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The sowing date and post-flowering water status affect the sugar and grain production of photoperiodic, sweet sorghum through the regulation of sink size and leaf area dynamics

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ABSTRACT

The combined production of grain and sugar by sorghum requires efficient leaf C acquisition (source) and allocation to productive sinks, namely the stem and the panicle. Photoperiod sensitivity, which regulates plant phenology and growth, is also likely to be a key regulator of such C source-sink relationships, while it is crucial to drought adaptation. This study set out to evaluate the contribution of plant leaf area and stem growth to the production of grain and sugar by sweet, photoperiodic sorghum depending on the sowing date and post-flowering water availability. Twelve West African accessions were studied in the field in Senegal during two consecutive rainy seasons, comparing two sowing dates and post-anthesis water regimes (irrigated, or not). Plant growth and development were monitored weekly up to flowering. Organ size and biomass, stem juiciness and sweetness were characterized at flowering and maturity. At flowering, early sowing enhanced plant leaf area, stem dry weight and sugar production, and plant leaf area expressed per unit of stem dry weight was positively correlated to stem sweetness, suggesting that a high pre-flowering source-to-sink ratio favors early sugar accumulation. Overall, a late sowing date reduced sugar and grain production more than post-anthesis drought, whereas early sowing enhanced both types of production. No post-anthesis competition was found between grain filling and stem sugar accumulation. However, under drought conditions, the maintenance of combined production was better for the most leaf stay-green accessions. It is suggested that the combined production of sugar and grain by sweet, photoperiodic sorghum in response to the sowing date and post-anthesis drought is firstly sink-driven but that source (plant leaf area) dynamics can enhance stem sugar accumulation and its maintenance under drought conditions. These results provide further insight into the traits to be combined in dual-purpose ideotypes dedicated to drought-prone environments.

1. Introduction

Sorghum is an important cereal crop in dryland areas of West Africa, used as a staple crop and for animal feed (Belton and Taylor, 2004). Its photoperiod (PP) sensitivity makes it adaptable to various environments in the region (Sanon et al., 2014). Sorghum is gaining increasing importance due to its combined production (grain, stem biomass and/or sweet juice) and resulting multipurpose suitability for industrial end-uses, including bio-ethanol, bio-products, brewing and livestock (Prakasham et al., 2014).

Improving sorghum for combined production of grain and sugar for West African drought-prone conditions requires that key yield components be identified, along with adaptive traits and the relationships between them. Maximizing or optimizing the combined production of grain and sugar may indeed mean associating (i) efficient acquisition of the C resource throughout the crop cycle, based on plant leaf area expansion, leaf photosynthetic efficiency and its maintenance thanks to post-flowering stay-green (Borrell et al., 2000b; Khanna-Chopra, 1982; Okiyo et al., 2010), (ii) efficient activity and sizing of the productive sinks, namely panicle size and filling, sugar reservoir, as defined by stem dry weight, juiciness and sweetness (Massacci et al., 1996).

Sugar accumulation in the sorghum stem is determined at internode level. An individual internode starts accumulating

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sucrose once its expansion is accomplished, with a variable rate depending on the genotype and the environment (Gutjahr et al., 2013a). In this respect, sugar accumulation in the sorghum stem depends on plant phenology which determines (i) the number of internodes expanded before flowering, i.e. the reservoir available for accumulating sugar and (ii) the time available to fill this reservoir. Accordingly, stem sugar production can already reach a plateau at anthesis in the case of long cycle, photoperiod-sensitive genotypes when sown early and under non-limiting conditions (Gutjahr et al., 2013b). In the case of genotypes with shorter cycles and/or depending on cropping conditions, stem sugar accumulation may however mainly occur between anthesis and physiological maturity (Tovignan et al., 2015; Zhao et al., 2009).

By impacting internode expansion, leaf senescence and C assimilation, drought can negatively impact sugar accumulation and production to a variable extent depending on its timing during the plant cycle (Almodares et al., 2013). In a situation where stem sugar accumulation mainly occurs after flowering, it can be expected that a post-flowering drought will severely impact sugar production, due to greater competition for C resources between sugar storage in the stem and grain filling.

Some agronomic solutions have been suggested to minimize the risk of post-flowering drought, by decreasing water demand before anthesis through planting density (van Oosterom et al., 2011) or maximizing sugar and juice accumulation by varying nitrogen supply (Holou and Stevens, 2012). Nevertheless, the risk of post-flowering drought in West African cropping systems is huge and challenging to meet future expectations in terms of the combined production of sugar and grain due to limited access to irrigation and fertilization (Comas et al., 2012).

