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Generation mean analysis of some physiological traits in the hybrid maize cv. SC704 under different water regimes

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Abstract

This research was carried out using seven generations of MO17 (the paternal line), B73 (the maternal line), F_1 (SC704), F_2, F_3, BC_1 and BC_2 to study the inheritance of chlorophyll fluorescence parameters and relative water content using generation mean analysis. The experiment was conducted in the research station of the University of Tabriz, Iran, with two replications for each generation under normal irrigation and two water deficit conditions. The existence of epistatic gene interaction was observed in controlling of F_0, F_m, F_V (in the severe stress condition), F_V/F_m (in the normal condition), F_V/F_0 (in the normal and severe stress conditions) and RWC (in the normal and moderate and severe stress conditions). Duplicate epistasis was observed for all studied traits under the normal and water deficit conditions except RWC in the severe stress condition. Therefore, exploiting non-additive gene action and delaying the selection to advanced generations for physiological traits in maize was suggested to adopt in the programs aimed at developing drought-tolerant lines and hybrids.

Keywords: Generation mean analysis; Heritability; Maize (*Zea mays* L.); Physiological traits; Water deficit stress

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Introduction

Various abiotic stresses such as drought, reduce the growth and yield of plants below the optimum level (Cramer *et al.* 2011). Maize (*Zea mays* L.) as one of the most important crops in the world, is drought sensitive, and its yield significantly decreases under water stress conditions (Shiferaw *et al.* 2011; Todaka *et al.* 2015). Drought causes degradation of photosynthetic pigments and thus decreases the light energy absorption on the photochemical apparatus and damages thylakoid membranes and centers of photosystem reaction (Batra *et al.* 2014). The chlorophylls and PSII absorb the light energy which can be used to drive photosynthesis processes. When this energy is lost from PSII, it appears as heat or emitted chlorophyll fluorescence (Kalaji *et al.* 2012). Chlorophyll fluorescence has been extensively used to study the variation in the efficiency of light processing and stress tolerance in plants (Lichtenthaler *et al*. 2005; Stirbet *et al*. 2018). Relative leaf water content (RWC) has also been utilized for the evaluation of drought tolerance in crops (Dhanda and Sethi 2002). Decreasing this trait causes stomata closure and CO2 assimilation declines under drought stress (Gindaba *et al*. 2004).

Studies about the inheritance of chlorophyll fluorescence components are very limited in maize. Hola *et al*. (2010) examined the response of several photosynthetic parameters of maize plants to drought stress in five inbred lines and their F1 hybrids. They reported that the nonadditive genetic effects were often more important than the additive effects for the photosynthetic characteristics. However, the genetic changed when the plants were exposed to drought conditions. Also, it was not possible to predict the response of F1 hybrids to drought based on the photosynthetic performance of their parents. Simic *et al*. (2014) conducted a quantitative trait loci (QTL) analysis on nine chlorophyll fluorescence parameters in maize at four environments that differed in weather conditions. The chlorophyll fluorescence parameters were analyzed among 205 recombinant inbred lines derived from the intermated B73 × Mo17 maize population. The results revealed 10 significant QTLs for seven chlorophyll fluorescence parameters, of which five were co-localized after combining over the four environments. These results indicated the role of polygenic inheritance in governing the chlorophyll fluorescence parameters under study. They also detected one pleiotropic locus on chromosome 7, coinciding with the gene gst23 that possibly related to efficient photosynthesis in different field conditions.

Generation mean analysis is a biometrical method for estimating the genetic effects including additive, dominance and especially epistatic interactions by using means of different generations (Mather and Jinks 1982; Viana 2000). Information about the nature and magnitude of gene actions involved in the tolerance to water deficit stress can be useful for breeding drought-resistant varieties in maize. Thus, a generation mean analysis was designed to study the inheritance of physiological characteristics in maize under different water regimes.

Materials and Methods

Plant material and experiment

Seven generations including B73 (the maternal line), MO17 (the paternal line), SC704 (F_1), F_2, BC_1, BC_2 and F_3 were grown in PVC pipes with 20 cm diameter and the height of one meter, under normal irrigation and two water regimes (55% and 75% of available water depletion) in the research station of the University of Tabriz. With consideration of a proper distance between the seeds, two maize seeds were sown per pipe to secure at least one plant appearance in each pipe. Then, thinning was done at the tillering stage and only one plant was left in a pipe. Eventually, 20 plants for each generation were evaluated. Plants were grown in similar conditions in terms of soil type, light, temperature and pipes size. Also, the experimental site was protected from the rainfall by a plastic cover throughout the cropping period.

