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Insights on Fructans and Resistance of Plants to Drought Stress

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Drought, one of the major abiotic stresses affecting plants, is characterized by a decrease of water availability, resulting in a decrease of the water potential (Ψ) of the cells. One of the strategies of plants in resisting to this low Ψ and related stresses is regulating their water-plant relation and the interplay between Ψsolutes and the turgor pressure (Ψp). This regulation avoids the dehydration induced by low Ψ and is resulting from the accumulation of specific molecules which induce higher tolerance to water deficit and also other mechanisms that prevent or repair cell damages. In plants, fructans, the non-structural carbohydrates (NSC), have other physiological functions than carbon reserve. Among these roles, fructans have been implicated in protecting plants against water deficit caused by drought. As an efficient strategy to survive to this abiotic stress, plants synthesize fructans in response to osmotic pressure in order to osmoregulate the cellular flux, therefore, protecting the membrane damage and maintaining Ψp. Although different studies have been conducted to elucidate the mechanisms behind this strategy, still the concept itself is not well-understood and many points remain unclear and need to be elucidated in order to understand the causal relation between water deficit and fructans accumulation during water scarcity. This understanding will be a key tool in developing strategies to enhance crop tolerance to stressful dry conditions, particularly under the changing climate prediction. This review aims to give new insights on the roles of fructans in the response and resistance of plants to water deficit and their fate under this severe environmental condition.

Keywords: fructans, abiotic stress, drought, resistance, plants

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INTRODUCTION

Fructans have a history of more than two centuries and some review articles have reported some historical aspects on fructans research (Meier and Reid, 1982; Pontis and Del Campillo, 1985; Pollock and Cairns, 1991). Prior to this exciting contemporary science, ancient peoples have been using fructans-containing plants as food, feed, and medicine. Indeed, the modern history of fructans began with their discovery by Rose (1804), and this history has known at the turn of the twentieth century considerable development when Edelman and Jefford proposed for the first time the mechanism of their metabolism in higher plants (Edelman and Jefford, 1964, 1968). More recently, fructans research has known a considerable progress particularly with the advancements of molecular biology moving fructans research from basic to applied science. Briefly and from the chemical and structural points of view, fructans are polyfructosylsucroses of varying molecular size build on a sucrose starter unit and are biochemically designated by 1F (1-β-D-fructofuranosyl)*n* sucrose oligomers where *n* may vary depending on their types and degree of polymerization in different plant species (**Figure 1**).

