

# PERFORMANCE OF FIVE GENERATIONS OF SELECTION FOR INCREASED STALK DIAMETER IN THE LANCASTER VARIETY OF MAIZE (*Zea mays*, L.), CROSSED WITH B73 INBRED

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**ABSTRACT** - Mass selection of 5% intensity for increased stalk diameter, controlling both parents, was conducted over five generations ( $S_1$  to  $S_5$ ) in the Lancaster maize (*Zea mays*, L.) variety. The five generations of mass selection plus the original Lancaster population ( $S_0$ ) were crossed with inbred B73 to assess the hybrid performance for both grain and forage harvest. The hybrids showed, significant ( $p \leq 0.05$ ) increases in stalk diameter, production traits (ear, stover, and total dry digestible matter yields), and plant size (number of leaves, ear height, and total height). Neutral detergent fibre (NDF) decreased significantly while other traits related to the nutritive quality of the stover did not change significantly. The traits showing significant differences in the hybrid populations are the same ones that showed significant differences with mass selection in the Lancaster populations "per se". With the exception of NDF, these differences ( $S_5 \times B73 - S_0 \times B73$ ) are of the same sign and smaller than those found in Lancaster populations "per se" ( $S_5 - S_0$ ). The results support the selection of stalk diameter for increased grain and forage yields.

**KEY WORDS:** Mass selection; Correlated response; Grain yield; Forage yield; Lancaster variety of maize.

## INTRODUCTION

Breeding directly for yield is difficult because of: lower heritability of ear and stover yields (HALLAUER and MIRANDA, 1981; BOSCH *et al.*, 1999), and the impossibility of selecting male parents because the trait is measured after flowering. Direct selection for yield is slow, making indirect selection, if possible, more advisable.

CASAÑAS *et al.*, (1998) conducted mass selection for increased stalk diameter in the Lancaster variety

of maize over five generations ( $S_0$  to  $S_5$ ). An applied selection intensity of 5% (on both male and female parents) increased the stalk diameter an average of 4% per generation. Overall increases in ear yield (16%), stover yield (31%), and total digestible dry matter yield (24%) were similar to the positive additive correlations found in previous studies by ALMIRALL *et al.* (1996) in the Lancaster population. Indirect responses to selection included increases for days to pollen shedding (4.3%), plant height (10%) and the number of leaves (13.8%). The only significant change in quality-related traits was a 4.3% increase in neutral detergent fibre (NDF).

In maize, the final objective of breeding an open-pollinated population is generally to obtain inbreds for producing better hybrids. For this reason, we studied the hybrid populations obtained by crossing the above-mentioned populations selected for increased stalk diameter (CASAÑAS *et al.*, 1998) with an inbred having a high specific combining ability with Lancaster germplasm. Our aim was to determine how the diameter and other traits contributing to yield vary in the hybrid populations in comparison with the Lancaster populations ( $S_0$  to  $S_5$ ) to evaluate the suitability of mass selection for stalk thickness for improving grain and forage yields in maize.

## MATERIAL AND METHODS

### Genetic material

The five populations obtained through selection for stalk thickness ( $S_1$  a  $S_5$ ) and the initial population ( $S_0$ ) (CASAÑAS *et al.*, 1998) were crossed with the inbred B73 (40 plants from each population were repeatedly pollinated by B73). These six hybrids ( $S_i \times B73$ ) were compared together with the original Lancaster population ( $S_0$ ). Only  $S_0$  was used as a check because the study of the generations of selection in the Lancaster variety (CASAÑAS *et al.*, 1998) found no significant generation  $\times$  location interaction for any trait except percentage of ear dry matter and number of leaves.

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### Comparative study

The comparative study of the six hybrids and  $S_0$  population was conducted from July through October 1999 under irrigation at Caldes de Montbui (location 1), Cardedeu (location 2) and La Roca del Valles (location 3), all in Northeast Spain. The previous study of  $S_0$  to  $S_5$  Lancaster populations (CASAÑAS *et al.*, 1998) had been conducted at the same locations and fields. Both experiments were also sown on the same dates though in different years.

Experimental design was a randomised complete block with six replications at each location. Each block included seven controlled rows (one for each population). Because of  $S_0$  was expected to have less vigour, it was represented by three rows at the beginning of each block, but only the central one row was controlled. The hybrid population next to the  $S_0$  was represented by two rows though only the row farthest, from  $S_0$  was controlled. The remaining hybrid populations were represented by a single row. Four border rows were placed along both sides of each block. Each row (plot) consisted of 42 competitive plants (density 83,300 plants/ha). One half of each plot (21 plants) was harvested at the optimal time for forage. The mature ears were later harvested from the remaining half-plot (21 plants).

