intermating do not modify the expected response to selection for thickness of the stem and days to flowering; this will enable us to save time and start the process in  $F_2$ . It seems that in this population the main loci involved in variation of each of these traits are not linked (or if they are, they have a very high frequency of recombination).

The situation is different for grain yield. Some of the loci involved in the control of this trait are presumably linked (linkage between quantitative loci involved in grain yield was reported in several studies, e.g., GRAHAM *et al.*, 1997); moreover, the genomes of Mo17 and Across 8443 La Posta are

complementary for heterosis. In both Mo17 and Across 8443 La Posta, the loci involved in yield would show heterogeneity for dominant and recessive linked alleles, so that in F<sub>2</sub>, in linkage disequilibrium, states of repulsion would predominate. In F<sub>2</sub> of B73 x Mo17, WOLF *et al.* (2000) reported a  $\sigma^2_D > \sigma^2_A$  which they attributed to linkage disequilibrium, while epistatic variance was of little importance. HANZELIN (1998), in an introgression of exotic germplasm into elite Brazilian populations found a reduction in the genetic variances for grain yield, which he attributed to changes in linkage equilibrium and epistatic interactions. This kind of interactions could also contribute to explain the differences between F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub> in our experiment.

The genetic variances affect the values of the additive genetic correlations between traits and the expected correlated responses to selection for stem diameter. In F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub> the additive genetic correlations between stem diameter and days to pollen shedding are significantly different from zero but are not significantly different from each other (Table 3). This leads to correlated responses in days to pollen shedding per unity of applied intensity of selection in stem diameter significantly different from zero but not significantly different between F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub> (Table 3). On the other hand, as the yield in F<sub>2</sub> shows negligible additive genetic variance, the expected correlated response to selection in grain yield per unity of applied intensity of selection in stem diameter is not significantly different from zero (Table 3). In F<sub>2</sub>Syn<sub>3</sub>, with a significant additive genetic correlation between both traits, the correlated response in grain yield per unity of applied intensity of selection in stem diameter is significantly different from zero (Table 3).

The comparison of the values of the genetic parameters of Mo17 x Across 8443 La Posta with the values obtained in an adapted variety such as Lancaster, which is supposedly in a state of linkage equilibrium, shows that the differences in generation F<sub>2</sub>Syn<sub>3</sub> of Mo17 x Across 8443 La Posta with respect to the structure of Lancaster are minimal (in Lancaster, heritability of stem diameter =0.36±0.12, pollen shedding =0.68±0.16, grain yield =0.21±0.12; and expected % increase per unit of selection intensity applied =4.35%, 2.5% and 6.91% respectively – ALMIRALL *et al.*, 1996 –). Thus, after four generations of intermating the semiexotic population generated by crossing the adapted inbred Mo17 with the exotic population Across 8443 La Posta shows similar heritabilities to those found in an adapted population in equilibrium.

TABLE 3 - A) Estimates of additive genetic correlations among traits with significant additive variance in F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub>. B) Expected correlated responses in days to pollen shedding and grain yield per unit of applied intensity of selection in stem diameter.

Traits	F <sub>2</sub>	F <sub>2</sub> Syn <sub>3</sub>
A) Stem diameter-days		
to pollen shedding	0.535±0.147	0.390±0.151
Stem diameter-grain yield	0	0.512±0.156
Days to pollen shedding-grain yield	0	0.376±0.152
B) Days to pollen shedding (days)		
	1.23±0.39	0.81±0.24
	3.07±0.50*	1.97±0.30
Grain yield (g)		
	0	10.07± 2.69
	0	11.86±2.80

\* Percentage expected increase with a pressure of selection of 5%.

*Achieved versus expected response to selection*

Performing a single cycle of selection for stem thickness in F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub> has generated two new populations (F<sub>2s</sub> and F<sub>2</sub>Syn<sub>3s</sub>) that do not differ significantly from one another (p≤0.05) for this trait (Table 4). The two initial generations (F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub>) also showed no significant difference (p≤0.05) for this

TABLE 4 - Results of the field comparison trial among unselected F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub>, and populations derived from selection for thick stem diameter.

