

Regulation of Sugar in Sweet Sorghum Crop - A Review

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Sweet sorghum (*Sorghum bicolor* L.) accumulates high concentration of sucrose along with the juice in their stem. Hence, the opportunity of extensive research is in the physiology, biochemistry and molecular aspect of sucrose accumulation. Instead of this, the relationship between leaf photosynthetic activity and sucrose accumulation in the culm is not well understood. Communication between source and sink may play very crucial role in regulating sucrose synthesis. Assimilates partitioning is the process by which the products of photosynthesis are exported from leaves through the minor veins to storage tissues. Key aspects of researchers are to improve carbohydrate partitioning by increasing source capacity or plant or by increasing sink strength. Increases of carbohydrate production may possible by increasing light interception either by increasing the number of leaves or total leaf area, stay-green traits, and by enhancing the capacity of photosynthesis of the plant to fix carbon. In this review, we discuss many aspect of sweet sorghum that make it an ideal crop for biofuel, ethanol and syrup production and also provide an overview of genetic diversity and resources available for engineering and marker-assisting breeding of sweet sorghum.

Keywords: Sweet sorghum, Sugar metabolism, Photosynthesis.

Sorghum (*Sorghum bicolor* L. Moench) is a C₄ herbaceous annual plant, and is popularly known by a particular names in particular country like great millet, kafir corn, durra, mtama, jowar, kaoliang and milo in West Africa, South Africa, Sudan, Eastern Africa, India, China, United States respectively (Purseglove, 1972). Being a C₄ plant, sweet sorghum has a highly efficient photosynthetic pathway and is very efficient in the utilization of soil nutrients also. Hence, plant contains high concentrations of soluble sugars (10–15 %) in the stalk juice. The name “sweet sorghum” is used to identify those varieties of

sorghum, which has juicy along with sugar content in the stalk. Partitioning of carbohydrate is the process by which the products of photosynthesis are exported from leaves through the minor veins to storage tissues. Key aspects of researchers are to improve carbohydrate partitioning by increasing source capacity or by increasing sink strength. Carbohydrate production may increase by increasing light interception either by increasing the number of leaves or total leaf area, stay-green traits, and by enhancing photosynthesis capacity of the plant to fix CO₂ (Sakamoto *et al.*, 2006; Hammer *et al.*, 2009; Zheng *et al.*, 2009; Zhu *et al.*, 2010; Raines, 2011; Ruan *et al.*, 2012a). The change in sugars content between the time period of anthesis and harvest is already established, while the content of reducing sugars decrease, and sucrose increases in the stem during maturation

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time in (Lingle *et al.*, 2012). Grain sorghums are used for human food, while forage sorghums are used for animal feed, and sweet sorghums for edible syrup. It requires less water than sugarcane and is tolerant to drought and flooding and also it is capable of re-growth as ratoon crops. In this respect, sweet sorghum is one of the best alternatives option (Rooney *et al.*, 2007; Zhang *et al.*, 2010; Linton *et al.*, 2011; Yu *et al.*, 2012).

Photosynthetic capacity

Storage organs are the anatomical structures that accumulate sugar from photosynthesis. They include fruits, seeds, roots, and stems. Stem acting as a storage organ is found in grasses, such as sweet sorghum (*Sorghum bicolor*) and sugarcane (*Saccharum officinarum*) (Slewinski, 2012). Being a C₄ plant, both species have the capacity to perform high speed of photosynthesis and accumulate high concentrations of fermentable sugars in the stem, mainly sucrose. Therefore both the plants are ideal plant for strong stem sinks, and being used for the production of ethanol as a biofuel (Waclawovsky *et al.*, 2010; Calviño and Messing, 2012). In sweet sorghum, photo-assimilate is used for plant growth and development during initial vegetative phase. Thereafter, internodes elongated and stem initiate sugar accumulation where most of the photo-assimilate stored in the form of sucrose (Hoffmann-Thoma *et al.*, 1996; Lingle, 1999; Almodares *et al.*, 2008; Almodares and Hadi, 2009; Calviño and Messing, 2012; Slewinski, 2012). Mature Internodes of sweet sorghum stem accumulate higher concentration of sucrose content in comparison to younger one (Hoffmann-Thoma *et al.*, 1996). Ali *et al.*, (2008) reported that a little variation is found in terms of sugar composition among the cultivated sweet sorghum varieties and on the basis of simple sequence repeats (SSRs) marker study he grouped in to two types of sweet sorghum group IX high sugar content and group VII low sugar content. Moreover, on the basis of molecular analysis i.e. based on SSR and SNP marker, sweet sorghum varieties categories in to three major groups (Murray *et al.*, 2009). While, on the basis of AFLP and SSR markers analysis, sweet sorghum classified into two types with various brix content (Pecina-Quintero *et al.*, 2012).

