IMPACT OF SELECTION FOR STOMATA FREQUENCY ON YIELD CHARACTERISTICS UNDER HEAT AND DROUGHT STRESSES IN BREAD WHEAT (*Triticum aestivum* L).

M. M. El-Defrawy

Genetics department, Faculty of Agriculture, Assiut University, Assiut, Egypt.

Email address: mmheldefrawy@yahoo.com

Abstract: Stomata spread allover leaves are important sources for plant canopy temperature depression which might contribute to heat stress tolerance. Two F₂ populations of bread wheat (Triticum aestivum L.) were subjected to two cycles of divergent selection for flag leaf stomata frequency. Plants were exposed to heat and drought stresses in order to study the impact of selecting for high and frequency low stomata on vield characteristics. The correlated responses in grain yield/plant and 100-kernel weight were determined.

The response to the first cycle of selection in the high direction in population 1 and 2 amounted to 16.03% and 11.63% of the bulk sample mean. respectively, which were consistently higher than that expected (8.29% and 5.598%). Higher observed response (7.16%) than expected (5.50%) was also observed for low stomata frequency in population 2. Such inflated responses might be attributed to dominance, epistasis or G x E. Asymmetrical responses to selection were evident with the deviation being greater in the high direction. Narrow-sense heritability, as calculated by parent-offspring regression, reached 0.45 and 0.266 in populations 1 and 2, respectively. However, the

realized heritability was higher in the high direction than that in the lower direction in both populations.

The observed responses of the second cycle of selection amounted to 12.71% and 9.39% from the bulk mean were greater than those expected (9.48% and 5.01%) in populations 1 and 2. respectively. In the low stomata frequency direction the observed responses (6.67% and 9.42%) were also higher than those expected (5.32% and Generally, the differences 3.63%). between high and low directions were highly significant over cycles of selection for both populations. The narrow-sense heritabilities were 0.50 and 0.36 in population 1 and 2, respectively. The realized heritability reached 0.62 and 0.44 in the low and high directions, respectively in population 2, while it remained unchanged in population 1. Further expected responses of 7.04% and 9.61% in the low and high directions, respectively in population 1, and of 5.60% and 6.58% in the low and high directions, respectively in population 2 under heat and drought stresses were estimated for the third cycle of selection.

The selected F₄ families of population 1 developed significantly higher 100kernel weight but lower grain yield/plant than population 2 in the low and the high direction as well as the two bulks. Such differences were only observed in the high direction where selection led to greater mean of stomata frequency in population 1 than in population 2. Selecting for stomata frequency did not show correlated responses in 100-kernel weight or in grain yield/plant. No correlated responses were detected for leaf area, which did not differ among selected families and the control or the other studied traits.

Key words: *T. aestivum*, selection, stomata frequency, grain yield/plant, kernel weight, heat and drought stress.

Introduction

Until the year 2020 at least, the demand for wheat is expected to grow bv approximately 1.6 percent/year worldwide and by 2 percent/year in developing countries (Rosegrant et al., 1995). Thus, there is an urgent need to develop new and efficient wheat breeding more methodologies to complement existing breeding techniques, as well as to identify new traits, which will drive faster yield gains.

Two of the most important stresses of wheat are heat and drought. Over 7 million ha of spring wheat are grown under continual heat stress, namely environments with mean daily temperatures of greater than 17.5°C in the coolest month (Fischer and Byerlee, 1991). In addition, terminal heat stress can be a problem in up to 40 percent of the irrigated wheat-growing areas in the developing world. Wheat yields can be severely reduced in moisturestressed environments (Morris et al., 1991), which affect at least 15 million ha of spring wheat alone in the developing world.

A strong body of evidence now indicates that physiological traits may early-generation complement phenotypic selection in wheat in the following three ways: (i) identifying traits that may serve as indirect selection criteria for yield; (ii) developing selection methodologies that increase the efficiency of parental and progeny selection; and (iii) providing insights into the physiological and genetic basis of rising yield potential (Reeves et.al., 2000 and Reynolds, 2002).

Stomatal frequency, as one of the morpho-physiological traits, was reported to have negative and nonsignificant association with yield at both genotypic and phenotypic levels in wheat (Nayeem and Nerker, 1988). Later, Khan and Shaik (1997), Khaliq et al. (2000) and Usman Khan et al., (2003) reported that stomatal frequency had positive direct effect on grain yield. These controversial results deserve more studies to elucidate the role of stomata frequency and the underlying genetic mechanism controlling it. Flag leaf stomata frequency was reported to be governed by additive gene action along with partial dominance in bread wheat (Tahir *et. al.*, 1995; Subhani and Chowdhry, 2000; Ambreen *et. al.*, 2002; and Iqbal, 2004) indicating that this character is amenable to selection.

Low stomata frequency on the upper epidermis can be beneficial by increasing water use efficiency, through the reduction of water loss (Kramer, 1969 and Monteiro et al., 1985). Under water deficit conditions, a signal from the roots (abscisic acid) triggers stomata closure which causes slower entrance and of CO_2 slow down photosynthesis (Fay and Knapp, 1993). In Triticum aestivum. shoot/root ratio, stomata frequency, and stomata aperture were found to be correlated with the potassium concentration in the leaves. Transpiration rate was also reported to be regulated by varied potassium and sodium concentrations (Brag, 1972). Jiang and Huang (2001) demonstrated that prior exposure to drought stress (drought preconditioning) enhanced heat tolerance in Kentucky bluegrass, which might be attributed to the maintenance of higher osmotic adjustment associated with accumulation of ion solutes, water soluble carbohvdrates and development of extensive roots deeper in the soil profile.

