GENETIC CORRELATION BETWEEN TRAITS IN THE ESALQ-PB1 MAIZE POPULATION DIVERGENTLY SELECTED FOR TASSEL SIZE AND EAR HEIGHT

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ABSTRACT: Full-sib and selfed (S_1) progenies were obtained from sub-populations of ESALQ-PB1, divergently selected for tassel size (T+ and T–) and ear height (E+ and E–), and used for estimating genetic and phenotypic correlation coefficients between traits. The analyzed traits were: EW- total ear weight (g/plant), PH- plant height (cm), EH- ear height (cm), TB- tassel branch number and TL- tassel length. The highest genetic (r_G) and phenotypic (r_F) correlation was observed for the combination PH x EH, as expected, with average of 0.800 and 0.778, respectively over sub-populations and locations. It is apparent that divergent selection for tassel size did not affect greatly the correlation between PH and EH in the full sib progenies, but in the inbred progenies the correlation was smaller in the sub-population selected for larger tassels. Genetic correlation between PH and EH with tassel traits was always positive but ranged from 0.020 to 0.668 in Piracicaba and from 0.06 to 0.309 in Rio Verde. Genetic correlation between PH and EH with yield (EW) also was positive in the range of 0.087 to 0.503. EH showed higher correlation with EW in relation to PH x EW and differences were larger in the sub-populations divergently selected for ear height. Correlation between tassel traits with other traits was positive in most of instances and a lack of consistency was observed among sub-populations. Generally the coefficients of genetic and phenotypic correlation differed substantially from the estimates in the base population ESALQ-PB1 before divergent selection for tassel size and ear placement. Divergent selection affected the correlation between traits under unpredicted and varying magnitudes.
Key words: *Zea mays*, genetic correlation, divergent selection, tassel size, ear height

CORRELAÇÃO GENÉTICA ENTRE CARACTERES NA POPULAÇÃO DE MILHO ESALQ-PB1 APÓS SELEÇÃO DIVERGENTE PARA TAMANHO DO PENDÃO E ALTURA DA ESPIGA

RESUMO: Progênies de irmãos germanos e de autofecundação (S_1) foram obtidas de sub-populações de ESALQ-PB1 após seleção divergente para tamanho do pendão (T+ e T–) e altura da espiga (E+ e E–) e utilizadas para estimar os coeficientes de correlação genética e fenotípica entre caracteres. Foram analisados os caracteres: EW- peso de espigas (g/planta), PH- altura da planta (cm), EH- altura da espiga (cm), TB- número de ramificações do pendão e TL- comprimento do pendão. Como esperado, as maiores correlações genéticas (r_G) e fenotípicas (r_F) foram observadas para a combinação PH x EH, com médias de 0,800 e 0,778 , respectivamente, em várias sub-populações e locais. Aparentemente, a seleção divergente para tamanho do pendão não afetou fortemente a correlação entre PH e EH nas progênies de irmãos germanos, mas nas progênies endogâmicas a correlação foi menor na sub-população selecionada para pendão grande. A correlação genética entre PH e EH com os caracteres do pendão foram sempre positivas mas variaram de 0,020 a 0,068 em Piracicaba e de 0,060 a 0,309 em Rio Verde. A correlação genética entre PH e EH com produção (EW) também foi positiva, na faixa de 0,087 a 0,503. EH mostrou maior correlação com EW em relação a PH x EW e as diferenças foram maiores nas sub-populações que sofreram seleção divergente para altura da espiga. A correlação entre os caracteres do pendão com outros caracteres foi positiva na maioria dos casos e uma falta de consistência foi observada entre sub-populações. Em geral, os coeficientes de correlação genética e fenotípica diferiram substancialmente das estimativas na população base ESALQ-PB1 antes da seleção divergente para tamanho do pendão e posição da espiga. A seleção divergente afetou a correlação entre caracteres sob magnitudes imprevisíveis e variáveis.
Palavras-chave: *Zea mays*,correlação genética, seleção divergente, tamanho do pendão, altura da planta

INTRODUCTION

Maize (*Zea mays* L.) is, among the cultivated species, one that has undergone a fantastic improvement in yield through artificial selection (Hallauer & Miranda Filho, 1995). Cultural practices also have greatly contributed to increase yield in the maize crops during this century. More recently, attention has been given to plant architecture toward a better efficiency in the utilization of solar energy and photosynthetic capacity (Donald, 1968; Wittner, 1974; Paterniani, 1974, 1981; Miranda Filho, 1974; Sampaio, 1986). Also, intentionally or not, changes have occurred in tassel size for a better utilization of photosynthates (Mock & Pearce, 1975).

