

From Storage to Survival: Understanding Non-Structural Carbohydrates in Cereal Crops

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Abstract

Carbon, acquired by plants through photosynthesis, primarily fuels their metabolic processes and builds structural biomass. Yet, a fraction becomes non-structural carbon compounds (NCCs), including neutral lipids and non-structural carbohydrates (NSCs). NSCs, like starch and soluble sugars, are found across various cellular compartments, each with specific functions. Starch acts as a long-term carbon storage, while soluble sugars, such as sucrose, fructose, and glucose, serve diverse roles in plant growth, defense, and transport. In challenging conditions, NSCs become vital, acting as a plant's "food pantry." Reduced growth sink activity during stress leads to NSC accumulation, crucial for survival. Osmolytes, derived from external carbohydrates, safeguard plants against desiccation and freezing by stabilizing proteins and cell membranes. NSCs are essential for overall plant well-being, as established by earlier research. Investigating their distribution, especially in crops like cereals, provides insights into growth optimization. Understanding sugar transporters and NSC regulation offers the potential to enhance crop productivity and resilience, with profound implications for future agriculture. In essence, non-structural carbohydrates are like the secret ingredients that ensure a plant's equilibrium amidst environmental fluctuations. Unlocking their mysteries promises improved farming practices, resilient crops, and a sustainable future.

Key words: Non-structural carbohydrates, Classification, Transport, Cereals

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1. Introduction

The primary role of carbon absorbed by plants through photosynthesis is to serve as a fundamental element for their metabolic processes, including respiration, as well as for the construction of structural biomass. However, a smaller portion of this carbon is reserved as non-structural carbon compounds (NCC). These NCCs encompass various components, notably neutral lipids, which are prevalent in only a select few taxonomic groups, and non-structural carbohydrates (NSC). NSCs, such as starch, soluble sugars, and fructans, are distributed across various cellular compartments within plant cells, including plastids, cytosol, apoplast, and vacuoles. Starch,

a particular type of NSC, functions as a storage reservoir within plants and becomes especially valuable during adverse conditions. Soluble sugars, on the other hand, play a multifaceted role in supporting growth, defense mechanisms, and transportation processes. During unfavorable circumstances, NSCs effectively act as a "food pantry," aiding stationary plants in adapting to challenging environments. In instances like drought, the accumulation of NSCs, resulting from reduced growth sink activity, becomes instrumental in a plant's survival. Plants also employ osmolytes, such as sugars and sugar alcohols derived from externally acquired carbohydrates, to



shield themselves from desiccation and freezing damage. These compounds accomplish this by stabilizing protein complexes and cell membranes. In both normal and stressful conditions, NSCs prove to be indispensable for the growth and development of plants, playing a pivotal role in their overall well-being. carbohydrates in plants. Starch, a non-soluble polysaccharide, functions as a long-

term storage resource within plants. In contrast, sucrose, fructose, and glucose are typically the primary soluble sugars available. These non-structural carbohydrates play pivotal roles in various aspects of plant growth and development. They are essential for maintaining normal plant functions, particularly when plants encounter challenging environmental conditions.

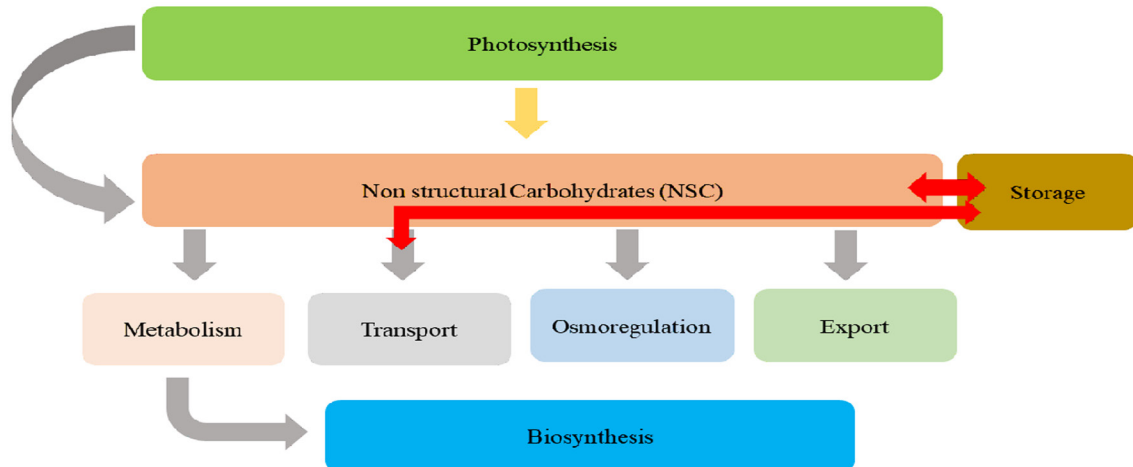


Fig 1: NSC Allocation: Regulation vs. Overflow in Plants

2. Classification

Carbohydrates can be categorized into two main groups: structural and non-structural carbohydrates. Structural carbohydrates serve as the foundational building blocks for plants, composing vital elements like cell walls and membranes. In contrast, non-structural carbohydrates serve multiple functions, including providing energy, supporting defense mechanisms, and enhancing tolerance to abiotic stressors. Non-structural carbohydrates encompass

a range of compounds, including monosaccharides, disaccharides, oligosaccharides, and polysaccharides. Among these, glucose and fructose are prominent monosaccharides found in plants, while sucrose serves as a representative disaccharide within the category of non-structural carbohydrates. Oligosaccharides, exemplified by substances like raffinose, and sugar alcohols such as inositol, sorbitol, and mannitol, are also prevalent among non-structural.

