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# Crop yield: challenges from a metabolic perspective

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Considering the dual use of plants, as bio-factories for foods and feedstock for bio-refining, along with a rising world population, the plant biotechnology field is currently facing a dramatic challenge to develop crops with higher yield. Furthermore, convergent studies predict that global changes in climate will influence crop productivity by modifying most yield-associated traits. Here, we review recent advances in the understanding of plant metabolism directly or indirectly impacting on yield and provide an update of the different pathways proposed as targets for metabolic engineering aiming to optimize source–sink relationships.

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## Yield components and modeling

Recently, efforts to directly increase yield per hectare have been achieved by the enhancement of harvest index (Box 1). However, food and bioenergy production must increase substantially in the next few years in order to supply the increasing global demand for commodities. It is well accepted that source production and sink utilization of carbohydrates are tightly coordinated and, given that the majority of food and feed comes from sink organs, these determine biomass production and, ultimately, yield. Here, yield is defined as the absolute capacity of a crop/genotype to produce biomass under optimum conditions and this review particularly focuses on harvestable sink organs. The source–sink relationship is regulated by a highly complex signaling network involving carbon/nitrogen (C/N) status and nutrient availability [1].

The ideal condition for improving crop yield would be the optimization of all metabolic events together with the environmental conditions. This includes optimizing rates of all important processes and also their interactions and duration, which are generally determined by genetically based mechanisms (G) often affected by the environment (G × E). However, crop management (*M*) must be rationally included in the yield equation: yield = G × E × M. Different kinds of crop modeling are intent on evaluating yield under current and mimicked future environmental conditions [2,3]. The extent to which these models can predict yield effects largely depends on the importance of feedback regulation regarding light interception and conversion to biomass [4]. However, integration of metabolism variables into these models is just now being assessed (reviewed by [5]). An exemplary case is that of wheat productivity, for which yield has reached a plateau in the last 4–5 years despite increasing very rapidly during the last 50 years [3]. Models applied to a broad metabolic data set, from different accessions of *Arabidopsis* subjected to restrictions in N and C supplies, confirmed that biomass negatively correlates with starch and protein contents supporting the hypothesis that these metabolic traits are integrative signals that capture information about the levels of many low-molecular-weight metabolites [6,7]. Likewise, a kinetic model based on enzyme activity measurements and subcellular compartmentalization also linked growth with sucrose metabolism in tomato fruit [8] and demonstrated that during cell expansion, fruit experiences a decrease in sucrose import and glycolysis, suggesting that much of the C is imported very early in development (cell division). Moreover, the study also incorporated kinetic parameters of tonoplast carriers allowing the proposal that these proteins are involved in the stage-dependent enzyme reprogramming that occurs during tomato fruit development [9], emphasizing the importance of knowledge on compartmentalization kinetics to understand sink growth.

Biomass production is related to photosynthesis, by means of source activity. However, either insufficient sink strength and elevated source activity or inhibition of sugar transport lead to accumulation of carbohydrates in leaves resulting in the feedback downregulation of photosynthesis and of photosynthetic efficiency [10]. Additionally, biomass production is constrained by environmental factors that also alter source–sink partitioning

**Box 1 Yield components definition**

Yield is determined by the size and activity of the harvestable organs. The former is a physical factor that comprises cell number and size, and the latter is a complex physiological factor including carbohydrate metabolism and storage capacity. Definitions of yield components vary according to the reference crop species and are determined in specific phenological stages during plant development. Here we define those main traits which impact the final harvestable biomass per area unit.

(1) Density at harvest: final plant number per unit area.
(2) Individual production per plant:

  2.1 Number of harvestable organs per plant (e.g. stems in sugar cane, panicles and ears in cereals, fruit in tomato and tubers in potato).
  2.2 Number of spikelets per panicle/ear (in cereals).
  2.3 Weight of harvestable organs (e.g. 1000 grains in cereals, stems in sugar cane, fruit in tomato and tubers in potato).

(3) Harvest index = total harvestable weight × 100/aerial biomass.

[11]. Thus, the experimental evidence clearly shows that yield should be placed in the context of whole-plant source–sink interrelationships. In order to approach a comprehension of agronomic yield, recent advances in carbohydrate production, partitioning and consumption aiming to optimize the source–sink relationship are reviewed in the next sections.

