HERITABILITY AND MODE OF GENE ACTION DETERMINATION FOR GRAIN FILLING RATE AND RELATIVE WATER CONTENT IN HEXAPLOID WHEAT

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Mode of gene action, heritability and determination of the effective breeding strategy for improvement of physiological and traits specifically in drought stress conditions is very important. Therefore, this study was conducted by using two drought susceptible and tolerant wheat cultivars. Cultivars Sakha8 (tolerant) and Pishtaz (susceptible) as parents along with F1, F2, BC1 and BC2 generations were sown in a randomized complete block design with three replications in drought stress conditions. Results of analysis of variance indicated significant difference between generations as well as degree of dominance revealed over-dominance for the both traits. Fitting simple additive-dominance model designated that this model was not able to account for changes of traits relative water content and mean of

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grain filling rate. It was revealed that m-d-h-i-j model for relative water content and m-d-h-i model for mean of grain filling rate are the best models. Estimation of heritability and mode of gene action indicated that selection for improvement of traits studied in stress condition and specifically in early generations have medium genetic gain. In conclusion, grain filling rate is better than relative water content as indirect selection criteria to improve plant grain yield in drought stress condition.

Key words: Bread wheat, generation mean analysis, drought tolerance, gene action

INTRODUCTION

Drought usually is the most important abiotic stress that affects crop production. Hence, selection for drought resistance and production of tolerant cultivars with high yield potential is the main objective of breeding programs. Many researchers (PASSIOURA, 1996; QUARRIE et al., 1999; RICHARDS, 1996) believed that tolerance to drought stress must be done via genetic improvement of physiological traits.

Harvest index and biological yield introduced as the most important traits in this connection (QUARRIE et al., 1999). In small-grained cereals increase in harvest index may causes yield improvement, without increase in plant water use (QUARRIE et al., 1999, RICHARDS, 1996). On the other hand, breeding for biological yield improve plant water use efficiency (QUARRIE et al., 1999). Therefore, selection criteria must be improving these traits. Relative water content and mean of grain filling rate are the proper criteria for this aim (GOLPARVAR, 2003; DHANDA and SETHI, 1996; SLAFER et al., 1998).

Indirect selection in early generation through traits correlated with seed yield is one of the most important strategies in plant breeding. Knowledge about inheritance and genetic control of different traits is prominence for plant breeders. Alteration in environment parameters cause change genetic architect of traits (AMAWATE and BEHL, 1995; CHOWDHRY et al., 1999; REDHU, 1988; WALIA et al., 1995). Genotype×environment interaction is the main reason for these changes, especially accured in stress conditions (SHARMA et al., 2002).

BHUTTA and MISHRA (1995) and COLLAKU (1994) emphasized on over-dominance and non-additive gene effects for yield and it's components in bread wheat cultivars under drought and non-drought environments. DHANDA and SETHI (1996, 1998) reported additive gene effects and high narrow-sense heritability for harvest index, biological yield and relative water content in drought stress condition that indicates possibility of genetic improvement of traits mentioned.

The aims of this study were genetic assessment of the traits relative water content and mean of grain filling rate and determination of the effective breeding strategy for genetic improvement of these traits in drought stress condition.
MATERIALS AND METHODS
The P₁, P₂, F₁, F₂, BC₁ and BC₂ generations were obtained from cross between Sakha8 (drought tolerance) and Pishtaz (drought susceptible) cultivars. Six generations were grown in randomized complete block design. Homogenous generations (P₁, P₂ and F₁) were grown in two rows and heterogeneous generations (BC₁, BC₂ and F₂) in four, four and six rows, respectively. Intra and inter row distance of 5 and 20 cm were applied in this study. 300 kg/ha of ammonium phosphate fertilizer before planting and 300 kg/ha nitrogen half before and half after planting were used. Irrigation was achieved in order to seed germination. Seeds did not receive another water via irrigation but used from humidity stored in soil and precipitation (163 mm). Relative water content was measured using method proposed by SCHNOFELD et al. (1988):

\[
\text{RWC} = \frac{\text{FreshWeight} - \text{DryWeight}}{\text{SaturatedWeight} - \text{DryWeight}}
\]

Mean of grain filling rate was estimated by using below formula (CHOWDHRY et al., 1999; LAZAR et al., 1995):

\[
\text{GFR} = \frac{\text{Seedyield}}{\text{GrainFillingDuration}}
\]

Generation mean analysis was carried out using methods proposed by MATHER and JINKS (1982). Genetic parameters were estimated according to weighted least square method. Joint scaling test was achieved to assess goodness of simple additive-dominance model. Method of KEARSY and POONI (1998) was used to computation gene effects and genetic variance components. Broad and narrow-sense heritability was estimated using method proposed by WARNER (1952).

