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Dissecting and modelling the comparative adaptation to water limitation of sorghum and maize: role of transpiration efficiency, transpiration rate and height

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ABSTRACT

Maize is considered less drought-tolerant than sorghum, but sorghum is commonly grown as a short triple dwarf (3dwarf) type, so difference in plant height confounds the species comparison. The objectives of this study were to experimentally determine effects of species and plant height differences on transpiration efficiency (TE) and transpiration rate per unit green leaf area (TGLA) and use findings to explain input parameters in a simulation study on the comparative adaptation of 3dwarf sorghum and maize in environments with contrasting water availability. Maize, tall double dwarf (2dwarf) and short 3dwarf sorghum genotypes were grown in two lysimeter experiments in 2011 in SE Queensland, Australia. Each plant was harvested after anthesis and total transpiration, shoot and root dry mass were measured to estimate TE. Daily TGLA was used to compare transpiration rates. Species and height had limited effect on TE, but significantly affected TGLA. This was associated with differences in biomass allocation. The similar TE but higher TGLA in maize compared with 3dwarf sorghum meant it potentially produces more biomass, consistent with published differences in biomass accumulation and radiation use efficiency (RUE). The simulation study, which used similar TE for maize and 3dwarf sorghum, but captured differences in TGLA through differences in RUE, predicted crossover interactions for grain yield between species and total water use. The greater TGLA of maize decreased grain yield in water-limited environments, but increased yields in well-watered situations. Results highlight that similarity in TE and differences in TGLA can influence comparative adaptation to water limitation.

KEYWORDS: Biomass allocation; drought adaptation; height; maize; radiation use efficiency; sorghum; transpiration efficiency; water use; yield potential.

1. INTRODUCTION

Maize and sorghum are major summer crops in rainfed farming systems around the world. With an ever-increasing population, combined with diminishing land and fresh water reserves, efficient use of available water resources is becoming critically important (Lobell *et al.* 2014). In the grain belt of eastern Australia, where timing and severity of the occurrence of

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water limitation are highly variable, sorghum is the dominant dryland summer crop (Chapman *et al.* 2002; Hammer *et al.* 2014). Sorghum is considered more drought-tolerant than maize, but maize has a greater yield potential and hence higher return to growers (Muchow 1989a; Farré and Faci 2006). Better understanding of the underlying physiological determinants of the perceived differences in adaptation to water limitation would provide insights for investigating the viability of maize as an alternative summer dryland season crop in eastern Australia and in other parts of the world where both crops are commonly grown, such as Argentina (Parra *et al.* 2020) and Africa and Asia (Choudhary *et al.* 2020).

The enhanced tolerance of sorghum to water limitation compared to maize has been associated with a shorter crop cycle and lower crop growth rate, both of which impact on the total amount of water transpired. This is important, as grain yield under end-of-season drought stress is closely related to the amount of water available for transpiration to sustain growth during grain filling (Turner 2004; Hammer 2006; Borrell *et al.* 2014). The shorter crop duration of sorghum is predominantly associated with a shorter grain filling period (Muchow 1989a); however, post-anthesis water availability may still not be maintained when precipitation is low. The lower crop growth rate of sorghum is reflected in a lower radiation use efficiency (RUE), indicating that it produces less biomass per unit of light intercepted (Muchow and Sinclair 1994). The RUE of commercially grown triple dwarf (3dwarf) sorghum is 1.2–1.4 g MJ^{-1} (Sinclair and Muchow 1999; Hammer *et al.* 2010), compared to 1.8 g MJ^{-1} for maize (Lindquist *et al.* 2005). This difference in RUE could be associated with their difference in crop height, as CSH13R, a tall single-dwarf sorghum hybrid from India, has a RUE of 1.6–1.8 g MJ^{-1} (Hammer *et al.* 2010). The transpiration efficiency (TE, amount of biomass produced per unit of water used) is observed to be quite similar for sorghum and maize (Tanner and Sinclair 1983; Choudhary *et al.* 2020), even though genotypic differences in TE have been reported for both species (Bunce 2010; Geetika *et al.* 2019). Hence, the greater crop growth rate of maize has been associated with greater transpiration rates, although it is unclear whether any such differences would be a species or height effect. In theory, greater transpiration rates associated with greater biomass growth can hasten the onset of water limitation in maize crops.

The implication of any such differences on crop adaptation to water limitation stress is attributed to complex genotype (G) × environment (E) × management (M) interactions on grain yield, which are best explored using crop growth simulation models. The APSIM modelling platform (Holzworth *et al.* 2014) is ideally set up to do this, as it contains advanced models for both sorghum (Hammer *et al.* 2010) and maize (Soufizadeh *et al.* 2018) crops with comparable modular structure and scientific underpinning. Therefore, the aims of this study were to experimentally determine the effects of species and plant height differences on TE and transpiration rates, and to use findings to explain input parameter values in a simulation study to quantify the consequences of any such differences on G × E × M interactions for grain yield across a range of environments with contrasting water availability.

2. MATERIALS AND METHODS

2.1 Genotypes

Two experiments were conducted in 2011 in a solarweave enclosure at Gatton (27°33′S, 152°20′E) in south-east Queensland, Australia. They included eight maize hybrids, seven 2dwarf sorghum genotypes and 16 3dwarf sorghum genotypes. However, one 3dwarf genotype was excluded in both experiments and one 3dwarf genotype was excluded in one experiment because of severe symptoms of calcium deficiency. The maize genotypes were all elite hybrids that were expected to have high TE, despite differences in drought tolerance (Table 1). The sorghum genotypes predominantly contained inbred lines that included parents of mapping populations and elite breeding lines and were known to span a range in TE (Table 1). Eleven of the 3dwarf genotypes were in common with the study reported by Geetika *et al.* (2019).

