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# THE INHERITANCE OF YIELD AND YIELD COMPONENTS OF FIVE WHEAT HYBRID POPULATIONS UNDER DROUGHT CONDITIONS

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## ABSTRACT

The magnitude of genetic inheritance and expected genetic advance are important for the prediction of response to selection in diverse environments and provide the basis for planning and evaluating breeding programs. This work investigated the inheritance of traits related to drought in wheat under natural drought conditions. Cross combinations were made to produce $F_1$ and $F_2$ hybrid populations, which were evaluated in a randomized completed block design with three replications at University of Agriculture, Faisalabad, Pakistan. Six wheat varieties/lines and six derived $F_2$ hybrids were studied to ascertain heritability and genetic advance for plant height, days taken to maturity, number of tillers per plant, spike length, number of grains per spike, 1000-grain weight, and grain yield per plant. Data were collected and subjected to statistical genetic analyses. Heritability estimates and expected genetic advance for plant height, days taken to maturity, number of tillers per plant, 1000-grain weight and grain yield per plant were high for the entire cross combinations while the estimates for spike length and number of grains per spike were relatively low. Our results suggest that improvement for these characters should be faster because of higher heritabilities and greater phenotypic variation. Prospects of genetic improvement for all the characters studied are evident. The most promising cross combinations were WL60 × LU26S and WL61 × LU26S. These traits, therefore, deserve better attention in future breeding programs for evolving better wheat for stress environments.

[*Keywords*: *Triticum aestivum*, plant breeding, drought resistance, yield components, genetic gain, heritability]

## INTRODUCTION

There has been a phenomenal increase in wheat production during the last three decades. The unprecedented rise in productivity and production of wheat owes a great deal to the short stature wheat introduced in the mid sixties. The major benefits of this green revolution were, however, harvested under high fertility irrigated conditions. These rapid initial gains attracted most of the breeders to evolve wheat technology for rich optimal agronomic conditions, which certainly was the right approach to achieve much needed food autarky. But due to limited irrigation network, almost entire fresh addition to wheat acreage has been managed from marginal moisture stricken areas. Almost one third of which is devoid of any supplemental irrigation and depends entirely on the winter rains which are often erratic and obviously vulnerable to spontaneous fluctuations in weather elements moreover, not judiously distributed over the wheat growth span. Atmospheric water and soil moisture often coupled with sharply ascending temperatures towards maturity frequently cause steep decline in wheat production.

Assurance of optimal moisture at critical stages of growth and grain development can greatly minimize the losses inflicted by unfavorable temperature regimes. Research inputs for developing stress tolerant varieties have only been modest and the situation now calls for concerted efforts to develop technology for better production under drought conditions. This is well known that under severe and even moderate stress of moisture, wheat plant brings about certain morphological changes to withstand these conditions.

Several morphological parameters such as plant height, number of tillers per plant, days taken to maturity, number of spikelets per spike, number of grains per spike, 1000-grain weight and grain yield has been identified which in some way contribute to the moisture stress tolerance of the wheat plant. Drought stress reduces main stem height in crops by decreasing the number of nodes and/or internode length. Drought stress leads to a very low dry matter value because of decreased stem height and stem diameter associated with limited leaf expansion and reduced tiller number. It also decreases the number of spikelets in different ways and this reduction is closely correlated with lower dry matter produced. Low spikelet number is essentially linked to the decreased number of flower produced. Reduced number of grains per spike, grain weight and yield indicates that low dry matter accumulation was the main cause for low pod and seed number. Drought at grain filling stage reduces the cell size and number and results in shriveled grains with small size and reduced weight and early maturity (Day and Intlap 1970; Hang and Miller 1983; Cooper *et al.* 1994; Foulkes *et al.* 2001; Foulkes *et al.* 2002; Tretowan *et al.* 2002; Foulkes *et al.* 2004). Considerable work done on drought related characters of wheat have been reported by Campbell and Read (1968), Fischer and Tuener (1978), Kissana *et al.* (1982), and Hang and Miller (1983).

