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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

Table 1
Characteristics of the studied accessions.

N°	Name	Origin	Race	Photoperiod-sensitivity	Plant height	Cycle duration
SS1	FELLAH ROUGE 2	SN	D	High	Tall	Medium
SS2	SARAKOLE M'BILOR	SN	D	Moderate	Tall	Medium
SS3	FELLAH	SN	D	High	Tall	Medium
SS4	SEVIL YOUDOWA	SN	DB	High	Tall	Medium
SS5	NIENIKO	SN	G	High	Tall	Late
SS6	BASSI TIN	SN	G	High	Tall	Late
SS7	BF95-11/110	BF	B	Moderate	Tall	Medium
SS8	SARIASO 10	BF	GC	Moderate	Moderate	Medium
SS9	TENEYA	MLI	CB	High	Tall	Late
SS10	GRD 1045 (IS23536)	ETH	C	High	Tall	Medium
SS11	F221	MLI	B	High	Tall	Late
SS12	E36-1	ETH	C	Moderate	Short	Medium

Plant height: short: <2 m; moderate: from 2 to 3 m; tall: >3 m. Photoperiod-sensitivity: moderate: Kp from 0.4 to 0.6; high: Kp from 0.6 to 1. Kp is photoperiodism coefficient. Cycle duration: Medium: from 70 to 110 days; Late >110 days. Race: B: Bicolor, C: Caudatum, D: Durra, G: Guinea, DB: Durra-Bicolor, CB: Caudatum-Bicolor, GC: Guinea-Caudatum. Origin: BF: Burkina-Faso, SN: Senegal, ETH: Ethiopia, MLI: Mali.

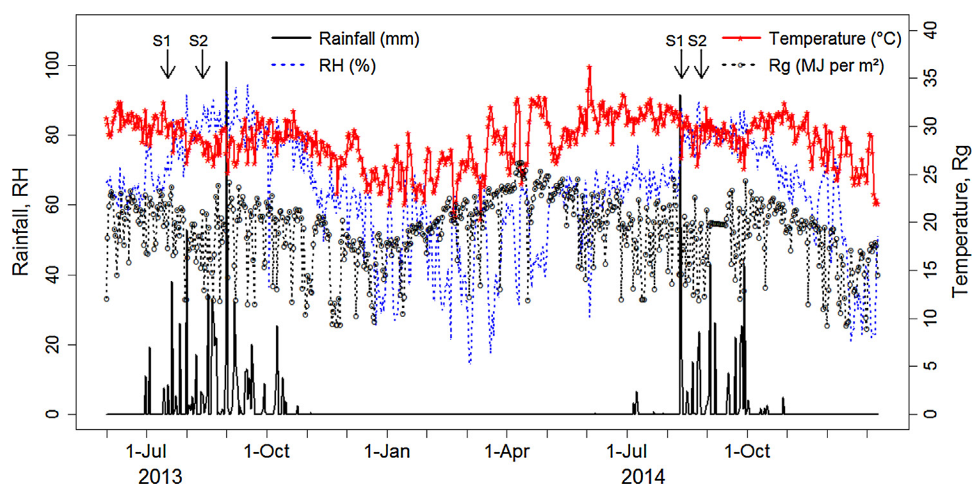

Fig. 1. Daily weather conditions at Bambey station from June 1st, 2013 to December 31st, 2014. Average temperature, average relative humidity (RH), global radiation (Rg) and daily rainfall. S1 and S2 represent the first and second sowing dates respectively for 2013 and 2014 rainy seasons.

Diviner tubes were randomly positioned in the central inter-row of six plots (one tube per plot) of the NI treatment, considering the two sowing dates and the three replicates of two reference accessions: one of the tallest (SS6) and one of the shortest (SS8) accessions, expected to consume soil water differently. Only 2 Diviner tubes were randomly positioned in the IR treatment (one in SS6 plot and one in SS8 plot). Accordingly, soil water content was measured weekly every ten cm on a rooting profile 160 cm from the soil surface. As already mentioned, soil characteristics were similar in 2013 and 2014 and it can be assumed that they had a similar wilting point and field capacity. However, as no reliable data could be obtained for the latter, diviner measurements were used only to compare treatments, accessions and years in terms of mm of water available per m of soil in 160 cm of the rooting depth (Fig. 2A and B). In 2014, this was supported by measurements of the predawn leaf water potential using a Scholander pressure chamber, on a plant randomly chosen in the central row of the same plots in both the NI and IR treatments (Fig. 2C and D). This methodological choice did not provide a quantification of the drought level for each accession but an indication of its variability between accessions and years.

Daily minimum and maximum temperatures were used in each year to compute the average daily air temperature (Ta) and, using a base temperature (Tb) considered as 10 °C (Sanon et al., 2014), to compute the thermal time (TT, °Cd, Fig. S1) cumulated since emergence (by cumulating the daily difference between Ta and Tb).

2.3. Data collection

2.3.1. Plant phenology, morphology and leaf area estimation

In each plot, four plants in the central row were tagged at thinning for dynamic characterization of plant development and morphology. Tillers were counted weekly, but as tillering was low no more tillers were alive at the end of the vegetative phase and the plants could be considered as mono-culms. Once a week, appeared, ligulated and green (GLN) leaves were counted on the main stem. It was thus possible to compute the leaf appearance rate or development rate (DR, °Cd) up to flag leaf rank. DR was computed as the slope(s) of the (bi)linear regression between cumulated thermal time and the appeared leaf number, for each plot considering the data of the 4 plants together (see example in Fig. S2). For this purpose, piecewise regression was applied using the "segmented" package in R (Muggeo, 2008) to detect the breakpoint at which the development rate changed. However, as a breakpoint was not systematically detected, only early DR was addressed and thereafter called DR.