## Morphogenetic influence on yield

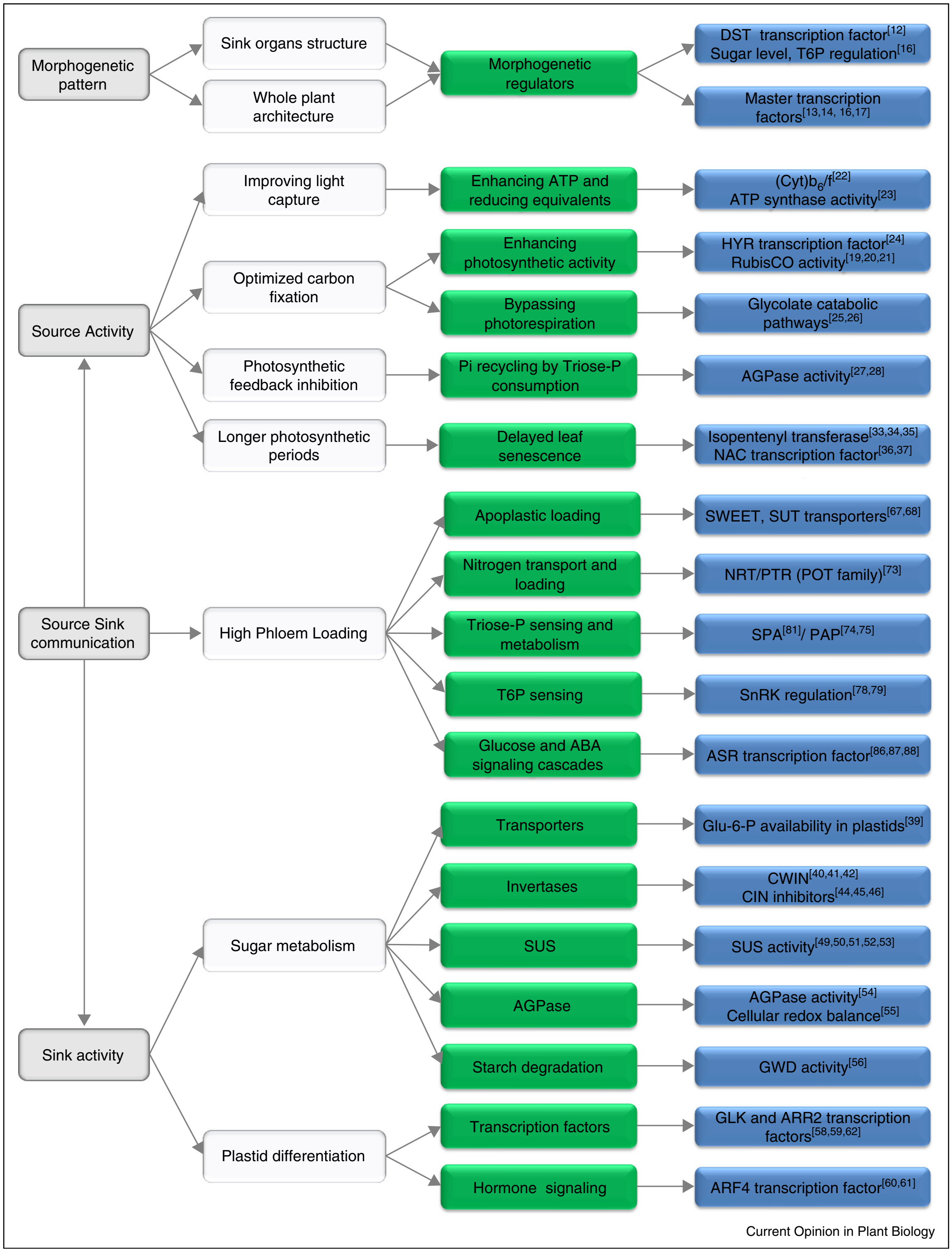
Several players and mechanisms by which morphogenetic patterns are determined have been revealed in recent years (Figures 1 and 2) and have been shown to modulate different yield components (Box 1), appearing as interesting targets to improve sink strength. In rice, panicle branching and number of grains per panicle are controlled by the transcriptional activator *DROUGHT AND SALT TOLERANCE* (*DST*). This is explained by elevated cytokinin levels in the reproductive shoot apical meristem, controlled by the *GRAIN NUMBER 1A/CYTOKININ OXIDASE 2* gene (*Gn1a/OsCKX2*) which is in turn activated by *DST* [12•]. Similarly, in wheat, supernumerary spikelet formation is controlled by *WHEAT FRIZZY PANICLE*, a member of the *APETALA2/ETHYLENE RESPONSE FACTOR* family [13]. *HvAP2*, a member of this same gene family that is regulated post-transcriptionally by miR172, controls barley spike architecture, directly affecting the density of grains along the inflorescence [14]. Through alterations in protein metabolism, overexpression of the *SPIKELET NUMBER* gene (*SPIKE*) led to increases in spikelet number, leaf size, root dry weight and the number of vascular bundles, indicating an enhancement of source size and translocation capacity as well as sink size in rice [15].