RESULTS AND DISCUSSION
Analysis of variance (Table 1) showed significant difference between treatments (generations) for traits. Significant difference between treatments designated genetic variability in genetic materials for the traits studied.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>relative water content</th>
<th>Mean of grain filling rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reps.</td>
<td>2</td>
<td>0.99</td>
<td>0.06</td>
</tr>
<tr>
<td>Treatments</td>
<td>5</td>
<td>52.8**</td>
<td>0.16**</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>3.95</td>
<td>0.02</td>
</tr>
</tbody>
</table>

** significance at 1% probability level
Degree of dominance \( \left( \frac{H}{D} \right) \) indicated over-dominance effect and more important role of non-additive gene effects in genetic control of the traits (Table 2).

**Table 2. Components of diversity and estimation of broad and narrow-sense heritability for traits studied in cross Sakha8×Pishtaz for six generations**

<table>
<thead>
<tr>
<th>Traits</th>
<th>( V_A )</th>
<th>( V_D )</th>
<th>( V_E )</th>
<th>( \sqrt{\frac{H}{D}} )</th>
<th>( H_b )</th>
<th>( H_n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative water content (%)</td>
<td>28.70</td>
<td>32.30</td>
<td>47.60</td>
<td>1.60</td>
<td>58</td>
<td>27.20</td>
</tr>
<tr>
<td>Mean of grain filling rate (gr day(^{-1}))</td>
<td>0.04</td>
<td>0.04</td>
<td>0.04</td>
<td>1.51</td>
<td>67.70</td>
<td>34.30</td>
</tr>
</tbody>
</table>

\( V_A, V_D \) and \( V_E \): Additive, dominance and environment variances, respectively.

\( \frac{H}{D} \): Degree of dominance

\( H_b \) and \( H_n \): Broad and narrow-sense heritability, respectively.

Hence, degree of dominance designated average dominance. REDHU (1988) and DHANDA and SETHI (1996 and 1998) reported similar results for these traits.

Simple additive-dominance model didn’t account for genetic changes for relative water content and mean of grain filling rate. Therefore, six-parameter genetic model fit for these traits (Table 3). After eliminating the non-significant interactions from six-parameter models, m-d-h-i-j and m-d-h-i determined as the best models for relative water content and mean of grain filling rate, respectively. EHDAIE and WAINE (1994), DHANDA and SETHI (1996 and 1998) and YADAV and NARSINGHANI (1999) also recommended relatively similar genetic models for these traits.

Component \( [h] \) was highly significant for all the traits. On the other hand, additive component \( [d] \) was non-significant for all the traits revealed low importance of additive gene effects in genetic control of traits studied (SHARMA, 1998). Dominance component \( [h] \) was significant for the traits designated hybrid production possibility for these traits (YADAV and NARSINGHANI, 1999). Additive×additive interaction effect is important for plant breeders and genetic improvement of traits via selection (DHANDA and SETHI, 1998; YADAV and NARSINGHANI, 1999). Among the traits studied these interaction effect was significant only for relative water content and mean of grain filling rate (Table 3).
Table 3. Estimation of genetic effects in six parametric model of generation mean analysis

<table>
<thead>
<tr>
<th>Traits</th>
<th>$[m]$</th>
<th>$[d]$</th>
<th>$[h]$</th>
<th>$[i]$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative water content (%)</td>
<td>$61.05** \pm 2.71$</td>
<td>$-1.42** \pm 0.89$</td>
<td>$-9.83** \pm 3.53$</td>
<td>$-6.48** \pm 2.91$</td>
</tr>
<tr>
<td>Mean of grain filling rate (gr day$^{-1}$)</td>
<td>$0.29** \pm 0.07$</td>
<td>$0.02** \pm 0.02$</td>
<td>$-0.25** \pm 0.09$</td>
<td>$-0.27** \pm 0.07$</td>
</tr>
</tbody>
</table>

and **: Non-significant and significant at 1% probability level, respectively.

