doi: 10.17221/796/2016-PSE

Grain sorghum transpiration efficiency at different growth stages

Sushil THAPA[1,2,*], Bob A. STEWART[1], Qingwu XUE[2]

[1]Dryland Agriculture Institute, West Texas A&M University, Canyon, USA
[2]Texas A&M AgriLife Research and Extension Center, Amarillo, USA
*Corresponding author: sushil.thapa@ag.tamu.edu

ABSTRACT

Thapa S., Stewart B.A., Xue Q.W. (2017): Grain sorghum transpiration efficiency at different growth stages. Plant Soil Environ., 63: 70–75.

Transpiration efficiency (TE) is an important physiological trait associated with drought tolerance of plants. Currently, little is known about the grain sorghum TE and its dynamics with the age of plants. To compare the sorghum TE at different growth stages, four studies (two in the greenhouse and two in the growth chamber) were conducted under controlled environmental conditions. Plants were grown in lid-covered boxes and harvested at six-leaf, flag leaf, grain filling and maturity stages. The mean shoot TE values were 4.47 and 4.10 kg/m^3 for two greenhouse studies, and 4.85 and 4.30 kg/m^3 for two growth chamber studies, respectively. The shoot TE was not different among four growth stages within each study, suggesting that sorghum plants used the same amount of water per unit of biomass production for different growing periods. Because crops grown under dryland environments often run out of water during reproductive periods, result supports the ideas that soil water availability at later growth stages is crucial to achieve the yield potential of dryland sorghum.

Keywords: C_4 plant; water stress; shoot to root ratio; *Sorghum bicolor*; vapour pressure deficit

Sorghum [*Sorghum bicolor* (L.) Moench], a C_4 plant, is the world's fifth most important cereal crop in terms of worldwide production and one of the most drought-tolerant and water-efficient cereals grown in semiarid environments (Peng and Krieg 1992, Blum 2004, Rooney 2004). In the U.S. Southern Plains and many other regions of the world, sorghum is usually cultivated under rain-fed conditions. The yield of sorghum grown under such conditions strongly depends on the rainfall during the growing season and soil water stored from previous season rains (Xin et al. 2008).

Transpiration efficiency (TE), an indispensable phenomenon associated with drought tolerance of plants (Mian et al. 1998), is the amount of above-ground biomass (kg dry matter) per unit of water transpired (m^3) (Kemanian et al. 2005, Xin et al. 2009). Enhancing TE, especially in dryland environments, is likely to have a large impact on improving grain yield, because a high TE trait would either enable plants to delay water stress symptoms or produce more biomass from the same amount of available soil moisture, or a combination of both (Xin et al. 2008). Improvement in genetic make-up as well as crop management practices can lead to a higher TE.

Reported TE values of sorghum at physiological maturity ranged from 3.21 to 7.55 kg/m^3 (Balota et al. 2008, Xin et al. 2009, Vadez et al. 2011). However, little is known about the sorghum TE and how, or if, it changes with the stage of growth. Since there is a positive association between TE and total biomass production in water-limited environments (Wright et al. 1994), the relation between TE and dry matter production should be carefully investigated throughout the growth stages. Further, despite its drought tolerance, sorghum yields in drylands are low, mainly due to the lack of soil water at later growth stages. Hence, it was hypothesized that sorghum TE was

doi: 10.17221/796/2016-PSE

independent to the different growth stages. The objective was to compare TE and shoot to root ratio (S:R) among four growth stages (six-leaf, flag leaf, grain filling, and grain maturity) of grain sorghum under controlled environmental conditions.