2.2 Experiment details

Details of the experimental set-up have been provided by Chenu *et al.* (2018). Individual plants were grown in lysimeters of around 51 liters. This was well above the threshold size below which biomass allocation to roots can be affected (Yang *et al.* 2010). Prior to filling, each lysimeter was lined with a plastic bag to facilitate removal of the soil at harvest. Lysimeters were filled to a constant weight with air-dried soil and *ca.* 42 g of Osmocote Plus® (Scotts Australia, Baulkham Hills, NSW Australia) slow release fertilizer (16 % N, 3.5 % P, 10 % K) was added in six evenly distributed layers, along with *ca.* 40 g of dolomite to minimize symptoms of calcium deficiency. After filling, pots were watered up to slightly below the drained upper limit (DUL) of the soil, which was determined from a reference lysimeter that had holes drilled in the bottom and was filled with the same amount of soil but without plastic liner. The reference lysimeter was watered and left to drain, and the amount of water to be added to the experimental lysimeters was determined from the difference in weight before watering and after draining. As soil in each lysimeter compacted during watering, soil was added to each lysimeter after the soil had wetted up and water was added pro rata. Five seeds were planted in the middle of each lysimeter on 10 March 2011 (Exp1) and 16 September 2011 (Exp2). Emerged seedlings were gradually thinned until one plant per lysimeter was left when *ca.* three leaves had fully expanded, at which stage the soil surface was sealed with thick plastic to minimize soil evaporation.

Each lysimeter was positioned on its own load cell, located on trolleys that carried eight load cells each (two rows of four lysimeters). The set-up contained eight rows of two trolleys, such that there were 16 rows of eight lysimeters (128 in total). Plant-to-plant spacing was around 50 cm within a trolley and *ca.* 1 m for plants on adjacent trolleys. Experiments were laid out as a group-balanced block design where genotypes were blocked into three classes (maize, 2dwarf sorghum, 3dwarf sorghum) and four replications. Each replication (32 lysimeters or four trolleys) included one trolley with eight maize genotypes, one trolley with seven 2dwarf sorghum genotypes plus a filled lysimeter with no plant, and two adjacent trolleys with 16 3dwarf sorghum genotypes. Lysimeter weights were recorded automatically every 15 min (Chenu *et al.* 2018) and once the weight of a lysimeter dropped below a preset value of around 1.5 kg below DUL, 500 mL of water was automatically added. This ensured that plant available water was maintained above a level that would trigger drought stress, but slightly below DUL to minimize any risk of water logging. In both experiments, pests were controlled chemically and no significant outbreaks occurred. To minimize symptom of calcium deficiency, a solution of 0.3 % $Ca(NO_3)_2$ was sprayed into the whorl of each axis (main shoot and tillers) at daily intervals in both experiments. Plants were

Table 1. Name, origin and characteristics of the maize and sorghum genotypes used in the experiment, plus the average stem height and days from sowing to anthesis or tasselling in the two experiments. [a]Sum of all the individual main shoot stem nodes. Means across replications. [b]Only in Exp2.

Name	Stem height (cm)[a]		Days to anthesis		Origin	Characteristics
	Exp1	Exp2	Exp1	Exp2		
Maize						
32T16	264	282	56.8	65.0		Elite hybrid, drought-susceptible
32T83	208	242	58.0	62.0		Elite hybrid
33D11	213	226	58.7	64.3		Elite hybrid, drought-tolerant
33N09	255	271	57.0	65.5		Elite hybrid
33T56	240	250	56.0	64.0		Elite hybrid, drought-tolerant
34N61	268	287	58.0	65.0		Elite hybrid
P0582	273	276	55.8	63.0		Elite hybrid
P1508	215	238	57.8	62.0		Elite hybrid
2d sorghum						
Ai4	84	81	68.5	72.8	China	Photoperiod-insensitive, possible cold tolerance
IS8525	150	139	53.5	65.0	Ethiopia	Early-flowering parent of mapping population for ergot resistance
IS9710	86	86	74.0	79.5	Sudan	*Caudatum* line with high TE (Hammer *et al.* 1997)
PI291382	165	168	45.3	54.8	China	Shatter cane line with high TE (Xin *et al.* 2009)
PI391652	175	176	57.3	64.8	China	High TE line (Xin *et al.* 2009; Chenu *et al.* 2018)
PI584085	174	149	57.5	62.3	Uganda	*Caudatum* line with high TE (Xin *et al.* 2009)
PI656046	106	85	68.3	70.5	China	Lian Tangai. *Durra* line with high TE (Xin *et al.* 2009)
3d sorghum						
A1*FB963676/R931945-2-2	116	75	76.3	67.5	Australia	Hybrid of two lines included in the experiment
BTx623[b]		78		69.8	USA	Elite female line
BTx642 (B35)	72	70	73.3	67.3	Ethiopia	Highly stay-green, low-tillering, partially converted *durra* landrace
B923296	81	64	73.3	67.3	Australia	Elite stay-green parent Department of Agriculture and Fisheries (DAF) breeding programme
B963676	77	72	70.5	69.3	Australia	Elite stay-green female line with above-average TE (Chenu *et al.* 2018; Geetika *et al.* 2019)
Check	86	78	60.8	64.0	Australia	High-tillering standard commercial check hybrid
QL12	54	52	72.0	70.3	Australia	Early flowering line with low TE and high transpiration rate (Geetika *et al.* 2019)
R9188	75	60	61.0	65.8	USA	Partially converted derivative of sweet sorghum Rio
R931945-2-2	73	61	85.8	74.8	Australia	Elite low-tillering stay-green parent DAF breeding programme
R9403463-2-1	67	72	84.3	81.8	Australia	Elite moderately senescent parent DAF breeding programme
SC170-6–8	61	59	81.0	78.5	Ethiopia	High-tillering, partly converted *caudatum* line with low transpiration rate (Geetika *et al.* 2019)
SC237-14E	65	75	74.8	78.3	Sudan	*Caudatum* line with high TE (Hammer *et al.* 1997)
TAM422	74	62	66.8	67.5	USA	Early hybrid parent with low TE and lacking in stay-green drought resistance (Geetika *et al.* 2019)
Tx430	74	77	79.0	77.8	USA	Yellow endosperm. Widely used as parent commercially in the USA
Tx7000	85	66	69.5	73.8	USA	Early hybrid parent with low TE (Geetika *et al.* 2019)

harvested 5 days after anthesis of the main shoot (sorghum) or at first silking (maize). Harvest occurred in May–June 2011 (late autumn to early winter) in Exp1 and November–December 2011 (early summer) in Exp2. As a consequence, average daily maximum and minimum temperatures, daily radiation and maximum daily vapour-pressure deficit (VPD) were generally higher in Exp2 than Exp1 (Table 2).

