

Water and Radiation Use Efficiencies in Sorghum

Sruthi Narayanan,* Robert M. Aiken, P. V. Vara Prasad, Zhanguo Xin, and Jianming Yu

ABSTRACT

Increasing water and radiation use efficiencies (WUE and RUE, respectively) are critical to enhance crop production. Exploring genetic variability in WUE and RUE is necessary to improve these traits. The objectives of this research were to evaluate eight sorghum [*Sorghum bicolor* (L.) Moench] genotypes for biomass production, WUE, and RUE and to test whether the differences in WUE among sorghum genotypes were associated with increased biomass production or decreased water use under field conditions. The WUE was estimated as the slope of the regression of aboveground biomass on cumulative water use for specified sampling intervals. The RUE was estimated as the slope of the regression of aboveground biomass on cumulative intercepted photosynthetically active radiation (IPAR). Sorghum genotypes showed significant differences in biomass production, WUE, and RUE. The WUE varied from 3.39 ± 0.80 to 5.42 ± 0.80 g kg⁻¹ in 2009 and from 4.04 ± 0.58 to 7.63 ± 0.58 g kg⁻¹ in 2010. Similarly, RUE varied from 2.13 ± 0.33 to 3.53 ± 0.31 g MJ⁻¹ IPAR in 2009 and from 2.08 ± 0.35 to 3.83 ± 0.33 g MJ⁻¹ IPAR in 2010. Among the eight sorghum genotypes tested in this study, IS 27111 and IS 27150 had the largest biomass production, WUE, and RUE. The WUE was more strongly correlated to biomass production than to water use. This result implies that it is possible to improve WUE without compromising biomass production. The sorghum genotypes evaluated for biomass production, WUE, and RUE in this study offer useful plant materials for identifying the mechanisms causing differences in these traits.

INCREASING ANY COMBINATION of crop WUE (the amount of biomass produced per unit water used) and RUE (the amount of biomass produced per unit radiation intercepted) under water-sufficient conditions can enhance land productivity. Increased WUE associated with water stress conditions often results in reduced yield (Blum, 2005). Sorghum, one of the most drought-tolerant cereal crops currently under cultivation (Blum, 2004), is reported to have high WUE (Hammer et al., 1997; Henderson et al., 1998; Mortlock and Hammer, 1999; Rooney, 2004) and RUE (Hammer and Vanderlip, 1989; Rosenthal et al., 1989, 1993; Kiriya et al., 1989; Muchow, 1989). Sorghum is the fifth major cereal crop in the world in terms of production and acreage. It is used as a staple food in Africa and Asia and as feed, forage, and biofuel in the United States.

Evaluating the genetic variability in sorghum for WUE and RUE can support utilization of traits that increase productivity. Intraspecific variation in WUE (Briggs and Shantz, 1913; Peng and Krieg, 1992; Hammer et al., 1997; Xin et al., 2009) and RUE

(Hammer and Vanderlip, 1989; Sinclair and Muchow, 1999; Hammer et al., 2010) has been reported in sorghum. Robust measurement of WUE and RUE in field studies is challenging, however, due to the lack of simple and rapid screening criteria and measurement techniques (Hall et al., 1990; Sinclair and Muchow, 1999) as well as the complexity of these traits. Consequently, there is limited knowledge of the genetic variability in both WUE and RUE in sorghum under field conditions.

Water use efficiency can be increased by increased biomass production with the same amount of water use, the same amount of biomass production with decreased water use, or a combination of both (Blum, 2005). Xin et al. (2009) evaluated 341 sorghum genotypes for transpiration efficiency (TE, the ratio of biomass produced to water transpired) based on biomass production in controlled environments and reported that TE had little correlation with water transpired and a large correlation with biomass produced. They concluded that increased biomass production rather than decreased transpiration accounted for increased TE. This result is in contrast with the selection of increased TE genotypes using the C isotope discrimination method that are often associated with decreased transpiration, growth, and biomass production (Condon et al., 2002; Impa et al., 2005; Blum, 2009). Tanner and Sinclair (1983) reported that WUE or TE within a species is relatively constant and cannot be manipulated. Xin et al. (2009), however, identified considerable genetic variability in TE for sorghum under controlled environments and reported that TE can be improved through improving biomass production. They further concluded that identifying high-TE genotypes based on biomass accumulation is a useful approach to select for high TE in sorghum. These results widen the scope for improving TE or WUE through exploiting traits or mechanisms that improve

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Abbreviations: IPAR, intercepted photosynthetically active radiation; LAI, leaf area index; RUE, radiation use efficiency; TE, transpiration efficiency; WUE, water use efficiency.

biomass production. Because the results of Xin et al. (2009) were from controlled environments and were conducted at the eight-leaf stage, to strengthen their inference these results need to be confirmed under field conditions and on fully developed plants.

The objectives of this study were to evaluate sorghum genotypes for biomass production, WUE, and RUE and to test under field conditions whether the differences in WUE among sorghum genotypes were associated with increased biomass production or decreased water use. We hypothesized that genetic variability exists in sorghum genotypes for WUE and RUE, and that WUE is more strongly correlated with biomass production than with water use.