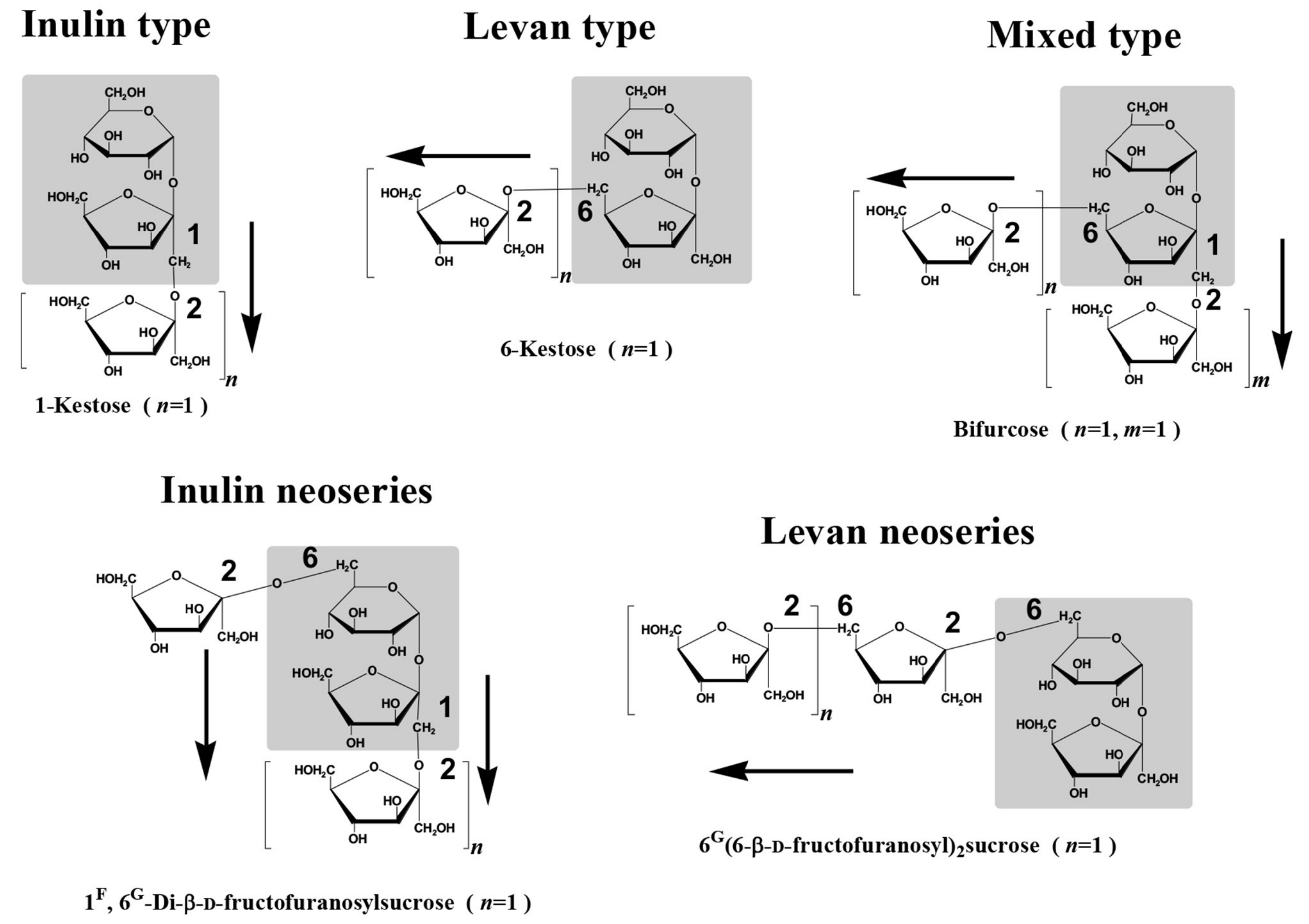

FIGURE 1 | Molecular structures of the different types on fructan polymers found in higher plants.

Fructan polymers are found in c.a. 15% of flowering plants, and the type and degree of polymerization vary with the species. In Asteraceae, inulin-type fructans of different degree of polymerization have been identified (Banguela and Hernández, 2006). For example, in chicory and Jerusalem artichoke low DP ranging from 10 to 30 units are found (Ernst et al., 1995; Vergauwen et al., 2003; Monti et al., 2005), while higher DP up to 200 units have been found in globe artichoke (Frehner et al., 1984). In contrary, in Monocot plants species such as Alliaceae, Asparagaceae, and Agavaceae more complex fructans are synthesized like inulin neo-series, and other branched types (see **Figure 1**). For example, in onion and garlic (Alliaceae) and asparagus (Asparagaceae) species, inulin and inulin neo-series are found ranging from 9 to 12 units in onion (Shiomi, 1989; Benkeblia and Shiomi, 2006), from 10 to 30 units in garlic (Das and Das, 1978; Baumgartner et al., 2000), and from 12 to 22 units in asparagus (Shiomi, 1993). In Agavaceae, another fructan-containing species, different types of fructan polymers were reported. Inulin type was found to be the principal fructan in *Agave americana*, however, inulin neo-series and other branched fructan types were identified in *Agave vera cruz* and *Agave tequilana* (Aspinall and Das Gupta, 1959; López et al., 2003).

As storage reserve, fructans are accumulated during the growth stage of the sink, then are catabolized during the regrowth and the development. However, fructans were found to have functions other than carbon storage: they have been implicated in protecting plants against water deficit or low temperature, inducing resistance to drought or cold stress/freezing (Hendry, 1993; Hendry and Wallace, 1993; Vijn and Smeekens, 1999) and as osmoregulators (Hendry, 1993; Livingston and Henson, 1998; Hincha et al., 2000). Although their metabolism and enzymes compartmentation have been elucidated (Frehner et al., 1984; Wagner and Wiemken, 1986), the molecular mechanisms behind their putative physiological roles still remain unclear.

