Trends in Plant Science

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Review

# Source–Sink Regulation in Crops under Water Deficit

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**To meet the food demands of an increasing world population, it is necessary to improve crop production; a task that is made more challenging by the changing climate. Several recent reports show that increasing the capacity of plants to assimilate carbon (source strength), or to tap into the internal carbon reservoir (sink strength), has the potential to improve plant productivity in the field under water-deficit conditions. Here, we review the effects of water deficit on the source–sink communication, as well as the respective regulatory mechanisms underpinning plant productivity. We also highlight stress-tolerant traits that can contribute to harness source and sink strengths towards producing high-yielding and drought-tolerant crops, depending on the drought scenario.**

## Highlights

Plants have evolved intricate systems to balance carbon assimilation (source strength) and usage (sink strength), however, drought disrupts this equilibrium, causing large losses in plant productivity.

Recently, our increasing understanding of the molecular mechanisms underlying plant responses to drought show that plants that are able to maintain source and sink strengths under stress are more resilient and productive.

## Source and Sink Strength

**Source strength** (see Glossary) and **sink strength** underpin plant production and are influenced by environmental conditions. Because recent projections estimate a continuing world population increase [1], plant production as a basis for food and feed needs to be significantly increased [2]. Plant yield is influenced by agronomic practices, such as irrigation, fertilization, and pest control, but also by the capacity of plants to capture light, to use its energy to assimilate carbon, and to allocate this carbon into harvestable organs [3,4]. Owing to suboptimal agronomic practices and because carbon assimilation and allocation can still be improved, crop productivity is often far from reaching its maximum potential [3–5]. Carbon assimilation is carried out by **source organs**, such as fully developed leaves, which assimilate $CO_2$ from the atmosphere, convert it into glucose and other sugars, and export them to **sink organs**, such as roots, stem, fruits, and seeds, where they are stored and used for organ growth [6] (Figure 1A). Along the plant life cycle, the same organ can shift from sink to source and vice versa. For example, newly developed leaves start as carbon sinks, because they cannot assimilate enough nutrients for their own growth, but as they develop, they assimilate excess carbon that is exported to other growing plant organs, as such becoming carbon sources. Later in development, or under nutrient-deficiency conditions, leaves can start to senesce and to act only as sources, exporting sugars and other nutrients to the remaining plant organs. The same organ can also be simultaneously a source of a particular nutrient, but a sink for another nutrient. This can be the case of fully developed leaves, which are at the same time sources of carbon and sinks of inorganic nitrogen, which is imported from the roots [7]. The nutrient movement within the plant is enabled by the plant vascular system, namely the **xylem** that transports water and nutrients from the roots to the shoots, and the **phloem** that mainly transports nutrients produced in the shoots to the remaining parts of the plant [8] (Figure 1A). To ensure that the nutrients reach the organs where they are needed, source–sink transport has to be tightly regulated.

The balance between source and sink dynamics becomes evident when one of the processes is perturbed. On the one hand, increasing $CO_2$ concentration [9], light quality, light intensity, or photoperiod [10–12] leads to improved carbon fixation and, consequently, to enhanced plant growth and yield [3], while growth stops shortly after carbon depletion [13], showing that plant growth is

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modulated by the carbon availability in the source organs. On the other hand, an increased sink demand promotes photosynthesis in source organs [14,15], whereas reduced sink strength causes sugars to build up in source organs, leading to the downregulation of photosynthesis-related genes and photosynthetic rate [7,14], indicating that the carbon requirements from the sink organs also influence the activity of the source leaves. Thus, overall, there is a high positive correlation between source strength (carbon assimilation and export) and sink strength (sugar import and usage) [16].

Source and sink strengths are highly responsive to environmental changes [17], and they are particularly susceptible to water-deficit conditions [17,18]. Under mild water deficit, plant growth is already severely impaired while photosynthesis performance is still preserved [16,19,20], indicating that when there is not enough water available for plant development, the balance between sink and source strength is disrupted [16]. Because the decline in source and sink strengths during water deficit leads to important reductions in crop yield [21], and drought episodes are becoming more frequent and severe [22,23], future crop varieties have to be more resilient to this stress. Until recently, drought-tolerant plants were often reported to have reduced growth and yield [24,25]. Well-known examples are the overexpression of genes that confer stress tolerance but lead to dwarfed and less productive plants [26–28], suggesting a tradeoff between stress resilience and yield or a side effect caused by the gene overexpression. Given that several high-yielding, drought-tolerant varieties of wheat and rice have been reported to have the ability to maintain growth and photosynthesis during stress [29,30], it seems clear that there is room to tailor sink and source strengths to have highly productive, drought-tolerant crops. To better understand how source and sink strength can be modulated to improve yield under water-deficit conditions, we review here the current knowledge about the mechanisms driving plant responses to drought at source, transport, and sink levels individually, as well as the regulatory mechanisms linking the source–sink relationship. Furthermore, we provide an overview on how this knowledge is used to design drought-tolerant crops.

