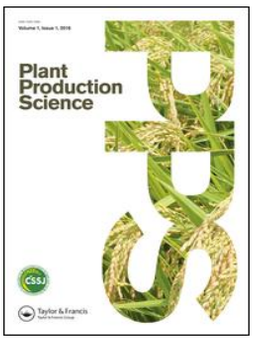

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Path analysis of genotype × environment interactions in rainfed durum wheat

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ABSTRACT

This study was investigated to analyze genotype × environment (GE) interactions for grain yield and its components and to investigate the mechanism by which the stability of grain yield is achieved in rainfed durum wheat. Twenty-four durum wheat genotypes (breeding lines, old, and new varieties) along with one old bread wheat cultivar were tested in 21 diversified rainfed environments during 2010–2013 cropping seasons. The data were analyzed by path analysis model which is composed of a main effect and four multiplicative effects. The flowering time (X1), maturity time (X2), plant height (X3), and 1000-kernel weight (X4) were assumed to be sequential characters for the development of grain yield productivity (*Y*) in rainfed durum wheat. A high relationship ($p < .01$) between observed and expected yields of genotypes in different environments confirmed the validity of the causal scheme adopted in the analysis. Comparison the estimates of components provided information on the degree of response of each genotype to the environmental stresses. The results indicated that higher grain yields are associated with higher kernel weight (v_4), which resulted from early flowering (v_1), and so more emphasis should be given to these traits for the improvement of yield potential in durum wheat under highland rainfed conditions of Iran. Positive correlation of stability variance (σ^2) with v_4 component indicated that the kernel weight is the main contributor towards GE interaction for grain yield in rainfed durum wheat.

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Durum wheat; GE interaction; path analysis; yield; genotypic components

Introduction

The development of high-yielding cultivars requires a thorough knowledge of the existing genetic variation for yield and its components (Shukla et al., 2006). Grain yield is a result of the combined effects of genotype, environment, and their interaction. The importance of the genotype × environment (GE) interaction is that it causes different reactions of genotypes when they are grown in different environments. The efficiency of a breeding program depends mainly on the direction and magnitude of the association between yield and its components and also the relative importance of each factor involved in contributing to grain yield (Agrama, 1996). The GE interaction is induced by differential responses of genotypes to environmental factors present during the development for component traits (Ehdaei et al., 1999).

Environmental stresses that occur during the sequential development of yield components constitute the major ingredients of GE interaction of yield. Several researchers (Ehdaei et al., 1999; Grafius, 1969; Lynch & Tai, 1989; Tai, 1975; Tai et al., 1994; Thomas et al., 1971) presented the concept of a sequential development process of yield components. Tai (1971) developed a statistical model based on the path analysis approach (Wright, 1934), which has been used successfully to study GE interaction of yield and its components for a set of genotypes evaluated in a range of environments. There are two important assumptions of the model: (i) the chronological sequence in the development in yield components is X1 to X2 to X3 to X4 and yield, *Y*, is final multiplicative product of sequential development process i.e. $Y = X1 \times X2 \times X3 \times X4$; and (ii) the environmental response can be separated into independent groups i.e. R1, R2, R3, and R4, where each group supports the development of a component trait. The path analysis method has been used to investigate GE interaction in potato under water stress (Lynch & Tai, 1989) and heat stress conditions (Tai et al., 1994) and in wheat under different level of nitrogen (Ehdaei et al., 1999).

