Study of gene action for various physiological traits in Zea mays

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Abstract: Improvement of physiological traits in maize plays an important role in enhancing grain and fodder yield. Gene action provides an opportunity to a plant breeder to develop higher yielding maize genotypes and was computed by using analysis of variance technique and 6×6 North Carolina matting design II analysis. In order to study gene action for physiological traits an experiment was conducted in the research area of Department of Plant Breeding and Genetics, University of Agriculture Faisalabad, Pakistan during crop growing season 2011-12 and 2012-2013 using completely randomized block design with three replications. It was reported from the evaluation of F1 hybrids that higher photosynthetic rate was recorded for B-327 (32.21 μ g CO₂s⁻¹), EV-1097 × B-316 (33.13 μ g CO_2s^{-1}), leaf temperature for B-11 (49.57 °C), Sh-139 × F-96 (49.60 °C), chlorophyll contents for EV-347 (57.77 mg g-1fr.wt), Raka-poshi (57.87 mg g-1fr.wt), stomata conductance for E-336 \times EV-340 (0.410 mmol m⁻² s⁻¹) and E-336 × F-96 (0.350 mmol m⁻² s⁻¹), transpiration rate for E-336 × EV-340 (14.72 mm d⁻¹), E-336 × F-96 (14.78 mm d^{-1}), sub-stomata CO₂ concentration for Sh-139 × Pop/209 (281.7 µmol mol⁻¹ CO₂), F-96 (254.0 µmol mol-1 CO₂) and water use efficiency was recorded for E-336 \times EV-340 (312.2 %) and B-327 \times F-96 (204.9 %). It was concluded that inbred lines B-11, E-336, B-316 performed well for physiological traits. Genetic advance and heritability was found higher for photosynthetic rate, stomata conductance, transpiration rate, sub-stomata CO_2 concentration and water use efficiency. Male additive effects were found higher for chlorophyll contents, water use efficiency, sub-stomata CO_2 concentration and photosynthetic rate. Female additive effects, male \times female interaction and cumulative additive effects were also found higher for chlorophyll contents, sub-stomata CO₂ concentration, transpiration rate. Dominance and degree of dominance was also found higher for leaf temperature, chlorophyll contents and photosynthetic rate. These additive effects and the degree of dominance indicated that selection via heterosis breeding may be helpful to develop synthetics with higher grain and fodder yield.

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1. Introduction

Corn (Zea mays) is a crop of imperative importance throughout the world, with higher impact in developing countries like Pakistan where rapidly growing population has outstripped available food. Maize is the third essential cereal crop in Pakistan after wheat and rice. It contributes 5.67 % to the value of agriculture product. Last year only, it was grown on 1083000 hectares with an annual production of 4271 thousand tons and an average yield of 3940 kg ha⁻¹ (Anonymous, 2011-12). Maize is disregarded as food for humans while it is used to feed livestock; and it is also worn as an industrial raw material to produce various types of by-products. Its highest (9.9 %) crude protein content occurs from early to full blooming stages, and it decreases to 7 % at milk stage (grain formation stage) and to 6 % at maturity. The grain is formed by 82 % endosperm, 12 % embryo, 5 % bran testa and 1 % tip cap; and in total it contains 72% starch, 10% protein, 4.80% oil, 9.50% fiber, 3.0% sugar, and 1.70% ashes, (Chaudhary, 1983; US-Bureau of Chemistry, 2010). Maize production of Pakistan is lower as compared to other maize growing countries due to non-availability of project funds and potential germplasm. Grain yield is related with diverse physiological, morphological and agronomic traits of maize. By improving these traits the production of maize genotypes may be improved. Heritability, genetic advance and gene action provides a great prospect to a plant breeder to select genotypes on the basis of strong correlation among grain yielding and its contributing traits (Grzesiak *et al.* 2007; Ali *et al.* 2011a,b; Ali *et al.* 2012 and Ali *et al.* 2014). The prescribed study was carried out to assess gene action in maize accessions for physiological traits of maize.

2. Material and methods

The present study was conducted in the experimental area of the Department of Plant Breeding and Genetics, University of Agriculture Faisalabad to assess the maize genotypes for physiological traits for the period of the crop season in February 2011-12. The experimental material was composed for 80 accessions including ten check varieties (Table 1). The accessions

were grown in the field following three replications in a completely randomized block design. The plant-to-plant distance and row-to-row distance was kept 25 cm and 75 cm respectively. The data from 10 randomly selected plants were recorded for the following traits, viz., chlorophyll content (mg g⁻¹ fr. wt.) by using chlorophyll meter; photosynthetic rate (μ g CO₂ s⁻¹), stomata conductance (mmol m⁻² s⁻¹), transpiration rate (mm day⁻¹), sub-stomata CO₂ concentration (μ mol mol⁻¹ CO₂), water use efficiency (%) and leaf temperature (°C) at maturity stage by using IRGA (Infrared Gas Analyzer) from experiment 1. The genotypes performed batters were selected for development of F_1 hybrids. The selected parents were crossed following a 6 × 6 North Carolina matting design II (Comstock and Robinson, 1952) during the growing season in August 2011-12. The parents and F_1 crosses as given below and were evaluated in the field experiment for all above given traits during growing season in February 2012-13 (Table 2). The data was statistically analyzed by using analysis of variance technique (Steel *et al.* 1997). The genetic advance was calculated by using Falconer (1989) formula. Heritability was recorded by using Burton, (1951) technique. Gene action was calculated by using Comstock and Robinson, 1952 technique.