Elevated temperatures accelerate senescence, reduce the duration of viable leaf area and diminish

photosynthetic activities (Harding et al., 1990). Heat stress also affects the quality of the harvested product, reducing bread making quality by affecting gliadin synthesis (Blumenthal et. al., 1993) and starch quality by affecting the ratio of A (large) to B (small) starch granule types (Stone and Nicolas, 1995). Rheological dough properties were affected by heat stress in field conditions (Castro, 2006). Numbers of leaf and tiller primordia are determined before spikelet initiation but their subsequent growth and development are controlled bv temperature and day length during the differentiation of spikes into spikelets. Similarly, floret number within each spikelet is established by anthesis, at which time the potential grain number per spike is established. High photosynthetic rates at high temperatures do not necessarily support high rates of crop dry matter accumulation. All stages of development sensitive are to temperature, development generally accelerates as temperature increases (Abrol and Ingram, 1996). Although there is a large and valuable literature physiological responses on to temperature, we are far from having a comprehensive understanding of how crops respond to temperature (White and Reynolds, 2001).

Al-Yassin *et. al.*, (2005) concluded that, holding all other factors affecting response to selection

concerns about the constant. magnitude of heritability at lowvielding locations are not justified and should not prevent them from being used as selection sites. No firm conclusions were drawn as to the effectiveness of selection for stomata frequency under heat and drought and their impact on vield characteristics. Therefore, the present study was designed to evaluate morpho-physiological response to divergent selection for stomata frequency under heat and drought stresses.

Materials and Methods

Materials used:

Four local landraces of bread wheat (Triticum aestivum L.) were chosen from the germplasm accessions collected from farmers' fields in stressful area in Upper Egypt in 1993 (Omara, 1994). The four landraces were evaluated for heat tolerance under field conditions as: 1) susceptible which heat group comprised: P₁ (WA50), P₂ (WA81), and 2) heat tolerant group which comprised: P₃ (45-3-4), P₄ (WA90). In 2001-2002 Season, two crosses were established among the four parental landraces, namely cross1: $P_3X P_1$ and cross2: $P_4X P_2$. The F_1 's were grown in 2002-2003 season in order to produce F₂ seeds. Normal agronomic practices were adopted.

II- Selection procedure:

In 2003-2004 season, 200 spaced seeds were sown for each of the two

 F_2 populations into the clay-loam fertile soil of Assiut University Experimental in Farm late (December 23^{rd}) sowing date so as to allow the late sown plants to be subjected to the heat stress which usually develop later in the season. The recorded temperatures during February and March 2004 indicated that heat waves have occurred with temperature rising above 34 °C for several days which coincided with the post flowering stages of plant development. At anthesis, fully expanded flag leaf of the main culm of each plant was excised and its bottom part was placed in a capped vial containing Carnoy's solution and was transferred to the laboratory for stomata frequency estimation. At maturity, plants were individually harvested and grain yield per plant was determined. The highest and in lowest five plants stomata frequencies were selected (an 2.5% intensity of selection) for the high and low directions in each population. From each population, an equal number of seeds of each of the 200 F₂ plants was pooled to form the F₃ bulk.

In 2004-2005 season, the five families selected in both directions for each cross, along with the F_3 bulks were planted on the late sowing date (December 22^{nd}) in a randomized complete block design (RCBD) with three replications. Each entry was planted in two rows 3m long, 30cm apart and plants were spaced at 5cm. Fully expanded flag

leaf of the main culms of five plants per replicate were excised for estimating stomata frequency. At maturity, grain yield per plant was determined on individual plant basis. Combined selection (between and within families) was practiced by picking the lowest three and the highest three families (3/5) for stomata frequency from population1 (pop1) and from population2 (pop2). The best three plants (3/15) were then selected within each family and their seeds were bulked to obtain the highest three and the lowest three families in each population (an 3/5*3/15 = 12% selection intensity).

In 2005-2006 season, seeds of the selected F₄ families along with their relevant F₄ bulks were planted on the late sowing date (25th December) in a triplicate RCBD. Each entry was planted in five rows 3m long, set 30cm apart and plants were spaced at 5cm. Irrigation regime was as follows: first irrigation was at the 42^{nd} day from establishment, then irrigation was applied at the 81st, 99th and 120^{th} days, thus simulating a strong drought stress. At anthesis, fully expanded five main stem flag leaves were scored for leaf area and stomata frequency. At maturity grain yield was scored on previous plants. A sample of five main stem ears was collected at 10 days intervals, beginning from anthesis onwards, for five consecutive scores to estimate their length, fresh and dry weight.

III- Stomata frequency estimation:

frequency Stomata was determined on flag leaves at anthesis using a light microscope (40X objective) in 10 microscopic fields with an average of 10 fields/mm²/leaf. Difference in stomata frequencies among high and low directions in both populations was statistically tested using t-test in groups. To test whether selected family variances were significantly different from those of the bulks F test was used according to Kearsey and Pooni (1996).

IV-Heritability estimation

Heritability was estimated by parent-progeny regression b_{po} (F₂-F₃), and b_{po} (F₃-F₄). Realized heritability was calculated using F₂ (or F₃) plants and their respective F₃ (or F₄) progeny means.