$m$, $d$, $h$, $i$, $j$ and $l$: mean, sum of additive, dominance, additive×additive, additive×dominance and dominance×dominance effects, respectively.

Overall, small additive effect for polygenic traits (Table 3) is predictable, because parameters that determine gene effects are average effect of total segregating loci. Therefore, because additive parameter or interaction effect related with additive effect is the function of dispersion degree of increasing genes between parents, additive effect estimates may be small (CHUGAN, 2002; GHANADHA, 1999; AMAWATE and BEHL, 1995; MATHER and JINKS, 1982).

Estimation of additive effect for relative water content and is negative (Table 3), while these traits have positive additive genetic variance. This problem is due to in generation mean analysis additive parameters or interaction effect related with additive effect is the function of dispersion degree of increasing genes between parents. On the other hand, genetic variances are not affected by equilibrate effect and are mean of squares of loci that expressed in form of sum of additive effect deviation (CHUGAN, 2002; GHANADHA, 1999; AMAWATE and BEHL, 1995; MATHER and JINKS, 1982).

Estimation of broad-sense heritabilities (Table 2) indicated higher importance of genetic effects in control of traits. Comparison between broad and narrow-sense heritabilities revealed equal importance of additive and non-additive effects in genetic control of traits that disagreement with results of degree of dominance estimation. Narrow-sense heritability designated average genetic efficiency for traits studied in stress conditions specifically in early generations.
DHANDA and SETHI (1998) reported possibility of selection for improvement of relative water content in early generations that disagreement with results of present study.

High mean on grain filling rate prevents decrease in grain weight and yield specifically in terminal stress conditions. Genotypes having higher value of these traits show higher drought tolerance (LAZAR et al., 1995; QUARRIE et al., 1999). Grain yield has low narrow-sense heritability specifically in stress condition. Because of that indirect selection is proposed for genetic improvement of this trait in stress environments (GOLPARVAR, 2003; DHANDA and SETHI, 1996; EHDAIE and WAINES, 1994; RICHARDS, 1996).

In conclusion, we can propose indirect selection via traits mean of grain filling rate to genetic improve the grain yield in stress condition. High and significant correlation between grain yield and other traits have been emphasized in many researches (GOLPARVAR et al., 2003; DHANDA and SETHI, 1996, 1998; LAZAR et al., 1995; QUARRIE et al., 1999). Considerable non-additive genetic effects and non-significant additive effects observed in this study suggests that selection in advanced generations may be more appropriate because effective selection in early generations of segregating material can be achieved only when additive gene effects are substantial and environmental effects are small.

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NASLEDIVANJE I NAČIN DEJSTVA GENA KOJI KONTROLIŠU BRZINU NALIVANJA I RELATIVNI SADRŽAJ VLAGE U SEMENU HEKSAPLOIDNE PŠENICE

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I z v o d

Način dejstva gena, naslednost i utvrđivanje efektivne strategije oplemenjivanja na unapređenje fizioloških osobina i osobina specifičnih za tolerantnost prema stresu izazvanog sušom su veoma značajan factor u oplemenjivanju pšenice. U ovim istraživanjima tako i u stepenu dominantnosti su kao eksperimentalni material korišćene dve sorte pšenice tolerantne i osetljive na sušu. Sorte Sakha8 (tolerantna) i Pishtaz (osetljiva) kao roditeljske linije F1, F2, BC1 i BC2 generacija su posejane u potpunom random blok u tri ponavljanja u uslovima stresa na sušu. Rezultati analize varianse ukazuju na značajne razlike kako između generacija tako i na stepen dominantnosti pokazujući over – dominantni efekat gena za ispitivane osobine. Testiranje jednostavnog modela aditivno – dominantnog efekta je pokazalo da nije bilo moguće da se utvrde promene osobina koje se odnose na relativni sadržaj vode i proseka brzine nalivanja semena. Pokazalo se da su modeli m-d-h-i-j za relativni sadržaj vode i m-d-h-i model za prosečnu brzinu nalivanja semena najbolji. Utvrđivanje naslednosti i načina dejstva gena je pokazalo da selekcija na poboljšanje ispitivanih osobina u uslovima stresa a posebno u ranijim generacijama ima srednju genetičku dobit. U zaključku, brzina nalivanja semena je bolja od relativnog sadržaja vode kao indirektni kriterijum u selekciji poboljšanja prinosa zrna u uslovima stresa na sušu.