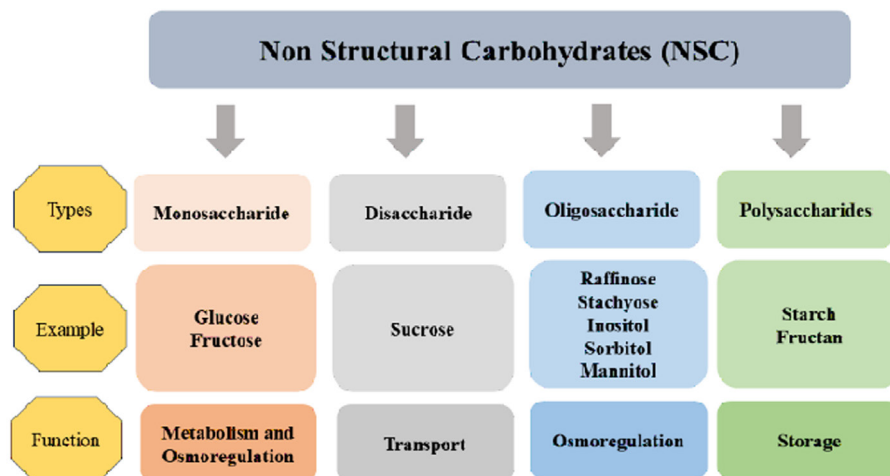


Fig 2: Classification and Function of Different NSC



3. Transport

In the realm of plant biology, transport plays a pivotal role. Plants harness the process of photosynthesis within their green tissues to generate sugars, commonly known as photosynthates. These sugars are subsequently dispatched to various parts of the plant, serving either as a source of growth or as reserves in the form of starch. The regions where photosynthates are produced are termed “sources,” while those where they are consumed or stored are termed “sinks.” The mechanism responsible for conveying photosynthates from sources to sinks is referred to as “translocation,” which can be classified based on membrane components and metabolic energy involvement. Within this complex transport system, the phloem, a specialized plant tissue, serves as the conduit for sugar transport, classified into passive, mediated, and active transport types based on specific membrane components and metabolic energy utilization.

The phloem, often referred to as the plant’s conducting tissue, facilitates the long-distance transport of sugars. It relies primarily on sieve elements, which differ in structure between angiosperms and gymnosperms. Sieve elements in angiosperms consist of highly specialized sieve tube elements, while gymnosperms employ less specialized sieve cells. These sieve elements are complemented by parenchyma cells, companion cells, and in some cases, fibers, sclereids, and laticifers. The characteristic sieve area in the cell wall is essential, facilitating pore connections between conducting cells. In angiosperms, sieve plates with larger pore areas are particularly significant, found where sieve tube elements converge to form a continuous tube. These sieve plates play a vital role in allowing sugar transport between cells. Companion cells, on the other hand, contribute to the transport of photosynthates from mature leaf cells to the sieve elements of minor leaf veins, with three types of companion cells found: ordinary cells, transfer cells, and intermediary cells. Ordinary and transfer cells facilitate sugar transport from the apoplast to the symplast in the source, while intermediary cells are involved in transporting sugars from mesophyll cells to sieve elements.

When it comes to transported sugars in plants, only a select few are transported over long distances through the phloem. Sucrose takes the lead as one of the primary sugars, often forming the basis for other mobile sugars

with varying numbers of galactose molecules. For instance, raffinose includes one galactose molecule in addition to sucrose, stachyose includes two, and verbascose includes three. Hexose sugars like glucose and fructose are typically not transported due to their reducing properties, although there have been some reports of limited hexose sugar transportation in specific plant species. Furthermore, certain sugar alcohols, including mannitol and sorbitol, are also transportable.

The mechanism governing sugar transportation in plants is elucidated by the pressure flow model, initially proposed by Münch in 1930. This model, often referred to as the Münch hypothesis, outlines the movement of photosynthates like sucrose from mesophyll cells in the green parts of plants to sieve-tube companion cells associated with sieve-tube elements in vascular bundles. This transportation occurs through a proton-sucrose symporter. Subsequently, sugars diffuse from companion cells into the sieve tubes via plasmodesmata, linking the companion cells to the sieve-tube elements. Within the phloem sieve tube elements, a low cytoplasmic content and pores connected by sieve plates enable pressure-driven bulk flow and the translocation of phloem sap. The unloading of sugars at the sink end can occur through active diffusion or active transport, depending on the sucrose concentration relative to the phloem. Passive diffusion predominates when sucrose concentrations are lower, while active transport prevails when concentrations are higher at the sink end.

Phloem loading, the process of moving sugars from chloroplasts in mesophyll cells to the sieve elements of the phloem, occurs during daylight hours. Triose phosphates formed via photosynthesis are transported from chloroplasts to the cytoplasm, where they are converted into sucrose, the transport sugar. Additionally, glucose, originating from starch in chloroplasts, is converted to sucrose and other sugars like raffinose, stachyose, and verbascose within the cytoplasm. Sucrose, among others, is then transported to sieve elements in the smallest veins of the leaf, representing a short-distance transport step. Once loaded into the sieve elements, sucrose, along with other sugars, embarks on a journey away from the source, a process referred to as export. This long-distance translocation of sugars to various sinks via vascular bundles is essential for plant growth and metabolism.



Phloem loading can take two forms: apoplastic and symplastic, depending on the type of sugar transported and the plant family. Apoplastic phloem loading involves sugar movement from mesophyll cells to sieve elements through intracellular spaces in an energy-dependent manner, utilizing a sucrose-H⁺ symporter. Symplastic pathways have been reported for transporting sugars like raffinose and sucrose to the phloem through minor vein intermediary cells, contingent upon the presence of open plasmodesmata between different cells. Within the broader context of phloem loading, the polymer-trapping model (Figure 3) elucidates the process by which sugars synthesized in mesophyll cells are transported to intermediary cells via bundle sheath cells and plasmodesmata. Inside the intermediary cells, sucrose and galactose are employed to synthesize various sugars like raffinose and stachyose, characterized by their large size and anatomy, preventing them from diffusing back but allowing them to move into sieve elements.