The main objectives were to (i) study GE interaction for grain yield and its components in durum wheat under diversified rainfed environments and (ii) identify superior genotypes to environmental constraints in the highland

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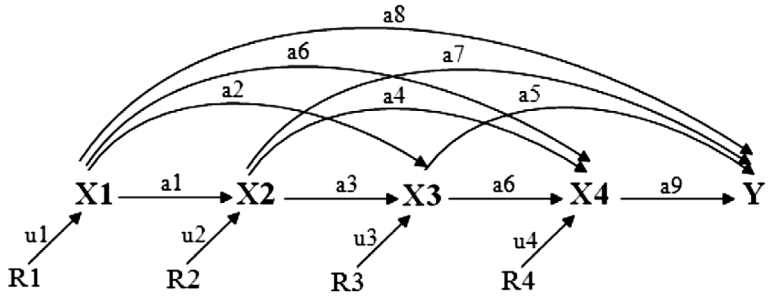

Figure 1. A causation diagram showing the relationship among three independent groups (R1, R2, R3, and R4) of environmental resources, yield components (X1, X2, X3, and X4) and yield. The lower case letters on the various single-arrow paths are path coefficients.

rainfed conditions of Iran, where drought and cold are two limiting factors.

Materials and methods

Plant materials and climatic conditions

Twenty-four durum wheat genotypes including 21 breeding lines (G1–G21), one new (G22) and 2 old cultivars (G23, G24), along with one popular old bread wheat variety (G25) were tested over 7 rainfed research stations, representative of major rainfed durum wheat-growing areas in Iran, during 3 cropping seasons (2010–2013), resulting in 21 different environments (combination of location-year). At each environment, experimental layout was a randomized complete block design with three replications. Plot size was 7.2 m^2 (6 rows, 6 m long, and 20-cm row spacing). Management practices recommended for each location were followed in all yield trials. The grain yields were measured per plot and converted to kg ha^{-1} for the statistical analyses.

Precipitation (October–June) among the environments varied from 177 to 399 mm, and average minimum temperatures ranged from −2.5 to 8.5 °C and average maximum temperatures varied from 8.4 to 24.5 °C, respectively, across environments. The low rainfall and low temperature in most of the stations resulting in both drought and cold stresses which are both limiting factors for durum wheat production in highland cold rainfed areas of Iran.

Data analysis

The performances of 5 traits for 25 genotypes over 21 environments were compared. The traits recorded for the genotypes at each environment included days to heading (DTH), days to maturity (DTM), plant height (PLH), 1000-kernel weight (TKW), and grain yield (YLD). The analysis of variance (ANOVA) procedure was applied to test the significance of genotype (G), environment (E), and GE interaction effects for each of the five traits.

To study the relationship between yield and the components of yield, the model proposed by Tai (1975) was used. The causal relationship between the grain yield and its four components is diagrammed in Figure 1. The multiplicative product of the yield components resulted in total yield. The u1, u2, u3, and u4 are the path coefficient from R1 to X1, R2 to X2, R3 to X3, and R4 to X4, respectively, and a1, a2, …, a9 are the path coefficients between X1, X2, X3, X4, and *Y*. The path coefficients which measure directly the effects of R1, R2, R3, and R4 on yield (*Y*) can be determined by calculating at first the products of path coefficients along each of the possible compound paths connecting the *R*'s to yield (*Y*) and then adding up the products of all the compound paths from R1, R2, R3, or R4 to *Y*.

The model separates environmental components into independent groups and estimates their contribution to the development of individual component traits. In Tai's model, the yield of the *i*th genotype ($i = 1 \ldots l$) in the *j*th environment ($j = 1 \ldots m$) is composed of a mean genotypic effect, μ; four multiplicative terms of the GE interaction formed by four genotypic components, v_{1i}, v_{2i}, v_{3i}, and v_{4i}; four environmental components, r_{1j}, r_{2j}, r_{3j}, and r_{4j}; and an experimental error, e_{ij}. It can be expressed as:

$$Yij = \mu + v_{1i}r_{1j} + v_{2i}r_{2j} + v_{3i}r_{3j} + v_{4i}r_{4j} + e_{ij}$$

The environmental components are measured in standard deviation units and genotypic components represent the efficiency of the genotype to utilize one standard unit input of the four environmental components during the ontogeny of yield development. The genotypic components are estimated by path analysis (Wright, 1921). The environmental components are then estimated by least squares using the observed yields and estimates of the genotypic components. For details see Tai (1975). The validity of the path analysis model to represent the observed results was assessed by the degree of correlation between observed and fitted data of each of the genotypes for each of the traits. This was carried out by calculating correlation coefficients between observed and fitted

Table 1. Combined ANOVA for grain yield and its components and description of phenotypic data for each component.