MATERIALS AND METHODS

Crop Culture

Field studies were conducted in 2009 and 2010 at the Kansas State University Northwest Research Extension Center, Colby, KS (39°24' N, 101°4' W, 963 m asl) on a Keith silt loam soil (fine-silty, mixed, superactive, mesic Aridic Argiustoll). The previous crop for the 2009 study site was sorghum in one half of the site and sunflower (*Helianthus annuus* L.) in the other half. The previous crop for the 2010 study site was maize (*Zea mays* L.). Tillage in both years included two passes with a disk harrow followed by a roller packer to break clods. Tillage was done on 10 June in 2009 and 1 April and 3 May in 2010. Eight sorghum genotypes (TX 7000, TX 399, TX 2862, PI 584085, Liang Tang Ai, TX 7078, IS 27150, and IS 27111), representing a range of vegetative TE values (Z. Xin and R. Aiken, personal communication, 2000), were planted in 6.1- by 6.1-m plots on 25 June 2009 and in 6.1- by 3.0-m plots on 28 May 2010. Plots were arranged in a randomized complete block design in 2009. Due to a planting error in 2010, some blocks did not receive all the genotypes. Therefore, plots were arranged in an incomplete block design in 2010. There were five blocks (replications) in both years. All genotypes except IS 27111 were photoperiod insensitive. Bulk rows were planted between plots to avoid edge effects on crop growth and resource use. Sorghum seeds were sown at a depth of 2 cm using a planter with a fluted coulter and double disk opener. The planting rate was 125,000 seeds ha⁻¹, with a spacing of 10 cm between plants and 76 cm between rows. Rows were oriented in a north-south direction. Nutrient application included 102 kg N ha⁻¹ and 34 kg P ha⁻¹ banded before planting in both years. Weed control consisted of a pre-emergent application of atrazine [6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5-triazine-2,4-diamine, 4.68 L ha⁻¹] and S-metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N'*[(1*S*)-2-methoxy-1-methylethyl]acetamide, 1.52 L ha⁻¹] and post-emergent application of fluroxypyr 1-methylheptyl ester (2-[(4-amino-3,5-dichloro-6-fluoro-2-pyridinyl)oxy]acetic acid, 1-methylheptyl ester, 1.02 L ha⁻¹) in both years. Supplemental in-season irrigation was provided during mid-vegetative growth (38 mm) and just before anthesis (25 mm) for one half of the plots (Treatment 1, five replications) and during mid-vegetative growth (25 mm) for the other half (Treatment 2, five replications) in 2009. In 2009, however, rainfall totals were large and negated any irrigation differences. Thus, irrigation treatment was removed from the data analysis in 2009. Therefore, in 2010, all plots were kept well watered. Irrigation was provided via the furrow method. The irrigation system had equal numbers and distribution of water-emitting tubes in all plots. The emission tubes were examined for constant and equal amounts of water delivery to each furrow.

The amount of water to each plot was monitored with a discharge gauge and regulated through manually operated control valves.

Observations and Calculations

Periodic observations of crop phenological development were recorded at approximately biweekly intervals for two identified plants in each plot (10 samples per genotype). Plant height was determined as the distance between the soil and the flag leaf ligule.

In 2009, biomass was measured by destructive harvest at booting (60 d after planting [DAP]) and post anthesis (82 DAP; as indicated by photoperiod-insensitive genotypes). Plants in the center rows were machine harvested for biomass measurement. Biomass at mid-vegetative growth (35 DAP) was determined from observed values of plant height (distance between soil and ligule of the top mature leaf) and average stem diameter and a calibrated linear relationship (Table 1) between aboveground biomass and the product of plant height and average stem diameter. Separate equations were derived for each genotype for estimating the biomass by this method. In 2010, the crop stand was not adequate to use machine harvest for the measurement of biomass. Therefore, the biomass harvest followed the method of Lindquist et al. (2005) in this year; e.g., five consecutive plants were hand harvested at approximately biweekly intervals from each plot between 35 and 105 DAP. The row length of harvested plants was measured. Plants were harvested from rows in which the crop stand was considered adequate. Each harvested row was bordered at least by two other rows, or bulk rows, to avoid edge effects. Biomass was calculated on a land-area basis, using row spacing and row length of harvested plants. At grain maturity, the harvested portion of the row had at least 1-m length, and more than five plants were sampled for biomass. Harvested plants were dried to constant weight at 60°C.

Leaf area index (LAI) was measured by a plant canopy analyzer (LI-COR LAI-2000), approximately biweekly beginning from 35 DAP in 2009, and approximately weekly beginning from 40 DAP in 2010. This instrument estimates LAI as a function of canopy transmittance of diffused solar radiation (Welles and Norman, 1991). Measurements of LAI were made on all plots in both years. Measurements with the LAI-2000 were made at three locations within each plot. These locations were ensured to have an adequate crop stand. Measurements at each location consisted of a single reading of diffused radiation above the canopy and four readings of diffused radiation below the canopy. All readings were

Table 1. Relationship between aboveground biomass (y) and the product of plant height and average stem diameter (x) of sorghum genotypes grown at Colby, KS, in 2009.

