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PHENOTYPIC AND GENETIC RELATIONSHIPS BETWEEN YIELD COMPONENTS IN MAIZE

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SUMMARY

Physiological components of kernel development – LAG period, effective filling period duration (EFPD) and grain filling rate (GFR) – ear moisture release (△ U), ear size (row number and kernels per row), days from emergence to silking and number of leaves, were examinated on 45 F_1 hybrids (10 × 10 diallel cross) in order to study their genetic relationships with yield. Combining ability analysis revealed that all trait variability derived mainly from g.c.a. effects. LAG period and EFPD were the traits most affected by genotype-environment interaction.

Covariation analysis (path method) based on mean phenotypic values and on *g.c.a.* effects yielded similar information. It is shown that GFR and EFPD are both related to plant yield, but GFR made the most important contribution. On the contrary, a significant relationship between yield and LAG was not detected. Ear size components were also positively related to yield and had negative effects on GFR. These results indicate that, for our material, the dry matter accumulation rate is the main limiting factor of yield.

Considering *s.c.a.* effects, kernel number per row made the most important contribution.

INTRODUCTION

The grain yield of a maize plant can be considered as the result of two major components, i.e., the number and development potential of the caryopses and the quantity of photosynthates translocated to the ear in the period following fertilization. Kernel development is regulated by three physiological phases characterizing the reproductive period: i) lag period, which goes from silking to the start of dry matter accumulation, ii) the period of linear dry matter accumulation and iii) the period showing a reduction of the dry matter filling rate that ends with physiological maturity, which in maize is marked by the formation of the black layer (JOHNSON & TANNER, 1972).

The relative importance of the parameters characterizing these components of kernel development, their genetic and environmental variability and relationships with other physiological and morphological traits are informations needed to define plant maize ideotypes (MOCK & PEARCE, 1975) and to plan breeding work based on production components. A review of the information concerning these aspects was given by TOLLENAAR (1977). Studies concerning the variability of the length of the reproductive period have furnished contrasting results. However, it is clearly established that this trait is an important yield component (GUNN & CHRISTENSEN, 1965; HANWAY & RUSSELL, 1969; CROSS, 1975; DAYNARD & KANNENBERG, 1976). Genetic differences with regard to the kernel filling period length and/or the kernel filling rate have been found by HILLISON & PENNY (1965), HALLAUER & RUSSELL (1962), JOHNSON & TANNER (1972), CARTER& POTENELEIT (1973), OTTAVIANO et al. (1976) and POTENELEIT & EGLI (1979).

For environmental conditions prevailing in short growing season areas a detailed genetic analysis of the three parameters describing kernel development, i.e., lag period, grain filling rate and length of the filling period, was carried out by CROSS (1975) on a diallel set of hybrids typical of the North Corn Belt area. He found significant combining ability effects for all these traits, but a significant correlation with yield was found only for filling period length.

This information needed to improve the definition of the maize ideotype (MOCK & PEARCE, 1975) for temperate zones, such as the Corn Belt and the Po Valley, is not available. Moreover, correlations between these physiological parameters, yield and other morphological and physiological traits have generally been based on phenotypic values, while for breeding purposes correlations based on genetic effects are desirable.

In this paper we have considered both these aspects by analyzing a diallel set of hybrids obtained from ten inbred lines largely used in temperate zones. The characters studied are those describing kernel development. Morphological ear and plant traits are also considered. The structure relating each trait to plant production has been determined by means of path coefficient analysis.

MATERIALS AND METHODS

A set of 45 F1's obtained by crossing 10 inbred lines (R71, B14, B37, B73, B77, NI72, H3025, Mo17, H55, H95) according to the diallel cross design without reciprocal was grown in a randomized complete block design with three replications. The experiment was repeated in three environments, i.e., two years (1977 and 1978) at Vimodrone (Milano) and one year at Landriano (Pavia). Plots were formed of two twenty-plant rows spaced 70 cm apart. Plant density was 5 plant per m^2. Observations were made on the following traits: a) silking time (days) from emergence; b) plant morphological traits: leaf number and number of ears; c) weight of 50 kernels (50 KW) sampled from the middle part of the ear at 25, 32, 39, 46, 53 and 60 days from silking; d) number of kernels per row (NK/R), number of rows per ear (RN) and kernel weight per plant (KW/P). a) was measured on all plants of each plot. b) on five plants, c) on three ears and d) on five plants at maturity. For all observations only garded plants were used. Kernel weight is the weight found after drying at 80 °C for 48 hours.