Plant height was measured weekly from the soil surface to the ligule of the last ligulated leaf. The size of the last ligulated leaf (blade length and width) was also measured weekly. Individual leaf blade area was estimated as the product of blade length, width and an allometric factor of 0.69 (Kim et al., 2010). The frequency of measurements made it possible to measure the area of almost all leaves on the main stem and a polynomial regression was established

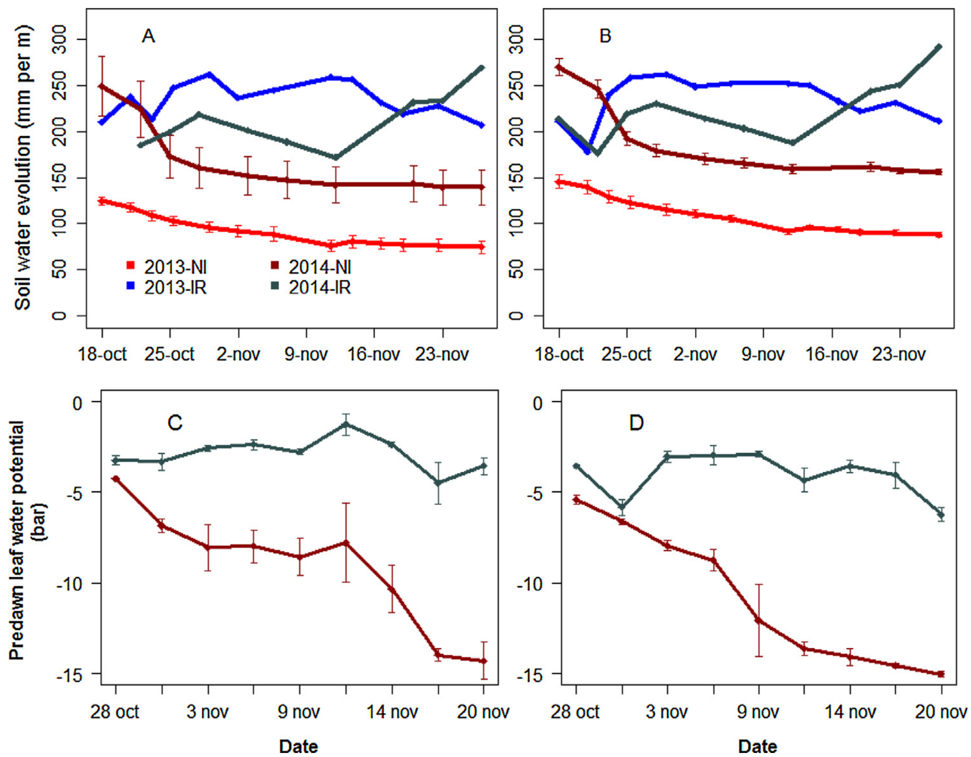

Fig. 2. Post-anthesis soil water content in each water treatment (NI: non irrigated, IR: irrigated) in 2013 and 2014 for the reference accessions SS6 (A) and SS8 (B); predawn leaf water potential measured during post-anthesis drought in 2014 for SS6 (C) and SS8 (D). Presented data are average value with standard error.

between leaf rank and area and the area of missing leaves could be estimated (**Fig. S3**). This choice was supported by the shape of the per-leaf area profile reported by previous authors on sorghum (Kim et al., 2010; Lafarge et al., 2002). The total plant leaf area (PLA) could then be estimated as the sum of the area of green leaves at a given stage.

Phenological stages, such as flag leaf ligulation, anthesis (FLO) and grain physiological maturity (MAT), were noted when 50% of the plants in the plot had reached the given stage.

2.3.2. Biomass, stem sugar content and stem morphology

At FLO and MAT, three plants per plot were selected to measure leaf, stem and panicle fresh weight and dry weight. They were sun dried and then left in an oven at 70 °C for 48 h for the dry weight. Fresh stems were weighed then crushed to measure the extracted juice weight of the three plants, as described in Tovignan et al. (2015). Stems were then dried similarly to the other organs to obtain their dry weight (SDW). Stem fresh (SFW) and dry weights were used to compute stem humidity (% of stem fresh weight). Brix was measured using a refractometer (Erickson et al., 2012) on a drop of extracted juice. Sugar content (SCT in g) and sugar concentration (SCC in mg g^{-1} DW) were calculated by the equations used in Gutjahr et al. (2013b):

$$SCT = \frac{Brix \times 8.827 \times (SFW - SDW)}{1000} \quad (1)$$

where 8.827 is the slope of the regression line between Brix and sugar concentration in g L^{-1}.

$$SCC = \frac{SCT}{SDW} \times 1000 \quad (2)$$

At anthesis, stem diameter was measured at a median position on the stem. The number of expanded internodes on the stem (IN) was counted and the average internode length (INL) estimated by dividing the plant height measured at the base of the peduncle.

2.3.3. Estimation of variation between anthesis and maturity

The variation in sugar accumulation, grain filling and green leaf area (i.e. stay-green) between anthesis and maturity was computed for each accession and treatment as follows:

$$VarX = ((X_{maturity} - X_{anthesis})/X_{anthesis}) \times 100 \quad (3)$$

where X is the considered variable measured at anthesis or maturity.

2.4. Data analysis

The variance analysis was performed firstly year by year. For variables measured from sowing up to anthesis, the sowing date (S), accession (A), replicate (R) and their interactions were tested. In this respect, the experimental design was a split plot resulting in 24 treatment combinations with six replicates. The sowing date was the main plot and the accession the subplot. The drought (D) stress study was initiated only from anthesis and consequently the experimental design became a split-split-plot with three replicates. Forty-eight treatment combinations were generated and the water regime was considered as the main plot, the sowing date as the subplot and the accession as the sub-subplot. The data for the two years were combined to test the year effect. The year was considered as the main plot, the water regime as the subplot, the sowing date as the sub-subplot and the accession as the sub-sub-subplot.