The association between traits is an important aspect to deal with in breeding programs, because genetic change in a given trait may change positively or negatively other traits (Vencovsky & Barriga, 1992). In addition, in most breeding programs the strategy is based on selection for several traits simultaneously and, therefore, knowledge on the genetic association between traits is inevitably useful for the establishment of selection criteria. The basic causes of genetic correlation are pleiotropy, and linkage disequilibrium (Falconer, 1964; Vencovsky, 1978; Hallauer & Miranda Filho, 1995).

One important application of the genetic correlation in breeding programs refers to indirect selection for traits of low heritability and consequently low direct response to selection. Selection for another trait may result in indirect response in the low heritable trait, provided the following conditions are satisfied: i) traits under consideration must be highly correlated genetically; ii) heritability of the secondary trait must be higher than the trait of higher interest (Falconer, 1964; Vencovsky & Barriga, 1992). In maize, for example, two secondary traits were identified for indirect selection to increase yield: prolificacy (Paterniani, 1981) and tassel size (Geraldi et al., 1985).

Although many authors have referred to a negative association between tassel size and yield potential (Leonard & Kiesselbach, 1932; Hunter et al., 1973; Fakorede & Mock, 1978; Lordelo & Miranda Filho, 1981; Geraldi et al., 1985), positive association of those traits also have been reported (Lordelo & Miranda Filho, 1981; Sampaio, 1986; Soares Filho, 1987). There are evidences that the correlation between yield and tassel size tends to be higher and negative under stresses caused by unfavorable environments (Soares Filho, 1987). Brunini et al. (1983) emphasized that environmental factors such as photoperiod, solar radiation and rainfall affect decisively the yield potential of a corn crop and consequently the association between traits may change if there is a differentiated variety response to the environmental factors.

Souza Júnior et al. (1985) reported on a negative correlation between tassel size and prolificacy which were explained by a larger amount of indol-acetic-acid (IAA) produced by larger tassels and causing inhibition of prolificacy, or vice-versa (Anderson, 1967). Other studies referring to the correlation of tassel size with other characters are sometimes contradictories. The correlation between tassel branch number with plant height, ear height and ear placement was reported as positive by Obilana & Hallauer (1974), Ayala Osuna et al. (1986); Miranda Filho & Andrade (2000). However, the same associations were positive in some cases and negative in other cases, as reported by Lordelo (1982), Aguilar Morán (1984), Sampaio (1986), Soares Filho (1987), and Araújo (1992). Some estimates of additive and phenotypic correlation between tassel branch number with plant height, ear height, and grain yield are summarized in TABLE 1. The objectives of this work was to study changes in the genetic correlation between traits after divergent selection for tassel size and ear height in the maize population ESALQ-PB1.

TABLE 1 - Ranges for the estimates of r_A (additive genetic correlation) and r_F (phenotypic correlation, family means) of tassel branch number and other quantitative traits (plant height, ear height, and grain yield).

Characters		Nº of estimates	Range	Average
Plant height	r_A	13	-0.184 to 0.363	0.054
	r_F	17	-0.111 to 0.289	0.138
Ear height	r_A	13	-0.269 to 0.436	0.108
	r_F	17	-0.037 to 0.308	0.204
Grain yield	r_A	13	-0.642 to 0.112	-0.197
	r_F	20	-0.339 to 0.290	-0.046

MATERIAL AND METHODS

Four sub-populations were derived from ESALQ-PB1, after six cycles of divergent selection for tassel size and ear height. Sub-populations were designated by