		Grain yield (kg/ha)		DTH (Day)		DTM (Day)		PLH (cm)		1000-kernel weight (g)	
Source	df	MS	%§	MS	%	MS	%	MS	%	MS	%
Genotype	24	393,304**	2.5	46.9**	.3	15.6**	0	1027.7**	18	80.0**	10.2
Environment	20	15,187,400**	81.2	20915.1**	99.1	39583.4**	99.6	4400.5**	64.1	615.4**	65.7
GE	480	127,016**	16.3	5.2**	.6	6.3**	.4	51.2**	17.9	9.4**	24.1
Linear	24	278,354**	11	4.9ns	4.7	23.1**	18.2	185.7**	18.1	4.7ns	2.5
Deviation	456	119,051	89	5.3	95.3	4.4	81.8	44.1	81.9	9.6	97.5
Total	524										
Mean		1542		194		222		64.6		33.2	
Minimum		1289		191		220		57.9		30.4	
Maximum		1969		197		224		83.8		37.3	
CV (%)		8.9		.8		.4		10.8		5.9	

§Percentage relative to total sum of squares or GE interaction.
**Significant at $p = .01$.
ns: non-significant.

data for individual genotypes across three replicates over three seasons. Shukla's (1972) stability variance was estimated based on grain yield for each genotype. The yield stability information was then used to compare the results of the genetic and environmental component estimates of the GE interactions.

Results

Variance components

The results of combined ANOVA for grain yield and its components are given in Table 1. Highly significant differences ($p < .01$) were observed among genotypes, environments and GE interaction effects for yield and its components (Table 1). Depending on trait, the environments accounted for the 64.1–99.6% of total sum of squares (SS), followed by GE interaction which captured .4–24.1% and genotype accounted for .05–18.0%. This indicates that for all traits, the environment accounted for most of the variation followed by GE and genotype effects. The linear regression of GE interaction accounted for 2.5–18.2% of GE interaction variation, depending on trait, whereas the residual of the variation around regression slope explained 81.8–97.5% of variation. Large portion of GE interactions was due to a non-linear component which can be regarded as a very important parameter for selection of stable genotypes.

The mean, minimum, maximum, and coefficient of variation (CV%) for yield and its components (X1, X2, X3, and X4) also are presented in Table 1. The mean yield for genotypes was 1542 kg ha^{-1} and ranged from 1289 to 1969 kg ha^{-1} across 21 environments. The values for DTH (X1) varied from 191 to 197 days, for DTM (X2) ranged from 220 to 224 days, for PLH (X3) was varied from 57.9 to 83.8 cm and for 1000-TKW (X4) varied from 30.4 to 37.3 g across 21 environments. The coefficient of variation (CV%) was the least for components X2 followed by X1 and moderate for X4 and was high for X3, indicating high variation in genotypes for components X3 followed by X4.

Estimates of genotypic components of GE interaction

The genotypic components of GE interaction for 25 tested genotypes are presented in Table 2. The validity of the estimations was verified by the high correlation between observed and fitted yields of individual genotypes. The correlations between observed mean yields and the values fitted by the model for 25 genotypes was high except for genotype G24, although was significant ($r = .50$; $p < .01$). This genotype was late in flowering, had the highest PLH, and low yield productivity. The genotype G25 (bread wheat old variety) gave the highest mean yield across environments. The breeding lines G8, G2, and G3 were in the group of second highest yield. Old durum variety (G24) and breeding lines (G18, G19) were poor in yield productivity.