Results and Discussions

Response to selection

After the 1st cycle of selection, the F_3 family means of stomata frequency ranged from 78.224 to 82.757 in the low direction of population1 with an average of 81.232 versus 85.8 for the F_3 bulk, indicating a significant reduction 5.36% from the bulk mean. Meanwhile, the family means in the high direction ranged from 99.2 to 100.2 with an average of 99.6, indicating a significant increase 16.03% from the bulk mean (Tables and Figs.1 and 2). Similar significant responses of 7.25% and 11.63%

respectively were also observed in population 2 (Tables 1 and 2). In both populations there were highly significant differences between the mean of high and low selections (Table 2).

| Table(1): Means of stomata frequency (stomata/mm ²) for different families |
|---|
| selected for high and low stomata frequency in populations 1 and |
| 2 in the first (F_3) and second (F_4) cycles of selection. |

| | | stomata frequency | | | | | |
|---------------------|--------------|-------------------|----------|----------|----------|--|--|
| Selection direction | Families No. | F | 3 | F_4 | | | |
| | | Pop. (1) | Pop. (2) | Pop. (1) | Pop. (2) | | |
| | 1 | 82.716 | 76.940 | 79.0257 | 85.517 | | |
| Low | 2 | 82.757 | 73.169 | 80.470 | 78.173 | | |
| | 3 | 78.224 | 76.539 | 77.261 | 78.173 | | |
| | 1 | 99.244 | 89.456 | 96.997 | 93.473 | | |
| High | 2 | 99.364 | 90.218 | 95.393 | 93.228 | | |
| | 3 | 100.166 | 92.865 | 93.547 | 90.046 | | |
| Bulk | 85.829 | 81.377 | 84.562 | 87.129 | | | |
| Mean Lov | 81.232 | 75.549 | 79.293 | 80.621 | | | |
| Mean Hig | 99.592 | 90.846 | 95.313 | 92.249 | | | |

The observed average responses to selection which amounted to 11.63% 16.03% and of the population mean were consistently higher than the expected 8.29% and 5.598% in the high stomata frequency direction of populations 1 and 2 respectively (Table 3). Such observed responses in the low direction were 5.36% and 7.16% as compared to the expected responses 6.96 and 5.50% in the two populations indicating that the higher than expected responses occurred in the late heading population 2 (Table 3). Such inflated observed responses in the high direction might be attributed to dominance, epistasis or G x E

Evidently, (Walsh. 2005). the contribution from epistasis is due to favorable combinations of alleles at different loci, specifically those alleles that interact epistatically to change the character in the direction favored by selection. According to Wilson (1972), selection was more successful for frequent than for infrequent stomata in Lolium perenne grown in controlled environment.

Asymmetrical responses to selection were evident with the deviation in the high direction being greater than in the low direction in the F_3 (Tables and Figs.1 and 2). According to Tewolde *et.al.*, (2006),

Table (2): Analysis of variance for stomata frequency in different families: family1, family2 and family3 selected for high and low stomata frequency in both populations in the first (F_3) and second (F_4) cycles of selection.

| L | Low direction High direction Ov | | | | | er all pop | ulation | | |
|-----------------------|---------------------------------|-----------|----------|------------|-----------------------|------------|---------|-------------|--|
| F ₃ | | | | | | | | | |
| Population 1 | | | | | | | | | |
| S. O. V. | d.f. | M.S. | S. O. V. | d.f. | M.S. | S. O. V. | d.f. | M.S. | |
| Blocks | 2 | 0.8381 | Blocks | 2 | 5.1421 | Blocks | 2 | 2.4049 | |
| Families | 3 | **29.4286 | Families | 3 | **142.5477 | Families | 5 | **311.8013 | |
| L vs B | 1 | **47.5508 | H vs. B | 1 | **426.1338 | L vs. H | 1 | **1516.7621 | |
| among L | 2 | **20.3675 | among H | 2 | 0.7547 | among L | 2 | 20.3675 | |
| | | | | | | among H | 2 | 0.7547 | |
| <u> </u> | | | | Popula | | | | | |
| Blocks | 2 | 1.7690 | Blocks | 2 | 11.3203 | Blocks | 2 | *22.8633 | |
| Families | 3 | **34.0463 | Families | 3 | *73.6626 | Families | 5 | **219.5902 | |
| L vs B | 1 | **76.4048 | H vs. B | 1 | **201.7708 | L vs H | 1 | **1053.0002 | |
| among L | 2 | 12.8671 | among H | 2 | 9.6085 | among L | 2 | 12.8671 | |
| | | | | | | among H | 2 | 9.6085 | |
| | | | | F 4 | | | | | |
| | | | | Popula | tion 1 | | | | |
| Blocks | 2 | 10.3805 | Blocks | 2 | 7.2525 | Blocks | 2 | 5.3455 | |
| Families | 3 | 29.0481 | Families | 3 | **92.6441 | Families | 5 | **248.5515 | |
| L vs B | 1 | *71.6446 | H vs. B | 1 | **260.0510 | L vs. H | 1 | **1209.3767 | |
| among L | 2 | 7.7498 | among H | 2 | 8.9406 | among L | 2 | 7.7498 | |
| | | | | | | among H | 2 | 8.9406 | |
| Population 2 | | | | | | | | | |
| Blocks | 2 | 1.6258 | Blocks | 2 | 17.8513 | Blocks | 2 | 13.7109 | |
| Families | 3 | *67.7186 | Families | 3 | 26.9753 | Families | 5 | **147.6513 | |
| L vs B | 1 | **95.2859 | H vs. B | 1 | 58.9922 ^{ns} | L vs. H | 1 | **608.4530 | |
| among L | 2 | 53.9349 | among H | 2 | 10.9668 | among L | 2 | 53.9349 | |
| | | | | | | among H | 2 | 10.9668 | |

L= low direction; H= high direction; and B= bulk

early heading, which was characterizing population 1 in this study, is an important and effective single trait defining wheat cultivars adapted to production systems prone to high temperature stress during the post-heading period. Successful selection was expected since Wilson (1971) and Subhani and Chowdhry

