Theoretical and Applied Genetics 42, 346–350 (1972)

Hybrid Prediction in Maize. Genetical Effects and Environmental Variations*

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Summary. This paper proposes a method for predicting the performance of multiple cross hybrids on the basis of single cross information, taking into account the specific interaction of the genotypes with the environment.

In the prediction model the genetical constants are those used for combining ability analysis, while genotype-environmental interaction terms are defined as linear regression of the genotypical effects on environmental variables.

The model was tested by considering the variations arising from the effects of population density; therefore the method was applied in a situation in which the problem was to select the best hybrid-population density combinations.

The results obtained show that the model is suitable to represent phenotypical response across densities.

However, the material used was not the most suitable to emphasize the improvement of the predictive power of the function when genotype-environmental parameters are considered.

Introduction

Predicting the performance of all hybrid combinations between a number of inbred lines is a practical problem that arises because the number of these combinations usually exceeds the practical limits of field evaluation.

Many methods of prediction have been proposed and some of them are currently used (Jenkins, 1934; Eberhart, 1964; Eberhart and Gardner, 1966; Hinkelmann, 1968). In general, theoretical values of all hybrid crosses are estimated on the basis of information obtained from a limited number of genotypes. The relative predictive power of these methods has been assessed and it has been shown that it varies according to the main genetical effects contributing to the differences between hybrids (Eberhart, 1964; Ottaviano et al. 1970). However, the results obtained using the different methods did not always agree sufficiently with the observed values. This means that certain factors not considered in the prediction formulas play an important role in determining the variation in the phenotypical values. These factors are epistasis, genotype-environmental interaction and sampling error (Eberhart et al. 1964; Eberhart and Hallauer, 1968).

The contribution of epistasis to the differences between observed and expected values can be reduced by including in the model parameters for this factor (Eberhart and Gardner, 1966), but the variation resulting from genotype-environmental interaction cannot easily be predicted.

A way of dealing with this problem is suggested by the observations of many authors who found that a significant proportion of genotype-environmental interactions variance can be linearly related to the mean effects of the environment or to some other environmental indexes (Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Ottaviano and Conti, 1968). Furthermore, it has been shown that the genotype-environmental effects can be partitioned according to the genetical parameters considered in the model (Bucio Alanis, 1966; Bucio Alanis and Hill, 1966; Perkins and Jinks, 1968, a and b; Bucio Alanis et al. 1969; Jinks and Perkins, 1970).

In the present work we have extended this approach to hybrid performance prediction, adopting the genetical model used for combining ability analysis. Plant spacing was used as the environmental variable, and the method proposed was applied to predict the performance of hybrid crosses in relation to plant spacing and to select the hybrid-plant spacing combinations which maximize yield.

Material and Methods

The 21 single crosses from all combinations between seven inbred lines of maize were the material used for this experiment. The parental lines, W23, W22, W374R, B2, OH-41, 38–11 and 33–16, will here be referred to as 1, 2, 3, 4, 5, 6 and 7, respectively.

Four different plant density levels were considered: 4, 6, 8 and 10 plants per m^2. The field lay-out was a split-plot with two replications in which plant densities were the whole plots. Each plot contained 42 sub-plots, two for each hybrid. These sub-units consisted of three rows of ten plants; the distance between rows was 80 cm, while that between the plants in the rows was varied so as to provide the four population densities. Hybrids within plots and plant densities within replications were completely randomized. The experiment was carried out in two successive years (1969 and 1970) at Vimodrone, Milano. Ears of five plants in the central row of each sub-plot were harvested and artificially dried to uniform moisture. The characters measured were ear weight per plant (gms) and weight of 50 kernels (gms).

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* This work was supported by a grant from the Consiglio Nazionale delle Ricerche (70.10298.06.115.140).

Statistics

The mean value of kk' single cross hybrid at the i^{th} level of plant density can be expressed by the following mathematical model:

$$Y_{(kk')i} = \mu + G_{kk'} + \varepsilon_i + l_{(kk')i}$$

where μ is the mean of all hybrids over all population rates; $G_{kk'}$ is the genotypic effect of kk' hybrid, $k = 1, 2, \ldots, n$; ε_i is the mean effect of the i^{th} population rate, $i = 1, 2, \ldots p$; $l_{(kk')i}$ is the effect of interaction between the i^{th} population rate with the kk' hybrid.