## Drought Tolerance Is Associated with Source Strength

At the earliest stages of water deficit, there is a decrease in root water uptake, which leads to impaired water movement within the plant, reduced **cell turgor pressure**, and consequently stomatal closure [31,32] (Figure 1B). Simultaneously, the endogenous levels of the hormone abscisic acid (ABA) increase, further signaling stomata closure. In this way, plants lose less water through the leaves but also obtain less carbon for photosynthesis [33]. In the long term, the reduction in $CO_2$ available for assimilation leads to a **Calvin cycle** slow down [34,35], excessive reduction of **photosystem** II, subsequent production of **reactive oxygen species (ROS)** causing cellular damage [36] (Figure 1B), and consequently, reduced source strength. Despite these mechanisms that reduce source activity, there is much evidence that source strength is resilient to drought [16,19,20]. In rice and foxtail millet (*Setaria italica*), photosynthesis-related genes are upregulated under water-deficit conditions in tolerant varieties, but downregulated in sensitive varieties [30,37]. This upregulation of photosynthesis-related genes in tolerant plants is thought to result in a lower reduction in photosynthetic rate during water deficit and might be a drought tolerance strategy. In addition, maize seedlings that undergo a water-deficit period have a higher photosynthetic rate after rewatering, compared with plants in the same developmental stage but fully grown under control conditions [38]. The increased photosynthetic rate is associated with the upregulation of photosynthesis-related genes, which may be a way of priming plants to quickly respond in case of stress alleviation. There are numerous examples of photosynthesis-related genes and proteins being either downregulated [20,39] or upregulated [30,37,38,40–42] under water-deficit conditions. The molecular mechanisms regulating these changes in gene expression still need to be investigated, but they are likely context dependent,

## Glossary

**Aquaporins:** water channels present in cellular membranes that facilitate water movement within and between different tissues.
**Calvin cycle:** a set of reactions occurring in the chloroplast stroma whereby $CO_2$, NADPH, and ATP are converted into triose phosphates, which are used to produce glucose.
**Cell turgor pressure:** hydraulic pressure within cells, usually reduced under drought conditions. Guard cells with a high turgor pressure lead to stomatal opening, whereas lowering the turgor pressure of guard cells causes stomatal closure.
**Osmoprotectant:** soluble molecules, such as some sugars and amino acids, that are neutrally charged, have low toxicity at high concentrations, and act as osmolytes. These molecules function to maintain the osmotic difference between the cytosol and the extracellular fluid.
**Phloem:** channels in the vasculature of a plant, necessary to transport nutrients assimilated by source organs to the sink organs.
**Photosystems:** protein complexes located in the thylakoid membranes of chloroplasts that carry out the photosynthetic light reactions. These reactions use light energy and water to generate ATP and NADPH necessary for carbon assimilation in the Calvin cycle.
**Reactive oxygen species (ROS):** highly reactive molecules containing oxygen. When the photosystems and the electron transport chain are over-reduced, there is the production of hydroxyl radical (•OH), hydrogen peroxide ($H_2O_2$), and superoxide radical ($•O_2^-$) that can react with DNA, RNA, and proteins causing cellular damage and photoinhibition.
**Sink organ:** developing or storage organs such as young leaves, roots, seeds, and fruits that import nutrients from source organs.
**Sink strength:** the ability of sink organs to import nutrients and water from source organs. This activity is determined by size, metabolic activity, and storage capacity of the sink organs.
**Source organ:** plant organs capable of exporting nutrients or photoassimilates, which are not needed for their own growth, to sink organs. Mature leaves are examples of carbon source organs.
**Source strength:** capacity of source organs to assimilate $CO_2$, convert it into

and influenced by the level of water deficit, plant species, developmental stage, and level of drought tolerance.

Although only a few mechanisms regulating source responses to drought have been elucidated [33–36], it seems that maintaining the level of carbon assimilation by promoting photosynthesis, while reducing water loss (stomatal closure) and the harmful effects of ROS, may contribute to improve drought tolerance. Recently, it was shown that constitutive overexpression of transcription factors (TFs) from NAC (NAM, ATAF, and CUC), homeobox, and nuclear factor (NF)-Y families [43–48], as well as overexpression of ZmNF-YB16 driven by a stress-inducible promoter [49], leads to an increased yield under water-deficit conditions, with no yield penalty in the absence of stress in crops grown in drought-prone areas. This drought tolerance is observed when plants

sugars and export them to sink organs, depending on the size, assimilation rate and export rate of the source organ, as well as the availability of water and nutrients in the environment.
**Xylem:** constitutes part of the vascular tissue within the plant that transports water and nutrients taken up by the roots to other plant organs.