ESALQ-PB1 (E+): selection for increasing ear height end/or ear placement

ESALQ-PB1 (E–): selection for decreasing ear height end/or ear placement

ESALQ-PB1 (T+): selection for increasing tassel size

ESALQ-PB1 (T–): selection for decreasing tassel size

Full sib progenies were obtained through biparental crosses from each sub-population. In ESALQ-PB1 (T+) and ESALQ-PB1 (T–), S_1 progenies were also obtained by selfing individual plants. The six sets totaled 921 progenies that were evaluated in 18 experiments following the completely randomized block design with three replications, at Piracicaba, SP, and Rio Verde, GO. The numbers of progenies of each set in each experiment are shown in TABLE 2.

Experimental plots were represented by a single row 4.0 m long with 20 plants per plot (0.20 m between plants) after thinning. The following traits were analyzed: PH-plant height (cm), EH-ear height (cm), TB-tassel branch number, TL-tassel length (cm), and EW-total ear weight (g/plant). Except for EW, the experimental units were represented by means of three plants per plot. In Rio Verde (GO), only PH, EH and TB of full sib progenies were evaluated.

The statistical model for variance and covariance analyses following the randomized complete block design is $Y_{ij} = m + p_i + b_j + e_{ij}$, where Y_{ij} is the observed mean of the i^{th} progeny in the j^{th} replication, m is the general mean, p_i is the random effect of the i^{th} progeny, b_j is the random effect of the j^{th} replication, and e_{ij} is the error term. In the analysis of variance the mean squares for progenies (M_P) and Error (M_E) have the following expectations: $E(M_P) =$

TABLE 2 - Number of full-sib (FS) or selfed (S_1) progenies in each experiment representing six sets (divergently selected sub-populations).

Sub-populations	Progeny	Experiments				Total
ESALQ-PB1 (E+)	FS	50	51	51	28	180
ESALQ-PB1 (E-)	FS	57	56	55	-	168
ESALQ-PB1 (T+)	FS	55	54	56	-	165
ESALQ-PB1 (T-)	FS	55	56	54	53	218
ESALQ-PB1 (T+)	S1	54	-	-	-	54
ESALQ-PB1 (T-)	S1	49	49	38	-	136

$\sigma^2 + 3\,\sigma_P^2$ and $E(M_E) = \sigma^2$. In the same way, the corresponding expected mean products (P_P and P_E) in the analysis of covariance have the expectations $E(P_P)$ = cov + 3 cov_P and $E(P_E)$ = cov. In the formulations, σ^2 and cov refer to the variance and covariance of effects relative to the error term. In the same way, σ_P^2 and cov_P refer to the genetic variance and covariance relative to progeny effects. The coefficients of correlation were then calculated by

Genetic correlation coefficient -------- $r_G = \frac{cov_{P(XY)}}{[\sigma^2_{P(X)}\sigma^2_{P(Y)}]^{\frac{1}{2}}}$

Phenotypic correlation of progeny means - $r_F = \frac{P_{P(XY)}}{[M_{P(X)}M_{P(Y)}]^{\frac{1}{2}}}$

X and Y refer to pairs of characters

RESULTS AND DISCUSSION

Observed means for six traits in sub-populations of ESALQ-PB1, divergently selected for tassel size (T+ and T–) and ear height (E+ and E–) are shown in TABLE 3. The direct effect of divergent selection on means of selected traits and the correlated response on other non-selected traits can be visualized in TABLE 3. Also, Farias Neto & Miranda Filho (2000) already presented comparisons involving inbred and non-inbred progenies, leading to estimates of inbreeding depression. Therefore, our attention here focuses on results of genetic (r_G) and phenotypic (r_F) correlation (TABLE 4).

