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RESEARCH ARTICLE

Transpiration efficiency of sorghum [*Sorghum bicolor* (L.) Moench] in relation to plant type and genotype

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Abstract: Sorghum is a major crop in dry land farming systems where grain yield is limited by water availability around anthesis. Genotypic differences in transpiration efficiency (TE) have been reported for sorghum, but it is unclear whether the TE of tall double dwarf (2d) genotypes is different to that of short triple dwarf (3d) ones. The objectives of this study are to determine whether (i) plant type in terms of plant stature has a significant effect on TE, and (ii) genotypic differences in TE are associated with leaf conductance or photosynthetic capacity. Individual plants of seven tall 2d genotypes and 14 short 3d genotypes were grown in lysimeters. Plants were well watered and harvested 5 ± 1 days after flowering of the main shoot. At harvest, total transpiration (T), leaf area and biomass were measured. TE, photosynthetic capacity and conductance were calculated. The TE did not differ between 2d and 3d plant types. Differences in TE among genotypes of both sorghum plant types were observed. These differences were associated with differences in photosynthetic capacity, rather than conductance and were not linked to stay-green expression. As stay-green expression can be a consequence of plant size, it indicates that TE and plant size are potentially independent traits of drought adaptation, highlighting the possibility of simultaneous selection for these two traits.

Keywords: Conductance, drought adaptation, photosynthetic capacity, plant stature, sorghum, transpiration efficiency.

INTRODUCTION

Sorghum is a major summer crop in rainfed farming systems around the world (Hammer *et al*., 2014; Geetika *et al*., 2019). In the grain belt of eastern Australia, it is the dominant dryland summer crop. Rainfall in sorghum cultivated areas of eastern Australia is highly variable (205 to 800 mm). As a result, crops can experience a wide range of patterns of water supply during the growing season and timing and intensity of drought stress can be variable (Chapman *et al*., 2000).

Crop production in water limited environments is the product of total transpiration (T), transpiration efficiency (TE) and harvest index (HI) (Passioura & Angus, 2010). In this context, grain yield is linked to post anthesis transpiration or crop water used (Turner 2004; van Oosterom *et al*., 2011). Water stress at early reproductive phases can contribute to major yield losses (Borrell *et al*., 2014), because the crop growth rate, and in particular the panicle growth rate at anthesis determines grain number (Vega *et al*., 2001; Andrade *et al*., 2002; van Oosterom & Hammer, 2008). Tall 2d sorghum tends to have greater grain yield than short 3d sorghum, but this is predominantly associated with increased grain mass, rather than grain number (George-Jaeggli *et al*., 2011). Within the above framework, grain yield can be increased by restricting pre-anthesis water use to maximise post anthesis water availability (Hammer, 2006). Simulation studies for wheat (*Triticum aestivum* L.) indicated a yield increase of 50–60 kg/ha per millimetre of extra water uptake after anthesis (Manschadi *et al*., 2006). Crops that have higher potential biomass production prior to anthesis utilise more water and as a consequence have less soil water available for reproductive growth

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(Hammer, 2006; van Oosterom *et al*., 2011). Hence, under water limited conditions, increased post anthesis transpiration as a fraction of total transpiration could be an important aspect of drought stress.

As a tillering crop, plant size of sorghum can be reduced by restricting tillering (Hammer *et al*., 1997). Tillering is associated with the carbon supply/demand balance of the crop (Kim *et al*., 2010). However, in environment × management conditions that are not conducive to tillering, such as high plant density and high temperatures (Kim *et al*., 2010), water saving through reduced tillering has limited value for rainfed farming systems. Under such conditions, TE and its components become more important factors of drought adaptation in breeding programmes (Blum, 2009; Lobell *et al*., 2014). Within the context of growth rates around anthesis, increased TE can delay the onset of drought stress if it is associated with reduced water use, or increase the growth rate for the same water use. Both mechanisms can potentially increase the crop growth rate around anthesis, and hence the panicle growth rate and therefore grain number. Genotypic differences in TE have been reported for sorghum (Hammer *et al*., 1997; Balota *et al*., 2008; Xin *et al*., 2009), but little information is available on the crop physiological mechanisms that determine these differences and whether 2d and 3d sorghum differ in TE. The genotypic variation for TE in sorghum could be associated with differences in photosynthetic capacity (Hammer *et al*., 1997; Xin *et al*., 2009), conductance (Mortlock & Hammer, 1999), or leakage of CO_2 to the bundle sheath (Henderson *et al*., 1998). At the leaf level, TE is the ratio of photosynthetic capacity and conductance (Polley *et al*., 1996). At the plant level, photosynthetic capacity can be estimated as biomass production per unit leaf area and conductance as transpiration per unit leaf area. Therefore, an experiment was conducted to measure TE and associated parameters of photosynthetic capacity and conductance at the plant level for a range of tall double dwarf (2d) and short triple dwarf (3d) sorghum genotypes. The aims of this study were to determine if sorghum plant types differ in TE, and if so, whether there is any genotypic differences in TE associated with plant stature or with components of TE (conductance or photosynthetic capacity).