Genotype	Relationship†	R ²
TX 7000	$y = 0.286 (0.009) x$	0.96
TX 2862	$y = 0.356 (0.012) x$	0.95
PI 584085	$y = 0.2960 (0.004) x$	0.91
Liang Tang Ai	$y = 0.2350 (0.008) x$	0.94
TX 7078	$y = 0.3140 (0.012) x$	0.93
TX 399	$y = 0.2910 (0.008) x$	0.96
IS 27150	$y = 0.4340 (0.014) x$	0.95
IS 27111	$y = 0.3510 (0.011) x$	0.95

† To calibrate the relationship between aboveground biomass and the product of plant height and average stem diameter, five plants were hand harvested at approximately biweekly intervals from each plot, between 32 and 81 d after planting, after measuring plant height and average stem diameter. Harvested plants were dried individually to constant weight at 60°C to determine dry weight. Values in parentheses represent standard error of the slope. The intercept was not significant for this relationship.

taken within 2 min to minimize atmospheric variation. Readings were screened to exclude apparent transmittance >1. The LAI was solved analytically using LI-COR software to obtain a single LAI value for each plot. Because the instrument is sensitive to all light-blocking objects in its view, and no corrections were made in the LAI estimates for stem area, the LAI measured in this study represents the foliage area index.

For the estimation of transmittance (τ), solar radiation above and below the canopies was measured using a line quantum sensor (LI-COR LI-191SA). Measurements were made on 36, 49, and 60 DAP in 2009 and on 47, 60, and 69 DAP in 2010. Transmittance was measured on all the plots at locations with an adequate crop stand in both years. A single line quantum sensor was used to make a single measurement of the incident radiation at the top of the canopy, followed by four consecutive measurements below the canopy in each plot. The fraction of photosynthetically active radiation (PAR) transmitted by the canopy (τ) was calculated by dividing each below-canopy reading by the above-canopy reading, and the average was taken as the estimate for the plot. Transmittance measurements were made on days with clear sky in both years. Transmittance values (solar azimuth >20° relative to south, and solar zenith angles between 25 and 40°) were used for the calculation of a canopy extinction coefficient (k), which was used for the estimation of IPAR. The extinction coefficient was calculated by the Beer–Lambert equation:

$$k = \frac{-\ln(\tau)}{\text{LAI}} \quad [1]$$

Weather data were obtained from the Cooperative Observer Site (Colby 1SW, located within 500 m of the field), associated with the National Weather Service. Daily incident PAR (400–700 nm; in MJ m⁻²) was calculated from daily solar radiation (SR; obtained from weather station records), assuming that PAR comprised 47% of SR (Howell et al., 1983). Daily IPAR was estimated as (Campbell and Norman, 1998)

$$\text{IPAR} = 0.47 \text{SR} \left[1 - \exp(-k \text{LAI}) \right] \quad [2]$$

The daily LAI values used in Eq. [2] were obtained through interpolation of the observed LAI values. Cumulative IPAR was calculated from daily values of IPAR, beginning from emergence. The RUE for each genotype was determined as the slope of biomass (accumulated after the first sampling and up to 81 DAP in 2009 and 89 DAP in 2010) regressed against the corresponding cumulative IPAR (Lindquist et al., 2005).

Soil water content was measured at approximately biweekly intervals during 32 to 81 DAP in 2009 and 45 to 89 DAP in 2010 using neutron thermalization (503DR Hydroprobe, CPN Corp.). Soil was excavated by a hydraulic-driven tube (38-mm diameter) in each plot to a depth of 3.5 m, into which a vertical aluminum tube (38-mm diameter and 3.65-m length) was inserted, providing access to the soil profile. The volumetric water content (m³ m⁻³) at 0.30-m depth intervals was determined by the neutron attenuation method, from 0.30 m below the soil surface to the 3-m depth. The total stored soil water (m) was calculated as the product of the depth interval (0.3 m) and the sum of individual volumetric

water content values at 0.3-m intervals. Stored soil water was calculated using measurements to a depth of 2.4 m. Access tubes were installed in crop rows that were bordered by other rows on both sides and where the crop stand was considered adequate to represent root water uptake. Soil water depletion for a given plot between two sampling dates was calculated as the difference between stored soil water between the sampling dates.

Crop water use, at approximately biweekly intervals, was determined as the sum of soil water depletion, irrigation, and precipitation during the time interval. No corrections were made for drainage, runoff, or evaporative losses of water in the estimates of crop water use. Thus, our field determinations of crop water use included drainage, runoff, and evaporation. Cumulative water use was calculated as the sum of biweekly crop water use between 32 and 81 DAP in 2009 and 45 and 89 DAP in 2010. The WUE (biomass based) was estimated, for the duration of the measured crop water use interval, as the slope of the regression of above-ground biomass (relative to the initial value; 35 DAP in 2009 and 45 DAP in 2010) on cumulative water use; biomass values corresponding to cumulative water use values were calculated by linear interpolation between measurements. In both years, the beginning of seasonal WUE estimation was near canopy closure.

Statistical Analyses

Analysis of variance was performed on genotypes using the MIXED procedure in SAS (Version 9.1.3, SAS Institute) for growth, water use, and IPAR variables at all measurement dates separately. Separation of means used the LSD test ($P < 0.05$) in the PDMIX 800 macro (Saxton, 1998). Genotype was treated as a fixed effect, and replication was treated as a random effect. Irrigation was considered as a whole-plot treatment and genotype was considered as a split-plot treatment in 2009; because no difference was detected in growth, water use, IPAR, WUE, and RUE variables between irrigation treatments in 2009, the data were pooled across irrigation treatments. An extinction coefficient was estimated and compared among different genotypes using the MIXED procedure in SAS, with LAI as a covariate. The REG procedure in SAS was used to regress biomass against water use or cumulative IPAR for the estimation of WUE or RUE, respectively; homogeneity of slopes was evaluated by analysis of covariance, using the GLM procedure, and constructing a t -test using a pooled standard error for interacting effects of biomass and covariate (either cumulative water use or cumulative IPAR). To determine the relative contribution of biomass production and water use to WUE, regression analysis (REG procedure in SAS) was performed between WUE and biomass and between WUE and water use.