The role of sugar-mediated signaling pathways in flowering control is well documented. In *Arabidopsis thaliana*, high levels of sucrose accelerate flowering through the trehalose-6P (T6P) signal, which inhibits the transcription of miR156, allowing expression of the *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE* (*SPL*) transcription factor [16]. T6P also regulates the expression of several flowering-time genes throughout the plant. In leaves, this signal molecule induces the *FLOWERING LOCUS T* (*FT*), which is a long-distance signal transported to the shoot meristem that triggers flowering [16]. Likewise, tuning the ratios between the flower-promoting *SINGLE FLOWER TRUSS* (*SFT*) (*FT* tomato homolog) and the flower-repressing *SELF PRUNING* (*SP*) results in an optimal balance of the flowering signals, defining a partially determinate plant architecture that leads to maximum yields without compromising the source strength [17•]. In the above examples, the photoperiodic and metabolic signals converge to ensure optimal conditions for flowering and, hence, affect overall yield. Notwithstanding these findings, until we fully understand the mechanisms underlying source and sink bottlenecks and partitioning that allow enough C supply to sink organs, this cumulative body of knowledge cannot be rationally exploited for increasing yield.

## Improving yield by enhancing source strength

Many factors of plant physiology affect source strength (Figures 1 and 2). Photosynthesis efficiency, by means of increasing photosynthesis per leaf area, might be attained by improving light capture, optimized C fixation and decreasing photosynthetic feedback inhibition. Engineering ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) for improved forms has been a main objective for enhancing photosynthetic efficiency. Although some interesting advances have been achieved, due to the complex quaternary structure of this enzyme, composed by a plastid-encoded large subunit (LSU) and a nuclear-encoded small subunit (SSU), and the still limited chloroplast transformation for crop species, more effort should be made to translate RubisCO engineering into enhanced yield [18]. The co-expression of the *Synechococcus elongates* LSU and SSU genes, together with the assembly chaperone (RbcX) or an internal carboxysomal protein (CcmM35) in transplastomic tobaccos resulted in higher rates of $CO_2$ fixation per unit of enzyme [19]. Additionally, the engineering of the plastidial LSU in tobacco or the incorporation of the nuclear SSU from *Sorghum bicolor* in rice resulted in faster carboxylation and catalytic turnover rates of the enzyme, respectively [20•,21]. However, the capacity of electron transport seemed insufficient to support the increased enzyme capacity in the transgenic plants [21]. Thus, some interesting works have explored the bottlenecks of the light harvest system and indicated the cytochrome (Cyt)$b_6$/f complex and the δ-subunit of chloroplast ATP synthase as potential targets for enhancing ATP and production of reducing equivalents especially when $CO_2$ fixation is not limited [22,23]. Recently, a master regulator of photosynthetic C metabolism was identified in rice. Transgenic lines overexpressing

