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-Jaeggl 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.
(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 CO₂ 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 lysimetry facility in a shade house at Gatton (27°33’S, 152°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 preset 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(NO₃)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                  |            |                                                                                 |
| A4                          | 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 ºC for 48 h.
TE was calculated as the ratio of biomass and seasonal transpiration using only shoot biomass (TE\textsubscript{shoot}) or using both shoot and root biomass (TE\textsubscript{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.

| Plant type | Days to flowering | Biomass (g plant\textsuperscript{-1}) | Leaf area (m\textsuperscript{2} plant\textsuperscript{-1}) |
|------------|-------------------|----------------------------------------|-----------------------------------------------|
| 2d sorghum |                   |                                        |                                               |
| IS9710     | 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                                        |
| Probability species | < 0.0001 |                                         | < 0.0001                                      |
| Probability genotype | < 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 gh                          | IS8525 0.511 ij                              |
| PI391652   | 58.3 kl           | PI391652 131.52 hi                    | AI4 0.479 j                                  |
| IS8525     | 54.5 i            | 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 bcd                 | 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 dfgf                    | B923296 0.759 defg                            |
| QL12       | 73.0 fghi         | Tx7000 182.71 efgf                    | B963676 0.736 efgf                           |
| 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 hj                                |
| 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’s 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).

Plant factors affect transpiration efficiency of sorghum

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) (9.2–9.4 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.
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\(_{\text{total}}\) and either photosynthetic capacity (Figure 1) or conductance (Figure 2) varied. In general, TE\(_{\text{shoot}}\) was positively associated with photosynthetic capacity (R\(^2 = 0.43\), p < 0.01, Figure 1), except for Ai4 (2d), which had low TE\(_{\text{total}}\) despite having the highest photosynthetic capacity. This was because of an extremely high conductance for Ai4 (Table 7, Figure 2). Similarly, the low TE\(_{\text{total}}\) of QL12 (3d) was associated with
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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 cdef
PI391652 12.46 cdef
IS8525 11.51 cdef
PI291382 5.11 cdef

3d sorghum
Tx430 34.3 a
SC170-6-8 24.81 b
SC237-14E 21.95 bc
A1*FB963676/R931945 21.75 bc
R931945 21.64 cde
R931945-2-2 19.93 cde
R9403463-2-1 19.93 cde
Tx7000 18.72 cde
B923296 17.54 cde
B963676 17.21 cde
Buster 14.21 cde
B35 12.89 cd
QL12 12.34 de
TAM422 11.61 ef
R9188 11.19 ef

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

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

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

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 CO₂ concentration over the past 30 years (Forster & Ramaswamy, 2007), as TE increases with increasing atmospheric CO₂ levels (Eamus, 1991). The two 3d hybrids (A1*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*FB963976/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.
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     |                         |                         |
| PI656046       | 10.30 a                 | 11.18 a                 |
| IS9710         | 9.63 abcdef             | IS9710                  |
| PI391652       | 9.63 abcdef             | PI391652                |
| PI584085       | 9.54 abcdef             | PI584085                |
| IS8525         | 8.77 cdefg              | PI291382                |
| PI291382       | 8.68 cdefg              | IS8525                  |
| A4             | 8.67 cdefg              | A4                      |
| 3d sorghum     |                         |                         |
| B963676        | 10.06 ab                | A1*FB963676/R931945     |
| B923296        | 9.86 abc                | B963676                 |
| A1*FB963676/R931945 | 9.82 abcdef             | B963676                 |
| SC237-14E      | 9.77 abcde              | Buster                  |
| Buster         | 9.35 abcdef             | SC237-14E               |
| SC170-6-8      | 9.30 abcdef             | SC170-6-8               |
| R9188          | 9.17 bcdefg             | R9403463-2-1            |
| R9403463-2-1   | 8.96 bcdefg             | R9188                   |
| TAM422         | 8.84 cdefg              | R931945-2-2             |
| B35            | 8.54 cfg                | TAM422                  |
| Tx7000         | 8.54 cfg                | B35                     |
| R931945-2-2    | 8.41 fg                 | Tx7000                  |
| Tx430          | 8.37 fg                 | Tx430                   |
| QL12           | 7.73 g                  | QL12                    |

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...
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 CO₂ 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 (B9223296) 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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