METHODOLOGY

Experimental details

The experiment was conducted in a semi controlled lysimetery facility in a shade house at Gatton (27^{0}33'S, 152^{0}20'E), Queensland, Australia. It included seven double dwarf (2d) and 14 triple dwarf (3d) sorghum genotypes. The genotypes contained two hybrids, whereas the remainder were inbred lines that represented a diverse range of germplasm, including parents of mapping populations and elite breeding lines (Table 1). The experimental design was a modified split plot with plant type (2d sorghum, 3d sorghum) as main plots and genotypes as subplots. The experiment had four replications and a blank reference pot was included in each 2d sorghum main plot.

Genotypes were grown as individual plants in lysimeters. Lysimeters had a size of around 51 litres, which did not restrict root growth (Yang *et al*., 2010). Prior to filling, each pot was lined with a plastic bag to facilitate removal of the soil at harvest. The pots were filled with air dried soil to a weight of 61 kg. Approximately 42 g of Osmocote plus (16 % N, 3.5 % P, 10 % K) slow releasing fertilizer and 40 g of dolomite (to minimise symptoms of calcium deficiency) were added to each pot in six evenly distributed layers during soil filling. After filling, pots were watered up to slightly below the drained upper limit (DUL) or field capacity. The DUL was determined from a reference pot that had holes drilled in the bottom and was filled with the same amount of soil but without plastic liner. The pot was watered, and left to drain, and the amount of water to be added to the experimental pots was determined from the difference in weight before watering and after draining. As the soil in each lysimeter compacted during watering, an additional 8 kg of soil was added to each pot and water was added pro rata to achieve the DUL.

Five seeds were planted in the middle of each pot, and after emergence, these were gradually thinned until one plant per pot was left when two to three leaves had fully expanded. At that stage, the soil surface of each lysimeter was covered and sealed with thick plastic to minimise soil evaporation. Each lysimeter pot was placed on its own load cell, and weight was recorded automatically every 15 min. Once the pot weight dropped below a pre-set value (around 1.5 kg below DUL) 500 mL of water was automatically added. Hence, water content of soil in the containers was maintained above the lower limit (LL) or wilting point. Pots were thus watered as required, and plant available water was maintained at a level at which drought stress did not occur, but was slightly below DUL to minimise the risk of water logging. If the fraction of available soil water is higher than 0.3, the transpiration rate is not changed (Sinclair & Ludlow, 1986). Therefore, addition of 500 mL of water could maintain the plant without water deficit. Water was added through a porous plastic tube (2 cm diameter) that was buried down to a depth of 10 cm above the base of pots. Hence, water could be absorbed into soil and capillary action could help to move water up to the root zone of plants. As sorghum is sensitive to calcium (Ca) deficiency, a solution of 0.3 % $Ca(NO_3)_2$ was sprayed into the whorl of each axis at daily intervals to minimize Ca deficiency symptoms. Nonetheless, one plant showed severe symptoms of Ca deficiency and had to be discarded.

