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A comparative analysis of transpiration response to atmospheric increasing vapor pressure deficit conditions in cereal crops

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Abstract
Plant adaptation to drought depends on both inherited and adaptive characteristic of water conservative traits. Expression of limited transpiration rate (TR) under high vapor pressure deficit (VPD) conditions could be one of the potential sources of soil water conservation for drought tolerance. Large genetic variation for limited TR has been identified in the comparison of three major C3 cereals viz., maize, pearl millet and sorghum under elevating VPD. The total amount of water transpired under elevating VPD by these three cereals not found dependent on leaf area, in fact, it was reflected more by the variation in transpiration rate. Pearl millet showed better adaptation of limitation of TR than maize and sorghum under high VPD regimes.

Keywords
Cereals, transpiration, vapor pressure deficit, breakpoint and variability.

Introduction
Maize, Pearl millet and Sorghum are important cereal crops for food and feed in arid and semi-arid tropics. The C3 crops are evolved to cope-up with high temperature, low CO2 and high irradiance environment. However, when it comes to drought (atmospheric and soil), they do suffer equally as the C4 cereals. Water stress limits the crop yield and plays a significant role in the potential yield gap. Drought tolerance is a complex trait and regulated by many component traits (Monteith, 1995; Vadez et al., 2014). Identification of component traits to drought-tolerance and utilisation into crop breeding program is essential for sustainable agriculture. One such trait identified in recent years is the transpiration response to increasing atmospheric evaporative demand (also called vapor pressure deficit, VPD) is the difference between the vapor pressure inside the leaf to saturated air pressure of the atmosphere which drives the transpirational pull. Plant transpiration increases with increasing VPD (Sinclair and Bennett, 1998) but genetic variation has been reported in many crops in the transpiration response to high VPD conditions. Some genotypes indeed restrict their transpiration under high VPD, by partial stomata closure, and then limit their maximum transpiration rate. This trait contributes to soil water conservation, water is conserved in early crop stages and effectively used for later critical stages (Richards and Passioura, 1989; Sinclair et al., 2005). Kholova et al. (2010) identified genetic variation for limited transpiration rate in pearl millet which is linked to the water use at the vegetative stage. Gholipoor et al. (2013) evaluated thirty-five single cross maize hybrids for limited transpiration rate in response to increasing high VPD and reported VPD threshold for limiting TR range of 1.7 to 2.5 kPa. Gholipoor et al. (2010) and Choudhary et al. (2013) identified VPD sensitive and insensitive lines by screening twenty-six sorghum genotypes, and the expression of limited transpiration trait ranged from VPD threshold of 1.6 to 2.7 kPa in sensitive lines. Shekoofa et al. (2014) compared the expression of limited transpiration trait in a controlled test environment to the field conditions. This study showed a similar trend of expression and possibility to compare the studied lines under a range of conditions. In particular, it looked at the trade-off between the maximum transpiration trait and the photosynthesis-driven plant growth, i.e. trade-offs between carbon dioxide entry in the plant and water losses at the stomata level. Several attempts have also been made to address these trade-offs between water conservation and biomass accumulation so that utilisation from the soil profile get maximize and no water remains available in the soil profile once the crop has matured. Sinclair et al. (2005) conducted a simulation study for the limited transpiration traits.
in sorghum and reported 9-13% yield benefits under arid regions with a very minimum penalty under well-watered conditions.

Similarly, Kholova et al. (2014) simulated the same traits for post rainy sorghum cultivars reported for grain yield and fodder. The model showed the close relationship between the crop yield and amount of water available at post flowering crop growth stage subjected to limited water conditions. The primary objective of the present study is to compare the genetic variation in three major crops of semi-arid tropics for transpiration response to elevating VPD conditions.