Lag period in days (LAG), grain filling rate (GFR) in g/day and effective filling period duration (EFPD) in days were computed for each hybrid in each replication, according to the procedure described by JOHNSON & TANNER (1972). Grain filling rate was estimated by fitting a linear equation to kernel weight, considering only the sampling dates in the linear filling period, i.e., 25, 32, 30 and 46 days from silking. EFPD was obtained as the ratio between kernel weight at maturity and GFR. LAG period was estimated on the basis of the regression equation as the value of X (days) corresponding to 5% of kernel weight at harvesting (final sampling). Water emission was evaluated as the percentage difference in humidity ($\triangle$ U) between kernels at the second and the fourth sampling dates.

Combining ability analysis was carried out for each trait according to the procedure described by GRIFFING (1956). To study relationships between traits, three sets of data were used, i.e., hybrid means (m_{ij}) over environments, general combining ability effects (g_i) and specific effects (s_{ij}). The effects were obtained from hybrid means over environments. Similar to the procedure adopted by CERVATES et al. (1978) for taxonomical analysis, these three sets (matrices) of values formed the raw data for structural analysis according to the path methods of WRIGHT (1918). This method is equivalent to regression analysis performed on standardized variables where two or more regression equations are involved (TURNER & STEVENS, 1955; OTTAVIANO et al., 1977).

RESULTS

Means over hybrids and environments, general combining ability effects and coefficient of determination (R_g^2) for the model including only general combining ability (*g.c.a.*) are reported in Table 1. Table 2 shows the analysis of variance. It shows that differences between hybrids are largely due to the average effects of the lines. Although significant for many traits, specific effects make an important contribution to hybrid variation only for grain yield per plant, while for LAG and EFPD no significant effect was detected. For genotype-environment interaction only the item relating to *g.c.a.* was significant for all traits.

G.c.a. effects describe the genetical features of the parental lines with regard to the yield components studied. For instance Mo17, a parental line well known for its good combining ability and early physiological and agronomic maturity in relation to its silking time, shows the minimum value for GFPD and the highest values for water emission ($\triangle$U) and GFR. B73, one of the best combiners with Mo17, obtains good values of combining ability for production by means of the increase of kernel number due to high number of rows. NI72, a line selected from an Italian population (Nostrano dell'Isola) produces hybrid progeny showing long ears (KN/R). In general it is observed that in this material high values of combining ability for production are reached by means of different combinations of morphological and physiological traits.

Relationships between traits were studied according to the diagram in Fig. 1. Yield per plant (KW/P) is considered as the result of kernel weight at maturity (50KW), RN and KN/R. Number of ears has not been included in the diagram because the hybrid material used is generally single eared. Moreover, statistical analysis did not show any contribution of this trait to plant yield. Kernel weight at maturity (50KW) is considered as the result of LAG, GFR and EFPD. Single path coefficients (standardized partial coefficient of regression) and correlations are reported in the diagram. Compound paths can be easily obtained as moment products (WRIGHT, 1918).

Table 3 shows the values of these coefficients computed on the basis of mean values, *g.c.a.* effects and *s.c.a.* effects. The residual variance, which includes the effects due to factors not considered in the diagram plus the random variation, is given as *res* = $1-R^2$. The least significant value is not the same for the three sets of data because of the different degree of freedom of the residual. In general the structure of covariation depicted on the basis of *g.c.a.* effects is similar to that obtained from hybrid means. Ear size components represent 66% of plant yield variation (*res.* 1 = 0.34) and 88% when *g.c.a.* values are considered. This increase in degree of determination is probably due to a lower sampling error for array means than for single hybrid values. Taking into

Table 1. General combining ability effects based on over environment hybrid means.

Lines	Silking time (days)	50 kernel w.t. (g)	Kernel row n.	Kernel n. per row	LAG (days)	Grain filling rate (g/day) × 10	Eff. filling per. duration	Δ % humidity	Yield per plant (kg)
R71	0.371	-0.863	-0.365	0.005	1.129	-0.111	-1.821	0.499	-13.775
B14	0.412	1.600	-0.178	-3.433	-0.285	0.163	2.583	0.718	6.986
B37	-1.677	0.513	-0.053	0.143	0.493	0.187	-1.113	0.359	10.616
B73	-0.427	-0.175	0.923	-0.558	-0.414	-0.078	0.715	-0.266	3.506
B77	1.214	-0.800	-0.140	0.443	-0.571	-0.187	0.483	0.384	- 4.132
NI72	-1.224	-0.250	-0.428	5.043	-0.225	-0.144	1.228	-3.343	5.722
H3O25	0.109	-0.225	0.435	-1.245	-0.258	-0.154	1.411	-0.936	- 0.648
Mo17	-1.827	1.663	-1.790	2.030	0.639	0.637	-3.719	2.634	4.396
H55	2.320	0.075	-0.385	-0.208	-3.214	-0.048	0.869	-1.466	3.720
H95	-0.396	-1.538	1.211	-2.220	2.706	-0.265	-0.696	1.417	-16.441
hybrid means	61.11	14.92	16.27	43.90	8.73	3.244	46.11	0.180	0.224
R_g^2	0.84	0.78	0.80	0.69	0.34	0.62	0.59	0.84	0.30

