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

E. J. van Oosterom1*, M. R. D. L. Kulathunga2,3, K. S. Deifel1, G. B. McLean1,4, C. Barrasso5, A. Wu1, C. Messina6 and G. L. Hammer1,6

1The University of Queensland, Queensland Alliance for Agriculture and Food Innovation, Centre for Crop Science, Brisbane, QLD 4072, Australia
2The University of Queensland, School of Agriculture and Food Sciences, Brisbane, QLD 4072, Australia
3Fruit Research and Development Institute, Department of Agriculture, Kahanwila, 12418 Horana, Sri Lanka
4Agri-Science Queensland, Department of Agriculture and Fisheries, Toowoomba, QLD 4350, Australia
5German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany
6Corteva Agriscience, Agriculture Division of DowDuPont, 7250NW 62nd Avenue, Johnston, IA 50131, USA

*Corresponding author’s e-mail address: erik.van.oosterom@uq.edu.au

Guest Editor: Vincent Vadez
Editor-in-Chief: Stephen P. Long

Citation: van Oosterom EJ, Kulathunga MRDL, Deifel KS, McLean GB, Barrasso C, Wu A, Messina C, Hammer GL. 2020. Dissecting and modelling the comparative adaptation to water limitation of sorghum and maize: role of transpiration efficiency, transpiration rate and height. In Silico Plants 2020: diaa012; doi: 10.1093/insilicoplants/diaa012

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...
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(NO₃)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. aSum of all the individual main shoot stem nodes. Means across replications. bOnly 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                                       |
| 33TS6                       | 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**              |       |       |       |       |                                                   |
| A14                         | 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) |
| P1291382                    | 165   | 168   | 45.3  | 54.8  | China, Shatter cane line with high TE (Xin et al. 2009) |
| P1391652                    | 175   | 176   | 57.3  | 64.8  | China, High TE line (Xin et al. 2009; Chenu et al. 2018) |
| P1584085                    | 174   | 149   | 57.5  | 62.3  | Uganda, Caudatum line with high TE (Xin et al. 2009) |
| P1656046                    | 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 |
| B7x623 b                    | 78    | 69.8  |       |       | USA, Elite female line                             |
| B7x642 (B35)                | 72    | 70    | 73.3  | 67.3  | Ethiopia, Highly stay-green, low-tillering, partially converted duura 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 Rz |
| 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:

\[
\text{Leaf size} = 0.705 \times \text{length} \times \text{width} \quad \text{if length} \times \text{width} < 642 \\
\text{Leaf size} = -108.5 + 0.874 \times \text{length} \times \text{width} \quad \text{if length} \times \text{width} > 642
\]

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 TEwp 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...
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<sub>shoot</sub>) and whole-plant (root and shoot) dry mass (TE<sub>wp</sub>). 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 (ΣT/ΣGLA). 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<sub>shoot</sub>, TE<sub>wp</sub> 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 southeast 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 patch 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<sup>2</sup>, 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<sup>2</sup>, 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<sup>−1</sup> 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<sup>−1</sup> for 3dwarf sorghum and 1.85 g MJ<sup>−1</sup> 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 evapotranspiration (transpiration plus soil evaporation (mm)) were reported for each year.

3. RESULTS

3.1 Transpiration efficiency

Maize had significantly ($P < 0.05$) greater $TE_{\text{shoot}}$ than sorghum as observed in Exp2, but not in Exp1, where there was a trend ($P < 0.10$) towards greater $TE_{\text{shoot}}$ for sorghum (Table 3). In contrast, $TE_{\text{wp}}$ 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 $TE_{\text{shoot}}$ or $TE_{\text{wp}}$, 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 $TE_{\text{shoot}}$, but the association with $TE_{\text{wp}}$ was not significant ($P > 0.05$) in either experiment (Table 4). Within classes, maize genotypes did not differ significantly for $TE_{\text{wp}}$, but both 2dwarf and 3dwarf sorghum genotypes showed significant differences in $TE_{\text{wp}}$ in both experiments (Table 3). Across all sorghum genotypes, the range in $TE_{\text{wp}}$ 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 $TE_{\text{shoot}}$ and $TE_{\text{wp}}$ 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).

3.2 Transpiration rates and biomass partitioning

Significant differences in average daily TGLA were observed across the three classes of germplasm. Average daily TGLA ($\pm$ 5 % confidence interval) for 3dwarf sorghum was only 75 % of that of maize across all TGLA levels (slope of 0.75 $\pm$ 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 $\pm$ 0.043, Fig. 1C) and significantly lower than that of maize (slope of 0.77 $\pm$ 0.038, Fig. 1B).