According to the model used for combining ability analysis of a set of diallel crosses including F_1's only (Griffing 1956), the genotypic effects can be partitioned as follows:

$$G_{kk'} = g_k + g_{k'} + s_{kk'} .$$

Where g_k is the general effect of the line k, and $s_{kk'}$ the specific effect that occurs when the line k is mated with line k'. Assuming a model with fixed effects we have $\sum_k g_k = \sum_k s_{kk'} = 0$. If the value $Y_{(kk')i}$, referring to single plants or to units with the same number of plants, is a linear function of the environmental factor considered (X = number of plants per m²) it follows that:

$$\varepsilon_i = \bar{b}\,(X_i - \bar{X}) + \delta_i$$

and

$$l_{(kk')i} = (b_{kk'} - \bar{b}) \cdot (X_i - \bar{X}) + \delta_{(kk')i}$$

b is the regression coefficient of hybrid means on plant density and $b_{kk'}$ the coefficient of regression applied to the hybrid kk'; δ_i and $\delta_{(kk')i}$ are the deviation from regression at i^{th} population rate.

According to the genetical model adopted for $G_{kk'}$, the coefficient of regression $b_{kk'}$ can be partitioned as follows:

$$b_{kk'} = \bar{b} + b_{g_k} + b_{g_{k'}} + b_{s_{kk'}} .$$

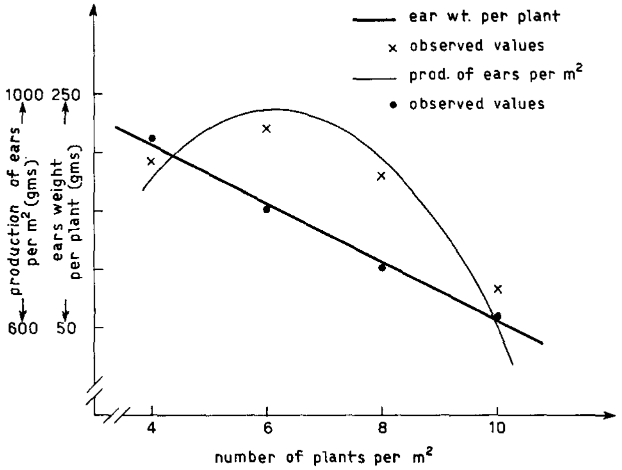

Fig. 1. Response of the single cross W 374R × OH-41 to plant spacing variation. The line describing the expected production of ears per m² is obtained by multiplying the expected ear weight per plant by the number of plants per m²

Where b_{g_k} is the coefficient of regression that measures the interaction of the general combining ability effect of the parent k linearly related to plant density, and $b_{s_{kk'}}$ the coefficient of regression referred to specific effect.

It follows that the expected mean value of the hybrid kk' at the i^{th} plant density rate level can be expressed by the following linear equation:

$$\begin{aligned}\hat{Y}_{(kk')i} = m + g_k + g_{k'} + s_{kk'} + \\ + \left(\bar{b} + b_{g_k} + b_{g_{k'}} + b_{s_{kk'}}\right) \cdot (X_i - \bar{X}) ,\end{aligned}$$

where $\sum_k b_{g_k} = \sum_k b_{s_{kk'}} = 0$. The condition is that the deviations from regression are negligible.

