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GENETICS OF SOME DROUGHT RESISTANT TRAITS IN WHEAT

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The genetics of four physiological traits (net photosynthesis, water-use-efficiency, relative water content and excised leaf water loss) and their correlation with agronomic traits in spring wheat was studied under drought.. The parent, F, and segregating generations of four crosses were grown in pots under glasshouse conditions. Generation means and variance analyses of the data suggested simple inheritance of the traits. The estimates of narrow sense heritability were very high which might be due to the presence of a few major genes involved for the inheritance of the traits. The traits were not correlated with agronomic traits so it should be easy to breed recombinant lines for improved drought resistance. Similar gene action and significant correlation among net photosynthesis, water-use-efficiency and relative water content suggested that under drought these traits might be controlled by some common major genes.

Key words: drought resistant traits, genetics, wheat

INTRODUCTION

Reports in the published literature suggest that further progress in increasing yield in wheat and other crops in drought prone areas through the development of drought resistant cultivars can be achieved by selecting for physiological characteristics related to drought resistance (Clarke, 1987; Mehta *et al.,* 1989). Net photosynthesis (Pn), water-use-efficiency (WUE), relative water content (RWC) and excised leaf water loss (ELWL) have been related to drought resistance (Clarke and McCraig. 1982; *Schonfeld et al., 1988;* Matin *et al.,* 1989; Ritchie *et al.,* 1990; Gent and Keyomoto, 1992; Mojayad and Planchon, 1994; Johnson *et al.,* 1995). Sufficient genetic variation exists for these physiological traits. The techniques for measuring these traits are now easy and fairly standardised. Hence it may be possible to manipulate this variation (Hubick *et al.,* 1988) for developing drought resistant cultivars.

However, systematic breeding for drought resistance utilizing variation for these physiological traits has not been enthusiastically undertaken. This may be largely attributable to the lack of understanding of the genetics of these traits (Acevedo, 1993). If the nature of genetic variation for drought resistant trait is known, breeding strategy can then be formulated for the development of drought resistant cultivar or for the introgression of the trait into an otherwise promising local cultivar.Very little information is available about the inheritance of drought related physiological traits. The experiments reported in this paper were conducted to investigate the genetics of the above said physiological traits.

MATERIALS AND METHODS

The F_1, F_2 and backcross generations (BC_1 and BC_2) involving four genotypes (Pk81, Pb85, Lu26S, and Low-ABA 18) were developed in the Dept. of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan during the years 1988-90. These genotypes were widely different for the traits studied (Malik *et al.,* unpublished results). The following two experiments were conducted:

Experiment A

The F_1, F_2 and backcross generations were grown in a randomized complete block design with four replications. Each cross was studied in a separate trial so that in total there were four experiments. The experiments were conducted during the summer of (June-Aug) 1992 in a glasshouse at the College Farm, University of Wales, Bangor, UK. The plants were grown in 12 cm plastic pots filled with 1500 g of air dry sandy loam soil.. Four seeds were planted in each pot but at the 3rd leaf stage two healthy seedlings were retained. There were 6 pots for each of the parents and F_1, 24 pots for each of the backcrosses and 64 pots for the F_2 population in each experiment. .

The seedlings were supplied with optimum irrigation and nutrition until the 4th leaf stage. From now on irrigation was withheld and water stress was allowed to develop. The moisture content in the pots was monitored and kept uniform throughout the population by measuring moisture potential of the soil in the pots by filter paper method given by Fawcett and Collis- George (1967). When the moisture potential of the soil in the pots approached -1.2 MPa, net photosynthesis and transpiration rate were recorded with infrared gas analysis system (Model LCA2). After this RWC (on the 4th leaf and ELWL (on the 3rd leaf) were measured. Twelve plants from each of the parents and F_1, 48 from each of the backcrosses and 128 from each of the F_2 were measured for each trait., RWC, ELWL and

WUE were calculated by the following formulae:

RWC = (FW-DW)/(TW-DW)
ELWL = (FW -WW)/DW
WUE = Net photosynthesis/transpiration rate

Where,
FW = Fresh weight of the leaf taken soon after excision,
DW = Dry weight at 70°C,
TW = Turgid weight of the leaf (taken after keeping in distilled water overnight), and
WW = Wilted weight of the leaf (after putting on laboratory bench for 6 hours)

Experiment B

These experiments were a repetition of the experiments described above. However, in these experiments only four generations (parents, F_I and F_2) were included. These experiments were conducted at the Penn-y-Fridd Field Station, University of Wales, Bangor, UK, during the summer (April-Aug.) of 1993 The plants were grown in 12 cm plastic pots filled with 1500 g of air dry John Innes Potting Compost NO.2. Three seeds were planted in each pot and at the 3rd leaf stage one healthy seedling was retained in each pot. For each cross, there were 12 pots for each of the parents and the F_1, and 100 pots for the tF_2 population. The seedlings were supplied with optimum irrigation and nutrition until the 4th leaf stage.