MATERIAL AND METHODS

Experimental design. Two studies in both greenhouse (GH) and plant growth chamber (GC; BioChambers TPC-37) facilities were conducted in 2015 and 2016 at West Texas A&M University (34.9814°N, 101.9160°W). The GH and GC temperatures were maintained at 20°C night minimum and 32°C day maximum. The mean relative humidity for crop growing periods was about 60% ranging from 25–80%. Light bulbs (600 W SONT) fixed at 2.0–2.5 m height were used in the greenhouse to maintain the lighting intensity of about 1000 μmol/m^2/s PAR (photosynthetically active radiation) at noon. Photoperiod was 6:00 to 21:00 h Central Standard Time (CST) for each day. Lighting intensities of 750 μmol/m^2/s PAR (6:00 to 8:00 h, and 19:00 to 21:00 h CST), 1500 μmol/m^2/s PAR (10:00 to 17:00 h CST), and 1125 μmol/m^2/s PAR (8:00 to 10:00 h, and 17:00 to 19:00 h CST) were used for GC studies. 1500 μmol/m^2/s PAR was the full intensity when all the lights were turned on. A continuous flow of fresh air was maintained in both experimental units to ensure that no CO_2 deficit developed.

Sixteen wooden boxes (100 × 24.3 × 28 cm) for the GH studies and 16 plastic boxes (46 × 30.5 × 20 cm) for the GC studies were used to grow sorghum plants. Calcined clay was used to grow plants with the volumetric water content of 42% (100% field capacity) at the time of seeding. This material is porous, has a low bulk density (0.68 g/cm^3 after packing), retains a large quantity of plant available water, is chemically inert and maintains good aeration and drainage properties needed for plant growth. Potential water leakage from wooden boxes was prevented by lining plastic sheets. Before adding water, 70 and 35 g of Miracle-Gro water soluble all-purpose plant food (N-P-K = 24-3.5-13%) was mixed uniformly with the calcined clay in wooden and plastic boxes, respectively. This fertilizer also contains some amounts of boron (B), copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo), and zinc (Zn).

The experimental design was randomized complete block design (RCBD) with four replications, where growth stages were considered as treatments. Sorghum (cv. DK-S36-06) was planted on July 17, 2015 for the first (GH1 and GC1) studies and on November 6, 2015 for the second (GH2 and GC2) studies. The cultivar was selected based on its adaptation in the semi-arid climates of the U.S. Southern Plains. Before planting, all boxes were weighed using a common balance. For the GH studies, in each box, six plants were grown in two clumps (three plants per clump), 50 cm apart and 25 cm from each end of the box. For GC studies, three plants were grown in a clump at the centre of each box. Volumetric water content in each box was maintained between 35–42% (83–100% field capacity), ensuring that sorghum plants were never water stressed. Boxes were covered with lids having holes (20 cm^2) for growing plants. In order to prevent evaporation, the holes were covered with plastic tape, leaving only a small opening sufficient for emerging seedlings. The tape was readjusted as the plants grew. Boxes were sealed to the lids, so all water lost from the boxes was assumed to be transpiration. At the six leaf stage (S1), plants from four boxes were harvested and four additional boxes were harvested at the flag leaf stage (S2), grain filling stage (S3), and physiological maturity stage (S4). The harvesting plan was prepared before seeding. Though there was a small variation among four studies, on average, plants were harvested at 35 (S1), 55 (S2), 75 (S3),

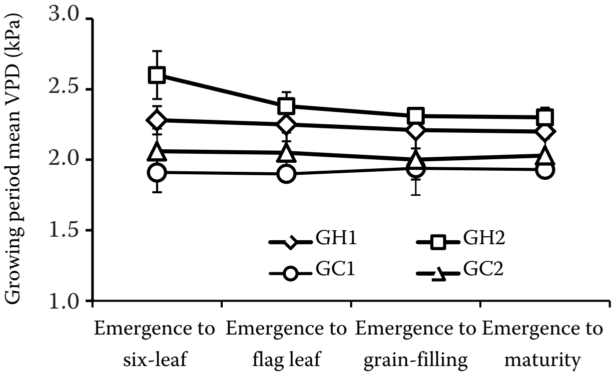

Figure 1. Sorghum growing period mean vapour pressure deficit (VPD) for greenhouse and growth chamber studies. GH1 – greenhouse first study; GH2 – greenhouse second study; GC1 – growth chamber first study; GC2 – growth chamber second study. Six-leaf – 35, flag leaf – 55, grain filling –75, maturity stages – 105 days after planting

doi: 10.17221/796/2016-PSE

and 105 (S4) days after planting (DAP). Flowering started about 65 DAP, so 65–105 DAP was considered as grain filling period.