### Traits studied

In the half-plots harvested for grain production the following traits were recorded plant by plant (except days to flowering):

- Days to flowering (ps). Recorded as the number of days from planting to 50% of plants shedding pollen.
- Stalk diameter in millimetres (d). The thinnest diameter in the central part of the first elongated internode of the stalk.
- Number of leaves to the ear (el).
- Total number of leaves (tl).
- Height to the ear in cm (eh).
- Total height in cm (th).
- Dry ear yield in g/plant (ey). Ears were harvested long after the appearance of the black layer.
- Percentage dry matter in the ear (%edm).

The traits number of leaves to the ear and total number of leaves were transformed according to the expression  $\sqrt{(x+(3/8))}$  to improve their statistical analysis. Values appearing in the tables are the non transformed ones.

All half-plots of a particular population and location were harvested for forage at the same time. The hybrid populations showed similar maturity ranges and the locations presented only small environmental differences for this trait; therefore, harvest encompassed a period of only 3 days, except for the  $S_0$  population, which was harvested (on average) 3 days later than the latest hybrid population. After harvest the following traits were recorded:

- Dry ear yield in g/plant (ey). Plants were harvested approximately at the late-dough stage, considered the optimum for forage production.
- Dry stover yield in g/plant (sy). For dry yield determinations plants were dried at 60°C, for 72 hours.

A representative sample of the stover of each half-plot was chopped as if for silage, dried at 60°C for 72 hours in a forced-air oven and ground to pass a 1-mm screen of a mill. With this material, duplicate determinations were performed on the following traits:

- Neutral detergent fibre of the stover, expressed as a percentage (NDF) (VAN SOEST and WINE, 1967).
- Stover dry matter digestibility, expressed as a percentage (Ddm) (AUFRÈRE, 1982).
- Cell wall digestibility, expressed as a percentage (Dcwc) (SNEDECOR, 1983). Cell wall digestibility =  $100 - (100 - (\text{digestible organic matter} + 9)) \times (100 - \text{ash content})/\text{NDF}$ ; digestible organic matter =  $0.875 \times \text{stover digestibility} + 9.19$  (AUFRÈRE and DEMARQUILLY, 1989).

- Total digestible dry matter yield in g/plant (TDdmy), calculated from the stover and ear yields and their respective digestibilities according to the expression  $\text{TDdmy} = \text{ey} \times 0.83 + \text{sy} \times \text{Ddm}$ . The ear was assumed to have a constant digestibility value (DEINUM and BAKKER, 1981), since a constant value of ear digestibility has been reported for a wide range of dry matter content (DEMARQUILLY, 1969; AERTS *et al.*, 1976; WHITE and WINTER, 1980).
- Whole plant digestibility (ear + stover) as a percentage of the whole plant weight (TD).

### Statistical treatment of data

The traits were analysed according to the linear equation

$$x_{ijkl} = m + g_i + l_j + b_{k(j)} + gl_{ij} + e_{l(ijk)},$$

where

$g_i$  = population effect,

$l_j$  = location effect,

$b_k$  = block effect within location, and

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

Calculations were performed using the GLM procedure of the SAS statistical package (SAS INSTITUTE, 1985).

To compare the hybrid populations with the Lancaster populations from CASAÑAS *et al.* (1998), the  $S_0$  population was used in the current experiment. The reported values corresponding to the Lancaster populations ( $S_0$  to  $S_5$ ) (CASAÑAS *et al.*, 1998) were transformed in proportion to the mean differences between the  $S_0$  of both experiments.

## RESULTS AND DISCUSSION

The genotype effect was significant ( $p \leq 0.01$ ) for all traits (Table 1 and 2). The location effect was significant for all traits except for ear yield in harvesting for grain ( $p = 0.08$ ). The block effect was significant ( $p \leq 0.05$ ) for all traits except cell wall content (NDF) of the stover, whole plant digestibility (TD), and number of leaves to ear. The interaction genotype  $\times$  location was not significant for any of the traits studied ( $p \leq 0.05$ ).

Stalk diameter, the trait that was the object of selection in the Lancaster population, increased progressively from the initial hybrid generation to the fifth generation hybrid. The total increase in the hybrid populations was 1.78 mm (Tables 1 and 3), compared with 4.82 mm for the Lancaster populations.