Physiologically, fructans accumulate in plants as long-term or short-term carbohydrates reserve and are remobilized during the sprouting or regrowth. They are stored either in underground organs such as roots and tubers, or in stems, tiller bases and leaf sheaths (Incoll et al., 1989; Bancal et al., 1992; Morvan-Bertrand et al., 2001; Ranwala and Miller, 2008; Joaquim et al., 2014). Beside these roles, some studies have shown that fructan polymers might also be involved in the regulation of osmosis during flower opening (Le Roy et al., 2008), and the protection of plants against abiotic stresses (Hincha et al., 2003). In addition to these roles, some studies also investigated the possible alterations of the fructans pool and the photosynthetic responses of plants. For example, the depression of the photosynthesis did not affect the levels and fructans and the high DP pool was maintained even though mono- and disaccharide pools were affected (Marschall et al., 1998; Thomas and James, 1999; Marschall, 2010). In a similar study on different varieties of wheat and chicory, the depression of photosynthesis did not affect the accumulation of fructans, although hexoses pool was negatively correlated to the photosynthesis rate (Martínez-Carraseo et al., 1993; Monti et al., 2005).

As carbohydrate reserve, fructans are remobilized during regrowth of ryegrass (Chalmers et al., 2005; Trethewey and Rolston, 2009), cereals (Iannucci et al., 2016), or sprouting of onion (Pollock and Lloyd, 1994; Shiomi and Benkeblia, 2005; Yasin and Bufler, 2007), asparagus (Suzuki et al., 2013), and Jerusalem artichoke (Luo et al., 2018). Unlike in bacteria and fungi where two fructan hydrolases -one exo- and one endo-types- are found, different studies have demonstrated that in plants only the fructan exohydrolases (FEHs) releasing fructose units have been identified (Edelman and Jefford, 1968). These enzymes are supposed to not only breakdown fructans, but some evidences have shown they might play roles in plants signaling and defense (Van den Ende et al., 2004).

In general, plants are affected by biotic (e.g., resistance to diseases, parasites, insects, and weeds) or abiotic [e.g., better adaptation to heat, drought, salinity, acidity, heavy metals, waterlogging, and nutrient (especially nitrogen and phosphorus) availability)] stresses (Shao et al., 2008, 2009; Jahangir et al., 2009). Consequently, biotic and abiotic stresses cause significant losses in crops and productivity (Dita et al., 2006). Globally, the recent studies are predicting that water deficit or drought will increase in severity with the rising temperatures by 2100 (IPCC, 2019a). The effects of climate change will be reflected by either acute or chronic impacts associated with variable precipitation events and longer periods of drought. Africa will be among the most affected regions and yields of major crops will decrease significantly by more than 50% in 2050 and might reach 90% in 2100 for the major crops (Li et al., 2009; IPCC, 2019b). Therefore, improving water use efficiency (WUE) of crops is an imperative and needs to be addressed urgently, as this plant trait is seen as one of the most important solutions in addressing water scarcity and drought (Eslick and Hockett, 1974; Hamdy et al., 2003; Tuberosa and Salvi, 2006). On the other hand, there is a pressing need to improve WUE of either rain-fed or irrigated crops and breeding new varieties with optimal WUE by using either conventional breeding or molecular engineering seems to be the most environmentally friendly and sustainable solution to face water shortage and drought caused by climate in the future (Chaerle et al., 2005). However, prior to develop new crops or improve WUE of plants, we need to understand and decipher all the mechanisms developed by plants to face drought and their strategies to survive during short- and long-term dry periods. Indeed, plants encounter many unfavorable growth conditions including drought as one of the major abiotic environmental stress which limit their growth and development (Krasensky and Jonak, 2012). From the biological point of view, abiotic stresses include multiple ones, however, water deficit constitutes likely the major abiotic factor affecting plants (Sharma and Lavanya, 2002).

Under water scarcity, the biological roles of water as solvent, transporter, electron donor, and evaporative coolant were well-demonstrated to be impaired by environmental conditions (Hsiao, 1973; Bohnert et al., 1995). Nevertheless, sensitivity of plants to water deficit varies with the species and their responses to this abiotic stress, and therefore, they encoded different capabilities in their perception, signaling, and response to drought (Zhu, 2002; Shinozaki and Yamaguchi-Shinozaki, 2007; Shanker et al., 2014). Thus, plants respond to low water availability by modifying the concentration, composition, and distribution of the primary and secondary metabolites (Almeida et al., 2020). Within the context of climate change and the prediction of higher frequency of drought in many regions of the world, the challenge of metabolomics is to profile the widest range of primary and secondary metabolites that are present within plants during drought, and the comprehensive analysis shall reflect the exact biological fate of the plant system at both a defined developmental stage and under drought stress (Bowne et al., 2012). Experimental research and several biochemical studies reported that drought stress induce the accumulation of different metabolites in vascular and non-vascular plants (Bohnert and Jensen, 1996), and identifying the mechanisms underlying plant resilience to water deficits (Chaves and Oliveira, 2004), understanding carbon sequestration by plants per unit of transpired water (Condon et al., 2004) and the regulatory networks and specific metabolites involved in crop drought tolerance (Valliyodan and Nguyen, 2006) need to be further investigated.