In this agronomic context, breeders are expected to provide sorghum genotypes with high accumulation of sweet juice in the stem up to flowering and a good maintenance of green leaf area after anthesis (i.e. stay-green ability). The latter should ensure C assimilation during grain filling while maintaining or even increasing stem sweetness and juiciness (Borrell et al., 2000a). However while stay-green has been extensively studied with respect to its involvement in ensuring grain production (Borrell, 2014; Thomas and Howarth, 2000; Tolk et al., 2013) or sugar production (Harris et al., 2007; Kassahun et al., 2010), it has been poorly addressed in the case of sweet, PP-sensitive sorghum intended for dual purpose. As regards grain sorghum, Blum et al. (1997) reported that a large amount of stem carbohydrate was remobilized from the stem for grain filling when the photosynthetic source was affected by drought. This remobilization process under post-flowering drought conditions was confirmed by Beheshti and Behboodi (2010) who reported, in addition, that ultimate grain yield remained reduced by drought when compared to well-watered conditions. These authors suggested, however, that carbohydrate remobilization ability was a key trait for improving sorghum grain yield in drought-prone environments. Kouressy et al. (2008) suggested, in the case of West African accessions, that stay-green was not sufficient to ensure grain filling under post-anthesis drought conditions because grain yield is more sink- than source-limited in such genetic material and that, accordingly, competition with carbohydrate storage in the stem is low. By contrast Borrell et al. (2000b) suggested that, under post-anthesis drought conditions, stay-green ability in hybrids was positively correlated not only to better grain yield but also to higher stem biomass accumulation after anthesis when compared to hybrids with higher leaf senescence after flowering.

Our study set out to analyze the contribution of green leaf area dynamics and stem morphology to the combined production of sugar and grain by sweet, PP sorghum, depending on the sowing date and post-flowering water availability. To that end, twelve African sorghum landraces and sweet reference cultivars with different levels of photoperiod sensitivity and stay-green ability were studied with two sowing dates and post-flowering water treatments in the field in Senegal, in two consecutive years. The results are discussed with respect to the identification of morphological or developmental traits optimizing stem sugar production in a context of sweet, dual purpose sorghum for West Africa.

2. Materials and methods

2.1. Plant material

The twelve African sweet sorghums studied are listed in Table 1. This panel was selected from 143 cultivars tested in preliminary trials in the 2012 rainy season according to the following criteria (partially presented by Tovignan et al. (2015)). The cultivars were selected for a similar phenology in order to synchronize flowering time with the end of the rainy season and facilitate the study of a post-anthesis drought effect. However, they slightly differed in their PP sensitivity (moderate to high). They were also chosen for their good stem sugar production, while having a contrasting morphology (in terms of internode number and size).

2.2. Weather conditions, experimental design and management

This study was conducted in the rainy seasons of 2013 and 2014 between July and December at the CNRA research station in Bambey, Senegal (14°42′N, 16°28′W; 20 m above sea level). The climate in that area is Sudan-Sahelian with a short rainy season extending from mid-June to mid-October with monomodal rainfall distribution peaking in August. The cumulative rainfall recorded in 2013 was 668 mm, as opposed to 374 mm in 2014, due to a later and weaker rainy season. The rainfall, mean temperature, average relative humidity and global radiation distribution for the two years are given in Fig. 1 and translated into cumulated thermal time, radiation and water supply in Fig. S1.

In 2013, the soil in the field trial was sandy (86.3%) with low clay (10.2%), low loam (2.6%), low organic matter (0.49%) and low nitrogen (0.30‰) with a slightly alkaline pH (7.8). The experimental site was changed in 2014, but the soil characteristics of the two years were very similar. The soil in 2014 was sandy (88.1%) with low clay (7%), low loam (2.33%), low organic matter (0.61%) and low nitrogen (0.35‰) with a slightly alkaline pH (7.38). A split-split-plot design with three replicates was used to study three factors: post-anthesis water regime (2), sowing date (2) and accession (12). Two sowing dates were used. In 2013, the two sowing dates (S) were separated by almost a month (S1: July 17 and S2: August 12) while in 2014, due to the lateness of the rainy season, there were only fifteen days between sowing dates (S1: August 6 and S2: August 21).

Each unit plot comprised three rows 4.4 m in length each, 0.8 m apart, with a distance of 0.4 m between hills in the row. A space of 1.5 m was left between adjacent plots. Stressed and control treatments were separated by 15 m to prevent undesirable water transfers during the post-anthesis drought stress study. Around 15 days after emergence, the plots were thinned to three plants per hill. Fertilization consisted of an application of 150 kg ha^{-1} of NPK (15-10-10) after sowing. After thinning, 50 kg ha^{-1} of urea was applied and the same amount was provided during vegetative growth. Weeds were manually removed every two weeks after sowing. The drought (D) study started in mid-October with the end of the rainy season and anthesis. Before anthesis, the entire field was irrigated with 25 mm per week when the dry spell lasted a week. After anthesis, stressed plots (NI) were allowed to dry down and the controls (IR) were irrigated with 25 mm per week.

Soil water content was determined using a Diviner 2000 (Sentek Pty. Ltd., Adelaide, SA) from flowering to physiological maturity. Six