Table 1: Name, origin, and characteristics of the sorghum genotypes used in the experiment

Name	Origin	Characteristics
2d sorghum		
Ai4	China	2-dwarf, photoperiod insensitive, possible cold tolerance
IS8525	Ethiopia	Early flowering parent of mapping population for ergot resistance
IS9710	Sudan	High TE line (Hammer *et al*., 1997)
PI291382	China	Shatter cane line with high TE (Xin *et al*., 2009)
PI391652	China	High TE line (Xin *et al*., 2009)
PI584085	Uganda	Caudatum line with high TE (Xin *et al*., 2009)
PI656046	China	Durra line with high TE
3d sorghum		
A1*FB963676/R931945 (hybrid)	Australia	Hybrid of two lines included in the experiment
BTx642	Ethiopia	Highly stay-green, low tillering, partially converted durra landrace.
B923296	Australia	Elite stay-green, heat sensitive, narrow root angle parent DFAF breeding program
B963676	Australia	Good heat tolerance, wide root angle, widely used commercial female.
MR Buster (hybrid)	Australia	High-tillering standard commercial check hybrid
QL12	Australia	Early flowering source of stay-green drought resistance
R9188	USA	Partially converted derivative of sweet sorghum Rio
R931945-2-2	Australia	Elite low-tillering stay-green parent DFAF breeding program
R9403463-2-1	Australia	Elite moderately senescent parent DFAF breeding program
SC170-6-8	Ethiopia	High tillering, heat sensitive, wide root angle, partly converted caudatum line
SC237-14E	Sudan	Caudatum line with high TE (Hammer *et al*., 1997)
TAM422	USA	Early hybrid parent lacking in stay-green drought resistance
Tx430	USA	Yellow endosperm. Widely used as parent commercially in the USA
Tx7000	USA	Early hybrid parent lacking in stay-green drought resistance

Observations and measurements

The number of visible fully expanded, and senesced leaves on the main shoot and all tillers of every plant were counted twice a week. A leaf was counted as visible leaf when its tip was visible inside the whorl of the previous leaf, as fully expanded leaf when its ligule was visible above the ligule of the previous leaf, and as senesced leaf when > 50 % of its lamina had died. Tillers were labelled according to leaf axil from which they appeared. For example, tiller 3 (T3) appeared from the axil of leaf 3. The length and maximum width of each fully expanded leaf were measured non-destructively on all plants. Leaf area of each leaf was estimated from the measured length and width, multiplied by a scaling factor of 0.71 (0.635 for flag leaves) (van Oosterom *et al*., 2011).

Daily transpiration per plant was calculated as the decline in pot weight for that day, plus any water added. Transpiration throughout the season was calculated as the sum of these daily values, adjusted for the fresh shoot mass at harvest, dry root mass at harvest, and any change in weight of the empty reference pots.

Plants were harvested 5 days after 50 % of anthers in the main shoot panicle were visible. Plants were cut below the base of the stem and shoot fresh weight was determined (after removal of soil). Roots of each plant were washed thoroughly until all the debris and soil particles were removed. Shoot and root dry masses of each plant were determined after drying in a dehydrator at 60 ^{0}C for 48 h.

TE was calculated as the ratio of biomass and seasonal transpiration using only shoot biomass (TE_shoot) or using both shoot and root biomass (TE_total). The two components of TE; photosynthetic capacity and conductance, which at the plant level, can be represented by biomass per unit leaf area (B/LA) and transpiration per unit leaf area (T/LA), respectively were calculated.

Data were analysed in SAS v.9.3. using the General Linear Model (GLM) procedure for ANOVAs and means separated using Duncan's multiple range test for genotypic differences.

Table 2: ANOVA of plant type and genotypic differences in phenology, total biomass, and leaf area