Material and Methods
Two experiments (Exp I and Exp II) were conducted at Controlled Environment Research Facility (CERF), International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India (17°30’ N; 78°16’ E; altitude 549 m) during March to April and July to August 2015. A total of sixty-six genotypes were selected which comprised of 28 inbred lines of tropical and temperate maize and 19 lines of tropical pearl millet contrast for transpiration efficiency (Table 1). Seeds were sown in the 7” plastic pots filled with approx. 5-6 kg of vertisol: sand in the ratio of 2:1 with Complete Randomized Design (CRD). Before sowing, the soil was well fertilized with Di-Ammonium Phosphate (DAP) and Muriate of Potash (MOP) in the concentration of 0.3 g per kg of soil. Three hills were raised at the time of sowing and finally thinned to two plants per pot in Exp I and single plant per pot in case of Exp II. The plants were maintained under well-watered conditions throughout the experiment.

At V5-V7 (vegetative stage of 5-7 fully developed leaves) plant stage, the uniform pots were selected, saturated with water and allowed to drain overnight. Soil evaporation was restricted by covering the soil surface around the stem with a plastic sheet covered with a 2-cm layer of plastic beads. The plants were grown in a glasshouse and shifted to plant growth chamber (Conviron, Controlled Environments, Winnipeg, MB, Canada) for one day. After acclimation, the transpiration response to increasing VPD was assessed in the range of 0.7 kPa to 4 kPa (Exp I) and 0.6 kPa to 3.6 kPa (Exp II) for one-hour intervals (15 min transition time). The lower level humidity was maintained with the help of dehumidifier (Daikin, India). The light flux density ranged from 450-500 μ mol m⁻² s⁻¹ at canopy level in a growth chamber. The protocol for transpiration response to increasing VPD was followed same as described in the earlier studies by Kholova et al. (2010); Gholipoor et al. (2010); Choudhary et al. (2013) and Shekoofa et al. (2014) in cereal crops. The transpiration response was measured by a gravimetric method using 0.01 precision balances (FBK, Kern & Sohn GmbH, Balingen, Germany) to five plants per genotype. The first weight was considered as field capacity weight, and the pots were weighted at every one-hour interval for each VPD level to access the transpiration response. The fresh leaves were separated from the plant part at the end of the experiment, and total leaf area was measured using a leaf area meter (LI-3100, Li-Cor, Lincoln, Nebraska, USA).

The gravimetric transpiration measurement of plants was expressed in Transpiration Rate (TR) as transpiration (mg) per unit leaf area (m²) and per unit of time (s). The VPD was calculated as per equation (given by Monteith and Unsworth, 1990).

\[
\text{VPD} = \frac{100 - RH}{SVP} \times SVP
\]

Analysis of variance (ANOVA) was done using SAS 9.3 PROC GLM (SAS Institute, Inc., Cary, NC, USA) followed by least significant test (LSD) test to find the significant difference among and between the crop species. The transpiration response to increasing VPD was categorized into three VPD levels as low VPD (<1.5 kPa), medium VPD (1.5 kPa to 2.5 kPa) and high VPD (>2.5 kPa) to find the difference at each level. The transpiration rate to increasing vapor pressure deficit was subjected to two-segmented linear regression equation using GraphPad Prism version 6.03 (Graph Pad Software, Inc., San Diego, CA). The value of (Breakpoint)BP was the breakpoint between the two linear regression equations. The slope of the two linear regressions was statistically compared (P <0.05). If the two slopes are statistically different, the response is best represented by a nonlinear regression model. If the two slopes are not significantly different the response is best represented by a simple linear regression model.