RESULTS

Environmental Conditions

The maximum and minimum temperatures (max./min.) during the sampling period varied between 18.9/12.2 and 37.8/20.0°C in 2009 and 19.4/3.3 and 40.0/21.7°C in 2010 (Fig. 1). Total precipitation (Fig. 2) was 194 mm in 2009 (within 82 DAP) and 241 mm in 2010 (within 105 DAP). The large amount of rainfall prevented the two irrigation treatments (well watered and limited irrigation) from being differentiated in 2009. In 2010, all plots were maintained as well watered throughout the growing season. No pest or pathogen problems were observed in either year during the entire cropping season.

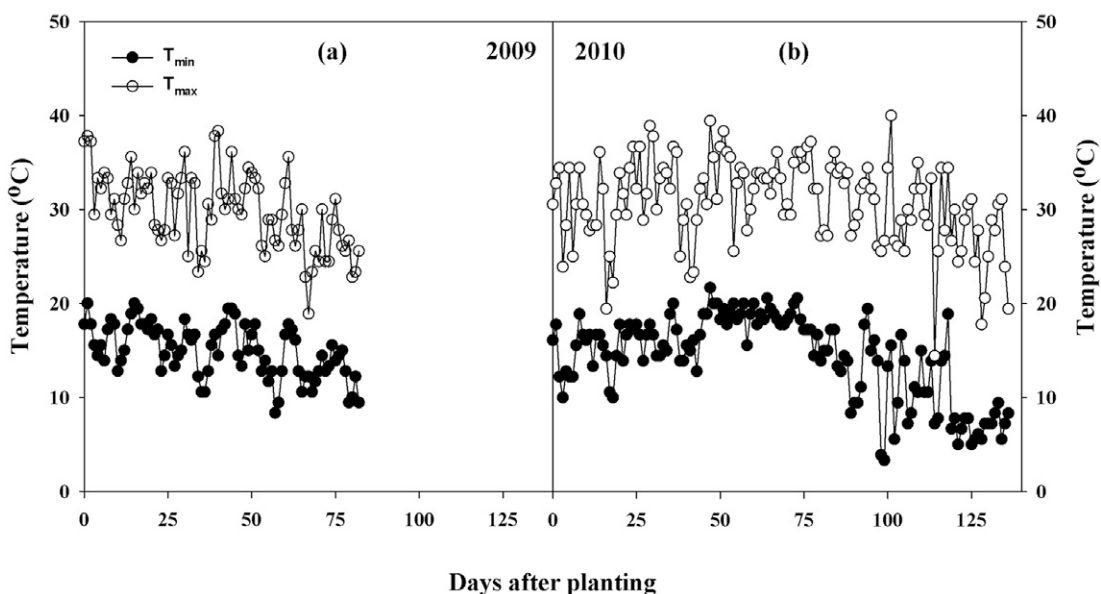


Fig. 1. Daily minimum (T_{\min}) and maximum (T_{\max}) temperatures from planting through the end of the season (82 d after planting [DAP] in 2009 and 136 DAP in 2010) for sorghum genotypes grown at Colby, KS, in (a) 2009 and (b) 2010.

Phenological Development

Emergence was noted at 8 DAP in both years. Genotype PI 584085 was removed from the 2010 study because it had <20% crop stand. All photoperiod-insensitive genotypes flowered within 65 DAP in both years. The photoperiod-sensitive genotype IS 27111 flowered around 85 DAP in both years. Due to frost, plants did not survive to grain maturity in 2009. This prevented the aboveground biomass sampling for all genotypes at grain maturity in 2009.

Biomass Production

Sorghum genotypes showed significant variation for biomass production. Genotypes started differing in biomass production from the second sampling date (60 DAP in 2009 and 48 DAP in 2010) onward in both years (Fig. 3a and 3b). After that point, the genotypes IS 27150 and IS 27111 had greater biomass production than the other genotypes during the entire cropping season in both years (Fig. 3a and 3b; Table 2). In 2010, there was one additional biomass sampling at grain maturity, in which the results (reported in Fig. 3b) were consistent with the results of the biomass measurements. Genotypes IS 27150 and IS 27111, with greater biomass production, also had greater plant height than other genotypes in 2009 and 2010 (Table 2).

Leaf Area Index, Cumulative Intercepted Photosynthetically Active Radiation, and Crop Water Use

Genotypes differed in LAI on all measurement dates (except for the first measurement at 40 DAP in 2010) in 2009 and 2010. In both years, the LAI of the genotypes IS 27150 and IS 27111 was greater than the others during initial growth (Fig. 3c and 3d). The LAI of genotypes IS 27150 and IS 27111 decreased to half of the maximum value within 30 d of the maximum LAI.

