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Review

Source–Sink Communication: Regulated by Hormone, Nutrient, and Stress Cross-Signaling

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Communication between source organs (exporters of photoassimilates) and sink organs (importers of fixed carbon) has a pivotal role in carbohydrate assimilation and partitioning during plant growth and development. Plant productivity is enhanced by sink strength and source activity, which are regulated by a complex signaling network encompassing sugars, hormones, and environmental factors. However, key components underlying the signaling pathways that regulate source–sink communication are only now beginning to be discovered. Here, we discuss recent advances in our understanding of the molecular mechanisms regulating sugar mobilization during seed development and seedling establishment in cereals, which provide the majority of nutrition for humans. Insights into these mechanisms may provide strategies for improving crop productivity.

The Plant Life Cycle Is Accompanied by Source–Sink Transition

As sessile, self-sufficient, and resilient organisms, plants require the dynamic coordination of numerous signal transduction pathways to capture energy and **nutrients** (see Glossary), to orchestrate their growth and development, and to cope with changing environments. At the beginning of their active growing life, plants develop from an embryo, which depends on the metabolism of nutrients transported from storage organs, such as seeds (Figure 1A). During active vegetative growth and development, plants rely on the energy gained from CO_2 fixation into carbohydrates via photosynthesis in **source organs** and the translocation of photoassimilates, mainly sucrose, from the site of synthesis through the phloem to **sink organs** for their utilization (Figure 1B). During the reproductive stage, sugars and other nutrients are remobilized from mature leaves to developing seeds (Figure 1C).

In plants, sugars including sucrose, glucose, fructose, and trehalose, and their derivatives not only serve as metabolic resources and structural constituents of cells, but also have hormone-like regulatory activities. Sugars modulate most of the fundamental processes throughout the entire life cycle of plants, including embryogenesis, germination, vegetative growth, reproduction, senescence, and responses to diseases and environmental stimuli [1]. In general, sugars upregulate genes involved in biosynthesis, transport, storage of reserves, and cell growth, and downregulate those associated with photosynthesis and reserve mobilization and stress responses, whereas sugar starvation has the opposite effect [2–5]. Consequently, the path of sucrose transfer from its source to its utilization in sink organs is a central feature of the

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With the rapidly expanding world population, food production must be substantially increased in the coming several decades to meet increasing global demands for food.

Source–sink interactions modulate carbon (C) assimilation, translocation, partitioning, and storage throughout the plant and have a pivotal role in determining the productivity of harvestable organs.

Crop yield is dependent on the source–sink relation, which is influenced by environmental changes.

Understanding mechanisms by which plants control source activity and sink strength in the context of global climate changes, such as water limitation and high temperature, is of agronomic significance for the development of efficient breeding programs for improving crops.

Many examples have demonstrated that manipulation of source activity and sink strength could significantly enhance crop productivity. However, crop productivity is determined by the combinatorial functions of multiple genes involved in signaling and metabolic pathways, which are still not well understood. Additionally, yield increase has not been evaluated in field trials in most studies. Therefore, more work is needed for the translation of basic findings to open field trials.

http://dx.doi.org/10.1016/j.tplants.2015.10.009

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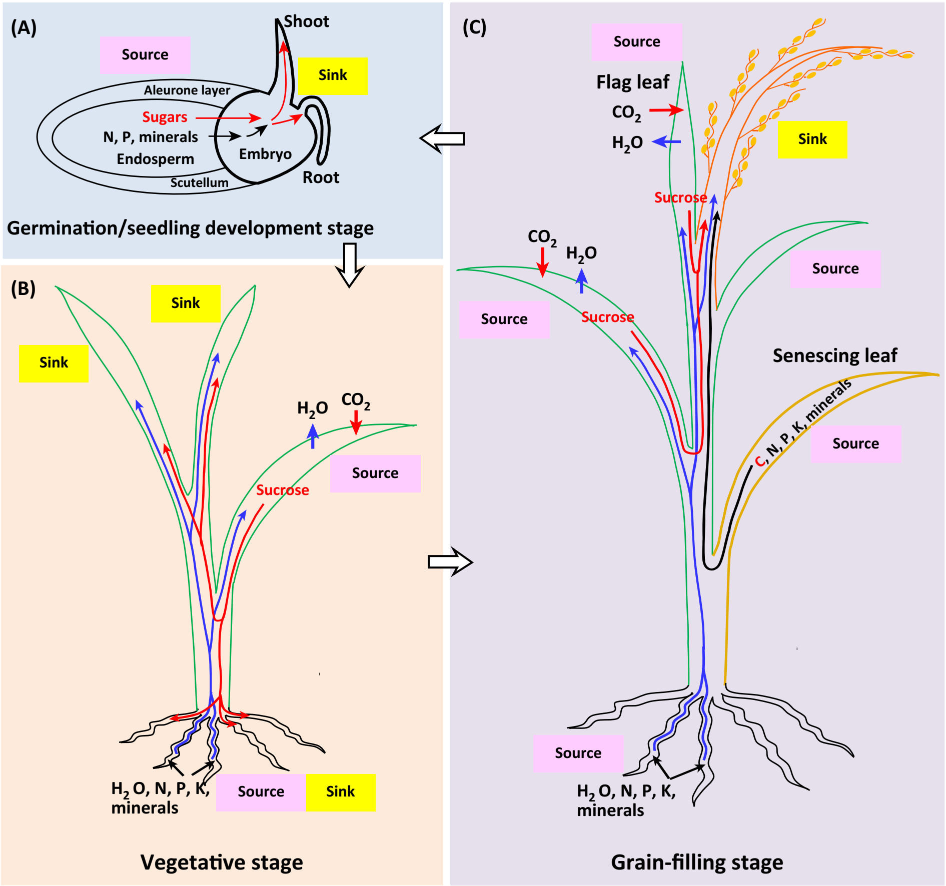

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Figure 1. Translocation of Sucrose and Other Nutrients from Source to Sink Organs in the Life Cycle of Cereals. (A) At the germination and/or seedling development stage, carbon (C), nitrogen (N), phosphorus (P), and minerals produced from hydrolysis of stored nutrients in the endosperm (source) are transported to the embryo (sink) to support initial growth of seedlings. (B) At the vegetative stage, sucrose synthesized via photosynthesis in mature leaves (source) is translocated to developing leaves (sink) through the phloem. At this stage, growing roots serve as C sinks as well as the source for minerals that are transported to shoots together with H_2O through the xylem. (C) During the grain-filling stage, sucrose is produced by photosynthesis in mature leaves and is translocated to developing grains (sink). At this stage, the flag leaf is the main source of sucrose for grain filling. Various nutrients, particularly N, and minerals in senescing leaves (source) are also remobilized to developing grains. In (B,C), red lines indicate the path of sucrose translocation from source to sink, blue lines indicate the path of water transport from roots to the whole plant, and the black line indicates the path of nutrient remobilization from senescing leaves to developing grains.

source–sink communication that determines grain yield [6,7]. Sugars are not the only metabolites that are involved in source–sink relations; nitrogen (N) uptake, transport, and recycling also sustain plant growth and impact eventual grain yield [8].

The balance of source production and sink utilization of carbon (C) is tightly coordinated through an integrated signal network in which hormones, sugar, and environmental cues converge to regulate developmental and stress adaptive processes [1]. These signaling pathways determine the direction of nutrient flow and metabolic pathways (Figure 2). Insight into these mechanisms is not only important for elucidating the molecular basis of the signaling networks regulating source–sink communication, but is also a prerequisite for devising genetic manipulation strategies of source–sink nutrient allocation toward crop improvement. Emerging studies on these