Chlorophyll fluorescence parameters

Chlorophyll fluorescence was measured on a fully developed leaf using a hand-held chlorophyll fluorometer (Opti-Sciences, OS-30p). The leaves were adapted in dark for 15 min at first and then fluorescence was recorded at 650 µmol m^{-2} s^{-1}. Fluorescence values recorded included: F_0:

minimum fluorescence, F_m: maximum fluorescence, F_V: variable fluorescence = (F_m - F_0), F_V/F_m: maximum quantum yield of photosystem II (PS II) and F_V/F_0: maximum primary yield of the photochemistry of PS II.

RWC

The measurement of RWC was accomplished by excising 1-cm disks from the fresh leaves. Five disks from each pipe were weighed immediately and the fresh weight (FW) was measured. Then, the leaf disks were placed in the distilled water for 24 h and the turgid weight (TW) was obtained. Finally, the samples were dried in an oven at 72 °C for 24 h and their dry weight (DW) was recorded. RWC was determined as follows (Salisbury and Ross 1998):

$$RWC = ((FW - DW) / (TW - DW)) \times 100$$

Statistical and genetic analysis

Generation mean analysis was carried out using the weighted least squares method considering the inverse of the variance of the means within each generation as the weight (Mather and Jinks 1982). In this method, the overall average for each trait is shown as follows: $Y = m + \alpha\,[d] + \beta\,[h] + \alpha^2\,[i] + 2\alpha\beta\,[j] + \beta^2\,[l]$

Where, Y= the generation mean, m= F∞ metric, d= additive effects, h= dominance effects, i= additive × additive interaction, j= additive × dominance interaction, 1= dominance × dominance interaction and α, 2αβ and β^2 are coefficients of genetic parameters. To verify the goodness of fit of the model, a joint scaling test was carried out for each trait at each irrigation level (Cavalli 1952). All genetic parameters were tested for significance using a t-test.

Results and Discussion

The results showed that the scaling tests for the three-parameter model were not significant for F_V under the normal and mild stress conditions (55% AWD), F_V/F_m under both stress conditions and F_V/F_0 under the mild stress condition, which indicates the lack of epistasis for these traits (Table 1). The scaling tests were significant for the other studied traits suggesting the inadequacy of the additive-dominance model or the presence of epistasis type of gene effects.

Estimates of genetic effects based on the three- or six-parameter models for the studied traits under different water regimes are given in Table 2. The generation mean analysis suggested the importance of both main effects (dominance and additive effects) and non-allelic interaction for most of the studied traits. However, for almost all characters the dominance effects were higher in magnitude as compared to the additive gene effects under different water regimes. The opposite signs of [h] and [l] revealed duplicate epistasis for all traits in the normal and water deficit conditions except RWC in the severe stress condition. Negative and positive signs of the [h] parameter showed that partial dominance was towards the decreasing F_0, F_m, F_V and RWC and increasing of F_V/F_m and F_V/F_0 in the cross under consideration, respectively.

F_0: The best-fit model for this trait was the six-parameter model [m-d-h-i-j-l]. Additive × additive

Table 1. Scaling tests (±SE) for physiological traits in maize generations at different water regimes.

