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Dynamic changes in the starch-sugar interconversion within plant source and sink tissues promote a better abiotic stress response

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Abstract

Starch is a significant store of sugars, and the starch-sugar interconversion in source and sink tissues plays a profound physiological role in all plants. In this review, we discuss how changes in starch metabolism can facilitate adaptive changes in source-sink carbon allocation, for protection against environmental stresses. The stress-related roles of starch are described, and published mechanisms by which starch metabolism responds to short- or long-term water deficit, salinity, or extreme temperatures are discussed. Numerous examples of starch metabolism as a stress response are also provided, focusing on studies where carbohydrates and cognate enzymes were assayed in source, sink, or both. We develop a model that integrates these findings with the theoretical and known roles of sugars and starch in various species, tissues, and developmental stages. In this model, localized starch degradation into sugars is vital to the plant cold stress response, with the sugars produced providing osmoprotection. In contrast, high starch accumulation is prominent under salinity stress, and associated with higher assimilate allocation from source to sink. Our model explains how starch-sugar interconversion can be a convergent point for regulating carbon use in stress tolerance at the whole-plant level.

Keywords: starch metabolism; salinity; drought; extreme temperatures; source-sink relations; T6P/SnRK

Abbreviations

^{14}C	^{14}Carbon
3-PGA	3-Phosphoglyceric acid
ADPG	ADP-glucose
AGPase	ADP-glucose pyrophosphorylase
AMY	α-amylase
BAM	β-amylase
cINV	Cytosolic invertase
cwINV	Cell wall invertase
CAM	Crassulacean acid metabolism
DBE	Debranching enzyme
G-1-P	Glucose-1-phosphate
G-6-P	Glucose-6-phosphate
GBSS	Granule bound starch synthase
GWD	Glucan water dikinase
HXK	Hexokinase
INV	Invertase
ISA	Isoamylase
NSC	Non-structural carbohydrates
Pho	Starch phosphorylase
Pi	Inorganic phosphate
PMG	Phosphoglucomutase
PWD	Phosphoglucan water dikinase
RFOs	Raffinose family oligosaccharides
ROS	Reactive oxygen species
T6P/ SnRK	Trehalose-6-phosphate / Sucrose non-fermenting related kinase
TOR	Target of rapamycin

SBE	Starch branching enzyme
SPS	Sucrose phosphate synthase
SS	Starch synthase
SuS	Sucrose synthase
UDPG	UDP glucose
vINV	Vacuolar invertase

1. INTRODUCTION

Starch is a glucose homopolymer that is deposited as discrete granules in plastids. It is the major storage carbohydrate in many plant species, and can represent up to 90% of the total dry weight in organs of perennation (Martin and Smith, 1995; Streb and Zeeman, 2012). For many years, storage starch was the primary focus of investigation because it was the direct source of more than 50% of the calories consumed by the human population (Zeeman et al., 2007a). Recently, however, the starch pools synthesized in photosynthetic source tissues and in non-storage sinks have been shown to be key drivers of overall plant productivity (Sulpice et al., 2009).

Each starch granule consists of millions of polymerized glucose monomers. In contrast to glycogen, which is stored in fungi and animals, starch permits the long-term storage of a higher number of glucose molecules per unit of space (Ball et al., 2011; Cencil et al., 2014; Colleoni and Ball, 2009), with no chemical or osmotic disturbance to the cell. Although polymerized within the granule, these glucose molecules can be quickly accessed as needed to prevent starvation (Zeeman et al., 2007b). Starch likely conferred an evolutionary advantage to plants, which are sessile and thus unable to forage for food.

Because starch evolved as a carbon and energy stockpile in many plants, it seems reasonable that during periods of environmental stress, when assimilation of carbohydrates becomes compromised, starch metabolism can buffer against the adverse effects of stress-induced carbon depletion (Hare et al., 1998; Krasavina et al., 2014; Thomashow, 1999; Wanner and

Junttila, 1999). Starch can act as a sugar source when carbon is needed, or as a sugar sink when sugars are in excess, which may permit an optimal use of these carbon reserves (MacNeill et al., 2017).

Recent reviews have demonstrated the importance of starch for abiotic stress tolerance (Thalmann and Santelia, 2017), and as a modulator of source-sink interactions (MacNeill et al., 2017). In this review, we integrate these concepts by addressing the following question: Can starch metabolism improve the abiotic stress response 1) by regulating starch-sugar interconversion within source and sink tissues, and/or 2) by changing source-sink relations? To answer this, we first examine starch metabolism in source and sink tissues, and its role in plant growth, development, and fitness. Next, we illustrate how changes in sugars and starch can confer a mechanistic advantage under unfavorable conditions, providing examples of associated changes in enzyme activity, as proof of concept. We then summarize the existing evidence to show how the reconfiguration of whole-plant carbon flow can be accompanied by modulation of the starch-sucrose dynamic under stress. Finally, we provide a snapshot of how this could be driven at the molecular level. Our review shows that the redistribution of carbon in source and sink via starch metabolism has merit as a model for stress tolerance.

We wish to note that in this review, carbon distribution into various metabolic pathways is termed *carbon partitioning*, while its distribution from source to sink is termed *carbon allocation*.

2. STARCH METABOLISM AND ITS ROLE IN PHYSIOLOGICAL PROCESSES

Starch granules can be found in almost every tissue of a plant at some phase over its life cycle, and when and where the starch is deposited and subsequently metabolized to sugars shows surprising versatility (Smith and Martin, 1993). Therefore, the pathway of starch metabolism, its regulation and role, varies depending on the tissue, developmental stage, and external factors (Hedhly et al., 2016; Kuang and Musgrave, 1996; Smith, 1999; Tang et al., 2009), as explored below.

2.1 Source tissues

Source tissues produce assimilates from photosynthesis. A portion of these assimilates is used for growth and energy *in situ*, some is stored as starch, and the remainder is allocated to sink tissues, mainly as sucrose (Figure 1A). The partitioning of photoassimilates between sucrose and starch is highly regulated, with the ratio of 3-phosphoglyceric acid to phosphate being a key regulatory checkpoint (3-PGA:Pi) (Figure 1A). These compounds allosterically, and differentially regulate the enzyme ADPglucose pyrophosphorylase (AGPase), which has a high degree of control over starch biosynthesis (Mugford et al., 2014). Under carbon sufficiency, 3-PGA is used to synthesize sucrose for long-distance export to sinks, and, simultaneously, to stimulate source-leaf plastidic starch synthesis. When sink activity is reduced, or when photosynthesis is inhibited at night or due to stress, sucrose export slows and Pi increases in the plastid (Sonnewald and Willmitzer, 1992). This reduces the 3-PGA:Pi ratio and inhibits starch biosynthesis. When sucrose is depleted, starch is then broken down to release stored carbon (Sonnewald and Willmitzer, 1992). Leaf starch is described as 'transitory' because it is accumulated during the day and degraded at night (Smith and Martin, 1993).