Table 1. Maize	accessions used	in screening	experiment

F-121	F-146	EV-324	F-98	F-143	B-308	E-341	Sawan-3
F-127	B-303	EV-335	B-96	F-113	B-304	E-351	Pak-Afgogee
F-128	B-327	EV-323	F-135	F-111	B-312	E-322	Gold Isalamabad
F-150	B-316	EV-334	VB-06	F-114	EV-344	E-346	Islamabad. W
F-142	B-306	EV-330	B-121	F-136	EV-343	E-336	VB-51
F-151	B-313	EV-329	B-15	F-122	EV-310	BF-337	EV-1097
F-118	B-314	EV-338	B-11	F134	POP/209	BF-248	EV-7004Q
F-117	B-305	EV-340	Sh-213	F-147	EV-342	BF-212	Raka-Poshi
F-130	B-321	E-349	Sh-139	F-105	EV-347	BF-236	BS-2
F-140	B-326	E-352	SWL-2002	F-148	F-96	BF-238	POP/2007

Table 2. Parents and F₁ crosses used in evaluation experiment

Sr. No.	Genotypes	Sr. No.	Genotypes	Sr. No.	Genotypes
1	Pop/209	17	B-11×F-96	33	B-327×EV-340
2	B-316	18	B-11×EV-347	34	B-327×E-322
3	EV-340	19	B-336×Pop/209	35	B-327×F-96
4	E-322	20	B-336×B-316	36	B-327×EV-347
5	F-96	21	B-336×EV-340	37	Raka-poshi×Pop/209
6	EV-347	22	B-336×E-322	38	Raka-poshi×B-316
7	B-11	23	B-336×F-96	39	Raka-poshi×EV-340
8	B-336	24	B-336×EV-347	40	Raka-poshi×E-322
9	EV-1097	25	EV-1097×Pop/209	41	Raka-poshi×F-96
10	B-327	26	EV-1097×B-316	42	Raka-poshi×EV-347
11	Raka-poshi	27	EV-1097×EV-340	43	Sh-139×Pop/209
12	Sh-139	28	EV-1097×E-322	44	Sh-139×B-316
13	B-11×Pop/209	29	EV-1097×F-96	45	Sh-139×EV-340
14	B-11×B-316	30	EV-1097×EV-347	46	Sh-139×E-322
15	B-11×EV-340	31	B-327×Pop/209	47	Sh-139×F-96
16	B-11×E-322	32	B-327×B-316	48	Sh-139×EV-347

3. Results and discussions 3.1 Screening experiment

Significant differences were found for all physiological traits (Table 3). Chlorophyll content is represented in Figure 1, the highest chlorophyll content was recorded for F-113, and followed by B-303; while the lowest value of chlorophyll content

was F-98, followed by Pak-Afgoee. The mean for chlorophyll content ($45.735 \pm 1.00 \text{ mg g}^{-1}$ fr. wt.) was recorded at tasseling stage. The higher estimate of heritability (98.65 %) and genetic advance (23.891 %) were found for chlorophyll content. It was found (Figure 2) that the highest photosynthetic rate was recorded for F-151 followed by EV-335; while the

lowest value of photosynthetic rate was B-11 followed by F-127. The higher photosynthetic rate also implies that the increasing chlorophyll content caused increases in growth and development (Grzesiak et al. 2007; Veronica et al. 2009; Wali et al. 2010; Ali et al. 2011a; Ali et al. 2012b and Ali et al. 2013b, c.d.e). The mean for photosynthetic rate $(16.718\pm0.2470\mu g CO_2)$ s^{-1}) was recorded at tasseling stage. The higher estimate of heritability (99.90%) and genetic advance (92.12%) were found for photosynthetic rate (Table 3). The mean for stomata conductance (0.172 ± 0.03873) mmol m⁻² s⁻¹) was recorded at tasseling stage. The higher estimate of heritability (79.30%) and genetic advance (64.198%) were found for stomata conductance (Table 3). Ahsan et al. (2013); Akbar et al. (2009); Ali et al. (2011a,b,d,e) and Ali et al. (2012a) reported similar results. The higher values of heritability and genetic advance indicated that the stomata conductance may be helpful to enhance crop yield and productivity. It was suggested from the Figure 3 that the highest stomata conductance was recorded for Pop-209 followed by F-155 while the lowest value of stomata conductance was EV-335 followed by Sh-139. The higher stomata conductance indicated higher photosynthetic rate and accumulation of organic compounds (Akbar et al. 2009; Veronica et al. 2009; Wali et al. 2010 and Ahsan et al. 2011). The mean for leaf temperature $(48.385\pm0.12040C)$ was recorded at tasseling stage.

The higher estimate of heritability (98.0%) and lower genetic advance (3.046%) were found for leaf temperature (Table 3). The higher values of heritability and genetic advance indicated that leaf temperature may be helpful to enhance crop yield and productivity. Findings were found similar to Ali *et al.* (2011a,b); Grzesiak et al. (2007) and Wang et al. (2007). It is shown in Figure 4 that the highest leaf temperature were recorded for Sh-139 followed by Islamabad W, while the lowest value of leaf temperature was F-121 followed by F-127. The higher leaf temperature also implies that chlorophyll content is increased, and that caused the increase in growth and development of crop plants (Moulin et al. 2009 and Veronica et al. 2009). The mean for transpiration rate (9.392±0.03873 mm day⁻¹) was recorded at tasseling stage. The higher estimate of heritability (99.60%) and genetic advance (47.798%) were found for transpiration rate (Table 3). Ahsan et al. (2013); Akbar et al. (2009); Ali et al. (2012a,b) and Ali et al. (2013a) reported similar