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

| Experiment | $TE_{\text{whole plant}}$ | $TE_{\text{shoot}}$ |
|------------|--------------------------|---------------------|
|            | $R^2$ | $P$  | $R^2$ | $P$  |
| Maize      |       |      |       |      |
| Exp1       | 0.06  | ns   | 0.32  | ***  |
| Exp2       | 0.00  | ns   | 0.49  | ***  |
| Sorghum    |       |      |       |      |
| Exp1       | 0.02  | ns   | 0.19  | ***  |
| Exp2       | 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 signifi-
cantly 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 regres-
sion, 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 (F(62/61) = 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 sor-
ghum 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 accumula-
tion prior to stem elongation as the combined dry mass of leaf blades
and leaf sheaths of main shoot phytomers 1–8, and leaf area produc-
tion 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 of maize and were thus close to the slopes of the relevant regressions for TGLA in Fig. 1. After the onset of stem elonga-
tion, 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.

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 gov-
erned 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 posi-
tive 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
decayed 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 bet-
ter able to maintain its harvest index at low total crop water use. Maize

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 ≤ 37.9; FEL = −7.008 + 0.399 * DAS if DAS ≥ 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 ≤ 44.0; FEL = −13.466 + 0.474 * DAS if DAS ≥ 44.0; \( R^2 = 1.00 \) Sorghum: FEL = −2.460 + 0.257 * DAS; \( R^2 = 1.00 \).
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. *P < 0.05; **P < 0.01; ***P < 0.001.

| genotype | 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 |     | **   |      |      |
| Height effect, followed by species effect |      |      |      |      |
| 2dwarf vs. maize | ns   |      |      |      |
| Genotype (maize) | ***  | ***  | ***  | ***  |
| 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 TEwp

Across the two experiments, there were no consistent species effects on TEwp (Table 3). Differences were significant in Exp1, where sorghum had significantly (P < 0.05) greater TEwp than maize, but not in Exp2, where maize tended to have greater TEwp 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 TEwp 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 TEwp.

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 TEwp were not a consequence of differences in plant height per se, because 2dwarf sorghum genotypes on average had the same TEwp as 3dwarf genotypes (Table 3), despite the generally taller stature (Table 1). The observation that the difference between 2dwarf and 3dwarf sorghum for TEwp was in both experiments smaller than the difference for TEGl 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 TEGl 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 CO₂ inside the stomatal cavity and ambient CO₂ (c/cₐ) 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 CO₂ diffusion into leaves. The greater TGLA of the maize...
Adaptation to water limitation of sorghum and maize

...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 counterparts, 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)

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.
than for 3dwarf sorghum (0.2 g m⁻² °C day⁻¹ (van Oosterom and Hammer 2008), or 0.4 g per plant per day at 10 plants per m² 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 seed set 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 cropped 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).

ACKNOWLEDGEMENTS

The authors acknowledge support for this work by the Australian Research Council Linkage Project and ARC Centre of Excellence for Translational Photosynthesis.

SOURCE OF FUNDING

This work was supported by the Australian Research Council Linkage Project 100100495 and ARC Centre of Excellence for Translational Photosynthesis, CE140100015.

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.

LITERATURE CITED

Birch CJ, Andrieu B, Fournier C. 2002. Dynamics of internode and stem elongation in three cultivars of maize. Agronomie 22:511–524.

Borrell AK, Mullet JE, George-Jaeggl B, van Oosterom EJ, Hammer GL, Klein PE, Jordan DR. 2014. Drought adaptation of stay-green cereals is associated with canopy development, leaf anatomy, root growth and water uptake. Journal of Experimental Botany 65:6261–6263.

Bunce J. 2010. Leaf transpiration efficiency of some drought-resistant maize lines. Crop Science 50:1409–1413.

Chapman SC, Cooper M, Hammer GL. 2002. Using crop simulation to generate genotype by environment interaction effects for sorghum in water-limited environments. Australian Journal of Agricultural Research 53:379–389.

Chenu K, Van Oosterom EJ, McLean G, Deifel KS, Fletcher A, Geetika G, Tirfessa A, Mace ES, Jordan DR, Sulman R, Hammer GL. 2018. Integrating modelling and phenotyping approaches to identify and screen complex traits: transpiration efficiency in cereals. Journal of Experimental Botany 69:3181–3194.