Data collection. The air temperature and RH in GH and GC were measured every 30 min using three sets of LASCAR EL-USB-2+ sensors starting seedling emergence through final harvest. Sensors were placed vertically at 1.5 m height above the ground level. Temperature and RH data were converted to vapour pressure deficit (VPD) using the equations described by CronkLab (2016). VPD is the difference between the amount of moisture present in the air and how much moisture the air can hold when it is saturated (Prenger and Ling 2009).

$$SVP = 610.7 \times 10^{7.5T/(237.3 + T)} \quad (1)$$

$$VPD = [(100 - RH)/100] \times SVP \quad (2)$$

Where: SVP – saturated vapour pressure (kPa); T – temperature (°C); VPD – vapour pressure deficit (kPa); RH – relative humidity (%).

The final box weight was recorded before each harvest. Water used (transpiration) was calculated by subtracting the final box weight from the initial weight plus total water added during the growing period. Since water has density of 1 g/cm^3 (i.e. 1 g/mL), weight of water is equivalent to its volume. After harvesting, plant samples were separated into shoot and root systems. Roots were collected by washing the calcined clay on a mesh screen. Plant samples were oven dried at 70°C until the constant weight was recorded. The shoot to root ratio (S:R) was calculated on a dry weight basis. TE was calculated on a shoot basis (TE_{shoot}) as the ratio of shoot mass to transpiration and on a