results. The higher values of heritability and genetic advance indicated that transpiration rate may be helpful to enhance crop yield and productivity. The genotypes with greater transpiration rate may also be used for the development of drought resistant fodder genotypes. The broader leaf may have larger stomata, due to which the transpiration rate and photosynthetic will be enhanced, therefore the genotypes with greater stomata conductance and transpiration rate may be used in rainfed areas to fulfill the fodder and forage requirement of livestock. It was suggested from figure 5 that the highest transpiration rates were recorded for Pop-209 followed by EV-347 while the lowest value of transpiration rate was EV-335 followed by Sh-139. The mean for sub-stomata CO₂ concentration $(113.3\pm1.414 \text{ }\mu\text{mol mol}^{-1} \text{ CO}_2)$ was recorded at tasseling stage. The higher estimate of heritability (99.98%) and genetic advance (113.418%) were found for sub-stomata CO₂ concentration (Table 3). Ahsan et al. (2013) and Ali et al. (2013a,b,c) reported similar results. The higher values of heritability and genetic advance indicated that sub-stomata CO₂ concentration may be helpful to enhance the crop yield and productivity. It indicated that due to higher value of sub-stomata CO₂ concentration caused to increase the photosynthetic that leads rate towards the improvement of fresh and dry biomass of plant. It was suggested from figure 6 that the highest sub-stomata CO₂ concentration were recorded for BF-236 followed by F-127 while the lowest value of sub-stomata CO₂ concentration was BF-248 followed by B-306. The mean (53.322±2.2439) for water use efficiency was recorded at tasseling stage. The higher estimate of heritability (99.37%) and genetic advance (93.231%) were found for total dry matter (Table 3). The higher values of heritability and genetic advance indicated that water use efficiency may be helpful to enhance the crop yield and productivity. It was suggested from figure 7 that the highest water use efficiency were recorded for F-96 followed by while E-351 the lowest value water use efficiency was F-142 followed by EV-335. The fodder yield was also increased on higher water use efficiency as the photosynthetic rate increased that caused to increase the green fodder and dry matter yield per plant. Findings were found similar to Muraya et al. (2006); Ojo et al. (2007); Ali et al. (2011c,e); Ali et al. (2012b) and Ali et al. (2013c).









Figure 7. Water use efficiency (%)

SOV	Chl. C	LT	PR	SC	TR	SSCC	WUE
MSS	79.655**	1.4669*	154.259**	0.0126*	13.197**	10724.94**	1583.85**
GM	45.735	48.385	16.718	0.172	9.392	113.3	53.322
SE	1.00	0.1204	0.2470	0.03873	0.1688	1.414	2.2439
GV	39.291	0.719	77.069	0.00499	6.571	5361.861	789.405
GCV	13.71	1.75	52.51	41.08	27.29	64.63	52.692
PV	39.827	0.733	77.129	0.00629	6.599	5362.472	794.445
PCV	13.80	1.77	52.53	46.14	27.35	64.63	52.859
EV	0.537	0.0145	0.0607	0.0013	0.0283	0.611	5.04
ECV	1.60	0.25	1.47	20.99	1.79	0.69	4.21
$h^2_{bs\%}$	98.65	98.00	99.90	79.30	96.60	99.98	99.37
SE h ² _{bs %}	0.017724	0.131	0.0127	1.538	0.0433	0.0015	0.0056
GA%	23.891	3.046	92.122	64.198	47.798	113.418	93.231

** = Significant at 5% significance level, * = Significant at 1% significance level, Chl. C = Chlorophyll contents (mg g⁻¹ fr. wt.), LT = Leaf temperature (°C), PR = Photosynthetic rate (μ g CO₂ s⁻¹), SC = Stomata conductance (mmol m⁻² s⁻¹), TR = Transpiration rate (mm day⁻¹), SSCC = Sub-stomata CO₂ concentration (μ mol mol⁻¹ CO₂), WUE = Water use efficiency (%),M.S.S = Mean Sum of Squares, GM±SE = Grand mean ± Standard error, GV = Genotypic variance, GCV = Genotypic coefficient of variance, PV = Phenotypic variance, PCV = Phenotypic coefficient of variance, EV = Environmental Variance, ECV + Environmental coefficient of variance, h²_{bs %} = Broad sense heritability, SE h²_{bs %} = Standard error for broad sense heritability, GA = Genetic advance %

3.2 Evaluation of parents and f₁ hybrids

The results related to the mean performance of the parents and F₁ hybrids as suggested from Table 4 that highly significant differences were found among parents and F₁ hybrids for all physiological traits. The results indicated that the average of chlorophyll contents was recorded as 46.141±0.5833mgg⁻¹fr.wt. The higher heritability (99.10%) and moderate type of genetic advance (17.56%) was found for chlorophyll contents (Table 4). Higher values of heritability indicated that selection of genotypes for higher chlorophyll contents may be helpful to improve green fodder yield of maize. Higher chlorophyll contents also indicated that the photosynthetic rate, sub-stomata CO₂ concentration, transpiration rate, leaf and stem weight and leaf area will be higher (Ojo et al., 2007; Akbar et al., 2009; Wali et al., 2010; Ali et al. 2012b and Ahsan et al. 2013). It was indicated from Table 6 that higher chlorophyll contents were recorded for EV-347 $(57.77 \text{mgg}^{-1} \text{fr.wt}), \text{ B-11} (54.90 \text{mgg}^{-1} \text{fr.wt}), \text{ B-11} \times$ EV-347 (54.83mgg⁻¹fr.wt), EV-1097 × B-316 (54.73mgg⁻¹fr.wt) and Raka-poshi (57.87mgg⁻¹fr.wt) while lower for EV-1097× Pop/209 (36.40mgg⁻¹fr.wt), Sh-139 \times Pop/209 (36.14mgg⁻¹fr.wt) and Sh-139 \times F-96 (32.46mgg⁻¹fr.wt). The higher chlorophyll contents indicated that F_1 hybrids B-11 × EV-347 and EV-1097 \times B-316 may be used for higher green fodder vield per plant (Rahmeeh et al., (2000); Khan et al., (2001); Gautam (2003); Parkash et al., (2004); Malik et al., (2004); Ali et al. (2011d,e); Ali et al.