There are three main steps on the process of phloem unloading (i) sugars in sieve elements move from sieve elements of sink tissues the process called as sieve element unloading (ii) transportation of sugars to the sink cell via short distance transport (iii) the imported sugars are stored or metabolized in the cells of sink. The sink varies can be vegetative tissue such as tip of root, young leaves

and storage organs like stems and roots, reproductive organs like fruits and seeds. There is no one method of phloem unloading because sink vary so widely. Phloem unloading can be symplastic or apoplastic. The unloading pathway is completely symplastic leaves of tobacco and sugar beet. In some of the sink some part of loading is apoplastic. The apoplastic step is present at the end of sieve element-companion complex but this pattern has not yet gained experimental supports. Unloading is passive via plasmodesmata because it flow from sieve element where concentration is high to sink cell having low concentration. In apoplastic pathway sugar cross two membrane of cell and the sink cell plasma membrane. When sugars are transported into the vacuole of the sink cell, they must also traverse the tonoplast thus transport in apoplastic pathway is energy dependent. The apoplastic pathway is of two types. Type 1 – In this type the unloading is called apoplastic because transport of sugars from sieve element companion cell complex to the successive sink cells is apoplastic. After that sugars move back to symplast of adjoining cells continuing symplastic pathway again. Type 2 – The type 2 pathways also have apoplastic step but movement from sieve element to companion cell is symplastic. Further the pathway is of two types types 2A in which apoplastic step close to sieve element-companion cell complex and in type 2B apoplastic step that is further removed.

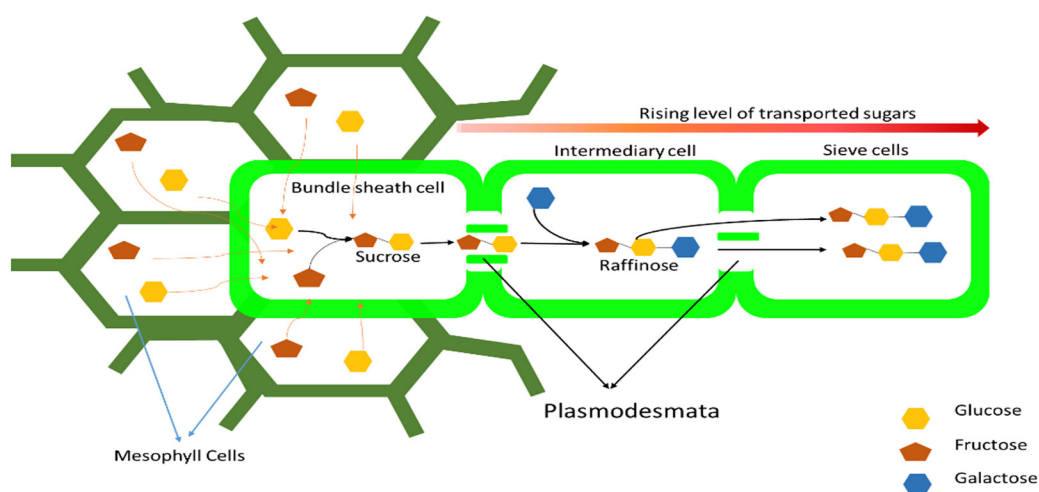


Fig 3: Polymer trapping mechanism in plants

3.1 Role of Sucrose Transporters

Sucrose transport across plasma membranes or within intracellular compartments is dependent on specific transporters, which play a crucial role in sugar flow and

accumulation, as outlined by Milne *et al.* in 2017. These transporters are found in all three phloem sections and are especially vital in tree crops where sucrose loading occurs via symplastic pathways in the collection phloem.



Disrupting symplastic pathways is necessary in some cases, such as in growing seeds, to efficiently transfer photo-assimilates, emphasizing the significance of these sucrose transporter genes. A notable example is OsSUT2, responsible for transporting sucrose across the tonoplast. Disruption of this transporter can severely disrupt sugar transfer and crop yield, as demonstrated in rice by Eom *et al.* in 2011.

3.2 *SWEET* Proteins in Sucrose Export

SWEETs (Sugars Will Eventually be Exported Transporters) constitute a novel family of sugar transporters found in plants like *Arabidopsis* and rice. They are responsible for the export of sucrose from the transport phloem to the apoplast. In *Arabidopsis*, mutants with reduced sucrose export exhibit downregulated photosynthesis due to starch accumulation, underscoring the crucial role of the SWEET family in enhancing photosynthesis. Sucrose discharged into the apoplastic space can either be assimilated by sink cells or bound to hexose and carried by specific carriers via invertase. In some crop species like sugar cane and sugar beet, sucrose can be stored in the vacuoles of storage cells to support sink growth and development.

4. The Fate of Sucrose in The Sink

In some plants the incoming sucrose is hydrolyzed into glucose and fructose by an enzyme called invertase. The glucose and fructose are substrate for enzyme hexokinase. Plants have another enzyme called as sucrose synthase (SuSy) which cleaves the molecule of sucrose. Sucrose synthase found in the cell wall and cytoplasm of cell and catalyses the reversible conversion of sucrose and UDP to UDP-glucose and fructose. The produced UDP glucose become the starting point in predominate route for synthesis of polysaccharides such as starch. Families of enzymes collectively known as fructosyl transferases synthesize fructan directly from sucrose. Fructan are polysaccharides consists of linear and branched polymer unit of fructose having glucose unit at the the head of the chain. In plant kingdom there are five classes of fructan namely inulin, levan, mixed levan, inulin neoseries and levanneoseries which differ from each other in chain length, branching and fructosyl linkages. Van den Ende *et al.* (2004) reported that fructan is cleaved by enzyme called fructanexohydrolases which sequentially remove fructose monomers unit from the end of the fructan chain (Figure 4).