Choudhary S, Guha A, Kholova J, Pandravada A, Messina CD, Cooper M, Vadez V. 2020. Maize, sorghum, and pearl millet have highly contrasting species strategies to adapt to water stress and climate change-like conditions. Plant Science 295:110297.

Cooper M, Messina CD, Podlich D, Totir LR, Baumgarten A, Hausmann NJ, Wright D, Graham G. 2014. Predicting the future of plant breeding: complementing empirical evaluation with genetic prediction. Crop and Pasture Science 65:311–336.

Cooper M, Tang T, Gho C, Hart T, Hammer G, Messina C. 2020. Integrating genetic gain and gap analysis to predict improvements in crop productivity. Crop Science 60:582–604.

Farré I, Faci JM. 2006. Comparative response of maize (Zea mays L.) and sorghum (Sorghum bicolor L. Moench) to deficit irrigation in a Mediterranean environment. Agricultural Water Management 83:135–143.

Geetika G, van Oosterom EJ, George-Jaeggl B, Mortlock MY, Deifel KS, McLean G, Hammer GL. 2019. Genotypic variation in whole-plant transpiration efficiency in sorghum only partly aligns with variation in stomatal conductance. Functional Plant Biology 46:1072–1089.

George-Jaeggl B, Jordan DR, van Oosterom EJ, Broad IJ, Hammer GL. 2013. Sorghum dwarfing genes can affect radiation capture and radiation use efficiency. Field Crops Research 149:283–290.

Hammer G. 2006. Pathways to prosperity: breaking the yield barrier in sorghum. Agricultural Science 19:16–21.

Hammer GL, Dong Z, McLean G, Doherty A, Messina C, Schussler J, Zinselmeier C, Paszkiewicz S, Cooper M. 2009. Can changes in
canopy and/or root system architecture explain historical maize yield trends in the U.S. corn belt? Crop Science 49: 299–312.

Hammer G, Farquhar G, Broad I. 1997. On the extent of genetic variation for transpiration efficiency in sorghum. Australian Journal of Agriculture Research 48: 649–655.

Hammer GL, McLean G, Chapman S, Zheng B, Doherty A, Harrison MT, van Oosterom E, Jordan D. 2014. Crop design for specific adaptation in variable dryland production environments. Crop and Pasture Science 65: 614–626.

Hammer GL, van Oosterom E, McLean G, Chapman SC, Broad I, Harland P, Muchow RC. 2010. Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops. Journal of Experimental Botany 61: 2185–2202.

Henderson S, von Caemmerer S, Farquhar GD, Wade L, Hammer G. 1998. Correlation between carbon isotope discrimination and transpiration efficiency in lines of C4 species Sorghum bicolor in the glasshouse and the field. Australian Journal of Plant Physiology 25: 111–123.

Holzworth DP, Huth NI, deVoil PG, Zurcher EJ, Herrmann NI, Doherty A, Moore AD, Brown H, Whish JPM, Verrall S, Fainges J, Bell LW, Peake AS, Poulton PL, Hochman Z, Thorburn PJ, Gaydon DS, Dalglish NP, Rodriguez D, Cox H, Chapman S, Teixeira E, Sharp J, Chictoa R, Vogeler I, Li FY, Wang E, Hammer GL, Robertson MJ, Dimes J, Whitbread AM, Hunt J, van Rees H, McClelland T, Carberry PS, Hargreaves JNG, MacLeod N, McDonald C, Harsdorf J, Wedgwood S, Keating BA. 2014. APSIM - evolution towards a new generation of agricultural systems simulation. Environmental Modelling and Software 62: 327–350.

Jeffrey S, Carter J. 2001. Using spatial interpolation to construct a comprehensive archive of Australian climatic data. Environmental Modelling and Software 16: 309–330.

Jobson EM, Johnston RE, Oiestad AJ, Martin JM, Giroux MJ. 2019. The impact of the wheat Rht-B1b semi-dwarfing allele on photosynthesis and seed development under field conditions. Frontiers in Plant Science 10: 51.

Kakani VG, Vu JC, Allen LH Jr, Boote KJ. 2011. Leaf photosynthesis and carbohydrate fluxes of CO2-enriched maize and grain sorghum exposed to a short period of soil water deficit during vegetative development. Journal of Plant Physiology 168: 2169–2176.

Kulathunga L. 2013. Role of transpiration efficiency and dry matter partitioning in drought adaptation of 2dwarf and 3dwarf sorghum. MPhil thesis, The University of Queensland, Australia, 77 pp.

Lafarge T, de Raissac M, Tardieu F. 1998. Elongation rate of sorghum. Australian Journal of Experimental Botany 47: 72–78.