2.3 Leaf area measurements

The number of fully expanded leaves (ligule visible above that of the previous leaf) was counted twice a week on each axis of every plant in both experiments. The length and maximum width of each fully expanded leaf were measured non-destructively and individual leaf area was estimated from the measured length and width, multiplied by a scaling factor of 0.71 (0.635 for flag leaves) for sorghum (van Oosterom *et al.* 2011). For maize, a factor of 0.68 was used for flag leaves, whereas for all other leaves, a bilinear relationship was used based on data from previous experiments:

$$\text{Leaf size} = 0.705 * \text{length} * \text{width} \quad \text{if length} * \text{width} < 642$$
$$\text{Leaf size} = -108.5 + 0.874 * \text{length} * \text{width} \quad \text{if length} * \text{width} > 642$$

Daily green leaf area (GLA) per plant was interpolated from individual leaf sizes and the number of fully expanded leaves. The area of expanding leaves was estimated based on observations that this area is equivalent to the fully expanded area of the next 1.6 sequential leaves following the last fully expanded leaf (Muchow and Carberry 1990).

2.4 Transpiration

Daily transpiration (T) per plant was calculated as the decline in lysimeter weight from midnight to midnight, adjusted for any water applied during that period. The daily increase in plant dry mass was considered to be negligible relative to the amount of water used, considering that observed TE_{wp} had a range of 6–10 g kg^{-1} (Table 3). To account for differences in plant size, associated with plant-to-plant variation and with increased plant size over time, leaf area-based transpiration rates were obtained by dividing daily T for each plant by its GLA for that day (transpiration per unit green leaf area, TGLA, g m^{-2}), assuming that GLA was constant throughout each day. Total transpiration of each plant throughout the experiment was calculated as the sum of the daily water use data, adjusted for the fresh shoot mass and dry root mass at harvest, and the average change in weight of the lysimeters with no plants.

2.5 Biomass sampling

At harvest (5 days after anthesis for sorghum, first silking for maize), plants were cut below the base of the stem and shoot fresh weight was

Table 2. Environmental conditions of the two experiments included in this study. [a]29 March to 21 May 2011 in Exp1; 15 October to 28 November 2011 in Exp2. End dates represent date when 50 % of plants were harvested. Excludes some days with missing records.

	Experiment 1	Experiment 2
Sowing date	10 March 2011	16 September 2011
Harvest date	28 April to 10 June 2011	14 November to 22 December 2011
Mean daily maximum temperature (°C)[a]	28.7	31.8
Mean daily minimum temperature (°C)[a]	15.1	18.7
Mean daily radiation (MJ m^{-2})[a]	10.2	17.9
Mean daily maximum VPD (kPa)[a]	2.46	3.19

Table 3. ANOVA for TE for whole plant (including roots) and the shoot only, and root-to-total biomass ratio (RWR) for maize, 2dwarf and 3dwarf sorghum genotypes measured in two lysimetry experiments. [ns]$P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

	$TE_{\text{whole plant}}$ (g kg^{-1})		TE_{shoot} (g kg^{-1})		RWR	
	Exp1	Exp2	Exp1	Exp2	Exp1	Exp2
Maize	9.48	7.24	8.58	6.18	0.095	0.145
2dwarf sorghum	10.13	7.02	9.32	5.93	0.081	0.154
3dwarf sorghum	10.08	7.11	9.04	5.78	0.140	0.191
Species effect, followed by height effect						
Maize vs. sorghum	*	ns	ns	*		
2dwarf vs. 3dwarf	ns	ns	ns	ns		
Height effect, followed by species effect						
3dwarf vs. (maize and 2dwarf)					*	***
2dwarf vs. maize					*	ns
Genotype (maize)	ns	ns	**	***	ns	*
Genotype (2dwarf)	**	***	***	***	ns	***
Genotype (3dwarf)	**	***	ns	*	***	***

determined after removal of any attached soil. Roots were washed out from the soil and any organic matter was removed. This was done on screens to minimize loss of roots. Shoot and root dry mass of each plant were determined after drying in a fan-forced dehydrator at 60–70 °C for at least 48 h. Biomass data for the main shoot were obtained individually for the blade, sheath and stem of each phytomer. For tillers, data for each organ (blade, sheath, stem) were aggregated across phytomers.

2.6 Data analysis and interpretation

Transpiration efficiency was calculated as the ratio of biomass (B) and total water transpired (T), and was calculated using both shoot dry mass (TE_{shoot}) and whole-plant (root and shoot) dry mass (TE_{wp}). The ratio between root and total dry mass (RWR, root weight ratio) was calculated as a measure of dry mass partitioning.

To look at differences in TGLA across the three classes of genotypes (maize, 2dwarf sorghum and 3dwarf sorghum), average daily TGLA across all plants for each class was calculated by dividing total daily water use across all plants for each class by their total leaf area for that day ($\Sigma T/\Sigma GLA$). This was done for days from 2 to 30 April 2011 (Exp1) and 16 October to 24 November 2011 (Exp2). Before these start dates, plants were so small that (i) plant leaf area (including the area of expanding leaves) could not be estimated accurately from observed leaf length and leaf width data, and (ii) daily water use could not be estimated accurately from changes in pot weights, thus resulting in unreliable estimates of TGLA. Days with prolonged periods of missing records for transpiration due to data logging issues were excluded. Daily TGLA for each pair of classes was plotted and regressions were forced through the origin, such that the slope of each regression was taken as the relative TGLA of one class compared to another, using data across the two experiments.

In order to link class differences in TGLA to differences in biomass partitioning, biomass production per unit leaf area produced (BLA) was estimated for two phases of crop development that were separated by the approximate onset of stem elongation (see Results). For the first phase prior to stem elongation, BLA was estimated as the combined dry mass at harvest of the leaf blades and leaf sheaths of the first eight phytomers of the main shoot (see Results), divided by the total leaf area of these phytomers. To estimate BLA for the second phase, after the onset of stem elongation, dry mass and leaf area accumulation were taken as total plant dry mass and leaf area (including roots and tillers) at harvest, minus the values estimated for the first phase of development. This assumed that the dry mass of leaf blades and sheaths of these first eight phytomers at the onset of stem elongation was similar to their weight at harvest, just after flowering, before the onset of grain growth.