Pearson correlations were estimated between variables measured separately up to anthesis and at maturity.

All the analyses were performed using R v 3.02 (http://www.R-project.org/; R Core Team, 2013).

The scatterplots showing accession performance for sugar and grain production across sowing dates, water treatments and years were performed using SigmaPlot 12® (Systat Software Inc., San Jose, CA, USA).

Table 2
Accession (A), sowing date (S), SxA, replicate (R), year effects and average values per sowing date for phenological, morphological and stem sugar related traits at anthesis in 2013 and 2014 trials. S1: July 17 and August 6 and S2: August 12 and August 21, respectively in 2013 and 2014. DR: Development Rate (°C d^{-1}), PLA: Plant green Leaf Area (cm^2), IN: internode number, INL: Internode average length (cm), SDW: Stem Dry Weight (g), SCT: Stem sugar content (g), SCC: Stem sugar concentration (mg g^{-1} DW).

	2013						2014						Year
	Mean		Anova				Mean		Anova				
	S1	S2	S	A	SxA	R	S1	S2	S	A	SxA	R	
Phenology													
Vegetative phase duration (d)	75	57	***	***	***	ns	68	58	***	***	**	*	***
DR (°C d^{-1})	0.023	0.020	***	***	***	ns	0.022	0.028	***	*	ns	ns	***
Morphology													
Flag leaf rank	25	20	***	***	***	ns	23	20	***	***	**	*	***
Flag leaf area (cm^2)	233	177	***	***	***	*	193	189	ns	***	***	ns	***
Green leaf number	10.0	7.8	***	**	**	ns	10.3	9.5	***	ns	ns	ns	***
PLA (cm^2)	4365	2826	***	***	***	ns	3616	3497	ns	***	*	ns	ns
Plant height (cm)	352	300	***	***	ns	*	225	203	**	***	ns	**	***
Stem diameter (mm)	17.2	15.4	***	***	ns	ns	15.4	14.6	ns	***	ns	ns	***
IN	15	12	***	***	***	***	12	11	***	**	ns	*	***
INL (cm)	19	18	ns	***	ns	ns	15	14	ns	***	ns	ns	***
SDW (g)	114	72	***	***	***	ns	64	57	*	***	ns	ns	***
Sugar production													
Brix (%)	12	10	***	***	ns	ns	13	12	ns	**	ns	ns	***
Stem humidity (%)	77	71	***	***	ns	ns	77	76	ns	***	***	ns	***
SCT (g)	32	21	***	***	***	ns	25	20	***	***	***	*	*
SCC (mg g^{-1} DW)	273	296	***	***	ns	*	400	343	***	***	***	ns	***

ns: $P > 0.05$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

3. Results

3.1. Weather conditions

Fig. 1 shows that photo-thermal conditions were similar in the 2013 and 2014 trials, resulting in similar cumulated thermal time and radiation when expressed in days after sowing (Fig. S1). Fig. 2A and B indicates that the soil water content from the surface to a depth of 160 cm in the non-irrigated treatment in 2013 was lower compared to 2014, and that in 2014 the two water treatments were less contrasting than in 2013. Nevertheless, the water supply was lower in 2014, due to lower rainfall and slightly reduced irrigation (because of technical problems) compared to 2013 (Fig. S1). The variation in soil water content between the two reference accessions in the non-irrigated treatment was significant ($P < 0.001$) for both years. Fig. 2C and D shows that in 2014 the predawn leaf water potential decreased gradually from dry down onset at anthesis until maturity and reached around −15 bar during the dough grain stage, i.e. severe plant water stress for both accessions.

3.2. Sowing date effect on plant growth, development and sugar production up to anthesis

The sowing date (S), accession (A), AxS interactions and year effects were tested on variables studied up to anthesis and are presented in Table 2. Replicate effects (R) were rarely significant (Table 2). Almost all the studied variables were influenced by the year. In both years, the duration of the vegetative phase was lengthened by early sowing (S1). S1 extended the vegetative phase by 18 and 10 days on average in 2013 and 2014, respectively, compared to S2. The number of organs produced by the plants was also significantly influenced by sowing. In 2013, the accessions produced 5 more leaves and 3 more internodes on average and in 2014, 3 more leaves and 1 more internode in S1 compared to S2 respectively (cf. flag leaf rank and internode number in Table 2). The green leaf number (GLN), flag leaf area and plant leaf area (PLA) were also enhanced by early sowing, but this was significant in 2013 only. The median stem diameter was also enhanced by early sowing, but to a minor extent, while the average internode length (INL) was not (Table 2). In both years, plant height and stem dry weight (SDW) at anthesis were increased by early sowing (S1), which was again more pronounced in 2013 compared to 2014. Traits related to stem sugar production (Brix, stem humidity, sugar content (SCT), and sugar concentration (SCC)) were all enhanced by early sowing (albeit not significantly affected in 2014 for Brix and stem humidity). All traits related to plant growth, development and sugar production displayed an accession effect. The effect of sowing date × accession interaction was significant for almost all of the traits in 2013, except plant height, internode size (diameter, length) and traits related to sugar concentration (Brix, stem humidity, SCC). In 2014, this interaction was significant for the duration of the vegetative phase, flag leaf rank and area, plant leaf area, stem humidity, sugar content and sugar concentration.