The range of component v_1 was larger than those of v_3, v_2, and v_4. Thus, the genotypes showed more varied responses to the environmental stresses for the flowering time which is the most important trait under rainfed condition. All genotypes showed negative estimates of v_1 component, indicating all genotypes used a negative unit of this component to escape from terminal drought and heat stresses. Breeding lines G2 and G9 had the highest value for v_1, indicating early flowering had the highest impact in yield productivity of these promising durum wheat breeding lines and, in contrast, this component with $v_1 = -.077$ had the least impact on yield productivity of old bread wheat cultivar (G25). In contrast to v_1, the all genotypes showed positive estimates of v_2 and v_3, thus the yield productivity of all genotypes was positively more influenced by v_2 and v_3 components. Breeding lines G2 and G9 had the

Table 2. Mean grain yield, genotypic components of GE interaction, and stability variance for 25 genotypes across 21 rainfed environments, and correlation coefficients between observed and fitted data for each of the genotypes.

Genotypes		Mean yield	Genotypic components of GE interaction					Correlation
Code	Type	(kg/ha)	v_1	v_2	v_3	v_4	σ^2 ($\times 10^{-4}$)	Coefficient
G1	Breeding line	1476bcd[§]	−.371	.307	.701	−.149	27.1	.79**
G2	Breeding line	1676b	−.715	.471	.61	−.173	25.2	.76**
G3	Breeding line	1648b	−.5	.354	.528	−.012	39.6	.62**
G4	Breeding line	1418bcd	−.338	.336	.666	.014	23.9	.72**
G5	Breeding line	1546 bcd	−.489	.368	.716	−.053	27.0	.78**
G6	Breeding line	1475 bcd	−.385	.284	.65	−.093	26.1	.72**
G7	Breeding line	1594bc	−.382	.28	.61	−.17	28.7	.71**
G8	Breeding line	1690b	−.466	.192	.598	−.148	25.4	.69**
G9	Breeding line	1529bcd	−.715	.482	.613	−.098	25.6	.72**
G10	Breeding line	1407 bcd	−.465	.266	.64	−.222	27.2	.79**
G11	Breeding line	1559 bcd	−.54	.315	.553	−.218	35.0	.73**
G12	Breeding line	1504 bcd	−.587	.322	.635	−.209	32.6	.77**
G13	Breeding line	1467 bcd	−.5	.327	.463	−.176	35.6	.61**
G14	Breeding line	1590bc	−.39	.366	.733	.031	20.2	.78**
G15	Breeding line	1625bc	−.484	.299	.584	−.087	37.5	.70**
G16	Breeding line	1469 bcd	−.651	.449	.642	−.096	31.6	.79**
G17	Breeding line	1590bc	−.541	.33	.619	−.129	38.9	.77**
G18	Breeding line	1357 cd	−.413	.359	.666	−.258	18.9	.81**
G19	Breeding line	1358 cd	−.418	.356	.745	−.132	29.3	.85**
G20	Breeding line	1558bcd	−.218	.289	.569	.032	35.2	.62**
G21	Breeding line	1507bcd	−.133	.176	.646	.077	29.0	.67**
G22	New cultivar	1596bc	−.561	.428	.585	−.117	33.8	.75**
G23	Old variety	1642bc	−.342	.267	.591	−.115	22.4	.69**
G24	Old variety	1289d	−.216	.308	.456	−.036	50.0	.53**
G25	Old variety	1969a	−.077	.207	.514	.19	64.4	.50**
Mean		1542	−.436	.325	.613	−.094	31.6	.72**

[§]Means in same column followed by common letters are not significant based on Duncan's test at 5% level of probability.
**Significant at $p = .01$.

highest value for v_2, suggesting the importance of number of DTM in yield productivity of these genotypes. These two genotypes were the earliest in flowering (highest negative v_1 value) and latest in maturity (highest positive v_2 value), which suggest highest grain filling period for these two genotypes which toward to high yield productivity in G2 (third rank in yield productivity). The lowest values for v_2 belonged to G21, G8, and G25, while for v_3 belonged to G24, G13, and G25. The greatest values of v_4 was correspond to G25, followed by G21, G20, G14, and G4, suggesting the importance of kernel weight in determination of yield productivity in these genotypes.