This review aims to give recent and new insights on the roles of fructans in plants resistance to water deficit and their resilience to dry conditions. This review will also report recent evidences on the drought-protecting role of fructans and the mechanisms triggering these roles at organ and cellular levels.

HOW DO PLANTS RESPOND TO DROUGHT STRESS?

In response to water scarcity, plants have developed different but efficient mechanisms to adapt to this abiotic stress by activating resistance mechanisms at molecular and tissue levels. These mechanisms are multiple and metabolic adaptation, and regulation and molecular responses by triggering the biosynthesis of specific metabolites, are one of the most important of these multiple mechanisms (Seki et al., 2007; Nishizawa et al., 2008; Gargallo-Garriga et al., 2014; Fàbregas and Fernie, 2019).

Water deficit causes a reduction of the photosynthesis rate in the leaves and a decrease in the diffusion of atmospheric CO_2 to the carboxylation site of RUBISCO (Flexas et al., 2004), and the decrease in the diffusion of CO_2 is resulting from the stomatal closure (Chaves et al., 2003). The closure of stomata is likely the first response to water deficit and is mediated by ABA one the first phytohormones playing major roles in mediating plants response to stresses and synthesized in response to drought (Yoshida et al., 2014). ABA is known to trigger first the cascade of drought signaling (Urano et al., 2009; Lim et al., 2015; Shang et al., 2016; Li et al., 2017), and was shown to promote fructans accumulation by inducing further the expression of the 1-FFT (Fructan:fructan 1-fructosyltransferase) and 1-SST (Sucrose:sucrose 1-fructosyltransferase) genes in agave (Suárez-González et al., 2014). Indeed, drought stress is more complex that it seems, and plants' capacity to trigger physiology processes allowing tolerance to face drought stress are still not well-elucidated (El-Sayed et al., 2014). Although extensive literature is readily available on dehydration stress in a wide range of species, drought resistance still remains a complex mechanism and metabolomics techniques are one of the most used approaches to decipher this mechanism. On the other hand, the biosynthesis of protecting and stress-induced metabolites are induced by the expression of numerous stress-responsive genes in order to re-establish homeostasis and slowing down energy consuming processes which in turn induce tolerance to abiotic stress (Taylor et al., 2000; Hummel et al., 2010; Skirycz and Inzé, 2010; Seiler et al., 2011). By reducing energy consumption, carbon assimilation is redirected to activate protective mechanisms and stress-protecting metabolites among them fructans (Pilon-Smits et al., 1995; Van den Ende and Valluru, 2009; Keunen et al., 2013).

More generally, the induction of the production of stress-protecting metabolites or osmoprotectants is triggered by a cascade of signals starting by the induction of many genes expression involved in water scarcity response. Indeed, metabolites profiling and biology system studies have been good approaches for understanding the pathways of the molecular system mediating drought stress (Bowne et al., 2012). Different metabolomics studies showed that carbohydrates were among the most increased metabolites in response to drought stress (Rolland et al., 2006; Obata and Fernie, 2012; Ullah et al., 2017), and the levels of carbohydrates synthesis increases with the drought stress severity (Todaka et al., 2017).