Analysis of variance was done using the General Linear Model (GLM) procedure in SAS 9.4 (SAS 2013). Genotypes were divided into three classes (maize, 2dwarf sorghum and 3dwarf sorghum) and significance of differences among these three classes (two degrees of freedom) was analysed using two orthogonal contrasts with one degree of freedom each. For traits for which the species difference was most important (TE_{shoot}, TE_{wp} and BLA prior to stem elongation) the contrasts used were maize versus sorghum (2dwarf and 3dwarf combined), followed by the contrast of 2dwarf versus 3dwarf sorghum. For traits for which height was expected to be the major cause for genotypic differences (RWR, BLA after stem elongation), the contrasts used were short (3dwarf sorghum) versus tall (maize and 2dwarf sorghum combined), followed by the contrast of maize versus 2dwarf sorghum. In the analyses, the class × rep error term was used for the contrast among classes (main blocks), whereas for genotypic differences within classes, the remaining error term was used, which consisted of the sum of the genotype (class) × rep error terms. Regressions analyses for comparison of TGLA across the three classes were done using the REG procedure in SAS 9.4 (SAS 2013).

2.7 Simulation studies

To analyse the effects of species and height differences on grain yield across a range of environments, simulation runs were performed for standard 3dwarf sorghum and maize hybrids using the APSIM-Sorghum (Hammer *et al.* 2010) and APSIM-Maize (Soufizadeh *et al.* 2018) models, respectively. These models are part of the APSIM cropping systems simulation platform (Holzworth *et al.* 2014) and version 7.9 was used in this study. Simulations were conducted for two locations in the summer grains belt in eastern Australia: Dalby in south-east Queensland (27.18°S, 151.26°E) and Gunnedah in the Liverpool Plains in Northern New South Wales (30.96°S, 150.25°E). For both locations, simulations were conducted for the period 1986–2016 (31 years), using daily weather data from the SILO patched point data set (http://www.longpaddock.qld.gov.au/silo/index.html) (Jeffrey and Carter 2001) that were infilled where observed data were not available. For the Liverpool Plains, simulations were conducted using a starting soil water of 150 mm and a soil water holding capacity of 250 mm. All simulations were conducted assuming no nitrogen limitations and fully irrigated conditions to allow expression of yield potential for this high-yielding environment. For Dalby, a 2 × 2 factorial design was used that included two starting soil water amounts (75 and 150 mm) and two water regimes (irrigated, rainfed) to generate a diverse range of moisture environments and yield levels. A soil water holding capacity of 250 mm was used, and, where irrigation was simulated, it was applied to refill the soil profile when the fraction of available soil water dropped below 50 %. In total, this yielded 155 (5 × 31) simulation runs for each crop (maize, 3dwarf sorghum).

Simulations for sorghum and maize were set up using standard agronomic practices and a standard hybrid for each species. Sorghum simulations were conducted using a plant density of 5 plants per m^2, a row spacing of 1 m, and were parameterized for the 3dwarf hybrid MR Buster (Hammer *et al.* 2010) assuming one productive tiller per plant. Maize simulations were conducted using a plant density of 8 plants per m^2, a row spacing of 0.75 m, and were parameterized for hybrid Pioneer 3394 (Hammer *et al.* 2009). Based on experiment results, a common TE was used for both species (Table 3), which was set at 9 g kg^{-1} at a VPD of 1 kPa (Tanner and Sinclair 1983). To reflect observed differences in TGLA (Fig. 1), RUE was set at 1.25 g MJ^{-1} for 3dwarf sorghum and 1.85 g MJ^{-1} for maize, consistent with previously reported values (Hammer *et al.* 2010; Soufizadeh *et al.* 2018). All simulated crops were sown on 1 October each year, and soil water was reset at sowing each year for all simulations so that simulated results reflected only the effects of seasonal climate variability. For each simulation run, total biomass and grain mass at maturity as well as total crop evapotranspiration (transpiration plus soil evaporation (mm)) were reported for each year.

3. RESULTS

3.1 Transpiration efficiency

Maize had significantly ($P < 0.05$) greater TE_{shoot} than sorghum as observed in Exp2, but not in Exp1, where there was a trend ($P < 0.10$) towards greater TE_{shoot} for sorghum (Table 3). In contrast, TE_{wp} of sorghum was significantly ($P < 0.05$) greater than that of maize in Exp1, but species differences were not significant in Exp2. Differences in phenology (Table 1) generally had no effect on TE (data not shown). Plant height *per se* also had no effect on either TE_{shoot} or TE_{wp}, as 2dwarf and 3dwarf sorghum genotypes did not differ significantly for both traits in both experiments (Table 3). However, plant height did affect the root-total biomass ratio (RWR), which was significantly greater for 3dwarf sorghum genotypes than for the taller maize and 2dwarf sorghum genotypes in both experiments (Table 3). Within species and using individual plant data, RWR was significantly ($P < 0.001$) negatively associated with TE_{shoot}, but the association with TE_{wp} was not significant ($P > 0.05$) in either experiment (Table 4). Within classes, maize genotypes did not differ significantly for TE_{wp}, but both 2dwarf and 3dwarf sorghum genotypes showed significant differences in TE_{wp} in both experiments (Table 3). Across all sorghum genotypes, the range in TE_{wp} was 9.2–11.2 g kg^{-1} in Exp1 and 5.9–8.3 g kg^{-1} in Exp2, indicating a range of 2.0–2.4 g kg^{-1} within each experiment. Even though differences in RWR were highly significant ($P < 0.001$) across the 3dwarf sorghum genotypes in both experiments and across 2dwarf genotypes in Exp2 (Table 3), inclusion of roots had little effect on the ranking of genotypes for TE. For Exp1, the Spearman rank correlation between TE_{shoot} and TE_{wp} for individual plants was $r = 0.99$ ($n = 28$, $P < 0.0001$) for 2dwarf sorghum plants and $r = 0.91$ ($n = 55$, $P < 0.0001$) for 3dwarf sorghum plants. For Exp2, rank correlations were slightly lower but still highly significant ($r = 0.90$, $n = 28$, $P < 0.0001$ for 2dwarf plants; $r = 0.90$, $n = 60$, $P < 0.0001$ for 3dwarf plants).