There are multiple isoforms of each starch biosynthetic enzyme, as shown in Figure 1A: ADPglucose pyrophosphorylase (AGPase), starch synthases (SSs), starch branching enzymes (SBEs), and starch debranching enzymes (DBEs) (Orzechowski, 2008; Pfister and Zeeman, 2016; Smith, 2012; Streb and Zeeman, 2012; Zeeman et al., 2002). The suite of enzyme isoforms varies among species, leaf developmental stage, and time of day (Colleoni and Ball, 2009). In source tissues, the structure, size and morphology of the granule synthesized lends itself to rapid degradation (Zeeman et al., 2002). Many enzymes are involved in the disassembly of the starch granule, which occurs at night, under environmental stress or during senescence (Figure 1A). The collection of enzymes and the nature of starch granule attacks differ, depending on whether starch is degraded during the night, or during environmental stress (Thalmann and Santelia, 2017). β-amylases (BAM), which hydrolyze starch to release

maltose, have been extensively studied (Fulton et al., 2008), while α-glucan phosphorylase and glucan water dikinase are also major players (Figure 1A). The produced maltose and glucose in plastids are exported to the cytosol to provide hexose phosphates for partitioning into various pathways as shown in Figure 1A (Streb and Zeeman, 2012; Zeeman et al., 2010; Zeeman et al., 2007b).

There is some bifurcation among species in terms of the physiological role of leaf starch (Graf and Smith, 2011). In *Arabidopsis*, where up to 40% of assimilated carbon may be used to synthesize starch during the light period (Dong et al., 2018), starch is used primarily to fuel nighttime growth processes (Graf and Smith, 2011; Sulpice et al., 2009). In contrast, starch in rice leaves accumulates to less than 1% of fresh weight (Cook et al., 2012), and may primarily serve to reduce sugar overflow and its inhibitory effect on photosynthesis (Cook et al., 2012; Okamura et al., 2015). *Arabidopsis*, tobacco, tomato, and potato have 'starch-leaves' and barley, rice, and wheat have 'sugar-leaves' (Cook et al., 2012; Okamura et al., 2015; Stitt et al., 1987), descriptors that reflect not only the ratio of starch-to-sugars in that organ, but also the primary role of transitory starch. In plants with Crassulacean acid metabolism (CAM), starch is degraded to regenerate the carbon acceptor phosphoenolpyruvate for the nocturnal fixation of carbon dioxide, in addition to having the above roles (Weise et al., 2006).

Shifts in the leaf sugar-to-starch flux occur at a critical juncture in carbon availability, allowing starch levels to also be used as a proxy for cellular carbon status (Sulpice et al., 2009). Typically, faster-growing individuals will partition carbon to sugars for rapid metabolic use, while slower-growing individuals have a comparatively reduced need for energy and will partition more carbon into the starch reserve (Purdy et al., 2015; Rebolledo et al., 2012; Sulpice et al., 2009). For these reasons, Sulpice et al. (2009) describe starch as an integrator of growth for *Arabidopsis*, and this role may be applicable to other species.

2.2 Sink tissues

Storage organs, as non-photosynthetic sinks, depend on imported carbon from source tissues to provide the substrates for the biosynthesis of all compounds, including starch (Figure 1B). Sucrose synthase (SuS) and invertase (INV) metabolize sucrose to hexose phosphates, and these enzymes are critical elements of 'sink strength' i.e. the capacity to import assimilates (Koch et al., 1996). Hexose phosphates or cytosolic ADPG (in cereals) are imported into the plastid for starch biosynthesis (Beckles et al., 2001a; Beckles et al., 2001b), via dedicated transporters (Shannon et al., 1998). The starch degradation pathway in storage organs varies from that in leaves (Smith et al., 2005; Smith et al., 2003; Zeeman et al., 2010; Zeeman et al., 2007b). Some starch turnover may occur throughout the development of all starch-storing organs (Lloyd and Kossmann 2015, Thalmann and Santelia 2017b), with perhaps a higher degradative flux in organs that store 'transitory-storage' starch (see section 3), such as *Lotus japonica* embryos and tomato fruits (Andriotis et al., 2010; Lloyd and Kossmann, 2015; Luengwilai and Beckles, 2009; Thalmann and Santelia, 2017). The role of starch in different organs varies and is instrumental in plant progression through the lifecycle as shown in Figure 2.

Intra-organ diversity in starch metabolism also exists. Guard cells have different diel patterns of starch accumulation, breaking it down during the day but accumulating it at night, a trend opposite to that found in the surrounding mesophyll cells (Santelia and Lunn, 2017). Within wheat peduncles one region acts as a starch-source and the other as a sink (Scofield et al., 2009). Species with C_4 leaf metabolism fix carbon in mesophyll cells, but store most of the starch in the bundle sheath cells (reviewed in Weise et al., 2006). Futher illustration of the spatial regulation of starch metabolism was seen in rice mutants, where a loss of culm starch was compensated for by higher accumulation of leaf starch (Cook et al., 2012; Rosti et al., 2007). These studies, described here and summarized in Figure 2, collectively underscore the idea that the substantial plasticity of starch metabolism over space and time is in keeping with its evolutionary role as a 'famine-' or 'stress-' protectant.

3. ADAPTIVE ROLE OF THE STARCH-TO-SUGAR INTERCONVERSION UNDER STRESS

Stress-induced regulation of starch metabolism can increase cellular sugars or increase starch accumulation. As mentioned previously, there are important biological implications for the shift in the ratio of these biomolecules. Much emphasis has been placed on the role of sugars in surviving abiotic stress, but there are examples where enhanced stress response was accompanied by increasing starch biosynthesis. Some of these 'protective' mechanisms will be described under section 4, but are also emphasized in Table 1A and 1B for clarity. Because sugars are metabolites, sensors, and regulators (O'hara et al., 2013), it is not easy to contextualize how changes in concentrations alter their effects on various plant processes under stress occuring across different micro-, macro-, spatial and temporal scales; however, we attempt to do so in Figure 3. Plants normally maintain sugar levels within an optimal range (Figure 3). When exposed to stress, the cellular sugar level may change in different ways: 1) Unfavorable conditions often restrict photosynthesis. As a result, sugar concentration may decrease to 'sugar deficit' levels, that trigger a sugar starvation response, and if extended, lead to 'sugar depletion' (Figure 3). 2) Reduced utilization of sugars as a result of anemic growth under stress may lead to sugar overaccumulation. These high sugar concentrations may be advantageous, providing 'sugar osmoprotection' until they reach harmful concentration which can lead to 'sugar injury' (Figure 3). In stress-tolerant lines or species which have adaptive responses to stress (Balibrea et al., 2000; Pattanagul and Thitisaksakul, 2008; Thitisaksakul et al., 2017a), the starch-to-sugar conversion may be accelerated to promote sugar accumuation to delay a 'sugar deficit', but feedback systems may elicit an increased flux of sugars to starch to postpone the occurrence of 'sugar injury' (Figure 3).

Stress-induced starch degradation increases carbon flux into the hexose phosphate pool (Figure 1), and the spectrum of sugars produced from this pool will reflect the species, tissue, and type of stress experienced (Keunen et al., 2013; Krasavina et al., 2014). Different sugars affect physiological processes in distinct ways as shown in Table 1A: 1) Raffinose family oligosaccharides (RFOs) are superior osmolytes and ROS scavengers compared to other

sugars (Asami et al., 2018; Keunen et al., 2013); 2) The ratio of hexose to sucrose can influence organ size through their distinct regulation of cell osmotic potential and mitotic activity (Beckles et al., 2012; Ruan, 2014); 3) There are also sugar-specific signaling transduction pathways: for example, the Hexokinase (HXK) and the Target of Rapamycin (TOR) pathways are regulated by glucose, the Trehalose-6-phosphate / Sucrose non-fermenting related kinase (T6P/SnRK) pathway by trehalose, and the hexokinase-autonomous sucrose-specific pathway by sucrose (Baena-Gonzalez et al., 2007; Chiou and Bush, 1998; Martin and Hall, 2005; Martinez-Noel and Tognetti, 2018; Rolland et al., 2006; Wingler, 2018). Clearly, the secondary effect of concentration changes in these respective sugars will be highly context-dependent.