The measure of genetic variation and sufficient understanding of their mode and extent of inheritance is, therefore, important in planning and execution of a potent breeding project. The present research work was designed to identify some morphological characters having impact on drought tolerance and to estimate the extent of their heritability. The characters studied were plant height, number of tillers per plant, spike length, days taken to maturity, number of grains per spike, 1000-grain weight, and grain yield per plant. Reliable heritability estimates obtained through this research will not point to only the scope of assembling genetic characters imparting stress tolerance but also enable us to make predictions about the possible progress in this effort.

## MATERIALS AND METHODS

The experimental material was comprised of six varieties/lines of wheat namely LU26S, WL59, WL60, WL61, WL62, and WL63. LU26S was a famous variety of the irrigated areas having medium height, white bold grains; excellent bread making quality due to high gluten percentage and high yields was hybridized with other genotypes. These lines have profuse tillering, medium sized red colored grains and are best suited for drought areas.

Following cross combinations were made to raise $F_1$ and $F_2$ generations, namely: (1) WL59 × LU26S, (2) WL 60 × LU26S, (3) WL61 × LU26S, (4) WL62 × LU26S, and (5) WL 63 × LU26S. The $F_2$ progenies along with their parents were grown in the experimental area of Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan under natural drought conditions in a triplicate randomized complete block design. Seed was dibbled in 30 cm apart. Distance between plants was 22.5 cm. The experimental population received normal agronomic and plant protection care, except irrigation water. To maintain the identity, each plant was tagged and numbered. Three hundred plants from $F_2$ population of each cross (100 plants from each replication) and 30 plants from each parent (10 plants from each replication) were selected at random for recording data on the seven morphological traits like plant height, days taken to maturity, number of tillers per plant, spike length, number of grains per spike, 1000-grain weight, and grain yield per plant.

- Plant height of the main tiller at maturity was measured in centimeters from the base of the stem up to the apex excluding awn from the 100 plants from each replication and cross.
- Days taken to maturity were recorded from the time of complete emergence to the date when more than 50% plants were ready for harvest. Hundred randomly selected plants from each replication and cross were used for this purpose.
- Number of tillers per plant was counted from the randomly selected plants.
- Spike length of the main spike of the selected plant excluding awn was measured at maturity in centimeters. The plants used for recording data on tillering were also used for this parameter.
- Number of grains per spike was counted from the spikes used for measuring spike length. The total number of grains recorded was divided by the number of spikes, the average was computed.
- For 1000-grain weight, a single sample of 1000 grains was counted in grams from the yield of the selected plants.
- Regarding grain yield per plant, at maturity, all the randomly selected plants per cross and replication were harvested manually, threshed separately and their yield recorded in grams. The average yield was then computed. Data were tabulated. Means, standard deviations, variances and coefficients of variability for parents and $F_2$ populations were computed.

Heritability estimates in broad sense were computed using the formula described by Mahmud and Kramer (1951) as follows:

$$h^2 = \text{var. } F_2 - \sqrt{(Vp1 \times Vp2)} \,/\text{var. } F_2$$

Where:

$h^2$ = heritability
p1 = parent 1
p2 = parent 2,
var. $F_2$ = variance of $F_2$
Vp1 = variance of p1
Vp2 = variance of p2

Genetic advance at 10% selection intensity was calculated according to formula given by Burton and Devane (1953) as follows:

$$G = SD \times h \times i$$

SD = standard deviation
h = heritability
i = constant value that reflects the selection intensity. The value for i (1.7) in this study was used in 10% selection intensity.

## RESULTS AND DISCUSSION

Means, standard deviations, variances, coefficient of variability, heritability estimates and genetic advance values for various drought related traits in five wheat crosses are presented in Table 1 and 2. Heritability estimates for plant height were high in order. The cross WL59 × LU26S had the highest heritability estimate (90.93) followed by the cross WL60 × LU26S which had the value of (88.08). The lowest heritability estimate (75.19) was, however, observed from the cross WL63 × LU26S. The highest genetic advance value of 14.09 was observed in the cross WL59 × LU26S while the lowest 11.13 was observed in the cross WL61 × LU26S.

