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Line × Tester Analysis of Stomatal Conductance, Chlorophyll Content, Photosynthetic Efficiency, and Transpiration Rate Traits in Maize

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KeyWords Inheritance analysis, Photosynthetic properties, Physiological breeding, *Zea mays indentata* Sturt

Abbreviations CC: chlorophyll content, PE: photosynthetic efficiency, SC: stomatal conductance, TR: transpiration rate

Abstract

This study evaluated seven inbred lines of maize (*Zea mays* L.), three testers and 21 hybrids produced by line × tester mating design. Stomatal conductance, chlorophyll content, photosynthetic efficiency, and transpiration rate traits of parents and progenies were observed. The study was conducted in Konya, in the mid-Anatolian region of Turkey. The mean values of the stomatal conductance, chlorophyll content, photosynthetic efficiency, and transpiration rate measurements were evaluated using Duncan's multiple range test for grouping parent and offspring groups. The variance for general combining ability, the variance for specific combining ability, the relative variance, additive variance, dominance variance, $\sqrt{D/A}$, narrow-sense heritability and broad-sense heritability parameters of the population, along with the heterosis rates of the progenies, were calculated for each trait. The parental general combining abilities and specific combining abilities of the progenies were determined. We observed parents with significant and positive general combining abilities [3.4 (stomatal conductance, transpiration rate); 14.20 (photosynthetic efficiency, transpiration rate)] and their progenies with significant and positive specific combining abilities [3.4 × FRMo 17 (stomatal conductance, transpiration rate); 3.4 × ADK 451 (transpiration rate); 14.20 × FRMo 17 (transpiration rate)]. Results of the study showed the possibility of using physiological properties as selection criteria.

Introduction

Maize (*Zea mays* L.) is the most widely-produced cereal globally and is the primary staple food in many developing countries. It is a versatile crop with high genetic diversity, enabling its cultivation in tropical, subtropical, and temperate climates worldwide (Izhar and Ckahraborty, 2013). Approximately one billion tonnes of maize is produced globally per year, making it the highest-produced cereal species. Maize production in Turkey was 6.4 million tonnes in 2016 (TMO, 2017). Maize has a wide range of uses compared with other cereal crops; it is used as human food, animal fodder, and for several industrial purposes. The wide utility of maize is due to its broad global distribution, low price when compared with other cereals, diverse grain types, and wide range of biological and industrial properties (Assefa et al., 2017). Maize grains contain 70% starch, 10% protein, 5% oil, 10% fibre, 3% sugar and 2% ash (Musila et al., 2010). Identifying physiological properties related to grain yield and understanding the combining ability effects of these physiological

features would assist maize breeders in identifying and selecting appropriate genotypes for parent and hybrid development at an early growing stage of maize (Long et al., 2006). Welcker et al. (2005) reported that physiological traits like the photosynthetic rate, CC (chlorophyll content), TR (transpiration rate) and SC (stomatal conductance) play an important role in yield. Cai et al. (2014) stated that SC is associated with carbon assimilation; increasing SC would improve ventilation and transportation of CO₂. Because CO₂ is a basic ingredient for photosynthesis, increased SC could potentially increase biomass, resulting in higher yield (Sharma-Natu and Ghildiyal, 2005; Cai et al., 2014). The measurement of PE (photosynthetic efficiency), is a popular technique in plant physiology because researchers can use it to gain a better understanding of PSII (photosystem II) processing. A better understanding of PSII processing can lead to improved understanding of the basic mechanisms of photosynthesis, plant reactions to their environments, and genetic and ecological variations (Adams and

Demmig-Adams, 2004). This technique is of interest to breeders because of its potential use as a genetic screening method (Baker and Rosenqvist, 2004). The transpiration effect is one of the factors that promote grain yield under limited water conditions. It has been previously reported that yield is a feature that includes water usage, transpiration effect, and harvest index components. The TR can differ according to the species and is linked to carbon assimilation and SC properties (Jones, 1998). Patil et al. (2012) reported that the high-yield potential of single-cross maize hybrids has increased maize productivity. Such hybrids are advantageous to seed companies and growers alike, mainly because of the inability to use farm-saved seeds and increased yield, respectively. Effective parental selection is essential to produce single-cross hybrids that have high yields. Breeders focus on the production of inbred parents with high GCA (general combining ability) levels and hybrids with high SCA (specific combining ability) levels and high Hs (heterosis). The present study was conducted to evaluate various maize parents and F1 progenies for different physiological traits (CC, SC, TR, PE) at the tasselling stage.