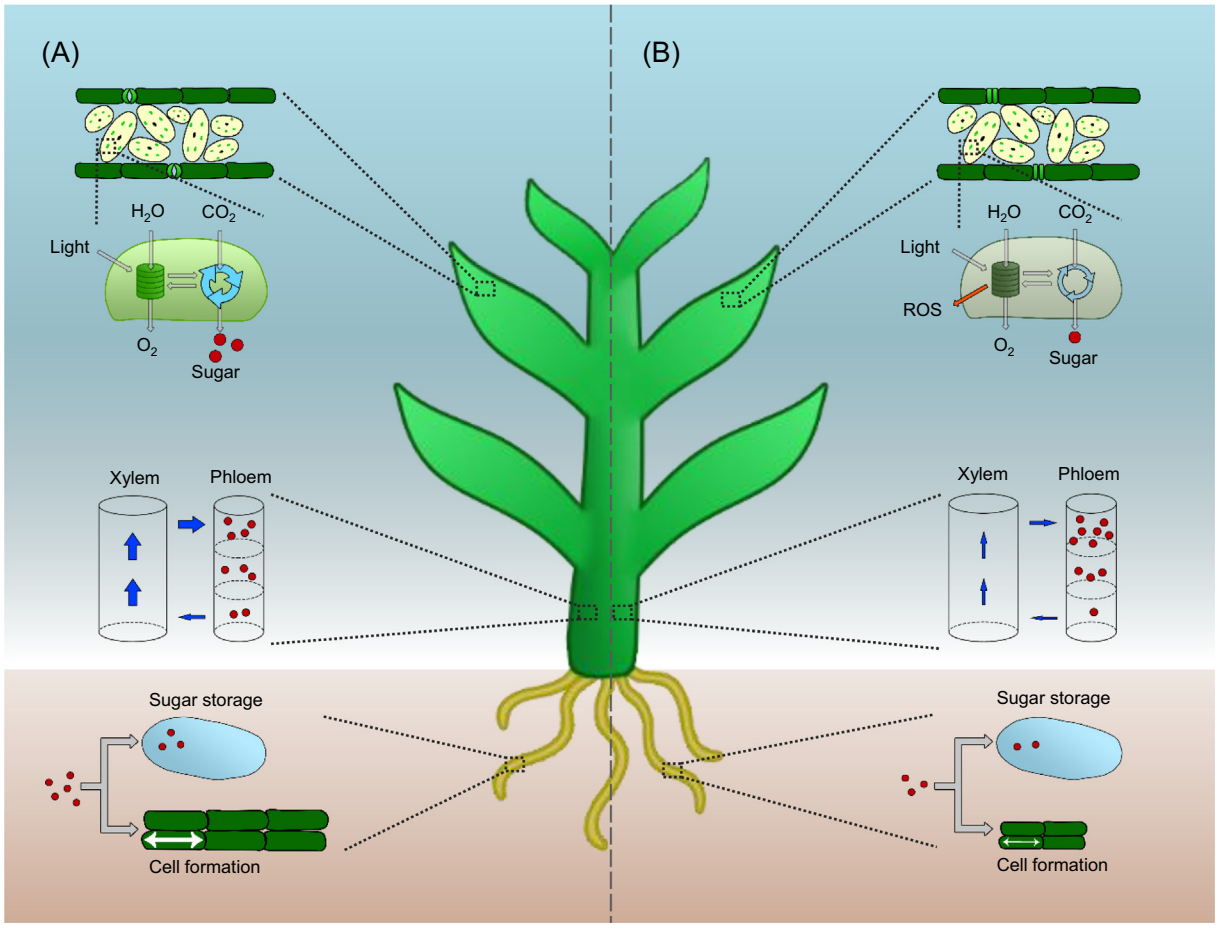


Figure 1. Overview of the Source–Sink Relationship in the Absence or Presence of Drought. (A) In the absence of drought, stomata present in the leaf epidermis are open (leaf inset), and $CO_2$ is fixed into sugars by the photosynthetic reactions (chloroplast inset). These sugars are transported through the phloem (stem inset) to sink organs such as roots (root inset), where they are stored in the vacuoles or as starch in plastids or incorporated for plant growth. (B) During drought, stomata are closed (leaf inset) leading to reduced $CO_2$ reaching the Calvin cycle, over reduction of photosystems and reactive oxygen species (ROS) production (chloroplast inset). Decreased water movement through the xylem increases phloem viscosity and the sugar gradient within the phloem vessels (stem inset). In sink organs such as roots (root inset), cell division and expansion are impaired as a result of reduced capacity to use sugars as well as lower cell turgor pressure. In the chloroplast inset, green stacked disks represent the thylakoids and blue circular arrows represent the Calvin cycle. The greyed out chloroplast indicates photosynthesis impairment during drought. Red circles represent sugars; wide and narrow dark blue arrows represent abundant and diminished water movement, respectively. The blue oval-like shape represents a vacuole and the white double-headed arrow represents cell turgor pressure. Thickness of the white arrow indicates level of pressure.