Relationship between source and sink

The rate of sucrose accumulation often increases near anthesis in culm internodes, which

is a period in which least demand appear in reproductive sinks (Vieter *et al.*, 1989). However, photoassimilate can be remobilized to reproductive sink that accumulated in the culm tissue during anthesis if photoassimilate export from the source leaves is low [Vieter *et al.*, 1989 and Sowder *et al.*, 1997). A good relationship between source and sink tissue is essential because supply of photoassimilate from source is depending upon the consumption of the intermediate (Hofmeyr and Cornish-Bowden, 2000). Leaves are the major source of carbohydrate supply while sink demand includes growth, respiration and storage in plant. In sugarcane, culm parenchyma cell may be a strong additional demand component of sucrose. This kind of additional storage, contribute a lot to maintain a high sink demand of sucrose in the stem resulting a high yield of sucrose (Fig. 1). The frequency of end product formation is governed by feedback inhibition of the supply process by the concentration of the intermediate metabolite, which is determined by the balance between supply and demand (Fig. 1A). In plants, demand is likely to be the result of metabolic activities such as growth, respiration and storage, especially in high carbon accumulating species such as sugarcane. In this regard, Feedback inhibition is indicated as a sensitivity function of supply to the concentration of the intermediate, sucrose i.e. sucrose (Hofmeyr, 1998).

Sugar transport and storage in the stem

Sweet sorghum and sugarcanes may vary in respect of high levels of sucrose in their stems. In mature sugarcane stems, sucrose transport follows a predominantly symplastic movement when moving from the phloem into the storage parenchyma cells (Lingle, 1989; Rae *et al.*, 2005; Patrick *et al.*, 2013). This hypothesis is supported by evidence observed from the study of sap collected from the xylem of sugarcane stems, which was very close with the phloem (Welbaum *et al.*, 1992), moreover, it was observed that a fluorescent dye loaded into leaves is unloaded in the phloem of stem and move symplastically via plasmodesmata into the stem parenchyma cells (Rae *et al.*, 2005). During the sucrose accumulation in the stem, parenchyma cell apoplast facilitate as an additional storage compartment that increases sink strength. At maturity stage, when sucrose accumulates at higher concentration in the stem

apoplast, reverse translocation of sucrose into the phloem is inhibited by the lignified and suberized cell walls (Rae *et al.*, 2005; Walsh *et al.*, 2005; Patrick *et al.*, 2013). Biochemical studies shown that the sucrose must be store in parenchyma cells by crossing the plasma membrane cell in the stem of sweet sorghum, that itself indicate the support of sugar transporter (Hoffmann-Thoma *et al.*, 1996). Sucrose transporters are the H⁺/sucrose symporter that is able to translocate sucrose across the membrane (Lalonde *et al.*, 2004; Sauer, 2007; Braun and Slewinski, 2009). There are six class of popular sucrose transporter (SUTs) i.e. is SUT1, SUT2, SUT3, SUT4, SUT5, SUT6 have been proposed that encode protein located in the plasma membrane and tonoplast in sorghum genome (Braun and Slewinski, 2009). The transporters are involved in the high sucrose accumulation in sweet sorghum was tested by transcriptional analysis and concluded that SUT1 and SUT4 are highly correlated with sugar content in sweet sorghum stem (Qazi *et al.*, 2012). Some other sugar transporter proteins i.e. SWEETs and TMTs are recently shown to transport sucrose across the membrane (Wingenter *et al.*, 2010 and Chen *et al.*, 2012). Even though, exact role of additional sucrose transporters in sucrose transfer is not yet

established in the stem (Braun, 2012; Chen *et al.*, 2012).