(2000) found a considerable additive genetic variation for stomata Bkagwat and frequency. Bhatia (1993) also obtained two selections in the F_9 generation exhibiting significantly higher stomata frequencies than the higher parent. Such successful selection was also expected since both additive and

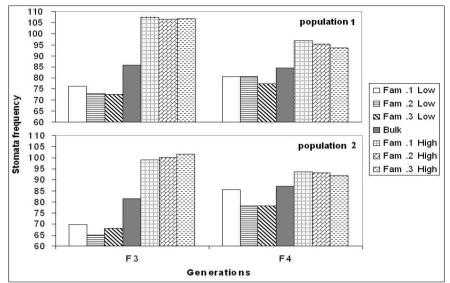


Fig. (1): Means of selected families for high and low stomata frequency (stomata/mm²) in populations 1 and 2 in the first (F_3) and second (F_4) cycles of selection.

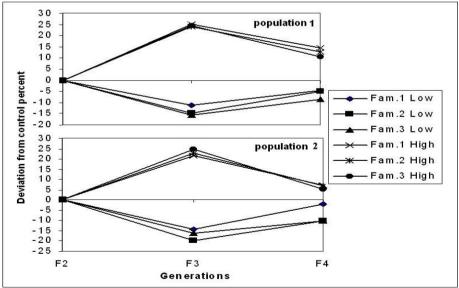


Fig. (2): Stomata frequency deviation percentage from the bulk sample for families selected for high and low directions in populations 1 and 2 in the first and second cycle of selection (F₃ and F₄).

non-additive variances were controling stomata frequency (Iqbal, 2004, and Riaz 2003), additive gene action along with partial dominance was reported by Tahir et. al., (1995) and Ambreen et. at.. (2002).The inconsistent results obtained in this study might be attributable to random genetic drift and/or to the presence of (G x E) which was reported to affect such a trait in alfalfa leaves (Gindel. 1968).

Variances within selected families were not significantly different from those of the bulk which was rather unexpected in the high and low directions of the late flowering populations 2 (Table 3). A similar trend was obtained, in one of the three families, in the low and high directions, while the other two families showed reduced variances in population 1. As rare alleles might have increased in frequency due to the genetic drift, the frequency of the extreme genotypes might have increased and so inflated the additive variance.

The narrow sense heritability calculated by parent-offspring regression was moderate ($h^2=0.45$) in population 1 but low ($h^2=0.266$) in population 2. However, the realized heritability was higher in the high direction, reflecting the effect of inflated responses to selection, and lower in the low direction (Table 3). These results are in accordance with those of Riaz (2003) who found moderate narrow-sense heritability (0.52) under drought stress. As well, heritability for stomata frequency based on parent-progeny regression was reported to be 0.42 (F_3 — F_4) which increased to 0.81 (F_4 — F_5) in bread wheat (Bkagwat and Bhatia, 1993). However, Iqbal (2004) obtained high narrow and broad– sense heritability estimates of 0.89 and 0.94 for such a trait in spring wheat under non-stressed conditions.

significant The responses obtained in the first cycle of selection under heat stress prompted the superimposition of moisture stress, which concurrently occurs with sporadic heat waves in arid regions, in the second cycle of selection. Family means of stomata frequency ranged from 77.26 to 80.47 in the low direction with an average of 79.29 and ranged from 93.55 to 97.00 with an average of 95.313, in the high direction, versus 84.56 for the bulk of population 1 (Table1). After the second cycle of selection, the significant observed response which averaged 12.71% of the population mean was higher than the expected 9.48% in populations 1 in the high stomata frequency direction (Table 2 3). The observed average and response of 9.39% exceeded also the expected 5.01% in population 2 in the high direction but such difference was not significant (Table 3 and 2). the low stomata frequency In direction observed responses 6.67% and 9.42% respectively, were higher

M. M. El-Defrawy (2006)

than those expected 5.32% and 3.63% in population 1 and 2, respectively. Generally, the difference between high and low direction was highly significant all over the cycles of selection in both populations (Table2).

Responses to selection in the second cycle were less than those obtained in the first cycle which might probably be due to the effect of drought on stomata frequency per wheat leaf in accordance with Ouarrie and Jones (1977) who found that water stress reduced the number of stomata per leaf. Moisture stress decreased also the length and breadth of stomata, leaf water potential and relative water content in Solanum melongena L. (Prakash and Ramachandran, 2000). The variety with the lesser stomatal frequency and higher total leaf resistance to water loss had nevertheless faster net photosynthesis than the variety with the greater stomatal frequency. demonstrating the importance of the so-called mesophyll resistance in maize (Heichel, 1971).

Generally, there were no significant differences between selected and bulk variances overall families and populations in the second cycle of selection which might be due also to the severe stress to which plants were exposed. Heritability was also inflated whether calculated parentas realized offspring regression or

lend heritability which further additive support to the inflated variance. The narrow-sense calculated as parentheritability offspring regression was moderate $(h^2=0.497)$ in population 1 and low $(h^2=0.363)$ in population 2, but still higher than those observed in the first cycle of selection. Similar increase for h^2 of this trait was reported by Bkagwat and Bhatia, (1993). Here again, the realized heritability was higher (0.620) in the low stomata direction of population 2, reflecting the inflated response to selection and indicating that drought stress reversed the situation which was apparent in the first cycle of selection in this population. In the other cases, the realized heritability became slightly higher than those estimated by parent-offspring regression basis. For some abiotic stresses and many biotic stresses, higher in heritability was the presence of stress (Baker, 1993). Kanemasu et. al., (1969) have reported that varieties that offer more resistance to water flow from stomata into the atmosphere have beneficial traits towards drought tolerance. Drought improved watersoluble carbohydrates mobilization efficiency in the peduncle. penultimate, and lower internodes by 33, 17, 11%, respectively (Ehdaie et. al., 2006). Prior exposure to drought stress (drought preconditioning) affected turfgrass tolerance to subsequent heat stress (Jiang and Huang 2000, 2001).