Plant height in wheat has been observed to be affected by moisture stress to a considerable extent. The varieties adapted to the water stress environments are generally short in stature as compared to the ones, which are adapted to optimal moisture conditions (Foulkes *et al.* 2004). The height of the culms, size of the leaves, the distance between the veins and the stomata openings are all affected when they are developing under limited water supplies. When wheat plants are stressed for water at vegetative and flowering stages, shorter plants are obtained, as a result of low moisture absorption, lower soil nutrient uptake, reduced cell size and reduced photosynthesis (Day and Intlap 1970; Sheikh *et al.* 2000). Heritability estimates computed for plant height in present study are in accordance with the findings of Fedin (1976) who reported high heritability estimates for this character.

Heritability estimates are fairly high for number of tillers per plant (Table 2). The highest value of 85.76 was obtained from the cross WL62 × LU26S followed by 83.40 from the cross WL60 × LU26S. The lowest value of 73.57 was obtained from the cross WL59 × LU26S. The highest genetic advance value of 10.33 was obtained from the cross WL60 × LU26S while the lowest value of 6.25 from the cross WL61 × LU26S.

Number of tillers per plant is also a drought related character. Tiller production is important in the development of plant and determines the productivity of the plant (Rajaram *et al.* 1996). Plants grown under moisture stress conditions produce less number of tillers compared to normal crop (Campbell and Read 1968). The results are also indicative that through proper selection procedures this character can be fixed in genotypes especially tailored for low moisture situations.

It is also obvious from Table 2 that there were moderate to high heritability estimates for spike length. The highest value of 80.75 was observed in the cross WL61 × LU26S, while the lowest 55.97 was formed in the cross WL62 × LU26S. The highest genetic advance value 2.53 was computed from the cross WL61 × LU26S while the lowest value 1.10 was obtained from the cross WL62 × LU26S.

Spike length is a character of considerable importance, as the larger spike is likely to produce more grains and eventually the higher yields per plant. Genotypes retaining larger spikes under moisture stress are likely to be more productive under stress environments (Foulkes *et al*. 2001). Better heritability values recorded point to the possibility of improvement in this parameter. Attention, therefore, may be focused on this important trait while synthesizing genotypes for stress stricken areas. The present

**Table 1. Means and standard deviations for various drought related traits in five wheat crosses.**

| Crosses/lines | Plant height (cm) | | Days taken to maturity | | No. of tillers/plant | | Spike length (cm) | | No. of grains/spike | | 1000-grain weight (g) | | Grain yield/plant (g) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| WL-59 × LU26S | 105.90 | 9.12 | 158 | 3.22 | 28.30 | 5.52 | 13.20 | 1.15 | 50.14 | 16.40 | 39.10 | 3.67 | 47.90 | 9.25 |
| WL-60 × LU26S | 104.40 | 8.98 | 166 | 3.43 | 22.80 | 7.49 | 12.40 | 1.28 | 47.46 | 15.55 | 47.30 | 2.21 | 51.40 | 12.70 |
| WL-61 × LU26S | 107.90 | 8.71 | 162 | 3.82 | 24.12 | 4.97 | 12.45 | 1.85 | 56.70 | 13.25 | 41.30 | 3.53 | 44.70 | 14.10 |
| WL-62 × LU26S | 103.16 | 8.44 | 160 | 3.62 | 31.61 | 7.05 | 12.98 | 1.16 | 76.90 | 14.06 | 47.30 | 2.12 | 49.75 | 13.27 |
| WL-63 × LU26S | 111.00 | 7.59 | 155 | 3.31 | 22.40 | 6.67 | 13.40 | 1.20 | 52.26 | 13.58 | 34.89 | 2.68 | 43.06 | 12.81 |

SD = standard deviation

**Table 2. Coefficients of variability, heritability estimates and genetic advance values for various drought related traits in five wheat crosses.**