4. ADAPTIVE CHANGES IN STARCH CONTENT UNDER STRESS

The accumulation or reduction of starch under various stresses has been found in many studies (reviewed in Thalmann & Santelia; 2017 and shown in Table 1B). A reduction of starch and increase in sugars could be due to 1) reduced starch biosynthesis, or 2) higher starch degradation to sugars. Stress-associated starch accumulation has also been found under various environmental stresses. In this section, we discuss examples of these processes (listed in Table 2), providing a mechanistic basis for some of these observations.

4.1 Increased sugar levels from reduced starch biosynthesis

Water deficit has been documented to repress starch biosynthesis and increase sugars in potato tubers and in spinach, barley, and rice leaves (Geigenberger et al., 1997). AGPase activity was reduced and SPS activated in spinach and potato (Geigenberger et al., 1997; Zrenner and Stitt, 1991), and both SS and AGPase activity were decreased in rice (Sheoran and Saini, 1996), leading to a higher sugar-to-starch ratio. In barley, unlike the other species, there were decreases in both starch and sucrose, but increases in hexoses, suggesting that sucrose hydrolysis provided the sugar for osmoprotection under water deficit (Villadsen et al., 2005).

Salinity-induced restriction of starch biosynthesis has not been as widely reported, and the

studies identified used high concentrations of salt (Table 2). The application of 200 mM of sodium chloride reduced GBSS activity and led to reduced starch content in rice seedlings (Chen et al., 2008). A treatment of 100 mM NaCl in citrus calli reduced the activity of AGPase (5-fold) and caused defects in starch synthesis (Libalweksler et al., 1994). Neither of these studies reported whether sugar levels increased, which is the presumed rationale for reducing carbon flux to starch (Table 1A).

Severe heat stress causes many starch metabolism-related enzymes to function sub-optimally in developing cereal grain (Thitisaksakul et al., 2012). In a range of studied, starch synthase in wheat and barley, GBSSI in barley and rice, SBEII in maize and rice, and AGPase in maize, rice, wheat, and barley, were all inhibited by high temperature, which reduced starch biosynthesis and increased the pool of sugars in the grain (reviewed in Thitisaksakul et al., 2012). The sugars may potentially protect the embryo via multiple processes, at the expense of reserve storage (Table 1A and Section 3).

4.2 Increased sugar levels from accelerated starch degradation

Drought can activate starch-degrading enzymes, leading to an increase in sugars. These enzymes include α-glucan phosphorylase (Zeeman et al., 2004), α-amylase3 (Thalmann et al., 2016), and β-amylase1 (Zanella et al., 2016), the transcripts for which were shown to be activated in osmotically stressed *Arabidopsis* leaves (Table 2). Increased starch mobilization could have sustained both osmolyte accumulation and carbon export to sinks (Table 1A). An in-depth study of the role of β-amylase1 under osmotic stress found that the maltose produced from starch degradation was directed towards the synthesis of proline needed for osmoprotection (Zanella et al., 2016). In another study, data generated by $^{13}CO_2$ labeling of water-stressed clover strongly suggested that starch degradation contributed to increased sugar levels as a direct response (Lee et al., 2008).

Cold stress is widely known to trigger starch degradation. Some β-amylase (BMY) isoforms have been repeatedly shown, through gene expression and functional studies, to be activated

by cold (Fowler and Thomashow, 2002; Jung et al., 2003; Kaplan and Guy, 2004; Kaplan et al., 2006; Seki et al., 2001; Seki et al., 2002). In rice, a *BMY8* mutant (Kaplan and Guy, 2005) and a transgenic line overexpressing *OsMYB30*, a transcription factor that suppresses the expression of *BMY2*, *BMY6*, and *BMY10* (Lv et al., 2017), were incapable of breaking down starch, and both genotypes were cold sensitive. The idea that starch degradation is integrated into a cold-stress response was further shown in poplar, where the *CBF1* transcription factor, a key hub in the plant cold stress tolerance gene network, was shown to directly target *BMY,* providing a clear connection to cold-induced starch degradation and a cold-adaptive response (Peng et al., 2014). Starch glucan water dikinase (GWD) also has a role in plant cold response (Yano et al., 2005). GWD phosphorylates glycosyl residues in the starch granule, priming it for degradation (Zeeman et al 2007a). Mutants lacking this enzyme had higher starch and lower sugars than the wildtype, and were also more cold-susceptible (Yano et al., 2005). These data support the idea that increasing the carbon flux to sugars via starch breakdown helps plants to survive under chilling stress (Table 1A).

4.3 Higher starch accumulation

Mild water deficit, rather than severe drought, can activate the key enzymes of the sucrose-to-starch pathway, such as SuS, SS, SBE, and AGPase, in cereal grain post-anthesis (Thitisaksakul et al., 2012). Studies in wheat (Yang et al., 2004) and rice grain (Zhang et al., 2012) showed that higher activities of the enzymes in this pathway led to greater starch accumulation under water deficit. This phenomenon of increased starch accumulation under mild drought was also seen in *Arabidopsis* mutants, albeit through a loss of β-amylase activity in the guard cells. These lines maintained starch content under drought, as there was minimal degradation of sugars (Prasch et al., 2015; Valerio et al., 2011). Less sugar in the guard cells of these mutants reduced stomatal opening, decreased water loss, and resulted in a better drought response (Prasch et al., 2015; Valerio et al., 2011).

Salinity stress has been shown to induce starch accumulation in source and sink tissues, which can reduce stress-induced growth inhibition (Table 1B). Compelling data for this comes from

339 comparing salinity-tolerant and -sensitive genotypes from a diverse group of species,
340 including *Thellungiella*, rice, tomato, and (transgenic) *Arabidopsis*. *Thellungiella halophile,* a
341 halophytic relative of *Arabidopsis*, increased its accumulation of leaf starch when treated with
342 high concentrations of salt (200, 400, 600 mM), which led to high levels of both starch and
343 sugars (Wang et al., 2013). The accumulation of these carbohydrates was determined to be an
344 important component of the salt-adaptive response of this species. A salt-tolerant rice cultivar,
345 'Pokkali', also accumulated more starch in leaves when grown on high salt compared to the
346 sensitive cultivars studied, permitting continued photosynthesis in the tolerant genotype
347 (Pattanagul and Thitisaksakul, 2008). A similar result was seen in tomato (Balibrea et al.,
348 2000). Both the salt-tolerant and -susceptible tomato genotypes increased sugars in the mature
349 leaves (presumably source leaves) as salinity progressed over 21 days. However, the tolerant
350 line had 2- and 3-fold higher starch content (Balibrea et al., 2000). In salt-tolerant transgenic
351 *Arabidopsis* that ectopically expressed a plastid-localized protein kinase (MSK4) cloned from
352 *Medicago sativa*, starch increased 4-fold to adjust to 150 mM salt stress, with an
353 accompanying increase in sugars (Kempa et al, 2007). In all of these examples, conversion of
354 a portion of the sugars to starch can minimize the physiological disruption of excess sugars in
355 the source leaf as described in Figure 3 and Table 1B. Another interesting phenomenon is the
356 role of starch as an ion 'flocculant.' When common reed (*Phragmites australis* [(Cav.) Trin.
357 ex Steudel]), is exposed to high concentrations of harmful ions (Table 1B), these ions may
358 become entrapped by starch or starch-derived glucan, thus preventing them from being
359 systemically spread throughout the plant and upsetting cellular osmotic balance. High sodium
360 ion (Na+) concentrations stimulated starch accumulation in common reed, with the Na+
361 becoming entombed within the starch granule (Kanai et al., 2007). Cadmium stress also led to
362 higher stem starch in this species and to the subsequent production of a starch-dericed alpha-
363 glucan that enmeshed the cadmium (Higuchi et al., 2015). It is not known if starch "ion-
364 trapping" is exclusive to common reed or if it operates general in plants, but it is intriguing,
365 and it provides further examples of the versatility of starch as a stress-protectant.
366