Drought stress resulted in a significant increase in the thermal stability of Photosystem II in wheat (Dulai *et. al.*, 2006).

By comparing the absolute mean values, it was apparent that a significantly higher stomata frequency was reached in population 1 than that in population 2 after the second cycle of selection (Tables Whereas. significant 1&4). no difference was detected between the low direction in population 1 and that of population 2, the bulk exhibited also a similar trend (Tables 1&4). These results indicated the success of divergent selection for changing this trait under both heat drought and stresses. Further responses to selection based on 13.33% selection intensity are expected to amount to 7.04% and 9.61% in the low and high stomata directions, respectively in population 1, and to 5.60% and 6.58% in the low and high stomata directions. respectively in population 2 under both heat and drought stresses in the third cycle of selection.

Table(4): Testing the differences between population 1 (Pop.1) and population 2 (Pop.2) means for stomata frequency, grain yield per plant and 100-kernel weight among the selected families in the low direction [Low(Pop.1) - Low(Pop.2)], in the high direction [High(Pop.1) - High(Pop.2)] and among non-selected bulks [Bulk(Pop.1) - Bulk(Pop.2)] after the second cycle of selection.

| | Obtained t values for each character | | | | | |
|----------------------------|--------------------------------------|--------------------------|----------------------|--|--|--|
| Pop.1 mean – Pop.2 mean | Stomata frequency | Grain yield per plant | 100-kernel weight | | | |
| Low(Pop. 1) - Low(Pop.2) | -1.25 | -5.74** | 3.47** | | | |
| High(Pop. 1) - High(Pop.2) | 2.02* | -7.54** | 9.01** | | | |
| Bulk(Pop. 1) - Bulk(Pop.2) | -1.2 | -4.2** | 5.8** | | | |

t test for [Pop.1 mean – Pop.2 mean] : *= significant (P<0.05), **= highly significant (P<0.01)

Correlated response to selection

I- 100-kernel weight

Correlated responses in 100kernel weight for the different families selected for the high and low stomata frequency directions in populations1 and 2 in the first and second cycles of selection are presented in Table (5). The first cycle of selection did not produce correlated responses in 100-kernel weight in population 1 in either Both high directions. and low selections did not deviate from each from other or the control. Meanwhile, significant reductions of 1.37% and 2.51% of the bulk mean were obtained in the low and high directions respectively, in population 2 (Tables 5 and 6). selected Surprisingly, families within low direction in population 1 and both low and high directions in population 2 showed significantly different performances as revealed by the highly significant among low as well as among low and high families mean squares (Table 6), indicating different genetic for assimilate potentialities partitioning in these families. The different performances of selected families might reflect their differential sensitivities to elevated temperatures or light conditions after anthesis. Schlüter et. al., (2003) working with а mutant of Arabidopsis sdd1-1 having 2.5-fold higher stomatal densities reported that upon exposing it to constant light intensities it did not differ significantly from the wild type. Whereas, plants receiving low light quantities during their development of the photosynthetic apparatus, elevated stomatal density caused only minimal differences in stomatal conductance since the synthesis of involved many proteins in photosynthesis, for example Rubisco, depends on stimulation by light. They concluded that stomatal

initiation could be of particular importance for plants where leaves develop over a relatively short period but serve longer as a source of carbohydrates. This study stresses upon the other systems governing assimilates accumulation in addition stomata frequency. Such to which might conditions have occured due to enhanced growth by high temperatures in this study may explain the differential assimilates accumulation in selected families in high and low directions. Meanwhile, high temperature of soil alone (26/38°C) or high temperature of both air and soil (38/38°C) caused a reduction in the chlorophyll content grain-filling duration. and and increased carbohydrate remobilization. Genotypic differences in the responses to high soil temperature and high air/soil temperature were also observed (Tahir et. al., 2006). Evidently, moderate to high heat stress at mid-grain fill increased thousand kernel weight. However, higher heat stress under controlled environment caused a decrease in thousand kernel weight, without any difference in relation to duration or timing of stress (Castro 2006). Cereals possess a degree of developmental plasticity that allows for increases in kernels/spike or kernel weight to compensate for losses in tiller number if conditions environmental and assimilate availability improves after the stem elongation stage (Kirby and Jones, 1977).

Table (5): Means of 100-kernel weight for different families selected for high and low stomata frequency in populations1 (Pop.1) and 2 (Pop.2) in the first (F₃) and second (F₄) cycles of selection.

| (10).2) in the first (13) the second (14) cycles of selection. | | | | | | | |
|--|--------------|-------------------|---------|---------|---------|--|--|
| | | 100-kernel weight | | | | | |
| Selection direction | Families No. | F | 3 | F_4 | | | |
| | | Pop (1) | Pop (2) | Pop (1) | Pop (2) | | |
| | 1 | 4.99 | 4.18 | 4.82 | 4.61 | | |
| Low | 2 | 4.98 | 3.89 | 4.69 | 4.19 | | |
| | 3 | 4.47 | 3.70 | 4.64 | 4.19 | | |
| | 1 | 4.71 | 4.04 | 4.99 | 4.46 | | |
| High | 2 | 4.75 | 4.19 | 4.86 | 4.33 | | |
| | 3 | 4.80 | 3.80 | 5.42 | 4.04 | | |
| Bulk | 4.82 | 4.13 | 4.87 | 4.39 | | | |
| Mean Low | 4.81 | 3.92 | 4.72 | 4.33 | | | |
| Mean High | 4.75 | 4.01 | 5.09 | 4.28 | | | |