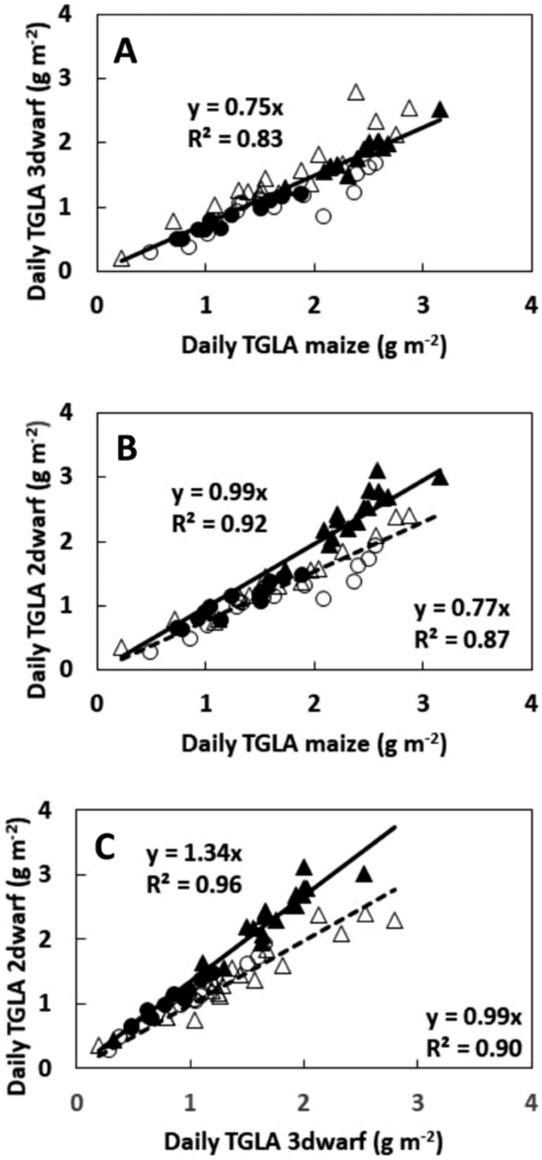

Figure 1. Daily transpiration per unit green leaf area (TGLA) for (A) 3dwarf sorghum versus maize, (B) 2dwarf sorghum versus maize and (C) 2dwarf versus 3dwarf sorghum for Exp1 (○●) and Exp2 (Δ▲), for the period before (○Δ) and after (●▲) the onset of stem elongation. Last day of early phase is 17 April 2011 (38 DAS) in Exp1 and 2 November 2011 (47 DAS) in Exp2.

3.2 Transpiration rates and biomass partitioning

Significant differences in average daily TGLA were observed across the three classes of germplasm. Average daily TGLA (±5 % confidence interval) for 3dwarf sorghum was only 75 % of that of maize across all TGLA levels (slope of 0.75 ± 0.032, Fig. 1A). The observation that the ratio was common across the two experiments and across days within experiments indicated that this ratio was independent of time of year and development stage of the crop, respectively. For the comparison of 2dwarf sorghum with maize and 3dwarf sorghum, however, there was a distinct effect of development stage on the ratio of the TGLA (Fig. 1B and C). This was particularly the case in Exp2, but the trend was similar in Exp1. During early development stages (prior to 17 April 2011 in Exp1 and 2 November 2011 in Exp2), TGLA of 2dwarf sorghum was similar to that of 3dwarf sorghum (slope of 0.99 ± 0.043, Fig. 1C) and significantly lower than that of maize (slope of 0.77 ± 0.038, Fig. 1B). After

Table 4. Association of RWR with $TE_{whole\ plant}$ and TE_{shoot} for both maize and sorghum in each of the two experiments. Data across individual plants. $^{a\ ns}P > 0.05$; $^{***}P < 0.001$.

		$TE_{whole\ plant}$		TE_{shoot}	
Experiment	*n*	R^2	P^a	R^2	P^a
Maize					
Exp1	32	0.06	ns	0.32	***
Exp2	31	0.00	ns	0.49	***
Sorghum					
Exp1	83	0.02	ns	0.19	***
Exp2	88	0.01	ns	0.31	***

these dates, however, TGLA of 2dwarf sorghum increased to the level of the maize, as the slope of the relationship did not differ significantly from unity (0.99 ± 0.044, Fig. 1B), but it was significantly greater than 3dwarf sorghum, as the slope of the relationship (Fig. 1C) was significantly greater than unity (1.34 ± 0.041). This was further supported by a covariance analysis, which showed that for both pairs of classes, the two individual regressions gave a significantly better fit than a single regression, as the *F*-ratio between the Error Mean Square (EMS) of a single regression and that of the two individual regressions was significant for the comparison of 2dwarf sorghum with both maize ($F(60/59) = 1.97$, $P < 0.01$) and 3dwarf sorghum ($F62/61) = 3.27$, $P < 0.001$). In contrast, for the relationship between maize and 3dwarf sorghum, two individual regressions did not significantly improve the fit.

In order to determine if the timing of this transition in TGLA of 2dwarf sorghum represented a shift in the biomass allocation of 2dwarf sorghum relative to maize and 3dwarf sorghum, we estimated biomass produced per unit leaf area (BLA) before and after this moment. The timing of the transition around 17 April in Exp1 and 2 November in Exp2 (Fig. 1) coincided with an increase in the leaf appearance rate of maize, which occurred around 38 days after sowing (DAS) or 17 April 2011 in Exp1 and 44 DAS or 30 October 2011 in Exp2 (Fig. 2). This increase in the rate of leaf collar emergence of maize has been linked to the early stages of stem elongation (Birch *et al.* 2002). At the timing of this change in the leaf appearance rate, maize had on average 8.1 (Exp1) and 7.4 (Exp2) fully expanded leaves and sorghum 9.4 (Exp1) and 8.9 (Exp2) (Fig. 2). Because stem elongation of a phytomer in sorghum occurs once its leaf blade is fully expanded (Lafarge *et al.* 1998) and because biomass accumulation to stems in sorghum starts from *ca.* phytomer 7 onwards (Kulathunga 2013), we defined biomass accumulation prior to stem elongation as the combined dry mass of leaf blades and leaf sheaths of main shoot phytomers 1–8, and leaf area production as the combined area of leaf blades of these same phytomers. Dry mass and leaf area accumulation after the onset of stem elongation were taken as total plant dry mass and leaf area (including roots and tillers) at harvest, minus the values estimated for the pre-stem elongation period.

