J. Agric. Sci. Technol. (2001) Vol. 3: 43-49

Genetic Properties of Drought Resistance Indices

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ABSTRACT

Inheritance of several yield-based drought resistance indices was studied by a half-diallel method using seven winter wheat varieties. The parental lines were such chosen as to represent a broad range of drought stress resistance. The experiment was conducted in a split-plot design at the research farm, Faculty of Agriculture, Zanjan University, Iran, in 1998. Irrigated vs. rainfed regimes were considered as the main plots. The F_1 hybrids and parental varieties constituted the subplots. From the grain yield data, some drought resistance indices such as geometric mean productivity (GMP), mean productivity (MP), standard superiority measure (SP), stress susceptibility index (SSI), stress tolerance index (STI), superiority measure (P), and tolerance (TOL) were calculated. Genetic components of variance and heritabilities were estimated using Gardner and Eberhart's Method 3, Model II. Significant differences among parents and F_1s were observed for all indices except for SSI and TOL. Significant general combining abilities (GCA) were obtained for GMP, MP, P, SP, STI, and TOL but not for SSI. Therefore, except for SSI, other indices could be regarded as heritable. The specific combining ability (SCA) effects were also highly significant for GMP, MP, P, SP, and STI. However, additive variances were more important than dominance ones. Narrow-sense heritability estimates were very low for SSI, low for TOL, but moderate for GMP, MP, P. SP, and STI. Thus selection based on the latter indices could be more promising than on SSI and TOL. It seems that SP and STI might be better yield-based drought resistance indices to be employed in plant breeding programs, because of their moderate narrow-sense heritabilities and the inherent ability of selecting high yielding genotypes in either stressed or non-stressed conditions.

Keywords: Combining ability, Diallel, Drought resistance, Genetic properties, Wheat.

INTRODUCTION

In semiarid regions, dry farming is often practiced for wheat production. In these areas, precipitation being low and irregular, water deficit becomes the most important limitation to crop, including wheat production (5) and therefore breeding for drought resistant wheat is an important task and objective in these semiarid regions (2,14). On the other hand, good selection criteria are needed to identify drought resistant genotypes.

Levitt (15) noted that drought resistance can be defined as: the water stress necessary to produce a specific plastic strain. The choice of parameters used to quantify the level of stress and the intensity of strain are somewhat arbitrary. Drought tolerance or resistance in native plant species is often defined as survival, but in corp species it must be defined in terms of productivity (18).

Several indices have been utilized to evaluate genotypes for drought resistance based on grain yield such as geometric mean productivity (7), mean productivity (20),

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standard superiority measure (9), stress susceptibility index (8), stress tolerance index (7), superiority measure (16), and tolerance (20). According to Richards (19), selection for yield automatically integrates all the known and unknown factors that contribute to drought resistance. These indices have been compared by some researchers (7,19), but their genetic properties and consistencies have not been studied. This could be one of the main reasons for the lack of significant progress in developing drought resistant plants.

Heritability of a quantitative trait such as grain yield directly determines the efficiency of selection for that trait. Traits with high heritability are easier to be improved than those with lower heritability. Most cultivars in self-pollinated crops, such as wheat, are pure lines produced by selection methods following hybridization. Thus, selection is mainly based on the presence of additive genetic variance in these methods. Higher genetic advances could be realized when employing characters with higher rather than lower narrow-sense heritability. The objective of this study was, to estimate the genetic parameters and especially the narrow sense heritability of the important yield-based drought resistance indices using diallel method.

MATERIALS AND METHODS

A half- diallel cross of 7 winter wheat lines was made in 1997 at the research farm, Faculty of Agriculture, Zanjan University, Iran (Latitude 36^0 41´; Altitude 1620 m). For each cross, more than 600 F_1 seeds were produced in order to be able to evaluate F_1 hybrids for their agronomic performance. The parents were: (1) P_{8-5}/Kavkaz, (2) 4839 Sarakhs, (3) Ska/Aurifen, (4) Sabalan, (5) Sardari, (6) MV_{17}, and (7) Alamoot. These cultivars represented a broad range of response to drought stress (11).