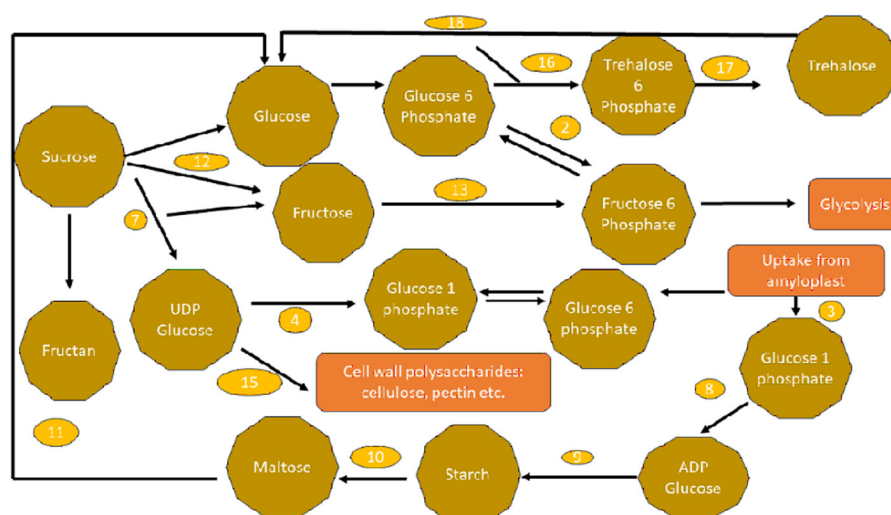


Fig 4: Fate of sucrose in sink

5. NSC in crop plants

The capacity of plants to accumulate substantial levels of non-structural carbohydrates (NSC) is regarded as a valuable agronomic trait in crops. Plant species exhibiting high NSC accumulation and tolerance to abiotic stresses have been identified (Volaire and Lelievre 1997). Both C3 and C4 grasses typically contain sucrose concentrations ranging from 12 to 15% of their dry weight under

conditions of 10°C days and 5°C nights (Chatterton *et al.* 1989). Typically, C3 cool grasses tend to store fructans, with fructan accumulation occurring before reaching a threshold of 15% NSC (Chatterton *et al.* 1989). In contrast, C4 warm-season grasses do not accumulate fructans and may only accumulate fructooligosaccharides in small amounts. C3 and C4 grasses differ in their respiration mechanisms, allowing C4 grasses to conserve energy



under hot conditions, while C3 grasses tend to utilize all their carbohydrates. Certain tropical grasses store high levels of starch, while NSC levels in perennial grasses are relatively low (Wilson and Ford 1971). Grasses such as Rhodes, Paspalum, and Bermuda (C4 grasses) accumulate significant amounts of starch in their leaves under high-temperature stress.

5.1 Maize

Modern maize, as we know it today, has evolved from its ancestor, teosinte. Initially, maize cultivation focused on harnessing the soluble sugars found in the maize stem (Williaman *et al.* 1924). In maize, the total carbohydrate content in the stem consists of a combination of starch and reducing sugars, with sucrose being transported apoplastically. The allocation of sugar in maize stems is mediated by sucrose transporters located on the plasma membrane of companion cells, sieve element parenchyma cells, and tonoplasts. In maize, a specific sucrose transporter, ZmSUT1, has been identified. ZmSUT1 is active in maize leaves and plays a role in phloem loading (Slewinski *et al.* 2012). Manipulating the relationship between sources (sites of sugar production) and sinks (sites of sugar utilization) provides valuable insights into sugar partitioning in maize. For instance, defoliated maize plants accumulate less sucrose compared to plants with intact foliage (Jones and Simmons, 1983). Similarly, removing the ear of a maize plant yields a similar effect compared to a controlled plant (Hume and Campbell 1972). Stem carbohydrates have limited direct impact on maize yield potential but play a more significant role in ensuring yield stability under unfavorable environmental conditions. High-yielding maize varieties typically exhibit lower levels of stem carbohydrates, which decrease over time. In contrast, lower-yielding maize varieties tend to accumulate higher levels of carbohydrates in their stems, with this accumulation gradually increasing during the grain-filling phase. Maize offers significant potential for breeding lines with enhanced yield and direct stem sucrose production, along with other desirable traits, owing to the wide range of genotypic and phenotypic variation available.

5.2 Sorghum

Sorghum encompasses various types, including forage, grain, sweet, and fiber sorghum (Dolciottiet *al.* 1998). Among these classifications, grain and sweet sorghum are the most commonly cultivated. The primary distinction

between these two lies in how carbohydrates are allocated. In grain sorghum, carbohydrates are primarily partitioned into the grain, whereas sweet sorghum has two major sinks: the grain and the stem. This differential sugar partitioning results in sweet sorghum having higher carbohydrate levels in both the upper internodes and the apical panicle grain compared to grain sorghum. Sorghum employs an apoplastic pathway to transport, store, and remobilize sucrose within the stem. Genetic manipulation of leaf angle can contribute to achieving higher sucrose levels in sweet sorghum. Sorghum varieties with a “stay-green” trait tend to accumulate high concentrations of carbohydrates. This is likely due to a reduced need for sucrose mobilization within the stem, coupled with an enhanced photosynthetic capacity (Duncan *et al.* 1981). Grain sorghum exhibits a remarkable ability to tolerate drought (Massaciet *al.* 1996). One plausible hypothesis for this resilience is that the sugars stored in the stem may assist in drawing water into the canopy. Consequently, the sugars within the vegetative tissues play a crucial role in overall water management within the plant, thereby contributing to its drought tolerance.