Materials and Methods

This study was conducted at the Prof. Dr. Abdulkadir AKCIN field trial area of the Selcuk University Agriculture Faculty Crop Science Department, during the 2016 growing season. Seven inbred lines of dent corn (*Zea mays indentata* Sturt.), three testers (FRMo 17, FRB 73, ADK 451), and 21 hybrids were studied (Table 1).

Plant Materials

The seven inbred lines and three testers were crossed to produce 21 F1 hybrid progenies following the line × tester mating design developed by Kempthorne (1957) in 2015 growing season. The various maize accessions were grown in a randomized complete block design with three replications in 2016. Seeds of each genotype were sown by hand in the second week of May with a spacing of 70 × 20 cm. Each replicate plot of a particular accession consisted of two 5 m long rows. Cultural practices, as described by Kirtok (1998), were followed.

Collecting of Data

All measurable characteristics were determined on each of the five plants per row in each plot during tasselling. Stomatal conductance was recorded as mmol / m²s, using a Porometer device by Decagon Devices. Chlorophyll content was recorded as Spad, using a Spad Meter Spad-502 device by Minolta. Maize

Table 1 - Maize inbred lines and test crosses used in the study

Inbred lines	Test crosses
3.2	3.2 × FRMo 17*
	3.2 × FRB 73*
	3.2 × ADK 451**
3.4	3.4 × FRMo 17
	3.4 × FRB 73
	3.4 × ADK 451
3.6	3.6 × FRMo 17
	3.6 × FRB 73
	3.6 × ADK 451
14.2	14.2 × FRMo 17
	14.2 × FRB 73
	14.2 × ADK 451
14.20	14.20 × FRMo 17
	14.20 × FRB 73
	14.20 × ADK 451
14.21	14.21 × FRMo 17
	14.21 × FRB 73
	14.21 × ADK 451
14.26	14.26 × FRMo 17
	14.26 × FRB 73
	14.26 × ADK 451

* Origin USA

** Origin Turkey

leaves were enclosed in the dark for 30 min., and PE was recorded as Fv / Fm rates, using a Plant Efficiency Analyser (PEA) device by Hansatech Instruments Ltd. TR was recorded as H₂O m⁻²s⁻¹, using a Li-Cor 6400 XTQ device by Li-Cor.

Statistical Analysis

SPSS version 20.0 was used for analyzing all the statistical data. Statistical analysis was performed using analysis of variance for randomized complete block design. The mean value of each genotype for each parameter was grouped according to Duncan's multiple range tests. The heritability parameters [U² GCA (variance of general combining ability), U² SCA (variance of specific combining ability), RV (relative variance), U² A (additive variance), U² D (dominance variance), UD / A, GCA, SCA, h² (narrow-sense heritability) and H² (broad-sense heritability)] were calculated as described by Singh and Chaudhary (1979) and Hussain and Sulaiman (2011). The RV rate was calculated as described by Fasahat et al. (2016). The Hs rate was calculated as described by Iqbal et al. (2010) using Microsoft Excel and the formulae below. The Student's t-test was used to test the significance of the GCA, SCA and Hs rates, etc.