The experiment, on a silty-loam soil was conducted in October, 1997. A split-plot design, arranged in 3 randomized complete blocks, was used. Irrigated (non-stress) and rainfed (stress) regimes were considered as main plots. Twenty eight genotypes, including 21 F_1 hybrids plus 7 parental lines represented the subplots. Each subplot consisted of two 98 cm long, 18 cm apart rows. Seventy kgs of N/ha and 150 kgs of P_20_5 /ha were applied to the soil prior to planting. From mid-May 1998 (anthesis) until the end of growing season only the non-stressed plots were irrigated. This was when tensiometers indicated a soil water suction of 50 KPa. At each irrigation, about 30-40 mm of water was applied to the non-stressed plots, totaling to 200mm of irrigation waterduring the whole period. After harvest the grain yield was recorded for every subplot. The seven drought resistance indices were calculated for every genotype using the corresponding non-stressed and stressed subplots in each block. The resulting data were analyzed as obtained from a randomized complete block design.

The drought tolerance indices were calculated as follows:

1)Stress Susceptibility Index (8):

$SSI=\frac{1-Y_s/Y_p}{SI}$ where: SI = Stress Intensity $= 1-\bar{Y}_s/\bar{Y}_p$

2) Mean Productivity (20): $MP=\frac{Y_s+Y_p}{2}$

3) Tolarance (20): TOL = Y_p- Y_s

4) Superiority Measure (16):

$$P_i=(\sum_{j=1}^{n}(X_{ij}-M_j)^2)/2n$$

5) Standard Superiority Measure (9): SP = Similar to P but uses standardized data

6) Geometric Mean Productivity (7):

$GMP=\sqrt{(Y_s)(Y_p)}$.

7) Stress Tolerance Index (7):

$STI=\frac{(Y_s)(Y_p)}{(\bar{Y}_p)^2}$, where:

Y_p = yield of a given genotype in a non-stressd environment.

Y_s = yield of a genotype in drought stressed environment.

$\bar{Y}_p$= mean yield in non-stressed environment.

$\overline{Y}_s$ = mean yield in drought stressed environment.
n = number of environments.
X_{ij} = grain yield of ith genotype at the jth environment, and
M_j = grain yield of the genotype with maximum yield at jth environment.

Genetic components of variance and heritabilities were estimated using Gardner and Eberhart's Method 3, Model II (10). The data were analyzed using a computer package developed by Burow and Coors(3).

RESULTS AND DISCUSSION

The growing season rainfall in 1997-1998 was 306 mm, very close to the long term mean (311 mm for a 30 year period), thus it was considered a typical season in the study area. According to Begg and Turner (1) drought resistance could be categorized based on the growth stage in which it occurs, e.g. early season (pre-anthesis), midseason (flowering), late season (grain filling) or intermittent. At the experimental site the drought is mainly of the mid or late season type and usually occurs during flowering and/or grain filling period.

In 1997, there was enough rainfall until mid-May, corresponding to anthesis period, tensiometers indicating no considerable soil moisture deficit. Up to this time, therefore, non-stressed plots did not need to be and were not irrigated. Afterwards no effective rainfall occured in the area, thus during grain filling period, the non-irrigated plots were under drought stress with an intensity (SI) of 0.45.

Analysis of variance for various yield-based drought tolerance indices for parental lines and their F_1 hybrids is shown in Table 1. There were significant differences among parents and F_1s for all indices except for SSI and TOL. Initial studies, have also indicated the existence of variation for drought response among the parents under study (11). F_1s' vs. parents' mean squares were not significant for any of the drought indices indicating no average heterosis for these criteria. Partitioning of F_1 sum of squares into general and specific combining abilities (GCA and SCA, respectively) resulted in significant GCA effects for GMP, MP, P, SP, STI, and TOL but not for SSI. Therefore, except for SSI, other indices could be regarded as heritable. The SCA effect was also highly significant for GMP, MP, P, SP, and STI. This suggests that both additive and non-additive gene effects were involved in the expression of these indices. The additive and dominance genetic variances were estimated by Method 3, Model II of Gardner and Eberhart (10), Table 2. Additive variances were more important than non-additive (dominance) ones for these indices. The ad-

Table 1. Pertinent mean squares of seven winter wheat lines and their F_1 diallel hybrids for different yield-based drought tolerance indices grown at Zanjan University,research farm, Zanjan, Iran, in 1997-1998.