When the 4th leaf was fully expanded, irrigation was withheld and water stress was allowed to develop. The moisture content in the pots was monitored and controlled as described in experiment A. When the moisture potential of the soil approached -1.2 MPa, net photosynthesis, transpiration rate, RWC and ELWL were recorded as in experiment A. Twelve plants from each of the parents and F_I and 100 from each of the F_2 were measured for each trait. The drought stress was then relieved by watering and the plants were grown up to maturity. The data about spike length, number of grains per spike, number of spikelets per spike, 100-grain weight and plant height were also recorded at maturity.

A generation means analysis of the data was done as described by Mather and Jinks (1982) using a computer programme supplied by Dr JW Snape, Cambridge Laboratory, Norwich, UK to study the inheritance of the traits. A weighted least squares analysis of variance as described by Mather and Jinks (1982) was also run but only on the experiment containing six generations (parents, F_1, F_2, BC_1 and BC_2) using a computer programme supplied by Dr. HS Pooni, University of Birmingham, UK. Narrow sense (h^2_n) and F infinity generation heritability (h^2/X) estimates were calculated using the components of variance from the best fit model of weighted least squares analysis using the formulae:

h^2_n,
1) = 0.5/(0.5D +. E) (when a simple DE model was adequate without a significant dominance component)
2) = 0.5/(0.5 +. 0.25H +. E) (when a DHE model had to be fitted)
h^2 = D/ (D +. E)

The genetic correlation (rG) between two characters, x and y, was calculated by the formula:

rG = eo'iG(x,y)/.jVG(x) Vft·(y)

Where,
Cov G(x,y) = Cov (x,y)F_2 - Cov (x.y) E
Cov (x,y)E = (1/4) [Cov (x.y) PI +. Cov (x.y) P_2 +. 2Cov (x,y) Fa

CovG(x,y), Cov(x,y) E, Cov(x,y)P_1, Cov(x,y)P_2, Cov(x,y)F) and Cov(x,y)F_2 are covariances of x and y associated with genetic effects, non-genetic effects, PI' P_2, F/, F_2, generations, respectively and VG(x) and VG(y) are genetic variances of x and y, respectively.

RESULTS AND DISCUSSION

Significant differences (P<0.05) were found among generation means in all the crosses for various traits (Table 1) except in the crosses Pk81 x Pb85 and Pk81 x Low-ABAI8 for relative water content, and in Lu26S x Pb85 and Lu26S x Low)ABA 18 for excised leaf water loss (results not shown). The mean performance of the parents, F_I, F_2 and back crosses for the traits were constant across the crosses (Table 1).' The results of generation means analysis are given in Table 2.

In case of WUE the two-parameter model (m and [d]) fitted consistently in all the crosses for both the years (1992 and 1993). This shows that the variation between the genotypes is only additive. For the other traits as well, simple two-parameter (m and [d]) or three-parameter model (m, [d] and [h]) were adequate to explain the variation between genotypes except for the cross Pk81 x Pb85 in the data of 1993 for Pn trait in which additive x additive and for the same cross in the data of 1992 for RWC, additive x dominance interactions were involved. The results of the present study corroborate the earlier findings. Ehdaie *et al.* (1993) have also reported additive component of genetic variance and absence of epistasis in the inheritance of WUE in wheat. Schonfeld *etal.* (1988) have reported additive genetic interactions along with the additive and

Table I. Generation means of net photosynthesis (Pn umole m-?s-'), water-use-efficiency (WUE, mmol CO/mol HP), relative water content (RWC, %) and excised leaf water loss (ELWL, gig) in four crosses, Pk81 x Pb85 (1), Pk81 x Low-ABAI8 (2), Lu26S x Pb85 (3) and Lu26S x Low-ABAI8 (4) of wheat

