HERITABILITY OF WATERLOGGING TOLERANCE IN WHEAT
(*Triticum aestivum* L.)

Aydin UNAY[1*], Serap SIMSEK[2]

[1]*Aydın Adnan Menderes University, Faculty of Agriculture, Department of Field Crops, Aydın, TURKEY*
[2]*Aydın Adnan Menderes University, Institute of Natural and Applied Sci., Aydın, TURKEY*
*Corresponding author: aunay@adu.edu.tr

ABSTRACT

One of the most important objectives of wheat breeding is tolerance to waterlogging stress in high rainfall during critical stages and poorly drained areas. This study was conducted to estimate heritability parameters of characters associated with waterlogging tolerance by 5 x 5 complete diallel analysis in wheat (*Triticum aestivum* L.). The genetic material was evaluated for SPAD, CCI, MTS, Fe root and shoot contents, Mn root and shoot contents under waterlogging during Zadox Growing Stage 12 and 31 for 10 days and untreated conditions. The differences among genotypes for most of the studied characters were found to be significant under both treatments. The heritability of observed characters was controlled by both additive and dominance genes under two treatments. Also, significant reciprocals differences depend on items (c) and (d) showed the presence of maternal effects for observed characters. Consequently, the determination of maternal parents was very important for waterlogging tolerance. Moderately broad sense heritability (h^2_b) and low magnitude narrow-sense heritability (h^2_n) values indicated that non-additive gene effects were more considerable on the inheritance of studied characters. Therefore, the selection in later generations was recommended for waterlogging tolerant in the wheat breeding program.

Keywords: Diallel, heritability, maternal effect, waterlogging, wheat

INTRODUCTION

Waterlogging is the leading cause of yield losses in the saturated soils with poor drainage, and its prevalence is expected to increase by global climatic change (Parry et al., 2007). At present, waterlogging is a factor limiting production in humid, temperate regions, excessive rainfall resulting in waterlogged soils, and can reduce the wheat yields by 20 to 25 % in the top 10 wheat producers (Setter et al., 1999; Bailey-Serres and Voesenek, 2008). It is shown that wheat is one of the most intolerant crops to soil waterlogging (Thompson et al., 1992). It is recognizable that the percentage of drainage systems per cultivated area for Turkey has been decreased (Valipour, 2014). In Aydin and all wheat area of the coastal zone of Turkey, especially heavy rains of January and February damages winter wheat at the tillering stage (Musgrave, 1994).

In waterlogged soils, gas-filled pores are eliminated, and gas exchange between soil and air are limited within a few hours following flooding (Ponnamperuma, 1972). Soil redox potentials decreased sharply and shoot concentrations of Mn and Fe increased above critical toxicity concentrations after waterlogging in alkali soil (Setter et al., 1989; Sharma and Swarup, 1989; Stieger and Feller, 1994; Setter and Waters, 2003). However, N uptake and redistribution of N within the shoot are restricted, early senescence of leaves is obtained in flooded wheat (Fageria, 2001), and waterlogging causes leaf chlorosis due to chlorophyll degradation (Li et al., 2008).

Waterlogging tolerance of wheat cultivars is a very important breeding objective in high rainfall environments. The direct selection for the yield of wheat may not be effective under the waterlogging conditions, because the inheritance of yield is very low, and waterlogging tolerance is a complex character which is related to many morphological and physiological traits of wheat (Collaku and Harrison, 2005). In the studies evaluating response to waterlogging, varietal differences of wheat were reported (Huang et al., 1994; Sayre et al., 1994; Thomson et al., 1992; Yavas et al., 2012; Ozseven and Genctan, 2018). It was reported that genes controlling waterlogging tolerance of wheat are in all the group 5 chromosomes, especially 5D (Poysa, 1984). The number of green leaves on the main stem associated waterlogging tolerance was controlled by a single dominant gene (Cao et al., 1992) whereas Boru (1996) reported a total of four major genes involved for leaf chlorosis in waterlogging tolerance.