Correlation between plant height (PH) and ear height (EH)

The correlation coefficients (r_G and r_F) between PH and EH were the highest among the combinations of traits in this study. Estimates of r_G and r_F averaged 0.800 and 0.778, ranging from 0.755 to 0.870 and 0.675 to 0.911, respectively, over sub-populations and locations. It is apparent that divergent selection for tassel size did not affect greatly the correlation between PH and EH in the full sib progenies, but in the inbred progenies the correlation was smaller in the sub-population selected for larger tassels. Also, r_G and r_F were smaller in the sub-population selected for decreasing ear height. In general, a high correlation between PH and EH has been reported by many authors. Estimates of the additive genetic correlation (r_A) and phenotypic correlation summarized by Moraes (1989) averaged 0.82 and 0.78, respectively. Also, Hallauer & Miranda Filho (1995) presented a high average genetic correlation of the order of 0.81. Miranda Filho & Andrade (2000) reported on estimates of r_A and r_F of 0,842 and 0.803 between PH and EH in the base population ESALQ-PB1.

Correlation between plant height (PH) and ear height (EH) with tassel traits (TB, and TL)

The correlation coefficients between PH and EH with tassel branch number were always positive but not consistent among sub-populations. The highest correlations of EH with TB were observed with inbred progenies. Also, for both inbred and non-inbred progenies in Piracicaba the genetic correlation was higher in the sub-population selected for larger tassels. However, in Rio Verde, the highest positive correlation (0.301) was for EH x TB in the sub-population (T–). In general, correlation coefficients between EH and TB were higher than for PH and TB. Estimates of r_A and r_F in the base population ESALQ-PB1 were 0.379 and 0.339 for PH x TB and 0.436 and 0.382 for EH x TB, respectively (Miranda Filho & Andrade, 2000). The correlation of PH and EH with tassel length (TL) was estimated in only three and two sub-populations, respectively, and the estimates of r_G were all positive and above 0.40, except for PH x TL in the sub-population ESALQ-PB1 (T+) with inbred progenies (r_G = 0.127). Estimates of r_A in the base population ESALQ-PB1 were 0.273 and 0.101 for PH x TL and EH x TB, respectively (Miranda Filho & Andrade, 2000).

Correlation between plant height (PH) and ear height (EH) with ear yield (EW)

The association of plant height and ear height with yield tends to be always positive. Hallauer & Miranda Filho (1995) reported genetic correlation of 0.26 and 0.31 for the combinations PH x EW and EH x EW, respectively, on the average of 23 experiments. The association of these traits in our experiments comprised only non-inbred progenies, where r_G varied from 0.087 to 0.503 among sub-populations. EH showed higher correlation with EW than PH, and differences were larger in the sub-populations divergently selected for ear height. When looking to the sub-populations divergently selected for tassel size, a higher genetic correlation of PH and EH with EW was observed in ESALQ-PB1 (T+). Estimates of r_A in the base population ESALQ-PB1 were 0.594 and 0.506 for PH x EW and EH x EW, respectively (Miranda Filho & Andrade, 2000).

Correlation between tassel traits (TB, TL) and EW

The genetic correlation coefficients between TB and TL were low but negative (r_G = -0.015) in ESALQ-PB1 (T+) and positive (r_G = 0.232) in ESALQ-PB1 (T–), the two sub-populations representing the divergent selection for tassel size. The later was closer to the r_A estimate (0.217)

TABLE 3 - Observed means for six traits* in sub-populations at two locations (Piracicaba, SP and Rio Verde, GO).

Sub-population	Progeny	Location	PH	EH	TB	EW	TL
ESALQ-PB1 (T+)	FS	PIRACICABA	197.0	107.9	35.1	147.8	42.0
ESALQ-PB1 (T+)	FS	RIO VERDE	201.9	113.4	43.0	-	-
ESALQ-PB1 (T-)	FS	PIRACICABA	187.6	87.7	7.4	139.9	41.8
ESALQ-PB1 (T-)	FS	RIO VERDE	189.5	91.3	8.9	-	-
ESALQ-PB1 (E+)	FS	PIRACICABA	237.4	138.6	22.5	170.9	-
ESALQ-PB1 (E+)	FS	RIO VERDE	221.5	128.6	23.1	-	-
ESALQ-PB1 (E-)	FS	PIRACICABA	165.2	64.1	14.3	130.0	-
ESALQ-PB1 (E-)	FS	RIO VERDE	159.8	70.3	18.3	-	-
ESALQ-PB1 (T+)	S1	PIRACICABA	165.7	97.8	32.2	-	40.5
ESALQ-PB1 (T-)	S1	PIRACICABA	159.6	76.4	6.3	-	38.2
Check		PIRACICABA	169.7	85.2	19.4	194.9	43.6
Check		RIO VERDE	184.8	88.5	15.7	-	-

*PH- plant height (cm), EH- ear height (cm), TB- tassel branch number, EW- ear weight (g/plant) and TL- tassel length (cm).