DROUGHT STRESS AND FRUCTANS ACCUMULATION

One of the biochemical responses of plants to drought is the biosynthesis of non-structural carbohydrates (NSC) as osmo-protectants and adjusting the osmotic pressure by synthesizing osmo-protectants to avoid cell dehydration (Muller et al., 2011; Hou et al., 2018). Although not specific to fructans, the roles of the osmo-protecting molecules consist of stabilizing the cell membranes and cellular proteins from the denaturating effects of drought (Yancey, 1994). Additionally, osmo-protectors are thought to have many other roles like restoring the cellular redox by scavenging the reactive oxygen species (ROS), and balancing osmosis in order to preserve turgor, resulting in stabilization of protein and cellular structures (Pinhero et al., 1997; Zhu et al., 2003; Li et al., 2013). Among the accumulated metabolites as osmo-protectors, numerous carbohydrates, including fructose, sucrose, trehalose, raffinose, and fructans that are of high solubility, have been shown to accumulate in response to the increase in the osmotic pressure resulting from the dehydration (Rook et al., 1998; Nishizawa et al., 2008; Valluru and Van den Ende, 2008). The causation of fructans accumulation and drought stress was established by using plants transformed with bacterial fructosyltransferase genes (Cairns, 2003; Khan et al., 2015). In the 1990s, Pilon-Smits et al. (1999) used SacB gene from *Bacillus subtilis* to produce fructans in tobacco (Ebskamp et al., 1994; Pilon-Smits et al., 1995), potato (Van der Meer et al., 1994), and sugar beet (Pilon-Smits et al., 1999) which accumulated fructans under drought-induced condition and increased their resistance to water deficit. Studies carried out on the effects of drought on fructans biosynthesis in fructans non-accumulating and transformed plants using genes of fructans-accumulating plant species have also showed similar results. Wheat-derived genes encoding fructans biosynthesis enzymes were transferred into tobacco plants which synthesized fructans under drought-induced stress (Bie et al., 2012). He et al. (2015) isolated a *Psathyrostachys huashanica* sucrose:fructan-6-fructosyltransferase (Ph-6-SFT) and transferred it into tobacco (*Nicotiana tabacum* L.). By comparing the wild to the transgenic tobacco plants, they noted that the transformed plant exhibited a much higher tolerance of drought and this tolerance was associated with the accumulation of carbohydrate suggesting this approach might be applied as a genetic tool for improving stress tolerance in other crops. Similarly, the isolation of the fructan: fructan 1-fructosyl-transferase (1-FFT) gene from Jerusalem artichoke and its overexpression in the leaves of transgenic tobacco increased their fructans biosynthesis under simulated drought (Sun et al., 2020). In non-transformed plants, the response and accumulation of fructans in response to drought stress was first reported by Virgona and Barlow (1991) who observed that turgor of wheat stem was maintained with an increase in NSC. Later, other research reported similar results on drought-induced fructans biosynthesis in chicory (De Roover et al., 2000), wheat (Zhang et al., 2015; Hou et al., 2018), *Vernonia herbacea* (Garcia et al., 2011), and lettuce (Blanch et al., 2017).

However, these numerous studies did not elucidate the mechanisms of how fructans contribute to enhancing drought stress tolerance either in the transformed plants which accumulate low level of fructans or non-transformed plants which accumulate significant levels of these osmo-regulators. On the hand, the mechanism by which these osmolytes provide protection is still unclear and not completely understood (Ramanjulu and Bartels, 2002; Du et al., 2004; Reddy et al., 2004; Arbona et al., 2013; Fedotova, 2019), although it is hypothesized that fructan polymers might act by regulating water potential, signaling molecules and/or ROS scavengers, therefore, affecting the metabolism of plants under drought conditions (Bolouri-Moghaddam et al., 2010; Van den Ende, 2013; Ahmad et al., 2020).

FRUCTANS METABOLISM AS DROUGHT PROTECTIVE MECHANISMS

Demel et al. (1998) first suggested an interesting *in-vitro* model on the protective role of fructans during drought. From the results of their experiment, the authors suggested that fructans cause a very large increase in surface pressure of lipid monolayers, hence hypothesizing that lipid condensation and phase transitions might be prevented by membrane-fructan interaction, thus inducing the drought protective effect. Later, a similar model of the protective effect of fructans on liposomes by assessing their stability during either air draying or drying and rehydration was suggested (Hincha et al., 2002, 2007). Results showed that low DP 3, DP 4, and DP 5 fructans exhibited higher protective action by preventing leakage of a soluble marker from liposomes and liposome fusion. The same study is however suggesting that this protective action of fructans depends on their size and origin, and their compartmented protective properties might differ significantly compared to the purified fractions (Hincha et al., 2007). Getting a deeper insight into the mechanism of this protective effect on the cellular membrane during dehydration, different fructans have been tested on phosphatidylcholine-based model systems. Results clearly showed that inulin-type fructans protected the membrane barrier and inhibited vesicle fusion by their presence between the lipid bilayers during drying, thus, confirming their membrane-protecting role during dehydration (Vereyken et al., 2003). Indeed, the protective action of fructans was attributed to their capacity to insert between the lipids of the membrane. The hypothesis of the membrane stabilization by fructans during drought is based on their capacity of binding lipid molecules forming a glass, therefore, reducing the movement of the membrane molecules and this pseudo-rigidity is behind their protective effects (Hinrichs et al., 2001; Vereyken et al., 2003).