5.3 Sugarcane

Sugarcane is a prominent source of commercially produced sucrose, accounting for nearly 70% of global sucrose production (Carson and Botha 2002). Sugarcane is known for its remarkable ability to accumulate high concentrations of sucrose in the parenchyma cells of its stems. In fact, sucrose levels within the stem can reach up to 50% of the stem’s dry weight (Inman-Bamber *et al.* 2009). Unlike sorghum and maize, sugarcane employs a different transport mechanism. Sugarcane relies on a symplasmic transport pathway (Walsh *et al.* 2005). Within sugarcane, the ShSUT1 sucrose transporter is situated on the plasma membrane of storage parenchyma cells. This transporter plays a critical role in the storage and mobilization of sucrose. While hexose transporters are significantly expressed in sugarcane, their precise functions have yet to be fully elucidated. Additionally, the flux of sugars across the tonoplast membrane is regulated by sugarcane orthologs of AtSUC4, AtTMT1, and AtTMT2, and their activities are influenced by the concentrations of sucrose and hexose inside the cell (Schulz *et al.* 2011). Conventional breeding methods for improving sugar yield in sugarcane have reached a plateau. This



limitation may be attributed to sugarcane having reached its physiological limit in terms of sucrose concentration. Further enhancements in yield can potentially be achieved through modifications in plant morphology rather than physiological processes. Hybridization of sugarcane with other closely related genera such as *Erianthus*, *Sclerostachya*, *Narenga*, and *Miscanthus* has shown promise. Notably, hybrids of *Saccharum* (sugarcane) and *Miscanthus* have demonstrated cold tolerance, making them suitable for cultivation in subtropical regions.

5.4 Rice

Rice stands as one of the most vital food crops, providing a substantial portion of the calories (ranging from 35% to 60%) consumed by nearly half of the global population (Fageria et al., 2003). What sets rice apart from other plants is its distinctive carbohydrate partitioning strategy. In rice, carbohydrates are stored in the form of sucrose within the leaves and as a combination of starch and sucrose within the stem (Scofield et al. 2009). The transport mechanism in rice operates through symplasmic pathways. Notably, the management practices employed in rice cultivation have a significant impact on carbohydrate partitioning. For instance, rice production accounts for approximately 80% of water usage in Asia. Future rice cultivation practices may increasingly involve partial drying of the crop during its life cycle. This partial drying process enhances the mobilization of carbohydrates from the stem, resulting in higher yields and improved harvest indices. Research by Park et al. in 2011 found that rice cultivars grown under normal conditions tend to accumulate high levels of non-structural carbohydrates (NSCs) left in the straw. Additionally, studies have shown that NSCs present in the stem before anthesis can have a significant impact on the final sink strength, increasing the survival of spikelets under unfavorable conditions. The accumulation of high levels of NSCs can also influence the size of cells and starch granules within the spikelets. Despite these insights, there remain significant gaps in our understanding of

carbohydrate partitioning in rice and how the dynamics of its life cycle affect rice yields.

5.5 Wheat and Barley

Wheat and barley are two crucial crops that provide a substantial portion of grain-based calories in temperate and cooler regions across the globe. Carbohydrate storage mechanisms and remobilization processes in wheat stems have been extensively studied, more so than in any other grass species (Blum et al. 1994). This heightened research focus may be attributed to the early discovery of a direct correlation between the ability to maintain stable yields and carbohydrate storage in wheat under various environmental stresses (Binding et al. 1977; Asseng and Herwaarden 2003). Wheat genotypes that accumulate high levels of non-structural carbohydrates (NSCs) typically exhibit shorter stature, produce fewer but more fertile tillers, and undergo early flowering. High NSC wheat lines boast a higher harvest index because a significant portion of photosynthates is allocated to grain development (Rebetzke et al. 2016). In optimal conditions, photosynthesis alone can support grain development (Slafer and Andrade 1991). However, when unfavorable conditions cause a drop in photosynthesis rates, the stem's stored carbohydrates become crucial for maintaining the maximum fill rate of the kernels. One of the primary reasons for yield losses in wheat is floret abortion and sterility, often resulting from carbohydrate deficiencies. Addressing these issues remains a key objective in wheat cultivar improvement (Gonzalez et al. 2011). Wheat cultivars with high NSC accumulation demonstrate better grain filling and yield stability when grown under water-deficient conditions. However, when cultivated under normal conditions, the yield of wheat cultivars with high stem NSC is comparable to that of low NSC lines, indicating that there are no inherent yield penalties associated with high NSC levels in the absence of stress (Foulkes et al. 2007). In the case of barley, carbohydrates in the stem play a pivotal role in sustaining photosynthesis

Table 1: Composition of Different NSC in Some Major Crops (Halford et al. 2010)

Plants	Glucose	Fructose	Maltose	Sucrose
Wheat (<i>Triticum aestivum</i>)	1.49–4.84	0.80–1.89	2.81–6.40	21.90–25.65
Rye (<i>Secale cereale</i>)	0.64–33.43	0.61–7.02	0.74–21.05	26.81–49.52
Maize (<i>Zea mays</i>)	0.66–6.92	0.56–3.46	ND	12.91–89.60
Rice (<i>Oryza sativa</i>)	6.60–14.90 (Total reducing sugars)			15.10–58.60



during the later phases of grain filling. In wheat, barley, and oats, stem NSCs predominantly exist in the form of fructans. Other types of carbohydrates have a minimal impact on NSC reserves and show little variation between high and low stem NSC lines (Ruuska *et al.* 2006).