| Crosses/lines | | Plant height (cm) | Days taken to maturity | No. of tillers per plant | Spike length (cm) | No. of grains per spike | 1000-grain weight (g) | Grain yield per plant (g) |
|---|---|---|---|---|---|---|---|---|
| WL59 × LU26S | CV% | 8.61 | 2.03 | 25.50 | 8.71 | 32.53 | 9.39 | 19.31 |
| | $h^2$ | 90.93 | 68.81 | 73.57 | 76.69 | 60.55 | 94.52 | 87.11 |
| | GA | 14.09 | 3.76 | 6.87 | 1.49 | 16.88 | 5.89 | 13.69 |
| WL60 × LU26S | CV% | 8.60 | 2.06 | 32.85 | 10.33 | 32.76 | 4.48 | 33.71 |
| | $h^2$ | 88.08 | 49.48 | 83.40 | 68.29 | 74.05 | 75.05 | 96.81 |
| | GA | 13.44 | 2.88 | 10.61 | 1.48 | 19.57 | 2.81 | 20.76 |
| WL61 × LU26S | CV% | 8.13 | 2.35 | 21.61 | 14.85 | 23.36 | 8.55 | 31.54 |
| | $h^2$ | 75.19 | 77.79 | 74.17 | 80.75 | 39.57 | 91.10 | 97.38 |
| | GA | 11.13 | 5.05 | 6.25 | 2.53 | 8.91 | 5.46 | 23.34 |
| WL62 × LU26S | CV% | 8.18 | 2.26 | 23.30 | 8.94 | 18.28 | 5.80 | 26.67 |
| | $h^2$ | 85.50 | 61.60 | 85.76 | 55.97 | 54.70 | 76.09 | 90.66 |
| | GA | 12.26 | 3.79 | 10.27 | 1.10 | 13.07 | 3.01 | 20.45 |
| WL63 × LU26S | CV% | 7.16 | 2.13 | 27.32 | 8.95 | 25.98 | 7.70 | 29.74 |
| | $h^2$ | 82.87 | 70.49 | 76.75 | 68.05 | 80.84 | 88.50 | 97.04 |
| | GA | 11.20 | 3.96 | 8.70 | 1.38 | 18.66 | 4.03 | 21.13 |

CV = coefficient of variability, $h^2$ = heritability, GA = genetic advance

results are in accordance with the earlier findings of Borojevic (1983) and Li and Yang (1985).

Moderate to high heritability estimates were noted for number of grains per spike (Table 2). In this study the highest estimate of 80.84 was obtained from the cross WL63 × LU26S while the lowest value of 39.57 was observed in the cross WL61 × LU26S. The highest genetic advance value of 19.57 was observed for cross WL60 × LU26S, while the lowest value of 8.91 was noted for the cross WL61 × LU26S.

Number of grains per spike is an important component of yield. Yield is the product of tillers per unit area, grains produced per spike and grain weight. So any change in grain number will ultimately affect yield (Rajaram *et al*. 1996). The wheat grown in drought stricken areas usually suffers a great deal on account of reduced number of grains per spike (Sharma and Bhargava 1996). Seed number is much more influenced by factors affecting the growth, but the influence of water limitation is more important. A water stress for 3 days, 2 days before ear emergence in wheat reduces seed number in proportion to the reduction in inflorescence weight (Fischer and Turner 1978). The wheat plants developing under water stress conditions gave reduced grain yield, due to reduction in heads per unit area and fewer seeds per head (Day and Intlap 1970). Sidwell *et al*. (1976) has also reported similar findings. From the present studies it is clear that sufficient variation for number of grains per spike was present in $F_2$ populations and effective selection for this trait could be practiced for improvement.

Table 2 also indicates that heritability estimates for days taken to maturity ranged from 49.48 to 77.79 with genetic advance values ranging from 2.88 and 5.05 for the crosses WL60 × LU26S and WL61 × LU26S respectively. Generally, the plants maturing early would escape the deleterious effects of environmental and soil drought as compared to the ones that mature late. Wheat plants stressed for water at different stages of growth matured earlier than the plants under normal conditions. It is evident that earlier maturity of wheat may be caused by soil moisture deficit during seed development (Day and Intlap 1970).

Keeping in view the heritability estimates recorded in the present studies, it can be stated that selection for this parameter can be effectively done in hybrid populations. However, one has to plan cautiously as drastic curtailment in growth period may provide an escape from drought injury but can also adversely affect the yield through reduced accumulation of total dry matter. Almost similar results have earlier been reported (Das and Rehman 1984).