Generation	Stem diameter mm	Pollen shedding* days	grain yield g/plant
F <sub>2</sub> Syn <sub>3s</sub>	27.49a*	86.71a	115a
F <sub>2s</sub>	27.32a	85.61b	89b
F <sub>2</sub> Syn <sub>3</sub>	25.73b	84.41c	106ab
F <sub>2</sub>	25.41b	84.18c	97ab

\* Interval from planting.

\* Figures followed by the same letter are not significantly different according to the Newman-Keuls test (p≤0.05).

TABLE 5 - Comparison of expected and achieved increase in thickness of the stem diameter in F<sub>2</sub> and F<sub>2</sub>Syn<sub>3</sub>. The same for correlated response in days to pollen shedding and grain yield.

	Stem diameter (mm)	Days to pollen shedding	Grain yield (g/plant)
F <sub>2</sub> expected	1.68±0.37	2.58±0.42	0
F <sub>2s</sub> achieved	1.91±0.30	1.44±0.36	-7±9.2
F <sub>2</sub> Syn <sub>3</sub> expected	1.65±0.50	1.67±0.25	12.6±2.9
F <sub>2</sub> Syn <sub>3s</sub> achieved	1.76±0.30	2.30±0.36	9±8.9

trait (Table 4), as would be expected given the genetic structure of  $F_2$  and the fact that no selection had been carried out to develop  $F_2\text{Syn}_3$ . Comparison of the achieved and expected responses to selection for the thickness of the stem diameter reveals that both in generation  $F_2$  and generation  $F_2\text{Syn}_3$  the expected and realized responses coincide and the differences are within the limits of the estimation error (Table 5). The results confirm that the main loci responsible for variation in the stem thickness in the semiexotic population are not strongly linked.

A significant delay in pollen shedding with respect to the starting populations was seen to parallel the thickening of the stem, in both population  $F_{2s}$  and  $F_2\text{Syn}_{3s}$ . Moreover, values for this trait are significantly higher in  $F_2\text{Syn}_{3s}$  than in  $F_{2s}$  (Table 4). Comparison of the expected and realized values for days to pollen shedding after selection for stem thickness shows no significant difference in either  $F_{2s}$  and  $F_2\text{Syn}_{3s}$  (Table 5). Our knowledge of the genetic structure of populations  $F_2$  and  $F_2\text{Syn}_3$  enabled us to accurately predict their behaviour after undergoing selection.

With respect to grain yield, the values obtained in the four populations studied overlap (Table 4). The population  $F_2\text{Syn}_{3s}$  is the most productive, but it is not statistically different from either  $F_2$  or  $F_2\text{Syn}_3$ . No correlated response to selection for stem diameter thickness is expected in  $F_2$ , though it is expected in  $F_2\text{Syn}_3$ . Although this response was observed, it was not statistically different from zero (Table 4). As was stated above, the lack of correlated response in  $F_2$  can be attributed to linkage disequilibrium in repulsion phase. When equilibrium has been reached and the expected correlated response becomes significant ( $12.6 \pm 2.9$  g/plant, with a selection pressure of 5% for stem thickness – Table 5 –), a value of  $9 \pm 8.9$  g is realized, which is not statistically different from zero, but which is also not significantly different from the expected response of 12.6 g (Tables 4 and 5). Data suggest that a real advance is achieved, but due to the high residual of the ANOVA for grain yield, the increase is not statistically significant ( $p \leq 0.05$ ). This would mean that the correlated response in grain yield on performing selection for stem thickness previously found in the Lancaster variety (CASAÑAS *et al.*, 1998) could also be obtained in the semiexotic population Mo17 x Across 8443 La Posta. Nevertheless, to take advantage of this situation for breeding for higher grain yield in the semiexotic population, several generations of intercrossing are needed to reach linkage equilibrium for this trait. In the present study four generations of intermating were sufficient.

ACKNOWLEDGEMENTS - Financial support from CICYT (projects AGF94-0405 and AGF98-0993) is acknowledged.

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