Genetic components like genotypic coefficient of variance (GCV), the phenotypic coefficient of variance (PCV), heritability (h² Broad sense) and genetic advance (GA % mean) were estimated as suggested by Johnson et al.(1955), Burton, (1952) and Lush (1940). The coefficient of variation (CV %) was categorised into low (0-10), moderate (11-20) and high (>20) as suggested by Sivasubramanian and Madhava Menon, (1973). The heritability % were categorised into low (0-30), medium (30-60) and high (more than 60) as suggested by Robinson et al. (1949). The genetic
Results and Discussion

Analysis of variability revealed significant ($P<0.05$) differences among all the lines for leaf area (LA, cm$^2$) under investigation in both the set of experiments. In this study, the genetic variability parameters like PCV and GCV were calculated and showed high values for LA, T and TR respectively. In the case of the maize crop, the high heritability and high genetic advance per cent mean were observed for LA, T and TR. Moderate to high heritability and high genetic advance were recorded for LA, T and TR in case of pearl millet and sorghum respectively. The analysis of variance and estimated variability parameters are given in Table 2 and 3. The transpiration (T, g) and transpiration rate (TR, mg m$^2$ sec$^{-1}$) showed large variation in the studied genetic material. The variability in canopy development, transpiration and transpiration rate were also discussed. With regard to canopy development, at the first set of experiment (Exp I; March to April), the mean leaf area was recorded highest in pearl millet (1425±485cm$^2$) followed by sorghum (1139±437cm$^2$) and maize (788±316cm$^2$). The LSD test showed a significant difference among three crops ($P<0.05$). Similarly, second set of experiment (Exp II; August-September) showed highest mean leaf area in pearl millet (547±146cm$^2$) followed by sorghum (476±87cm$^2$) and maize (417±128cm$^2$). The leaf area was not statistically different between sorghum and maize in the second set of experiment.

The plant water loss (transpiration) of maize in the course of the day was comparatively less than pearl millet and sorghum under a range of low, medium and high VPD levels in the both sets of experiments. The water loss in maize plant ranged between 9.8 and 13.7 g/day (Low to High VPD) in Exp I, whereas it ranged between 12.4 and 17.6 g/day (Low to High VPD) in the case of Exp II. The water loss in both pearl millet and sorghum plants were comparatively similar in both the experiments and statistically non-significant to each other.

The measurement of transpiration rate in plants was expressed as per unit leaf area. In both the experiments (Exp I and II), the maize TR was higher than sorghum TR under both low and high VPD conditions and was significantly different among the crops ($P<0.005$) used in the study. When the plants exposed to increasing VPD conditions, the maize and sorghum TR were similar, and they were non-statistically different to each other in both the experiments.
were 27°C/65% and 28°C/80% respectively. Due to the difference in temperature and humidity between experiments, the data were analyzed individually, and results are discussed as experimental wise under each crop category.

Maize
In Experiment I, among 28 inbred lines of maize, nine lines expressed a limited TR and other 19 lines showed a linear increase in TR under elevating VPD. The VPD threshold at which those nine lines showed a limitation in TR was observed in the range of 1.93 (MBS847 and LP1233) to 2.95 kPa (VL 109150). The same set of inbred lines in Exp II, eight among 28 lines showed BP in range of 2.26 (VL 108320) to 3.10 (EP 1) kPa. The lines EA1197, PH207, VL 109150 and VL 12153 showed BP in both the experiments.

Sorghum
Large genotypic variation for limited TR trait under increasing VPD conditions in sorghum lines was noticed. In Exp I, eight lines exhibited a limited TR with VPD threshold range of 2.10 (IS 25910 and IS 8348) to 2.73 (IS 14276) kPa, and six genotypes exhibited VPD threshold in the similar range of 2.22 (IS 3147 and IS 27791) to 2.88 (IS 8348) kPa in Exp II. Among nineteen sorghum lines, three lines (IS 27791, IS 3147 and IS 8348) exhibited a limited TR in both the experiments. The slope above the breakpoint ranged from 2.63 mg m⁻² sec⁻¹ kPa⁻¹ for IS 8348 and 3.19 mg m⁻² sec⁻¹ kPa⁻¹ for IS 3147 in the first experiment. The line IS 8348 had a negative slope in case of the second experiment.