### Grain harvest

There was a significant trend toward increased yield with the selection cycles in the material harvested for grain (Table 1). As reported in the experiment on the Lancaster populations (CASAÑAS *et al.*, 1998), a correlated response was only seen in the earlier generations; no response was seen in the last

TABLE 1 - Mean values of the traits measured in plants harvested for grain yield in the Lancaster population ( $S_0$ ) x B73 inbred testcrosses and the  $S_0$  population.

Entry	Pollen shedding days	Stalk diameter mm	Leaves to the ear no.	Total leaves no.	Ear height cm	Total height cm	Ear dry matter %	Ear yield g/plant
$S_0$	75.74	22.65	8.24	14.46	139	260	73	116
$S_0$ xB73	70.11	22.78	8.45	14.52	153	276	72.1	152
$S_1$ xB73	70.11	22.38	8.80	14.83	161	282	72.7	158
$S_2$ xB73	70.50	23.57	8.68	14.68	157	279	71.4	161
$S_3$ xB73	71.05	24.03	8.87	14.99	164	286	71.4	170
$S_4$ xB73	70.33	24.22	9.05	15.15	163	285	71.1	165
$S_5$ xB73	71.00	24.56	9.11	15.23	168	289	71.1	167
lsd ( $p \leq 0.05$ )	0.62	0.48	0.18	0.19	4	5.5	0.8	9

two generations. The total increase was 15 g representing a 65% of the 23.2 g found in the Lancaster populations (Table 3). During selection, a gain of 9.9% in the crosses was achieved with respect to the starting value in  $S_0$  x B73.

The maturity range, (days-to-flowering and % moisture of the ear at harvesting) showed a significant trend toward increased values with the selection cycles (Table 1). The total increase in days to flowering in the hybrids (0.89 days) was only 26% of that in the Lancaster populations (3.35 days), whereas ear yield total increase (15 g) was a 65% of that in the Lancaster populations (23.2 g) (Table 3). Maturity and yield usually have a positive correlation (HALLAUER and MIRANDA, 1981), and the increase in days to flowering increased yields of the hybrids. However, a large part of the advances achieved in ear yield with Lancaster is expressed in the hybrid

populations whilst the lengthening of the maturity range is much reduced in the hybrids.

Similarly, number of leaves to the ear, total number of leaves, ear height, and total plant height increased significantly ( $p \leq 0.05$ ) in the hybrids throughout the five cycles of selection (Table 1). The increase in ear height (15 cm), representing a relative increase  $((S_5 \times B73 - S_0 \times B73) / S_0 \times B73)$  of 9.8%, was less than in the Lancaster populations (20 cm and 14.5%), but is unfavourable response because high ear insertion increases lodging.

Crossing the Lancaster generations of selection with B73 increased stalk diameter and the other traits with each selection cycle, with the exception of percentage of dry matter in the ear (%edm), which decreased due to the significant increase in the maturity range. The increase (decrease) in the population crosses was less than in the Lancaster populations. The gains in ear

TABLE 2 - Mean values of the traits measured in plants harvested for forage yield in the Lancaster population ( $S_0$ ) x B73 inbred testcrosses and the  $S_0$  population.

Entry	EAR		STOVER			EAR + STOVER	
	Yield g/plant	Yield g plant	NDF %	Dewc %	Ddm %	Total digestible dry matter yield g/plant	Total digestibility %
$S_0$	91	132	53.5	36.7	51.0	147	59.6
$S_0$ xB73	122	138	56.7	35.0	47.1	166	64.1
$S_1$ xB73	132	140	57.2	34.2	46.1	174	64.1
$S_2$ x B73	132	144	55.7	33.6	47.0	177	64.2
$S_3$ xB73	135	156	55.7	33.5	47.0	186	63.8
$S_4$ xB73	131	156	54.7	33.2	47.4	184	64.1
$S_5$ xB73	138	161	55.6	33.4	47.1	190	63.7
lsd ( $p \leq 0.05$ )	8	8	1.4	1.8	1.8	9	0.8

TABLE 3 - Initial value ( $S_0$  and  $S_0 \times B73$ ) and overall increase between the initial and the fifth generation of selection in Lancaster and testcrosses. Increases in Lancaster populations were transformed from CASAÑAS et al. (1998) according to  $S_0$  current results.