are subjected to water deficit at either the reproductive stage [44,45] or earlier, after seedling establishment, and maintained until yield parameters are evaluated [46–49]. The higher drought tolerance of the TF-modulated plants is associated with improved stomatal responses, reduced photosystem damage, and a higher photosynthetic rate (Table 1). These exciting results indicate that source adaptations to drought can be fine-tuned to improve tolerance and yield. However, the direct targets of these TFs still need to be identified to increase the current knowledge about the specific mechanisms driving source responses to drought, and to minimize pleiotropic effects and potential yield penalties upon modulation of TFs [26,27]. Using tissue-specific or inducible promoters or targeting a subset of downstream genes of these TFs may provide the way forward to uncouple drought tolerance and yield penalty. Indeed, galactinol synthase (GOL), which is involved in the synthesis of **osmoprotectants** of the raffinose family oligosaccharide class, is a direct target of dehydration responsive element binding (DREB)2A [27], a TF from the DREB family,

Table 1. Genes and Associated Traits that Confer Drought Tolerance and Improved Yield in Field-Grown Crops

| Function | Gene name | Species | Yield in WW | Yield in WD | Physiology | Growth | Refs |
|---|---|---|---|---|---|---|---|
| **Transcription factor** | *AtEDT1/ HDG11* | Rice<br>Cotton<br>Alfalfa | ↑ Grain yield<br>↑ Tiller number | ↑ Grain yield<br>↑ Tiller number<br>↑ Biomass yield | ↑ Photosynthesis<br>↓ Stomatal density<br>↑ Stomatal size<br>↓ Stomatal conductance | ↑ Root dry weight<br>↑ Root length<br>↑ Root diameter<br>↑ Root number<br>↑ Leaf area<br>↑ Plant height<br>↑ Shoot dry weight | [46–48] |
| | *HvSNAC1* | Barley | NA | ↑ Seed number<br>↑ Seed weight<br>↑ Tiller number | ↓ Stomatal conductance<br>↑ RWC<br>↑ Quantum yield | = | [43] |
| | *OsNAC10* | Rice | ↑ Seed weight<br>↑ Spikelet number | ↑ Seed weight<br>↑ Spikelet number | ↑ Quantum yield<br>↑ Recovery after rewatering | ↑ Root diameter | [72] |
| | *OsNAC5* | Rice | ↑ Seed weight<br>↑ Spikelet number | ↑ Seed weight<br>↑ Spikelet number | ↑ Quantum yield | ↑ Root diameter | [73] |
| | *OsNAC9* | Rice | ↑ Grain yield | ↑ Grain yield | ↑ Quantum yield | ↑ Root volume<br>↑ Root dry weight<br>↑ Root length<br>↑ Root diameter | [74] |
| | *OsTF1L* | Rice | = | ↑ Grain yield | ↑ Photosynthesis<br>↓ Stomatal conductance<br>↓ Water loss<br>↑ Quantum yield | ↑ Lignin content | [44] |
| | *ZmNF-YB16* | Maize | ↑ Seed weight | ↑ Seed weight | ↑ Photosynthesis<br>↑ Stomatal conductance<br>↑ RWC<br>↑ Quantum yield | ↑ Root length<br>↑ Plant height | [49] |
| | *ZmNF-YB2* | Maize | NA | ↑ Grain yield | ↑ Photosynthesis<br>↑ Stomatal conductance | = | [45] |
| | *ZmARGOS8* | Maize | ↑ Grain yield | ↑ Grain yield | NA | ↑ Plant height | [106] |
| **Enzyme** | *AISAP* | Rice | ↑ Panicle number | ↑ Grain yield<br>↑ Panicle number | ↑ Photosynthesis<br>↓ Stomatal conductance | ↑ Shoot dry weight | [101] |
| | *AtGOLS2* | Rice | ↑ Grain yield | ↑ Grain yield | ↑ Photosynthesis<br>↑ RWC<br>↑ Quantum yield | ↑ Plant height | [50] |
| | *LOS5/ABA3* | Soybean | = | ↑ Pod number | ↓ Stomatal conductance<br>↑ RWC | ↑ Shoot dry weight | [100] |
| | *TPP1* | Maize | ↑ Grain yield | ↑ Grain yield | ↑ Photosynthesis | ↑ Shoot dry weight | [96,97] |

Abbreviations: NA, not available; RWC: relative water content; WD, water-deficit conditions; WW, well-watered conditions. ↑, increased, =, maintained, ↓, decreased.