$$\begin{aligned} \text{GCA (line)} &= [X_i \dots / (T \times R)] - [X \dots / (T \times L \times R)] \\ \text{GCA (tester)} &= [X_j \dots / (L \times R)] - [X \dots / (T \times L \times R)] \\ \text{SCA (hybrid)} &= [(X_{ij} / R) - (X_i / (T \times R)) - (X_j / (L \times R)) - (X \dots / (T \times L \times R))] \\ U^2 \text{ GCA} &= [(1 + F) / 4]^2 \times U^2 A \\ U^2 \text{ SCA} &= [(1 + F) / 2]^2 \times U^2 D \\ \text{RV} &= 2 U^2 \text{ GCA} / (2 U^2 \text{ GCA} + U^2 \text{ SCA}) \\ \text{Hs (\%)} &= [(F_1 - \text{MP}) / \text{MP}] \times 100 \\ h^2 &= U^2 A / U^2 P \\ H^2 &= (U^2 A + U^2 D) / U^2 P \\ U^2 A &= (2 U^2 L + 2 U^2 T) / 2 = U^2 L + U^2 T \\ U^2 L &= [Ms(L) - \text{Mse}] / R \times T = \frac{1}{2} U^2 A \quad A U^2 A \\ &= 2 U^2 L \\ U^2 t &= [Ms(T) - \text{Mse}] / R \times L = \frac{1}{2} U^2 A \\ U^2 A &= 2 U^2 T \\ U^2 D &= U^2 LT = [Ms(L \times T) - \text{Mse}] / R \\ U^2 E &= \text{Mse} / R \\ U^2 P &= U^2 A + U^2 D + U^2 E \end{aligned}$$

Results and Discussion

Stomatal Conductance

Results of the variance analysis of all traits (SC, CC, PE, and TR) are summarised in Table 2. For each trait, variations among genotypes were statistically significant ($P < 0.01$), which promoted investigation into parents and progenies. Relative variance (0.531) of the population in SC was less than 1. Fasahat et al. (2016) stated that an RV ratio closer to one had a greater ability to predict GCA alone, whereas a ratio of less than 1 suggested SCA action. To be $U^2 \text{ SCA}$ (148.058) $>$ $U^2 \text{ GCA}$ (83.888) indicated an additional influence of non-additive gene effects on the trait.

Table 2 - Analysis of variance for features at the parents and their F_1 progenies of maize

Sources	d.f.	SC	CC	PE	TR
Replications	2	0.180	5.436	0.351	0.151
Genotypes	30	12.751**	2.059**	41.010**	74.496**
Error	60
Total	92
CV (%) ^c		15.81	7.82	0.59	8.28

^c Coefficient of variation.

** $P < 0.01$.

SC: stomatal conductance; CC: chlorophyll content; PE: photosynthetic efficiency; TR: transpiration rate