7. Stem Carbohydrate Storage and Utilization for Grain Production

To effectively mobilize stem reserves into grains, it is imperative to have ample carbohydrate storage in place before the onset of grain loading. This prerequisite is closely related to traits that enhance the potential for high yield even before the flowering stage (anthesis). In the stems of wheat plants, the predominant type of non-structural carbohydrates (NSCs) is comprised of fructans, constituting the majority of these reserves (Ruuska *et al.* 2006; Joudi *et al.* 2012). Fructans can make up as much as 85% of the total NSCs during the peak accumulation stage (Goggin *et al.* 2004), whereas sucrose accounts for a mere 10% (Cruz-Aguado *et al.* 2000). Notably, research by Dreccer *et al.* in 2009 revealed that in wheat lines with high water-soluble carbohydrate (WSC) content, both individual grain weight and the contribution of WSCs to overall yield were significantly greater compared to lines with low WSC content. Consequently, in harvests with high WSC content, the pool of stored stem carbohydrates played a more substantial role in determining the final average individual grain weight (11.5% compared to 8.2% in low WSC lines). Furthermore, drought-tolerant wheat cultivars tend to have taller stems with higher NSC levels compared to sensitive cultivars under both normal and stressful conditions (Dreccer *et al.* 2009).

The accumulation of NSCs in wheat stems typically occurs during the period from jointing to grain filling, although the total amount varies depending on the specific wheat genotype and prevailing environmental conditions (Gupta *et al.* 2011). Different internodes within the stem exhibit varying levels of NSC accumulation and subsequent remobilization (Joudi *et al.* 2012). Interestingly, the peduncle and penultimate internode together make up approximately 45% of the total mass of the stem, while the lower internodes account for the remaining 55% (Goggin *et al.* 2004). It is noteworthy that the peduncle and penultimate internode serve as primary sites for NSC accumulation (Zhang *et al.* 2015). During the anthesis stage under normal conditions and in the middle of the

grain-filling period under water-deficient conditions, the concentration of WSCs in the lower internodes displayed highly significant associations with thousand-grain weight (TGW). Thus, it is crucial for the length of lower internodes to be sufficient to store an adequate quantity of stem NSCs to provide assimilates during the grain-filling phase (Ehdaie *et al.* 2008).

8. Role of NSC in abiotic stress tolerance

8.1 Drought

Drought stress poses a significant challenge to agricultural ecosystems, disrupting the carbon balance and potentially leading to plant mortality. Investigating how plants can withstand drought stress has become a crucial focus for agricultural improvement. Drought events are becoming more frequent and severe, causing vegetation to become transient and transforming crops from carbon sinks into carbon sources (Kannenber *et al.* 2020). During drought, plants experience a shortage of available water, leading to reduced stomatal conductance and photosynthesis. This reduction significantly limits the availability of carbon for essential plant metabolic processes (Sala *et al.* 2020). Additionally, drought-induced xylem cavitation and embolism hinder the transport of nutrients and non-structural carbohydrates (NSCs) between plant organs (Deng *et al.* 1990). As a result, maintaining carbon balance and hydraulic transport in plants under water stress becomes extremely challenging (Galiano *et al.* 2011). Non-structural carbohydrates (NSCs), including soluble sugars like glucose, fructose, and sucrose, as well as insoluble starch, play a pivotal role in plant metabolism. They provide energy, regulate substrate metabolism, and serve as a source-to-sink system for carbon transport. NSCs also play a significant role in buffering the effects of changes in carbon balance, helping plants cope with environmental stress (Halford *et al.* 2011; McDowell *et al.* 2011; Dietze *et al.* 2014; Quentin *et al.* 2015). The relationship between NSC distribution and drought stress remains not fully understood. Abid *et al.* (2017) conducted a study on wheat to explore whether pre-anthesis drought priming enhances grain filling response to post-anthesis drought stress by modifying carbohydrate-metabolizing enzyme activities in wheat source and sink parts. Their research revealed that drought stress during grain filling affected enzymatic activities, leading to reduced carbohydrate translocation from the source and limited grain accumulation in



wheat. However, the impact of drought stress was less severe in primed plants (under mild drought conditions) than in non-primed plants (under control conditions). Primed plants exhibited higher NSC levels, including fructan and sucrose, and more active enzymes, such as sucrose-phosphate synthase, sucrose fructosyltransferase, and soluble-acid invertase in the stem. These findings suggest that pre-drought priming can alter source-sink relationships, enhancing dry weight accumulation during grain filling under post-anthesis drought stress in wheat. Stored non-structural carbohydrates (NSCs) significantly influence the grain yield of cereal crops, contributing more than 50% under stressful conditions and 5-33% in non-stressful conditions (Hirano *et al.* 1998; Wardlaw and Willenbrink 2000; Zhang *et al.* 2009). This holds true not only for cereals like rice and wheat but also for vegetables such as potatoes. During reproductive drought, grain yield becomes more reliant on reserves in lower leaves and culms rather than flag leaves, emphasizing the transfer of stem reserves to the grain under stressful conditions. These findings suggest that culm and leaf reserves serve as a short-term buffer to maintain a source of photosynthate for developing organs (Wardlaw and Willenbrink 2000). Previous research has suggested that carbohydrate deficiency can accelerate plant aging. This is supported by several studies, including Thimann *et al.* (1997) and Fujiki *et al.* (2000). Drought stress has been shown to reduce photosynthesis and chlorophyll content in leaves, hasten leaf senescence (Yang *et al.*, 2002), and promote the mobilization of stored carbohydrates in stems, potentially resulting in earlier loss of stem weight (Kaur *et al.*, 2012). Additionally, drought stress can shorten the grain-filling period (Wardlaw *et al.* 2000) leading to reduced 1000 grain weight, fewer grains per spike, and decreased straw yield.