In both years, no differences were detected among genotypes in transmittance of above-canopy incident radiation to ground level. Therefore, a common extinction coefficient (k) was derived for all genotypes for a period from emergence to 82 DAP in 2009 and 80 DAP in 2010. The value of k (\pm SE) was greater in 2009

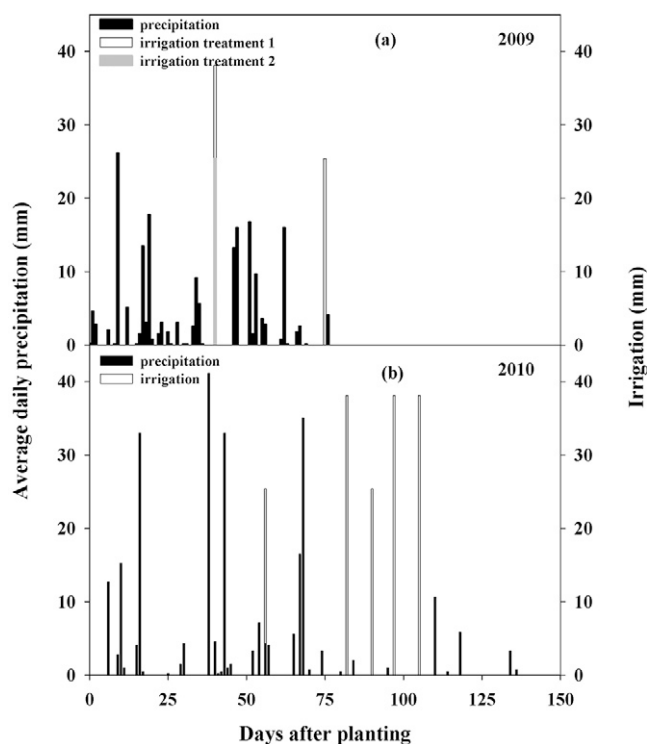


Fig. 2. Daily precipitation and irrigation from planting through the end of the season (82 d after planting [DAP] in 2009 and 136 DAP in 2010) for sorghum genotypes grown at Colby, KS, in (a) 2009 and (b) 2010. There were two irrigation treatments—Treatment 1, well watered and Treatment 2, limited irrigation—in 2009 while there was only one irrigation treatment—well watered—in 2010.

(0.891 ± 0.029) than in 2010 (0.668 ± 0.025). The larger estimates of k in 2009 may be due to the larger number of dead leaves on plants, observed in 2009 compared with 2010, which might alter leaf angles and the interception of radiation (Muchow and Sinclair, 1994; Lindquist et al., 2005); the delayed planting and

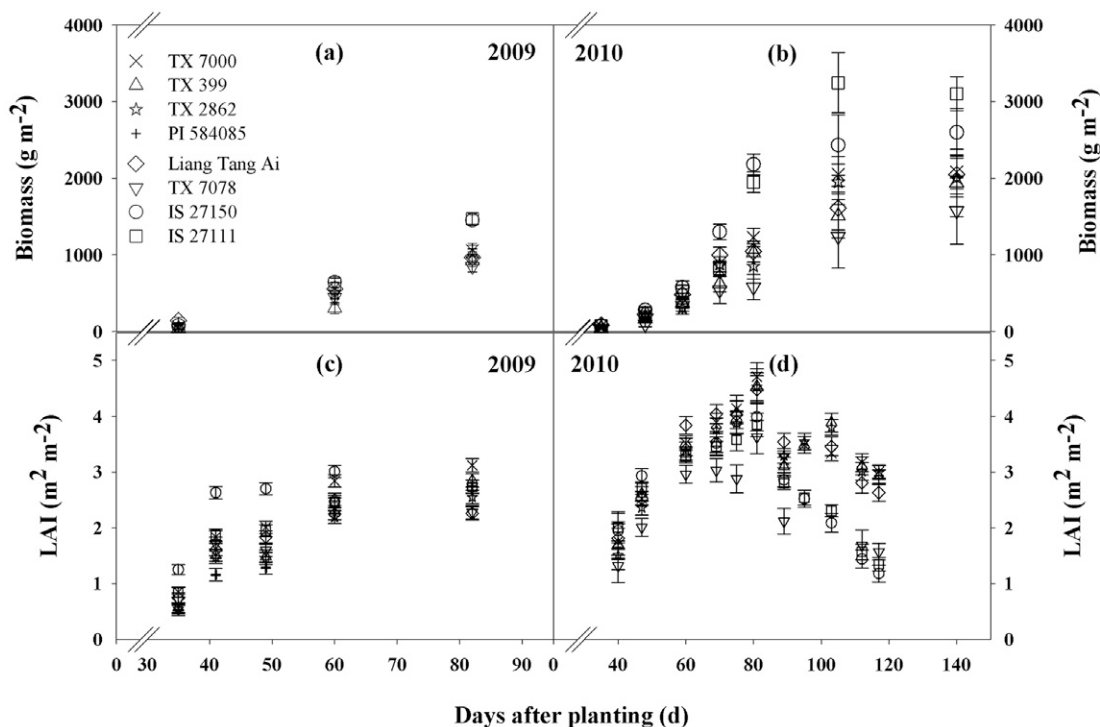


Fig. 3. Observed (symbols [LSMEANS] and standard error bars) (a,b) biomass production and (c,d) leaf area index (LAI) of sorghum genotypes at Colby, KS, in 2009 and 2010.