Another inevitable consequence of drought response in plants is the production of reactive oxygen species (ROS) and this production is linked to ABA signaling (Cruz de Carvalho, 2008; Hasanuzzaman et al., 2014; Kaur and Asthir, 2015; Hussain et al., 2019). This excess production of ROS known as oxidative burst, is one of the responses of plants to drought triggering defense reaction in plants. Under drought stress, the induction of ROS-generating systems or attenuated ROS scavenging is associated with the damaging oxidative effect and the modifications of cell biomolecules leading the disruption of cellular homeostasis, causing damages to cell and even its death (Mittler, 2017; Janku et al., 2019). Consequently, plants developed two main strategies to control excessive ROS production and reducing cell damages. The first detoxification strategy is achieved by a complex enzymatic system including numerous enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR; Noctor and Foyer, 1998). The second detoxification strategy is achieved by some primary and secondary metabolites possessing antioxidant and scavenging properties such as ascorbic acid, glutathione, carotenoids, tocopherols, and phenolic compounds (Noctor and Foyer, 1998; Isah, 2019). Therefore, this capacity to maintain an antioxidant activity by scavenging ROS has been associated to tolerance of plants to drought and other abiotic stresses as well (Sharma et al., 2012; Noctor et al., 2014). From the biochemical point of view, the metabolic compartmentation of ROS are the chloroplasts, mitochondria, and peroxisomes under light condition, while under darkness, the mitochondria are the main compartment of ROS production (Choudhury et al., 2014). Consequently, during environmental stresses an overproduction of ROS in plants due to disruption of cellular homeostasis, triggers undesirable processes such as lipids peroxidation, proteins oxidation, damage to nucleic acids, enzymes inhibition, and even programmed cell death (PCD) activation ultimately leading to death of the cells [Sharma et al., 2012; see Hasanuzzaman et al. (2020)]. Enhanced production of ROS has also been shown to increase the production of malondialdehyde (MDA) considered as an indicator of oxidative damage and a marker-metabolite of membrane lipid peroxidation (Moller et al., 2007; Ayala et al., 2014; Morales and Munné-Bosch, 2019).

Interestingly, numerous studies have reported the antioxidant (AOA) power of sugars (Faraji and Lindsay, 2004; Couée et al., 2006; Cherkas et al., 2020) by quenching ROS and contributing to stress tolerance (Bolouri-Moghaddam et al., 2010), and this AOA activity seems to be enhanced when sugars interact with phenolic compounds (Faraji and Lindsay, 2004; Lončarić et al., 2018). More interestingly, fructans were also reported to possess antioxidant properties *in vitro* (Stoyanova et al., 2011; Peshev et al., 2013; Pasqualetti et al., 2014).

Fructans, and other sugars as well, have been shown to be better $^\circ$OH radical scavengers in comparison with $O_2^\circ -$ (Stoyanova et al., 2011). Since plants do not possess an enzymatic $^\circ$OH scavenging mechanisms, high concentrations of non-enzymatic antioxidants mechanism are used to neutralize ROS (Gechev et al., 2006). Furthermore, *in-vitro* studies demonstrated good ROS scavenging properties of fructans (Peshev et al., 2013), and similar reactions are thought to occur in planta, especially at higher concentrations (Uemura and Steponkus, 2003). This capacity of fructans for capturing ROS in a wide range of stresses was also highlighted by the study of Nemati et al. (2018) who noted an increase of fructans accumulation accompanied by increased OH radical scavenging activity in 4-day-old seedlings of wheat during drought stress.

Although numerus studies have demonstrated the membrane-protecting roles of the antioxidant activities of fructans, two questions remain yet to be fully answered. Since fructans are synthesized and stored in the vacuolar compartment (Darwen and John, 1989), the first question is how fructans polymers are transported from the vacuole to reach the plasma membrane?