Correlations between growth, development and sweetness-related traits at anthesis are presented in Table 3 for 2013 and Table S1 for 2014. Correlations were in general stronger in 2013. In both years, the plant leaf area was mainly explained by the duration of the vegetative phase and thus by the green leaf number. The main difference between years was the relationship between the development rate and these variables, which was positive in 2013 and negative in 2014. These results remained similar when considering sowings separately in each year (not shown). In both years, sugar content was positively correlated to stem dry weight, and to plant height in 2013 only. Sugar content was significantly correlated to sugar concentration in 2014 only ($P < 0.05$). The latter was even negatively correlated to stem dry weight in 2013 ($P < 0.05$). Stem humidity strongly contributed to sugar concentration in both years ($P < 0.001$). It was nevertheless negatively correlated with all traits related to the leaf and internode number (only significant in 2013) and not correlated with internode morphology (diameter, length) in both years. Stem diameter contributed to sugar content in 2014 only. Plant leaf area was positively correlated to sugar content and stem dry weight, but not correlated to sugar concentration. However, the latter was positively correlated to the ratio between

Table 3
Correlations between phenological, morphological and sugar related traits at anthesis across 12 sweet sorghum accessions studied at two sowing dates (S1: July 17; S2: August 12) in 2013. FLA: Flag Leaf Area (cm^2), GLN: Green Leaf Number per plant, PLA: Plant Leaf Area (cm^2), SDW: Stem Dry Weight (g per plant), IN: Internode number per plant, INL: average internode length (cm), SCT: Stem sugar Content (g per plant), SCC: Stem sugar Concentration ($mg\,g^{-1}$ DW).

	DR	Vegetative phase	FLA	GLN	PLA	PLA/SDW	Stem diameter	IN	INL	Plant height	SDW	Brix	Stem humidity (%)	SCT
Vegetative phase	0.474*													
FLA	0.354	0.643**												
GLN	0.566**	0.701***	0.410*											
PLA	0.573**	0.642**	0.482*	0.944***										
PLA/SDW	−0.034	−0.382	−0.237	0.186	0.263									
Stem diameter	0.401	0.267	0.331	0.644**	0.659**	0.389								
IN	0.741***	0.836***	0.556**	0.814***	0.761***	−0.217	0.475*							
INL	0.193	0.075	−0.091	−0.229	−0.347	−0.623**	−0.434*	0.123						
Plant height	0.581**	0.594**	0.273	0.323	0.199	−0.590**	−0.060	0.697***	0.785***					
SDW	0.506*	0.888***	0.650**	0.568**	0.552**	−0.595**	0.146	0.796***	0.182	0.641**				
Brix	0.185	0.520**	0.379	0.431*	0.462*	0.092	0.415*	0.399	−0.396	−0.025	0.355			
Stem humidity (%)	−0.403	−0.735***	−0.269	−0.458*	−0.377	0.320	−0.136	−0.662***	−0.155	−0.574**	−0.661***	−0.638**		
SCT	0.442*	0.788***	0.770***	0.591**	0.627**	−0.450*	0.298	0.700***	0.000	0.411*	0.881***	0.433*	−0.381	
SCC	−0.320	−0.438*	0.037	−0.214	−0.071	0.461*	0.198	−0.469*	−0.557**	−0.741***	−0.481*	0.121	0.678***	−0.062

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

plant leaf area and stem dry weight, i.e. the amount of green leaf area per unit of stem dry weight (only significant in 2013, $P < 0.05$). However, the biggest plants (SDW, PHT) were associated with the smallest ratio between plant leaf area and stem dry weight ($P < 0.01$ in 2013). Accordingly, the accessions with the highest production of stem sugar at anthesis (sugar content) were, in 2013, the tallest ones with the highest internode number, i.e. with the longest vegetative phase, whereas in 2014 they were those with the thickest, sweetest internodes (highest sugar concentration) with the highest humidity.

3.3. Sowing date and post-anthesis drought effect on leaf area, grain and sugar production

The effects of post-anthesis drought (D), sowing date (S), accession (A) and their interactions were tested on plant traits related to post-anthesis leaf area, sugar and grain production and to their variation between FLO and MAT (Table 4). The year effect was also tested and significant for all the studied variables ($P < 0.001$). Replicate effects are not presented and were not significant for most traits.

In both years, the benefit of early sowing (S1) observed at anthesis (Table 2) on plant sugar production (SCT) and traits related to stem sugar concentration (SCC, varSCC) was maintained at maturity (Table 4). Panicle dry weight (PDW) was also enhanced by S1. This effect was in general smaller in 2014 compared to 2013 (significant in both years for sugar content only). In both years, the variation in plant leaf area between anthesis and maturity (varPLA) was smaller (more reduced PLA) in S1 compared to S2. Accordingly, the positive effect of S1 observed at anthesis was maintained up to maturity in 2013 only, as in 2014 the plant leaf area was even smaller at maturity in S1 compared to S2. The abovementioned sowing date effect was observed in both water treatments and years.

Post-anthesis drought only slightly affected sugar production, i.e. sugar concentration and its variation between anthesis and maturity (varSCC), as well as Brix and stem humidity. Accordingly, the sugar content was not affected by drought except in 2013 ($P < 0.05$). Similarly, grain production was only slightly affected by drought. Indeed, panicle dry weight was reduced by around 9% in 2013 ($P < 0.05$) and was even increased in 2014. This pattern was true both in S1 and S2. By contrast, the plant leaf area was greatly reduced by drought in both sowings and years (around 50 and 40% reduction in 2013 and 2014 respectively). The variation in plant leaf area between anthesis and maturity (varPLA) was thus smaller ($P < 0.001$) in the non-irrigated treatment (71 and 77% in 2013 and 2014 respectively) compared to the controls (around 40 and 60% in 2013 and 2014 respectively).

The accession effect was significant for all variables in both years. The effects of the sowing date × accession (SxA) or post-anthesis drought × accession (DxA) interactions were not significant except for the plant leaf area at maturity, for its variation between anthesis and maturity, for Brix (only by DxA) and for sugar content in 2013. Accordingly, across sowing dates and water treatments, accessions SS9 and SS10 maintained the highest leaf area at maturity and the lowest variation in post-anthesis leaf area under drought conditions (Fig. S3).