Table (6): Summary of the analysis of variance for 100-kernel weight in different families selected for high and low stomata frequency in populations1 and 2 in the first (F₃) and second (F₄) cycles of selection.

| Low direction | | | High direction | | | Over all population | | |
|---------------|------|-----------|----------------|--------|-------------|---------------------|------|------------|
| F_3 | | | | | | | | |
| Population 1 | | | | | | | | |
| S. O. V. | d.f. | M.S. | S. O. V. | d.f. | M.S. | S. O. V. | d.f. | M.S. |
| Blocks | 2 | 0.3469 | Blocks | 2 | 0.8575 | Blocks | 2 | 0.2180 |
| Families | 3 | 17.8524** | Families | 3 | 0.7554 | Families | 5 | 11.2655** |
| L vs B | 1 | 0.0239 | H vs B | 1 | 1.1406 | L vs H | 1 | 1.6684 |
| among L | 2 | 26.7667** | among H | 2 | 0.5628 | among L | 2 | 26.7667** |
| | | | | | | among H | 2 | 0.5628 |
| | - | | Р | opulat | | | | |
| Blocks | 2 | 5.7891 | Blocks | 2 | 9.5947** | Blocks | 2 | 11.0689** |
| Families | 3 | 14.7110** | Families | 3 | 8.5184** | Families | 5 | 12.0299** |
| L vs B | 1 | 9.7095* | H vs B | 1 | 3.2616* | L vs H | 1 | 3.4322 |
| among L | 2 | 17.2117** | among H | 2 | 11.1468** | among L | 2 | 17.2117** |
| | | | | | | among H | 2 | 11.1468** |
| | | | | F_4 | ŀ | | | |
| | | | Р | opulat | tion 1 | | | |
| Blocks | 2 | 0.044636 | Blocks | 2 | 0.003417 | Blocks | 2 | 0.002214 |
| Families | 3 | 0.036223 | Families | 3 | 0.202729 | Families | 5 | 0.238179* |
| L vs B | 1 | 0.05728 | H vs B | 1 | 0.105625 | L vs H | 1 | 0.636944** |
| among L | 2 | 0.025694 | among H | 2 | 0.251281 | among L | 2 | 0.025694 |
| | | | | | | among H | 2 | 0.251281* |
| | | | Р | opulat | tion 2 | | | |
| Blocks | 2 | 0.002615 | Blocks | 2 | 0.024214 | Blocks | 2 | 0.018389 |
| Families | 3 | 0.125961 | Families | 3 | 0.1035 | Families | 5 | 0.131893* |
| L vs B | 1 | 0.009801 | H vs B | 1 | 0.030976 | L vs H | 1 | 0.011858 |
| among L | 2 | 0.184041* | among H | 2 | 0.139761 | among L | 2 | 0.184041* |
| | | | | | h direction | among H | 2 | 0.139761* |

L= low direction; H= high direction; and B= bulk

After the second cycle of selection, a highly significant difference was obtained between high (5.09g) and low (4.72g) stomata directions for 100-kernel weights, although each of which did not deviate significantly the control (4.87g)from in populations 1. By comparing the absolute mean values, it was apparent that a significantly higher 100-kernel weight was reached in population 1 than that in population 2 after the second cycle of selection in the low and the high direction as well as the two bulks (Tables 5 and 4). Kernel weight can be reduced when the length of the grain filling period is restricted by drought and heat stress after anthesis (Warrington et al., 1977). These results are also in accordance with Guttieri et. al., (2001) who suggested that the overall moisture-deficit-induced reduction in vield was primarily due to reduction in kernel weight. According to Duggan and Fowler, (2006) large differences in kernels/spikelet and kernel weight indicated that these two variables were responsible for yield adjustments to dryland stress during the spikelet and kernel development phase. Hundred-kernel weight is a vital vield component and is more or less stable character of wheat cultivars. Under drought 100- kernel weight may be affected to a greater extent due to the shortage of moisture which forces plants to complete its grain formation in relatively lesser time (Riaz, 2003).

Such results might suggest that selection operating on the genetic system underlying the control of stomata frequency and 100-kernel weights might have changed their allelic frequencies differently, genetic drift have also also been responsible for such differential performances or that the other systems controlling photosynthesis show plasticity in this regard.

Grain yield/plant

No correlated response to selection for stomata frequency were obtained grain vield/plant. However, in significant differences were detected among families selected for high and low stomata frequency in population 2 after the first cycle of selection, differential indicating assimilates partitioning among these families as was previously observed for100kernel weight (Tables 7 and 8). Following the first cycle of selection, means of grain yield/plant in low stomata frequency direction (25.92g and 31.06g) were slightly higher than those of the high (23.82g and 27.54g) as well as those of the bulk (24.55 g and 25.94 g) in population 1 and 2 respectively. However. such differences non-significant. were After the second cycle of selection, such slight increases over the bulk disappeared in population 1 where both high (19.79g) and low (20.91g)stomata frequency directions were slightly lower in grain yield (21.42g for the bulk). Whereas, in population

| Grain vield | | | | | | | | |
|---------------------|--------------|---------|---------|----------------|---------|--|--|--|
| Selection direction | Families No. | F | | F ₄ | | | | |
| | | Pop (1) | Pop (2) | Pop (1) | Pop (2) | | | |
| | 1 | 26.73 | 35.75 | 21.25 | 31.55 | | | |
| Low | 2 | 24.89 | 32.02 | 20.06 | 35.94 | | | |
| | 3 | 26.13 | 25.41 | 21.43 | 34.39 | | | |
| | 1 | 21.54 | 24.05 | 20.18 | 34.86 | | | |
| High | 2 | 22.87 | 24.83 | 17.03 | 31.66 | | | |
| | 3 | 27.04 | 33.75 | 22.17 | 38.35 | | | |
| Bulk | 24.55 | 25.94 | 21.42 | 31.02 | | | | |
| Mean Low | 25.92 | 31.06 | 20.91 | 33.96 | | | | |
| Mean High | 23.82 | 27.54 | 19.79 | 34.96 | | | | |