Heat tolerance may be engendered by higher accumulation of starch. This was borne out in tomato pollen grain (Nepi et al., 2001). Heat-tolerant tomato cultivars, in contrast to susceptible genotypes, maintained pollen starch content under heat stress, contributing to improved fecundity (Firon et al., 2006; Giorno et al., 2013; Kumar et al., 2015; Pressman et al., 2002). Paradoxically, an initial and brief exposure to elevated temperatures can stimulate a transient increase in cereal grain starch. This phenomenon has been seen in barley (Wallwork et al., 1998), rice (Bahuguna et al., 2017), and wheat (Nicolas et al., 1984), and was supported by increases in starch biosynthetic enzyme activity (Wallwork et al., 1998). In barley, there was an uptick in SuS, AGPase, GBSS, and SBE activity (Wallwork et al., 1998). As the stress progressed, heat became detrimental to the activity of starch enzymes, and starch content was reduced. It is possible that exposure to a mild or short-term stress can also have a 'hormetic' effect on grain starch, as seen here, and also under mild salinity in rice (Thitisaksakul et al., 2015), and mild water deficit in wheat and rice (Yang et al., 2004; Yang et al., 2001; Zhang et al., 2012). This could prime carbon storage for later use should stress intensity increase or become prolonged (Table 1B).

Cold stress can also trigger higher starch accumulation. Quinoa cotyledon incubated at 5°C showed a transient increase in starch content for two days, but after six days of exposure to chilling, starch decreased in concert with increased sugar content (Rosa et al., 2009a). Starch accretion after two days of cold treatment may be an early cold-stress response designed to 'bank' sugars as starch (acting as a sugar sink) for later osmoprotection (Figure 3). The increases in starch and sugars at various timepoints were synchronous with AGPase and SPS activities, respectively, in the chilled cotyledons compared to the unstressed control (Rosa et al., 2009a). Cold also triggered starch accumulation in sensitive tomato species possibly as a protective response (Venema et al., 1999). Starch content in leaves was four- to five-fold higher in the cold-sensitive *Solanum* spp., but was unchanged in three cold-adapted wild species studied (Venema et al., 1999). Further, sugar levels and photosynthesis were not altered in the tolerant species, but either increased or decreased in the susceptible ones (Venema et al., 2000a; Venema et al., 1999; Venema et al., 2000b). Leaf starch hyperaccumulation in the chilled sensitive genotypes could be a short-term way to cope with

injurious sugar concentrations due to cold-induced growth cessation (Figure 3 and Table 1B). A time-course of isotopic labeling to monitor carbon flow into different compounds and between tissues would provide clarification.

5. ALTERATIONS IN STARCH METABOLISM & SOURCE-SINK RELATIONS IN PLANT RESPONSE TO ABIOTIC STRESS

Stress induces changes in the source-sink relationship (Ceusters et al., 2017). Stress often decreases photosynthetic capacity, reducing source-sugar supply and allocation to sinks (Ceusters et al., 2016), sometimes with consequences for plant allometry (Barnabas et al., 2008; Lloyd, 1980; Moles et al., 2018). The sinks often respond by reducing their activity and strength. This leads to the sub-optimal operation of phloem sugar transporters (Gong et al., 2015; Yamada et al., 2010), or to a loss of phloem integrity e.g. callose deposition (Lemoine et al., 2013), further blocking phloem from loading at the source, and compounding leaf sugar buildup. Excess source sugars may protect sensitive membranes and proteins from dehydration due to cold, drought, salinity, or even heat, but they are largely inaccessible for growth, and may instead eventually inhibit photosynthesis, short-circuiting further photoassimilation (Lemoine et al., 2013; Paul and Foyer, 2001). In many species, starch metabolism is an integral link that connects carbohydrates in the source with those allocated to the sink (Schlosser et al., 2012). Its judicious metabolism may optimize carbon use, and lessen the harmful effect of stress exposure (Figures 4, 5, and Section 3).

Environmental stress can also change carbon partitioning in addition to changing carbon allocation among tissues. This can be facilitated by the selective or sequential metabolizing of starch in either the source, the sink, or both. For example, in the sink, the effective sugar concentration is kept low by its conversion to starch, and this in turn could increase the flux of assimilates from the source, where concentrations are high, to the sink. Whether the starch in a particular tissue acts as a 'sugar source' or a 'sugar sink' as part of the stress response, will be determined in part by the developmental stage of the plant, which in turn is mediated by hormonal signaling pathways (Yu et al., 2015), will partially determine if the starch in a

particular tissue acts as a 'sugar source' or 'sugar sink' as part of the stress response (Yu et al., 2015). As shown in Figure 4, the culm and root in young cereals are the primary sinks and are nurtured from the starch stores in the germinating grain. When transitioning to the reproductive stage, the flag leaf, and especially the culm, become the primary source for the rapidly developing flowers and grain. Stress imposed during the transition from the juvenile to the adult stage, will cause carbon to be redirected the towards adaptive mechanisms to survive the unfavorable period, rather then investing them into reproduction (Figure 4). In this section, we examine examples of starch redistribution among tissues, sometimes with an accompanying shift in biomass, as a response to abiotic stress. Evidence derived from seedlings and the reproductive stage are described separately because of source-sink developmental transitions (Figure 4).

5.1 Drought.

Seedling stage. In wheat seedlings under mild water deficit, Hu *et al.,* (2015) showed there to be an accompanying increase in carbohydrate metabolism in source organs and a subsequent export to roots, which increased the relative growth rate of the latter (Hu et al., 2015). Leaf growth was inhibited, but lateral root development was stimulated, presumably to permit better foraging for water. Another example can be seen in drought-tolerant rice seedlings exposed to a water potential range of -0.47 to -0.52 MPa (Xu et al., 2015). Stressed seedlings had lower starch in the stems and leaves, and a higher proportion of dry matter and soluble sugar in the roots. This was supported by an increase in leaf SPS and root INV activity, and the transport of more sucrose from leaves to roots. Similar results were shown in rice seedlings (Luquet et al., 2008), where a decrease in source leaf starch, and an increased starch buildup in both sink leaves and roots was likely a mechanism for surviving drought.

