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PLEIOTROPIC EFFECTS OF *Rht* DWARFING GENES ON GRAIN YIELD AND ITS COMPONENT TRAITS IN WHEAT UNDER RAINFED ENVIRONMENT

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ABSTRACT

Evaluation of random dwarf (*Rht*) and tall (*rht*) wheat lines under irrigated (nonstress) and rainfed (water stress) environments showed that *Rht1* and *Rht2* dwarfing genes have negative effect on grain yield under water stress conditions. The greater decline in the grain yield of *Rht* lines was due to significant and greater reduction in biological yield caused by reduced number of lighter tillers and yield per spike due to reduction in number of florets and grains per spike (*Rht1*) or grain weight (*Rht2*) and early maturity. It is concluded that the poor biological and grain yields of *Rht* dwarf lines under water stress may emanate from their greater sensitivity to the factors associated with diminished soil moisture content. However, in *Rht* dwarf lines under water stress conditions, variability for stress susceptibility index (S) and its negative association with grain yield were noted. This suggested that it should be possible to select *Rht* containing semidwarf lines with high yield potential and greater tolerance to water stress conditions.

Key words: Wheat, *Rht* genes, pleiotropic effects, grain yield, sensitivity, water stress.

Despite the wide spread adoption of high yielding semidwarf wheats for irrigated and high fertility conditions, their suitability for replacing the traditional drought-tolerant tall wheats is still questioned. The semidwarf wheats, relative to their tall counterparts, have been shown to be more susceptible to water stress conditions [1-3]. However, Innes and Blackwell [4] and Allen *et al.* [5] reported that dwarf lines were less susceptible to drought than either the semidwarf or tall lines. Further, it is argued that under drought although the percentage yield losses may often be greater, the absolute yields of semidwarfs were usually higher than those of tall lines [6-8].

In view of this, the present study was conducted to study the pleiotropic effects of major dwarfing genes (*Rht1* and *Rht2*) on grain yield and its component characters and to assess the suitability of semidwarf wheats for water stress conditions.

MATERIAL AND METHODS

The material for the present study was comprised of random F_7 semidwarf (17 *Rht1* and 7 *Rht2*) and tall (9 *rht1* and 14 *rht2*) lines as well as their parental genotypes. Each of the random lines could be traced to individual F_2 plants of the cross K 68 (*rht*) × HD 2009 (*Rht1*) and K 68 (*rht*) × WH 147(*Rht2*). The *Rht* and *rht* genotypes of each of the semidwarf and tall lines, respectively, were confirmed following seedling GA-response test [9].

Presowing irrigation was given in the experimental field and the soil moisture was judged to be optimum at the time of sowing of the experiments. The random semidwarf (*Rht*) and tall (*rht*) lines along with their parents were separately evaluated in randomized block design experiments with three replications under irrigated (nonstress) and rainfed (water stress) environments. In each replication, each line was evaluated in a single row plot of 1.5 m length with row to row and plant to plant distances of 30 cm and 15 cm, respectively. In experiments conducted in the nonstress environment, the required irrigations were applied while for water stress experiments no irrigation was applied from sowing until maturity. The rainfall during the crop season, in the preceding three years, ranged from 47.0 mm to 147.8 mm with an average of 101.1 mm. The total rainfall during the crop season of the present experiment was only 46.0 mm, creating a water stress environment in the absence of irrigation.

The data on 11 characters (Table 1) were recorded on all plants except the border plants. The data on culm length and spike characters were recorded on the main culm of each plant. The data on grain weight were recorded on a random sample of 100 grains from the bulk of grains from each line. Data on the remaining characters were recorded on whole plants.

The plot means were used for statistical analyses. The values for the tall (*rht*) genotype K 68, being the common parent in the two hybrids, were pooled over the different experiments separately under irrigated and rainfed conditions to obtain the mean values. The mean values for the various characters were compared using t-test. The values of stress susceptibility index (S), a parameter of stress susceptibility, were calculated following Fischer and Maurer [10] as given below.

$$S = (1 - Y_d/Y_p)/Di$$

where Y_d is grain yield in water stress environment, Y_p is grain yield in non stress environment and; Di is stress intensity index [11] calculated as given below:

$$Di = 1 - X_d/X_p$$

where X_d and X_p are the average grain yield values over all entries under water stress and non stress environments.