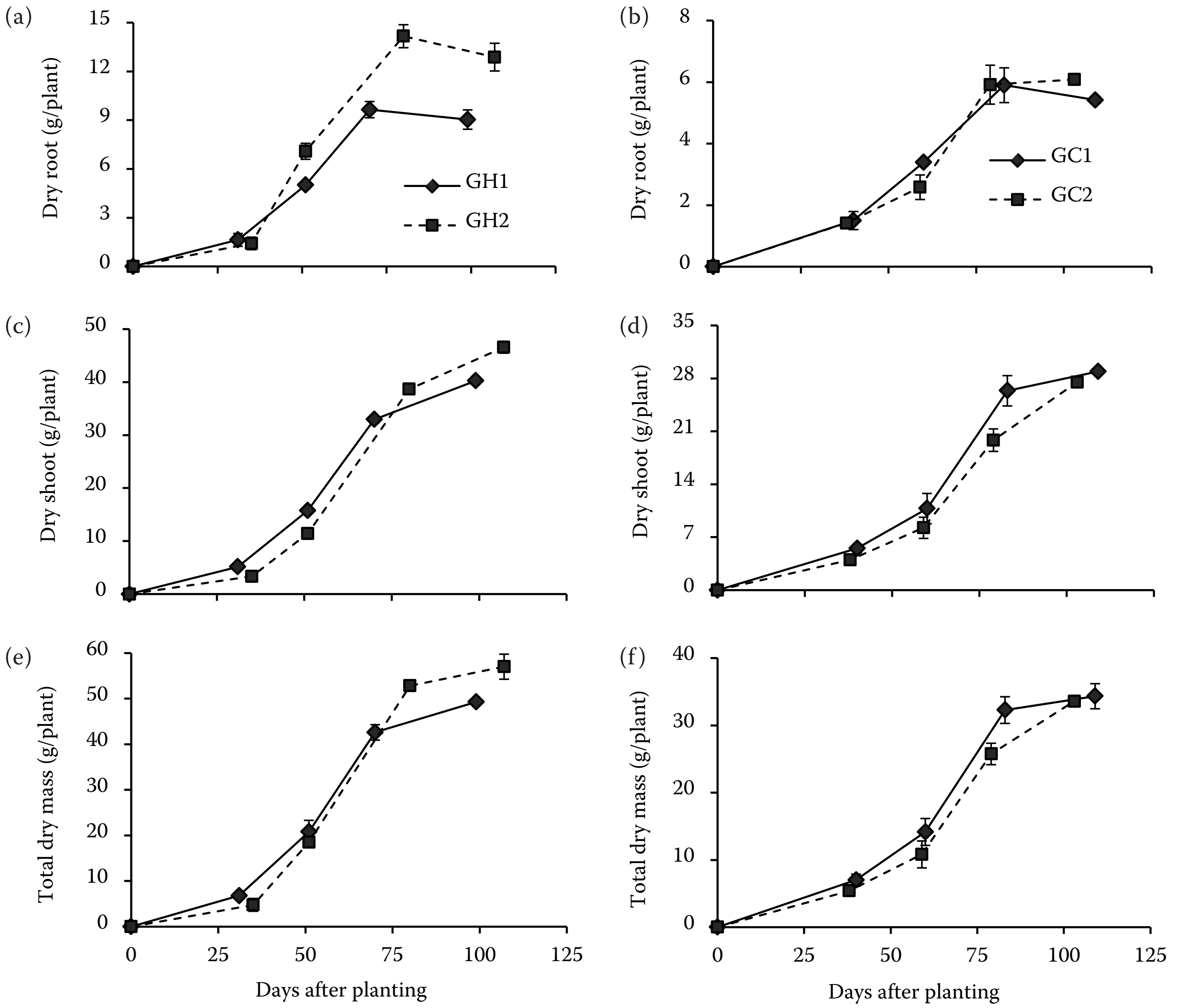

Figure 2. Dry root, shoot, and total mass of sorghum plants for greenhouse (GH) studies (a, c, e) and growth chamber (GC) studies (b, d, f). Shoot included leaves, stems, and generative organs of both main plants and tillers. Very few plants produced tiller(s) in GC studies, but most of the plants had tiller(s) in GH studies

doi: 10.17221/796/2016-PSE

Table 1. Means of shoot:root ratio (S:R); shoot transpiration efficiency (TE_{shoot}), and total transpiration efficiency (TE_{total}) of sorghum plants as affected by plant growth stage for greenhouse (GH) studies

Effect	Greenhouse study 1 (GH1)			Greenhouse study 2 (GH2)		
	S:R ratio (g/g)	TE_{shoot} (kg/m^3)	TE_{total} (kg/m^3)	S:R ratio (g/g)	TE_{shoot} (kg/m^3)	TE_{total} (kg/m^3)
Emergence – S1	3.22 ± 0.34^b	4.39 ± 0.15^a	5.66 ± 0.16^{ab}	2.40 ± 0.22^b	3.96 ± 0.33^a	5.60 ± 0.36^b
Emergence – S2	3.20 ± 0.42^b	4.57 ± 0.17^a	6.02 ± 0.33^a	2.61 ± 0.13^c	4.12 ± 0.22^a	6.08 ± 0.15^a
Emergence – S3	4.97 ± 0.28^a	4.44 ± 0.13^a	5.34 ± 0.16^b	3.60 ± 0.13^b	4.10 ± 0.10^a	5.49 ± 0.19^b
Emergence – S4	5.32 ± 0.50^a	4.52 ± 0.16^a	5.38 ± 0.18^b	4.14 ± 0.12^a	4.20 ± 0.09^a	5.43 ± 0.16^b

S1 – six leaf stage; S2 – flag leaf stage; S3 – grain filling stage; S4 – grain maturity stage. In each column, means with different letters are significantly different at $P < 0.05$

total dry weight basis (TE_{total}) as the ratio of total mass to transpiration (Xin et al. 2008). TE_{shoot} between subsequent growth stages was also calculated by subtracting shoot mass from current harvest to the previous harvest, and then divided by water transpired between these stages. Shoot or aboveground biomass included leaves, stems, and generative organs of both main plants and tillers.

Analysis of variance (ANOVA) was conducted using SAS 9.3 (SAS Institute, Inc. 2009). Growth stage was considered as fixed and replication as a random effect. The mean separation test was done using the least significance difference (*LSD*) and differences were considered significant at $P < 0.05$.

RESULTS AND DISCUSSION

Environmental conditions. The mean VPD from seedling emergence to different growth stages, was similar for each study except GH2 (Figure 1). At the beginning of the GH2 study, the temperature control system in the greenhouse did not work properly so temperature was higher than the set temperature for about two weeks. This temperature resulted in a mean VPD of 2.68 kPa from emergence to six-leaf stage compared to about 2.33 kPa for other growing periods.