Reproductive stage. Drought can also cause increased carbon allocation to reproductive organs for storage as starch. For example, under water stress, drought-resistant beans were shown to efficiently mobilize leaf carbon towards the seeds, while the sensitive cultivar did not (Cuellar-Ortiz et al., 2008). Pulse-chase labeling of leaves showed reduced ^{14}C in the leaf

454 starch, in parallel with increased ^{14}C-starch content in immature pods. This shift in ^{14}C
455 towards the sink was matched by higher sink-to-source biomass in the resistant cultivar
456 compared to the sensitive line. Yang *et al*. (2001) also demonstrated, through ^{14}C feeding and
457 enzyme assays, that under a mild water deficit, there was enhanced starch remobilization to
458 sugars in rice culm, accelerated rate of import into the grain, and higher grain starch
459 accumulation (Yang et al., 2001).
460
461 **5.2 Salinity.**
462 **Seedling stage**. Preferential allocation of starch to sinks was observed in transgenic rice
463 seedlings overexpressing a glycogen synthase kinase 3-like (GSK3-like) homologue
464 (Thitisaksakul et al., 2017a). Some members of this subfamily have been identified as either
465 positive or negative regulators of plant response to salinity stress, and in some examples, the
466 changes have been associated with higher starch and sugars (Kempa et al., 2007;
467 Thitisaksakul et al., 2017a). The isoform studied in rice, *OsGSK5*, was associated with higher
468 root starch accumulation in seedlings (Thitisaksakul et al., 2017a). When plants were exposed
469 to a short-term, high-salinity shock (150 mM NaCl), ^{14}C-labelled leaf photoassimilates were
470 exported at a higher rate to the roots and stored as starch. The roots of the transgenic line had
471 improved biomass, which the authors proposed could be helpful in terms of adaptation to
472 salinity stress.
473
474 In a study of a salt-tolerant and a salt-sensitive tomato genotype exposed to different salinity
475 levels, the authors concluded that, in spite of higher SPS activity, photosynthesis in the
476 tolerant line was maintained under salinity (50 and 100 mM NaCl), because the higher starch
477 accumulated in the mature source leaf could buffer against the interference of sugars in
478 photosynthesis (Balibrea et al., 2000). Further, there was greater root biomass in the tolerant
479 line with a lower proportion of total carbohydrates and insoluble matter (which is presumed to
480 consist mainly of starch) compared to the sensitive tomato. This may be explained by the
481 efficient use of carbon for growth in the former, whilst the failure to use carbohydrates led to
482 the accumulation of starch and sugar in the sensitive line. Relatively low starch content is

typically characteristic of tissues undergoing rapid growth (Purdy et al., 2015; Rebolledo et al., 2012; Sulpice et al., 2009).

Reproductive stage. In mature tomato plants exposed to 50 or 100 mM NaCl, the allocation of assimilates was monitored by ^{14}C-pulsing of leaves (Gao et al., 1998). Initially, most of the label was allocated to the root, but after fruit development, the ^{14}C label was preferentially allocated to the fruit. Interestingly, ^{14}C partitioning to starch was increased via accelerated AGPase activity in the immature fruits. This result was confirmed in studies of Micro-Tom tomato by Yin *et al.* (2010), where high concentrations of salt stimulated starch accumulation in unripe fruit. This was accompanied by increased ^{13}C-labelled sugar import from source tissues. *AGPase* was up-regulated at the transcriptional level via an ABA-dependent pathway due to the osmotic effect of high salt concentration. These changes in sink activity after salt exposure are hormone-mediated, and are driven by alteration in sucrose transporters and sucrolytic activity (Albacete et al., 2014; Ghanem et al., 2009).

5.3 Temperature stress

Heat. Carbohydrate-driven changes in source-sink relations may also be an adaptive response to heat stress. For example, the remobilization efficiency of non-structural carbohydrates (NSC) from source tissues during grain filling under heat was found to vary in tolerant and sensitive wheat (Tahir and Nakata, 2005; Tahir et al., 2005). A similar observation was made by Plaut et al. (2004), where stress-tolerant wheat increased the transport rate of NSC from stems and leaves to the kernel, compared to the stress-susceptible genotype (Plaut et al., 2004). This response would ensure maximal grain yield, ensuring 'reserve security' for the germinating seedling (Figures 2 and 4).

When multiple heat-tolerant and heat-sensitive rice cultivars were compared side-by-side, the tolerant lines all had lowered NSC content in the stem culm under high temperature, due to increased remobilization to the grain (Tanamachi et al., 2016). Heat did not interfere with the starch-related enzyme activity in the tolerant genotypes compared to the susceptible ones. Prior studies show that the transcripts of the *AGPS2b* (*AGPase subunit 2b*) and *Amy3E (α-*

511 *amylase 3E*) genes normally decrease and increase, respectively, under heat stress, and are
512 associated with lower grain starch (Thitisaksakul et al., 2012). These transcripts were not
513 altered by heat stress in the most tolerant genotypes, but were in the most susceptible ones
514 (Tanamachi et al., 2016). Starch accumulation in the tolerant genotypes was unaffected,
515 contributing to heat tolerance by maintaining the sink strength.

516 This observation was also made in a different study of rice. The grain starch content of a heat-
517 tolerant genotype was unaltered after high night temperature, but decreased 30% in the
518 sensitive genotype 20 days post fertilization (Bahuguna et al., 2017). CwInv, vInv and SS
519 enzyme activities measured in the flag leaf (source) and the panicles (sink) were impaired in
520 the susceptible line, but either were unaltered, or showed minor changes in the tolerant line
521 (Bahuguna et al., 2017). Interestingly, in the sensitive line, sugar content of the rachis (source)
522 was low, while in the spikelet (sink), it was high, and the opposite was true for the resistant
523 line (Bahuguna et al., 2017). This suggests that the resistant genotypes maintained grain
524 starch biosynthesis in the grain under stress, thereby utilizing imported sugars, which
525 contributed to their tolerance.
526

527 **Cold.** When petunia response to a low temperature treatment was investigated, reduced
528 source-sink allocation was found: more sugars and starch accumulated in source leaves, while
529 starch content decreased in the sink apex (Bauerfeind et al., 2015). Reduced cwINV activity
530 in the sink confirmed the reduced sugar import and utilization, and indicated a prioritization of
531 carbon for the source at the expense of sink growth. Higher 'source-sugars' could bolster the
532 sensitive photosynthetic tissues against chilling injury through their osmoprotectant
533 properties, which has been demonstrated to be a core element of plant cold stress response
534 (Kaplan et al., 2006; Nagler et al., 2015; Peng et al., 2014). The higher starch in the source, in
535 turn, could act as a dynamic metabolic sink to keep sugar levels within the protective range
536 (Figure 3).

537 Based on how starch may alter source-sink relations under the various abiotic stresses
538 discussed above and in Figure 3, we develop a model to show that the starch-sugar conversion

in source and sink tissues can regulate carbon availability and balance at the whole plant level. Under stress, one outcome (shown in Figure 5A), is inhibited sink growth, which reduces demand from the source, leading to high source sugar accumulation. Sugar may also accumulate from stress-induced 1. blockage of starch biosynthesis, 2. acceleration of starch degradation, or 3. the amplification of cycles of starch synthesis and degradation. In sink tissues, reductions in starch biosynthesis, and the breakdown of existing starch reserves all have been demonstrated to promote sugar accumulation (See Figure 5A legend). The increased sugar in source and sink can act as osmoprotectants and provide substrates for respiration which may be advantageous (Figure 3). Figure 5B shows adaptive mechanisms related to higher starch accumlation. The elevated sugar levels that initially provide osmoprotection may eventually feedback inhibit photosynthesis. To prevent further impedment of photoassimilation, sugars can be converted and stored as starch. They may also be exported to the sinks where their unloading can be accelerated due to sink-starch biosynthesis. This modulation of whole plant carbon relations can maintain sink strength and reduce biomass loss during the reproductive growth stage.