Table 2. Least square means (LSMEANS) for plant height, biomass, crop water use, and cumulative intercepted photosynthetically active radiation (IPAR) of sorghum genotypes grown at Colby, KS, in 2009 and 2010.

Genotype	Plant height		Biomass		Crop water use†		Cumulative IPAR‡	
	2009	2010	2009 (32–81 DAP)	2010 (45–89 DAP)	2009 (32–81 DAP)	2010 (45–89 DAP)	2009 (32–81 DAP)	2010 (45–89 DAP)
	cm		g m ⁻²		kg m ⁻²		MJ m ⁻²	
TX 7000	71 cd§	81 de	976 bc	1335 bc	236 abc	212 b	400 b	476 ab
TX 2862	70 cd	87 de	890 bc	1307 bcd	218 c	220 ab	363 de	473 ab
PI 584085	74 cd	–	1012 b	–	224 bc	–	349e	–
Liang Tang Ai	79 c	110 c	910 bc	1127 cd	227 bc	232 ab	378 cd	484 a
TX 7078	66 cd	74 e	797 c	981 d	230 bc	240 ab	370 d	448 c
TX 399	57 d	77 e	862 bc	1154 cd	243 ab	221 ab	377 cd	471 ab
IS 27150	179 b	207 b	1344 a	1717 a	239 abc	238 ab	422 a	476 ab
IS 27111	278 a	319 a	1399 a	1516 ab	256 a	246 a	391 bc	468 b
LSD	18	16	199	303	21	32	18	15

† No corrections were made for drainage, runoff, or evaporative losses of water in the estimates of crop water use.

‡ Cumulative IPAR was computed beginning from the indicated time period.

§ LSMEANS estimates followed by different letters are significantly different according to a LSD test at $P < 0.05$.

drier growing environment in 2009 compared with 2010 might have hastened the onset of leaf senescence in crops in 2009.

Genotypes differed in cumulative IPAR in both years (Table 2). Because IPAR, for a given year, was calculated from LAI and a constant k , the differences in IPAR among genotypes was determined by the differences in LAI alone. Genotypes did not show much variation for water use in either year (Table 2).

Water Use Efficiency and Radiation Use Efficiency

Genotypes differed in growth in relation to water use (Fig. 4a and 4b) and cumulative IPAR (Fig. 4c and 4d) in 2009 and 2010; genotypes also differed in WUE and RUE (Table 3). Genotype IS 27150 had greater WUE than TX 7078 in both years; genotypes

IS 27150 and IS27111 had greater RUE than TX 7078 and TX 399 in both years.

Because WUE is the ratio between biomass production and water use, it can be increased by increased biomass production with the same amount of water use, the same amount of biomass production with decreased water use, or a combination of the two. To analyze which factor contributed more toward large WUE values under field conditions, we regressed WUE against biomass production and water use. Water use efficiency was strongly related to biomass and not significantly related to water use (Table 4). Similarly, RUE had a stronger correlation with biomass than with cumulative IPAR (Table 4).

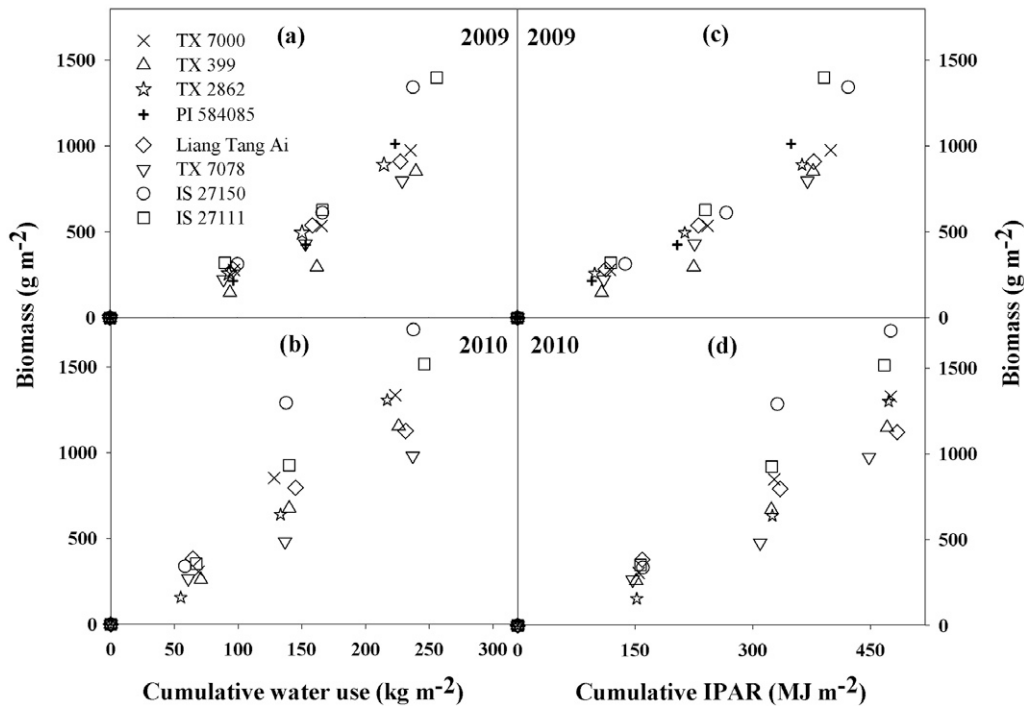


Fig. 4. Derivation of (a,b) water use efficiency (WUE) and (c,d) radiation use efficiency (RUE) among sorghum genotypes; WUE was derived as the slope of the regression of biomass on cumulative water use, while RUE was derived as the slope of the regression of biomass on cumulative intercepted photosynthetically active radiation (IPAR).