Biomass and S:R ratio. For all four studies, shoot, root, total biomasses, and S:R ratio were significantly ($P < 0.05$) affected by the main effect of plant growth stage. Mean shoot mass at the final harvest (S4) was greater for GH2 than for GH1, which was mainly because the sorghum plants in GH2 produced more tillers (1.87 tillers/plant average) than in GH1 (0.62 tillers/plant average). Most of the plants in the GC studies did not produce tillers. For all studies, root mass declined after S3, (Figures 2a,b), but total biomass (shoot + root) increased from S1 through S4 (Figures 2e,f) due to the continuous increase in shoot mass (Figures 2c,d). As a result, S:R ratios were higher at later growth stages (S3 and S4) than earlier (S1 and S2) (Tables 1 and 2).

An increase in S:R ratio with the advancement of plant age was reported in previous studies (Yoshida

Table 2. Means of shoot:root ratio (S:R); shoot transpiration efficiency (TE_{shoot}), and total transpiration efficiency (TE_{total}) of sorghum plants as affected by plant growth stage for growth chamber (GC) studies

Effect	Growth chamber study 1 (GC1)			Growth chamber study 2 (GC2)		
	S:R ratio (g/g)	TE_{shoot} (kg/m^3)	TE_{total} (kg/m^3)	S:R ratio (g/g)	TE_{shoot} (kg/m^3)	TE_{total} (kg/m^3)
Emergence – S1	3.72 ± 0.15^c	4.75 ± 0.35^a	6.02 ± 0.48^a	2.85 ± 0.36^c	4.54 ± 0.39^a	6.16 ± 0.35^a
Emergence – S2	3.21 ± 0.22^c	4.78 ± 0.16^a	6.27 ± 0.30^a	3.21 ± 0.29^{bc}	4.18 ± 0.15^a	5.37 ± 0.32^{ab}
Emergence – S3	4.57 ± 0.56^b	5.04 ± 0.27^a	6.29 ± 0.45^a	3.56 ± 0.33^b	4.25 ± 0.37^a	5.44 ± 0.42^{ab}
Emergence – S4	5.42 ± 0.55^a	4.88 ± 0.29^a	5.79 ± 0.44^a	4.61 ± 0.48^a	4.22 ± 0.15^a	5.18 ± 0.27^b

S1 – six leaf stage; S2 – flag leaf stage; S3 – grain filling stage; S4 – grain maturity stage. In each column, means with different letters are significantly different at $P < 0.05$

doi: 10.17221/796/2016-PSE

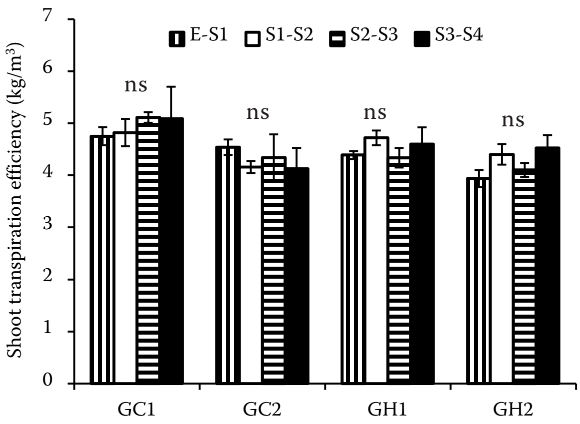

Figure 3. Means of shoot transpiration efficiency (TE-shoot) between two subsequent growth stages for different studies. E – emergence; S1 – six-leaf; S2 – flag leaf; S3 – grain filling; and S4 – maturity stages; GC1 – growth chamber first study; GC2 – growth chamber second study; GH1 – greenhouse first study; GH2 – greenhouse second study; ns – not significant

1975, Fageria 1992). Fageria (1992) found that S:R ratio was influenced by soil phosphorus levels, cultivars, and plant age. Amanullah and Stewart (2013) grew grain sorghum in the greenhouse and found S:R ratios of 1.10, 4.34, and 3.47 at 30, 60, and 90 days after emergence, respectively. Yang et al. (2010) harvested sorghum shortly after flowering, and found S:R ratios ranging from 3.09 to 4.59, which were comparable to the current S:R ratios (Tables 1 and 2). For example, S:R ratios at grain filling stage (after flowering) were 4.67, 3.60, 4.57, and 3.56 for GH1, GH2, GC1, and GC2 studies. According to Waldren (1983), during early growth stages, roots grow rapidly and few, if any, die, so the size of the root system increases exponentially. As the plant reaches flowering, roots begin to die as fast as the new roots are produced so that the size of the root system remains constant. As the plant reaches later growth stages, the number of roots dying exceeds the number being produced and the overall size of the root system declines.