Source of Variation	Df	GMP	MP	P $\times 10^{-4}$	SP	SSI $\times 10^3$	STI $\times 10^3$	TOL
Reps	2	585	475	598	10.36	1	14	365
Genotypes	27	1448 **	1554 **	599 **	7.47 **	48	89 **	1080
Parents	6	1483 **	1462 **	532 **	8.28 **	91	87 **	1107
F_1s vs Parents	1	347	364	88	1.71	9	23	45
F_1s	20	1492 **	1641 **	645 **	7.51 **	37	94 **	1123
Error 1	54	257	238	88	1.11	75	17	652
GCA	6	3107 *	3439 *	1232 *	14.56 *	45	197 *	2226 *
SCA	14	800 **	871 **	393 **	4.49 **	34	49 **	650
Error 2	40	255	224	83	0.98	89	17	705

* and **: Significant at 0.05 and 0.01 probability levels, respectively. GCA : general combining ability. SCA: specific combining ability. GMP: geometric mean productivity. MP: mean productivity. P: superiority measure. SP: standard superiority measure. SSI: stress susceptibility index. STI: stress tolerance index. TOL: tolerance.

[DOR: 20.1001.1.16807073.2001.3.1.5.8]

Table2. Estimates of additive genetic variance (σ^2_A), non-additive genetic variance (σ^2_D),phenotypic variance on a plot mean basis (σ^2_{ph}), broad-sense heritability (h^2_B), and narrow-sense heritability (σ^2_N), for different drought resistance indices from wheat dialled grown at Zanjan University, research farm, Zanjan, Iran, in 1997-1998.

Component	GMP	MP	P	SP	SSI	STI	TOL
σ^2_A	307.5 ± 242.5	342.4 ± 368.3	1118797 ± 968926	1.34 ± 1.14	0.001 ± 0.004	0.020 ± 0.015	210.0 ± 174.4
σ^2_D	181.7 ± 102.6	215.5 ± 111.0	1032716 ± 498999	1.17 ± 0.57	0	0.011 ± 0.006	0
σ^2_{ph}	744.5 ± 269.5	782.4 ± 294.7	2983357 ± 1105630	3.49 ± 1.30	0.089 ± 0.022	0.048 ± 0.017	915.0 ± 254.5
h^2_B (%)	66 ± 36	71 ± 38	72 ± 38	72 ± 38	1.6 ± 0.09	64 ± 35	23 ± 28
h^2_N (%)	41 ± 31	44 ± 33	38 ± 31	38 ± 31	1.6 ± 0.04	41 ± 31	23 ± 25

GCA: general combining ability. SCA: specific combining ability. GMP: geometric mean productivity. MP: mean productivity. P: superiority measure. SP: standard superiority measure. SSI: stress susceptibility index. STI: stress tolerance index. TOL: tolerance.

ditive variance is the main determinant of the observable genetic properties of the population and its response to selection (6). The conspicuity of additive inheritance indicates the possibility of improving drought tolerance through breeding programs and by using the heritable indices considered in this study.

Broad and narrow-sense heritability estimates are presented in Table 2. Estimates were very low for SSI, low for TOL, and moderate for GMP, MP, P, SP, and STI. Genetic advances are directly related to the magnitude of narrow-sense heritabilities (13). Thus, it seems that selection for drought resistance based on GMP, MP, P, SP, and STI will be more fruitful than based on SSI and TOL.

For a trait or parameter to be useful in the selection of superior genotypes, it must be heritable as well as repeatable across samples of the environments (12). In this experiment SSI exhibited negligible heritability, and TOL was less heritable than GMP, MP, P, SP, and STI, as determined by narrow-sense heritability estimates (Table 2). Also, through a good drought tolerance index one should be able to identify superior genotypes in both drought prone and favorable environments.