Traits	Lancaster $S_0 + (S_5 - S_0)$	Testcrosses $S_0 \times B73 + (S_5 \times B73 - S_0 \times B73)$
Pollen shedding (days)	75.74 + 3.35	70.1 + 0.89
Stalk diameter (mm)	22.65 + 4.82	22.78 + 1.78
Leaves to the ear	8.24 + 1.87	8.47 + 0.66
Total leaves	14.46 + 2.03	14.57 + 0.71
Ear height (cm)	139 + 20.1	153 + 15
Total height (cm)	260 + 25.2	276 + 13
Ear yield (grain harvest) (g plant)	116 + 23.2	152 + 15
Ear yield (forage harvest) (g plant)	91 + 15.2	122 + 16
Stover yield (g plant)	140 + 42.2	138 + 23
Ddm (%)	51 - 0.78*	47.1 + 0*
NDF (%)	53.5 + 2.35	56.7 - 1.1
Dcwc (%)	36.75 + 1.22*	35.0 - 1.6*
TDdmy (%)	147 + 34.7	166.1 + 24

\* Not significant ( $p \leq 0.05$ ).

yield were found only in the first generations of selection, being null in the last two generations, as was found in the Lancaster populations. For practical purposes, the trait that attenuates the differences between the hybrids with respect to the results in the Lancaster populations was the maturity range, and those that maintain the differences were ear height and ear yield.

#### Forage harvest

In the hybrid material harvested for forage, ear yield is lower than in the material harvested for grain (Tables 1 and 2), because translocation of starch was incomplete (Table 3). As in the material harvested for grain, ear yield in the hybrids harvested for forage increased significantly ( $p \leq 0.05$ ) as a function of the cycle of selection (Table 3), with a total amount of 16 g during selection. This represents a 13.1% increase over  $S_0 \times B73$ , which is greater than the increase seen in the material harvested for grain (9.9%). However, the corresponding estimation in the material harvested for grain was probably better, because of the difficulty of harvesting forage maize in the same phenological state.

Stover yield increased significantly through the generations of selection. The total increase of 23 g, was 50% of that achieved in the generations of selection in Lancaster (Table 3). An overall increase of 16.7% was seen with respect to the initial generation ( $S_0 \times B73$ ).

Regarding nutritive value and composition of the stover, only NDF showed significant differences between hybrid generations (Table 2). Hybrids in ad-

vanced generations of selection had less fibre than the initial generations (Table 2). This is in contrast with the findings in the Lancaster populations, where the opposite occurred (Table 3). This could be possibly explained by some kind of epistasis caused by the crosses of the inbred B73. Nevertheless, on a practical level, the increases or decreases in NDF are minor (-1.1 percentage points in the hybrids, and +2.35 percentage points in the Lancaster populations) (Table 3).

The total digestible dry matter yield increased with each cycle of selection (Table 2). Because this trait is strongly correlated with the other yield-related traits (Table 4). When the yield-related traits increased with the advancement of the selection cycles, there was a parallel increase in TDdmy.

When comparing the correlations of the mean phenotypical values of the Lancaster  $\times$  B73 populations with those of the Lancaster populations themselves (Table 4), a similar behaviour (positive correlations) in the morphological traits, the yield-related traits, and between the morphological and yield-related traits occurred. The traits related to nutritive quality, however showed opposite behaviours. Neutral detergent fibre and Dcwc show negative correlations with morphological and yield-related traits in the hybrid populations and positive correlations in the Lancaster populations. Therefore, the hybrid populations with thicker stalks have higher yields but with less cell wall and less digestible cell walls, whereas the Lancaster populations show a greater percentage of cell wall and the cell wall is more di-

gestible. In both types of material, the proportion of cell wall (NDF) and its digestibility (Dcwc) are positively correlated, but the Ddm depends more on the first variable than on the second (Table 4), as would be expected.

#### *General effects of the cross*

For the traits not related to the nutritive quality of the stover (i.e., ear yield, forage yield, days to pollen shedding and to late-dough stage, ear height, total height, number of leaves to the ear and total number of leaves), the difference between the initial and final generations in the hybrids is of the same sign as in the generations of selection in the Lancaster populations, though not as great (Table 3). The traits that come closest to the results obtained in the Lancaster populations are ear height and ear yield.

Neutral detergent fibre decreases gradually in the hybrids as the diameter increases, while contrarily NDF increases with diameter in the Lancaster populations (Table 3; CASANAS *et al.*, 1998). The same is true of Dcwc, although in this case the difference is not statistically significant. This leads to significant correlations of both traits with stem diameter, but of opposite sign in both populations

(Table 4). Epistasis probably is at the cause of this difference in behaviour.