Plant type	Days to flowering	Biomass (g plant^{-1})		Leaf area (m^2 plant^{-1})	
2d sorghum	61.5 b		152.61 b		0.591 b
3d sorghum	74.6 a		193.54 a		0.850 a
CV	3.68		17.45		16.48
Probability block	0.0262		0.4258		0.57
Probability species	< 0.0001		< 0.0001		< 0.0001
Probability genotype	< 0.0001		< 0.0001		< 0.0001
2d sorghum					
IS9710	75.0 efg	IS9710	264.00 b	IS9710	0.960 bcd
Ai4	69.5 ij	PI584085	187.49 defg	PI584085	0.807 def
PI656046	69.3 ij	PI656046	179.58 efgh	PI656046	0.696 fghi
PI584085	58.3 kl	Ai4	142.46 ghi	IS8525	0.511 ij
PI391652	58.3 kl	PI391652	131.52 hi	Ai4	0.479 j
IS8525	54.5 l	IS8525	113.95 i	PI391652	0.455 j
PI291382	45.8 m	PI291382	49.28 j	PI291382	0.226 k
3d sorghum					
R931945-2-2	86.5 a	Tx430	327.59 a	Tx430	1.600 a
R9403463-2-1	85.3 ab	SC170-6-8	260.00 b	SC170-6-8	1.138 b
SC170-6-8	82.0 bc	A1*FB963676/ R931945	246.81 bc	SC237-14E	1.082 bc
Tx430	80.0 cd	SC237-14E	236.27 bcd	R9403463-2-1	0.956 bcd
A1*FB963676/ R931945	77.3 de	R931945-2-2	220.25 bcde	Tx7000	0.923 cde
SC237-14E	75.8 ef	R9403463-2-1	204.24 cde	A1*FB963676/ R931945	0.914 cde
B35	74.3 efgh	B923296	198.23 cdef	R931945-2-2	0.851 def
B923296	74.3 efgh	B963676	189.70 defg	B923296	0.759 defg
QL12	73.0 fghi	Tx7000	182.71 efg	B963676	0.736 efgh
B963676	71.5 ghij	Buster	152.82 fghi	Buster	0.700 fghi
Tx7000	70.5 hij	B35	126.33 i	B35	0.583 ghij
TAM422	67.8 j	QL12	115.25 i	TAM422	0.559 ghij
R9188	62.0 k	TAM422	114.63 i	R9188	0.537 hij
Buster	61.8 k	R9188	114.14 i	QL12	0.493 ij

Values within a column followed by the same letters are not significantly different at 5 % level according to Duncan multiple range test

RESULTS AND DISCUSSION

Phenotypic characters

Time to flowering was significantly different among plant types (Table 2) and genotypes within each plant type. 2d sorghum flowered earlier than 3d sorghum. The late flowering of 3d sorghum was associated with low temperatures around flowering in late autumn - early winter, in particular some of the 3d sorghum genotypes (Table 2).

2d sorghum on average produced significantly less biomass and leaf area per plant than 3d sorghum (Tables 2 and 3). This was associated with the faster growth in 2d sorghum, and their lower leaf number on the main shoot, while the productive tiller number was similar in both plant types (Table 3). Biomass production and leaf area also differed significantly among genotypes, partly because of the differences in anthesis date and hence harvest date. However, some 3d genotypes produced similar biomass to that of 2d sorghum (Table 2).

Table 3: ANOVA on plant differences in plant height, tiller number, and main shoot dry mass allocation to the stem (height excludes panicle and is stem only)

	Total leaf number	Plant height (cm)	Productive tiller number	Main shoot dry mass to stem (%)
2d sorghum	12.18b	169.36a	3.00a	62.67a
3d sorghum	14.76a	78.43b	3.05a	44.63b

Values within a column followed by the same letters are not significantly different at the 5 % level according to Duncan multiple range test

Plant type differences in shoot and root mass were generally consistent with differences in total biomass (Table 4). The relatively high coefficient of variation (CV) for shoot mass (18 %) was most likely a consequence of differences in tillering among individual plants across replications. The CV for root mass (26.57) was approximately 50 % greater than for shoot mass, suggesting an acceptable level of accuracy for root mass. Dry matter partitioning to roots (Table 4) showed significant differences among plant types, with root/shoot ratio of 2d sorghum significantly lower than for 3d sorghum (Table 4).

Within plant types, significant genotypic differences were observed in root mass, shoot mass and root/shoot ratio (Table 4). Nonetheless, genotypic variation in root/shoot ratio was generally small. The main exceptions were 3d sorghum genotypes R931945-2-2 and QL12, as both had high root/shoot ratio. Both these genotypes were low-tillering (Table 2).

Transpiration and transpiration efficiency

Plant type differences in seasonal transpiration (Table 5) to a large extent reflected differences in phenotypic characters and hence plant size at harvest. Transpiration was significantly greater in 3d than in 2d sorghum. Genotypes of both 3d and 2d sorghum showed significant differences in transpiration (Table 5). Genotype Tx430 (3d), which flowered relatively late had the highest transpiration and the early flowering genotype PI291382 (2d) the lowest.