Year	Trait	Cross	Pt'	P_2	F_1	F_2	BC_1	BC_2	Pop. effects	LSD (0.05)
1992	Pn	1	4.32	1.91	3.31	3.30	3.95	2.97	**	1.62
		2	4.71	2.21	2.87	3.34	3.51	2.81	**	1.31
		3	3.45	1.51	2.76	2.64	2.83	1.92	**	1.22
		4	4.19	2.01	2.36	3.01	3.65	2.41	**	1.35
1993		1	5.11	2.89	4.32	4.58			**	1.36
		2	4.92	3.21	3.78	3.52			**	1.27
		3	4.59	2.31	3.68	3.92			**	1.32
		4	4.21	2.58	3.12	3.39			**	1.18
1992	WUE	1	1.58	0.96	1.31	1.32	1.41	1.23	**	0.33
		2	1.54	1.01	1.31	1.26	1.34	0.98	**	0.31
		3	1.38	0.88	1.10	1.13	1.16	0.92	*	0.29
		4	1.32	0.92	1.01	0.96	1.04	0.99	*	0.21
1993		1	1.61	0.97	1.41	1.39			**	0.32
		2	1.51	1.51	1.12	1.25			**	0.26
		3	1.21	0.75	1.01	1.15			**	0.34
		4	1.26	0.96	1.01	1.11			**	0.21
1992	RWC	3	87.5	82.2	83.1	84.1	86.4	81.1	*	3.29
		4	85.4	79.3	80.5	80.9	82.2	79.1	**	3.51
1993		3	81.2	77.3	78.4	79.5			*	2.68
		4	80.1	76.4	77.2	77.1			**	2.21
1992	ELWL	1	2.21	1.76	2.02	2.01	2.10	1.91	**	0.26
		2	2.19	1.84	2.12	1.91	1.95	1.91	*	0.21
1993		1	2.33	1.75	2.25	2.23			*	0.33
		2	2.13	1.78	2.01	2.10			**	0.28

a, PI =Pb85 in cross 3 and Low-ABA 18 in cross 4 for ELWL.. For the other traits PI = Pak81 and Lu26S.
* = P<0.05; ** = P<0.01.

dominance effects. However, dominance and additive x additive components were not significant in their results. Variance analyses of the data revealed that a DE (additive and non-genetic component) model was sufficient to explain the variation in various crosses for all the physiological traits (Table 3) except for net photosynthesis in the cross' Lu26S x Pb85 in which the dominance component was also significant but only at 0.05 probability level.. The generation means analysis showed that generally the additive components of variance were pronounced in the inheritance of the traits, nevertheless dominance also seemed to be involved in some traits. However, the dominance component of variance was not detectable in the analysis of second degree statistics. This discrepancy might arise from the estimation precision of the two analyses. The analysis of generation means is more robust than that of generation variances. The general fit of simple genetic models to the data for the physiological traits investigated in the present study shows that the genetic variance present within *Triticum aestivum* species for these traits is not complex at least under drought conditions.

Narrow sense heritability estimate for all the traits are given in Table 3. Heritability estimates for all the traits were generally consistent between crosses. Narrow sense heritability estimates were high for all the traits studied. Infinity generation heritability was also very high for all the traits. Schonfeld *et al. (1988)* have also reported high narrow sense heritability (64%) for relative water content in wheat.. Adequate fit of the simple DE model to the generation variances suggests that additive variance comprised a significant part of total genetic variance therefore, only narrow sense heritability estimates were computed.

High estimates of heritability support the results of generation means and variance analyses suggesting additive variance to be more pronounced in the inheritance of the traits. High heritability might be due to simple inheritance of the traits suggesting a few major genes involved. Consistency in the estimates of heritability across' the traits might be due to similar gene action. The accuracy with which measurements

Table ~. Estimates of the best fit model for generation means parameters by weighted least squares analysis in respect of net photosynthesis (Pn), water-use efficiency (WUE), relative water content (RWC) and excised leaf water loss (ELWL) in four crosses, Pk81 x Pb85 (1), Pk81 x Low-ABAI8 (2), Lu26S x Pb85 (3) and Lu26S x Low-ABAI8 (4) of wheat

Year	Trait	Cross	Genetic effects					χ^2
			m	[d]	[h]	[i]	[j]	(df)
1992	Pn	1	3.29±0.07	1.17±0.12**				4.13(4)
		2	3.51 ±0.13	1.12±0.13**	-0.59±0.25*			4.79(3)
		3	2.54±0.07	0.95 ±0.12**				3.47(4)
		4	3.19±0.11	1.12±0.12**	-0.59 ±0.22**			3.98(3)
1993		1	4.52±0.14	1.11 ±0.17**		-0.52±0.22*		0.62(1)
		2	3.85±0.10	0.87 ±0.13**				5.93(2)
		3	3.66±0.10	1.13±0.15**				4.37(2)
		4	3.33±0.10	0.82±0.14**				1.48(2)
1992	WUE	1	1.30±0.03	0.28±0.06**				1.32(4)
		2	1.25±0.03	0.28±0.05**				3.08(4)
		3	1.09±0.03	0.25±0.05**				1.43(4)
		4	1.01 ±0.04	0.22±0.07**				3.50(4)
1993		1	1.35±0.05	0.32±0.07**				1.51(2)
		2	1.~5 ±0.04	0.20±0.06**				0.55(2)
		3	1.02±0.04	0.23±0.06**				2.64(2)
		4	1.08±0.04	0.15±0.05**				1.58(2)
1992	RWC	3	84.83±0.27	2.65±0.31**	-1.78±0.53**		5.22± 1.29**	0.79(2)
		4	82.09±0.27	3.04±0.27**	-2.15 ±0.51 **			4.06(2)
1993		3	79.18±0.19	1.95±0.29**				4.64(2)
		4	78.13±0.26	1.85±0.28**	-1.19±0.49**			1.94(1)
1992	ELWL	1	2.00±0.04	0.22±0.07**				0.14(4)
		2	1.98±0.04	0.15±0.05**				3.93(4)
1993		1	2.06 ±0.07	0.29±0.08**	0.23±0.11 *			0.68(1)
		2	2.01 ±0.05	0.17±0.06**				1.30(2)