3.4. Variables contributing to grain and sugar production

Based on the results in Tables 2 and 4, a principal component analysis (PCA) was performed to cluster the twelve accessions depending on C source- and sink-related traits between anthesis and maturity and their relationship with final grain and sugar production, for each sowing date and water treatment in both years (Fig. 3). The first axis (Dim 1) explained 46.49% of the variability while Dim 2 explained 31.80%. Sugar content at anthesis (SCT.FLO) was mostly explained by Dim 2 whereas Dim 1 explained the variation in sugar concentration (varSCC) and in plant leaf area between anthesis and maturity (varPLA). Sugar production at maturity (SCT.MAT) was explained by both axes. Grain production at maturity was also explained by both axes, but to a minor extent (Dim 1 and Dim 2 with eigenvalues of 0.29 and 0.20 respectively).

The relationship between stem sugar concentration at anthesis and maturity is presented in Fig. 4 and S3 for 2013 and 2014 respectively, for each sowing and water treatment separately. The positive correlation suggested in Fig. 3 (Dim 1) was stronger in 2013 (Fig. 4) compared to 2014 (Fig. S3). The relationship between the variation in plant leaf area and sugar concentration between anthesis and maturity was also considered (Fig. 5 for 2013 and Fig. S4 for 2014). Interestingly, this relationship was positive and significant only under drought conditions, for both sowing dates, but stronger in 2013 compared to 2014.

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Table 4
Drought (D), sowing date (S), accession (A), their interaction and year effects on post-anthesis morphological and stem sugar related traits. PLA: Plant green Leaf Area (cm^2), SDW: Stem Dry Weight (g), SCT: Stem sugar content (g), SCC: Stem sugar concentration ($mg\,g^{-1}$ DW), PDW: Panicle dry weight (g). "Var" indicates the variation (%) of a given variable between anthesis and maturity. Average values are presented per sowing date (S1: July 17 and August 6 in 2013 and 2014 respectively; S2: August 12 and August 21 in 2013 and 2014 respectively), in each water treatment (NI: Non-Irrigated; IR: irrigated) and year.

	2013									2014										
	Mean				Anova					Mean				Anova					Year
	NI		IR		D	S	A	DxA	SxA	NI		IR		D	S	A	DxA	SxA	
	S1	S2	S1	S2						S1	S2	S1	S2						
Leaf area																			
varPLA (%)	−73c	−70c	−47b	−32a	***	***	**	**	**	−79c	−75bc	−689b	−51a	***	***	***	ns	ns	***
PLA (cm^2)	1091c	870c	2469a	1932b	***	***	***	*	***	707c	874c	1232b	1743a	***	***	***	ns	**	***
Sugar production																			
Brix (%)	17.9a	17.3a	17.2a	17.3a	ns	ns	***	*	ns	16.6a	17.2a	16.4a	17.0a	ns	ns	***	*	ns	**
Stem humidity (%)	77.2a	77.1a	78.5a	77.9a	*	ns	***	ns	ns	76.9a	75.0a	76.5a	75.7a	ns	*	***	ns	ns	***
SCT (g)	57a	31b	61a	36b	*	***	***	**	*	33a	28ab	30ab	27b	ns	**	***	ns	ns	***
varSCC (%)	116a	84b	109ab	91ab	ns	***	***	ns	ns	42a	41a	43a	38a	ns	ns	*	ns	**	***
SCC ($mg\,g^{-1}$ DW)	572a	544a	589a	552a	ns	*	***	ns	ns	526a	485a	508a	482a	ns	ns	***	ns	ns	***
Grain production																			
PDW (g)	42b	39b	51a	39b	*	***	***	ns	ns	32a	22bc	26ab	16c	**	***	***	ns	ns	***

ns: $P > 0.05$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

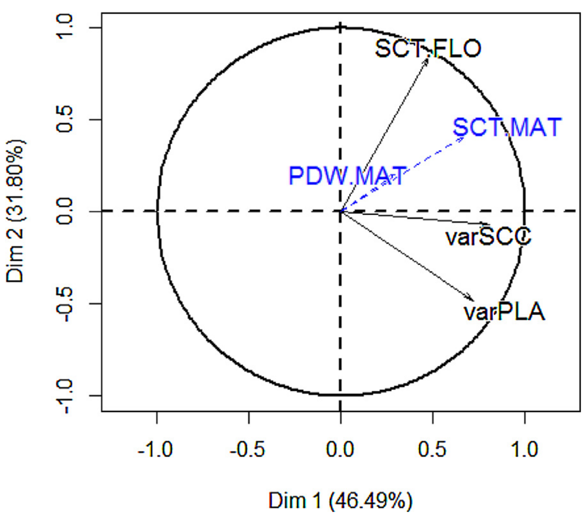

Fig. 3. Principal component analysis clustering the 12 studied sweet sorghum accessions depending on carbon source (varPLA) and sink (SCT, varSCC) related traits between flowering (FLO) and maturity (MAT) and their relationship with final grain and sugar productions (PDW.MAT and SCT.MAT respectively). SCT: Stem sugar Content in g per plant; SCC: Stem sugar Concentration in $mg\,g^{-1}$ DW; PDW: Panicle Dry Weight in g per plant; PLA: Plant Leaf Area in cm^2; var.# is the variation of a given trait between flowering and maturity (in% of this trait at flowering).

3.5. Dual purpose ability of accessions

Fig. 6 presents plant grain vs. sugar production for the 12 studied accessions for each sowing date, water treatment and year. It also compares each accession to the average performance of the 12 accessions in a given sowing and year, irrespective of water treatments (NI, IR).

Firstly, Fig. 6 confirms the low sowing date x accession or post-anthesis drought x accession interactions pointed out in Table 4, as the accessions were frequently localized in the same quarter delimited by average value lines. As regards sugar production, SS2 was the only accession systematically higher than the average line in all situations, which was explained more by a high production potential than by production maintenance under drought conditions. It was also the case of SS1, SS3, SS7, SS9 and SS10 but only in 7 (6 for SS3) situations out of 8. Among them, SS9 and SS10 were characterized by maintained good sugar production under drought conditions, related to a good stay-green ability (Fig. S2). For grain production, only SS3 was systematically positioned above the average line. Accessions SS2 and SS4 were also positioned above the average line in 6 of the 8 situations and SS1 in 5 of the 8 situations. Accordingly, SS2 showed the most stable dual purpose production across situations, followed by SS3 and SS1.