Previous studies on the inheritance of wheat waterlogging tolerance are scarce and of conflict results, probably due to different characters based on waterlogging, genotypes used and/or the environmental conditions. There are many questions about gene number of controls tolerance to waterlogging, gene action and maternal or reciprocal effect. Studies are usually focused on the inheritance of leaf chlorosis in terms of waterlogging tolerance in wheat. When maternal effects on waterlogging traits are not neglected, the most effective methods are complete diallel analysis. Therefore, specific objectives of this study were to estimate the suitable selection criteria, genetic information and effective wheat breeding programs in waterlogging tolerance of wheat.

MATERIALS AND METHODS

Five selected wheat varieties (*Triticum aestivum* L.) from previous studies (Pamukova 97, Hanlı and Beskopru) and standard for the coastal zone of Aegean Region (Stendal and Anopa) were mated in a 5 x 5 diallel design including reciprocals. The experiment consisted of two separate sets; control and waterlogging condition in 2012. Separate trials were conducted for control and waterlogging stress as applied by Betran et al. (2003), Rainey and Griffiths (2005), El-Satar (2017) and Tawfik and El-Mouhamady (2019) in diallel studies for different stress conditions. The design of experiments was Randomized Complete Block Design with three replications. The five parents and 20 F_1 populations were sown in plastic tanks (80 cm x 38 cm x 31 cm) filled with soil which waterlogging occurs regularly in previous years for waterlogging treatments and standard soil for control. The soils of waterlogging pots compacted by 1-4 mm/h infiltration capacity. The waterlogged pots were undrained and plants were waterlogged by maintaining water 5 cm above the soil surface during Zadox Growing Stage 12 and 31 for 10 days. Control treatments were maintained at the field capacity using soil moisture sensor (Decagon EC-5; Decagon Devices, Pulman, WA) to achieve optimum plant growth. The experimental soil was mixed with 90 kg N ha^{-1}, 90 kg P_2O_5 ha^{-1} and 90 kg K_2O ha^{-1} fertilizer before sowing, and 70 kg N ha^{-1} fertilizer was applied at the tillering stage. Each pot consisted of 64 plants in double rows.

Chlorophyll concentration (SPAD) and chlorophyll content index (CCI) of the uppermost fully expanded leaves was determined for 10 plants per pot at ten days week after the release of the waterlogging stress, using a Minolta SPAD-502 chlorophyll meter and Apogee-CCM 200, respectively. After them, sampled same 10 plants were removed with roots, and the uppermost fully expanded leaves were used for membrane thermostability index (Blum and Ebercon 1981). Fe and Mn content were determined separately in root and shoot of the wheat plant to determine the phytotoxic concentrations (Reuter et al., 1997).

A separate analysis was performed for each treatment. Data obtained from reciprocal hybrids and parental genotypes for each character were evaluated according to Jinks and Hayman (1953) diallel method I. TARPOPGEN statistical package program (Ozcan and Acıkgoz, 1999) was used for statistical analysis.

RESULTS AND DISCUSSION

It was revealed that waterlogging tolerance of crops was highly heritable (Cao et al., 1995; Boru, 1996) and there was sufficient genetic variability for waterlogging traits (Zhou et al., 2007; Amin et al., 2014). In our study, significant differences among genotypes of diallel mating design in all studied characters except MTS and Fe (shoot) for control and, CCI and Fe (shoot) for waterlogging conditions are pre-requisite for performing the diallel analysis for estimating the inheritance (Table 1). Also, non-significant genotypes mean squares of Fe (shoot) in both conditions were considerable.

The most significant a and b indicated that both additive and dominance genes were responsible for the heritability of observed characters in control and waterlogging conditions (Table 1). Similarly, both additive and non-additive gene effects govern the control of waterlogging tolerance by Cao et al. (1994) in wheat; Zhou et al. (2004) in barley; Anjos e Silva et al. (2006) and Zaidi et al. (2010) in maize. In contrast, waterlogging tolerance based on leaf chlorosis is controlled by additive gene effects in wheat (Boru et al., 2001; Zhou et al., 2007).