which is well known to be involved in the drought response. Unlike the overexpression of DREB TFs [26,27], the overexpression of *AtGolS2* in rice shows no yield penalty in well-watered conditions in the field, while plants have higher photosynthesis activity, increased biomass, and more panicles during water-deficit conditions than the control plants have, resulting in an improved yield stability [50]. Moreover, the results were obtained in two rice varieties and during different seasons, showing that the beneficial effect from the overexpression of *AtGolS2* is penetrant and robust [50]. Recently, targeting other components of the source strength, such as boosting recovery from photoprotection by overexpressing Photosystem II Subunit S together with enzymes from the xanthophyll cycle [51], or bypassing photorespiration by the introduction of alternative glycolate metabolic pathways [52,53], significantly improved tobacco and rice productivity in the field. Similarly, increasing the rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) assembly led to improved carbon assimilation and growth in maize [54]. In *Arabidopsis*, improving the rate of stomatal opening and closing in response to light, increases plant size and dry weight by reducing water loss through transpiration, without compromising photosynthesis [55]. The examples of how increased source strength leads to improved yield are exciting and it will be pivotal to assess these plants under water-deficit conditions. It is also important to translate findings on source strength improvement from *Arabidopsis* to crops and field conditions.

## Drought Reduces Nutrient and Water Transport

The reduced soil water availability during drought [56] results in a decreased water movement through the xylem, and subsequently, less water reaching the different organs [57], which decreases cell turgor pressure, influencing stomatal behavior [58] and cell expansion [59]. Additionally, the diminished water flow increases phloem viscosity, which reduces sugar transport [57]. The impairment in nutrient transport further affects the remaining source–sink communication, because it contributes to sugar build-up in source organs [17], consequently reducing source strength, and to less sugars reaching the sink organs [57], thus reducing sugar uptake and sink activity (Figure 1B).

Under water-deficit conditions, sugar transporters become more abundant [60], suggesting that there is pressure to maintain the nutrient flow from the sources to the sinks to preserve the source and sink strengths during drought. Nevertheless, the exact molecular mechanisms regulating this increased abundance in sugar transporters remain elusive. Recently, a positive correlation between transcript levels of genes encoding sucrose transporters and yield under field water-deficit conditions was reported in wheat [61]. In addition, maize plants mutant for different sucrose transporters showed a reduced growth and yield under field conditions, as a result of sugar accumulation in the leaves [62,63]. However, the opposite strategy of overexpression of sucrose transporters has not been successful to increase yield under field conditions so far [64,65]. The overexpression of SoSUT1 driven by a strong constitutive promoter increases sugar transport from leaves to tubers but has no effect on yield in potato [64]. Similarly, overexpression of AtSUT2 under the control of a phloem-specific promoter promotes sugar transport but reduces plant growth in *Arabidopsis* [65]. Possible explanations may be that growth is limited by other nutrients rather than sugars [65], or that improving sugar transport needs to be combined with enhanced source and/or sink strength. Complementary to improved nutrient transport through the phloem, water movement in the xylem and between different cell types has also the potential to be a target for drought tolerance. **Aquaporins** are important regulators of the water relations within the plant [66] and facilitate the transport not only of water, but also $CO_2$ and neutrally charged solutes across cell membranes [66,67]. Recently, increasing the abundance of these water channels in potato led to improved photosynthesis, growth, and yield under laboratory water-deficit conditions [67]. Although this result needs to be evaluated in the field, it suggests that improving water movement during water deficit alleviates the effects of this stress at the source and sink levels.