Table 3 - Mean features of parents and their F_1 progenies

Parents and Crosses	SC	CC	PE	TR
3.2	37.40 j - m	50.67 fgh	0.827 cde	0.557 mno
3.4	49.23 f - j	52.33 d - h	0.807 f	0.420 r
3.6	36.84 j - m	53.33 c - h	0.770 i	0.430 pqr
14.2	28.47 lm	49.33 gh	0.781 h	0.620 lmn
14.20	25.07 m	51.33 e - h	0.783 h	0.637 k-n
14.21	28.05 lm	54.67 c - h	0.793 g	1.153 cde
14.26	42.51 h - k	53.33 c - h	0.826 cde	1.050 ef
FRMo 17	48.29 f - k	53.33 c - h	0.824 de	0.540 n - q
FRB 73	38.62 i - l	55.33 b - h	0.833 bc	0.963 fg
ADK 451	56.18 d - g	53.33 c - h	0.837 ab	1.237 bcd
3.2 × FRMo 17	37.33 j - m	56.00 a - h	0.832 bcd	0.747 ijk
3.2 × FRB 73	76.52 bc	55.33 b - h	0.833 bc	1.124 de
3.2 × ADK 451	47.50 f - k	55.00 b - h	0.835 b	1.262 bc
3.4 × FRMo 17	80.44 abc	58.00 a - e	0.827 cde	1.335 b
3.4 × FRB 73	67.21 cde	53.67 c - h	0.832 bcd	1.123 de
3.4 × ADK 451	46.70 f - k	58.67 a - d	0.827 cde	1.653 a
3.6 × FRMo 17	35.60 klm	50.33 fgh	0.832 bcd	0.426 qr
3.6 × FRB 73	69.35 bcd	58.67 a - d	0.825 de	1.637 a
3.6 × ADK 451	51.59 f - i	49.00 h	0.826 cde	0.667 j - m
14.2 × FRMo 17	82.11 ab	62.00 ab	0.826 cde	0.458 o - r
14.2 × FRB 73	92.15 a	56.33 a - g	0.823 e	0.558 mno
14.2 × ADK 451	77.75 bc	60.00 abc	0.831 b - e	0.903 gh
14.20 × FRMo 17	60.12 def	54.00 c - h	0.827 cde	1.350 b
14.20 × FRB 73	36.21 j - m	51.67 d - h	0.837 ab	0.937 fgh
14.20 × ADK 451	47.96 f - k	56.67 a - f	0.844 a	0.843 hi
14.21 × FRMo 17	59.82 d - g	58.33 a - e	0.838 ab	1.147 cde
14.21 × FRB 73	59.58 d - g	63.00 a	0.831 b - e	0.703 jkl
14.21 × ADK 451	52.04 f - i	54.67 c - h	0.826 cde	0.697 jkl
14.26 × FRMo 17	53.81 e - h	50.33 fgh	0.838 ab	0.457 o - r
14.26 × FRB 73	46.33 g - k	57.00 a - f	0.833 bc	0.760 ij
14.26 × ADK 451	52.90 fgh	58.00 a - e	0.836 ab	0.547 nop
LSD (0.05)	13.52	7.01	0.007	0.11

SC: stomatal conductance; CC: chlorophyll content; PE: photosynthetic efficiency; TR: transpiration rate

The additive variance of SC was 167.775, while $U^2 D$ was 148.057. $U^2 A$ associated with the average effect of individual genes measures the breeding value of genotypes and is always fixable thorough selection (Sofi et al., 2007). To be $U^2 A > U^2 D$ indicates the presence of individual genes that add stability to the population for that trait. $U^2 A > U^2 D$ was measured as 0.939. Li et al. (2017) reported that a dominance degree of any character in the population of $0.20 \leq \sqrt{D} / A < 0.80$ indicates partial dominance, while $0.80 \leq \sqrt{D} / A <$

Table 4 - Estimation of GCA in parents and SCA in the F1 progenies for all traits

GCA (parents)	SC	CC	PE	TR
3.2	- 4.931**	- 0.587	0.002**	0.123
3.4	6.066**	0.746	- 0.003**	0.450**
3.6	- 6.534**	- 3.365**	- 0.004**	- 0.011
14.2	25.286**	3.413**	- 0.005**	- 0.281**
14.20	- 10.620**	- 1.921**	0.005**	0.123**
14.21	- 1.568	2.635**	...	- 0.072
14.26	- 7.699**	- 0.921	0.004**	- 0.333**
FRMo 17	- 0.253	- 0.460	...	- 0.075**
FRB 73	5.191**	0.492	- 0.001	0.057**
ADK 451	- 4.939**	- 0.032	0.001	0.018
SCA (combinations)				
3.2 × FRMo 17	- 16.199**	1.016	- 0.002**	- 0.222**
3.2 × FRB 73	17.548**	- 0.603	...	0.023**
3.2 × ADK 451	- 1.349	- 0.413	0.001	0.199
3.4 × FRMo 17	15.914**	1.683**	- 0.002**	0.039
3.4 × FRB 73	- 2.767*	- 3.603**	0.004**	- 0.304**
3.4 × ADK 451	- 13.147**	1.921**	- 0.002**	0.265**
3.6 × FRMo 17	- 16.326**	- 1.873**	0.004**	- 0.409**
3.6 × FRB 73	11.977**	5.508**	- 0.002**	0.670**
3.6 × ADK 451	4.350**	- 3.635**	- 0.002**	- 0.261**
14.2 × FRMo 17	- 1.640	3.016**	- 0.001	- 0.107**
14.2 × FRB 73	2.953**	- 3.603**	- 0.002**	- 0.139**
14.2 × ADK 451	- 1.313	0.587	0.003**	0.245**
14.20 × FRMo 17	12.274**	0.349	- 0.009**	0.382**
14.20 × FRB 73	- 17.073**	- 2.937**	0.002**	- 0.163**
14.20 × ADK 451	4.800**	2.587**	0.007**	- 0.218**
14.21 × FRMo 17	2.928**	0.127	0.007**	0.373**
14.21 × FRB 73	- 2.762**	3.841**	...	- 0.202**
14.21 × ADK 451	- 0.166	- 3.968**	- 0.007**	- 0.170**
14.26 × FRMo 17	- 3.082**	- 7.873**	0.007**	- 0.317**
14.26 × FRB 73	- 16.006**	- 2.159**	0.002**	- 0.146**
14.26 × ADK 451	0.694	- 0.635	0.004**	- 0.320**