Considering the relationships between two-way, three-way and double cross hybrids given by Eberhart (1964), the estimation of these parameters makes it possible to predict the mean values of all possible hybrid combinations for any rate of plant spacing included in the range considered in the experiment. Thus for double-cross hybrids at rate X_i we have:

$$\begin{aligned}\hat{Y}_{(kk' \cdot k''k''')i} = m &+ 1/2\,(g_k + g_{k'} + g_{k''} + g_{k'''}) + \\ &+ 1/4\,(s_{kk''} + s_{kk'''} + s_{k'k''} + s_{k'k'''}) + \\ &+ [\bar{b} + 1/2\,(b_{g_k} + b_{g_{k'}} + b_{g_{k''}} + b_{g_{k'''}}) + \\ &+ 1/4\,(b_{s_{kk''}} + b_{s_{kk'''}} + b_{s_{k'k''}} + b_{s_{k'k'''}})] \times \\ &\times (X_i - \bar{X}) .\end{aligned}$$

As the value $\hat{Y}_{(kk' \cdot k''k''')}$ refers to a single plant, the production per unit of land (m², hectare) can be obtained by multiplying the computed value by X_i (Fig. 1). This procedure should permit selection of the best hybrid-plant density combinations.

The genetical parameters g_k and $s_{kk'}$, are estimated on the basis of observed mean values over rates, according to the procedure reported by Griffing (1956). The least squares estimates of regression coefficients are:

$$\bar{b} = \frac{\sum_i \bar{Y}_i \cdot x_i}{\sum_i x_i^2} ; \qquad b_{g_k} = \frac{\sum_i g_{ki} \cdot x_i}{\sum_i x_i^2} ;$$

$$b_{s_{kk'}} = \frac{\sum_i s_{(kk')i} \cdot x_i}{\sum_i x_i^2} .$$

$\bar{Y}_i$ is the mean of all hybrids at the rate i; g_{ki} and $s_{(kk')i}$ are the effects of combining ability estimated at plant density i and $x_i = X_i - \bar{X}$. According to the mathematical model adopted, the 84 entries (hybrid-densities) can be partitioned in a way similar to the one indicated by Eberhart and Russell (1966). This analysis (Table 1) provides tests for general and specific combining ability, heterogeneity between b_{g_k}'s and between $b_{s_{kk'}}$'s, and deviation from linearity. As far as the test for differences between coefficients of regression (Ho: $\beta_{kk'} = \beta_{kk''} = \beta_{kk'''} \ldots$) is concerned, we do not meet with the complications mentioned

Table 1. *Analysis of variance of 7 × 7 F_1 diallel set grown at four population densities*

Items	d. f.	Mean square	
		ear weight	50-kernels wt.
(1) Population density	3	335447.81**	229.2609$^{n.s.}$
regression ($\bar{b}$)	1	938030.66**	653.1030*
deviations	2	34156.38**	17.3395$^{n.s.}$
Error (a)	6	2035.31	51.0180
(2) Crosses	20	3231.96**	43.0124**
g. c. a. (g_k)	6	8540.43**	122.1055**
s. c. a. ($s_{kk'}$)	14	956.91*	9.1154**
(1) × (2)	60	742.78*	3.4994**
regression ($b_{kk'}$)	20	912.96*	7.6348**
deviations	40	657.70$^{n.s.}$	1.4318$^{n.s.}$
(1) × g. c. a.	18	918.17*	7.1858**
regression (b_{g_k})	6	1218.50*	18.2046**
deviations	12	862.50$^{n.s.}$	1.6763$^{n.s.}$
(1) × s. c. a.	42	640.62$^{n.s.}$	1.9195*
regression ($b_{s_{kk'}}$)	14	782.01$^{n.s.}$	3.1049**
deviations	28	569.92$^{n.s.}$	1.3268$^{n.s.}$
Error (b)	324	488.57	1.4536
$R^2(\mu, g_k, s_{kk'}, \bar{b})$		0.8988	0.8608
$R^2(\mu, g_k, s_{kk'}, \bar{b}, b_{g_{k'}}, b_{s_{kk'}})$		0.9148	0.9477

n. s.: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$;
R^2 is the coefficient of determination.

by the authors above because the environmental variable (plant density) is not related to the observations.

Results

Sub-plot means from equal numbers of plants were the data used for the analysis. The total variance was partitioned according to the factors of variation considered in the experiment, i.e., year, replications, crosses and plant densities. This combined analysis did not reveal any significant interaction with regard to year, therefore the results reported in Table 1 related only to the items of genetical effects and plant density. The mean differences between densities are highly significant and the trend of this variation shows a slight deviation from a straight line when ear weight is considered. The differences between crosses account for general (g_k) and specific combining ability ($s_{kk'}$). The significance of genotype — density interaction (1 × 2) indicates that the response trend of both characters is not the same for all hybrids.