The v_1 and v_3 components were larger in absolute values than the corresponding v_2 and v_4 components, except for G25, G24, G21, G20, and G4. Therefore, most genotypes were sensitive to environmental stresses for flowering and plant stature, which affect grain weight in G18 followed by G10, G11, G12, and G13. According to all genotypic components (v_1–v_4), the old cultivars (G25, G24 and G23) and two breeding lines (G20 and G21) were the genotypes with reasonable tolerance to environmental stresses while sensitive genotypes were the breeding lines G2, G9, G16, G12, and G18. However, in general, a consistent pattern was observed between type of genotypes i.e. old cultivars vs. breeding lines. The old bread wheat cultivar (G25) was the highest yielder with the largest positive estimate of v_4, and smallest estimate in absolute value of v_1 component. The breeding lines G8, G2, and G3 had slightly lower mean yields than G25 but with lower v_4 and higher v_1 estimates. The new cultivar (G22) had moderate mean yield and moderate estimates of the four genotypic components. In contrast, G2 and G25 were the only two genotypes showing a high level of responses to all genotypic components of the GE interaction except for v_3 component. However, their reactions to the first and fourth environmental components were in opposite directions.

The genotypes G18, G14, G23, G4, and G2 with the lowest stability variance values were stable, while the genotypes G25 followed by G24, G3, G17, and G15 with the highest stability variance were unstable (Table 2). Correlation coefficients were calculated between mean yield and the four genotypic components of the GE interactions and stability variance (Table 3). Mean yield and stability variance were significantly correlated ($r = .397$; $p < .05$), indicating a positive trend between high yielding and stability performance in genetic materials. Stability variance negatively correlated with v_3 component and positively with v_4 component, indicating the importance of plant stature and kernel weight components in stabilizing grain yield across diverse environments. An interesting result was the highly positive correlation between the v_1 and v_4 indicating early in flowering which resulting in increasing kernel weight. The negative correlation between v_1 and v_2 showing that earlier in flowering essentially not resulting

in earlier maturity. The v_4 component showed positive correlation (r = .417; p < .05) with mean yield, indicating the importance of kernel weight in yield productivity under rainfed condition.

Estimates of environmental components of GE interaction

The agroclimatic characteristics, environmental index (EI), and estimates of the 4 environmental components (r_1, r_2, r_3, and r_4) of the 21 environments are given in Table 4. The correlations of EI with r_1, r_2, r_3, and r_4 were, respectively, −.118, −.098, −.568, and .085. Both r_1 and r_3 had a much greater absolute sizes than r_2 and r_4 in most environments. Only in few occasions were the influences of r_1 or r_3 smaller than or similar to that of r_2 and r_4. The r_1 component did not show a clear trend that could be associated with the environmental stresses, and the values for r_1 were slightly greater than the corresponding values for r_2, r_3, and r_4. Like r_1, r_2, and r_3 also did not show a clear trend with environmental stresses, but there was a general trend for r_3 which showed a negative values for moderate cold and warm environments (except for I12) and positive values for cold environments (except for A12 and S11). However, the third environmental component was apparently the most influential on grain yield productivity which had a significant negative correlation with the EI (r = −.568; p < .01) (Table 5). A moderate correlation (r = .535; p < .01) was observed

Table 3. Pearson correlation coefficients between genotypic components of mean grain yield and stability variance.

		Genotypic components			
	Mean yield	v_1	v_2	v_3	v_4
v_1	.085				
v_2	−.210	−.750**			
v_3	−.251	−.135	.176		
v_4	.417*	.638**	−.276	−.117	
Stability variance	.397*	.372	−.258	−.671**	.477*

*,**Significant at p = .05 and .01, respectively.

Table 4. Agroclimatic characteristics, environmental index, and environmental components of GE interaction for 21 test environments.