Presence of maternal effects (c) was also revealed by significant values of c item for all studied characters under control and waterlogging except CCI and Mn (root) in waterlogging conditions (Table 1). Similarly, reciprocal effects (d) were found to be significant for all characters except CCI and Fe (shoot) in control treatments and SPAD, MTS and Fe (shoot) in waterlogging conditions. Boru et al. (2001) revealed that the inheritance of leaf chlorosis in waterlogging tolerance did not influence by maternal effects or non-significant differences could be observed between reciprocal crosses. On the contrary, our results demonstrated the presence of maternal and reciprocal effects for chlorophyll content traits and Fe and Mn contents. In other words, the expression of waterlogging traits of F_1 can be controlled by both genetic and cytoplasmic factors.

Estimates of genetic components were found to be non-significant for studied characters in F_1's under control and waterlogging conditions (Table 2). The dominance genetic component of variation (H_1) was higher than the additive component (D) for all characteristics under both conditions except Fe (shoot) in waterlogging treatments. Dominance gene effects indicated that selection in later generations may be efficient for studied characters. The differences between additive genes and dominant genes (D-H_1) were found to be negative for all traits except Fe (root) in waterlogging stress.

Table 1. Mean squares of sources of variations for characteristics according to Hayman's model.

S.O.V.	df	SPAD	CCI	MTS	Fe (root)	Fe (shoot)	Mn (root)	Mn (shoot)
					Control			
Gen.	24	19.10**	16.11**	72.50	311.10*	125.17	4.54*	13.15*
a	4	73.1*	58.2**	333.3**	949696.5	469607.9**	9754.1**	2698.0*
b	10	34.7**	22.8**	150.2	801637.7**	396925.2	12165.9**	6695.0**
b_1	1	31.0	37.5	226.1	715716.0	803712.3	27159.0	18036.5*
b_2	4	65.4**	25.8*	106.2	474737.5*	556063.8	14118.8**	11278.0*
b_3	5	10.8*	17.5	170.2*	1080342.2	188256.9	7604.9	760.3*
c	4	120.1**	140.7**	376.3*	1421765.6**	536953.2**	30606.0**	2995.6**
d	6	42.7**	22.7	146.6*	816165.1**	169503.3	7388.5*	829.1*
Error	48	6.12	8.08	50.89	162.34	133.96	2.26	7.42
					Waterlogging			
Gen.	24	16.04**	3.46	67.75 *	390.05*	267.52	5.92**	5.58*
a	4	83.5**	22.9**	202.0*	1464591.7**	1123746.8**	11409.6*	1977.9**
b	10	52.8**	21.5*	227.9**	1326381.0**	689683.7**	32681.5**	1236.7*
b_1	1	112.3*	63.7*	335.6	2542749.2	469225.0	140400.1*	918.1
b_2	4	41.1*	10.4	241.8*	1706112.1*	1234126.3**	31298.7**	2195.6*
b_3	5	50.3*	21.9	195.2**	779322.5*	298221.3	12244.1*	533.3
c	4	50.7**	6.6	372.3**	1637550.4**	1501805.0*	3292.6	4358.9**
d	6	14.9	38.0**	50.3	401917.7*	310484.7	6787.1*	417.2
Error	48	6.85	2.54	32.22	200.05	199.65	1.77	2.96

*, **; significant at 5% and 1% probability level, respectively.

Table 2. Estimates of genetic parameters and ratios for characteristics.