Table (7): Means of grain yield for different families selected for high and low stomata frequency in populations1 (Pop.1) and 2 (Pop.2) in the first (F_3) and second (F_4) cycles of selection.

Table (8): Summary of the analysis of variance for grain yield in different families selected for high and low stomata frequency in populations 1 and 2 in the first (F_3) and second (F_4) cycles of selection.

| L | | Low direction High direction Over all | | | | | all noni | lation | |
|----------------|--------------|---|----------|----------|----------|----------|----------|--------------|--|
| F ₃ | | | | | | | an popu | nation | |
| | Population 1 | | | | | | | | |
| S. O. V. | · · · | | | | | | | M.S. | |
| Blocks | 2 | 3.4668 | Blocks | 2 | 5.6774 | Blocks | 2 | 5.9015 | |
| Families | 3 | 3.1801 | Families | 3 | 16.8750 | Families | 5 | 14.9175 | |
| L vs B | 1 | 4.2244 | H vs B | 1 | 1.1983 | L vs H | 1 | 19.8450 | |
| among L | 2 | 2.6579 | among H | 2 | 24.7134 | among L | 2 | 2.6579 | |
| | | | | | | among H | 2 | 24.7134 | |
| | | | Po | opulatio | n 2 | | | | |
| Blocks | 2 | 8.1948 | Blocks | 2 | 24.2596 | Blocks | 2 | 19.2149 | |
| Families | 3 | 74.4321* | Families | 3 | 60.0083* | Families | 5 | 78.8671* | |
| L vs B | 1 | 58.9824 | H vs B | 1 | 5.7600 | L vs H | 1 | 55.7568 | |
| among L | 2 | 82.1569* | among H | 2 | 87.1324* | among L | 2 | 82.1569* | |
| | | | | | | among H | 2 | 87.1324* | |
| | | | | F_4 | | | | | |
| | | | Po | opulatio | n 1 | | | | |
| Blocks | 2 | 3.946209 | Blocks | 2 | 33.05287 | Blocks | 2 | 57.76961 | |
| Families | 3 | 1.302369 | Families | 3 | 15.40945 | Families | 5 | 9.846337 | |
| L vs B | 1 | 0.583187 | H vs B | 1 | 5.987809 | L vs H | 1 | 5.667222 | |
| among L | 2 | 1.66196 | among H | 2 | 20.12027 | among L | 2 | 1.66196 | |
| | | | | | | among H | 2 | 20.12027 | |
| | | | | | | | I | Population 2 | |
| Blocks | 2 | 74.4391 | Blocks | 2 | 34.77211 | Blocks | 2 | 95.27161 | |
| Families | 3 | 16.42155 | Families | 3 | 34.05137 | Families | 5 | 20.29937 | |
| L vs B | 1 | 19.47996 | H vs B | 1 | 34.91234 | L vs H | 1 | 4.470382 | |
| among L | 2 | 14.89235 | among H | 2 | 33.62089 | among L | 2 | 14.89235 | |
| | | y U- high | | | | among H | 2 | 33.62089 | |

L= low direction; H= high direction; and B= bulk

2 both high (34.96g) and low (33.96g) stomata frequency directions were higher in grain yield versus 31.02g in the bulk of F_4 , but again the differences were non-significant. It seems that the relationship between stomata frequency and yield is tenuous. By comparing the absolute mean values, it was apparent that a significantly lower grain yield per plant was reached in population 1 than that in population 2 in the second cycle of selection in the low and the high direction as well as the two bulks (Tables 7&4). Evidently, selection for one trait (stomata frequency) might not affect other traits (100-kernel weight and grain yield) since high temperature significantly decreased grain yield by decreasing grain weight (Tahir. et. al., 2006).

No correlated responses were detected for leaf area, which did not differ among selected families and from the bulk (analysis of variance not presented) in disagreement with Bkagwat and Bhatia (1993) who found that stomata frequency was negatively correlated with the flag leaf blade area. It appears that leaf area generally decreased in the same way all over selected families and bulks due to the severe drought stress which blurred the variability in this trait in accordance with (Fischer, 1984) who reported that if growth resources (water, nutrients and radiation) are limited under heat stress, then the size of plant organs such as leaves, tillers, and spikes is reduced. Moreover, (Mosaad et. al., 1995) reported that leaf area decreased with increasing moisture stress in *Triticum aestivum* and *T. durum*.