SC: stomatal conductance; CC: chlorophyll content; PE: photosynthetic efficiency; TR: transpiration rate

1.20 indicates dominance and $\sqrt{D} / A \geq 1.20$ indicates super dominance. $U^2 SCA > U^2 GCA$, where $U^2 A > U^2 D$ causes less dominance compared with causing over dominance because the dominance gene effects are limited by additive gene actions. Ali et al. (2014) reported that SC, CC, and TR properties are under the influence of dominance effects in maize. Evaluation of SC variance components within the population revealed that heterosis breeding could be used as an effective method for this population to improve SC. Line 14.2 had significant and the highest positive GCA, followed

Table 5 - Heterosis rates of progenies in all traits

Combinations	SC (%)	CC (%)	PE (%)	TR (%)
3.2 × FRMo 17	- 12	7	...	36
3.2 × FRB 73	101**	4	...	47
3.2 × ADK 451	1	5	...	40
3.4 × FRMo 17	64**	9	1**	178**
3.4 × FRB 73	53**	...	1**	62
3.4 × ADK 451	- 11	11	...	99**
3.6 × FRMo 17	- 16	- 5	4**	- 12
3.6 × FRB 73	83**	7	2**	134**
3.6 × ADK 451	10	- 8	2**	- 19
14.2 × FRMo 17	113**	20**	2**	- 20
14.2 × FRB 73	174**	7	2**	- 29
14.2 × ADK 451	83	16**	2**	- 2
14.20 × FRMo 17	63**	3	2**	129**
14.20 × FRB 73	13	- 3	3**	17
14.20 × ADK 451	18	8	4**	- 9
14.21 × FRMo 17	56**	8	3**	35
14.21 × FRB 73	78**	14*	2**	- 33
14.21 × ADK 451	23	1	1**	- 41**
14.26 × FRMo 17	18	- 5	1**	- 42
14.26 × FRB 73	14	4	...	- 24
14.26 × ADK 451	7	8	...	- 52
Mean values	44	5	2	23

SC: stomatal conductance; CC: chlorophyll content; PE: photosynthetic efficiency; TR: transpiration rate

by line 3.4 (Table 4). Tan (2010) reported that combining ability is defined as the ability to transfer desired parental traits to F1 progenies. Stomatal characteristics set the limit for maximum SC for gas exchange, thus having the potential of affecting carbon gain and water-use efficiency (Verhoef, 1997; Erdal, 2016). Lines that have significant and positive GCAs (14.2, 3.4) have the potential to produce F₁ progenies that have high SC. Plants having high SC means that the stomata are opened and gas exchange is occurring, resulting in CO₂ uptake. CO₂ has a remarkable relationship with grain yield. We can hypothesize that genotypes with higher SC could produce more photosynthetic products under normal conditions. Owing to this, Lines 3.4 and 14.2 have garnered the attention of breeders who focus on physiological-based studies to improve grain yield. Hybrids which had significant and positive SCAs were 3.2 × FRB 73, 3.4 × FRMo 17, 14.20 × FRMo 17, 3.6 × FRB 73, 14.20 × ADK 451, 3.6 × ADK 451, 14.2 × FRB 73 and 14.21 × FRMo 17 (Table 4). Fasahat et al. (2016) reported that progenies with high SCAs, where both parents were good general combiners, may indicate the occurrence of additive × additive gene actions