The first clue to explain the solutes flux out of the vacuole is the primary functions of many cells of roots, tubers, and rhizomes to mobilize vacuolar components during the regrowth because as a storage compartment, vacuole is intimately involved in the export of the stored metabolites to their final destination either cytosol or apoplast (Etxeberria et al., 2012). Indeed, fructans are supposed to be transported out of the vacuole similarly to sugars. Because of their high concentration in the vacuole, solutes do not require active transporters. Functional analyses of monosaccharide transporters (Schulz et al., 2011) and sucrose-symporters (Schneider et al., 2011; Schulz et al., 2011) showed the ability of these transporters to efflux from the vacuolar compartment under appropriate conditions and this efflux is controlled by their concentration gradients. Therefore, it could be hypothesized that fructans might be transported and channeled by their specific transporter or passively through anion channels like other solutes

(Blumwald and Poole, 1985; van der Leij et al., 1998; Kataoka et al., 2004; Poschet et al., 2011). However, this hypothesis raises another question on the mode of action of these specific transporters, although the evidence of glucose transporter was reported in Arabidopsis (Poschet et al., 2011), further investigation is needed to elucidate the mode of actions of the potential transporters of fructans and this hypothetical transport pathway.

The second question is related to the ability of fructans to scavenge ROS. Although the question remains yet unclear and the scavenging mechanisms of ROS by sugars not clearly established. Nevertheless, from the chemical and biochemical points of view different studies established the association between soluble sugars accumulation and ROS induced by the high photosynthetic rate in the source leaves (Scarpeci and Valle, 2008; Van den Ende and Valluru, 2009), and similarly sugars starvation also induced ROS accumulation (Couée et al., 2006). On the other hand, sugars have also been found to interact with secondary metabolites known for their strong scavenging power and antioxidants capacities (Bolouri-Moghaddam et al., 2010; Peshev et al., 2013). A study conducted *in vitro* showed that sugars might act jointly with the phenolic compounds in ROS detoxification and the cytosolic antioxidant mechanisms (Van den Ende and El-Esawe, 2013). However, many studies suggest that sugars have direct role in ROS scavenging, but they also act indirectly by triggering other pathways such as the oxidative-pentose phosphate pathway (OPP) which in turn might trigger ROS scavenging (Debnam et al., 2004). Nevertheless, direct or indirect ROS-detoxification roles of sugars including fructans make a strong consensus, and a synergetic interaction between sugars and phenolics form a valuable part of the redox system contributing significantly to abiotic stress tolerance. Nevertheless, the chemical and biochemical mechanisms behind these actions remain still unclear and not clearly elucidated, therefore, requiring further investigation.

FRUCTANS METABOLISM AS CELLULAR MECHANISM OF DROUGHT ADJUSTMENT

Under drought conditions, higher plants were reported to decrease their photosynthetic rate consequently to the decrease of leaf water potential and relative water content (Lawlor and Cornic, 2002), however, there is still a controversy on whether drought limits photosynthetic CO_2 assimilation through stomatal closure or by metabolic impairment in C3 plants (Bunce, 1988; Flexas and Medrano, 2002; Lawson et al., 2003). The different studies are suggesting that the decrease in the photosynthesis rate is caused by stomatal closure in the earliest response of plants at mild to moderate drought, while the downregulation or inhibition of metabolic processes leading to a drastic decrease of RUBISCO is the response of plants to sever drought (Flexas and Medrano, 2002).

On the other hand, it is well-established that sugar metabolism is controlled by phytohormones, specifically abscisic acid (ABA) which is the principal regulator of enzymes and transcript involved in the synthesis pathways and accumulation of carbohydrates including fructans (Van Den Ende et al., 2002; Trouverie et al., 2003; Yang et al., 2004). Indeed, the hormonal regulation of fructans-metabolizing enzymes was first suggested by Bausewein et al. (2012), ABA appears to positively affect reserve of carbon storage in plants and promoting the accumulation of fructans by increasing gene expressions of 1-FFT and 1-SST (Suárez-González et al., 2014; Gasperl et al., 2016). For example, application of exogenous ABA induced an increase of fructans in chicory (Wei et al., 2016), however, in a recent study Mohammadi et al. (2021) reported on the hormonal interaction mechanisms for fructan content and their degree of polymerization (DP). Interestingly, the authors noted that inulin DP increased by an application of exogenous ABA which also interacted by changing and adjusting the effect of auxin (AUX) and ethylene (ETH) hormones. Using chicory as plant model, Michiels et al. (2004) have also demonstrated the response of 1-FEH to ABA and other plant growth regulators, highlighting the complexity of fructans metabolism and it's the regulation.