(2012a) and Ali et al. (2013a,c)). The results indicated that the average of leaf temperature was recorded as 48.448±0.1867°C. The higher heritability (91.90%) and lower type of genetic advance (0.99%) was found for leaf temperature (Table 4). Higher values of heritability indicated that selection of genotypes for higher leaf temperature may be helpful to improve green fodder yield of maize. Higher leaf temperature also indicated that the photosynthetic rate, sub-stomata CO₂ concentration and transpiration rate will be higher. The selection of genotypes on the basis of leaf temperature may be helpful in next generations (Ojo et al. 2007; Akbar et al. 2009; Wali et al. 2010; Ali et al. 2012 and Ahsan et al. 2013). It was shown from Table 6 that higher leaf temperature were recorded for Pop/209 (49.53°C), B-11 (49.57°C), Sh-139×F-96 (49.60°C), EV-1097 × B-316 (49.53°C) and Raka-poshi× Pop/209 (49.53°C) while lower for E-336 \times B-316 (47.47°C), E-336 ×F-96 (47.27°C) and E-336 × EV-340 (47.13°C). The higher leaf temperature indicated that F₁ hybrids Sh-139 \times F-96 and EV-1097 \times B-316 may be used for higher green fodder yield per plant in next generations (Rahmeeh et al. 2000; Khan et al. 2001; Gautam 2003; Parkash et al. 2004 and Malik et al. 2004).

The results indicated that the average of photosynthetic rate was recorded as 17.453 ± 0.5756 μ gCO₂s⁻¹. The higher heritability (99.60%) and genetic advance (69.28%) was found for photosynthetic rate (Table 4). Higher values of

heritability and genetic advance indicated that selection of genotypes for higher photosynthetic rate may be helpful to improve green fodder vield of maize. Higher photosynthetic rate also indicated that the sub-stomata CO₂ concentration, stomata conductance, leaf area, leaf and stem weight, green fodder yield per plant due to accumulation of organic compounds will be higher. The selection of genotypes on the basis of photosynthetic rate may be helpful to improve grain and fodder yield of maize (Ojo et al. 2007; Saleem et al. 2007; Ahsan et al. 2013; Akbar et al. 2009; Wali et al. 2010; Ali et al. 2012 and Ahsan et al. 2013). It was indicated from Table 6 that higher photosynthetic rate was recorded for B-327 (32.21 $\mu g CO_2 s^{-1}$), EV-1097 (30.82 $\mu g CO_2 s^{-1}$), EV-1097 × B-316 (33.13 $\mu g CO_2 s^{-1}$) and B-327 × E-322 $(30.45 \mu g CO_2 s^{-1})$ while lower for Raka-poshi × EV-347 (4.92 μ gCO₂s⁻¹), E-336 × EV-340 (4.72 $\mu gCO_2 s^{-1}$) and EV-1097 × Pop/209 (4.24 $\mu gCO_2 s^{-1}$). The higher photosynthetic rate indicated that F_1 hybrids $B-327 \times E-322$ and $EV-1097 \times B-316$ may be used for higher green fodder yield per plant in next generations (Saleem et al. 2007; Ahsan et al. 2013; Ali et al. 2011a; Ali et al. 2012 and Ahsan et al. 2013). The results indicated that the average of stomata conductance was recorded as 0.1722±0.005mmol m⁻²s⁻¹. The higher heritability (99.60%) and genetic advance (64.43%) was found for stomata conductance (Table 2). Higher values of heritability and genetic advance indicated that selection of genotypes for higher stomata conductance may be helpful to improve green fodder yield of maize. Higher stomata conductance also indicated that the sub-stomata CO₂ concentration, photosynthetic rate, leaf area, leaf and stem weight, green fodder vield per plant due to accumulation of organic compounds will be higher. The selection of genotypes on the basis of stomata conductance may be helpful to improve grain and fodder yield of maize (Akbar et al. 2009; Wali et al. 2010; Ali et al. 2012 and Ahsan et al. 2013). It was shown from Table 6 that higher stomata conductance was recorded for E-336 × EV-340 (0.410mmol m⁻²s⁻¹), Sh-139 × B-316 (0.333 mmol $m^{-2}s^{-1}$) and E-336 × F-96 (0.350mmol $m^{-2}s^{-1}$) while lower for E-336 × E-322 (0.063mmol $m^{-2}s^{-1}$), EV-340 (0.060mmol $m^{-2}s^{-1}$) and EV-1097 × B-316 (0.047 mmol $m^{-2}s^{-1}$). The higher stomata conductance indicated that F_1 hybrids E-336 × B-316. Sh-139 \times B-316 and E-336 \times F-96 may be used for higher green fodder yield per plant (Gautam 2003; Parkash et al. 2004 and Malik et al. 2004)).