Table 6 - Narrow and broad sense heritability of all traits

Heritability parameters	SC	CC	PE	TR
h^2	0.495	0.212	0.282	0.380
H^2	0.933	0.591	0.812	0.911

h^2 : narrow sense heritability H^2 : broad sense heritability

SC: stomatal conductance; **CC**: chlorophyll content;
PE: photosynthetic efficiency; **TR**: transpiration rate

concerning the trait in question. High-value hybrids between good and poor general combiner parents may be attributed to favorable additive effects from the good general combiner parent and favorable epistasis effects from the poor general combiner parent. High performance from hybrids between low × low parents may be due to dominance × dominance types of non-allelic gene interactions, resulting in over dominance. Consistent with this idea, we hypothesise that the observed SC values for the progenies of 3.2 × FRB 73, 14.20 × FRMo 17, 3.6 × FRB 73, 14.20 × ADK 451, 3.6 × ADK 451 and 14.2 × FRB 73 were under the influence of additive × additive gene effects, while the offspring of 3.4 × FRMo 17 was under the influence of additive × epistasis effects, whereas progeny of 14.21 × FRMo 17 was under the influence of dominance × dominance gene effects. Many different gene effects were observed in this population-based on SC values. It was observed that line 14.2, a good combiner, combined well with tester FRB 73 and produced progeny 14.2 × FRB 73, which had an observed SCA of 2.953 (Table 4). These results may reflect a high genetic distance among parents. Line 14.2 did not combine well with other testers (FRB 73 and ADK 451) for SC. Line 3.4, a good combiner, combined well with FRMo 17, not a good combiner, and produced progeny 3.4 × FRMo 17, which had significant and positive SCA (Table 4). Kulembeka et al. (2012) reported in their study that progenies with favorable SCAs could be utilized for heterosis breeding. Significant and positive heterosis rates determined progenies were 174% (14.2 × FRB 73), 113% (14.2 × FRMo 17), 101% (3.2 × FRB 73), 83% (3.6 × FRB 73), 78% (14.21 × FRB 73), 64% (3.4 × FRMo 17), 63% (14.20 × FRMo 17), 56% (14.21 × FRMo 17) and 53% (3.4 × FRB 73), respectively. Oliboni et al. (2012) reported that heterosis expressed in hybrids between individuals from different populations depends on the presence of genes with non-additive effects in controlling desirable properties and the genetic divergence between them. Narrow-sense heritability of the population determined for SC was 0.495 and for H^2 was 0.933. Ogunniyan and Olakojo (2014) reported that $H^2 > 0.800$ indicates high heritability of the trait. High heritability indicates that

the influence of the environment on the heredity of the trait is minimal, revealing that the population is suitable for SC selection in early generations