4. Discussion

This 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, photoperiodic sorghum, depending on the sowing date and post-anthesis water availability. Twelve West African accessions were studied in two consecutive years in the field in Bambey, Senegal. The main difficulty met in this study was inherent to field trials implemented on West African experimental stations where access to water is technically complex and the onset of the rainy season increasingly variable (Nicholson and Webster, 2007). Slight irrigation problems were encountered in 2014 (Fig. S1) resulting in less contrast between the two water treatments (Fig. 2). However, it was possible to set up two contrasting water treatments in each year. The level of water stress was variable among accessions but within a range enabling a reasonable comparison of accession responses to stress in a given year, as suggested by plant water stress measured on the two reference accessions (SS6 and SS8). The latter confirmed their contrast in plant size (Fig. 4) but not in plant leaf area at anthesis (Fig. S3). While the choice of field made it possible to grow plants in similar soils in both years, the two sowing dates adopted in 2014 were not those initially planned due to a late onset of the rainy season and were thus later (August) and only separated by 2 weeks (as opposed to 4 weeks in 2013). The plants were thus on average smaller in 2014 and therefore explored and consumed soil water differently compared to 2013. These sources of variation had to be taken into account in the way the results were interpreted regarding the variability in drought level and drought sensitivity. Nevertheless, this study provided further insight into the genotypic and environmental control of sugar and grain production by photoperiodic sweet sorghum, under conditions representative of the real agro-

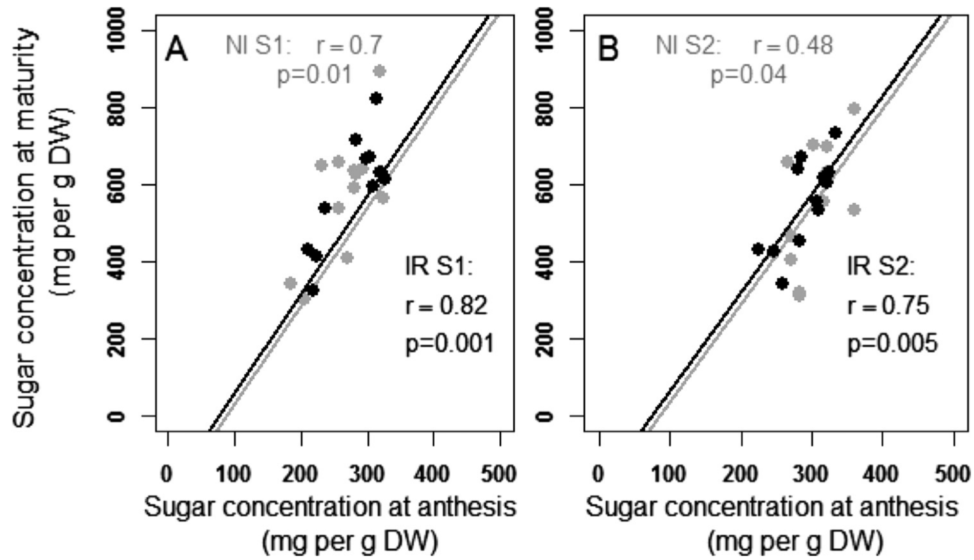

Fig. 4. Linear regression between sugar concentration at anthesis and maturity observed across the 12 studied sweet sorghum accessions in the 2013 field trial, under irrigated (IR) and non-irrigated (NI) treatments, for (A) the first (S1) and (B) the second (S2) sowing.

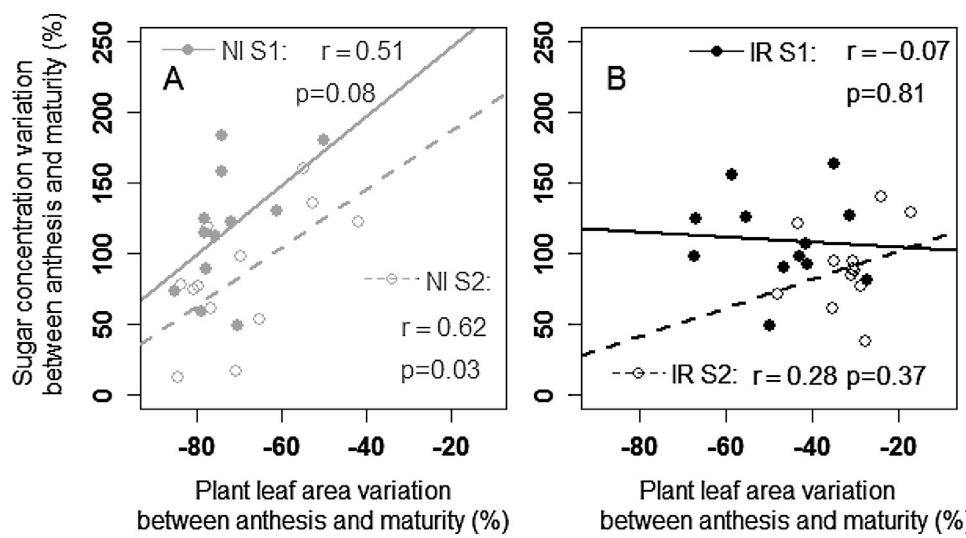

Fig. 5. Linear regression between the variation (from anthesis to maturity) in stem sugar concentration (Y axis) and plant leaf area (X axis) across the 12 sweet sorghum accessions studied in the 2013 field trial. S1 and S2 are respectively the early (July 17) and late (August 6) sowing dates. Data are presented for (A) non-irrigated (NI) and (B) irrigated (IR) treatments. Correlation coefficients (r) and p-values (p) are presented for each treatment for each sowing date.

ecological context. The benefit of stem morphology and plant leaf area for sugar accumulation was highlighted both before and after flowering and depending on the sowing date and water treatment. This is discussed below with respect to the identification of traits of interest when breeding for dual purpose (sugar, grain) photoperiodic sorghum for drought-prone environments as found in West Africa.