Transpiration efficiency. For each study, there was no significant ($P > 0.05$) difference in TE_{shoot} either from emergence to different growth stages (Tables 1 and 2) or between two subsequent growth stages (Figure 3). The mean TE_{shoot} from emergence to the final harvest for GH1, GH2, GC1, and GC2 studies were 4.47, 4.10, 4.85, and 4.30 kg/m^3, respectively. TE_{total} at different growth stages was significantly ($P < 0.05$) different for GH1, GH2, and GC2 studies due to the inclusion of root mass. Overall, TE_{total} was greater at earlier than the later growth stages (Tables 1 and 2). For all studies, shoot dry matter increased linearly with cumulative water used for transpiration (Figure 4).

Xin et al. (2008) harvested 14 sorghum genotypes four weeks after planting and found mean TE_{shoot} values of 5.9 and 6.7 kg/m^3 in the first and second experiments, respectively. The average TE_{total} was 7.7 and 8.1 kg/m^3, respectively. Xin et al. (2009) grew 25 sorghum lines in the greenhouse over two seasons and found the mean TE_{shoot} of 5.7 kg/m^3 and TE_{total} of 8.1 kg/m^3. From emergence to grain maturity in the current study, sorghum plants produced 1 g of biomass for every 221, 237, 205, and 236 g of water transpired when the crop growing period mean VPDs were 2.21 (GH1), 2.30 (GH2), 1.96 (GC1), and 2.03 (GC2) kPa, respectively. These values are close to the findings of Sinclair and Weiss (2010). They reported that C_4 crops grown in an average transpiration environment of 2 kPa VPD will produce 1 g of biomass for every 220 g of water transpired, but for an arid region with a transpiration environment of 2.5 kPa VPD, crops use about 280 g for each g of biomass production. Our study showed a linear relationship between aboveground dry matter (shoot) and total water transpired during the growing season, which was reported previously in different crops (Ben-Gal and Shani 2002, Kemanian et al. 2005, Haefele et al. 2009, Xin et al. 2009, Mantovani et al. 2014).

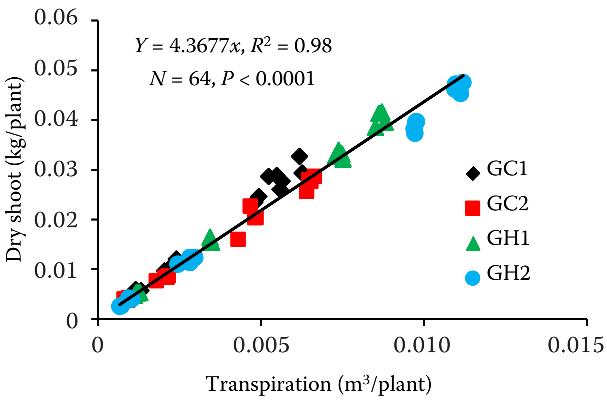

Figure 4. A linear regression between sorghum dry shoot mass and cumulative water used in transpiration during the crop growing period for all four studies. GC1 – growth chamber first study; GC2 – growth chamber second study; GH1 – greenhouse first study; GH2 – greenhouse second study

doi: 10.17221/796/2016-PSE

As hypothesized, under the controlled environmental conditions, sorghum TE of the aboveground biomass was essentially constant from emergence to physiological maturity. Sorghum plants that have harvest index of about 0.50 produce the half of the aboveground biomass during grain filling period (flowering to physiological maturity). When ET is constant as in this study, sorghum demands about 50% of total water during grain filling, which is approximately one-third of the total growing period. However, in drylands, plants often run out of soil water during the later growth stages such as reproductive and grain filling, and this is a main reason for dryland crops having lower harvest index compared to the irrigated crops. The results support research efforts for identifying possible genetic sources as well as crop management practices for improving TE in grain sorghum. However, the use of two or more cultivars is recommended for the further studies.