Table 3. Water use efficiency (WUE) and radiation use efficiency (RUE) of sorghum genotypes grown at Colby, KS, in 2009 and 2010.

Genotypes	WUE [†]		RUE [‡]	
	2009	2010	2009	2010
	g kg ⁻¹		g MJ ⁻¹ IPAR	
TX 7000	4.04 ± 0.81 (5)§	6.19 ± 0.63 (3)	2.41 ± 0.30 (5)	2.84 ± 0.33 (3)
TX 2862	4.06 ± 0.89 (4)	6.13 ± 0.63 (4)	2.42 ± 0.33 (4)	2.76 ± 0.33 (4)
PI 584085	4.35 ± 0.86 (3)	–	2.86 ± 0.35 (3)	–
Liang Tang Ai	3.95 ± 0.84 (6)	4.86 ± 0.59 (6)	2.39 ± 0.32 (6)	2.33 ± 0.32 (6)
TX 7078	3.44 ± 0.84 (7)	4.04 ± 0.58 (7)	2.13 ± 0.33 (8)	2.08 ± 0.35 (7)
TX 399	3.39 ± 0.80 (8)	5.20 ± 0.62 (5)	2.22 ± 0.32 (7)	2.44 ± 0.33 (5)
IS 27150	5.42 ± 0.80 (1)	7.63 ± 0.58 (1)	3.13 ± 0.29 (2)	3.83 ± 0.33 (1)
IS 27111	5.34 ± 0.75 (2)	6.30 ± 0.57 (2)	3.53 ± 0.31 (1)	3.26 ± 0.33 (2)
	<i>Analysis of covariance F tests (Type III), Pr > F</i>			
Effect				
Genotype	0.9977	0.5133	0.9712	0.9746
Covariate¶	<0.0001	<0.0001	<0.0001	<0.0001
Genotype × covariate#	0.5024	0.0156	0.0616	0.0330
R ²	0.937	0.982	0.974	0.975

[†] Canopy-level WUE was estimated as the slope (±SE) of the regression of aboveground biomass on cumulative water use for the specified sampling interval; SE values were estimated by solution for the interacting effects of genotype × covariate in analysis of covariance for aboveground biomass, with cumulative water use (specified sampling intervals) as the covariate.

[‡] Canopy-level RUE was estimated as the slope (±SE) of the regression of aboveground biomass on cumulative intercepted photosynthetically active radiation (IPAR); SE values were estimated by solution for the interacting effects of genotype × covariate in analysis of covariance for aboveground biomass, with cumulative IPAR as the covariate.

§ Values in parentheses are relative ranking of genotypes, based on numerical values of WUE or RUE.

¶ Covariate is cumulative water use for WUE and cumulative IPAR for RUE.

Significant effect of Genotype × covariate indicates slopes differed among genotypes.

DISCUSSION

This study demonstrated that sorghum genotypes differ in WUE and RUE under field conditions and that increased WUE based on biomass production per unit water use is related to increased biomass production rather than decreased water use. This contrasts with the selection of wheat (*Triticum aestivum* L.) genotypes with increased TE (C isotope discrimination method),

which exhibited decreased water use and biomass production (Blum, 2009). The results of this study indicate the potential to improve WUE without compromising biomass production and yield potential. The sorghum genotypes evaluated in this study offer useful plant materials for identifying the mechanisms resulting in increased WUE or RUE.

Table 4. Relationship between resource use efficiencies (water use efficiency [WUE] and radiation use efficiency [RUE]) and their components.

Relationship	2009		2010	
	R ²	RMSE	R ²	RMSE
x = biomass, y = WUE	0.942	0.200	0.942	0.309
x = water use, y = WUE	NA†	NA	NA	NA
x = biomass, y = RUE	0.900	0.169	0.970	0.113
x = CIPAR‡, y = RUE	NA	NA	0.695	0.361

† NA, not applicable. Slope and intercept of the regression between CIPAR and RUE were not significant. Therefore the regression line was not significant.

‡ Cumulative intercepted photosynthetically active radiation.

Xin et al. (2009) reported a stronger correlation of TE with increased biomass production than with reduced water use under controlled environments. Our study confirmed this inference under field conditions. Our study drew a similar inference for RUE also, because RUE had a stronger correlation with biomass than with cumulative IPAR. Xin et al. (2009) did not estimate RUE in their study. They confined their measurements for TE estimation within the early vegetative stage (eight-leaf stage). Our study estimated WUE considering crop growth until the early reproductive stage (up to 81 DAP in 2009 and 89 DAP in 2010).

Generally, the rank of the lines in biomass production and WUE (Table 3) was consistent between the 2 yr. The WUE values obtained from both years in this study (3.39–7.63 g kg⁻¹; Table 3) were within the range of those commonly reported for sorghum that range between 2.8 and 12.6 g kg⁻¹ (Hammer et al., 1997; Henderson et al., 1998; Mortlock and Hammer, 1999). The WUE values from 2009 (3.39–5.42 g kg⁻¹; Table 3) were consistently lower than those from 2010 (4.04–7.63 g kg⁻¹; Table 3). We attribute this to delayed planting (due to wet spring conditions) that resulted in diminished growth due to suboptimal growing conditions in 2009 (cool conditions late in the season; Fig. 1).