The simple correlation coefficients between S values and grain yield were calculated.

RESULTS AND DISCUSSION

In irrigated (nonstress) environment, the *Rht1* and *Rht2* (GA-insensitive major dwarfing genes), as expected, significantly reduced the culm length by 15.7 cm and 13.0 cm, respectively (Table 1). Similar trend was also noticed under rainfed (water stress) environment. Further, in nonstress environment the *Rht* containing dwarf lines gave slightly higher yield, though non significantly, than their tall (*rht*) counterparts (Table 1), which is consistent with the earlier results [12-18]. Under the water stress conditions, the grain yields of both the tall (*rht*) and dwarf (*Rht*) lines as well as their parental genotypes declined considerably (Tables 1 and 2). However, the reduction in grain yield was 13.7% and 3.6% greater in *Rht1* and *Rht2* lines, respectively, than in the corresponding tall lines. Thus under water stress conditions, the effect of the two major dwarfing genes (*Rht1* and *Rht2*) on grain yield was negative. It appears that the pleiotropic effects of *Rht* dwarfing genes may be altered due to stress factors associated with reduced soil moisture content.

Evidence is available to show that under optimum conditions, the positive effect of *Rht* dwarfing genes on grain yield is associated with reduction in grain size, which is more than compensated by increased number of grains per ear or tillers per plant [12-13, 16, 18]. In this study, in comparison to the tall (*rht*) lines, no significant change was noticed in any of the yield contributing characters (except an increase in harvest index in *Rht2* lines) in the semidwarf (*Rht*) lines under nonstress environment. However, in water stress environment the reduction in grain yield of both the tall (*rht*) and dwarf (*Rht*) lines was coupled with significant reduction in biological yield while maintaining similar or higher levels of harvest index. Further, the per cent reduction in biological yield, similar to the grain yield, was greater in dwarf (*Rht*) lines than in tall (*rht*) lines. Under optimum conditions, the *Rht* genes primarily reduce the rate of elongation of stem and vegetative dry matter accumulation resulting into increased ear: stem ratio and consequently higher yield [19]. Yet, it is stressed that under conditions in which shoot biomass is reduced, the grain yield of dwarf (*Rht*) lines may be less than those of tall (*rht*) lines. In the present study under the water stress conditions, the reduction in biological yield as also the grain yield is contributed by negative change in greater number of characters in dwarf (*Rht*) lines than in tall (*rht*) lines (Table 1). The reduction in biological yield in *Rht* dwarf lines is caused by decreased number of lighter tillers and yield per spike due to reduction in number of florets and grains per spike (*Rht1*) or grain weight (*Rht2*) and early maturity (Table 1), which is in conformity with earlier findings [1]. Thus, the mechanisms of biological and grain yield reduction in *Rht1* and *Rht2* containing

Table 1. Character means in random dwarf (*Rht*) and tall (*rht*) lines of wheat under irrigated and rainfed environments

Geno-types	Environ-ment	Grain yield per plant (g)	Culm length (cm)	Biolo-gical yield per plant (g)	Tillers per plant	100 grain weight (g)	Grains per spike	Yield per spike	Harvest index	Fertility %	Days to flowe-ring	Days to maturity
Rht1	Irrigated	15.57	91.08	43.21	12.62	3.82	54.37	2.13	0.37	53.64	75.67	137.61
	Rainfed	7.02	65.37	15.65	7.19	3.64	41.80	1.53	0.44	49.91	79.63	125.59
rht1	Irrigated	14.13	106.74	44.77	11.60	3.88	56.26	2.09	0.33	51.24	83.11	143.15
	Rainfed	8.30	72.38	23.86	8.79	3.88	49.50	1.79	0.38	49.89	81.89	133.63
Rht2	Irrigated	23.17	97.10	52.19	14.59	4.25	59.67	2.52	0.45	56.01	68.33	132.10
	Rainfed	6.67	74.20	16.69	5.49	3.13	53.09	1.68	0.40	55.99	69.76	119.62
rht2	Irrigated	22.20	110.13	60.85	13.65	4.60	57.14	2.58	0.38	54.91	79.88	134.14
	Rainfed	7.18	82.25	19.19	5.94	3.94	46.95	1.86	0.37	52.37	73.43	123.67

Table 2. **Character means for dwarf (*Rht*) and tall (*rht*) wheat genotypes used in crosses to derive random dwarf (*Rht*) and tall (*rht*) lines**