The results suggested that the average of transpiration rate was recorded as 9.597 ± 0.1175 mm day⁻¹. The higher heritability (99.80%) and genetic advance (36.83%) was found for transpiration rate (Table 4). Higher values of heritability and genetic

advance indicated that selection of genotypes for higher transpiration rate may be helpful to improve green fodder vield of maize. Higher transpiration rate also indicated that the stomata conductance, sub-stomata CO₂ concentration, photosynthetic rate, leaf area, leaf and stem weight, green fodder vield per plant due to accumulation of organic compounds will be higher. The selection of genotypes on the basis of transpiration rate may be helpful to improve grain and fodder yield of maize (Ojo et al. 2007; Akbar et al. 2009; Wali et al. 2010; Ali et al. 2012 and Ahsan et al. 2013). It was persuaded from Table 6 that higher transpiration rate was recorded for E-336 \times EV-340 (14.72 mm day⁻¹), Sh-139 × B-316 (14.29 mm day⁻¹) and E-336 \times F-96 (14.78 mm day⁻¹) while lower for E-336 × E-322 (5.650 mm dav⁻¹), EV-340 $(5.870 \text{ mm dav}^{-1})$ and EV-1097 × B-316 (3.670 mm day⁻¹). The higher transpiration rate indicated that F_1 hybrids E-336 \times B-316, Sh-139 \times B-316 and E-336 \times F-96 may be used for higher green fodder yield per plant (Parkash et al., (2004) and Malik et al., 2004).

The results conceived that the average of sub-stomata CO₂ concentration was recorded as $124.74\pm2.326 \text{ }\mu\text{mol} \text{ mol}^{-1} \text{ CO}_2$. The higher heritability (99.90%) and genetic advance (72.30%) was found for sub-stomata CO₂ concentration (Table 2). Higher values of heritability and genetic advance indicated that selection of genotypes for higher sub-stomata CO₂ concentration may be helpful to improve green fodder yield of maize. Higher sub-stomata CO₂ concentration also indicated that the transpiration stomata conductance, rate, photosynthetic rate, leaf area, leaf and stem weight, green fodder yield per plant due to accumulation of organic compounds will be higher. The selection of genotypes on the basis of sub-stomata CO₂ concentration may be helpful to improve grain and fodder yield of maize (Ahsan et al. 2008; Wali et al. 2010; Ali et al. 2012 and Ahsan et al. 2013). It was convinced from Table 6 that higher sub-stomata CO₂ concentration was recorded for B-327×EV-347 mol^{-1} CO₂), Sh-139×Pop/209 umol (246.7 $(281.7\mu mol mol^{-1} CO_2)$, F-96 $(254.0\mu mol mol^{-1} CO_2)$ and Sh-139 × E-322 (237.3 μ mol mol⁻¹ CO₂) while lower for E-336 × E-322 (36.0 μ mol mol⁻¹ CO₂), Sh-139 (35.67 μ mol mol⁻¹ CO₂) and B-11 × F-96 $(32.0 \text{ }\mu\text{mol mol}^{-1} \text{ CO}_2)$. The higher sub-stomata CO₂ concentration indicated that F_1 hybrids B-327 \times EV-347, Sh-139 \times Pop/209 and Sh-139 \times E-322 may be used for higher green fodder yield per plant (Parkash et al., (2004) and Malik et al., 2004).

The results show that the average of water use efficiency was recorded as 86.21±2.541%. The higher heritability (99.80%) and genetic advance (93.78%) was found for water use efficiency (Table 2). Higher values of heritability and genetic advance indicated that selection of genotypes for higher water use efficiency may be helpful to improve green fodder yield of maize. Higher water use efficiency also indicated that the transpiration rate, sub-stomata CO_2 concentration, stomata conductance, photosynthetic rate, leaf area, leaf and stem weight, green fodder yield per plant due to accumulation of organic compounds will be higher. The selection of genotypes on the basis of water use efficiency may be helpful to improve grain and fodder yield of maize (Wali *et al.* 2010; Ali *et al.* 2012 and Ahsan *et al.* 2013). It was swayed from Table 6 that higher water use efficiency was recorded for E-336 × EV-340 (312.2%), B-327 × F-96 (204.9%), EV-1097 × Pop/209 (195.4%) and Raka-poshi × EV-347 (194.25) while lower for E-336 × E-322 (20.11%), Sh-139 × F-96 (24.44%) and EV-1097 × B-316 (11.09%). The higher water use efficiency indicated that F_1 hybrids E-336 × EV-340, B-327 × F-96, EV-1097 × Pop/209 and Raka-poshi × EV-347 may be used for higher green fodder yield per plant (Rahmeeh *et al.* 2000; Parkash *et al.* 2004 and Malik *et al.* 2004).

SOV	Chl. C	LT	PR	SC	TR	SSCC	WUE
M.S.S	111.43*	12.31**	225.84*	0.018**	19.20*	769.27*	10043.8*
GM±SE	46.141±0.5833	48.448±0.1867	17.453±0.5756	0.1722 ± 0.005	9.597±0.1175	124.74±2.326	86.21±2.541
GV	36.804	0.394	74.948	0.006	6.386	4155.730	3341.486
GCV	13.148	1.296	49.603	46.031	26.332	51.679	75.850
PV	37.144	0.429	75.279	0.006	6.400	4161.139	3347.943
PCV	13.209	1.352	49.713	46.124	26.361	51.713	75.924
EV	0.340	0.035	0.331	0.001	0.014	5.409	6.457
ECV	1.264	0.385	3.298	2.931	1.225	1.864	3.334
$h_{bs\%}^2$	99.10	91.90	99.60	99.60	99.80	99.90	99.80
$\frac{SE}{h_{bs\%}^2}$	0.019	0.182	0.013	1.471	0.046	0.002	0.002
GA%	17.50	0.99	69.28	64.43	36.83	72.30	93.78

Table: 4. Genetic components for various physiological traits in parents and F₁ hybrids of maize