**Figure 1**



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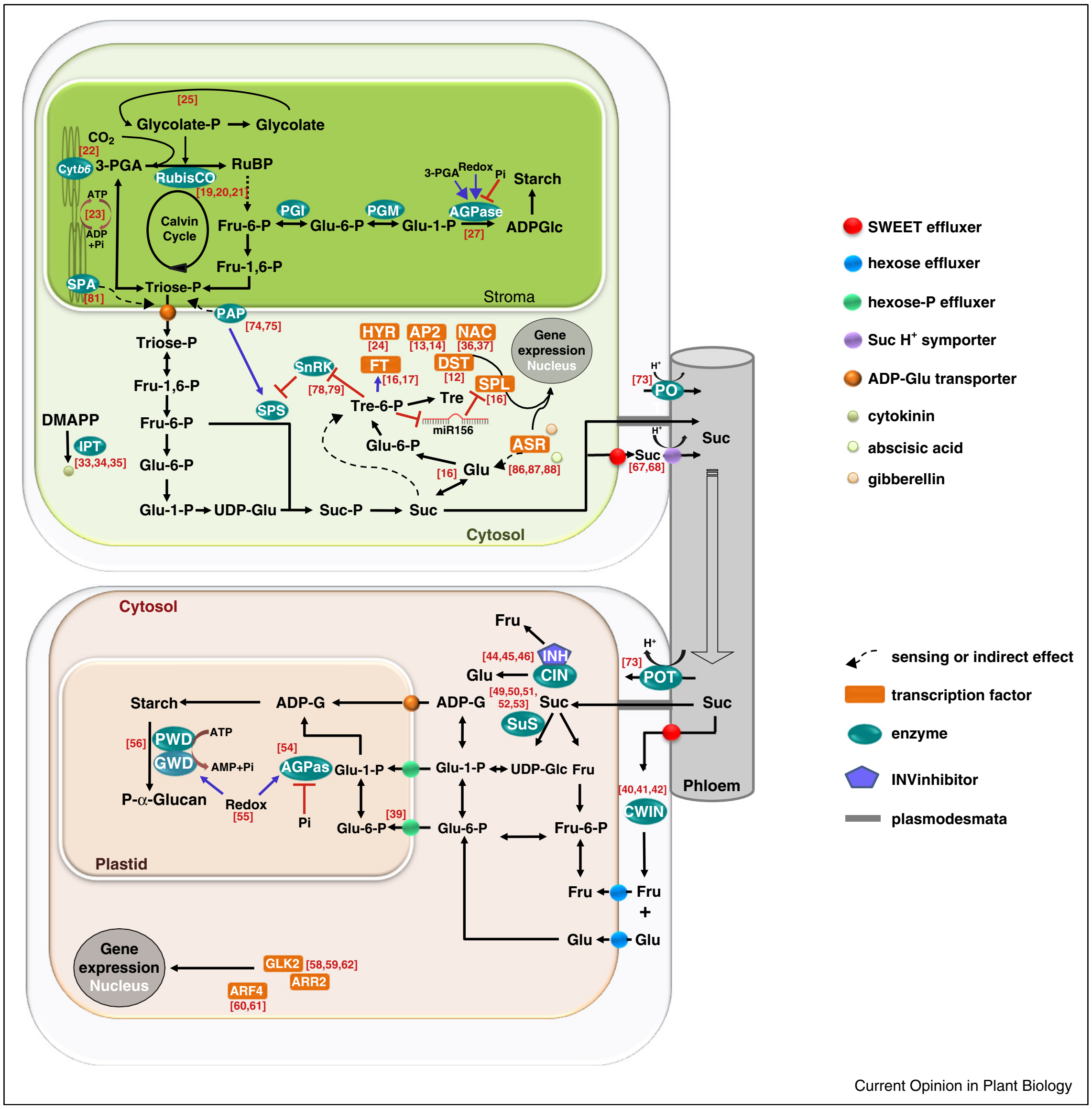
Overview of integrated strategies towards crop yield improvement. Currently known factors affecting yield through modulation of morphogenetic patterns, source and sink activities and source–sink communication. Numbers in brackets correspond to references cited in the text. Abbreviations (ordered as appearing in the figure). DST (drought and salt tolerance, zinc finger protein); (Cyt)b6/f (cytochrome b6f complex); HYR (higher yield rice); Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase); AGPase (ADP-glucose pyrophosphorylase); NAC (NAM, ATAF, and CUC transcription factors family); SUT (sucrose transporters); NRT/PTR (nitrate transporter/peptide transporter); POT (proton-dependent oligopeptide transporters); SPA (sugar partitioning affecting protein); PAP (purple acid phosphatase); SnRK (sucrose nonfermenting (SNF)-related kinase); ASR (abscisic acid, stress, ripening); CWIN (cell wall invertase); CIN (cytoplasmic invertase); SUS (sucrose synthase); GWD (glucan, water dikinase); GLK (Golden 2-like); ARR2 (Arabidopsis response regulator); ARF (auxin response factor).