6. SUGAR SIGNALING PATHWAY – RELATION TO STARCH MODULATION

How starch metabolism is integrated into stress signal transduction pathways to alter source-sink relations is still largely unknown, but recent data is helping to fill in the gaps. The T6P/SnRK1 signaling cascade in particular may be an important way of linking variation in starch metabolism to an appropriate stress response (Jamsheer and Laxmi, 2015), with an ensuing change in source-sink allocation (Griffiths et al., 2016a; Paul et al., 2017; Yu et al., 2015). The kinase SnRK1 and the metabolite T6P bind cooperatively with antagonistic effects (Delatte et al., 2011; Nunes et al., 2013; Zhang et al., 2009). The relative level of SnRK1 and T6P responds to energy changes, shifting tissues towards carbon conservation/storage under feast conditions (high T6P/SnRK1), or towards carbon utilization/remobilization under starvation (low T6P/SnRK1) (Paul et al., 2017). High T6P relative to SnRK activates storage pathways such as starch biosynthesis, especially in the sink (Bledsoe et al., 2017; Griffiths et al., 2016a; Lawlor and Paul, 2014; Martinez-Barajas et al., 2011) and likely in a tissue-

specific manner (Wurzinger et al., 2018). Conversely, reduced T6P signals 'starvation', activating SnRK1 for the mobilization of starch and other reserves to generate sucrose for transport to the cells that need it (Bledsoe et al., 2017; Griffiths and Paul, 2017; Yu et al., 2015). SnRK1 subunits can bind to starch granules and are associated with maltose, and could conceivably act as cytosolic sensors of released glucose (Avila-Castaneda et al., 2014).

Many experiments show one or more of the following: that T6P/SnRK1 a) responds to environmental stress (Im et al., 2014; Li et al., 2013; Lin et al., 2017; Nuccio et al., 2015; Paul et al., 2017), b) can activate changes in starch metabolism (Avila-Castaneda et al., 2014; Griffiths et al., 2016b; Henry et al., 2014; Lin et al., 2017; Loreti et al., 2018; Wang et al., 2017; Wang et al., 2012), and c) can activate changes in source-sink relations (Bledsoe et al., 2017; Griffiths et al., 2016b; Henry et al., 2015; Kretzschmar et al., 2015; Lin et al., 2014). More data is needed to strengthen the connectivity among these physiological and biochemical events (Griffiths and Paul, 2017; Griffiths et al., 2016a; Henry et al., 2015; Paul et al., 2017; Yu et al., 2015). Still, when all of the data are considered, it seems compelling that T6P/SnRK1 activity is a key regulator of assimilate distribution between sink and source to enhance survival under abiotic stress, and that starch metabolism, i.e. accelerated synthesis or remobilization, plays an indispensable role in the process (Yu et al., 2015).

7. FUTURE PERSPECTIVES

Unpredictable climate patterns, increasing urbanization, and rapid population growth mean that resources needed for intensive agriculture are becoming limited. Sporadic and persistent stresses will become increasingly commonplace, and plants will need to rapidly sense and transmit stress signals to the cell to allow the proper adjustment of growth for resilience. These adaptive responses will include changes in carbon use. However, our current knowledge of carbohydrate changes in the stress response, and the mechanisms underlying these changes, is fragmentary. We propose the following questions for consideration:

1. How does starch-sugar conversion change in the short and long term under stress conditions? Combining carbon flux analysis with changes in enzyme activity and components of the signal transduction pathways, e.g., T6P in source and sink, would provide a multidimensional view of how starch and its regulation varies under stress. It would also help pinpoint the spatial- and temporal-specific genetic engineering strategies required.

2. Can a plant with improved stress response be engineered by altering starch biosynthesis and sink-related enzyme activity? The activities of sucrose synthase, invertases, and their regulators are at critical metabolic junctures, keeping hexoses, sucrose, and starch pools in equilibrium (Figure 5). These proteins could be engineered to only express at high levels after stress activation to reduce pleiotropic effects on plant growth under normal conditions.

3. How is starch metabolism integrated into signal transduction networks? Posttranslational modification of starch by redox modulation will be important, and the mechanisms underlying it have been relatively well dissected (Skryhan et al., 2018). Still, there must be many hitherto undiscovered players at this nexus, including transcription factors, miRNAs, and other epigenetic agents. For example, BRZ-BAM7 and BRZ-BAM8 proteins have β-amylase domains but act as transcription factors to moderate growth within the brassinosteroid pathway (Reinhold et al., 2011). These proteins may act as metabolic sensors under stress-induced sugar starvation to help regulate growth (Reinhold et al., 2011). In cotton anthers, heat stress demethylates β-amylase, leading to starch degradation and increases in sugars (Ma et al., 2018), suggesting a role for epigenetic modulation of starch metabolism under stress. The following approaches may uncover genes that integrate carbohydrate metabolism and plant stress response: (a) intelligently designed mutant screens using a reporter gene fused to sugar-responsive promoters, (b) monitoring stress-induced changes at the epigenomic level, (c) developing gene co-expression networks generated under abiotic stress, and (d) using yeast two-hybrid and co-immuniprecipitation to target candidate proteins interacting with those involved in carbohydrate metabolism.

8. CONCLUSIONS

Starch serves a multitude of purposes throughout the life cycle of the plant. We propose that it functions as a protectant against abiotic stress, in part by its ability to influence whole-plant carbon allocation through its interconversion with sugars. Stress-induced flux of starch to sugars increases the concentration of the latter, and offers osmoprotection and rapid energy supplies for protective functions. Stress-induced starch accumulation has different effects dependent on tissue type. In the source, it can alleviate excess sugars that repress photosynthesis, while in non-photosynthetic tissues, it can maintain sink strength, act as statoliths in roots, and also provide a maximal carbon reserve for the next generation. These changes would enable short-term survival, but over a longer term, could influence whole-plant morphology, yield, and even crop quality. We developed a framework within which to interpret stress-induced changes in carbohydrate metabolism and how they may be advantageous in different situations. The signal transduction mechanisms underlying this movement of carbon have yet to be delineated, but the T6P-SnRK pathway may feature prominently in this role. Plants are confronted by an ever-changing environment and must battle a multiplicity of stresses. This requires having an arsenal of responses that can be deployed as needed. We have provided evidence to support the view that starch metabolism, as a mechanism for changing sugar availability, is a key convergence point in plant stress response.

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COMPETING INTERESTS

The authors declare that they have no competing financial, professional or personal interests.

FIGURE LEGEND

Figure 1. Starch biosynthesis and degradation pathways in source and sink tissues. A. Starch metabolism in photosynthetic source tissues. (Note: Several steps have been omitted for clarity). The Calvin cycle produces triose phosphate and other carbon substrates. AGPase-catalyzed synthesis of ADPG is the first step in the starch biosynthetic pathway, and is activated by a high 3-PGA:Pi. GBSS and SSs elongate glucan chains of starch, and SBE creates linkages in the starch semi-crystalline structure. DBEs maintain starch crystallinity (Mouille et al., 1996). GWD and PWD phosphorylate starch, and BAM with other enzymes (not shown) are needed to degrade starch completely into maltose and glucose. The degradation products are exported into cytosol to synthesize sucrose by SPS, or used for further metabolism. Sucrose can be loaded into phloem and transported into the sink tissues. **B. Starch metabolism in non-photosynthetic sink tissues.** Imported sucrose can be stored in the vacuole for future degradation, but can also be degraded by INV into glucose and fructose, or by SuS into fructose and UDPG, which provide substrates for metabolic processes in cytosol and starch synthesis in amyloplasts. Depending on species, lipid, protein, or sugar fluxes may predominate in the tissue during storage as opposed to starch. ADPG, ADPglucose; UDPG, UDP glucose; PGM, phosphoglucomutase; AGPase, ADP-glucose pyrophosphorylase; GBSS, ground bound starch synthase; SS, starch synthase; SBE, starch branching enzyme; AMY, α-amylase; BAM, β-amylase; Pho, starch phosphorylase*;* GWD, glucan water dikinase; PWD, phosphoglucan water dikinase; SPS, sucrose phosphate synthase; SuS, sucrose synthase; INV, invertase, vINV and cINV are vacuolar and cytosolic INV. **Key**: circles are membrane transporters; metabolites and biomolecules are in boxes; enzymes are in ovals; dashed lines indicate membrane transport; lines in red indicate the flux from starch-to-sugars.