Pearl Millet
Pearl millet lines, tested in two sets of experiment also showed a good range of variation for limited TR traits. Among nineteen lines, twelve lines expressed limited TR at high VPD where VPD threshold ranged from 1.83 to 2.72 kPa and recorded by IP 13520 and IP 7953 respectively. In Exp II only two lines IP 4542 and IP 6179 expressed limitation TR above 2.42 kPa, remaining seventeen lines showed a linear increase in TR with increasing VPD. The lines IP 4542 and IP 6179 were consistent in performance in both the experiments.

Genotypic variation for the sensitivity of transpiration to VPD also found in cereals crop like Pearl millet, Pennisetum glaucum (Kholova et al., 2010); Maize, Zea mays L. (Yang et al., 2012) and Sorghum, Sorghum bicolor (Choudhary et al., 2013). The hypothesis states that the restriction in transpiration under high VPD allowed by partial stomata closure saves soil moisture at the early vegetative stage, which can increase moisture availability for reproductive stages under the rainfed condition and can enhance yield (Richards and Passioura, 1989 and Sinclair et al., 2005). In this study, the restriction of the transpiration rate in crop plants for little or no increase in TR showed sizeable genetic variation. The variation in VPD breakpoint does not differ widely among these three crops. Four lines of maize (EA1197, PH207, VL 109150 and VL 12153), three lines of sorghum (IS 27791, IS 3147 and IS 8348) and two lines of pearl millet (IP 4542 and IP 6179) expressed sensitivity to elevating VPD by limiting TR consistently in both the sets of experiments. These lines may have the ability to conserve more soil water under high atmospheric VPD conditions compared to others. Water stress tolerance results from a complex combination of traits that influence supply and demand for water (Passioura 2012). The ability of a genotype to adapt to a particular water availability level eventually determines the level of tolerance of that genotype. Therefore, lines having a limited TR could further be evaluated for a given environment and selection could be based on the range of breakpoint exhibited. For this study, the heritability and genetic advance were also measured and were high, showing the potential of this trait to be used as an efficient secondary trait in breeding programs for the limited water environment.

References
Burton, G.W. 1952. Quantitative inheritance in grasses. Proc. of the 6th International Grassland Cong., 1: 277-284.

Choudhary, S., Mutava, R.N., Shekoofa, A., Sinclair, T.R. and Prasad, P.V. 2013. Is the stay-green trait in sorghum a result of transpiration sensitivity to either soil drying or vapor pressure deficit? Crop Sci., 53: 2129-2134.

Gholipoor, M., Choudhary, S., Sinclair, T.R., Messina, C.D. and Cooper, M. 2013. Transpiration response of maize hybrids to atmospheric vapor pressure deficit. J Agron Crop Sci., 199: 155-160.

Gholipoor, M., Prasad, P.V., Mutava, R.N. and Sinclair, T.R. 2010. Genetic variability of transpiration response to vapor pressure deficit among sorghum genotypes. Field Crops Res., 119: 85-90.

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

Kholova, J., Hash, C.T., Kumar, P.L., Yadav, R.S., Kočová, M. and Vadez, V. 2010. Terminal drought-tolerant pearl millet [Pennisetum
glaucaum (L.) R. Br.] have high leaf ABA and limit transpiration at high vapour pressure deficit. J. Exp. Bot., 61: 1431-1440.

Kholová, J., Murugesan, T., Kaliamooorthy, S., Malayee, S., Baddam, R., Hammer, G.L., McLean, G., Deshpande, S., Hash, C.T., Craufurd, P.Q. and Vadez, V. 2014. Modelling the effect of plant water use traits on yield and stay-green expression in sorghum. Funct Plant Biol., 41: 1019-1034.

Kudoyarova, G., Veselova, S., Hartung, W., Farhutdinov, R., Veselov, D. and Sharipova, G. 2011. Involvement of root ABA and hydraulic conductivity in the control of water relations in wheat plants exposed to increased evaporative demand. Planta., 233: 87-94.

Lush, J.L. 1940. Intra sire correlation and regression of offspring on dams as a method of estimating heritability of characters. Proc. Amer. Soc. Animal Production, 33: 293-301.