8.2 Heat Stress

Carbohydrates, particularly non-structural carbohydrates (NSCs) such as starch and sugars, play a critical role in plant metabolism, serving as indicators of the balance between carbon supply through photosynthesis and its utilization for plant growth. During vegetative growth, the stem acts as a temporary sink, storing excess photo-assimilates, and later transitions to a source during grain-filling and maturation, supplying carbohydrates to support growth (Slewisinski 2012). Heat stress can significantly impact wheat grain yield by reducing photosynthesis and

altering carbohydrate metabolism, with the extent of the impact varying depending on the cultivar and growth stage. For wheat, the ideal temperature range for anthesis and grain filling falls between 12°C and 22°C (Shewry 2009). Exposure to temperatures above 24°C during the reproductive stage can substantially reduce yield (Prasad and Djanaguiraman 2014). Wheat grain filling primarily relies on current photosynthesis in plant leaves and ears, along with the mobilization of stored carbohydrates to support growing grains. Under stress conditions, pre-anthesis stem carbohydrate reserves can be mobilized to mitigate yield losses. Wheat grains are composed of 65-75% starch, while rice grains contain 80-90% starch (Stone and Morell 2009; Costa *et al.* 2021). Research indicates that starch accumulation in wheat kernels peaks between 12 and 35 days after anthesis (Lu *et al.* 2019). However, high temperatures can negatively affect starch synthesis, particularly the activity of soluble starch synthase (SSS) (Denyer *et al.* 1994; Jenner 1994). Short periods of very high temperatures (35°C to 40°C) can detrimentally impact grain quality during grain filling. However, acclimation has been shown to enhance carbohydrate remobilization from the culm to developing grains during anthesis (Zhen *et al.* 2020). Elevated night temperatures can reduce transcript levels of ADP-glucose pyrophosphorylase and increase the synthesis of starch-degrading enzymes such as iso-amylase III, alpha, and beta-amylase in developing grains. Higher night temperatures can also shorten the duration of grain filling and reduce grain size more significantly than day temperatures (Impa *et al.* 2020). Wheat species exhibit a wide genetic diversity in their tolerance to high temperatures, affecting grain starch content, amylose and amylopectin deposition, and starch granule formation. High temperatures during grain filling have been reported to reduce starch content and alter the size distribution of starch granules in wheat grains (Hurkman *et al.* 2003). In rice, high-temperature stress negatively impacts yield, closely associated with reduced NSC translocation (Zhen *et al.* 2020). Stem NSC content increases, while panicle and stem NSC translocation efficiency decreases, resulting in a reduced contribution of stem-derived NSCs to grain yield. Severe heat stress transforms the stem into a carbohydrate sink during grain filling, and temperature stress at the booting stage inhibits NSC translocation due to reduced sink size (Zhen *et al.* 2020).



8.3 Salinity

Wheat is renowned for its moderate salt tolerance, with the ability to thrive even in the presence of high salinity levels in the field, reaching up to 100 mM NaCl (~ 10 dS m^{-1}) (Maas and Hoffman 1977). Salinity stress imposes osmotic stress, triggers increased reactive oxygen species (ROS) production, and results in ion toxicity (Sreenivasulu *et al.* 2000). Salt-tolerant plants respond to these challenges through various mechanisms, including ion compartmentalization, salt reduction, osmotic regulation, activation of antioxidant enzymes, and the synthesis of osmoprotective compounds (Sadak *et al.* 2015). Osmoprotectants function as safeguarding agents by participating in ROS detoxification, maintaining cellular osmotic balance, stabilizing proteins and enzymes, and preserving membrane integrity (Bohnert and Jensen 1996). Efforts have been made to enhance plant salinity tolerance by applying osmoprotectants, such as proline, trehalose, glycine-betaine, and other carbohydrates (Dawood and Sadak 2014). Trehalose (Tre), a non-reducing sugar, plays a significant role in stress tolerance across various plant species. Research has shown that foliar application of Tre can enhance wheat growth under salinity stress. It leads to increased levels of hydrogen peroxide free radicals, compatible osmolytes, antioxidant compounds (phenolics), and improved membrane stability (Sadak *et al.* 2019). Trehalose possesses unique properties that stabilize proteins, enzymes, and lipid membranes, shielding them from damage during desiccation (Fernandez *et al.* 2010). Studies indicate that foliar Tre treatment increases phenol concentrations in wheat leaves, a phenomenon also observed in other plants under salinity stress. Phenols play a crucial role in metabolic regulation and overall plant development, acting as substrates for antioxidant enzymes and assisting in mitigating salt stress injuries (Rady *et al.* 2011; Dawood and Sadak 2014; Abd Allah *et al.* 2015). In experiments conducted by Yan and Zheng (2016) Duman *et al.* (2011) and Luo *et al.* (2010), pre-treatment with Tre alleviated salt stress symptoms in wheat, with positive effects on physiological parameters like chlorophyll content, dry weight, biomass per plant, nitrogen content, and growth rate. Tre supplementation also improved potassium (K^+) accumulation, the K^+ /sodium (Na^+) ratio, and proline accumulation. The external application of Tre in wheat