682 **Figure 2. Role of starch in diverse heterotrophic tissues. A) Gametophytes**. Starch
683 biosynthesis increases sink capacity in pollen grain and ovaries early in development but is
684 degraded to sugars to fuel development (Datta et al., 2002; Lee et al., 2016; Niewiadomski et
685 al., 2005). **B) Guard Cells**. Starch is degraded to malate during the day, creating a positive
686 osmotic pressure that leads to water influx to guard cells and stomatal opening **(Daloso et al.,**
687 **2017; Horrer et al., 2016; Santelia and Lunn, 2017)**. **C) Other Starch-storing organs.** In
688 some tissues, starch is stored early in development and then degraded within an actively
689 developing sink, this includes fruits (e.g. apples, tomatoes, kiwi, and banana) (Dinar and
690 Stevens, 1981) and leguminous embryos (e.g. oilseeds like soybean and *Arabidopsis*)
691 (Andriotis et al., 2010; Andriotis et al., 2012; daSilva et al., 1997; Kuang and Musgrave,
692 1996; Luengwilai and Beckles, 2009; Martin and Smith, 1995). **D) Starch-rich perennating**
693 **organs: endosperm and tubers**. Store carbon and energy for the next generation during
694 germination or sprouting (Martin and Smith, 1995; Pfister and Zeeman, 2016). **E) Culms**.
695 Store assimilate in cereals for allocation to grain postanthesis (Cook et al., 2012; Nakano et
696 al., 1995). This starch enhances stress response (Blum, 1998) (Yang et al., 2001), lodging
697 resistance (Ishimaru et al., 2008; Kashiwagi et al., 2008; Ookawa et al., 2010), and influences
698 plant architecture by modulating tiller angle in rice (Higuchi et al., 2015; Okamura et al.,
699 2015). **F) Roots**. Starch statoliths may aid root depth perception (Baldwin et al., 2013; Berut
700 et al., 2018; Perrin et al., 2005) with implications for plant stress response.
701

702 **Figure 3. Adaptive responses of sugars in source tissues.** This image shows different
703 mechanisms by which sensitive and tolerant plants can survive environmental stress by
704 altering sugar and starch content. Plants will normally maintain sugar levels within an optimal
705 range. When exposed to stress (T_0; Time zero), the cellular sugar level may change in
706 different ways: 1) In stress-sensitive lines or species (shown as the straight line), unfavorable
707 conditions restricts photosynthesis and sugar concentration decreases to a range that can be
708 called a 'sugar deficit'. As the duration of the stress progresses, sugars become severely
709 limiting to levels that trigger a sugar starvation response (T_a), and then, finally, to sugar
710 depletion (T_b). In stress-tolerant lines or species which have adaptive responses to stress

(shown as the dash line), the starch-to-sugar conversion may be accelerated to replenish sugars for respiration and basic metabolism for survival, which could delay the timepoint when sugar reaches starvation levels (T_a'), or the time to depletion (T_b'). 2) In stress-sensitive lines or species (shown as the straight line), T_1 depicts the time at which sugar level exceed that needed for 'sugar sufficiency.' Sugar overaccumulation may be due to inhibited export, or reduced utilization of sugars as a result of anemic growth under stress. These high sugar concentrations may initially be for osmoprotection until the timepoint when it reaches the harmful 'sugar injury' levels (T_2), and thereafter, when the highest physiological levels of sugar are accumulated (T_3). In some stress-tolerant lines or species (shown as the dashed line), the rate of the starch-to-sugar conversion can be accelerated to promote sugar accumulation. Therefore, osmoprotection is invoked at an earlier timepoint (T_1'). When sugar levels are close to harmful, which could inhibit photosynthesis, starch accumulates to reduce the inhibition and postpone the occurrence of sugar injury (T_2').

Figure 4 Developmental source-sink transitions showing the movement of starch and sugars. Starch accumulation and utilization in many species can be used as a proxy for determining if that tissue acts as a sink or source, and can influence the direction of carbon flow between tissues. These biochemical and physiological processes will require adjustment under stress, but the nature of this adjustment will depend on source-sink interaction, which is predicated on plant developmental stage. **A)** The endosperm of imbibed seeds are sources, with almost no associated sink activity until the development of the embryo (Rosa et al., 2009b). **B, C)** In young seedlings, most leaves will act as sinks, but the strongest sink is the root. The injection of energy and carbon into the root from increased starch would help to acquire water and nutrients, and simultaneously reduce investment into tissues needed for photosynthesis at this early stage. **D)** In young cereals, the culm and root are the primary sinks, at the reproductive stage, the flag leaf and especially the culm are the primary source. **E)** At the reproductive stage, the carbon investment is predicted to be towards the perennating organ. Not shown are species where tubers and roots may be strong sinks during plant growth, but during resprouting, they become the primary source.

Figure 5. A model of how starch may alter source-sink relations under abiotic stress. The starch-sugar conversion in source and sink tissues can regulate carbon availability and balance at the whole plant level. **A**) **Biological processes leading to sugar accumulation**. **B) Mechanisms for alleviating excess sugar accumulation.** Numbers on the image indicate references in support of the model as follows: [1] (Chen et al., 2008); [2] (Libalweksler et al., 1994); [3] (Theerawitaya et al., 2012); [4] (Zeeman et al., 2004); [5] (Kakumanu et al., 2012); [6] (Todaka et al., 2000); [7] (Kempa et al., 2008); [8] (Zrenner and Stitt, 1991); [9] (Sicher, 2011); [10] (Oparka and Wright, 1988); [11] (Geigenberger et al., 1997); [12] (Wang et al., 2013); [13] (Pattanagul and Thitisaksakul, 2008); [14] (Kempa et al., 2007); [15] (Xu et al., 2015); [16] (Hu et al., 2015); [17] (Yang et al., 2004); [18] (Zhang et al., 2012); [19] (Gao et al., 1998); [20] (Thitisaksakul et al., 2017a).

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Role of sugars in stress response	Stress-induced changes in sugar content	Mechanism for better stress response	References
Signaling and regulatory molecules	↑ Monosaccharides and disaccharides	Sugars are integrated with stress signal transduction pathways, signaling carbon sufficiency or starvation and can have hormone-like actions.	(Kircher and Schopfer, 2012; Kunz et al., 2014; Mason et al., 2014; Morkunas et al., 2012; Rolland et al., 2006; Ruan, 2014; Smeekens et al., 2010; Smith and Stitt, 2007; Usadel et al., 2008)
Energy and carbon building blocks	↑ Monosaccharides and disaccharides	Sugars are the most efficient respiratory substrates needed for the biosynthesis of protective proteins and compounds, especially when photosynthesis is inhibited under stress.	(Lambers, 1985; Taiz and Zeiger, 2010)
Compatible solutes	↑ Various sugars	1. Sugars protect sensitive membranes and proteins and 2. Increase cell turgor pressure to maintain cell volume.	(Krasensky and Jonak, 2012) (Krasavina et al., 2014) (Tarkowski and Van den Ende, 2015); (Hasibeder et al., 2015; Hutsch et al., 2015; Jensen et al., 1996); (Balibrea et al., 2000; Chen et al., 2013; Kerepesi et al., 1998; Martinez-Ballesta et al., 2006; Sultana et al., 1999)
Reactive Oxygen Species (ROS)	↑ RFOs, sugar alcohols, and disaccharides	Sugars are the only options for offsetting the negative effects of °OH radicals, which can only be neutralized non-enzymatically.	(Keunen et al., 2013); (Asami et al., 2018; Keunen et al., 2013)