Environments			Annual climatic data		Traits					EI	Environmental components of GE interaction			
Code*	Status	Cropping season	Rainfall (mm)	Temperature (°C)	YLD (kg/ha)	DTH (Day)	DTM (Day)	PLH (cm)	TKW (g)		r_1	r_2	r_3	r_4
K11	MC	2010–11	342.5	11.8	1840	194	228	78	19	298	−.69	.288	−.322	.09
K12	MC	2011–12	302.9	11.0	2360	181	213	62	25	818	−.554	.153	−.219	.003
K13	MC	2012–13	394.3	13.4	774	181	218	48	34	−768	−.529	.129	−.194	.035
Mean in absolute size			346.6	12.1	1658	185	220	63	26		.59	.19	.25	.04
M11	C	2010–11	351.4	5.6	1979	220	252	65	36	437	−.711	.022	.231	−.425
M12	C	2011–12	251.0	4.0	859	217	242	42	31	−683	−.363	.146	.215	.014
M13	C	2012–13	351.1	6.4	1824	210	247	61	32	282	−.175	.256	.477	.386
Q11	C	2010–11	346.6	6.6	1565	220	251	63	29	23	−.206	−.29	.185	.396
Q12	C	2011–12	313.3	6.5	788	156	195	43	40	−754	−.19	−.181	.555	−.032
Q13	C	2012–13	256.1	8.4	2708	193	235	74	38	1166	.049	−.021	.499	.367
U11	C	2010–11	333.9	9.6	1234	212	250	78	41	−308	−.251	−.15	.238	.079
U12	C	2011–12	290.3	7.2	603	235	265	71	31	−939	.444	−.48	.446	.37
U13	C	2012–13	399.4	10.1	1529	218	253	69	36	−13	−.474	.325	.17	.196
A11	C	2010–11	177.0	8.5	1546	208	254	57	34	4	−.184	.235	.291	−.066
A12	C	2011–12	278.5	6.1	2362	214	259	69	35	820	−.107	−.099	−.291	.115
A13	C	2012–13	233.4	8.7	435	209	254	44	35	−1107	.301	.291	.706	−.193
S11	C	2010–11	229.0	11.1	1115	195	221	61	31	−427	.062	.229	−.044	.513
S12	C	2011–12	267.8	8.9	840	195	115	61	32	−702	.152	−.063	.209	.536
S13	C	2012–13	235.5	10.6	1441	189	218	62	35	−101	.257	−.244	.229	.263
Mean in absolute size			287.7	7.9	1388	206	234	61	34		.26	.2	.32	.26
I11	W	2010–11	384.3	13.5	3537	140	170	90	27	1995	.189	−.193	−.729	.241
I12	W	2011–12	328.9	12.9	974	121	142	54	37	−568	−.542	−.104	.049	−.181
I13	W	2012–13	396.1	13.6	2063	162	192	71	36	521	−.435	−.661	−.045	.099
Mean in absolute size			369.8	13.4	2191	141	168	72	33		.39	.32	.27	.17

*Code represent for the environments (combination of location-year). The initial letters in codes are stand for first letter of locations name and numbers of 11, 12 and 13 in environments codes are stand for 2011, 2012 and 2013 cropping seasons. K: Kermanshah; M: Maragheh; Q: Qamloo; U: Uromieh; A: Ardabil; S: Shirvan and I: Ilam. MC: moderate cold; C: cold; W: moderate warm; this classification is based on the regions of Iran, which the locations are located. The locations of Maragheh, Qamloo, Uromieh, Ardabil and Shirvan are located in highland rainfed areas of Iran with winter temperature less than <5 °C, while Kermanshah location is located in moderate cold region of Iran with winter temperature between 5 and 10 °C and Ilam location is located in the warm region of Iran with winter temperature more than 8 °C.

EI: environmental index; YLD: mean yield; DTH: days to heading; DTM: days to maturity; PLH: plant height; TKW: 1000-kernel weight.