Regression analysis of this component shows that this interaction is mainly attributable to heterogeneity between $b_{kk'}$'s. This means that the performance of each hybrid across the range of plant densities can be represented by a linear function in which the variation relating to plant spacing is expressed

Table 2. *Estimates of combining ability (g_k, $s_{kk'}$) and regression parameters ($\bar{b}$, $b_{g_{k'}}$, $b_{s_{kk'}}$) for 50-kernels weight*

		2	3	4	5	6	7		
$s_{kk'}$		0.438	−0.041	0.644	0.311	−0.936	−0.415	g_1	−1.721
$b_{s_{kk'}}$	1	−0.208	0.106	0.059	0.136	−0.091	−0.002	b_{g_1}	0.067
dev. M. S.		0.241	0.415	0.396	2.527	0.395	1.400	dev.	0.794
$s_{kk'}$			0.774	−0.050	−0.919	−0.526	0.284	g_2	−0.496
$b_{s_{kk'}}$	2		−0.127	−0.202	0.315	0.113	0.108	b_{g_2}	−0.001
dev. M. S.			0.068	0.235	1.218	0.170	0.614	dev.	1.266
$s_{kk'}$				−0.639	−0.099	0.572	−0.567	g_3	1.253
$b_{s_{kk'}}$	3			0.260	−0.139	−0.189	0.089	b_{g_3}	0.212
dev. M. S.				0.314	0.976	0.672	0.031	dev.	0.623
$s_{kk'}$					−0.999	0.514	0.529	g_4	−1.455
$b_{s_{kk'}}$	4				−0.203	0.261	−0.174	b_{g_4}	−0.162
dev. M. S.					4.742*	0.304	1.267	dev.	1.120
			$m = 11.672$ $\bar{b} = -0.623$						
$s_{kk'}$						0.957	0.749	g_5	0.374
$b_{s_{kk'}}$	5					−0.091	−0.018	b_{g_5}	−0.376
dev. M. S.						0.595	0.885	dev.	3.765
$s_{kk'}$							−0.580	g_6	1.146
$b_{s_{kk'}}$	6						−0.003	b_{g_6}	0.234
dev. M. S.							1.076	dev.	0.660
$s_{kk'}$								g_7	0.900
$b_{s_{kk'}}$								b_{g_7}	0.025
dev. M. S.								dev.	1.829

*: $P < 0.05$; m = mean of all observations.

by the regression $b_{kk'}(X_i - \bar{X})$. The remaining part of the analysis shows the partitioning of this interaction according to the genetical model adopted. The items (1) × g. c. a. and (1) × s. c. a. refer to the interaction of the general and specific combining ability effects, respectively, with rates of plant density. The regression analysis of these components shows different behaviour for the two characters considered. Variance due to the differences between b_{g_k}'s and between $b_{s_{kk'}}$ are both significant when 50-kernels weight is considered, but for ear weight the inclusion of $b_{s_{kk'}}$'s in the model does not bring about a significant reduction of the residual variances. All items referring to deviations from linear regression were not significant.

The least squares estimates of combining ability effects and regression coefficients for 50-kernels weight are shown in Table 2. For each regression coefficient the deviations from linearity mean squares are reported; in only one case were these variances significant when tested with the residual.

These results indicate that the complete model is required for predictive purposes when kernel weight is considered, but for the other character only b_{g_k} coefficients need be used to estimate the genotype-density interaction.

The reliability of the predicted values may be evaluated on the basis of the correlation between observed and expected means at each plant density rate. In order to measure the increase in predictive power obtained when genotype-environmental interaction parameters are included in the model, the correlations were computed considering both the model with only the combining ability parameters (m, g_k, $s_{kk'}$) and the model including the b terms. Invariably the second equation gave the best correlation values (Table 3) but these were not much higher than those obtained by the first model. This is because the amount of variation accounting for heterogeneity between regressions, although significant, resulted to be only a small amount of phenotypical variance (Table 1).