TABLE 4 - Estimates of the coefficients of genetic (r_G , upper) and phenotypic (r_F, lower) correlation in combinations of six traits in sub-populations of ESALQ-PB1 at two locations.

	Sub-populations*					
	T_{+F}	T_{-F}	E_{+F}	E_{-F}	T_{+S}	T_{-S}
			Piracicaba (SP)			
PHxEH	0.793	0.809	0.838	0.740	0.789	0.870
	0.783	0.781	0.822	0.717	0.775	0.820
PHxTB	0.135	0.020	0.041	0.088	0.092	0.160
	0.184	0.053	0.234	0.214	0.101	0.218
PHxEW	0.195	0.087	0.231	0.342	-	-
	0.174	0.122	0.361	0.314	-	-
PHxTL	0.438	-	-	-	0.127	0.581
	0.252	-	-	-	0.004	0.455
EHxTB	0.192	0.037	0.167	0.241	0.668	0.347
	0.205	0.158	0.370	0.285	0.210	0.326
EHxEW	0.293	0.176	0.388	0.503	-	-
	0.033	0.199	0.346	0.388	-	-
EHxTL	0.421	-	-	-	-	0.439
	0.082	-	-	-	-	0.281
TBxEW	-0.022	0.456	0.208	0.137	-	-
	0.010	0.118	0.223	0.287	-	-
TBxTL	-0.015	0.232	-	-	-	-0.014
	-0.010	0.034	-	-	-	0.071
EWxTL	0.027	-	-	-	-	-
	0.008	-	-	-	-	-
			Rio Verde (GO)			
PHxEH	0.843	0.764	0.805	0.755	-	-
	0.812	0.911	0.675	0.703	-	-
PHxTB	0.127	0.077	0.041	0.040	-	-
	0.041	0.085	0.234	0.102	-	-
EHxTB	0.065	0.301	0.151	0.132	-	-
	0.117	0.272	0.309	0.157	-	-

* T_{+F} : ESALQ-PB1 (T+)FS ; T_{-F} : ESALQ-PB1 (T–)FS; E_{+F} : ESALQ-PB1 (E+)FS; E_{-F} : ESALQ-PB1 (E–)FS; T_{+S} : ESALQ-PB1 (T+)S_1 ; T_{-S}: ESALQ-PB1 (T–)S_1

in the base population ESALQ-PB1 (Miranda Filho & Andrade, 2000). The genetic correlation TBxEW was calculated only for full-sib progenies and was small negative (-0.022) in ESALQ-PB1 (T+) and positive (0.137 to 0.456) in the other three sub-populations. In a study with the same sub-populations in the preceding cycle of divergent selection, Araújo (1992) found the same pattern of correlation between TB and EW. The only r_G estimate for TL x EW was in the sub-population ESALQ-PB1 (T+) and was small positive (0.027). Apparently, divergent selection for tassel size and ear height affected the original pattern of correlation between tassel traits and ear yield because all the estimates depart from the r_A estimates of 0.207 and 0.216 for TB x EW and TL x EW, respectively, as reported by Miranda Filho & Andrade (2000) for the base population ESALQ-PB1. Falconer (1964) emphasized that selection may change significantly the pattern of correlation between traits. However, the pattern of correlation between tassel size and yield depends also on the effect of environment and tends to be positive under favorable environments (Soares Filho, 1987).

Generally the coefficients of genetic and phenotypic correlation differed substantially from the estimates in the base population ESALQ-PB1 before divergent selection for tassel size and ear placement (Miranda Filho & Andrade,2000). Divergent selection affected the correlation between traits under unpredicted and varying magnitudes.

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