Table 5. Pearson correlation coefficients between environmental components of mean yield and environmental index.

Environmental components	EI	r_1	r_2	r_3
r_1	−.118			
r_2	−.098	−.262		
r_3	−.568**	.298	.049	
r_4	.085	.535**	−.168	−.044

**Significant at $p = .01$.

between the r_1 and r_4 indicating positive trend between flowering date and grain weight in tested environments. This leads to the conclusion that the impact on yield of this environmental component is associated with the magnitude of the genotypic component. In moderate and warm locations the r_1 component which supported the process of flowering was larger in absolute size than r_2, r_3, and r_4 components, while in cold locations the r_3 component which represents the plant stature was larger than other three components (Table 4). These results, however, indicate the importance of early flowering (r_1) to escape from drought and heat terminal stresses in moderate and warm locations than cold locations. The highest mean yield was obtained in warm (2191 kg ha^{-1}) followed by moderate (1658 kg ha^{-1}) and cold (1388 kg ha^{-1}) locations. In cold locations, the r4 component which supported the process of kernel weight was greater in absolute size than other three components.

Analysis of mean yields in test locations differing in winter temperature (consisting of December, January and February months) revealed a significantly positive association between the yield potential in moderate and warm locations (Figure 2). Therefore, it would be desirable to combine high yield with heat tolerance so that the varieties could be used in both locations with differing winter temperatures. No significant relationship was observed between genotypic mean yield in cold location with those in warm and moderate locations.

Discussion

Environmental variations seemed to be of importance in determining performance, and therefore, evaluation based on several years and locations is a necessary strategy to be pursued in the breeding program (Yue et al., 1997). Year-to-year climatic variation has a great impact on the degree of stress experienced by crops, hence the use of testing environments to represent stressed target environments. Since each environment consists of a combination of various factors, in other words, cold and drought stresses that influence adaptation and stability performance, it is difficult to specify all the differences between environments in relation to these factors. (Chapman et al., 1997). High yield of durum wheat under fluctuation environments requires not only high yield in a unique environment, but also the stability of relatively high yield across varied environments. The data from this experiment revealed a trend toward improved yield stability, as evidenced by the correlation of kernel weight and PLH with stability variance of yield. This indicates that the key strategies for yield stability improvement are most likely to be the kernel weight and PLH under rainfed conditions. High yielding breeding lines at warm and moderate cold locations had good tolerance ability throughout the whole stress season especially to terminal drought and heat stresses. The cold stress was more dominant than drought stress at cold locations, as none of the breeding lines did not surpass the bread wheat old variety (a beard wheat cultivar with good tolerance to cold stress and widely adapted to highland rainfed regions of Iran) indicating no genetic gain for cold tolerance in breeding lines compared to this popular cultivar.

Mean yield of five top yielding breeding lines at warm location was 2469 kg ha^{-1} and at moderate location was 1930 kg ha^{-1} and top old variety (G25) at warm and moderate cold locations produced 1884 and 1624 kg ha^{-1}, respectively. These results indicated yield improvements equal to 40 and 18% for first five top yielding breeding