* = p< 0.05; ** = P< 0.01.

of physiological traits are made affects experimental error. The degree of uniformity in the test environment also influences the experimental error. Any precaution that reduces experimental error will improve the estimate of heritability of a character (Fehr, 1987). The consistency in the estimates of heritability of the traits across the crosses may be attributable to keeping uniform environmental conditions in plant population across the crosses. The plants were grown in pots under glasshouse conditions and were allowed to stress at a uniform rate and a similar stress level was imposed in all plants by precise monitoring and adjustment of soil water content in the pots. Heritability of a trait is also affected by the environment where plants are grown. Heritability estimates for physiological traits, are expected to be higher under stress conditions due to the expression of stress responsive genes which might be a few in number with major effect. Schonfeld *et al.* (1988) have reported 5.1 and 64.4% heritability for relative water content under well-watered and drought conditions, respectively.

Pair-wise phenotypic and genetic correlations between morphological and physiological traits were worked out from the data of 100 F_2 plants from each of the crosses in experiment B. Pn was significantly and positively correlated with WUE and RWC. This suggests that maintenance of high RWC results in higher Pn and higher WUE. Pn, WUE, RWC and ELWL under drought were not significantly correlated with plant height, or any yield component. However, relative water content, Pn and WUE had a significant and positive correlation with each other in all the crosses. There was no significant correlation of excised leaf water loss with the other physiological traits. Spike length had a significant and positive correlation with grains per spike and spikelets per spike. Grains per spike were positively correlated with spikelets per spike in all crosses.

It may be concluded from the present study that the traits are genetically controlled and they have a high proportion of additive genetic variance and high heritability. Hence simple breeding procedures should

Table 3. Results of the best fit model following weighted analysis of components of variation, D (additive) and E (environmental) and heritability (ns, arrow sense and *Fa,* generation) for net photosynthesis (Pn), water-use-efficiency (WUE), relative water content (RWC) and excised leaf water loss (ELWL) in four crosses; Pk81 x Pb85 (1), Pk81 x Low-ABAI8(2), Lu26S x Pb85(3) and Lu26S x Low-ABAI8(4) of wheat

Year	Trait	Cross	Variance components		χ^2 (4dt)	Heritability	
			D	E		ns	Fa
1992	Pn	I	4.65±0.65**	0.48±O.1I **	6.89	82.9	92.8
		2	3.87 ±0.61 **	0.55±0.13**	4.00	77.9	87.6
		3	4.20±0.61 **	0.48±0.11 **	7.72	61.4	89.7
		4	4.61 ±0.62**	0.43±0.1O**	1.74	84.3	91.5
1992	WUE	I	1.28±0.16**	0.09±0.02**	0.77	87.7	93.4
		2	1.31 ±0.16**	0.08±0.02**	1.43	89.1	94.2
		3	1.47 ±0.18**	0.09±0.02**	3.26	89.1	94.2
		4	1.21 ±0.15**	0.08±0.02**	4.73	88.3	93.8
1992	EWC	3	16.83 ±2. 75**	2.53±0.58**	1.70	76.9	86.9
		4	19.95 ±2.92**	2.33±0.54**	1.18	81.1	89.5
1992	ELWL	I	1.69±0.23**	0.16±0.04**	3.04	84.1	91.4
		2	1.13±0.21 **	0.23 ±0.05**	0.57	71.1	83.1

**p<O.OI.

be appropriate to develop superior recombinant line for improved drought resistance. These traits are not correlated with yield components which suggest that the genes controlling these physiological characters have no linkage to the genes controlling the agronomic characters. Thus selection of plants for these physiological adaptations would not "adversely affect the yield potential and plants with any plant stature could be bred for these physiological adaptations. High estimates of *Fa* generation heritability reflect that a high proportion of genetic variance is fixable in the segregating lines. from a cross. The gene expression of Pn, WUE and RWC was generally the same under drought conditions and they were correlated with each other.. It seems that the variation of the genotypes for these traits might be controlled by some common major genes at a biochemical level or the genes for these traits might be very closely linked. Therefore, improvement in any of these traits may improve drought resistance of a genotype. "

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