An ANOVA for BLA (Table 5) showed that in both experiments BLA of maize prior to the onset of stem elongation was significantly ($P < 0.001$) greater than that of sorghum, whereas the difference between 2dwarf and 3dwarf sorghum was not significant in Exp1. Averaged across the two experiments, BLA was 85.5 g m^{-2} for maize, but only 63.4 g m^{-2} and 61.1 g m^{-2} for 2dwarf and 3dwarf sorghum, respectively. Values for sorghum were 0.74 (2dwarf) and 0.71 (3dwarf) of those for maize and were thus close to the slopes of the relevant regressions for TGLA in Fig. 1. After the onset of stem elongation, the BLA of 3dwarf sorghum in both experiments was significantly ($P < 0.001$) lower than that of maize and 2dwarf sorghum, which in turn did not differ significantly (Table 5). The ratio of BLA for 3dwarf sorghum and maize was 0.86 in Exp1 and 0.75 in Exp2, whereas the ratio between BLA values for 2dwarf and 3dwarf sorghum was 1.20 in Exp1 and 1.34 in Exp2. Particularly for Exp2, these ratios were close to the corresponding ratios for TGLA in Fig. 1.

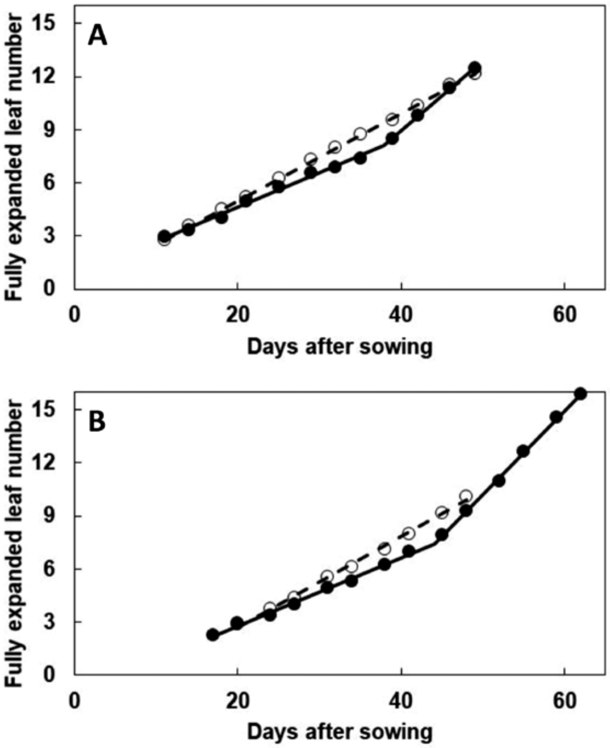

Figure 2. The number of fully expanded leaves (FEL) versus DAS for (A) Exp1 and (B) Exp2 averaged across all maize (●) and sorghum (○) genotypes. Regressions were truncated at the leaf numbers where the first plant for that species reached flag leaf. Regression equations are Exp1: Maize: $FEL = 0.735 + 0.195 * DAS$ if $DAS \leq 37.9$; $FEL = -7.008 + 0.399 * DAS$ if $DAS \geq 37.9$; $R^2 = 1.00$ Sorghum: $FEL = 0.078 + 0.247 * DAS$; $R^2 = 1.00$ Exp2: Maize: $FEL = -1.063 + 0.192 * DAS$ if $DAS \leq 44.0$; $FEL = -13.466 + 0.474 * DAS$ if $DAS \geq 44.0$; $R^2 = 1.00$ Sorghum: $FEL = -2.460 + 0.257 * DAS$; $R^2 = 1.00$.

3.3 Simulation studies

A comparison of simulated biomass accumulation of the maize and 3dwarf sorghum hybrids showed that below total crop water use of *ca.* 300 mm, shoot dry mass was closely associated with water use (Fig. 3), indicating that water availability was the major constraint to biomass accumulation. The similarity in the trend between maize and 3dwarf sorghum under these conditions of limited water availability is governed by their similar TE. In contrast, above 300 mm of total crop water use, biomass accumulation of sorghum reached a plateau, whereas for maize, the relationship between biomass and water use remained positive albeit weaker than at lower levels of water use (Fig. 3).

The greater biomass of maize than 3dwarf sorghum under well-watered conditions resulted in greater potential grain yield of maize (*ca.* 11.5 t ha^{-1}) than 3dwarf sorghum (*ca.* 8 t ha^{-1}), as the two crops had similar maximum efficiency in partitioning biomass to grains (or harvest index). Consistent with the results for biomass, grain yields declined for both crops once total crop water use dropped below 300 mm. However, there was a crossover interaction for grain yield, with grain yield of 3dwarf sorghum generally exceeding that of maize once water use fell below 250 mm (Fig. 3), because sorghum was better able to maintain its harvest index at low total crop water use. Maize

Table 5. ANOVA of biomass production per unit leaf area (BLA) prior to stem elongation and for the period from stem elongation onwards for maize, 2dwarf sorghum and 3dwarf sorghum genotypes. For calculation of BLA before and after onset of stem elongation, see text. $^{ns}P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

	BLA (g m^{-2}) before onset stem elongation		BLA (g m^{-2}) after onset stem elongation	
	Exp1	Exp2	Exp1	Exp2
Maize	86.2	85.0	278	344
2dwarf sorghum	62.4	64.3	288	345
3dwarf sorghum	63.5	58.6	240	258
Species effect, followed by height effect				
Maize vs. sorghum	***	***		
2dwarf vs. 3dwarf	ns	**		
Height effect, followed by species effect				
3dwarf vs. (maize and 2dwarf)			***	***
2dwarf vs. maize			ns	ns
Genotype (maize)	***	***	***	ns
Genotype (2dwarf)	***	*	***	***
Genotype (3dwarf)	***	***	***	***

generally failed to produce any grain yield if water use was less than *ca.* 200 mm.