Chlorophyll Content

It was observed that U^2 SCA (5.711) > U^2 GCA (1.595) and that RV (0.358) was less than 1, indicating that in this population, the CC trait was influenced by non-additive gene effects linked to U^2 SCA. The observed values of U^2 D (5.710) > U^2 A (3.189) supported these results as well. $\sqrt{D/A}$ (1.337) ≥ 1.20 demonstrated that the degree of dominance for CC was over dominance, suggesting the possibility of utilizing the population for heterosis breeding for CC. Line 14.2 had positive significance and the highest GCA, followed by line 14.21 (Table 4). GCA is controlled by genetic material and transmitted to offspring (Topal et al., 2004). SCAs of some progenies (14.21 × FRB 73, 14.2 × FRMo 17) of lines 14.21 and 14.2 were remarkable, as expected. Cai et al. (2014) stated that there is a remarkable relationship between photosynthesis, SC, and grain yield properties that promotes the investigation into physiological traits. Progenies of 3.4 × ADK 451 and 3.4 × FRB 73 were under the influence of dominance × dominance gene effects while 3.6 × FRB 73, 14.21 × FRB 73, 14.2 × FRMo 17 and 14.20 × ADK 451 were under the influence of additive × epistasis gene effects and, further, these progenies had significant and positive SCAs (Table 4). Within this population, dominance and epistasis effects were remarkable. Sofi et al. (2007) reported that additive effects are generally more important to open pollinated varieties, while in elite inbred lines dominance and epistasis effects are more important than additive effects. Progenies 14.2 × FRMo 17, 14.2 × ADK 451, and 14.21 × FRB 73 had significant and positive heterosis rates (Table 5). Lariepe et al. (2017) stated that heterosis rates of inter-group hybrids are higher than intra-group hybrids. SCA variation among inter-group hybrids is higher. Thus the parents of offspring with high SCAs in CC could have a high genetic distance, resulting in higher heterosis rates. Narrow-sense heritability of CC was 0.212 while H^2 was 0.591. Stansfield (1969) stated that $h^2 > 0.5$ indicates high heritability, $0.2 < h^2 < 0.5$ middle heritability and $h^2 < 0.2$ low heritability of the trait thus CC in this population has middle heritability which indicated that parents were responsible for 21% of the CC phenotype of the offspring.

Photosynthetic Efficiency

It was observed that U^2 SCA (2214×10^{-8}) > U^2 GCA (587×10^{-8}) and that RV (0.346) was less than 1, indicating that PE is under the influence of non-additive gene effects linked to SCA in this population. U^2 D (22×10^{-6}) > U^2 A (12×10^{-6}) supported these conclusions as well. Dominance variance is associated with intra-allelic gene interactions at segregating loci and measures breeding behavior of alleles in heterozygotes; it is practically applied in heterosis breeding (Sofi et al., 2007). To be dominance degree of the trait super dominance (\sqrt{D} / A (1.337) \geq 1.20) showed that heterosis could be an effective breeding strategy for PE in this population as well. Lines with remarkable GCAs are 14.20, 14.26, and 3.2 (Table 4). These lines can effectively transmit their genetic potential for PE to their offspring. Photosynthetic efficiency is linked to grain yield of crops. PE is determined by measuring the Fv / Fm rate, a biophysics parameter, and reveals the light absorption rate of PSII (Lepeduš et al., 2012). Parents whose PE potential is higher can be used sources of offspring with better potential grain yield. Progenies 14.20 × ADK 451, 14.21 × FRMo 17 and 14.26 × FRMo 17 had SCAs that were significant and positive, followed by offspring 3.6 × FRMo 17, 14.26 × ADK 451 and 3.4 × FRB 73. Progenies 14.20 × FRB 73 and 14.26 × FRB 73 had the lowest significant and positive SCAs (Table 4). Offspring which had remarkable SCAs also had remarkable heterosis rates (14.20 × ADK 451, 3.6 × FRMo 17, 14.21 × FRMo 17, 14.20 × FRB 73, 14.26 × FRMo 17 and 3.4 × FRB 73) (Table 5). Lines (formatted progenies with significant and positive SCA and heterosis rates) had significant GCAs, whereas all testers had non-significant GCAs. This situation indicates that all progenies with significant and positive SCA are influenced by additive × epistasis gene effects. Non-allelic genes that are not fixable were useful in this population in CC, and this finding is further supported by variance components for this population. Lines 14.20 and 14.26, which had significant and positive GCAs, produced offspring that had remarkable SCAs (14.20 × FRB 73; 14.20 × ADK 451; 14.26 × FRMo 17; 14.26 × FRB 73; 14.26 × ADK 451) (Table 4). These parents can be significant parental sources for breeders because they provide a robust gene pool to produce progeny with high PE. The higher PE potential of a genotype indicates more effective photosynthetic capacity. Breeders are interested in photosynthetic traits because of the connection between photosynthesis and yield. Narrow-broad sense heritability results in PE are presented in Table 6, and PE was observed to be of middle heritability ($0.2 < h^2 < 0.5$). Having a middle h^2 and H^2 with 0.812 indicated that environmental factors had a strong effect on PE phenotype.