Monteith, J.L. 1995. A reinterpretation of stomatal responses to humidity. Plant Cell Environ., 18: 357-364.

Monteith, J.L. and Unsworth, M. 1990. Principles of Environmental Physics. Edward Asner Publishers, London.

Pantin, F., Simonneau, T. and Muller, B. 2012. Coming of leaf age: control of growth by hydraulics and metabolites during leaf ontogeny. New Phytol., 196: 349-366.

Pantin, F., Simonneau, T., Rolland, G., Dauzat, M. and Muller, B. 2011. Control of leaf expansion: a developmental switch from metabolites to hydraulics. Plant Physiol., 156: 803-815.

Passioura, J.B. 2012. Phenotyping for drought tolerance in grain crops: when is it useful to breeders? Funct Plant Biol., 39: 851-859.

Richards, R.A. and Passioura, J.B. 1989. A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. Aust J Agr Res., 40: 943-950.

Robinson, H.F., Comstock, R.E. and Harvey, V.H. 1949. Estimates of heritability and degree of dominance in corn. Agron. J., 41: 353-359.

Shekooa, A., Balota, M. and Sinclair, T.R. 2014. Limited-transpiration trait evaluated in growth chamber and field for sorghum genotypes. Environ Exp bot., 99: 175-179.

Sinclair, T.R. and Muchow, R.C. 2001. System analysis of plant traits to increase grain yield on limited water supplies. Agron J., 93: 263-270.

Sinclair, T.R., Bennett, J.M. 1998. Water. In: Sinclair, T.R., Gardner, F.P. (Eds.), Principles of Ecology in Plant Production. CAB International, p.103-120.

Sinclair, T.R., Hammer, G.L. and E.J. van Oosterom. 2005. Potential yield and water-use efficiency benefits in sorghum from limited maximum transpiration rate. Funct Plant Biol., 32. doi:10.1071/fp05047.

Sivasubramaniam and Madhav Menon. 1973. Inheritance of short stature in rice. Madras Agric J., 60: 1129-1133.

Vadez, V., Kholova, J., Medina, S., Kakker, A. and Anderberg, H. 2014. Transpiration efficiency: new insights into an old story. J ExpBot., 65: 6141-6153.

Van Oosterom, E.J., Borrell, A.K., Deifel, K.S. and Hammer, G.L. 2011. Does increased leaf appearance rate enhance adaptation to postanthesis drought stress in sorghum? Crop Sci., 51: 2728-2740.

Van Oosterom, E.J., Carberry, P.S. and O’leary, G.J. 2001. Simulating growth, development, and yield of tillering pearl millet: I. Leaf area profiles on main shoots and tillers. Field Crops Res., 72: 51-66.

Yang, Z., Sinclair, T.R., Zhu, M., Messina, C.D., Cooper, M. and Hammer, G.L. 2012. Temperature effect on transpiration response of maize plants to vapour pressure deficit. Environ Exp Bot., 78: 157-162.
Table 1. Genotypes used in this study