4.1. Sugar accumulation in the stem before flowering depends on the sowing date effect on both plant leaf area and stem growth

When practicing early sowing (S1), the duration of the vegetative phase was longer for the accessions with higher photoperiod-sensitivity, which accordingly produced more organs (leaves and internodes) and thus taller and bigger plants with a larger leaf area (PLA) at anthesis. The effect of the sowing date on organ size was less and only concerned leaves of upper ranks, as represented by the flag leaf (FLA, Table 3, Fig. S2), which contributed to a minor extent to the increase in plant leaf area. This was already reported by Gutjahr et al. (2013b) and Tovignan et al. (2015).

The early development rate (DR), controlling the leaf appearance rate in a major part of the vegetative phase, was statistically different among accessions and observed year, S and SxA effects (Table 3). It was increased by early sowing (S1) in 2013 only, i.e. when S1 was one month earlier than S2. Clerget et al. (2008) carried out 26 monthly sowings over two years with three African sorghum varieties under Malian conditions and also found that early sowing enhanced the initial development rate. This is also partially in line with Gutjahr et al. (2013b) who also reported (in a panel of 14 African sorghum accessions) a positive effect of early sowing on the development rate, but proportionally to the photoperiod-sensitivity of the accession: the more photoperiod-sensitive it was the more the development rate was enhanced by early sowing. This could not be entirely confirmed in our study as all the studied accessions were photoperiod-sensitive, whereas the accessions studied by Gutjahr et al. (2013b) displayed a larger range

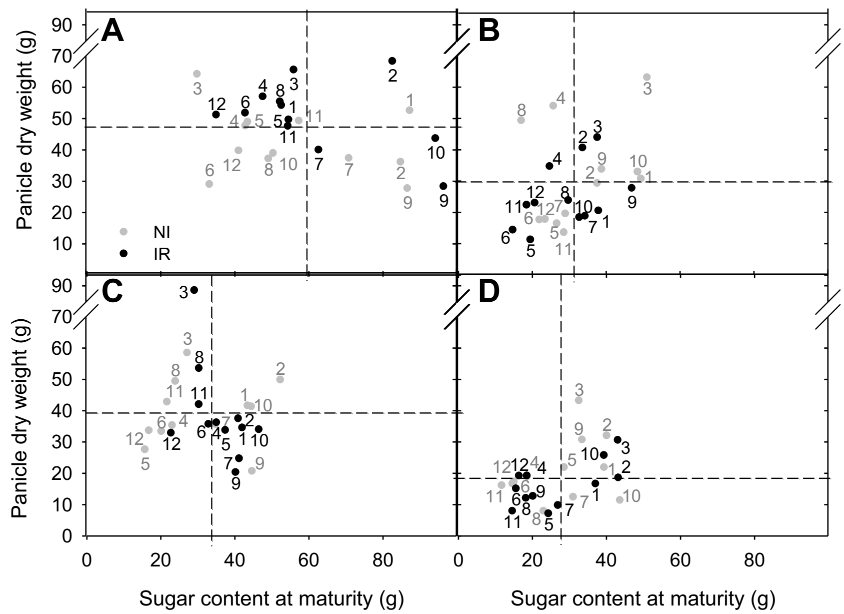

Fig. 6. Dual-purpose performance (stem sugar production vs. panicle dry weight at maturity, both in average in g per plant) of the 12 sweet sorghum accessions studied under irrigated (IR) and non-irrigated (NI) conditions. A: first sowing in 2013 (July 17); B: first sowing in 2014 (August 6); C: second sowing in 2013 (August 12) and D: second sowing in 2014 (August 21). Dotted lines represent the average productions in X and Y axis.

of photoperiod-sensitivity. Moreover, Gutjahr et al. (2013b) computed the development rate in a simplified way as the ratio between flag leaf rank and the duration of the vegetative phase (in thermal time), which is not entirely comparable to that computed in our study. Unfortunately, the computation of the late development rate attempted in our study was not robust enough to integrate it in the analyses.

By contrast with what was observed in 2013, the plant leaf area at anthesis in 2014 was neither correlated to the duration of the vegetative phase nor to the development rate. This was explained by the later sowings practiced and the shorter gap between them, resulting in a narrower range of vegetative phase duration and a limited effect of the variation in development rate. However, the plant leaf area at anthesis remained correlated to leaf number (flag leaf rank, GLN) more than to leaf size. Also, it can be suggested that the development rate may promote the plant leaf area, as reported by van Oosterom et al. (2011) under a low planting density.

In both years, the plant leaf area at anthesis was not correlated to sugar concentration in the stem (SCC) but was only positively correlated to stem dry weight and sugar content (i.e. to stem size and sugar reservoir, Table S1). Interestingly, the plant leaf area, when expressed per unit of stem dry weight (i.e. cm^2 of green leaves per g of stem dry weight, as an indicator of C source-sink ratio at anthesis), was positively correlated to sugar concentration (significantly in 2013 only, Table 3, S1). This suggests that the plant leaf area should favor stem sugar accumulation before anthesis in the case of tall, long cycle accessions, with a large sugar reservoir to fill. However, as the biggest plants in 2013 did not show the highest plant leaf area and stem dry weight ratio (Table 3), whereas genetic variability was observed at anthesis both for stay-green ability (ratio between green and total leaf number on the stem, not shown) and leaf area (Table 3), it is suggested that a genetic gain can be achieved for the plant leaf area at anthesis to maximize pre-flowering sugar accumulation. These results need to be confirmed and supported by other experiments, for example comparing different levels of leaf pruning and incoming light in accessions with variable stem size.