R_g^2 stands for coefficient of determination estimated for the model including g.c.a. effects.

Table 2. Combining ability analysis (mean squares).

Items	D.F.	Silking time (days)	50 kernel w.t. (g)	Kernel row n.	Kernel n. per row	LAG (days)	Grain filling rate (g/day)	Eff. filling per. duration	△ %humidity	Yield per plant (kg)
Hybrids	44	35.67**	20.05**	12.68**	115.57**	37.71*	0.01451**	87.22	0.00461**	0.00398**
g.c.a	9	124.34**	76.09**	49.69**	386.29**	66.34**	0.05204**	245.52**	0.01890**	0.00574**
s.c.a.	35	12.86**	5.64**	3.17**	45.96**	30.34	0.00485**	46.01	0.00094**	0.00352**
Env. × Hyb.	88	3.45*	2.51**	1.34*	18.66	27.04	0.00304	78.32	0.00096**	0.00163**
Env. × g.c.a.	18	6.66**	6.62**	2.06*	37.83**	49.33**	0.00757**	123.49**	0.00245**	0.00378**
Env. × s.c.a.	70	2.62	1.45	1.15	11.16	21.30	0.00187	66.70	0.00223**	0.00108**
Residual	264	1.78	1.36	0.99	10.33	22.16	0.00267	67.75	0.00054	0.00065

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

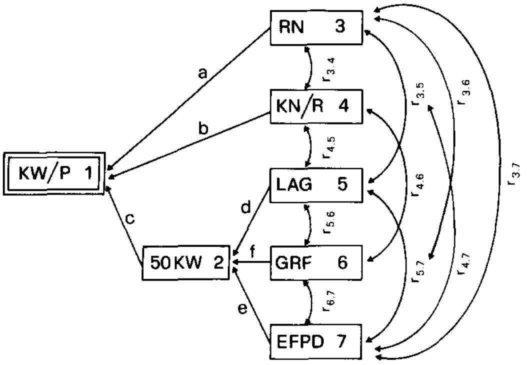

Fig. 1. Path diagram showing causal relationships of various characters to plant yield.

account *a*, *b*, *c* coefficient values, it appears that in this material all ear components significantly affect plant yield, 50KW making the most important contribution. The variation of this trait depends mainly on GFR; a smaller proportion of the variation is due to EFPD, while no significant contribution of LAG was detected. Negative effects on kernel weight arising mainly through GFR are the result, as may be expected, of ear size (RN): the compound path coefficient connecting RN and 50KW *via* GFR is $p_{3.6.2} = -0.63 \times 1.13 = -0.71$).

Considering the diagram based on *s.c.a.* values, KN/R has important effects on plant yield, therefore high positive specific combining ability for this trait is to be pursued. GFR and EFPD have the same effect on kernel weight as in the causal diagrams based on hybrid means and *g.c.a.* effects. However, as the variation of kernel weight is mainly due to *g.c.a.* effects, their contribution to plant yield is very low ($p_{6.2.1} = f \times a = 0.31 \times 1.04 = 0.32$.

Days from emergence to silking, although not accounting for a large portion of yield variation ($r^2 = 0.21$), was negatively correlated ($r = -0.41$) with this trait. Considering the yield components, negative correlations with silking date were found for 50KW, NK/R and GFR (r was -0.41, -0.48 and -0.45 respectively). As expected silking date

Table 3. Simple path coefficient values based on over environment hybrid means, g.c.a. and s.c.a. effects.