	SPAD	CCI	MTS	Fe (root)	Fe (shoot)	Mn (root)	Mn (shoot)
				Control			
E	2.50	2.65	19.25	51.80	50.23	746.64	284.66
D	0.47	2.41	18.50	11.80	26.04	731.73	2432.90
F	3.42	3.44	54.59	-11.80	40.35	721.21	3039.60
H_1	23.29	27.74	212.23	59.50	58.10	9257.40	4123.00
H_2	12.01	19.53	143.60	60.40	37.96	7682.50	3173.70
$D-H_1$	-22.82	-25.33	-193.73	-47.80	-32.60	-8525.70	-1690.10
h^2	0.60	0.97	3.76	17.60	25.80	1453.50	1100.40
$(H_1/D)^{1/2}$	7.016	3.393	3.39	2.28	1.49	3.56	1.30
$H_2/4H_1$	0.129	0.176	0.17	0.26	0.16	0.21	0.19
KD/KR	3.105	1.532	2.54	1.00	3.16	1.32	2.85
h^2/H_2	0.050	0.050	0.03	0.03	0.07	0.19	0.35
h^2_{BS}	0.626	0.576	0.46	0.48	0.40	0.52	0.38
h^2_{NS}	0.016	0.065	0.07	0.12	0.41	0.06	0.52
$r_{(Yr. Wr + Vr)}$	-0.403	-0.661	0.62	0.42	0.90	0.44	0.90
				Waterlogging			
E	2.29	2.194	11.79	73.90	73.61	856.23	103.42
D	0.80	1.634	59.66	48.80	12.30	3986	125.78
F	-0.50	1.861	81.34	91.00	36.70	6297.40	159.67
H_1	28.89	25.381	165.58	113.20	46.70	13793.60	1044.60
H_2	25.02	22.386	122.76	53.50	44.10	10253.90	765.42
$D-H_1$	-28.09	-23.747	-105.93	53.50	-34.40	-9.807	-918.84
h2	6.51	3.106	16.32	13.80	-13.20	9436.00	-0.90
$(H1/D)^{1/2}$	6.011	3.942	1.67	1.53	1.95	1.86	2.89
$H2/4H_1$	0.216	0.221	0.19	0.12	0.24	0.19	0.18
KD/KR	0.900	1.338	2.39	4.24	1.02	2.48	1.57
$h2/H_2=K$	0.260	0.139	0.13	0.25	-0.03	0.92	-0.001
h^2_{BS}	0.530	0.387	0.47	0.53	0.50	0.42	0.54
h^2_{NS}	0.020	0.048	0.31	0.49	0.14	0.27	0.09
$r_{(Yr. Wr + Vr)}$	-0.295	1.524	-0.54	0.34	0.14	0.90	0.10

The greater than unity $(H_1/D)^{1/2}$ values presented over-dominance for all characters under both conditions. The lower ratio of $(H_2/4H1)$ than 0.25 prevailed symmetrical distribution of positive dominant genes in parents. The ratios (KD/KR) for studied characters were higher than unity, indicating the majority of dominant alleles. The number of genes or groups controlling the inheritance of a character (h^2/H_2) was one group of genes for all characters.

Broad sense heritability (h^2_{bs}) for studied traits ranged from 0.38 (Mn shoot in control) to 0.626 (SPAD in control). Moderately h^2_{bs} values indicated that the effects of environment and genotype on the inheritance of studied characters were equal. At the same time, narrow-sense heritability (h^2_{ns}) was generally low magnitude and varied between 0.016 and 0.52. The high difference between h^2_{bs} and h^2_{ns} indicated that dominant gene effects were more considerable on inheritance for studied characters except Fe (root) in waterlogging and Fe (shoot) and Mn (shoot) in control. It was found that the narrow-sense heritability (h^2_{ns}) under waterlogging condition was higher than in the control condition for MTS, Fe (root) and Mn (root). The type of gene action for these characters appeared to be different under waterlogging than under normal condition, with additive effects being more important under dominance effects in non-stress (Betran et al., 2003). In addition, the fact that h^2_{ns} for Mn (shoot) is higher than h^2_{bs} indicates that additive x additive epistatic effect may also be effective in the inheritance of this character. The results of heritability degrees were in agreement with genetic parameters.

CONCLUSION

It was concluded that there were significant differences among genotypes for SPAD, MTS, Fe (shoot), Mn (root) and Fe (shoot) under waterlogging conditions. The selection of genotypes with high SPAD and MTS values, low Fe and Mn content in root and shoot can be successful for improving waterlogging tolerance in the wheat breeding program. Significant cytoplasmic components for SPAD, MTS, Fe (root), Fe (shoot) and Mn (shoot) in Hayman diallel analysis revealed that character expression in F_1 may be due to interactions between genetic and cytoplasmic factors. Thus the selecting maternal parents are very important in making crosses. The selection in later generations was recommended because of the higher dominant effect (H_1) and low magnitude h^2_{ns} under waterlogging conditions.

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