Drought directly affects the development of grain that naturally leads to the lower grain weight, ultimately reducing yield. Moisture stress at different stages of plant development resulted in the greatest reduction in grain-volume weight (Day and Intlap 1970). The wheat plants growing under water stress conditions resulted in shorter plants, lower grain yield, lower grain-volume weight, fewer heads per unit area, and fewer seeds per head. It is obvious from Table 2 that the heritability estimates for 1000-grain weight were high in order. These results find support from the earlier studies reported (Reddi *et al*. 1969; Pathak and Nema 1985). In the present studies the highest heritability (94.52%) was obtained from the cross WL59 × LU26S and the lowest (75.05%) was derived from the cross WL60 × LU26S. The highest genetic advance value (5.89) was obtained from the cross WL59 × LU26S where as lowest (2.81) was observed from the cross WL60 × LU26S. The high heritability in the crosses reflected that effective selection for this character is possible in appropriate cross combinations and new varieties may be evolved possessing higher 1000-grain weight along with resistance against drought.

Grain yield per plant is a character of prime importance and of special interest to the wheat breeder. Moisture stress is ultimately reflected in the depressed yields. Magnitude of yield depression is perhaps the most practiced measure of drought resistance of wheat plant (Uddin *et al.* 1992; Cooper *et al*. 1994; Reynolds *et al*. 2001; Foulkes *et al*. 2004). Harvest index in wheat declines as water application decreases. The reduction in harvest index suggests that grain yield is more sensitive to water stress than total plant yield (Tretowan *et al*. 2002). When wheat plant was stressed for water the reduced grain yield was produced by fewer heads per unit area, few seeds per head and lighter seeds (Day and Intlap 1970; Hang and Miller 1983). Grain yield was affected more than any other plant characteristics by moisture stress at all stages of growth (Denmead and Shaw 1960). Robins and Domingo (1962) observed 10-35% reduction in yield of wheat under different stress conditions. Assessment of Table 2 also indicates high heritability values for grain yield per plant that ranged from 87.11% (WL59 × LU26S) to 97.38% (WL61 × LU26S) and genetic advance values ranged from 13.69 (WL59 × LU26S) to 23.34 (WL61 × LU26S). Both heritability estimates and genetic advance values were of high magnitude and indicate that effective selection for high yielding genotypes was possible in these segregating populations. Almost similar results were earlier obtained by Sethi and Singh (1972) and Kissana *et al*. (1982). Grain yield is a highly complex character controlled by polygenes. Yet due attention has not been given to evolve drought resistant varieties.

The present studies suggest that high yielding cultivars can be developed which will also have the potential to resist the drought. Cross combinations WL60 × LU26S and WL61 × LU26S have shown high heritability for most of the drought related characters under focus in this study. It would be worthwhile to concentrate attention on these crosses to obtain recombinants with high yield potential, greater drought resistance, and better adaptability.

The lower values of heritability for some crosses can be attributed to the higher contribution of the maternal effects on the expression of these traits (Roach and Wulff 1987). This may suggest that selection for these traits would be less effective in early generations. In contrast, the higher heritability values indicate the genetic control of these traits with no significant contribution to their expression from reciprocal effects. In various species such as peanut (Hubick *et al.* 1988), wheat (Condon and Richards 1992; Rebetzke *et al.* 2006), and cowpea (Menendez and Hall 1996), high heritability have been reported due to the absence of maternal effects. Predominantly high heritability should ensure effective selection at early generations of breeding programs.

High heritability alone is not enough to make sufficient improvement through selection generally in advance generations unless accompanied by substantial amount of genetic advance (Bhargava *et al.* 2003). The utility of heritability therefore increases when it is used to calculate genetic advance, which indicates the degree of gain in a character obtained under a particular selection pressure. Thus, genetic advance is yet another important selection parameter that aids breeder in a selection program (Shukla *et al.* 2004). It has been emphasized that without genetic advance, the heritability values would not be of practical importance in selection based on phenotypic appearance. So, the genetic advance should be considered along with heritability in coherent selection breeding programs (Johnson *et al.* 1955). However, in general, it is considered that if a character is governed by non-additive gene action, it may give high heritability but low genetic advance, whereas if the character is governed by additive gene action, heritability and genetic advance both would be high. Since, in the present study expected genetic advance values were based on broad sense heritability, which incorporate both additive and non-additive components of gene actions; much reliance cannot be placed on expected genetic advance. But, the traits, which had high heritability and also showed high expected genetic advance, could be substantially considered for making selections as these traits were mainly influenced by the major effects of additive gene action.