Lobell DB, Roberts MJ, Schlenker W, Braun N, Little BB, Rejesus RM, Hammer GL. 2014. Greater sensitivity to drought accompanies maize yield increase in the U.S. Midwest. Science 344: 516–519.

McCaig TN, Morgan JA. 1993. Root and shoot dry matter partitioning in near-isogenic wheat lines differing in height. Canadian Journal of Plant Science 73: 679–689.

Messina CA, Sinclair TR, Hammer GL, Curan D, Thompson J, Oler Z, Gho C, Cooper M. 2015. Limited-transpiration trait may increase maize drought tolerance in the US corn belt. Agronomy Journal 107: 1978–1986.

Mirasdel DJ, Slafra GA. 1997. Radiation interception and radiation use efficiency of near-isogenic wheat lines with different height. Euphytica 97: 201–208.

Mirasdel DJ, Slafra GA, Lynch V. 1997. Rooting patterns in near-isogenic lines of spring wheat for dwarfism. Plant and Soil 197: 79–86.

Muchow RC. 1989a. Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical environment I. Yield potential. Field Crops Research 20: 191–205.

 Muchow RC. 1989b. Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical environment II. Effects of water deficits. Field Crops Research 20: 207–219.

Muchow RC, Carberry PS. 1990. Phenology and leaf area development in a tropical grain sorghum. Field Crops Research 23: 221–237.

Muchow RC, Sinclair TR. 1994. Nitrogen response of leaf photosynthesis and canopy radiation use efficiency in field-grown maize and sorghum. Crop Science 34: 721–727.

Parra G, Borrás L, Gambin BL. 2020. Maize long-term genetic progress explains current dominance over sorghum in Argentina. European Journal of Agronomy 119. Art. No: 126122.

Probert ME, Keating BA, Thornpom JP, Parton WJ. 1995. Modelling water, nitrogen, and crop yield for a long-term fallow management experiment. Australian Journal of Experimental Agriculture 35: 941–950.

SAS. 2013. Base SAS® 9.4 procedures guide: statistical procedures. Cary, NC: SAS Institute Inc.

Sinclair TR, Hammer GL, van Oosterom EJ. 2005. Potential yield and water-use efficiency benefits in sorghum from limited maximum transpiration rate. Functional Plant Biology 32: 945–952.

Sinclair TR, Muchow RC. 1999. Radiation use efficiency. Advances in Agronomy 65: 215–265.

Soufizadeh S, Munaro E, Massignam A, van Oosterom EJ, Chapman SC, Messina C, Cooper M, Hammer GL. 2018. Modelling the nitrogen dynamics of maize crops – enhancing the APSIM maize model. European Journal of Agronomy 100: 118–131.

Tanner CB, Sinclair TR. 1983. Efficient water use in crop production: research or re-search? In: Taylor HM, Jordan WR, Sinclair TR, eds. limitations to efficient water use in crop production. Madison, WI: American Society of Agronomy, 1–27.

Turner NC. 2004. Agronomic options for improving rainfall-use efficiency of crops in dryland farming systems. Journal of Experimental Botany 55: 2413–2425.

van Oosterom EJ, Borrell AK, Deifel KS, Hammer GL. 2011. Does increased leaf appearance rate enhance adaptation to post-anthesis drought stress in sorghum. Crop Science 51: 2728–2740.

van Oosterom EJ, Hammer GL. 2008. Determination of grain number in sorghum. Field Crops Research 108: 259–268.

Vega CRC, Andrade FH, Sadras VO, Uhart SA, Valentinuz OR. 2001. Seed number as a function of growth. A comparative study in soybean, sunflower, and maize. Crop Science 41: 748–754.
Wang N, Gao J, Zhang S. 2017. Overcompensation or limitation to photosynthesis and root hydraulic conductance altered by rehydration in seedlings of sorghum and maize. *The Crop Journal* **5**:337–344.

Wong SC, Cowan IR, Farquhar GD. 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**:424–426.

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

Yang Z, Hammer G, van Oosterom E, Rochas D, Deifel K. 2010. Effects of pot size on growth of maize and sorghum plants. In: George-Jaeggli B, Jordan DJ, eds. 1st Australian Summer Grains Conference, Gold Coast, Australia, 21–24 June 2010. Grains Research and Development Corporation. https://web.archive.org.au/awa/20120320190900mp_/http://grdc.com.au/uploads/documents/2010ASGCEditedPapersPDF/Yang_PotSize_edited_paper.pdf. Accessed 2 February 2021.