## Sink Organs Are Highly Sensitive to Drought

Because water deficit has a negative effect on photosynthesis and sugar transport, it is reasonable to think that this is the cause of the observed plant growth reduction upon drought. However, growth is often reduced prior to significant changes in photosynthesis [16,19,20]. In fact, in grapevine, shoot length is significantly reduced even before significant changes in leaf water potential are observed [40], emphasizing the extend of growth sensitivity to water deficit. In several species shoot growth is more affected than root growth [68], as observed by increased root to shoot ratios during water-deficit conditions [7,69], while in other species the root growth is more affected than the shoot growth [7,69]. This indicates that plant growth regulation under water-deficit conditions is organ and species dependent. Plant growth is defined by the capacity of cells to expand and divide [70]. As drought progresses, cells tend to lose water, lowering the turgor pressure necessary to expand; therefore, hydraulics play an important role in growth reduction during water-deficit conditions [71]. Nonetheless, prior to the growth reduction, the abundance of proteins associated with cell wall biosynthesis decreases [41], suggesting that beyond hydraulics, there are also early molecular signals involved in growth reduction. Additionally, genes and proteins associated with other processes necessary for plant grow, such as cell cycle, lignin biosynthesis, and protein synthesis, are also downregulated by drought [20,38,41]. It was recently reported that, in leaves exclusively developed under water-deficit conditions, growth reduction is caused by a decreased number of dividing cells, driven by major changes in cell cycle genes, as well as reduced cell expansion [38,39] (Figure 1B). Reduction in shoot area and consequently in the amount of water needed to sustain the plant may be a strategy to overcome water-deficit conditions. Nevertheless, increased plant height and leaf area, as well as root length and diameter, by constitutively overexpressing the homeobox TF AtEDT1/HDG11 [46–48], ectopically expressing TFs from the NAC family using a root-specific promoter [72–74], or introducing a quantitative trait locus for deep rooting in a shallow root rice cultivar [75], is associated with improved drought tolerance and crop yield under field conditions (Table 1), when water deficit is imposed after seedling establishment [46–48] or at the reproductive stage [72–75]. These results suggest that maintaining sink activity can be beneficial in some drought scenarios and it is possible that the severe growth reduction under drought conditions is an over-reaction, which might be a good target to improve drought tolerance. Since little is known about the targets of these TFs, it is possible that the obtained growth increase is not a direct effect of these TFs promoting growth, but rather an improvement of other pathways, for instance, at the level of carbon transport, which may alleviate the drought response. It is therefore important to uncover the molecular mechanisms directly targeted by these regulators. There are promising examples showing that specifically increasing the sink capacity of different crops may lead to high-yielding and drought-tolerant plants. Simultaneous overexpression of two sugar translocators in potato tubers increases plant yield and starch content [76], which has an even greater effect on productivity when combined with increased source strength [77]. Also, the cell cycle is a potential target to improve the sink strength. In *Arabidopsis*, many genes that positively affect organ size are involved in the regulation of cell proliferation [78], which may increase carbon usage and consequently nutrient flow, but it is yet unclear whether they also affect growth under water-limiting conditions. A notable exception is the cell-cycle-related gene *SIAMESE-RELATED1*, whose mutation leads to less growth inhibition under water-deficit conditions during early plant development [79]. However, whether and how cell cycle stimulation can improve drought tolerance is still largely unknown and deserves further attention.

## Drought Rewires the Source–Sink Regulation

In addition to the individual effects on the source–sink organs, water deficit also induces changes in the source–sink signaling. In the presence of sufficient water, there is a balance between source and sink capacities that is elegantly maintained by two kinases, sucrose-non-fermenting1-related

kinase1 (SnRK1) and target of rapamycin (TOR), in response to sugar levels (Figure 2). SnRK1 inactivates TOR and is repressed by trehalose-6-phosphate (T6P); an intermediate in the processes of sucrose conversion into trehalose. The mechanism linking T6P and SnRK1 was elusive until recently when T6P was found to prevent SnRK1 activation by directly binding to its catalytic subunit, KIN10, reducing its activity and phosphorylation [80]. T6P concentration is sensitive to changes in sugar abundance and is a precise proxy of the plant sugar status [81]. Low carbon levels, such as when photosynthesis is impaired or growth is boosted, are reflected in reduced T6P abundance (Figure 2A). The lower T6P concentration allows SnRK1 to repress TOR [82] and to phosphorylate other proteins, such as enzymes and TFs that constrain the cell cycle and cell wall formation, while promoting photosynthesis to reset the sugar levels [83,84]. Conversely, increasing photosynthesis or reducing growth leads to sugar accumulation (Figure 2B). In this case, T6P represses SnRK1, allowing TOR to be active and promote growth and development [85] by activating proteins associated with ribosomes and translation [86], as well as the brassinosteroid pathway [25]. Moreover, carbon build-up is also sensed by hexokinase that represses photosynthesis-related genes to reduce sugar production, while also modulating the levels of hormones such as auxin, cytokinins, and ethylene [87]. Also, hormones like auxin and ABA modulate the activities of the kinases SnRK1 and TOR [84,88], showing that sugar levels