REFERENCES

Amanullah, Stewart B.A. (2013): Shoot: root differs in warm season C_4-cereals when grown alone in pure and mixed stands under low and high water levels. Pakistan Journal of Botany, 45: 83–90.

Balota M., Payne W.A., Rooney W., Rosenow D. (2008): Gas exchange and transpiration ratio in sorghum. Crop Science, 48: 2361–2371.

Ben-Gal A., Shani U. (2002): Yield, transpiration and growth of tomatoes under combined excess boron and salinity stress. Plant and Soil, 247: 211–221.

Blum A. (2004): Sorghum physiology. In: Nguyen H.T., Blum A. (eds): Physiology and Biotechnology Integration for Plant Breeding. New York, Basel, Marcel Dekker, 141–223.

CronkLab (2016): Calculation of vapour pressure deficit. Available at: http://cronklab.wikidot.com/calculation-of-vapour-pressure-deficit

Fageria N.K. (1992): Maximizing Crop Yields. New York, Marcel Dekker.

Haefele S.M., Siopongco J.D.L.C., Boling A.A., Bouman B.A.M., Tuong T.P. (2009): Transpiration efficiency of rice (*Oryza sativa* L.). Field Crops Research, 111: 1–10.

Kemanian A.R., Stöckle C.O., Huggins D.R. (2005): Transpiration-use efficiency of barley. Agricultural and Forest Meteorology, 130: 1–11.

Mantovani D., Veste M., Gypser S., Halke C., Koning L., Freese D., Lebzien S. (2014): Transpiration and biomass production of the bioenergy crop Giant Knotweed IGNISCUM under various supplies of water and nutrients. Journal of Hydrology and Hydromechanics, 62: 316–323.

Mian M.A.R., Ashley D.A., Boerma H.R. (1998): An additional QTL for water use efficiency in soybean. Crop Science, 38: 390–393.

Peng S.B., Krieg D.R. (1992): Gas exchange traits and their relationship to water use efficiency of grain sorghum. Crop Science, 32: 386–391.

Prenger J.J., Ling P.P. (2009). Greenhouse Condensation Control: Understanding and Using 355 Vapor Pressure Deficit (VPD). Wooster, Ohio State University Extension Fact Sheet.

Rooney W.L. (2004): Sorghum improvement – Integrating traditional and new technology to produce improved genotypes. Advances in Agronomy, 83: 37–109.

Sinclair T.R., Weiss A. (2010): Principles of Ecology in Plant Production. 2nd Ed. Cambridge, Cambridge University Press.

Vadez V., Krishnamurthy L., Hash C.T., Upadhyaya H.D., Borrell A.K. (2011): Yield, transpiration efficiency, and water-use variations and their interrelationships in the sorghum reference collection. Crop and Pasture Science, 62: 645–655.

Waldren R.P. (1983): Corn. In: Teare L.D., Peet M.M. (eds): Crop – Water Relations. New York, John Wiley and Sons, 187–212.

Wright G.C., Rao R.C.N., Farquhar G.D. (1994): Water-use efficiency and carbon isotope discrimination in peanut under water deficit conditions. Crop Science, 34: 92–97.

Xin Z.U., Aiken R., Burke J. (2009): Genetic diversity of transpiration efficiency in sorghum. Field Crops Research, 111: 74–80.

Xin Z., Franks C., Payton P., Burke J.J. (2008): A simple method to determine transpiration efficiency in sorghum. Field Crops Research, 107: 180–183.

Yang Z., Hammer G., van Oosterom E., Rochais D., Deifel K. (2010): Effects of pot size on growth of maize and sorghum plants. In: Proceedings of the First Australian Summer Grains Conference, 21–24 June. Gold Coast, Australia.

Yoshida S. (1975): Factors that limit the growth and yields of upland rice. In: Major Research in Upland Rice. Philippines, International Rice Research Institute, 46–71.

Received on December 12, 2016
Accepted on February 7, 2017
Published online on February 24, 2017