Traits	Water Regimes	A	B	C	D
F_0 (µmol. m^2s^{-1})	Full irrigation	$-41.85 \pm 5.84^{**}$	$-18.1 \pm 7.66^{**}$	-10.55 ± 14.80^{ns}	8.55 ± 14.23^{ns}
	55% AWD	$-32.45 \pm 10.20^{**}$	-11.55 ± 9.81^{ns}	-30.20 ± 21.23^{ns}	$40.50 \pm 16.76^{**}$
	75% AWD	$-12.50 \pm 6.06^{*}$	$-17.25 \pm 7.09^{**}$	12.95 ± 14.76^{ns}	$28.65 \pm 14.32^{**}$
F_m (µmol. m^2s^{-1})	Full irrigation	-35.35 ± 30.81^{ns}	-25.35 ± 32.91^{ns}	40.60 ± 55.44^{ns}	$109.80 \pm 49.79^{**}$
	55% AWD	$-61.30 \pm 25.35^{**}$	$-64.85 \pm 25.51^{**}$	13.05 ± 44.61^{ns}	77.05 ± 42.42^{ns}
	75% AWD	-50.70 ± 29.04^{ns}	$-72.60 \pm 34.95^{**}$	$-144.30 \pm 56.86^{**}$	-8.90 ± 64.72^{ns}
F_v (µmol. m^2s^{-1})	Full irrigation	5.40 ± 31.60^{ns}	-7.30 ± 29.20^{ns}	51.80 ± 60.19^{ns}	95 ± 54.48^{ns}
	55% AWD	-28.85 ± 28.63^{ns}	-53.30 ± 27.57^{ns}	43.25 ± 45.70^{ns}	36.55 ± 42.47^{ns}
	75% AWD	-40.10 ± 31.75^{ns}	-66.35 ± 35.99^{ns}	$-119.65 \pm 54.81^{**}$	-29.25 ± 69.69^{ns}
F_v/F_m	Full irrigation	$0.05 \pm 0.02^{**}$	0.02 ± 0.02^{ns}	0.03 ± 0.04^{ns}	0.02 ± 0.04^{ns}
	55% AWD	0.02 ± 0.02^{ns}	-0.01 ± 0.02^{ns}	0.05 ± 0.03^{ns}	-0.03 ± 0.02^{ns}
	75% AWD	-0.007 ± 0.02^{ns}	-0.02 ± 0.02^{ns}	-0.02 ± 0.03^{ns}	-0.04 ± 0.04^{ns}
F_v/F_0	Full irrigation	$0.71 \pm 0.21^{**}$	0.21 ± 0.22^{ns}	0.46 ± 0.42^{ns}	0.40 ± 0.35^{ns}
	55% AWD	0.35 ± 0.27^{ns}	-0.12 ± 0.23^{ns}	0.70 ± 0.46^{ns}	-0.42 ± 0.35^{ns}
	75% AWD	-0.05 ± 0.18^{ns}	-0.07 ± 0.19^{ns}	$-0.86 \pm 0.36^{**}$	-0.47 ± 0.39^{ns}
RWC (%)	Full irrigation	$-24.22 \pm 3.65^{**}$	$-9.30 \pm 4.26^{**}$	$-38.42 \pm 7.59^{**}$	-6.98 ± 7.74^{ns}
	55% AWD	$-20.11 \pm 2.72^{**}$	$-15.88 \pm 2.64^{**}$	$-43.66 \pm 4.73^{**}$	-2.07 ± 5.62^{ns}
	75% AWD	$-10.32 \pm 2.50^{**}$	-3.75 ± 3.30^{ns}	$-26.83 \pm 5.39^{**}$	$-15.84 \pm 6.04^{**}$

ns, * and **: non-significant and significant at 0.05 and 0.01 probability levels, respectively; AWD: available water depletion; F_0, F_m, F_v, F_v/F_m and F_v/F_0: minimum fluorescence, maximum fluorescence value, variable fluorescence, the maximum quantum yield of photosystem II (PSII) and maximum primary yield of the photochemistry of PSII, respectively; RWC: relative water content.

and dominance × dominance interactions had a significant role in the genetic control of F_0 in all three water regimes. Asadi *et al.* (2015) reported a high additive gene effect for F_0 in wheat under normal conditions. Contrary, the non-additive gene effect was reported in sugarcane for F_0 by Zhang *et al.* (2010).

F_m: In the normal and mild stress conditions the six-parameter model [m-d-h-i-j-l] and in the severe stress conditions the five-parameter model [m-d-h-j-l] were the best-fit models for F_m. Dominance and dominance × dominance effects were significant and governed the genetics of this character. Therefore, exploiting the non-additive gene action can be effective for improving F_m. The same findings were documented by Hola *et al.* (2010) in five inbred lines of maize. The authors revealed that epistatic and dominance gene effects were important in controlling the chlorophyll fluorescence parameters.

F_V: The findings revealed that the three-parameter model [m-d-h] was fitted well for F_v under normal and mild stress conditions. Both additive and dominance gene effects were significant for this trait under the two aforementioned conditions. Whereas, in the severe stress condition the five-parameter model [m-d-h-j-l] was determined as the best model for this character. The dominance and dominance × dominance effects were also significant and had an important role in controlling F_v.