For the stomatal point of view, the regulation of stomata is complex, and its regulation varies with species and their response to water potential and ABA signal, thus, the mechanisms of the photosynthetic responses to drought is blurry (Liang et al., 1997; Reddy et al., 2004). It was admitted that low water potential in the soil triggers a root-to-leaf chemical (ABA) signal inducing a decrease of water potential and relative water content (RWC) in leaves (Epstein and Grant, 1973; Jones and Turner, 1978; Siddique et al., 2000), triggering therefore stomatal closure, and decrease in the photosynthesis rate (Downton et al., 1988; Cornic, 2000; Escalona et al., 2000).

Morphologically, drought was reported to decrease the rate of leaf expansion by reducing the expansion of the existing cells when root water potential decreases sharply (Munns and Sharp, 1993; Nelissen et al., 2018; Koch et al., 2019), while cell division rate is slowed down under mild drought (Schuppler et al., 1998; Tardieu et al., 2000).

From the metabolic point of view, the biosynthesis of solutes, namely osmoprotectors, is one of the strategies of plants to response and cope with osmotic stress resulting from drought. In order to prevent water loss and maintain cell turgor, plants accumulate numerous solutes, and fructans are one of these major compounds which play a role in osmotic adjustment, membrane protection and ROS scavenging (Pinhero et al., 1997; Hare et al., 1998). Different studies reported the high demand of osmolytes biosynthesis during drought with changes in carbohydrate metabolism and fructans accumulation (Hare et al., 1998; Xue et al., 2008; Ozturk et al., 2021), and interestingly this accumulation even though accompanied by a decrease in the photosynthesis rate, might increase yields of crops (Serraj and Sinclair, 2002). However, the mechanisms of solutes accumulation and osmotic adjustment are not fully understood, one of the hypotheses is that since drought reduces cell division and expansion, fructans accumulate because there are not consumed in growth although no evidence of 'competition' between growth and osmotic adjustment for metabolites was noted (Thomas, 1990). This observation agrees with the findings of Garcia et al. (2011) who reported an increase of fructans synthesizing enzymes (1-SST and 1-FFT) and a decrease in the fructans hydrolyzing enzymes (1-FEH) at the onset of the reduction in soil water and leaf water potential. These findings show well that fructan metabolism is undoubtedly thought to be involved in osmotic adjustment, and fructans are indirectly contributing to this adjustment (Spollen and Nelson, 1994).

CONCLUSION AND FUTURE PROSPECTS

Water scarcity is one of the most important abiotic stresses and might be a consequence of many events such as rainfall deficit or high temperatures. This multidimensional stress is associated to many physiological, biochemical, and molecular changes and responses to drought stress. Indeed, plants depict a wide range of responses drought stress and ability to withstand water scarcity which differs from species to species. Thus, many plants developed different mechanisms to better resist, cope and even resile to or from drought, and fructans biosynthesis is one of these developed biochemical mechanisms in order to maintain cell homeostasis under water-scarcity conditions. It is also well-established that occurrence of drought causes the osmotic disturbance and oxidative stress, and fructans have been demonstrated to play a role in counter-balancing these adversities.

Beside the significant advances made on fructans and their osmoprotective roles, and the various experimental approaches tested to understand the biochemical and molecular mechanisms behind these roles, yet numerous questions remain not answered. For proper understanding of the physiological, biochemical and molecular mechanisms of plants responses to drought and the roles and fate of fructans during and after drought, further investigations are needed. Among the major questions we need to elucidate (i) why fructans content increase during drought while photosynthesis decreases, (ii) how fructans are de-compartmentalized from the vacuoles to protect the membrane, (iii) what the mechanism of ROS scavenging by fructans is, and (iv) last but not least how fructans interact with phenolics to scavenge ROS. Indeed, different hypotheses have been suggested to clearly answer these questions, but more scientific evidences are need in order to clarify the blurry picture we have. Obviously, modern technologies including genomics, transcriptomics, proteomics and metabolomics might be very useful in elucidating these mechanisms and pathways. Consequently, with these techniques, it is likely possible to develop a sophisticated and efficient network in crops response to drought stresses and subsequently help significantly in the improvement of drought-tolerance and productivity of crops.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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