| S. No. | Genotype | Crop | Origin   | S. No. | Genotype | Crop | Origin       |
|--------|----------|------|----------|--------|----------|------|--------------|
| 1      | IP 6179  | Millet | Cameroon | 34     | IS 14556 | Sorghum | Cameroon    |
| 2      | IP 13520 | Millet | India    | 35     | IS 15428 | Sorghum | Cameroon    |
| 3      | IP 20349 | Millet | Yemen    | 36     | IS 3583  | Sorghum | CIRAD, France |
| 4      | IP 3110  | Millet | India    | 37     | IS 10978 | Sorghum | Germany    |
| 5      | IP 14311 | Millet | Cameroon | 38     | IS 3147  | Sorghum | CIRAD, France |
| 6      | IP 7953  | Millet | India    | 39     | SCMALAWI | Maize | Subtropical |
| 7      | IP 15857 | Millet | Tanzania | 40     | KY21     | Maize | Dent        |
| 8      | IP 8647  | Millet | Sudan    | 41     | LP1233   | Maize | South-American Flint |
| 9      | IP 6125  | Millet | Cameroon | 42     | CML245   | Maize | Tropical highlands |
| 10     | IP 6891  | Millet | Kenya    | 43     | MO17     | Maize | Dent        |
| 11     | IP 9651  | Millet | Nigeria  | 44     | FV2      | Maize | Flint       |
| 12     | IP 3471  | Millet | India    | 45     | PH207    | Maize | Dent        |
| 13     | IP 9391  | Millet | Ghana    | 46     | W64A     | Maize | Dent        |
| 14     | IP 13363 | Millet | Tanzania | 47     | ZN6      | Maize | Subtropical |
| 15     | IP 12395 | Millet | South Africa | 48     | B73      | Maize | Dent        |
| 16     | IP 9351  | Millet | Ghana    | 49     | EA1197   | Maize | Flint       |
| 17     | IP 4542  | Millet | India    | 50     | W117U    | Maize | Dent        |
| 18     | IP 4979  | Millet | Nigeria  | 51     | FV76     | Maize | Flint       |
| 19     | IP 18389 | Millet | Namibia  | 52     | MBS847   | Maize | Dent        |
| 20     | IS 393 (411) 659 | Sorghum | USA | 53     | EP1      | Maize | Flint       |
| 21     | IS 8347  | Sorghum | USA | 54     | FC16     | Maize | Flint       |
| 22     | IS 20743 | Sorghum | Pakistan | 55     | CH10     | Maize | Flint       |
| 23     | IS 25910 | Sorghum | Cameroon | 56     | FV252    | Maize | Dent        |
| 24     | SSM 275  | Sorghum | USA | 57     | VL 1018466 | Maize | -          |
| 25     | IS 20763 | Sorghum | Pakistan | 58     | VL 1054  | Maize | -          |
| 26     | IS 30619 | Sorghum | South Africa | 59     | VL 058725 | Maize | -          |
| 27     | IS 14276 | Sorghum | Algeria | 60     | VL 1018550 | Maize | -          |
| 28     | IS 27791 | Sorghum | Cameroon | 61     | VL 1018553 | Maize | -          |
| 29     | IS 29472 | Sorghum | South Africa | 62     | VL 511305 | Maize | -          |
| 30     | IS 31693 | Sorghum | Sudan    | 63     | VL 1022  | Maize | -          |
| 31     | IS 16044 | Sorghum | Lesotho | 64     | VL 109150 | Maize | -          |
| 32     | IS 16173 | Sorghum | Mali    | 65     | VL 12153 | Maize | -          |
| 33     | IS 8348  | Sorghum | Ethiopia | 66     | VL 1018113 | Maize | -          |
Table 2. One-way ANOVA for leaf area and transpiration traits in studied genotypes.