** = Significant at 5% significance level, * = Significant at 1% significance level, Chl. C = Chlorophyll contents (mg g⁻¹ fr. wt.), LT = Leaf temperature (°C), PR = Photosynthetic rate (μ g CO₂ s⁻¹), SC = Stomata conductance (mmol m⁻² s⁻¹), TR = Transpiration rate (mm day⁻¹), SSCC = Sub-stomata CO₂ concentration (μ mol mol⁻¹ CO₂), WUE = Water use efficiency (%),M.S.S = Mean Sum of Squares, GM±SE = Grand mean ± Standard error, GV = Genotypic variance, GCV = Genotypic coefficient of variance, PV = Phenotypic variance, PCV = Phenotypic coefficient of variance, EV = Environmental Variance, ECV + Environmental coefficient of variance, h²_{bs %} = Broad sense heritability, SE h²_{bs %} = Standard error for broad sense heritability, GA = Genetic advance %

3.3. Gene action

It was revealed from Table 5 that significant differences were found for all physiological traits. The results indicated that higher additive variance for male \times female interaction was 26.652 following female additive variance (5.874) and male additive variance was (1.270). The additive effect was recorded as 9.526 but higher dominance effect 106.607 was recorded for chlorophyll contents. The degree of dominance was recorded as 3.345 (Table 5). Higher values of dominance effect and degree of dominance indicated that over type of dominance gene action was shown for chlorophyll contents. Higher chlorophyll contents also indicated that photosynthetic rate, sub-stomata CO₂ concentration, water use efficiency and stomata conductance will also be higher. The over dominance and higher degree of dominance indicated that selection on the basis of chlorophyll contents may be helpful for the development of hybrid seed. Findings were found similar to Vafias and Ipilandis (2005); Welcker et al. (2005); Akbar et al. (2008); Wang et al., (2007); Ahsan et al. (2013); Akbar et al. (2009) and Moulin et al. (2009). The results indicated that higher additive variance for male × female interaction was 0.362 following female additive variance (0.015) and male additive variance was (0.057). The additive effect was recorded as 0.096 but higher dominance effect 1.449 was recorded for leaf temperature. The degree of dominance was recorded as 3.889 (Table 5). Higher values of dominance effect and degree of dominance indicated that over type of dominance gene action was shown for leaf temperature. Higher leaf temperature also indicated that photosynthetic rate, sub-stomata CO₂ concentration, water use efficiency, chlorophyll contents and stomata conductance will also be higher. The over dominance and higher degree of dominance indicated that selection on the basis of leaf temperature may be helpful for the development of hybrid seed.

Findings were found similar to Wang et al. (2007); Ahsan et al. (2013); Akbar et al. (2009) and Moulin et al. (2009). The results show that higher additive variance for male \times female interaction was 67.383 following female additive variance (-9.326) and male additive variance was (16.048). The additive effect was recorded as 8.962 but higher dominance effect 269.533 was recorded for photosynthetic rate (Table 5). The degree of dominance was recorded as 5.484. Higher values of dominance effect and degree of dominance indicated that over type of dominance gene action was shown for photosynthetic rate. Higher photosynthetic rate also indicated that sub-stomata CO₂ concentration, water use efficiency, chlorophyll contents and stomata conductance will also be higher. The over dominance and higher degree of dominance indicated that selection on the basis of photosynthetic rate may be helpful for the development of hybrid seed. Findings were found similar to Welcker et al. (2005); Akbar et al. (2008); Wang et al., (2007); Ahsan et al. (2013); Akbar et al., (2009) and Moulin et al., (2009). The results suggested that higher additive variance for male × female interaction was 0.0069 following female additive variance (-0.0001) and male additive variance was (0.0001). The additive effect was recorded as -0.0002 but higher dominance effect 0.0278 was recorded for stomata conductance. The degree of dominance was recorded as 12.926 (Table 5). Higher values of dominance effect and degree of

dominance indicated that over type of dominance gene action was shown for stomata conductance. Higher stomata conductance also indicated that sub-stomata CO₂ concentration. water use efficiency. photosynthetic rate and chlorophyll contents will also be higher. The over dominance and higher degree of dominance indicated that selection on the basis of stomata conductance may be helpful for the development of hybrid seed. Findings were found similar to Akbar et al. (2008); Wang et al. (2007); Ahsan et al. (2013); Akbar et al. (2009) and Moulin et al. (2009). The results indicated that higher additive variance for male \times female interaction was 7.344 following female additive variance (-0.463) and male additive variance was (-0.139). The additive effect was recorded as -0.802 but higher dominance effect 29.374 was recorded for transpiration rate. The degree of dominance was recorded as -6.052 (Table 5). Higher values of dominance effect and degree of dominance indicated that over type of dominance gene action was shown for transpiration rate. Higher transpiration rate also indicated that stomata conductance, sub-stomata CO₂ concentration, water use efficiency, photosynthetic rate and chlorophyll contents will also be higher. The over dominance and higher degree of dominance indicated that selection on the basis of transpiration rate may be helpful for the development of hybrid seed.

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SOV	Chl. C	LT	PR	SC	TR	SSCC	WUE
Replication	0.344ns	0.4734ns	1.81ns	0.00015ns	0.019ns	28ns	5ns
Males	104.107**	1.4043*	492.26*	0.02115**	19.574*	31591*	16491*
Females	186.982*	2.1541*	35.53*	0.01845**	13.750**	10267*	6365*
$M \times F$	81.241**	1.1319*	203.40*	0.02092**	22.076*	9368*	12868*
Error	1.286	0.0447	1.25	0.00007	0.045	19	25

Table: 5 (a). Analysis of variance for physiological traits in maize (North Carolina matting design-II)