Sugar metabolism in the stem

Metabolism and storage processes of sucrose in the stem are important step of sink strength. During initial growth of sweet sorghum and sugarcane stems, INVs contribute to strengthen the sink and stem size. However, later on sucrose is stored in the vacuoles of stem parenchyma cells. Out of the total store sucrose in the stem, only least amount is hydrolyzed during its transfer into the ripening stem (Lingle, 1989; Tarpley *et al.*, 1996; Tarpley and Vietor, 2007). Further, after the stems have matured and elongation has ceased, these tissues show low metabolic activity (Tarpley *et al.*, 1996), prompting the question as to whether sucrose metabolism remains an important driver of sink strength in maturing sweet sorghum and sugarcane stem tissues. The enzymes involved in sucrose metabolism are INV, sucrose synthase (SUS), sucrose phosphate synthase (SPS), and sucrose phosphate phosphatase (SPP). INV enzymes catalyze the cleavage of sucrose into glucose and fructose. Different types of INV enzymes are found in different places in the plant system like cell wall, vacuole, and cytoplasm (Ruan *et al.*, 2010; Vargas and Salerno, 2010;

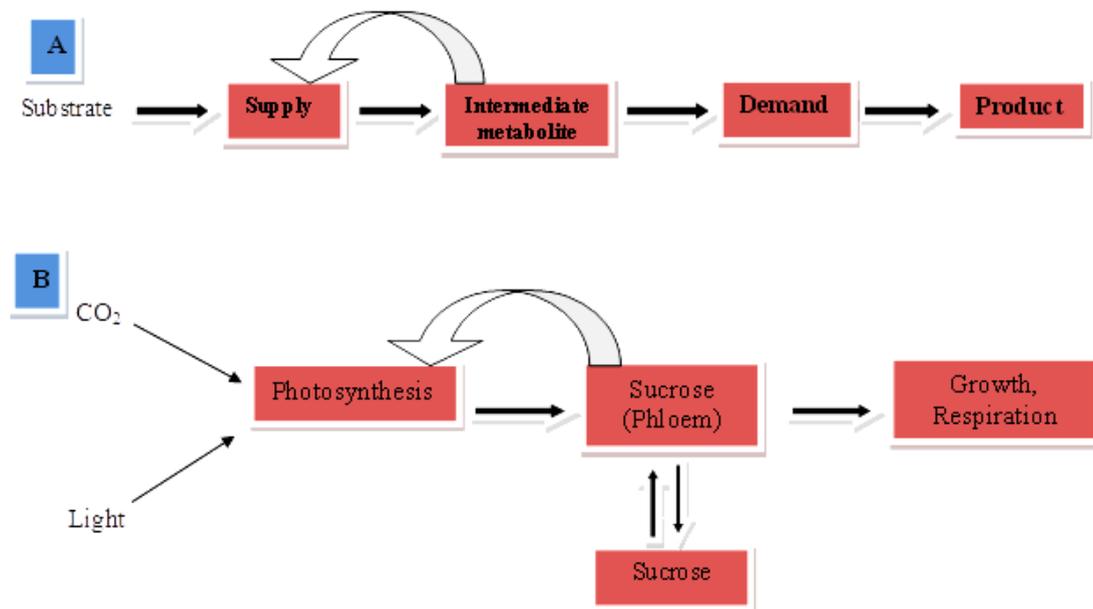


Fig. 1. A simplified model of metabolic supply and demand system modified from Hofmeyr (1998)

Patrick *et al.*, 2013). Winter and Huber, (2000) also reported that sucrose synthase is another enzyme that split sucrose into fructose and UDP-glucose. Ultimately, sucrose phosphate synthase and sucrose phosphate phosphatase play crucial role jointly in irreversible synthesis of sucrose from UDP-glucose and fructose-6-phosphate (Lunn and Mac Rae, 2003). Qazi *et al.*, 2012) reported that grain sorghum accumulates least amount of sucrose in the stem in comparison to sweet sorghum and the carbohydrates produced are moved toward storage in seeds.

CONCLUSION

Increased demand of energy resources in respect of biofuel throughout the world, sweet sorghum (*Sorghum bicolor* L.) became a most popular optional crop for the production of biofuel. Therefore, this crop compels researcher to do advanced research in this field. Because detailed study of physiological and biochemical analysis in addition to molecular investigation will help to understand or identify the novel characters in deep for better understanding of rate of photosynthesis in the leaves, source sink relationship between leaves and stem, sugar transport and storage in stem and sugar metabolism. The knowledge from above mentioned criteria shall also help to know how plant regulates the portioning of sugar inside the stem of sweet sorghum.

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