| Exp     | Source of variation | LA       | Low VPD | Medium VPD | High VPD | Total T | Low VPD | Medium VPD | High VPD | Average TR |
|---------|---------------------|----------|---------|------------|----------|----------|---------|------------|----------|------------|
| Exp I   | Crop MS             | 11937949.0 | 314.8   | 831.6      | 1045.9   | 43012.8  | 4972.6  | 5023.0     | 5940.3   | 5318.8     |
|         | Error MS            | 169464.0 | 9.9     | 17.8       | 22.1     | 933.2    | 392.1   | 607.3      | 501.8    | 458.9      |
|         | variance            | 70.5***  | 31.9*** | 46.7***    | 47.4***  | 46.1***  | 56.2*** | 8.3***     | 11.8***  | 11.6***    |
|         | CV%                 | 38.5     | 27.7    | 27.7       | 28.4     | 26.8     | 56.2    | 53.2       | 44.8     | 49.2       |
|         | SED                 | 56.8     | 0.4     | 0.6        | 0.6      | 4.2      | 2.7     | 3.4        | 3.1      | 3.0        |
|         | LSD (5% level)      | 111.7    | 0.9     | 1.1        | 1.3      | 8.3      | 5.4     | 6.7        | 6.1      | 5.8        |
|         | Maize               | 788.0 a  | 9.8 a   | 12.7 a     | 13.7 a   | 95.8 a   | 40.8 b  | 51.9 b     | 55.6 b   | 49.1 b     |
|         | Sorghum             | 1139.7 b | 12.7 b  | 16.9 b     | 18.7 b   | 128.0 b  | 34.4 a  | 45.4 ab    | 50.2 b   | 43.1 b     |
|         | P Millet            | 1425.3 c | 12.4 b  | 17.5 b     | 18.8 b   | 128.7 b  | 27.6 a  | 38.7 a     | 41.2 a   | 35.5 a     |
| Exp II  | Crop MS             | 467552.0 | 138.3   | 469.2      | 685.4    | 392.5    | 3799.4  | 6941.6     | 8518.0   | 6095.7     |
|         | Error MS            | 558822.0 | 30.7    | 55.2       | 63.8     | 47.1     | 652.0   | 910.7      | 1180.0   | 849.1      |
|         | variance            | 8.4***   | 4.5**   | 8.5***     | 10.7***  | 8.3***   | 5.8***  | 7.6***     | 7.2***   | 7.2***     |
|         | CV%                 | 50.4     | 41.4    | 40.9       | 40.1     | 40.0     | 42.6    | 37.3       | 38.7     | 38.0       |
|         | SED                 | 32.6     | 0.8     | 1.0        | 1.1      | 0.9      | 3.5     | 4.2        | 4.7      | 4.0        |
|         | LSD (5% level)      | 64.1     | 1.5     | 2.0        | 2.2      | 1.9      | 6.9     | 8.2        | 9.3      | 7.9        |
|         | Maize               | 417.2 a  | 12.4 a  | 16.3 a     | 17.6 a   | 15.4 a   | 62.2 b  | 81.8 b     | 89.0 ab   | 77.7 b     |
|         | Sorghum             | 475.6 ab | 14.5 b  | 19.8 b     | 22.1 b   | 18.8 b   | 52.3 a  | 71.5 a     | 78.8 a   | 67.5 a     |
|         | P Millet            | 546.6 b  | 13.8 ab | 19.5 b     | 21.4 b   | 18.3 b   | 63.9 b  | 88.7 b     | 98.0 b   | 83.6 b     |

Low VPD - <1.5 kPa; Medium VPD – 1.5-2.5 kPa; High VPD - >2.5 kPa.
Significance level – 5%
Table 3. Estimates of the phenotypic coefficient of variation (PCV %), the genotypic coefficient of variation (GCV %) and heritability (h²) for studied physiological traits.

