



Bigger is not always better: Reducing leaf area helps stay-green sorghum use soil water more slowly



Barbara George-Jaeggli^{a,c,*}, Miranda Yolanda Mortlock^b, Andrew Kenneth Borrell^c

^a Agri-Science Queensland, Department of Agriculture and Fisheries, Hermitage Research Facility, 604 Yangan Road, Warwick, Qld 4370, Australia

^b School of Agriculture and Food Sciences, The University of Queensland, Hartley Teakle Building 83, St Lucia, Qld 4072, Australia

^c Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, Hermitage Research Facility, 604 Yangan Road, Warwick, Qld 4370, Australia

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ABSTRACT

Stay-green, a trait that confers delayed leaf senescence and improved grain yield under post-anthesis drought, has been associated with smaller canopies at flowering and increased water uptake during the post-flowering period. It has been shown that the main stay-green quantitative trait loci reduce leaf area via reduced tiller number and smaller leaves. To show that these canopy characteristics are directly linked to water savings, we grew near-isogenic lines with and without stay-green introgressions in large lysimeter pots and measured their weekly pre-anthesis water use and main-stem and tiller leaf area. Paradoxically, age-related senescence of lower leaves in stay-green lines was accelerated before flowering, contributing to their smaller leaf area at flowering. This process of reducing leaf area by shedding old leaves lower in the canopy, has not previously been described for the stay-green introgressions. We found that tiller leaf area rather than transpiration efficiency, or transpiration per leaf area, was the main driver of weekly transpiration and the reduced pre-flowering water use in stay-green lines. In soils with good water-holding capacity, any water savings during the pre-anthesis period increases water availability during the post-anthesis period, therefore allowing plants to retain photosynthetic capacity for longer by “staying green” during grain filling.

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1. Introduction

Sorghum is a grain crop that is well adapted to hot and dry climates. For this reason, it is the main summer crop of the rain-fed agricultural production systems of north-eastern Australia, where it is an important rotational crop supplying feed grain to the livestock industry (Starasts, 2012). Sorghum is also a staple crop for more than 500 million people in over 30 countries, with particular significance in sub-Saharan Africa and central-western India.

Rainfall is highly variable and sporadic in these areas. However, where soils have good water-holding capacities, the crops can survive on stored subsoil moisture. The combination of dry atmospheric conditions and high average temperatures leads to a

particularly large difference in vapour pressure between the saturated leaf cavities and the less than saturated atmosphere (Sadras and McDonald, 2012).

To capture CO₂ for photosynthesis, leaves must open their stomata, but inadvertently lose water via transpiration. The rate of water loss is proportional to the vapour pressure deficit (VPD) of the atmosphere (Bierhuizen and Slatyer, 1965). While VPD drives transpiration through the leaf to the atmosphere, it has little effect on CO₂ uptake. As a consequence, plants grown in hot and dry environments often transpire wastefully.

Water use may be restricted either through shorter leaf area duration (earlier maturity), smaller leaf area, or reduced transpiration rates per leaf area, which in turn is affected by stomatal conductance and hydraulic conductivity of leaves and roots (Brodribb, 2009; Sack et al., 2015).

Apart from reducing total water use, which limits growth, some plants may be more efficient at converting the transpired water into carbon (Tanner and Sinclair, 1983). At the crop level, this efficiency is generally termed water use efficiency (WUE) and is

* Corresponding author at: Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, Hermitage Research Facility, 604 Yangan Road, Warwick, Qld 4370, Australia.

E-mail addresses: b.georgejaeggli@uq.edu.au (B. George-Jaeggli), m.mortlock@uq.edu.au (M.Y. Mortlock), a.borrell@uq.edu.au (A.K. Borrell).

defined as biomass divided by water used by the crop. Depending on the definition, biomass can either mean total biomass (including roots), just shoot biomass, or even simply grain yield. Water used may include plant transpiration, soil evaporation, irrigation, rainfall and moisture stored in the soil (Mortlock, 2014; Passioura, 1996; Sadras and McDonald, 2012; Vadez et al., 2014).

The efficiency with which individual plants turn transpired water into biomass, on the other hand, is generally termed transpiration efficiency (TE). It is also the genetic component of WUE (Vadez et al., 2014), which is why it is of particular interest to plant breeders and physiologists.

A third way to adapt to water limitation is to optimise the temporal distribution of transpiration so that water use is shifted to periods that are particularly critical for the formation of grain yield, such as during grain filling. It may be more important to maximise harvest index, and ultimately grain yield, than overall WUE (Rebetzke and Richards, 1999; Sadras and Connor, 1991; Siddique et al., 1990). This is particularly effective on soils that have good water-holding capacity, and any mechanism that conserves stored subsoil moisture for use during grain filling, may be beneficial for yield.

According to a crop modelling study, about 70% of sorghum crops grown in the northern grain belt of Australia are predicted to experience either mild or severe drought stress during the grain-filling period (Chapman et al., 2000), but many of the soils in that region have reasonable water-holding capacity.