Both situations of TE_shoot and TE_(total) in 2d and 3d sorghum showed similar TE (Table 6). Hence, TE was not associated with plant stature. However, there were significant genotypic differences in TE, and the values ranged from 7.7–10.3 g kg^{-1} for TE_shoot and from 9.2–11.2 g kg^{-1} for TE_(total) (Table 6). Among 2d genotypes, PI656046 had the highest TE_(total) (11.2 g kg^{-1}) and it was significantly greater than that of Ai4, IS8525 and PI291382, which had the lowest TE_(total) (9.5–9.6 g kg^{-1}). PI584085, PI391652, and IS9710 were intermediate (10.2–10.6 g kg^{-1}). Differences were comparable for TE_shoot. Among 3d genotypes, A1*FB963676/R931945, B923296 and B963676 had the highest TE_(total) (10.8–10.9 g kg^{-1}) and for the first two, the TE_(total) was significantly greater than Tx7000, QL12 and Tx430 (9.2–9.4 g kg^{-1}). Same trend was observed for TE_shoot.

Table 4: ANOVA of plant type and genotypic differences in shoot mass, root mass, and root/shoot ratio.

Plant type	Shoot mass (g plant^{-1})	Root mass (g plant^{-1})		Root/Shoot ratio	
2d sorghum	140.7 b		11.95 b		0.087 b
3d sorghum	173. 7 a		19.81 a		0.117 a
CV	18		26.57		20.83
Probability block	0.5531		0.1362		0.6135
Probability species	< 0.0001		< 0.0001		< 0.0001
Probability genotype	< 0.0001		< 0.0001		< 0.0001
orghum					
IS9710	241.5 b	IS9710	22.51 bc	IS9710	0.095 cdef
PI584085	175.8 cdef	PI656046	14.02 defg	Ai4	0.092 cdef
PI656046	165.6 defg	Ai4	11.89 efgh	IS8525	0.091 def
Ai4	130.6 fgh	PI584085	11.73 efgh	PI291382	0.091 cdef
PI391652	122.2 gh	IS8525	9.42 gh	PI656046	0.085 def
IS8525	104.5 h	PI391652	9.34 gh	PI391652	0.077 def
PI291382	44.5 i	PI291382	4.75 h	PI584085	0.068 f
3d sorghum					
Tx430	295.3 a	R931945-2-2	35.33 a	R931945-2-2	0.190 a
SC170-6-8	236.5 b	Tx430	32.30 a	QL12	0.190 a
A1*FB963676/R931945	222.0 bc	A1*FB963676/R931945	24.79 b	R9403463-2-1	0.137 b
SC237-14E	220.6 bc	R9403463-2-1	24.75 b	Buster	0.128 bc
R931945-2-2	184.9 cd	SC170-6-8	24.25 b	B35	0.126 bc
R9403463-2-1	179.5 cde	B923296	19.96 bcde	A1*FB963676/R931945	0.113 bcd
B923296	178.3 cdef	QL12	18.22 bcdef	Tx430	0.110 bcd
B963676	177.5 cdef	Buster	17.38 bcdefg	B923296	0.108 bcde
Tx7000	166.1 defg	Tx7000	16.61 bcdefg	SC170-6-8	0.104 bcdef
Buster	135.4 efgh	SC237-14E	15.64 cdefg	Tx7000	0.101 bcdef
B35	112.6 h	B35	13.72 defg	TAM422	0.094 cdef
QL12	104.8 h	B963676	12.20 efgh	R9188	0.094 cdef
TAM422	104.1 h	R9188	10.01 fgh	SC237-14E	0.071 ef
R9188	97.0 h	TAM422	9.82 fgh	B963676	0.070 ef

Values within a column followed by the same letters are not significantly different at the 5 % level according to Duncan multiple range test

Components of TE: photosynthetic capacity and conductance

Plant types showed significant differences in both photosynthetic capacity and conductance, with 2d sorghum on average having significantly greater values than 3d sorghum (Table 7). These differences represented the increased allocation of dry mass to stem in taller 2d sorghum (Table 3).