Paths	Means	g.c.a.	s.c.a.	Correlations	Means	g.c.a.	s.c.a.
a	0.515**	0.848*	0.142	$r_{3.4}$	-0.426*	-0.523	-0.174
b	0.592**	0.696**	0.633**	$r_{3.5}$	-0.251	0.016	0.112
c	0.797**	1.291**	0.311*	$r_{3.6}$	-0.634**	-0.751	-0.171
				$r_{3.7}$	0.276	0.511	-0.211
res. 1 ($1-R^2$)	0.342	0.117	0.354				
				$r_{4.5}$	0.245	-0.122	0.305
d	0.163	-0.054	0.282*	$r_{4.6}$	0.231	0.121	0.478**
f	1.135**	1.171**	1.041**	$r_{4.7}$	-0.216	-0.277	-0.118
e	0.701**	0.562**	0.850**	$r_{5.6}$	0.456**	0.031	0.516**
				$r_{5.7}$	-0.587**	-0.466	-0.521**
res. 2 ($1-R^2$)	0.029	0.014	0.111	$r_{6.7}$	-0.547	-0.554	-0.594

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

was positively (r = 0.72) correlated with leaf number. Water emission, expressed as $\triangle$ U, was found to be negatively correlated with LAG (r = -0.41), GFR (r = -0.34) and EFPD (r = -0.46).

DISCUSSION

The three components taken to represent kernel weight (LAG, GFR and EFPD) show genetic variation arising mainly from *g.c.a.* effects, which contribute also to the covariance of these traits with kernel production per plant. These results indicate that the values of these components can be genetically improved and that selection programs can be based on simple methods which take advantage of additive genetic variance. In connection with breeding programs, it is also important to note that LAG and EFPD showed the largest amount of genotype-environment interaction, while GFR was more stable. A similar result was obtained by PONELEIT & EGLI (1979) who found that EFPD, but not the rate of kernel growth, is influenced by plant density.

The accuracy of measurement procedures for the evaluation of kernel weight components should also be taken into account. EFPD and LAG, estimated on the basis of the regression equation, are expected to show a larger sampling error than GFR when the method adopted here is used. The measurement can be improved by a within-ear sampling (DUNCAN & HAIFILED, 1964) which also provides the possibility of single-plant evaluations. The efficiency of this procedure has been shown by DAYNARD & KANNENBERG (1976) who obtained a close correlation between EFPD and days from silking to black layer formation.

The correlation between yield and filling period length has been shown in several cases, whereas the significance of the grain filling rate has not been generally demonstrated (DAYNARD et al., 1976; JOHNSON & TANNER, 1972), although specific features of some hybrid varieties, which combine high yield with a relatively short filling period, lead to the conclusion that this component can play an important role (CROSS, 1975; DAYNARD & KANNENBERG, 1976). However, most of these studies refer to materials and environments in northern latitudes, where the length of the filling period is the limiting factor. In this work, relating to different materials and environments, path analysis revealed that both GFR and EFPD are related to yield, but that the former has the highest coefficient. Similar evidences was reported by PONELEIT & EGLI (1979), who found that differences in kernel weight between three inbreds of the same type as those used in this work and the three derived single cross hybrids were mainly due to differential kernel growth rate. Moreover, ear size has, as may be expected, negative effects on GFR, while it does not affect LAG and EFPD. This indicates, that, for our material and the environments where it was grown, the dry matter accumulation rate is the main limiting factor and, consequently, is one of the main traits to be taken into account in the context of breeding programs.

These results lead to the conclusion that a significant potentiality exists for the improvement of grain yield through increasing the efficiency of GFR. Therefore breeding strategy should envisage the incorporation of this trait in the breeding material and the selection of lines with high GFR. On the other hand more information is needed to define the most important morphological-physiological traits (photosynthetic activity, translocation efficiency of photosynthate into grain...) affecting the variability of GFR.

Data in the literature generally indicate a positive correlation between silking date and yield (CHASE, 1964; BRAWN, 1968; TANAKA & HART, 1971; DAYNARD & KANNENBERG, 1976). The negative value observed in this work derives from the effect of GFR and NK/R, which are negatively correlated with silking date. This indicates that in this material, belonging to the medium late group, selection for yield has influenced these components. This also confirms the observation that physiological components of kernel growth can be modified by selection without altering the length of the vegetative phase (CROSS, 1975; OTTAVIANO et al., 1975) and that the production of material with a short vegetative growth period and long grain filling period is feasible. This plant type could also benefit from a high rate of moisture loss, which has been shown to be genetically controlled and consequently modifiable by selection.

Finally, with regard to a statistical approach to the study of relationships between traits, it is important to point out that the simultaneous analysis of the variance of all components on the basis of a logical structure of covariation is the most suitable for measuring the weight of each component; for instance $r_{1.6} = 0.46$ while $P_{6.2.1} = 0.90$.

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