Stay-green (*Stg*) is a trait that has been associated with delayed leaf senescence, increased harvest index and improved grain yields of sorghum crops when water is limited towards the end of the growing season (Borrell et al., 2000a,b; Jordan et al., 2012). For this reason, it has been an important trait in the Australian sorghum breeding programme.

At least four major quantitative trait loci (*Stg1-4*) have been found which all individually induce delayed leaf-senescence (Harris et al., 2007). Field studies have shown that the *Stg* loci reduced the size of sorghum crop canopies at anthesis, mainly through reduced tillering and smaller upper leaves, which led to reduced water uptake during the pre-flowering period, and therefore increased water availability during the post-flowering period (Borrell et al., 2014a,b).

A similar association between leaf area at flowering, daily water use before flowering and grain yield was also observed in a recent study with soybean (He et al., 2017).

Most of these previous studies simply reported on the association between reduced canopy size at flowering and grain yield under post-flowering water limitation at the crop level, as it can be difficult to accurately measure the dynamic link between leaf area and plant transpiration excluding soil evaporation. In this study, we used single plants in large sealed pots (50L) to measure weekly water use via lysimetry (Mortlock, 2014). We used near-isogenic lines with four different stay-green QTL introgressed into RTx7000 (which is a highly senescent line) and RTx7000 as a control to examine the effects of the stay-green QTL on these dynamics. We were able to show a close link between increasing plant leaf area, and weekly water uptake during the pre-anthesis period. Plant green leaf area, in particular tiller green leaf area, and not TE or transpiration per leaf area, was the main driver of pre-anthesis water use. Paradoxically, we also discovered that age-related senescence of leaves before flowering was accelerated in lines with a stay-green introgression. Together, with the previously known mechanisms of smaller upper leaves and reduced tiller leaf area (Borrell et al., 2014a,b), this may contribute to the smaller canopy at flowering of stay-green lines.

2. Materials and methods

2.1. Treatments and experiment design

Two experiments in consecutive years were conducted to study the effects of stay-green introgressions on dynamics of leaf area and water use of sorghum lines. Near-isogenic lines with individual introgressions covering the four main stay-green quantitative trait loci (*Stg1-4* QTL) in a senescent background (RTx7000) and the senescent control (RTx7000) (Table 1) were grown in minilysimeters to measure transpiration (T), transpiration efficiency (TE), and canopy-related traits of each genotype. One genotype was grown per minilysimeter.

2.2. Experimental details

Two lysimeter experiments were conducted at Hermitage Research Facility (28°12' S, 152°06' E; 480 m above sea level) in south-east Queensland, Australia, during two consecutive summer seasons. Single plants were grown in mini-lysimeters (50-L pots) to determine water use (T), biomass, and TE. Exp1 was planted on 25 February 2006 and harvested on 24 May 2006 when plants had reached anthesis. Exp2 was planted on 22 February 2007 and harvested on 20 April 2007, as soon as all the plants had fully expanded flag leaves on the main stem.

The mini-lysimeters were arranged in three rows within two ventilated, plastic-covered growth tunnels. Rows were two metres and the pot centres one metre apart from each other, so the plants were basically grown in single plant stands. In Exp1, three replicates were grown in one growth tunnel and four replicates in the other growth tunnel; in Exp2, two replicates were grown in each growth tunnel. Both tunnels were orientated north-south and far enough apart from each other not to cause any shading. Front and sides of the growth tunnel were covered with white knitted shade cloth to allow air flow, while the top was covered with white solar weave (both materials Gale Pacific Pty Ltd, Melbourne, Australia). The solar weave excluded rainfall and transmitted approximately 70% of the incident solar radiation. The lysimeter pots were made from cylindrical PVC tubes, 300 mm diameter and 750 mm high, which were filled with a 3:1:1 mix of alluvial clay soil, loam and feedlot manure. Each plant was fertilised with 30 g of Osmocote Plus (16% N, 3.5% P, 10% K plus trace elements; Scotts Pty Ltd, Baulkham Hills, Australia).

Temperature and humidity sensors (Tinytag, Gemini Data Loggers Ltd, Chichester, UK) were installed inside each growth tunnel, and hourly and daily maximum and minimum temperatures and relative humidity were recorded. Maximum daily vapour pressure deficits for each growth tunnel were determined from the hourly temperature and humidity records (Rosenberg et al., 1983).

2.3. Water use measurements

The pots were fully saturated with water and drained to field capacity before the basal drainage hole was sealed. One plant per

Table 1
Genotypes grown in lysimeter experiments.

Genotype	Stg QTL	Description
RTx7000	RTx7000	Senescent hybrid
NIL 6078-1	<i>Stg1</i>	Entire <i>Stg1</i> QTL
NIL 2219-3	<i>Stg2</i>	Entire <i>Stg2</i> QTL
NIL 2290-19	<i>Stg3</i>	Entire <i>Stg3</i> QTL
NIL 6085-9	<i>Stg4</i>	Entire <i>Stg4</i> QTL

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