Across genotypes, the association between TE_(total) and either photosynthetic capacity (Figure 1) or conductance (Figure 2) varied. In general, TE_shoot was positively associated with photosynthetic capacity ($R^2 = 0.43$, $p < 0.01$), Figure 1), except for Ai4 (2d), which had low TE_(total) despite having the highest photosynthetic capacity. This was because of an extremely high conductance for Ai4 (Table 7, Figure 2). Similarly, the low TE_(total) of QL12 (3d) was associated with

Table 5: ANOVA of plant type and genotypic differences in total transpiration

Plant type	Total Transpiration (kg)
2d sorghum	14.60 b
3d sorghum	18.71 a
CV	21.88
Probability block	0.4575
Probability species	< 0.0001
Probability genotype	< 0.0001
2d sorghum	
IS9710	24.33 b
PI584085	17.59 cdef
PI656046	16.39 cdef
Ai4	14.89 def
PI391652	12.46 ef
IS8525	11.51 f
PI291382	5.11 g
3d sorghum	
Tx430	34.3 a
SC170-6-8	24.81 b
SC237-14E	21.95 bc
A1*FB963676/ R931945	21.75 bc
R931945-2-2	21.64 bc
R9403463-2-1	19.93 bcd
Tx7000	18.72 bcde
B923296	17.54 cdef
B963676	17.21 cdef
Buster	14.21 def
B35	12.89 ef
QL12	12.34 f
TAM422	11.61 f
R9188	11.19 f

Values within a column followed by the same letters are not significantly different at the 5 % level according to Duncan multiple range test

high conductance. In general, there was no association between TE_(total) and conductance (Figure 2).

Effect of genotypes on TE

TE_(total) ranged from 9.2–11.2 g kg^{-1} across sorghum genotypes. The observed TE was slightly greater than the standard TE of 9 g kg^{-1} for sorghum (Tanner & Sinclair, 1983) and could be due to low vapour pressure deficit (VPD) during autumn towards the end of the experiment, when plant size was highest. In addition, the higher values may reflect the increase in atmospheric CO$_2$ concentration over the past 30 years (Forster & Ramaswamy, 2007), as TE increases with increasing atmospheric CO$_2$ levels (Eamus, 1991). The two 3d hybrids (AI*FB963976/R931945 and Buster) showed above average TE that was not significantly different to that of PI656046, the genotype with the highest TE (Table 6). In addition, TE_(total) of A1*FB963676/R931945 (10.92 g kg^{-1}) was similar to that of B963676 and R931945-2-2, which were 10.76 g kg^{-1} and 10.02 g kg^{-1}, respectively (Table 3.6), whereas Xin *et al*. (2009) reported that the TE of ATx623/RTx430 (7.9 g kg^{-1}) was intermediate between that of its two parents BTx623 (8.1 g kg^{-1}) and RTx430 (7.8 g kg^{-1}). There is thus no evidence to suggest that differences in TE are associated with differences between inbred lines and hybrids.

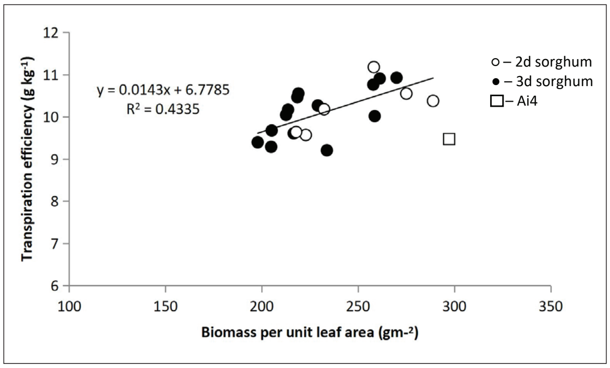

Figure 1: Biomass per unit leaf area vs transpiration efficiency (shoot+root)

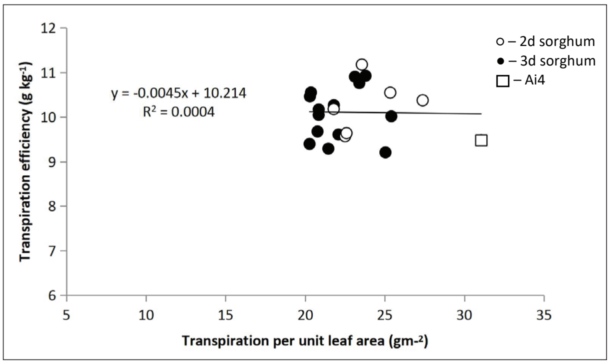

Figure 2: Transpiration efficiency (shoot+root) vs transpiration per unit leaf area