Transpiration Rate

We observed that U^2 SCA (0.121) > U^2 GCA (0.038) and the RV of the TR was 0.385 which is lower than 1 and indicates that non-additive gene actions effect TR in this population, which is consistent with our U^2 D (0.120) > U^2 A (0.075) observations. Lines 3.4 and 14.20 had significant and positive GCAs, and 3.4 × ADK 451, 14.20 × FRMo 17 produced by these lines also had significant and positive SCAs (Table 4) and under the influence of additive × additive and additive × epistasis gene effects, respectively. Other progenies with high SCAs were 3.6 × FRB 73, 14.21 × FRMo 17, and 3.2 × FRB 73 and all of those offspring were under the influence of epistasis × additive gene effects, while 14.2 × ADK 451 was under the influence of additive × epistasis gene effects. Many kinds of non-fixable gene effects observed among parents indicate the possible use of heterosis breeding in this population. Progenies with significant and positive heterosis rates were 3.4 × FRMo 17, 3.6 × FRB 73, 14.20 × FRMo 17 and 3.4 × ADK 451 (Table 5). This situation may be due to different types of gene effects on the gene pools of progenies. Line 3.4 had a significant and positive GCA and combined well with tester ADK 451 and with the progeny of 3.4 × ADK 451 and SCA of 0.265. The same line produced 3.4 × FRB 73, which had a significant and negative SCA (Table 4). Although both offspring were including line 3.4, they had different orientations from each other. This may be because of the high-low genetic distances of the parents. Fasahat et al. (2016) stated that parents with higher genetic distance could be better combined. Line 14.20, whose GCA is significant and positive combined well with all of the testers (Table 4). Progenies of line 14.20 with FRB 73 or ADK 451 had significant and negative SCAs, whereas progeny of line 14.20 with FRMo 17 had significant and positive SCA, although GCA of the tester was negative (Table 4). Passioura (1983) and Jones (1998) stated that to be water use efficiency, TR and harvest index (which correlates with yield) higher of genotypes indicated that the genotype could adapt to limited water conditions better than other genotypes and have higher yield potential. The TR changes according to species, CO₂ uptake, and SC properties. Narrow-sense heritability of TR in the population was 0.380 while H^2 was 0.911. The population had middle heritability for TR. A H^2 value of 91% indicated strong environmental effects on the gene process of TR. High TR rates in a plant may be added due to high leaf temperature (Sade, 2000), and plants can lose vapor from surfaces that contact the atmosphere and have a higher uptake of CO₂ and light. Some genotypes had higher TR, although at the same ecological conditions. This may be because of the different usage capacity of light, resulting in high photosynthetic activity.

Conclusions

Seven inbred lines (3.2, 3.4, 3.6, 14.2, 14.20, 14.21 and 14.26), three testers (FRMo 17, FRB 73 and ADK 451) and 21 F1 progenies produced by line × tester mating design were screened according to quantitative genetic elements with SC, CC, PE and TR traits. Lines 3.2 (PE), 3.4 (SC, TR), 14.20 (PE, TR), 14.21 (CC) and 14.26 (PE) had significant and positive GCAs at many features. Some progenies had significant and positive SCAs in some properties too. It was reported that features linked photosynthesis are also linked with yield and yield compounds. This population include parents that inherited genetic potentials of them to their progenies in SC, CC, PE and TR traits effectively because of their high GCAs. Some of the specific progenies with significant and positive SCAs showed desired properties of their parents as well. Those parents combined well with some of the testers and derived progenies with significant and high SCAs. Results of the study showed the possibility of using SC, CC, PE, and TR traits as selection criteria in breeding studies.

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