Genotypes	Environment	Grain yield per plant (g)	Culm length (cm)	Biological yield per plant (g)	Tillers per plant	100 grain weight (g)	Grains per spike	Yield per spike	Harvest index	Fertility %	Days to flowering	Days to maturity
K 68 (*rht*)	Irrigated	19.70^{**}	115.71^{**}	47.92^{**}	12.03^{*}	5.32	48.75^{*}	2.61	0.41	51.42	70.25	135.25^{*}
	Rainfed	9.69	81.98	23.26	9.20	4.95	42.00	2.08	0.42^{**}	49.46	71.33	129.75
HD 2009 (*Rht1*)	Irrigated	14.99^{**}	80.40^{**}	32.58^{**}	10.48^{**}	4.33	45.04	1.96	0.46	51.69	68.83	131.00^{**}
	Rainfed	8.99	62.35	17.42	6.68	3.84	44.89	1.74	0.53	55.44	70.17	123.00
WH 147 (*Rht2*)	Irrigated	23.63^{**}	87.99^{**}	54.58^{**}	12.50^{**}	4.64	53.50^{**}	2.47	0.45	51.61	72.75	131.75^{**}
	Rainfed	7.40	67.98	15.72	6.48	4.82	42.08	2.04	0.47^{**}	48.46	75.33^{**}	123.25

*, ** Significantly higher than corresponding value in the other environment at P = 0.05 & P = 0.01 respectively.

lines under water stress condition are not much different and begins with decline in first phenological yield component of wheat i.e. number of tillers. In lines containing either of the *Rht* genes, the decline in biological yield would, however, result into reduced number of grains per plant and consequently reduced grain yield. However, the greater reduction in grain yield of dwarf (*Rht*) lines than in their tall (*rht*) counterparts may emanate from greater sensitivity of dwarf lines to stress factors associated with diminished soil moisture content, which is in accordance with the earlier findings [1-3] and contrary to Innes and Blackwell [4] and Allen *et al.* [5].

It may be pointed out that yield in stress environments is dependent upon yield potential, stress susceptibility and stress escape and the stress susceptibility index (S) is not independent of yield potential [10]. In the present study, the values of stress susceptibility index (S) were variable for the various dwarf (*Rht*) and tall (*rht*) lines (Table 3), indicating variable response of genotypes to water stress condition.

Table 3. Ranges of stress susceptibility index (S) values in dwarf (*Rht*) and tall (*rht*) genotypes of wheat

Genotype	Range of S
Rht1	0.21-1.32
rht1	0.36-1.39
Rht2	0.89-1.11
rht2	0.87-1.13

In water stress condition, reduction in biological and grain yields in *Rht* dwarf lines was associated with significantly earlier maturity. Still considerable variation for days to flowering (66.0 to 99.7 days in *Rht1* and 62.0 to 79.3 days in *Rht2*) and from flowering to maturity (30.3 to 62.0 days in *Rht1* and 42.0 to 57.0 days in *Rht2*) was noticed among the *Rht* dwarf lines. In the rainfed (water stress) environment, the S values and grain yield of *Rht* dwarf lines were negatively and significantly associated (Table 4). Thus it should be possible to select *Rht* containing semidwarf lines with high grain yield potential and greater tolerance to water stress conditions.

Table 4. Correlation coefficients between stress suceptibility index (S) and grain yield of *Rht* dwarf and *rht* tall genotypes of wheat under irrigated and rainfed environments

Genotype	Irrigated	Rainfed
Rht1	0.37	–0.84**
rht1	0.12	–0.90**
Rht2	0.47	–0.88**
rht2	0.25	–0.86**

**Significant at P = 0.01.

The characters that lead to better performance under drought are believed to be related with the nature of drought [20-22]. Yet, it has been argued that rapid phenological development [23-25], rapid early dry matter accumulation [24, 26, 27], high ear-to-stem ratio at anthesis [28], rapid and prolonged grain growth and good ability to transfer assimilates to the grain resulting in a high harvest index [23, 24] are putatively important characters that could prove useful in augmenting yield in water limited environments. The utility of some of these characters in practical breeding programmes is currently being evaluated [29]. Results of these studies may also prove useful in developing strategies for breeding semidwarf (*Rht*) genotypes with high yield potential and greater tolerance to water stress conditions.

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