Table 6: ANOVA of plant type and genotypic differences in transpiration efficiency for shoot biomass (TE_shoot) and total biomass (TE_Total)

Plant type	TE_shoot biomass (g/kg)	TE_Total biomass (g/kg)	
2d sorghum	9.32 a		10.14 a
3d sorghum	9.05 a		10.09 a
CV	8.11		7.9
Probability block	0.0019		0.0008
Probability species	< 0.0001		< 0.0001
Probability genotype	< 0.0001		< 0.0001
2d sorghum			
PI656046	10.30 a	PI656046	11.18 a
IS9710	9.63 abcdef	IS9710	10.55 abcd
PI391652	9.63 abcdef	PI391652	10.38 abcd
PI584085	9.54 abcdef	PI584085	10.18 abcd
IS8525	8.77 cdefg	PI291382	9.64 bcd
PI291382	8.68 cdefg	IS8525	9.57 bcd
Ai4	8.67 cdefg	Ai4	9.48 cd
3d sorghum			
B963676	10.06 ab	A1*FB963676/R931945	10.93 ab
B923296	9.86 abc	B923296	10.91 ab
A1*FB963676/R931945	9.82 abcd	B963676	10.76 abc
SC237-14E	9.77 abcde	Buster	10.55 abcd
Buster	9.35 abcdef	SC237-14E	10.46 abcd
SC170-6-8	9.30 abcdef	SC170-6-8	10.27 abcd
R9188	9.17 bcdefg	R9403463-2-1	10.17 abcd
R9403463-2-1	8.96 bcdefg	R9188	10.05 abcd
TAM422	8.84 cdefg	R931945-2-2	10.02 abcd
B35	8.54 cfg	TAM422	9.68 bcd
Tx7000	8.54 cfg	B35	9.61 bcd
R931945-2-2	8.41 fg	Tx7000	9.40 cd
Tx430	8.37 fg	Tx430	9.29 d
QL12	7.73 g	QL12	9.21 d

Values within a column followed by the same letters are not significantly different at the 5 % level according to Duncan multiple range test

The presence of genotypic differences in TE of sorghum confirmed previous reports (Hammer *et al*., 1997; Henderson *et al*., 1998; Mortlock & Hammer, 1999; Xin *et al*., 2009) and the ranking of genotypes was consistent with those previously published. For example, Hammer *et al*. (1997) reported that IS9710, SC237-14E and R9188 had TE > 7.0 g kg^{-1}, whereas TAM422, Tx430 and QL12 had TE < 7.0 g kg^{-1}. Consistent with this Tx430 and QL12 had the lowest TE (Table 6), whereas TAM422 also had low TE. Similarly, Xin *et al*. (2009) found that the TE of 2d genotypes PI391652 and PI584085 (8.9 g kg^{-1}) was significantly greater than that of Tx430 (7.8 g kg^{-1}), whereas the TE of PI291382 (8.6 g kg^{-1}) was only marginally lower than that of PI391652 and PI584085. The consistency of TE values among genotypes between the current experiment and previously published

Table 7: ANOVA of plant type and genotypic differences in photosynthesis capacity and conductance.

Plant type	Photosynthetic capacity (g/m^2)	Conductance (kg/m^2)	
2d sorghum	240 a		24.89 a
3d sorghum	200 b		22.71 b
CV	9.14		13.32
Probability block	0.0029		0.0013
Probability species	< 0.0001		< 0.0001
Probability genotype	< 0.0001		< 0.0001
2d sorghum			
Ai4	270 a	Ai4	31.32 a
PI391652	260 ab	PI391652	27.18 ab
IS9710	250 abc	IS9710	25.40 bc
PI656046	230 bcde	PI656046	23.32 bc
PI584085	210 defg	PI291382	22.55 bc
IS8525	200 fghi	IS8525	22.47 bc
PI291382	190 ghi	PI584085	21.97 bc
3d sorghum			
A1*FB963676/R931945	240 bcd	R931945-2-2	25.27 bc
B963676	240 bcde	QL12	24.97 bc
B923296	230 cdef	A1*FB963676/R931945	23.86 bc
R931945-2-2	210 defgh	B963676	23.10 bc
SC170-6-8	200 efghi	B923296	22.95 bc
SC237-14E	200 fghi	B35	22.07 bc
QL12	190 ghi	SC170-6-8	21.83 c
Buster	190 ghi	Tx430	21.45 c
B35	190 ghi	R9403463-2-1	20.91 c
R9188	190 ghi	TAM422	20.82 c
TAM422	180 ghi	R9188	20.55 c
R9403463-2-1	180 ghi	Tx7000	20.30 c
Tx7000	180 hi	SC237-14E	20.29 c
Tx430	170 i	Buster	20.26 c