F_V/F_m: The five-parameter model [m-d-h-j-l] was best fitted for this trait in the normal conditions. The dominance gene effect and dominance × dominance interaction were significant and

Table 2. Estimates of genetic parameters (±SE), x^2 for the joint scaling test for physiological traits in maize at different water regimes using generation mean analysis.

Traits	Water Regimes	m	d	h	i	j	l	x^2	df
F$_0$ (µmol. m^{2}s^{-1})	Full irrigation	208.6 ± 5.85**	-2.54 ± 2.18^{ns}	-101.7 ± 17.27^{ns}	-23.83 ± 5.94**	-25.67 ± 8.54^{ns}	78.79 ± 13.38**	3.59^{ns}	1
	55% AWD	224.2 ± 7.08**	4.44 ± 2.51^{ns}	-99.4 ± 23.62**	-25.82 ± 7.22**	-21.05 ± 12.91^{ns}	72.35 ± 18.99**	0.32^{ns}	1
	75% AWD	244.8 ± 5.82**	8.39 ± 2.20**	-85.8 ± 16.89**	-27.12 ± 5.91**	4.06 ± 8.30^{ns}	54.04 ± 12.99**	1.36^{ns}	1
F$_m$ (µmol. m^{2}s^{-1})	Full irrigation	738.1 ± 22.31**	13.87 ± 8.60^{ns}	-212.1 ± 74.47**	-78.19 ± 22.86**	-10.57 ± 42.48^{ns}	131.6 ± 58.06**	0.16^{ns}	1
	55% AWD	788.9 ± 18.94**	22.53 ± 6.85**	-272.3 ± 61.39**	-80.51 ± 19.33**	3.22 ± 34.12^{ns}	188.3 ± 46.91**	1.60^{ns}	1
	75% AWD	727.0 ± 9.54**	-2.65 ± 9.81^{ns}	-120.1 ± 43.11**	-	23.22 ± 42.11^{ns}	129.0 ± 41.29**	0.19^{ns}	2
F$_v$ (µmol. m^{2}s^{-1})	Full irrigation	484.2 ± 7.38**	17.57 ± 8.21**	-9.10 ± 13.38^{ns}	-	-	-	6.35^{ns}	4
	55% AWD	513.5 ± 5.85**	20.22 ± 6.54**	-9.62 ± 11.55**	-	-	-	9.99^{ns}	4
	75% AWD	513.2 ± 10.20**	-9.52 ± 10.48^{ns}	-101.1 ± 44.79**	-	27.34 ± 45.08^{ns}	112.7 ± 42.36**	0.05^{ns}	2
F$_v$/F$_m$	Full irrigation	0.72 ± 0.006**	0.01 ± 0.007^{ns}	0.06 ± 0.03*	-	0.03 ± 0.02^{ns}	-0.06 ± 0.03**	0.50^{ns}	2
	55% AWD	0.72 ± 0.003**	0.004 ± 0.004^{ns}	0.003 ± 0.008^{ns}	-	-	-	4.40^{ns}	4
	75% AWD	0.70 ± 0.005**	-0.009 ± 0.005^{ns}	0.008 ± 0.008^{ns}	-	-	-	2.36^{ns}	4
F$_v$/F$_0$	Full irrigation	2.58 ± 0.06**	0.12 ±0.06*	0.76 ± 0.28**	-	0.50 ± 0.29^{ns}	-0.78 ± 0.27**	0.99^{ns}	2
	55% AWD	2.60 ± 0.05**	0.05 ± 0.05^{ns}	0.05 ± 0.10^{ns}	-	-	-	4.74^{ns}	4
	75% AWD	2.03 ± 0.10**	-0.14 ± 0.06**	0.44 ± 0.13**	0.33 ± 0.11**	0.03 ± 0.02^{ns}	-	1.24^{ns}	2
RWC (%)	Full irrigation	71.3 ± 3.34**	1.10 ± 1.15^{ns}	-27.02 ± 10.20**	0.73 ± 3.39^{ns}	-14.72 ± 5.35**	33.92 ± 7.52**	0.29^{ns}	1
	55% AWD	64.9 ± 2.44**	-3.57 ± 0.75**	-37.09 ± 7.19**	-1.93 ± 2.46^{ns}	-4.40 ± 3.52^{ns}	40.88 ± 5.33**	4.58^{ns}	1
	75% AWD	41.2 ± 2.61**	-4.27 ± 0.85**	2.88 ± 7.75^{ns}	8.73 ± 2.64**	-6.15 ± 3.86^{ns}	6.49 ± 5.70^{ns}	0.59^{ns}	1