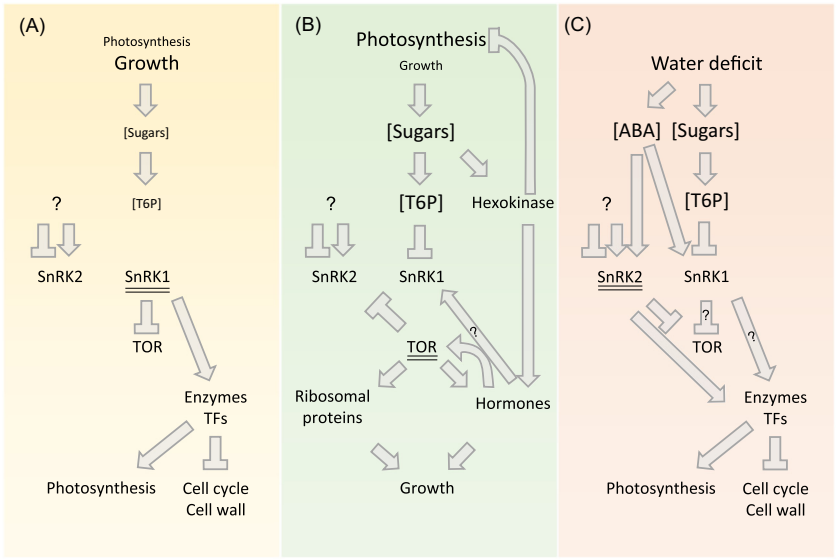


Figure 2. Regulation of the Source–Sink Communication by Sucrose-Non-Fermenting1-Related Kinase1 (SnRK1) and Target of Rapamycin (TOR). SnRK1 and TOR integrate sugar and hormone signaling to keep the balance between source and sink strengths. (A) Reduced photosynthesis or increased growth deplete the sugar pools, which is reflected in a low concentration of trehalose-6-phosphate (T6P). SnRK1 becomes active, represses TOR and phosphorylates proteins such as transcription factors (TFs) and enzymes. This downregulates high-energy-demanding processes, such as the cell cycle and cell wall formation, and promotes energy production by targeting photosynthesis. (B) A high concentration of sugar, due to increased photosynthesis or reduced growth, increases the concentration of T6P, which inactivates SnRK1. This inactivation allows TOR to target, for example, ribosomal proteins and hormones to promote growth, and to repress SnRK2. High sugar levels are also sensed by hexokinase, which regulates hormone signaling while repressing photosynthesis related genes to reduce source strength. (C) During water deficit, sugars accumulate leading to SnRK1 inactivation. However, the hormone abscisic acid (ABA) also accumulates, activating SnRK1, thus the contribution of SnRK1 for growth reduction under water-deficit conditions is still debated. ABA also activates SnRK2, which in turn represses TOR and modulates stomatal closure and plant growth during water deficit. Double underline highlights the main active kinase in each scenario. The size of the letters represents abundance. Question marks indicate unclear interactors or effects. Arrows represent positive effect while truncated lines represent negative effect.

and hormones are tightly integrated to regulate the source and sink capacities of plants in response to constantly changing environmental cues.

The higher concentration of ABA induced by water deficit promotes the activation of SnRK1 by inactivating one of its repressors [89]. Thus, it is reasonable that the growth reduction upon water deficit can be mediated by the growth repressor SnRK1 (Figure 2C). Nonetheless, under water-deficit conditions there is an increase in sugar availability [40,90] that should repress SnRK1 and thus promote growth. Given that growth is reduced during drought, the activation of SnRK1 by ABA may override its inhibition by sugars or, alternatively, another mechanism regulating this process may be in place. The involvement of SnRK1 in drought responses should therefore be further investigated. ABA also activates SnRK2 [89], which is known to mediate the drought response [91] by phosphorylating TFs and other proteins involved in stomatal closure and plant growth [91,92]. In addition, SnRK2 inactivates TOR under stress conditions, whereas in the absence of stress, TOR inactivates SnRK2 [93]. These reports, together with the fact that an effect of T6P on SnRK2 has not yet been reported [81], suggest that SnRK2 may play the role of SnRK1 during drought, independent of the sugar levels within the plant. In addition, some members of the SnRK2 family are known to act independently of ABA, thus integrating other signals, which are currently not fully understood [91,94]. Recently, the overexpression of one of the ten SnRK2 proteins present in rice increased yield under laboratory water-deficit conditions [95], and modulation of the T6P level in wheat and maize improved yield in both presence and absence of water deficit [96–98], indicating that these are important targets for plant improvement. Abolishing the enzyme activity while retaining the protein folding of T6P phosphatases, which phosphorylate T6P into trehalose, increases ear branching in field-grown maize without perturbing T6P levels, suggesting that apart from enzymatic activity, T6P phosphatases may have regulatory functions [99], expanding the complexity of metabolic regulation in plants.

Modulating different aspects of the ABA pathway has also been particularly successful. The overexpression of ABA biosynthesis and signaling regulators leads to overall improvements in source and sink capacity by reducing stomatal water loss, maintaining photosynthetic efficiency, and improving growth and biomass accumulation, thus converging into improved yield and drought tolerance in field-grown soybean and rice [100,101] (Table 1). Apart from the classical ABA-mediated drought response, the role of other plant hormones such as auxin, cytokinins, ethylene, gibberellins, and jasmonic acid in signaling drought responses is becoming evident [102–105]. Recently, the overexpression of *ZmARGOS8*, a negative regulator of the ethylene pathway [106], led to an increased yield under control, mild, and severe water-deficit field conditions in distinct locations and different maize inbred lines [106]. The creation of new *ZmARGOS8* variants with CRISPR-Cas9 has also increased yield under water-deficit field conditions [107]. Although the current knowledge about source–sink signaling during water deficit is still fragmentary, these examples indicate that targeting its regulation can improve stress tolerance and yield in field-grown crops under water-deficit conditions.