Table 3. *Correlations between observed and expected means of 21 single crosses*

Plants per m^2	Ear weight		50-kernels weight	
	R	R′	R	R′
4	0.881**	0.958**	0.848**	0.979**
6	0.579**	0.647**	0.901**	0.937**
8	0.790**	0.864**	0.919**	0.950**
10	0.821**	0.947**	0.910**	0.992**

R: expected values are obtained considering m, g_k, $s_{kk'}$;

R′: expected values are obtained considering m, g_k, $s_{kk'}$, $\bar{b}$, b_{g_k}, $b_{s_{kk'}}$.

Discussion

In this paper, a model including parameters for genetical effects and genotype-environmental interaction is proposed for estimating the trend of the phenotypical values across plant densities of all hybrid crosses between a set of inbred lines. The results obtained show that the effects of plant spacing on each hybrid can be represented by linear equations, the coefficients of which can be easily estimated from single-cross hybrids grown at different population rates. Fitting this model, the residual genotype-environmental interaction variance was of the same order as that of experimental error variance. However, the predictive power of the function, when compared with that of the model including only genetical parameters, was not much greater. This result was obtained because the proportion of genotype-plant density variance was very small, while that due to genetical effects accounted for most of the phenotypical variation.

Small differences in the phenotypical response to plant density variations are typical when the material tested comes from well established lines, as are the parents of the hybrids used for this experiment (Russell, 1969). The importance of genotype-density interaction increases if new lines from divergent material are evaluated in hybrid combinations.

This has been shown in many studies, particularly those by Russell (1968 and 1969), who found that the yield trend across plant densities displays large differences when single-ear types are tested with prolific types or when lines selected at low population densities are compared with those selected at high densities. In these situations the ranking of the material is expected to change with population density. Therefore, the selection of the best hybrids on the basis of predicted values obtained at a standard population density, without taking into account the relative variation of the phenotypical expression of the different crosses, leads to the discarding of many genotypes which attain their optimum yield at densities not considered in the experiment. This disadvantage would be removed if the prediction method provided the values of each hybrid cross at every population density, making it possible to select the best hybrid-density combinations.

The predictive values of the equation have been evaluated by correlation between the observed and estimated means, considering only two-way crosses. It is obvious that this is not the ideal test and that the inclusion of three-way and four-way crosses would have made possible a more appropriate evaluation. Besides, the stability parameters estimated using F$_1$'s might not be strictly appropriate for three-way and four-way crosses. In fact, since these crosses are a mixture of genotypes, they frequently display greater stability in relation to environmental variations (Sprague and Federer 1951). Further information on this point will be obtained during the coming year.

The prediction method suggested in this work requires accurate measurement of the environmental variable or, alternatively, that the levels of this variable be fixed *a priori*. It cannot be directly applied when dealing with genotype-interaction effects arising from the concomitant action of many environmental factors. This is the case, for example, with differences between locations in rainfall, the nature of the soil, temperature variations and so on. In these situations, for the regression analysis of the genotype-environmental interaction, it is proposed to relate the phenotypical variations to an environmental index obtained as the mean of all the varieties considered in the trial (Eberhart and Russell, 1966) or as the mean of a sample of varieties considered as standard (Bucio Alanis and Hill, 1966; Bucio Alanis et al. 1969; Jinks and Perkins, 1970). This second approach is more appropriate for the statistical assumptions on which the regression analysis is based (Freeman and Perkins, 1971).

For hybrid prediction, the biological assay of environmental effects may be performed by taking as a standard a sample of all possible crosses where the main genetical effects are equally represented. This group of genotypes can be obtained in different ways: one, suggested by Eberhart and Gardner (1966) and by Hinkelmann (1968), uses incomplete block designs to select a balanced sample of four-way crosses. The inclusion of these four-way crosses in the trial with all F_1's makes it possible for the predictive model to take into account constants for additive epistasis effects.

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Received February 29, 1972
Communicated by W. Seyffert

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