4. DISCUSSION

4.1 Little effect of species and plant height on TE$_{wp}$

Across the two experiments, there were no consistent species effects on TE$_{wp}$ (Table 3). Differences were significant in Exp1, where sorghum had significantly ($P < 0.05$) greater TE$_{wp}$ than maize, but not in Exp2, where maize tended to have greater TE$_{wp}$ than sorghum (Table 3). These finding are consistent with the assertion of Tanner and Sinclair (1983) that TE of both species is similar. Nonetheless, significant genotypic differences in TE$_{wp}$ were observed (Table 3) for sorghum, consistent with previous reports (Hammer *et al.* 1997; Xin *et al.* 2009; Geetika *et al.* 2019). The absence of genotypic differences among the maize hybrids was likely associated with the high level of selection to which these hybrids had been subjected, as opposed to the sorghum germplasm, which deliberately represented a range in TE$_{wp}$. The relatively higher TE of maize compared to sorghum under the higher VPD conditions of Exp2 (Table 2) was consistent with results of Choudhary *et al.* (2020), who concluded that maize restricts transpiration rate more than sorghum if grown under well-watered conditions at high VPD.

Any differences in TE$_{wp}$ were not a consequence of differences in plant height *per se*, because 2dwarf sorghum genotypes on average had the same TE$_{wp}$ as 3dwarf genotypes (Table 3), despite the generally taller stature (Table 1). The observation that the difference between 2dwarf and 3dwarf sorghum for TE$_{wp}$ was in both experiments smaller than the difference for TE$_{shoot}$ was a consequence of the significantly greater RWR of the shorter 3dwarf sorghum genotypes. This effect of plant height on RWR was consistent with observations by Miralles *et al.* (1997) and McCaig and Morgan (1993) for isogenic wheat (*Triticum aestivum*) lines that differed in the number of *Rht* dwarfing genes. It may indicate that in 3dwarf sorghum, roots became a sink for assimilates that were produced beyond the reduced shoot demand caused by a smaller sink size (Miralles *et al.* 1997). This supply-demand driven increase in the RWR would be similar to the situation under drought stress, when increased partitioning to the root can be an emergent consequence of small above-ground sink size as a result of poor seed set (van Oosterom *et al.* 2011). Under such circumstances, genotypic differences in TE$_{shoot}$ could be driven by differences in seed set. Because inclusion of roots had limited effect on genotype ranking for TE across 3dwarf sorghum, results support the conclusion of Chenu *et al.* (2018) that costs involved in extracting roots from soil are unlikely to be justifiable within the context of large-scale phenotyping of TE under well-watered conditions in breeding programmes, particularly if selection is predominantly among genotypes with similar height. However, the presence of significant genotypic differences in RWR within classes (Table 3) indicates that inclusion of roots can be important in more detailed crop physiology-focussed studies. The absence of consistent species differences in TE in our data set (Table 3) justifies the use of a common TE coefficient in the simulation studies.

4.2 Effects of species and plant height on transpiration rates were associated with biomass growth and partitioning

Crop species and plant height both significantly affected TGLA (Fig. 1). The species effect was expressed prior to stem elongation, the height effect once stem elongation had started, and both reflected differences in BLA (Table 5). The whole-plant TGLA observed in the current lysimeters is highly associated with stomatal conductance (Geetika *et al.* 2019) and consistent with the greater TGLA of maize compared to 3dwarf sorghum. Kakani *et al.* (2011) and Wang *et al.* (2017) reported greater stomatal conductance for maize than sorghum during vegetative development. This is reflected in the greater ratio between CO$_2$ inside the stomatal cavity and ambient CO$_2$ (c_i/c_a) of maize (0.4, Leakey *et al.* 2006; Wong *et al.* 1979) compared to sorghum (0.30–0.36, Henderson *et al.* 1998), as greater stomatal conductance increases CO$_2$ diffusion into leaves. The greater TGLA of the maize

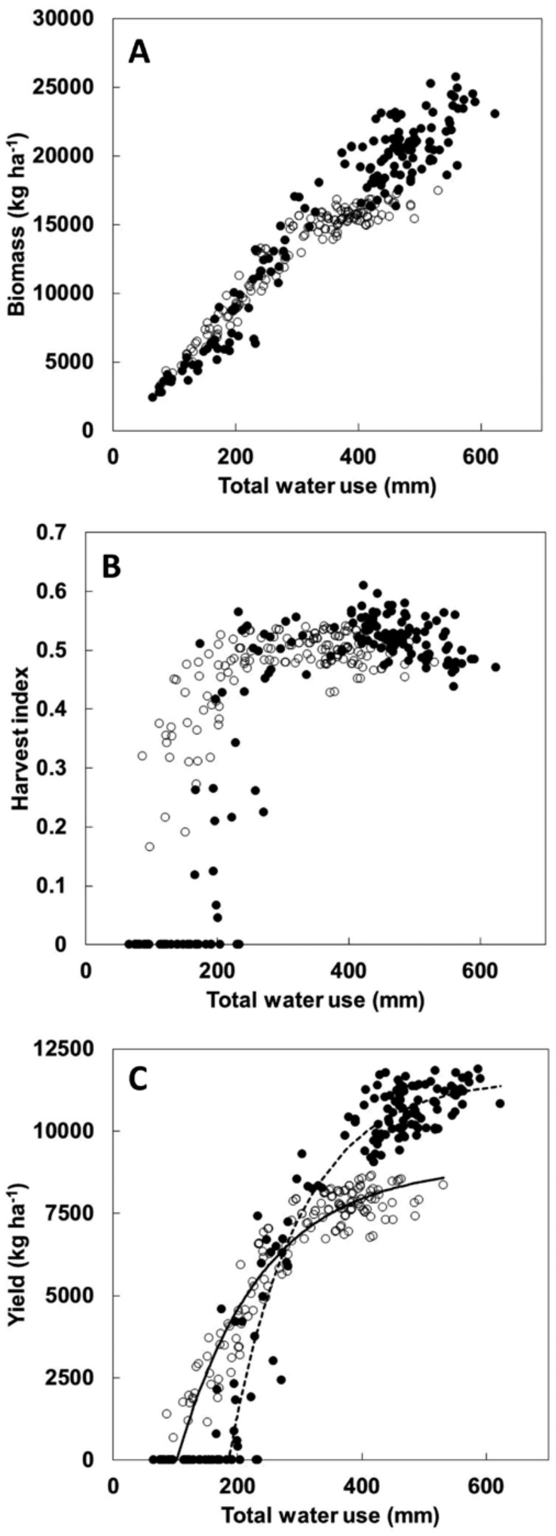

Figure 3. Simulated shoot dry mass (A), harvest index (B) and grain yield (C) of standard maize (●) and sorghum (○) hybrids versus total crop water use for simulations at Dalby and the Liverpool Plains.