See Table 1 for abbreviations.

involved in governing the genetics of F$_V$/F$_m$. Under both water stress conditions, the three-parameter model [m-d-h] was fitted for this character. Similar findings were reported by Vijayalakshmi *et al.* (2010) in winter wheat which showed a low additive gene effect for F$_V$/F$_m$. The quantum efficiency of PS II (Fv/Fm) has a major role in photosynthesis and it can be used as a screening tool to identify tolerant varieties to drought (Sharma *et al.* 2014). A low ratio of Fv/Fm shows low photosynthetic efficiency, thus, genotypes that have a higher ratio of Fv/Fm may be more tolerant to drought stress (Ristic *et al.* 2007; Kumar *et al.* 2012).

F$_V$/F$_0$: In the normal and severe stress conditions the five-parameter models [m-d-h-j-l] and [m-d-h-i-j] were regarded as the best models explaining the inheritance of this character, respectively. Thus, both main gene effects and epistatic interactions governed the control of this trait under these conditions. However, under the mild stress conditions, only the three-parameter model was best fitted for this trait.

RWC: Under normal and water deficit conditions the six-parameter model [m-d-h-i-j-l] was the best fitted this character. Both main effects were significant but the dominance effect was higher than the additive effect in the normal and mild stress conditions. Generation mean analysis in maize (Moharramnejad *et al.* 2018), as well as durum wheat (Salmi *et al.* 2019), under control and drought stress conditions showed the importance of dominance genes effects in operating the inheritance of RWC. In contrast to our results, the additive gene effect for RWC in wheat was reported by Said (2014) under the normal condition and Asadi *et al.* (2015) under both normal and water deficit conditions. It seems that the genetic effects vary according to crop species, varieties and the environmental conditions in which the research was conducted.

Conclusion

In this experiment, the importance of dominance and epistasis (duplicate) effect was recognized for most of the studied physiological traits under water stress conditions, which implies exploiting non-additive gene action and delaying the selection to advanced generations for these traits in maize aiming at developing drought-tolerant lines and hybrids in maize. However, the additive effect was more important in the inheritance of F_0 and F_V/F_m in the normal condition and early selection can be efficient for the improvement of these characters.

Conflict of Interest

The authors declare that they have no conflict of interest with any organization concerning the subject of the manuscript.

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تجزیه میانگین نسل‌ها برای برخی صفات فیزیولوژیک در هیبرید سینگل کراس ۷۰۴ ذرت تحت رژیم‌های آبی مختلف

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چکیده

تحقیق حاضر با استفاده از هفت نسل {MO17 به عنوان لاین پدری؛ B73 به عنوان لاین مادری؛ هیبرید SC704 (F1)؛ F2؛ F3؛ BC1؛ BC2} به منظور بررسی وراثت پارامترهای فلورسانس کلروفیل و محتوای آب نسبی توسط تجزیه میانگین نسل‌ها انجام شد. این آزمایش در ایستگاه تحقیقاتی دانشگاه تبریز با استفاده از طرح بلوک‌هایکامل تصادفی با دو تکرار در شرایط آبیاری نرمال و دو شرایط کمبود آب انجام شد. وجود اثرات متقابل اپیستازی در وراثت F0، Fm، FV (در شرایط تنش شدید)، FV/Fm (در شرایط عادی)، FV/F0 (در شرایط نرمال و تنش شدید) و RWC (در شرایط نرمال و تنش‌های ملایم و شدید) مشاهده شد. اپیستازی مضاعف در کلیه صفات مورد مطالعه به جز RWC در شرایط تنش شدید، مشاهده شد. این نتایج حاکی از لزوم بهره برداری از اثرات غیرافزایشی ژنتیکی و به تأخیر انداختن گزینش صفات فیزیولوژیکی مورد مطالعه به نسل‌های پیشرفته در برنامه‌های اصلاح ذرت برای تحمل خشکی می‌باشند.

واژه های کلیدی: تجزیه میانگین نسل‌ها؛ تنش کم‌آبی؛ ذرت؛ صفات فیزیولوژیکی؛ وراثت پذیری.