Table 1A: Proposed mechanisms to explain how stress-induced changes in sugars might alleviate plant stress response

Table 1B: Proposed mechanisms to explain how stress-induced changes in starch might alleviate plant stress response

Role of Starch in Stress	Stress-induced changes in starch	Mechanism for better stress response	References
Act as a sugar-sink	↑ Starch biosynthesis in source	Conversion of sugars to starch in source tissues may prevent the high sugar levels that can inhibit photosynthesis and also cause accelerated senescence.	(Rosa et al., 2009b)) ((Paul and Foyer, 2001)
Increase sink strength	↑ Starch biosynthesis in sinks	Increased sugar unloading at the sinks will alleviate a sugar backlog at the source to promote continued photosynthesis, especially under salt stress. The starch accumulated may be later degraded to sugars to provide nutritional support or to attract agents of dispersal (fruit).	(Gao et al., 1998; Thitisaksakul et al., 2017a; Thitisaksakul et al., 2017b; Yin et al., 2010)
Changing root growth and biochemistry	↑ Starch accumulation ↓ Starch degradation	1. Starch is stored in roots during stress for later remobilization to support root growth when favorable conditions are restored. 2. Under salinity, higher starch is proposed to increase starch statoliths and gravitropic response, and to direct root growth for the acquisition of nutrients, minerals, or water. It may also be degraded to act as a compatible solute.	1: (Luquet et al., 2008) 2: (Thitisaksakul et al., 2017b) (Baldwin et al., 2013)
Ion trapping	Ion induced increases in ↑starch accumulation	In reeds, Na+ ions were immobilized within starch granules, and exposure to Cadmium resulted in increased starch and the entrapping of Cd in a starch-derived glucan. Starch may prevent the systemic spread of harmful ions to sensitive tissues.	Salt: (Kanai et al., 2007); Cadmium: (Higuchi et al., 2015)
Altering plant allometry	Redirection of starch deposition to different tissues	1. Reduced starch storage in gametophytes led to flower abortion and to higher vegetative-to-reproduction tissue ratio. 2. Mobilization of starch from some tissues (leaf, stem) for transport and re-synthesis to starch in others e.g. in roots (for growth or storage) or in the grain to act as a reserve for the next generation.	(Barnabas et al., 2008; Geiger et al., 1996)

Providing an escape mechanism	↑ Synthesis during grain filling	1. Accelerated starch biosynthesis when stress is experienced *after* anthesis in the grain may be an escape mechanism, accumulating reserves for the next generation. 2. Mild stress applied during the vegetative cycle may have a hormetic effect, and lead to higher starch accumulation during grain filling.	1: (Barnabas et al., 2008; Yang and Zhang, 2010; Yang et al., 2004)) ((Thitisaksakul et al., 2012) 2: (Kunz et al., 2014)

Table 2. **Stress-induced changes in starch metabolism in source or sink tissues of various species**

Starch metabolism	Stress	Species	Tissue	Mechanism	References
Reduced biosynthesis	Drought	Spinach	Leaf	↓AGPase activity and 3-PGA:Pi; ↑sucrose and SPS.	(Geigenberger et al., 1997) (Zrenner and Stitt, 1991)
		Potato	Tuber	↓AGPase activity and 3-PGA:Pi; ↑sucrose and SPS.	
		Rice	Leaf	↓AGPase; ↓SS activity.	(Sheoran and Saini, 1996)
		Barley	Leaf	↑Hexose; ↓Starch and sucrose.	(Villadsen et al., 2005)
	Salinity	Rice	Seedling	↓GBSS transcript and activity; ↔ AGPase; ↔SS; ↔SBE	(Chen et al. 2008)
		Citrus	Calli	↓AGPase (5-fold); ↓ SS (3-fold); ↔α-amylase; ↔ β-amylase	(Libalweksler et al., 1994)
	Heat	Wheat	Grain	↓SS; ↓AGPase	(Reviewed in Thitisaksakul et al. 2012)
		Barley	Grain	↓SS; ↓AGPase; ↓GBSSI	
		Rice	Grain	↓SBEII; ↓AGPase; ↓GBSSI	
		Maize	Grain	↓SBEII; ↓AGPase	
Higher degradation	Drought	*Arabidopsis*	Leaf	↑α-glucan phosphorylase*	(Zeeman et al., 2004)
		Arabidopsis	Leaf	↑α-amylase 3*	(Thalmann et al., 2016)
		Arabidopsis	Leaf	↑β-amylase1*	(Zanella et al., 2016)
		Cucumber	Cotyledon	↑β-amylase	(Todaka et al., 2000)
		Rice mutant	Leaf	↓β-amylase; reduced fitness under low	(Kaplan and Guy,

	Cold	Tg. *Arabidopsis* Tg. Rice Tg. Tobacco	Leaf Leaf Leaf	temperature* ↓glucan water dikinase leads to cold-susceptibility* ↓BMY2,6,10; reduced cold fitness ↑PtrBAM1; enhanced cold tolerance	2005) (Yano et al., 2005) (Lv et al., 2017) (Peng et al., 2014)

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Starch metabolism	**Stress**	**Species**	**Tissue**	**Mechanism**	**References**
Higher accumulation	Drought	*Arabidopsis* Mutant	Guard Cells	↓β-amylase; Sugars, drought tolerance*	(Prasch et al., 2015; Valerio et al., 2011)
	Mild Drough	Wheat Rice	Grain Grain	↑SuS; ↑SS; ↑ SBE; ↑AGPase; ↔GBSS; ↔INV ↑SuS; ↑SS; ↑SBE; ↑AGPase	(Yang et al., 2004) (Zhang et al., 2012)
	Salinity	*Thellungiella* Rice Tomato Transgenic *Arabidopsis*	Leaf Leaf Leaf Leaf	↑Carbohydrates ↑Starch in Salt tolerant vs. susceptible line ↑Starch in Salt tolerant vs. susceptible line ↑Starch in tolerant transgenic vs. susceptible control line	(Wang et al., 2013) (Pattanagul & Thitisaksakul; 2008) (Balibrea et al., 2000) (Kempa et al., 2007)
	Heat	Tomato	Pollen	↑Starch in heat tolerant vs. susceptible genotype	(Firon et al., 2006)
	Mild Heat	Barley Wheat Rice	Grain Grain Grain	↑Starch; ↑SuS; ↑AGPase; ↑GBSS; ↑SBE; ↓SS activity ↑Starch ↑Starch	(Wallwork et al., 1998) (Nicolas et al., 1984) (Bahuguna et al., 2017)

	Cold	Quinoa Tomato	Cotyledon Leaf	4-fold ↑ Starch after 2D cold; ↑AGPase; after 6D, ↓starch and ↑sugars; ↑AGPase, SPS 4-5-fold ↑ Starch in cold-sensitive lines, in tolerant lines starch ↔	(Rosa et al., 2009a) (Venema et al., 2000a,b) Venema et al., 1999)

All directional changes are for enzyme activities assayed. Where transcripts were used, enzyme action was functionally validated in mutants and transgenic genotypes (see below).

* Mutants or transgenic lines lacking the expression of these genes impaired starch breakdown, leading to an altered stress response

Tg = Transgenic