|          | Maize |                  |                  |                  | Pearl millet |          |                  |                  |                  | Sorghum |          |                  |                  |                  |
|----------|-------|------------------|------------------|------------------|--------------|-------|------------------|------------------|------------------|---------|-------|------------------|------------------|------------------|
|          | Traits| Mean PCV | GCV | Mean | Mean | PCV | h² | GA % mean | Mean | GCV | Mean | PCV | h² | GA % mean | Mean | GCV | Mean | PCV | h² | GA % mean |
| I T (g)  | LA    | 788.02 | 0.58 | 0.68 | 0.73 | 101.18 | 1425.25 | 0.40 | 0.52 | 0.61 | 65.25 | 1139.73 | 0.34 | 0.52 | 0.44 | 46.65 |
|          | Low VPD | 9.79  | 0.35 | 0.46 | 0.59 | 56.18 | 12.39 | 0.23 | 0.33 | 0.51 | 34.34 | 12.74  | 0.33 | 0.42 | 0.62 | 54.04 |
|          | Medium VPD | 12.68 | 0.40 | 0.49 | 0.68 | 68.47 | 17.48 | 0.18 | 0.31 | 0.33 | 21.51 | 16.88  | 0.33 | 0.41 | 0.64 | 53.88 |
|          | High VPD | 13.68 | 0.38 | 0.49 | 0.61 | 61.24 | 18.84 | 0.23 | 0.36 | 0.43 | 31.31 | 18.69  | 0.27 | 0.36 | 0.56 | 42.31 |
|          | Total T | 95.76 | 0.37 | 0.47 | 0.64 | 61.24 | 128.65 | 0.20 | 0.32 | 0.41 | 26.89 | 128.03 | 0.29 | 0.37 | 0.61 | 47.13 |
|          | Low VPD | 40.75 | 0.67 | 0.90 | 0.55 | 103.12 | 27.62 | 0.51 | 0.70 | 0.54 | 77.84 | 34.42  | 0.34 | 0.53 | 0.43 | 46.38 |
|          | Medium VPD | 51.90 | 0.64 | 0.86 | 0.55 | 97.87 | 38.72 | 0.47 | 0.67 | 0.50 | 69.43 | 45.38  | 0.31 | 0.48 | 0.40 | 40.36 |
|          | High VPD | 55.58 | 0.54 | 0.71 | 0.59 | 85.54 | 41.18 | 0.45 | 0.63 | 0.50 | 65.12 | 50.24  | 0.30 | 0.46 | 0.41 | 39.35 |
|          | Average TR | 49.10 | 0.60 | 0.79 | 0.57 | 93.62 | 35.48 | 0.47 | 0.65 | 0.51 | 68.86 | 43.09  | 0.30 | 0.47 | 0.41 | 39.34 |
| II T (g) | LA    | 417.21 | 0.65 | 0.78 | 0.69 | 111.29 | 475.64 | 0.63 | 0.87 | 0.53 | 94.68 | 546.61 | 0.31 | 0.50 | 0.38 | 39.18 |
|          | Low VPD | 12.38 | 0.58 | 0.70 | 0.69 | 99.25 | 13.83 | 0.45 | 0.62 | 0.54 | 68.38 | 14.50  | 0.32 | 0.48 | 0.46 | 45.03 |
|          | Medium VPD | 16.28 | 0.57 | 0.68 | 0.69 | 97.14 | 19.51 | 0.48 | 0.64 | 0.58 | 75.90 | 19.83  | 0.27 | 0.44 | 0.37 | 34.22 |
|          | High VPD | 17.64 | 0.53 | 0.66 | 0.64 | 87.02 | 21.41 | 0.43 | 0.58 | 0.54 | 64.74 | 22.05  | 0.28 | 0.46 | 0.37 | 34.90 |
|          | Total T | 15.44 | 0.55 | 0.67 | 0.68 | 93.24 | 18.25 | 0.45 | 0.60 | 0.56 | 68.88 | 18.80  | 0.28 | 0.45 | 0.39 | 36.14 |
|          | Low VPD | 62.21 | 0.57 | 0.69 | 0.68 | 96.81 | 63.96 | 0.50 | 0.67 | 0.56 | 77.85 | 52.25  | 0.38 | 0.47 | 0.64 | 62.18 |
|          | Medium VPD | 81.81 | 0.54 | 0.64 | 0.69 | 92.20 | 88.71 | 0.46 | 0.58 | 0.65 | 77.19 | 71.49  | 0.30 | 0.41 | 0.54 | 45.07 |
|          | High VPD | 89.00 | 0.61 | 0.72 | 0.71 | 105.93 | 98.00 | 0.48 | 0.58 | 0.69 | 82.03 | 78.81  | 0.25 | 0.37 | 0.47 | 35.56 |
|          | Average TR | 77.67 | 0.57 | 0.68 | 0.70 | 98.03 | 83.56 | 0.47 | 0.58 | 0.65 | 77.88 | 67.52  | 0.30 | 0.40 | 0.55 | 45.19 |

GCV - Genotypic coefficient of variation; PCV - Phenotypic coefficient of variation; h² - heritability; GA % mean - Genetic advance % mean
Significance level – 5%