and 2dwarf sorghum after the onset of stem elongation compared to 3dwarf sorghum (Fig. 1) is likely to be predominantly associated with stomatal conductance. This would be consistent with the observation by Jobson *et al.* (2019) that short *Rht-B1b* wheat has significantly lower stomatal conductance than taller near-isogenic *Rht-B1a* wheat. In the wheat study, the short genotype also has significantly lower photosynthetic rates. The photosynthesis–stomatal conductance link could be an area of research to further dissect the comparative adaptation of maize and sorghum, as differences in organ size could potentially result in sink stimulation of TGLA and photosynthetic capacity. The observation that both before and after the onset of stem elongation these differences in TGLA were proportional to differences in BLA would support the hypothesis that species and height differences in TGLA (Fig. 1) were potentially an emergent consequence of differences in relative organ size.

The ratio in TGLA between 3dwarf sorghum and maize (Fig. 1A) reflected published differences in RUE, which is around 1.2–1.4 g MJ^{-1} for commercially grown 3dwarf sorghum (Sinclair and Muchow 1999; Hammer *et al.* 2010) and up to 1.8–2.0 g MJ^{-1} for maize (Lindquist *et al.* 2005). Similar to TGLA, these differences are likely to be at least partly associated with the difference in height, as Miralles and Slafer (1997) observed increased RUE of tall wheat genotypes compared to their short near-isogenic dwarf counterparts. However, George-Jaeggli *et al.* (2013) observed for sorghum that even though 2dwarf genotypes on average had significantly greater RUE than their near-isogenic 3dwarf counter parts, the effect of the *dw3* dwarfing gene on RUE was context-dependent. Consistent with this, Hammer *et al.* (2010) reported two tall single-dwarf sorghum genotypes with RUE close to either 3dwarf sorghum or maize. The cause for the low RUE of 3dwarf sorghum is still unclear, but possible mechanisms could include a feedback mechanism on biomass growth (photosynthesis), and hence conductance and TGLA, in response to accumulation of assimilates due to the reduced sink strength of the smaller stem. In the absence of consistent class differences in TE$_{wp}$ (Table 3), the observed height effect on TGLA (Fig. 1) is likely to represent an associated effect on RUE.

4.3 Species differences affected adaptation to water limitation

The association of yield with total crop water use is ubiquitous. Cooper *et al.* (2020) reported this for a more comprehensive range of environments and management practices simulated for maize in the USA and our simulated results are in line with the expected trends. Furthermore, we have revealed the interplay between RUE and TE could lead to a crossover in species × total crop water use interactions in grain yield (Fig. 3). For the environments and management practices simulated, 3dwarf sorghum yield (8 t ha^{-1}) was around 70 % of that of maize (11.5 t ha^{-1}) in the high-yielding range. As radiation became the main factor limiting crop growth in these water non-limiting situations, the species difference in biomass accumulation reflected the greater RUE of maize. The lower yield of maize under water limitation, when total crop water use is below 200–250 mm, was due to water stress effects on harvest index (Fig. 3). This reflects the observation that the threshold growth rate around flowering required for seed set is generally much higher for maize (1 g per plant per day, Vega *et al.* 2001; Cooper *et al.* 2014) than for 3dwarf sorghum (0.2 g m^{-2} °$Cday^{-1}$ (van Oosterom and Hammer 2008), or 0.4 g per plant per day at 10 plants per m^2 and average temperature of 25 °C). The negative effect of higher growth rate thresholds on seed set of maize in environments where biomass production is limited by water availability, will be exacerbated by its higher RUE and TGLA, which will increase water use during vegetative growth stages, causing an earlier onset of water stress if water is limiting. If this reduces growth rates around anthesis, this can have detrimental effects on seedset and grain yield, as illustrated by the high proportion of maize crops with no grain yield at low total water use (Fig. 3). The crossover interaction for grain yield observed in Fig. 3 is consistent with results from field experiments reported by Muchow (1989b). Although high TGLA and RUE of maize can increase potential grain yield compared to 3dwarf sorghum, there is a trade-off under water-limited conditions.

This crossover species × water availability interaction for grain yield in Fig. 3 is similar to the G × E interaction observed in simulations of genotypes within species that differ in TGLA. For both 3dwarf sorghum (Sinclair *et al.* 2005) and maize (Messina *et al.* 2015), simulation studies have shown that genotypes with low transpiration rates have a yield advantage under low-yielding, water-limited conditions, as the reduced rate of water use delays the onset of drought stress and increases water availability during grain filling. Under well-watered conditions, however, the reduced stomatal conductance, associated with low TGLA, will reduce assimilation and hence biomass accumulation. Indeed, under conditions where biomass production was radiation-limited, Sinclair *et al.* (2005) reported a gradual decrease in RUE for sorghum as an emergent consequence of stomatal closure. These results, together with the findings in this study, highlight the fact that effects of water availability on seed set weighs significantly on grain yield and multiple strategies exists in the underpinning physiology that could be explored for yield improvement.

However, the full G × E × M interactions need to be considered comprehensively for crop adaptation strategies. The greater TGLA of maize compared to 3dwarf sorghum, which is likely associated with its greater RUE, can increase grain yield in well-watered environments where biomass production is radiation-limited (Muchow 1989a; Hammer *et al.* 2010). However, this greater yield potential in well-watered situations comes at a cost of increased water use, and hence reduced soil water content at harvest. This can potentially have adverse consequences in a rainfed cropping systems where carry-over of water from one cropping season to the next is important for productivity of the subsequent crop (Probert *et al.* 1995).

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CONFLICT OF INTEREST

None declared.

CONTRIBUTIONS BY THE AUTHORS

E.J.vO. and G.L.H. conceived the ideas for the study, E.J.vO., M.R.D.L.K., K.S. and, G.B.M. conducted the experiments, E.J.vO., M.R.D.L.K., G.B.M. and C.B. conducted the analyses and data interpretation. All authors contributed scientific input during writing of the manuscript.

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