has been found to mitigate salinity stress by increasing the concentration of osmoprotectant solutes, including total soluble sugars, glucose, trehalose, proline, and free amino acids. Concurrently, it reduces lipoxygenase (LOX) enzymatic activity and malondialdehyde (MDA) content (Hasanuzzaman *et al.* 2017). The rise in carbohydrate concentration in leaf tissues is a response to the excessive accumulation of monovalent ions in the vacuoles. This accumulation lowers the vacuole's osmotic potential, which is counterbalanced by the accumulation of organic solutes, such as carbohydrates and proline, in the cytoplasm. These organic solutes function as osmolytes and protect enzyme systems and membranes. Another explanation for the increase in soluble carbohydrates (SCs) in flag leaves under salinity stress is their altered distribution between growing and storage tissues. Different wheat genotypes have demonstrated varying efficiency in transporting soluble carbohydrates to grains under salinity stress. For instance, the translocation of assimilates from the flag leaf to grains was less affected in CR and Kharchia cultivars compared to Ghods cultivar (Kafi *et al.* 2003). In a study involving two bread wheat cultivars (Inia-66 and Shole), salinity stress reduced the distribution of assimilates, leading to a decrease in the percentage of ^{14}C translocated from the flag leaves to the grains and, consequently, reduced ^{14}C content in the grains of both genotypes (Poustini 1990). Another investigation focused on the impact of salt stress on water-soluble carbohydrate (WSC) content in wheat seedlings from four different varieties. The study revealed that salt-tolerant wheat genotypes accumulated more WSC compared to sensitive genotypes. Salinity stress increased the content of sucrose, fructans, and reducing sugars, suggesting the potential of WSC as a marker for selecting salt-tolerant wheat genotypes (Kerepesi and Galiba 2000).

8.4 Logging and lodging

Waterlogging is a condition that poses adverse effects on plant growth and development, primarily by diminishing cellular energy levels through a reduction in total carbohydrate content. It occurs when soil becomes saturated with water, depriving plant roots of oxygen. This leads to severe hypoxia or anoxia within the roots, resulting in significant biological consequences (Hossain and Uddin 2011). When plant tissues experience oxygen deprivation due to waterlogging, they switch from



aerobic respiration to low-ATP-yielding fermentation. This transition triggers an energy crisis that inhibits root growth and function and disrupts the transport of nutrients and water to the shoot. In some cases, it can even lead to the death of certain roots. Notably, in wheat, waterlogging induces the accumulation of non-structural carbohydrates (NSCs), particularly sugars, in the shoots. According to Herzog *et al.* (2016), wheat plants showed a twofold increase in NSC levels within three days of soil waterlogging. This NSC boost was attributed to the buildup of fructans in both the roots and shoots of ten-day-old wheat seedlings during root hypoxia, providing an energy-efficient means of carbohydrate storage.

Plants that exhibit tolerance to flooding possess a critical trait: the ability to store high levels of non-structural carbohydrates (NSCs) in their shoots before, during, and after submergence. These plants achieve this by preserving chlorophyll in their leaves and slowing down shoot growth while submerged. Flood-tolerant varieties adopt a quiescent strategy during extended flooding to conserve carbohydrates and energy. Some varieties

also employ an escape mechanism by modifying their anatomical and morphological traits, facilitating gaseous exchange between submerged and non-submerged organs through elongation. Consistent carbohydrate supply during submersion is essential for their survival. Research has shown that the carbohydrate content shortly after submersion is positively correlated with plant survival, in contrast to carbohydrate levels during submersion itself (Oladosu *et al.* 2020).

Plants endowed with abundant non-structural carbohydrates (NSCs) and controlled elongation rates are more likely to endure prolonged flooding and deepwater stagnation. The capacity to store substantial NSCs and conserve energy by limiting underwater elongation are pivotal factors for survival in submerged conditions. Maintaining adequate energy levels during submersion takes precedence over the initial carbohydrate status before submersion. Additionally, down-regulating gibberellic acid (GA) biosynthesis during submersion may enhance survival, provided that the cultivars possess the potential to accumulate significant non-structural carbohydrates.

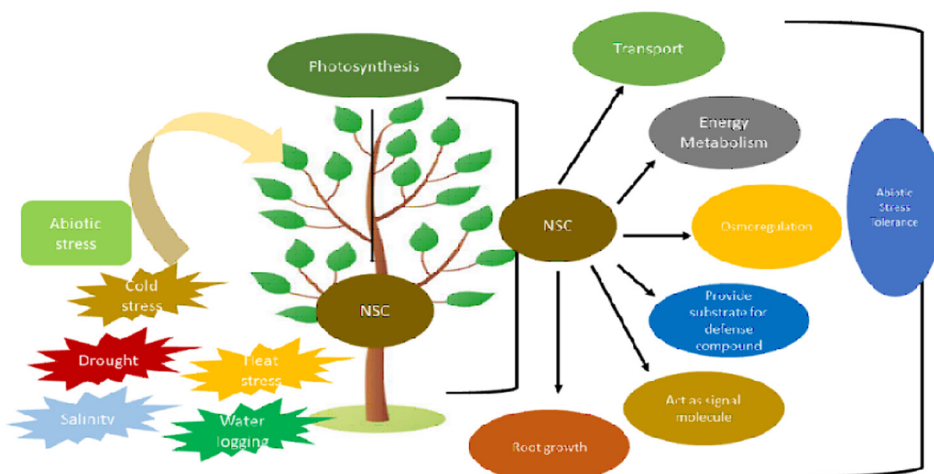


Fig 5: Role NSC in abiotic stress tolerance

Conclusion

Non-structural carbohydrates (NSCs) are like essential ingredients in all parts of a plant. They help us know how well a plant can handle tough environmental conditions. It's really important to study how NSCs are spread out in plants, especially in crops like cereals, to see how well they're growing. NSCs are like the plant's way of keeping everything in balance when the weather changes. But, we still have a lot to learn about how NSCs work, like how

they are controlled and used when plants are stressed. If we figure out how sugar transporters in plants respond and make sure things are balanced, we can make crops grow better. Making NSCs work more efficiently when plants are stressed is super important for their survival and how much they can produce. So, if we focus our research on NSCs, we can get better at understanding how plants make, move, and use sugar. This will give us valuable insights for making improvements in farming in the future.



Author contributions

The review was written and enriched by PS, RM and AK. All authors read, edited, and approved the final manuscript.

Conflict of interest

No

Declaration

The authors declare no conflict of interest.

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