(n) variable genetic components for physiological traits in	maize (North Caroling matting design_li)
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σ^2_{m}	1.270	0.015	16.048	0.0001	-0.463	1234.7	201.3
$\sigma_{\rm f}^2$	5.874	0.057	-9.326	-0.0001	7.344	50.0	-361.3
$\sigma^2_{m \times f}$	26.652	0.362	67.383	0.0069	-0.802	3116.0	4281.1
σ^2_{D}	9.526	0.096	8.962	-0.0002	29.374	1712.8	-213.3
$\sigma^2_{ m H}$	106.607	1.449	269.533	0.0278	-0.462	12464.1	17124.4
$\left[\sigma_{\rm H}^2/\sigma_{\rm D}^2\right]^{1/2}$	3.345	3.889	5.484	12.926	-6.052	2.698	-8.960

* = Significant at 1 % significance level, ** = Significant at 5 % significance level, ns = Non-significant, σ_m^2 = male additive variance, σ_m^2 = Female additive variance, $\sigma_{m\times f}^2$ = m×f interaction additive variance, σ_H^2 = Dominance variance, σ_D^2 = cumulative additive variance, $[\sigma_H^2/\sigma_D^2]^{1/2}$ = Degree of dominance, Chl. C = Chlorophyll contents (mg g⁻¹ fr. wt.), LT = Leaf temperature (°C), PR = Photosynthetic rate (µg CO₂ s⁻¹), SC = Stomata conductance (mmol m⁻² s⁻¹), TR = Transpiration rate (mm day⁻¹), SSCC = Sub-stomata CO₂ concentration (µmol mol⁻¹ CO₂), WUE = Water use efficiency (%)

Genotypes	PR	SC	TR	SSCC	WUE	LT	Chl.C
Pop/209	9.060 T	0.070 Z[\	5.990XY	90.00RS	66.13JK	49.53AB	52.90 DE
B-316	8.420 T	0.080 Z	6.350W	137.7 J	75.50 I	48.80DEFGHI	43.97 MNOP
EV-340	11.84 S	0.060 \]	5.870XY	49.00 Y	49.55MNO	49.57AB	46.93 JK
E-322	20.29 LM	0.160NOPQ	9.820MN	126.3 K	48.40MNOPQ	48.40GHIJK	37.77 ST
F-96	9.040 T	0.153PQRS	9.310 O	254.0 B	102.9 G	48.63EFGHIJ	44.77 LMN
EV-347	29.80CDE	0.283 D	12.32C	121.0 KL	41.33OPQRS	47.63MNOP	57.77 A
B-11	6.100 VW	0.120VWX	7.170UV	202.0 E	117.9 F	49.20ABCDEF	54.90 B
E-336	21.23 L	0.153PQRS	8.920PQ	78.00 T	42.03 OPQR	48.70EFGHI	44.77 LMN
EV-1097Q	30.82 BC	0.190 KL	10.36 L	65.33 UV	33.62 STU	48.27HIJKL	47.53 IJK
B-327	32.21 AB	0.220 HI	11.93DEF	75.33 T	37.06 RST	47.63 MNOP	48.83 HI
Raka-poshi	14.93OPQ	0.143RST	8.930PQ	92.33QRS	59.85 KL	48.67EFGHI	57.87 A
Sh-139	18.90 M	0.123VW	8.610 Q	35.67 Z	45.56NOPQR	48.63EFGHIJ	53.87 BCD
B-11×Pop/209	12.72 RS	0.147QRST	9.550NO	126.0 K	75.11 I	48.33GHIJKL	51.97 EF
B-11×B-316	24.78HIJ	0.223 HI	11.65FGH	54.67WXY	49.44MNOP	48.00JKLMN	48.83 HI
B-11×EV-340	15.99NOP	0.107 XY	7.440TU	47.67 Y	46.55 NOPQ	48.77DEFGHI	41.27 R
B-11×E-322	14.25PQR	0.243 EF	12.17CD	190.0 F	85.51 H	47.87 KLMNO	42.13 PQR
B-11×F-96	29.05DEF	0.227 GH	11.86DEF	32.00 Z	40.84 PQRS	47.70 LMNOP	41.83 QR
B-11×EV-347	15.99NOP	0.217 HI	11.03 IJ	236.3 D	68.96 IJ	47.60 MNOP	54.83 B
E-336×Pop/209	12.07 S	0.133 TUV	7.980 RS	57.67 WX	66.16 JK	48.57 FGHIJ	48.90 HI
E-336×B-316	27.37 FG	0.243 EF	12.10CDE	121.3 KL	44.22NOPQR	47.47 NOP	44.07 MNO
E-336×EV-340	4.720 WX	0.410A	14.72 A	36.00 Z	312.2 A	47.13 P	42.77 OPQR
E-336×E-322	28.12 EF	0.063 [\	5.650 Y	182.0 G	20.11 W	49.43 ABC	48.60 HIJ
E-336×F-96	23.68IJK	0.350 B	14.78 A	115.0 LM	62.45 JKL	47.27 OP	38.57 S
E-336×EV-347	8.230 TU	0.220 HI	11.57FGH	90.00 RS	140.6 E	47.60 MNOP	36.87 ST
EV-1097Q×Pop/209	4.240 X	0.127UVW	8.260 R	158.0 H	195.4 C	48.77DEFGHI	36.40 T
EV-1097Q×B-316	33.13 A	0.047]	3.670 Z	146.3 I	11.09 X	49.53 AB	54.73 BC
EV-1097Q×EV-340	23.16 JK	0.257 E	11.79EFG	142.0 IJ	50.93 MN	48.20 IJKLM	49.65 GH
EV-1097Q×E-322	20.01 LM	0.240 FG	11.29 HI	110.0 MN	56.45 LM	48.17 IJKLM	48.49 HIJ
EV-1097Q×F-96	6.300 VW	0.200JK	10.40 KL	104.0NOP	165.3 D	48.33GHIJKL	53.01 CDE
EV-1097Q×EV-347	14.33OPQR	0.170MNO	9.230 OP	235.0 D	64.40 JK	48.63EFGHIJ	53.91 BCD
B-327×Pop/209	16.97 N	0.113WXY	7.490 TU	95.00 QR	44.14NOPQR	48.63EFGHIJ	43.44 NOPQ
B-327×B-316	25.37 HI	0.240 FG	11.45 GH	156.0 H	45.14NOPQR	47.70 LMNOP	51.03 FG
B-327×EV-340	9.260 T	0.167MNOP	10.28 L	52.00 XY	111.1 F	48.20 IJKLM	46.40 KL
B-327×E-322	30.45 CD	0.123VW	8.160 R	192.0 F	26.81 UVW	48.87CDEFGH	44.17 MNO
B-327×F-96	6.060 VW	0.253EF	12.41 C	60.00 VW	204.9 B	48.20IJKLM	47.17 IJK
B-327×EV-347	8.950 T	0.157OPQR	10.20 L	246.7 C	114.1 F	48.40GHIJK	46.40 KL
Raka-poshi×Pop/209	13.60QRS	0.077 Z[6.340 W	102.7 OP	46.69NOPQ	49.53 AB	36.83 ST
Raka-poshi×B-316	22.86 K	0.173 MN	10.04 LM	153.3 H	43.94NOPQR	48.40GHIJK	51.97 EF
Raka-poshi×EV-340	10.01 1	0.217 HI	11.41 H	108.0 NO	114.1 F	48.20IJKLM	43.77 NOP
Raka-poshi×E-322	25.91 GH	0.103 Y	7.660 ST	146.01	29.55 TUV	48.97BCDEFG	41.57 QR
Raka-poshi×F-96	17.16 N	0.140STU	8.940 PQ	87.33 S	52.18 MN	48.//DEFGHI	50.78 FG
Kaka-poshi×EV-347	4.920VWX	0.153PQRS	9.550 NO	95.33 QR	194.2 C	48.50GHIJK	42.27 OPQR
Sh-139×Pop/209	25.93 GH	0.210 IJ	11.45 GH	281.7 A	44.18NOPQR	48.20IJKLM	36.14 I
Sh-139×B-316	12.62 KS	0.333 C	14.29 B	191.3 F	113.3 F	47.50 NOP	41.78 QK
Sn-139×EV-340	0.080 UV	0.083 Z	0.1/0 WX	/1.55 IU	92.40 H	49.60 A	32.46 U
Sn-159×E-522	10.08 NU	0.083 Z	0.300 W	237.3 D	40.42 QKS	49.3/ABCD	42.90 OPQK
Sh-139×F-96	28.02 F	0.080 Z	6.850 V	98.33 PQ	24.44 VW	49.23ABCDE	45.78 KLM
Sh-139×EV-347	26.12 GH	0.177LM	10.73 JK	102.3 OP	41.090PQRS	48.20 IJKLM	41.26 R