The RUE values reported here (2.08–3.83 g MJ⁻¹ IPAR; Table 3) are within the range of published values of seasonal RUE for sorghum that vary from 1.2 to 4.3 g MJ⁻¹ IPAR (Hammer and Vanderlip, 1989; Rosenthal et al., 1989, 1993; Kiniry et al., 1989; Muchow, 1989). The large RUE values (>3.0 g MJ⁻¹ IPAR; Table 3) associated with the genotypes IS 27150 and IS 27111 are even similar to those reported for maize (3.7 g MJ⁻¹ IPAR, Lindquist et al., 2005).

The stronger correlation of WUE to biomass than to water use (Table 4) implies that increased biomass production rather than decreased water use contributed more toward increased WUE in sorghum genotypes under field conditions. This implies that a substantial improvement in WUE is possible through the improvement in traits leading to increased biomass production. This study suggests that evaluating WUE based on biomass accumulation is a relevant approach to select for high-WUE sorghum genotypes under field conditions. Apparently, enhancing WUE through improving biomass production may have a large potential to increase sorghum biomass production under rainfed conditions because high-WUE sorghum plants accumulate large amounts of biomass with the same amount of soil water available to the plants during the growing season. By definition,

$$RUE = \frac{\text{biomass}}{\text{IPAR}} \quad \text{and} \quad WUE = \frac{\text{biomass}}{\text{water use}}$$

This gives, $RUE = (WUE \times \text{water use})/\text{IPAR}$. Thus, an association between RUE and WUE is expected based on the existing

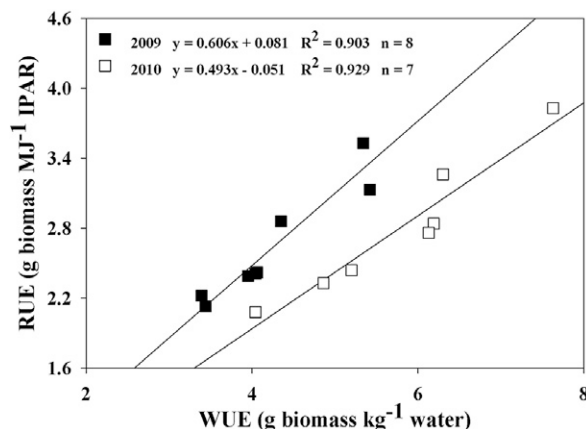


Fig. 5. Relationship between water use efficiency (WUE) and radiation use efficiency (RUE) among sorghum genotypes; WUE was derived as the slope of the regression of biomass on cumulative water use, while RUE was derived as the slope of the regression of biomass on cumulative intercepted photosynthetically active radiation (IPAR).

theory. Our field data provide evidence supporting this association (Fig. 5). We found a positive linear relationship between WUE and RUE of sorghum genotypes in this study (Fig. 5). The stronger correlation of RUE to biomass than to cumulative IPAR (Table 4) indicates that increased biomass production rather than decreased interception of radiation contributed more toward increased RUE in sorghum genotypes. Collectively, these results imply that selecting for high WUE based on biomass production also results in genotypes with high RUE.

The genotypes IS 27150 and IS 27111, with the largest biomass production, WUE, and RUE, also had the greatest plant height compared with other genotypes (Table 2). This result is consistent with recent studies on sorghum that reported increased biomass production (George-Jaeggli et al., 2011) and RUE (Hammer et al., 2010) in tall sorghum genotypes. Increased biomass production and RUE of tall sorghum genotypes could be related to increased productivity of open canopies with greater penetration of light into mid-canopy layers (Pattey et al., 1991; Rochette et al., 1996). The reasons behind significant genotypic effects on biomass and RUE, such as differences in net photosynthetic rate or root–shoot partitioning are subjects for future research. Increased biomass, WUE, and RUE in tall genotypes implies that improvement in sorghum yield potential under rainfed conditions might be possible through manipulation of plant height. Introduction of the stay-green character in sorghum and the associated decrease in lodging (Borrell et al., 2000) expand the scope of exploiting tall genotypes for improving biomass production.

This research focused on the WUE and RUE of sorghum genotypes based on biomass production, which is very important for sorghum used as a bioenergy crop (Rooney et al., 2007). Genotypes IS 27111 and IS 27150, with high biomass production, WUE, and RUE, can be utilized for breeding sorghum for forage and bioenergy production. Further studies are needed for improvement of grain-based WUE by converting the increased biomass production to increased grain yield with an improvement in harvest index. In addition, evaluating the relationship of WUE with biomass and water use and RUE with biomass and cumulative IPAR under different levels of water stress is a subject for future research.

In summary, we identified considerable genetic variability for biomass production, WUE, and RUE among sorghum genotypes under field conditions. Among the eight sorghum genotypes tested here, IS 27111 and IS 27150 had the largest WUE and RUE. Increased WUE among sorghum genotypes was more strongly associated with increased biomass production than with decreased water use. The sorghum genotypes evaluated for biomass production, WUE, and RUE in this study offer critical plant materials for identifying mechanisms causing differences in these traits.

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