Table 3 shows the parent lines, means for grain yield, in stressed (Y_s) and non-stressed (Y_p) environments, and drought resistance indices. The ranks of parents for GMP, MP, P, SP, and STI were identical and almost corresponded to the ranking for Y_s and Y_p. On the other hand, TOL and SSI exhibited rankings different than the other indices. Correlation coefficients, calculated from the data obtained for parental lines, are presented in Table 4. GMP, MP, P, SP, and STI were highly correlated with each other as well as with Y_s and Y_p. Thus, through these indices it is possible to distinguish high yielding genotypes in either condition. However, TOL and SSI were not strongly correlated with the above mentioned indices. The correlation coefficient of SSI with Y_s was high and negative while that of TOL with Y_p was high and positive. The correlation coefficients of TOL with Y_s and that of SSI with Y_p were negligible. According to Fernandez (7), genotypes can be categorized into four groups based on their performance in stressed and non-stressed environments: genotypes which express uniform superiority in both conditions (Group A); genotypes that perform favorably only in non-stressed environments (Group B); genotypes which yield relatively higher only in stressed environments (Group C); and genotypes that perform poorly in either condition (Group D). Fernandez (7) stated that an optimal selection criterion should be to distinguish Group A from the other three. He compared effectiveness of several stress tolerance criteria (GMP, MP, SSI, STI, TOL) and concluded that MP, SSI and TOL failed to identify

Table 3. Means of parental lines under study, for drought resistance indices and grain yield in strassed and non-stressed environments.

Parents Codes	GMP	MP	P	SP	SSI	STI	TOL	Y_s	Y_p
1	360.77	370.19	18221.54	2.4057	0.7961	0.4921	164.35	288.02	452.37
2	426.72	439.46	8566.49	1.1995	0.8516	0.6926	209.93	334.50	544.43
3	330.41	348.12	22923.69	3.4809	1.0126	0.4239	211.56	242.34	453.86
4	402.29	436.68	9619.75	1.7578	1.2360	0.6237	336.90	268.24	605.13
5	442.25	461.18	5334.28	0.7086	0.9431	0.7440	256.18	333.09	589.27
6	258.28	283.59	36708.59	5.6836	1.2385	0.2524	228.24	169.47	397.71
7	354.24	370.23	17195.50	2.4223	0.9457	0.4799	204.99	267.73	472.72
$LSD_{0.05}$	74.41	71.66	12311.50	1.7271	0.4483	0.2134	118.50	86.46	99.06

GMP: geometric mean productivity. MP: mean productivity. P: superiority measure. SP: standard superiority measure. SSI: stress susceptibility index. STI: stress tolerance index. TOL: tolerance. Y_s = yield in stressed environment Y_p : yield in non-stressed environment.

Table 4. Correlation coefficients among drought resistance indices and grain yield in stressed and non-stressed environments.

	GMP	MP	P	SP	SSI	STI	TOL	Y_s	Y_p
GMP	1.000								
MP	0.988	1.000							
P	-0.919	-0.935	1.000						
SP	-0.944	-0.931	0.963	1.000					
SSI	-0.350	-0.205	0.214	0.361	1.000				
STI	0.988	0.980	-0.898	-0.901	-0.324	1.000			
TOL	0.280	0.425	-0.407	-0.251	0.786	0.305	1.000		
Y_s	0.930	0.863	-0.801	-0.884	-0.664	0.908	-0.092	1.000	
Y_p	0.869	0.935	-0.879	-0.814	0.150	0.873	0.718	0.628	1.000

GMP: geometric mean productivity. MP: mean productivity. P: superiority measure. SP: standard superiority measure. SSI: stress susceptibility index. STI: stress tolerance index. TOL: tolerance. Y_s : yield in stressed environment. Y_p : yield in non-stressed environment.