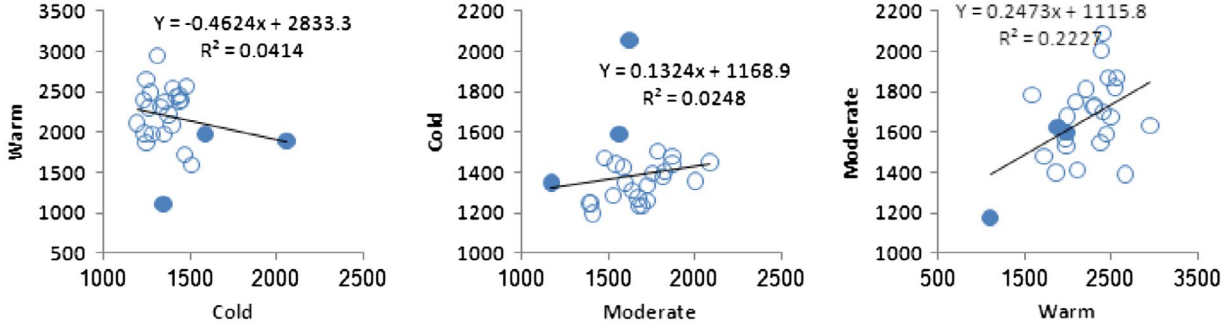

Figure 2. Relationships among responses of genotypic mean yields (kg ha^{-1}) at locations differing in winter temperature. Open circles: breeding lines and new cultivar; solid circles: old cultivars.

lines relative to top old variety (G25) in warm and moderate cold locations, respectively, while under cold stress conditions no yield improvement for breeding lines was observed. This result indicates that the cold stress is the most limiting factor than drought for durum production under highland rainfed conditions of Iran (Mohammadi et al., 2014). This supports this idea that positive genetic gains in breeding programs more limited in environments with more stresses. This agrees with the findings of Ceccarelli (1996), Munoz et al. (1998), Donmez et al. (2001), Voltas et al. (2002) and Pswarayi et al. (2008). However, achieving genetic gains in yield in stressful environments has been recognized to be a difficult challenge for plant breeders, while progress in yield gains has been much higher in non-stressed environments (Richards et al., 2002; Villegas et al., 2007).

The negative v_1 values for all genotypes and its values larger than v_2, v_3, and v_4 in absolute size suggests the genotypes showed more divergent responses to the changes in environmental effects influencing flowering than the other components for yield productivity. Variation in v_1 values among the genotypes was greatest, followed by v_3, v_2, and v_4, suggesting that genotypic differences in response to rainfed conditions associated more with flowering than other genotypic components. Most genotypes were more sensitive to a unit change of the first environmental component supporting flowering than the other components. These results, accompanied by the fact that the estimates of r_1 were larger and more variable than those of r_2, r_3, and r_4 over the environments, lead to the conclusion that the flowering time played a more important role in GE interactions of grain yield than other traits in durum wheat.

Positive association ($p < .05$) between mean yield and stability variance indicated a positive trend between high yielding and stability performance in genetic materials. This relation supports that genotype's performance responds in a consistent fashion to changes in the environments resulting in dynamic stability in genetic materials. This is in agreement with earlier reports on the correlations between mean yield and stability variance (Cross, 1977; Eagles et al., 1977; Eberhart & Russell, 1966; Mühleisen et al., 2014). Stability in grain yield under stress environments could be provided by a better ability of compensation in yield components (Matsuo, 1975). Many researchers have shown that grain yield of wheat depends on several grain yield components in different crop species (Aggarwal et al., 1987; Bansal & Sinha, 1991; Khanna-Chopra & Viswanathan, 1999; Klomsa-ard et al., 2013). This study indicated that kernel weight and flowering provided stability to the breeding lines G3 and G13, whereas plant stature contributed towards the stability of breeding lines G9, G10, G5, and G18.

Our findings clearly indicated that breeding lines as a group were more heat and drought tolerant than old varieties and, in contrast, old varieties were more cold tolerant than breeding lines. The results also clearly indicated that higher grain yields are associated with higher kernel weight (v_4), which resulted from early flowering (v_1), and so more emphasis should be given to these traits for the improvement of yield in durum wheat under rainfed conditions of Iran. Selection for high value kernel weight resulting from early flowering will enhance yield stability in breeding lines which is a major step towards facilitating the increasing abiotic stress expected from the predicted climate change. In conclusion, path analysis provided a useful picture for understanding GE interaction and grain yield components compensation in rainfed durum wheat, and hence these traits may be taken as indices of selection purposes. The responses of the individual genotypes did not reveal a common structure that would explain genotypic differences in tolerance to environmental stresses. However, the determination of genotypic strategies that maximize tolerance to environmental stresses deserves further research.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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