The paucity and partial information generated by stomata frequency studies, are due to the tedious work needed and its' hard applicability to great number of genotypes which diminish its use in large scale breeding programs and urge for more studies offering new avenues for crop improvement using marker assisted selection. We are still far from having a comprehensive understanding of how crops respond to temperature (White and Reynolds, 2001). Results demonstrated that heat tolerance of common wheat is controlled by multiple genes and marker-assisted suggested that selection with microsatellite primers could be useful in accelerating selection studies and developing improved cultivars (Yang et al., 2002). The genetic architecture of sotmata frequency should be dissected into a genetic network of interacting loci .These interactions, explored by epistatic QTL mapping, in a radial network may mediate a considerably larger selection response than predicted. А more in-depth genome-wide understanding of mechanisms necessitates explorations beyond the statistical estimates of these QTL effects. The ability of the loci in their network to release or suppress genetic variation is also related to the mechanisms shown by capacitors of cryptic genetic variation that have been described earlier in situations resulting from induced environmental or genetic perturbations (Carlborg et. al., 2006). genomic Stress-induced responses give more insight about transposon activation, transposition, and structural genome changes which may explain such unexpected selection results. Like other stress responses transposon-mediated alterations in transcriptional activity of affected genes might lead to avoidance or tolerance of the stress. Unlike many other stress responses, however. transpositional activation is a hit-ormiss approach to finding an appropriate way of handling an unusual challenge Madlung and Comai (2004). Using genetic mapping to dissect the inheritance of different complex traits. using molecular techniques, in the same segregating population can be a powerful means to distinguish common heredity from casual associations between such traits and might be a good alternative (Schlüter et. al., 2003).

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تأثير الانتخاب لتكرار الثغور على خصائص المحصول تحت الاجهادات الحرارية والمائية في قمح الخبز (Triticum aestivum L) . محد محمود حسيب الدفراوي

قسم الوراثة، كلية الزراعة، جامعة أسيوط، أسيوط، جمهورية مصر العربية

تعتبر الثغور المنتشرة على أوراق النبات مصدرا هاما لخفض درجة الحرارة بكنف النباتات، ولذا استخدمت عشيرتين في الجيل الثاني، إحداهما مبكرة الإزهار والثانية متأخيرة الإزهار ، لإجراء دورتي انتخاب في اتجاهين متعاكسين لصفة تكرار الثغور على ورقة العلم في نبات القمح. وقد عرضت النباتات للإجهادات الحراية والمائية وتم الانتخاب لمعرفة مدى ذلك في فصل العشيرة إلى عائلات مختلفة ومدى تأثير ذلك على خصائص المحصول. وجمعت أوراق علم من خمس سوق رئيسة في وقت إنتثار حبوب اللقاح ثم جمعت تلك النباتات لتقدير محصول الحبوب ووزن المائة حبة فيها عند النصج.

وكانت متوسطات الاستجابة المشاهدة للانتخاب في الدورة الأولى في العشيرة الأولى ومانت متوسطات الاستجابة المشاهد (المقارنة) أكبر من المتوقعة 2.9% و 5.59% في العشيرتين الأولى والثانية على التوالي في اتجاة زيادة تكرار الثغور. بينما ظهرت زيادة الاستجابة المشاهدة 7.16% عن المتوقعة 5.50% فقط في اتجاة نقصان الثغور في العشيرة الرابعة. ومن المحتمل أن تعزى تلك الزيائدة المتضخمة إلى السيادة والتفوق أو التفاعل بين الوراثة والبيئة. وكانت الإستجابة للإنتخاب غير متناظرة، إذ كان انحراف الإتجاة المزيد للثغور أكبر من الإتجاة المنقص لها. وكان معامل التوريث بالمعنى الضيق محسوبا كارتداد الأبناء على متوسط الأباء أعلى في العشيرة الأولى 0.45 عنة في الثانية 6.26% ، بينما كان معامل التوريث المتحقق أعلى في الاتجاة المزيد عن المنقص في العشيرتين على التوالي.

وكانت الاستجابة المشاهدة 12.71% و 9.39% في صورة انحراف عن الشاهد أكبر من المتوقعة في العشيرتين الأولى والثانية على التوالي في دورة الانتخاب الثانية في اتجاة زيادة الصفة. كما كانت الاستجاب المشاهدة أعلى في اتجاة نقصان الصفة 6.67% و 9.42% في العشيرتين على التوالي. وكان الفرق بين الاتجاة المزيد والمنقص للصفة معنويا جدا في العشيرتين مما يشير إلى جدوى الانتخاب. كما كان معامل التوريث بالمعنى الضيق أعلى في العشيرة الأولى 0.50 عنة في العشيرة الثانية 6.06. وكان معامل التوريث المتحقق أعلى في اتجاة زيادة 20.0 عنة في اتجاة في العشيرة الثانية 6.01. وكان معامل التوريث المتحقق أعلى في التقاريث المتحقق تجاة في العشيرة الأولى ومن المتوقع الحصول على مزيد من الاستجابة للإنتخاب فيما لو أجريت دورة ثالثة لو استخدمت شدة انتخاب 13.33% وباستخدام معامل التوريث المتحقق تغيرا ملموسا في الدورة الثانية من الانتخاب بمقدار 0.70% و 9.10% في الاتجاة المنقص والمزيد للثغور في المعثيرة الأولى و 5.60% و 5.8% وياستخدام معامل التوريث المتحقق المتحصل علية

وعموما كان وزن المائة حبة أعلى في نهاية التجربة في العشيرة الأولى منه في العشيرة الثانية في المنتخبات والشاهد بينما كان العكس حادثا بالنسبة للمحصول في اتجاة نقصان تكرار الثغور، إذ كان هذا الفرق معنويا فقط في اتجاة زيادة تكرار عدد الثغور حيث ادى الانتخاب إلى تكرار أعلى في العشيرة الأولى منه في الثانية. ولم يظهر الانتخاب الناجح والمعنوي لزيادة أو نقصان الثغور إلى أي استجابة متلازمة في وزن المائة حبة أو المحصول.