Similarly to the plant leaf area, plant stem vigor at flowering (stem dry weight, plant height) was enhanced by early sowing, particularly in 2013, due to the extension of the vegetative phase and increase in the development rate, resulting in a higher internode number. In addition, S1 enhanced the stem diameter, which also contributed to the increase in stem dry weight and thus the sugar reservoir, but to a minor extent (Table 3, S1). This variation in stem dry weight and plant height with the sowing date largely explained the variation in plant sugar production (SCT) at anthesis as previously reported by other authors (Gutjahr et al., 2013b; Han et al., 2012; Tovignan et al., 2015). This is also in line with Tsuchihashi and Goto (2005) suggesting that plant height is a key component trait of stem biomass and sugar production. The internode number was also positively correlated to sugar content at anthesis ($P < 0.001$), but not to internode length. This suggests that plant height is of greater benefit to sugar production based on the production of numerous rather than long internodes, supporting Tsuchihashi and Goto (2005) and Tovignan et al. (2015). Since both the internode number and average internode length were not or negatively correlated to sugar concentration and stem humidity, it can be suggested that a genetic gain in stem sugar production would be possible by better combining internode size, number, juiciness and sweetness. Further studies are thus needed to better understand the relationship between such internode traits.

4.2. *Stay-green contributes to maintaining grain and sugar production under drought conditions*

Post-anthesis drought significantly affected the variation in plant leaf area between anthesis and maturity (varPLA) and the plant leaf area reached at maturity, as previously reported but only for short, grain sorghum (Borrell et al., 2000a). Independently from the water treatment, varPLA was more negative for early sowing compared to late sowing. Nevertheless, the plant leaf area at maturity was higher on average with early sowing (Table 4). This different stay-green behavior between sowing dates might be explained by the fact that plants and thus leaves in the later sowing were younger at anthesis (due to a shorter vegetative phase) and accordingly would subsequently reach senescence later. However, this does not tally with the fact that varPLA was lower in 2013 than in 2014. Whether this might be explained by stronger water stress in 2014 cannot be fully answered (Fig. S3) and the hypothe-

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sis of a sowing date effect on post-flowering stay-green needs to be further explored. The variation in plant leaf area between anthesis and maturity varied significantly ($P < 0.05$) among accessions in the non-irrigated treatment in both years, whereas the difference was not significant in the irrigated treatment. Accordingly, the plant leaf area at maturity also displayed greater variation across accessions in the non-irrigated treatment where accessions SS9, SS10, SS7 and SS12 exhibited the best stay-green ability in both years.

Early sowing almost doubled sugar content at maturity in 2013 compared to late sowing, but this difference was less pronounced in 2014. Accessions accumulating a large quantity of sugar in the stem were generally characterized by the longest cycle and the highest stem dry weight, as already observed at anthesis and reported in previous studies (Prakasham et al., 2014; Gutjahr et al., 2013b; Tovignan et al., 2015). A significant accession effect was highlighted. Accessions SS1, SS2, SS7, SS9 and SS10 were among the best for both water treatments and years. Post-anthesis drought slightly affected ($P < 0.05$) sugar production at maturity (SCT) in 2013 but not in 2014. This might be explained by a reduction in stem humidity but not in sweetness (SCC) in 2013 (Table 4). The effect of drought on grain production was not significant and even positive in 2014. The latter result is surprising and might be explained by plant heterogeneity. Stay-green ability did not show any relationship with grain or sugar production under well-watered conditions, whereas under post-anthesis drought conditions, it was positively correlated to sugar accumulation (varSCC) in both years and sowings (Fig. 5). Interestingly, SS9 and SS10 were among the most stay-green under drought conditions and gave the best sugar production (maintenance) under drought conditions.

The variability found across the studied accessions in their suitability for dual production of grain and sugar was explained by: i) sink size (panicle, stem sugar reservoir) and the amount of sugar already accumulated in the stem up to flowering, and ii) post-anthesis sugar accumulation, which was more environment-dependent for the stem than for the panicle (Figs. 3–5). Accordingly, SS2 was the best accession across the situations explored in this study (Fig. 6) because of its long cycle and large stem reservoir (tall plant and the largest diameter). For the same reasons, accessions SS1 and SS3 also showed good (but less stable) dual purpose ability and were characterized by high post-anthesis sugar accumulation in the stem and the grains. Lastly, SS9 and SS10 were characterized by the best maintenance of sugar production under post-flowering drought conditions, due to their stay-green ability. For these reasons, these five accessions in particular should be of benefit to breeding programs dedicated to dual purpose sorghum for drought-prone environments.

5. Conclusion

This study demonstrated that the production of sugar and grain by photoperiodic, sweet sorghum depends both on stem morphology and leaf area dynamics as influenced by sowing date and/or post-anthesis water conditions. Leaf area dynamics were shown to promote sugar accumulation both before and after anthesis, depending on the sowing date and post-flowering water availability. Within the sweet, photoperiod-sensitive genetic material studied, the lengthening of the vegetative phase by early sowing was crucial for enhancing plant height and thus the sugar reservoir and production. It was confirmed that sugar accumulation in the stem starts before anthesis i.e., once the first internodes have completed their expansion. In this respect the amount of leaf area per unit of stem dry weight produced benefited sugar accumulation before anthesis. The occurrence of a post-anthesis drought slightly affected sugar and grain production, but accelerated leaf senescence. The accessions with the best maintenance of combined grain and sugar production under drought conditions were those with the largest carbon sinks (stem, panicle) set up at flowering, with the best stay-green aptitude after flowering. This study provided further insight into the way phenology, stem morphology and leaf area elaboration should be considered in the breeding context for dual purpose sorghum.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2016.04.015.

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