With knowledge, plant breeder can begin a more educated attempt to introduce these specific traits into more widely adapted genotypes and thus meet a goal for developing cultivars better adapted to dry land conditions. But the final test for any wheat variety for areas subjected to limited moisture supply will be found in whether it has ability to yield adequate returns under relatively dry conditions over a period of years.

## CONCLUSION

The genetic parameters discussed here are functions of environmental variability, so estimates may differ in other environments. Based on the high heritability and positive, moderately high additive genetic advance shown by the different characters, especially the plant height, 1000-grain weight and grain yield per plant components, we conclude that the determinant genetic effects of the phenotypic expression of these characters are fundamentally of the additive type. For this reason, a high response should be achievable after several selection cycles.

The development of varieties adapted to the arid conditions depends on improvement of potential yield and yield evaluation in differing environments. However, the inherent understanding of the limits of improving potential yield suggested that long range solution of yield improvement cannot be sustained by improving yield potential alone. Many other environmental variables should be controlled and optimized, so as to minimize the relative effect of genotype and environment interactions. In addition, the most promising cross combinations were WL60 × LU26S and WL61 × LU26S. These traits, therefore, deserve better attention in future breeding programs for evolving better wheat for stress environments.

## REFERENCES

Bhargava, A., S. Shukla, R.S. Katiyar, and D. Ohri. 2003. Selection parameters for genetic improvement in *Chenopodium* grain on sodic soil. J. Applied Hort. 5: 45-48.

Borojevic, K. 1983. Significance of experimental heritability estimates in wheat breeding. p. 19-24. Proc. 10th Cong. European Associ. Res. Pl. Bro, EUCARPIA, Wageningen, The Netherland.

Burton, G.W. and F.W. Devane. 1953. Estimating heritability in tall fescue (*Festuc arandinaca*) from replicated clonal material. Agron. J. 45: 478-481.

Campbell, C.A. and D.W.L. Read. 1968. Influence of air temperature, light intensity and soil moisture on the growth, yield and some growth related characteristics of Chinook wheat grown in growth chamber. Can. J. Plant Sci. 48: 299-311.

Condon, A.G. and R.A. Richards. 1992. Broad-sense heritability and genotype-environment interaction for carbon isotope discrimination in field-grown wheat. Aust. J. Agric. Res. 43: 921-934.

Cooper, M., D.E. Byth, and D.R. Woodruff. 1994. An investigation of the grain yield adaptation of advanced CIMMYT wheat lines to water stress environments in Queensland. II. Classification analysis. Aust. J. Agric. Res. 45: 985-1002.

Das, M.K. and L. Rahman. 1984. Estimates of genetic variability, heritability and genetic gain in common wheat. Bangladesh J. Agric. Res. 9: 15-18.

Day, A.D. and S. Intlap. 1970. Some effects of soil moisture stress on the growth of wheat (*Triticum aestivum* L. em Thell.) Agron. J. 62: 27-29.

Denmead, O.T. and R.H. Shaw. 1960. The effect of soil moisture stress at different stages of growth on the developmental and grain yield of corn. Agron. J. 52: 272-274.

Fedin, M.A. 1976. Heterosis in Wheat and Its Heredity Factors. Elsevier, New York. p. 291-302.

Fischer, R.A. and N.C. Turner. 1978. Plant productivity in the arid and semi arid zones. Ann. Rev. Plant. Physiol. 29: 207-213.

Foulkes, M.J., R. Sylvester-Bradley, and R.K. Scott. 2001. The ability of wheat cultivars to withstand UK drought: resource capture. J. Agric. Sci. 137: 1-16.

Foulkes, M.J., R.K. Scott, and R. Sylvester-Bradley. 2002. The ability of wheat cultivars to withstand drought in UK conditions: formation of grain yield. J. Agric. Sci. 138: 153-169.