## Concluding Remarks and Future Perspectives

Substantial evidence on the potential of fine-tuning source and sink strength, as well as the source–sink communication, to obtain high-yielding drought-tolerant crops has recently been reported [43–50,72–74,96,97,100,101,106]. Given the range of environments where agriculture takes place, plants can experience very distinct drought scenarios, ranging from mild to severe water stress, which can prevail at the beginning, middle, or at the end of the life cycle of the plant [108,109]. Factors such as soil depth and composition, nutrient availability, and temperature also influence the plant responses to water deficit, which can be beneficial in a given scenario but detrimental in another [108,109]. For example, reduced water loss is more beneficial during severe water deficit, whereas maintenance of photosynthesis is more beneficial in mild water-

### Outstanding Questions

Why do plants retain photosynthetic capacity, while growth is severely impaired under drought conditions?

What are the molecular mechanisms regulating the photosynthetic machinery during drought?

Improving sugar transport from the sources to the sinks is not enough to increase crop yield. Can changes in sugar transport lead to improved drought tolerance and yield? What is missing?

Although many TFs have been shown to increase yield during drought, their direct targets remain unknown. To have a deeper understanding of the mechanisms conferring drought tolerance, it is necessary to know which genes are being primarily regulated by these TFs. Can these target genes then be used to promote drought tolerance while avoiding yield penalties?

Is SnRK1 involved in reducing growth during drought?

Does SnRK2 also integrate drought signaling from other hormones apart from ABA?

deficit conditions. To keep a high photosynthesis performance under severe water stress may be detrimental [109]. As such, conceptualizing an ideotype for drought tolerance optimized for a multitude of scenarios may not be possible. Still, many traits associated with drought tolerance are similar for multiple species grown in different field conditions and can be proposed as targets towards further crop improvement. To maximize the sink and source strengths, as well as the water and nutrient transport, plants should have: (i) increased root length, diameter, and angle [46,47,49,56,72–75], to allow the roots to explore deeper and harder soils; (ii) tailored xylem and phloem, to deal with the increase in water and nutrient uptake [64,65,67]; (iii) improved biomass accumulation, to act as a carbon reserve during the reproductive stage [46–48,50,100,101,106], combined with enhanced carbon mobilization from the plant reserves to the developing seeds [97], to prevent grain abortion; (iv) optimal stomatal aperture and density, to reduce the water loss through transpiration, but without compromising photosynthesis [43,44,46–48,100,101]; and (v) increased abundance of proteins with osmoprotectant and/or ROS scavenging activities, to maintain the efficiency of photosystem II and reduce the cellular damage caused by ROS [43,44,50,73,74].

Obtaining drought-tolerant plants that combine individually strengthened source and sink activities, with improved communication between source and sink organs, can be eased by incorporating the increasing knowledge on stress-inducible and tissue-specific promoters, as well as on the function of different post-translational modifications, with recent technological improvements in plant modeling, high-throughput sequencing, gene stacking, CRISPR technology, new breeding techniques and high-throughput (laboratory and field) phenotyping platforms [110–115]. Moreover, the fact that drought tolerance is a complex trait with an intricate regulatory network of kinases, TFs, and hormones, makes it pivotal to further unravel the direct interactions between these players, as well as their downstream targets, to identify genes that contribute to stress tolerance. This knowledge will aid us to overcome potential yield and growth penalties, as well as to identify bottlenecks in the source–sink communication that can be targeted to improve drought tolerance and yield. A deeper understanding of the relationship between source and sink organs, and its control during drought, particularly the underlying molecular mechanisms, would answer open questions regarding the regulation of source and sink strengths (see Outstanding Questions), while enabling the generation of new hypotheses. Additionally, genes known to improve tolerance under laboratory water-deficit conditions [67,95] need to be evaluated under varying field-drought scenarios, while plants that have remarkable productivity as a result of improved source and/or sink strength [51,52,77], must be assessed for drought tolerance. Therefore, field trial evaluations should be standardized and made available to a broader scientific community [116] to optimize the already available resources towards improving source and sink strengths, as well as the overall source–sink communication. With the increasing number of plant phenotypic evaluations under varying environmental conditions, the challenge of standardizing data collection and making it publicly available should also be a priority [117,118]. In this way, data can be easily compared, reproduced, and used for meta-analysis that can aid in identifying important traits for drought tolerance. In the end, this global effort will allow the development of the future high-yielding, drought-tolerant crops (see Outstanding Questions).

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