#### *Evaluation of the method*

Selection for increased diameter improved yield in the first generations of selection. We were able to improve the Lancaster population for ear and stover yields, and half or more of this improvement was expressed in the Lancaster x B73 hybrid. The weak response for ear yield in advanced generations is not easy to explain. Several instances in literature, show that selection for one trait usually does not improve grain yield in advanced generations of selection, unless consideration is given to other traits as well as the trait emphasized in selection. Examples include selection for resistance to European corn borer (KLENKE *et al.*, 1986) and for ear length (LOPEZ-REYNOSO and HALLAUER, 1998).

In comparison with the yield-related traits, the increase in the maturity range that occurred with the selection of the Lancaster population for thicker stalks is much dampened by the crossing with B73, which is favourable. Increased height of ear insertion, of which 75% remains with respect to the Lancaster populations (Table 3), is undesirable. Ddm was not affected by selection, although NDF and

TABLE 4 - Mean phenotypic correlations between several traits in the six testcrosses (upper row) and Lancaster populations (lower row).

Trait	d	ps	th	tl	ey	ey'	sy	Ddm	NDF	Dcwc
Diameter (d)										
Pollen shedding (ps)	0.76 <b>0.96*</b>									
Total height (th)	0.75 <b>0.95</b>	0.72 <b>0.91</b>								
Total leaves (tl)	<b>0.81</b> <b>0.94</b>	0.55 <b>0.93</b>	<b>0.93</b> <b>0.95</b>							
Ear yield (grain harvest) (ey)	<b>0.82</b> <b>0.83</b>	<b>0.85</b> 0.68	<b>0.88</b> <b>0.90</b>	<b>0.81</b> <b>0.81</b>						
Ear yield (forage harvest) (ey')	0.64 0.58	0.76 0.42	<b>0.87</b> 0.68	0.70 0.66	0.75 <b>0.89</b>					
Stover yield (sy)	<b>0.94</b> <b>0.98</b>	0.79 <b>0.96</b>	<b>0.92</b> <b>0.90</b>	<b>0.93</b> <b>0.93</b>	<b>0.86</b> 0.77	0.75 0.55				
Stover dry matter digestibility (Ddm)	0.72 -0.77	0.30 -0.60	0.15 -0.80	0.38 -0.63	0.30 <b>-0.88</b>	-0.08 -0.61	0.52 -0.68			
Neutral detergent fibre (NDF)	<b>-0.87</b> <b>0.90</b>	-0.45 <b>0.83</b>	-0.51 <b>0.84</b>	-0.71 0.71	-0.68 0.73	-0.38 0.35	-0.77 <b>0.84</b>	<b>-0.81</b> <b>-0.88</b>		
Cell wall content digestibility (Dcwc)	<b>-0.81</b> <b>0.82</b>	-0.61 0.79	-0.78 0.64	<b>-0.85</b> 0.67	<b>-0.89</b> 0.56	<b>-0.81</b> 0.28	<b>-0.83</b> <b>0.89</b>	-0.35 -0.65	<b>0.81</b> <b>0.82</b>	
Total Digestible dry matter yield (Tddmy)	<b>0.88</b> <b>0.90</b>	<b>0.81</b> <b>0.83</b>	<b>0.95</b> <b>0.90</b>	<b>0.90</b> <b>0.93</b>	<b>0.96</b> <b>0.91</b>	<b>0.89</b> <b>0.84</b>	<b>0.97</b> <b>0.91</b>	0.33 -0.68	-0.70 0.67	<b>-0.90</b> 0.69

\* Bold figures: significant correlation coefficient  $p \leq 0.05$ .

Dwc are reduced significantly, probably because they compensate each other. It also seems that NDF and Dwc must be studied in each case, as they can present opposite responses (Table 3), which would be explained by epistasis.

## CONCLUSIONS

The advantages of selection for stalk thickness as a method for increasing both grain and forage yields (CASAÑAS *et al.*, 1998) were confirmed. A large part of the increase in yield gained by mass selection for stalk thickness in Lancaster was added to the heterosis shown by the pattern BSSS x Lancaster. At the same time, the increase in maturity range throughout the selection process in Lancaster, is lessened in the hybrids. As a large part of the advances achieved in yields with Lancaster carries over to the hybrid populations and the lengthening of the maturity range is reduced in the hybrids, the final result is favourable. The results confirm that selection for thicker stalks within populations is an easy procedure for improving yields. Genotype x location interaction with respect to diameter was not significant in the Lancaster "per se" or in the hybrids. Future selection for combining ability with complementary material and the later obtainment of inbreds could be effectively achieved working at a single location.

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