Foulkes, M.J., V. Verma, R. Sylvester-Bradley, R. Weightman, and J.W. Snape. 2004. Traits for improved drought tolerance of winter wheat in the UK. Proceeding of the 4th International Crop Science Congress. Brisbane, Australia.

Hang, A. and D.E. Miller. 1983. Wheat development as affected by deficit, high temperature sprinkler irrigation. Agron. J. 75: 234-239.

Hubick, K.T., R. Shorter, and G.D. Farquhar. 1988. Heritability and genotype - environment interactions of carbon isotope discrimination and transpiration efficiency in peanut (*Arachis hypogaea* L.). Aust. J. Plant Physiol. 15: 799-813.

Johnson, H.W., H.F. Robinson, and R.E. Comstock. 1955. Estimates of genetic and environmental variability in soybean. Agron. J. 47: 314-318.

Kissana, N.S., M. Tahir, and M.A. Chowdhry. 1982. Heritability of some quantitative characters in five crosses of wheat (*Triticum aestivum* L.). Pakistan J. Agric. Res. 3: 211-214.

Li, Z.L. and W.L. Yang. 1985. Studies on the heritability and genetic correlations of the main quantitative characters in winter wheat. Shanxi Nongye Kexue 2: 11-13.

Mahmud, I. and H.H. Kramer. 1951. Segregation for yield, height and maturity following a soybean cross. Agron. J. 43: 605-609.

Menendez, C.H. and A.E. Hall. 1996. Heritability of carbon isotope discrimination and correlations with harvest index in cowpea. Crop Sci. 36: 233-238.

Pathak, N.N. and D.P. Nema. 1985. Genetic advance in land races of wheat. Indian J. Agric. Sci. 55: 478-479.

Rajaram, S., H.J. Braun, and M.V. Ginkel. 1996. CIMMYT's approach to breed for drought tolerance. Euphytica 92: 147-153.

Rebetzke, G.J., R.A. Richards, A.G. Condon, and G.G. Farquhar. 2006. Inheritance of carbon isotope discrimination in bread wheat (*Triticum aestivum* L.). Euphytica 150: 97-106.

Reddi, M.V., E.G. Heyne, and G.H.L. Liang. 1969. Heritabilities and inter-relationships of shortness and other agronomic characters in F3 and F4 of wheat crosses. Crop Sci. 9: 222-225.

Reynolds, M.P., J.I. Ortiz-Monasterio, and A. McNab. 2001. Application of Physiology in Wheat Breeding. CIMMYT, Mexico, D.F.

Roach, D.A. and R.D. Wulff. 1987. Maternal effects in plants. Ann. Rev. Ecol. Syst. 18: 209-235.

Robins, J.S. and C.E. Domingo. 1962. Moisture and nitrogen effects on irrigated spring wheat. Agron. J. 54: 135-138.

Sethi, G.E. and S.B. Singh. 1972. Inter-relationship of quantitative traits with grain yield in Triticale. Indian J. Agric. Sci. 42: 281-282.

Sharma, H.P. and S.C. Bhargava. 1996. Relative sensitivity of wheat genotypes under moisture stress conditions. Annal. Biol. 12: 39-42.

Sheikh, S., I. Singh, and J. Singh. 2000. Inheritance of some quantitative traits in bread wheat (*T. aestivum* L em Thell) Ann. Agric. Res. 21: 51-54.

Shukla, S., A. Bhargava, A. Chatterjee, and S.P. Singh. 2004. Estimates of genetic parameters to determine variability for foliage yield and its different quantitative and qualitative traits in vegetable amaranth (*A. tricolor*). J. Genet. Breed. 58: 169-176.

Sidwell, R.J., E.L. Smith, and R.W. McNew. 1976. Inheritance and interrelationships of grain yield and selected yield related traits in a hard red wheat. Crop Sci. 16: 650-654.

Tretowan, R.M., G. Van, and S. Rajaram. 2002. Progress in breeding for yield and adaptation in global drought affect environments. Crop Sci. 42: 1441-1446.

Uddin, N., B.F. Carver, and A.C. Clutter. 1992. Genetic analysis and selection for wheat yield in drought-stressed and irrigated environments. Euphytica 62: 89-96.