papers indicates that genotypic differences in TE in the current experiment were reasonable, providing further confidence in the observed values.

Effect of plant stature on TE

Crop stature did not significantly affect TE, as 2d and 3d sorghum had on average a similar TE. TE_shoot was not significantly different between 2d and 3d sorghum which were 9.05 and 9.32 g kg^{-1}, respectively and this small difference could be accounted for by the difference in root/shoot ratio, as TE_(total) was similar for 2d and 3d sorghum (10.1 g kg^{-1}). This would suggest that the greater dry mass partitioning to roots of 3d sorghum compared with 2d sorghum could be a consequence of reduced sink size in the shoot, associated with shorter stems (Table 3). Although the inclusion of roots did not substantially alter the results for TE among sorghum genotypes, inclusion of roots in the calculation of TE may be particularly useful under abiotic stress, where increased partitioning to the root can be a consequence of poor seed set (van Oosterom *et al*., 2011).

Genotypic differences in TE were predominantly associated with differences in photosynthetic capacity (Figure 1), rather than conductance (Figure 2). The role of photosynthetic capacity on TE differences among genotypes found in this study was consistent with previous studies of Hammer *et al*. (1997) and Xin *et al*. (2009). In addition to this mechanism, Mortlock and Hammer (1999) reported that genotypic differences in TE of sorghum were associated with conductance and with leakage of CO_2 from the bundle sheath (Henderson *et al*., 1998).

Implications of differences in TE on drought adaptation

The present hybrids of cereal crops are close to a theoretical upper limit of harvest index (HI) of 0.5 (Hay, 1995). However, manipulation of pre-anthesis water use can affect actual HI irrespective of potential HI, because post-anthesis water availability is the main factor affecting grain yield of cereals under post-anthesis drought stress (Turner, 2004). The results of this study indicate that genotypic differences in TE of sorghum are predominantly associated with photosynthetic capacity and less with leaf conductance.

Stay-green, the ability of a crop to retain green leaf area during grain filling under drought stress, has been associated with drought adaptation of sorghum (Borrell *et al*., 2000). Hence, it is possible that the expression of stay-green is associated with increased TE. Among the four 3d sorghum genotypes known to exhibit the stay-green trait (Table 1), only one (B923296) had high TE in the present study. The other three genotypes (B35, R931945-2-2 and QL12) had below average TE. However, the three genotypes known to lack stay-green expression (R9403463-2-1, TAM422 and Tx7000) also had average or below average TE (Table 1). Hence, there was no apparent association between stay-green expression and TE. A likely explanation for this apparent contradiction is that drought adaptation can be achieved through a range of different mechanisms, including reduced pre-anthesis water use through either small plant size or early flowering (van Oosterom *et al*., 2011). The stay-green drought adaptation of QL12 is hence likely associated with its earliness (Borrell *et al*., 2000; van Oosterom, 2011), whereas for BTx642 (formerly known as B35) and R931945-2-2 this was associated with low tillering (Kim *et al*., 2010; van Oosterom *et al*., 2011). The current results thus indicate that plant size and TE might be two independent drought adaptation traits. This would allow breeders to combine these traits into a single genotype.

CONCLUSIONS

The transpiration efficiency of sorghum was not associated with plant height. Significant genotypic differences in transpiration efficiency were associated with differences in photosynthetic capacity, rather than conductance. The lack of association between transpiration efficiency and known expression of stay-green (which is linked to plant size) indicates that these are potentially independent mechanisms for drought adaptation.

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