genotypes with both high yield and stress tolerance potentials, whereas through STI, genotypes with these attributes could be identified. Clark *et al.*(4) assessed drought tolerance indices, P, SP and SSI using 25 hexaploid and 16 tetraploid wheat genotypes grown under dry *Vs*. irrigated conditions. They observed year-to-year variation in SSI within genotypes as well as changes in genotype ranking within years. Also, SSI did not differentiate between potentially drought tolerant genotypes and those of low yield potential from other causes, whereas P was correlated with mean yield in both hexaploid and tetraploid groups. However, P was strongly influenced by high yield environments, but standardization of the yield data resolved this problem. Several studies conducted in Iran measuring drought response of improved wheat varieties (11), pure lines derived from winter wheat landraces (21), and spring wheat landraces (17) showed that indices such as SSI and TOL were not efficient to be used in selecting genotypes with high yield capacity in either stressed or non-stressed environments. In contrast, STI and SP were identified as efficient indices. SSI and TOL indices only assess the plasticities of the genotypes under study, whereas a variety may rank first in both environments but still have higher SSI and TOL than other varieties.

In conclusion, based on our studies, it seemed that SSI and TOL were not useful indices to select for drought tolerant genotypes in plant breeding programs, because, SSI exhibited negligible heritability and TOL was less heritable than other indices usually not identifying genotypes with both high yield and drought tolerance characteristics. On the other hand indices like SP and STI were moderately heritable and are usually able to select high yielding genotypes in both environments. Therefore, based on the results obtained in this and previous studies (4,7,11,17,21), STI and SP seem to be useful yield-based drought tolerance indices to be employed in plant breeding programs for wheat.

The consistency or repeatability of the heritable indices could not be studied at this stage. To test this, the experiments should be repeated at different locations and years with different drought intensity levels.

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مشخصات ژنتیکی شاخص های مقاومت به خشکی

چکیده

نحوه توارث چندین معیار مقاومت به خشکی مبتنی بر عملکرد به روش نیمه دیالل با استفاده از هفت واریته گندم پاییزه مورد بررسی قرار گرفت. لاین‌های والدی به طور تصادفی از دامنه وسیعی از مقاومت به خشکی انتخاب شدند. آزمایش در سال زراعی ۷۷-۱۳۷۶ به صورت اسپلیت پلات با طرح پایه بلوک‌های کامل تصادفی در مزرعه تحقیقاتی دانشکده کشاورزی دانشگاه زنجان انجام شد. رژیم‌های آبیاری و بارندگی به عنوان دو کرت اصلی در نظر گرفته شدند. هیبریدهای F_1 و واریته‌های والدی درکرت‌های فرعی توزیع شدند. ازداده‌های مربوط به عملکرد شاخص‌های مقاومت به خشکی مانند میانگین هندسی عملکرد (GMP) ، میانگین عملکرد(MP) ، معیار برتری استاندارد (SP) ، شاخص حساسیت به تنش (SSI) ، شاخص تحمل تنش (STI) ، معیار برتری (P) و تحمل (TOL) محاسبه شدند. اجزای ژنتیکی واریانس و وراثت پذیری‌ها با مدلII روش ۳ گاردنر و ابرهارت برآورد شدند. برای تمام شاخص‌ها بجزSSI وTOL بین والدین و بین F_1 ها اختلاف معنی دار مشاهده شد. برایGMP، MP، P، SP، STI، TOL قابلیت ترکیب عمومی معنی داری بدست آمد، در حالیکه قابلیت ترکیب عمومی برایSSI معنی دار نبود. بنابراین به استثنای SSI دیگر شاخص‌ها می‌توانند وراثت پذیر در نظر گرفته شوند. واریانس‌های قابلیت ترکیب خصوصی نیز برایGMP ، MP، P، SP وSTI معنی دار بودند. با وجود این، واریانس‌های افزایشی مهمتر از واریانس‌های غالبیت بودند. برآوردهای وراثت پذیری خصوصی برای SSI بسیار پایین، برایTOL پایین و برای GPM، MP، P، SP، وSTI متوسط بودند. بنابراین، گزینش براساس شاخص‌های اخیر موثرتر از SSI وTOL خواهد بود. به نظر می رسد که SP و STI به علت داشتن وراثت پذیری خصوصی متوسط و توانایی گزینش ژنوتیپ‌های با عملکرد بالا در هر دو محیط واجد و فاقد تنش می‌توانند شاخص‌های مقاومت به خشکی مناسبی در برنامه‌های اصلاح نباتات کاربردی باشند.

[DOR: 20.1001.1.16807073.2001.3.1.5.8]