Table: 6. Statistical significance of parents and F1 hybrids of maize for various physiological and grain vielding traits

Chl. C = Chlorophyll contents (mg g⁻¹ fr. wt.), LT = Leaf temperature (°C), PR = Photosynthetic rate (μ g CO₂ s⁻¹), SC = Stomata conductance (mmol m⁻² s⁻¹), TR = Transpiration rate (mm day⁻¹), SSCC = Sub-stomata CO₂ concentration (μ mol mol⁻¹ CO₂), WUE = Water use efficiency (%)

Findings were found similar to Akbar et al. (2008); Wang et al., (2007); Ahsan et al. (2013); Akbar et al., (2009) and Moulin et al., (2009). The results indicated that higher additive variance for male \times female interaction was 3116.0 following female additive variance (50.0) and male additive variance was (1234.7). The additive effect was recorded as 1712.8 but higher dominance effect 12464.1 was recorded for sub-stomata CO₂ concentration (Table 5). The degree of dominance was recorded as 2.698. Higher values of dominance effect and degree of dominance indicated that over type of dominance gene action was shown for sub-stomata CO₂ concentration. Higher sub-stomata CO₂ concentration also indicated that transpiration rate, stomata conductance, water use efficiency, photosynthetic rate and chlorophyll contents will also be higher. The over dominance and higher degree of dominance indicated that selection on the basis of sub-stomata CO₂ concentration may be helpful for the development of hybrid seed (Akbar et al. 2008; Wang et al. 2007; Ahsan et al. 2013; Akbar et al. 2009 and Moulin et al. 2009). The results indicated that higher additive variance for male \times female interaction was 4281.1 following female additive variance (-361.3) and male additive variance was (201.3). The additive effect was recorded as -213.3 but higher dominance effect 17124.4 was recorded for water use efficiency (Table 5). The degree of dominance was recorded as -8.960. Higher values of dominance effect and degree of dominance indicated that over type of dominance gene action was shown for water use efficiency. Higher water use efficiency also indicated that transpiration rate, stomata sub-stomata concentration, conductance. CO_2 photosynthetic rate and chlorophyll contents will also be higher. The over dominance and higher degree of dominance indicated that selection on the basis of water use efficiency may be helpful for the development of hybrid seed (Welcker et al. 2005; Akbar et al. 2008; Wang et al. 2007; Ahsan et al. 2013; Akbar et al. 2009; Moulin et al. 2009 and Ali et al. 2014).

Conclusions

It was concluded that inbred lines B-11, E-336, B-316 performed well for physiological traits. Genetic advance and heritability was found higher for photosynthetic rate, stomata conductance, transpiration rate, sub-stomata CO_2 concentration and water use efficiency. The additive effects indicated that selection may be helpful to develop synthetics with higher grain and fodder yield while higher dominance and degree of dominance indicated that heterosis breeding should be proceeded to improve grain and fodder yield.

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