**Figure 2**



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Schematic model of metabolic pathways and transcription factors associated with the modulation of morphogenetic pattern, source and sink activities and source–sink communication. The regulatory points that have been shown to affect final yield are indicated. Numbers in brackets are the same as those for references reviewed in the text. Abbreviations are ordered alphabetically. AGPase (ADP-glucose pyrophosphorylase); AP2 (Apetala2); ARF (auxin response factor). ARR2 (Arabidopsis response regulator); ASR (abscisic acid, stress, ripening); CIN (cytoplasmic invertase); CWIN (cell wall invertase); (Cyt)b6/f (cytochrome b6f complex); DST (drought and salt tolerance, zinc finger protein); FT (flowering locus T); GLK (Golden 2-like); GWD (glucan, water dikinase); HYR (higher yield rice); IPT (isopentenyltransferase); NAC (NAM, ATAF, and CUC transcription factors family); NRT/PTR (nitrate transporter/peptide transporter); PAP (purple acid phosphatase); PGI (phosphoglucose isomerase); PGM (phosphoglucomutase); POT (proton-dependent oligopeptide transporters); PWD (phosphoglucan water dikinase); Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase); SnRK (sucrose nonfermenting (SNF)-related kinase); SPA (sugar partitioning affecting protein); SPL (squamosa promote binding protein-like); SPS (sucrose-phosphate synthase); SUS (sucrose synthase); SUT (sucrose transporters).

*HIGHER YIELD RICE* (*HYR*) gene showed higher CO$_2$ assimilation and photochemical efficiency of photosystem II (PSII) compared to wild type plants. *HYR* encodes an AP2/ERF (APETALA2/Ethylene Responsive Factor) transcription factor, which directly activates and represses other genes in a network involved in photosynthesis and carbon metabolism as well as in stress-protective pathways. The improved photosynthetic capacity of *HYR* overexpressing lines resulted in an increment of ~30% in grain yield under well-watered as well as drought-stressed conditions [24•]. Losses by photorespiration can reach over 25% of the fixed C [18]. To bypass these costs two alternative pathways have been introduced in *Arabidopsis* chloroplasts: (i) the entire glycolate catabolic pathway from *Escherichia coli* [25] and (ii) overexpression of the native glycolate oxidase, the malate synthase from *Cucurbita maxima* and a bacterial catalase [26•]. Promising results have been found in both cases; plants exhibited higher biomass production and showed enhanced $CO_2$ fixation and growth improvement. However, evidence that such a strategy will prove successful in crop plants is still lacking.

The overexpression of the ADP-glucose pyrophosphorylase, a key enzyme in regulating starch biosynthesis, under the control of the RubisCO SSU promoter in *Arabidopsis* and *Oryza sativa* resulted in higher photosynthetic capacity and increased biomass and yield [27]. These data raised the hypothesis that enhancing the transient starch accumulation in leaves alleviates feedback inhibition of photosynthesis, stimulating the recycling of inorganic phosphate (Pi) by the consumption of triose-P and promoting more vegetative and reproductive growth during the night [28••]. Similarly, the improvement of water use efficiency by the manipulation of stomatal behavior was demonstrated as an indirect way to increase photosynthesis efficiency, especially under drought stress conditions. In this sense, the expression of a hexokinase controlled by a guard cell-specific promoter in transgenic *Solanum lycopersicum* plants resulted in a 30% reduction of stomatal conductance and decreased transpiration without affecting photosynthesis and plant growth parameters [29].

The maintenance of photosynthetic activity for longer periods by delaying leaf senescence might also lead to C assimilation improvement. In mature leaves, photoassimilate export is followed by a phase of N remobilization; this transition corresponds to the initiation of senescence [30]. Genotypes in which the C–N transition point is delayed, named functional stay-greens, extend the transfer of photosynthetic assimilates from sources to harvestable sinks contributing to yield improvement [31,32]. A hormone-based strategy has been applied in several crop species where the gene encoding cytokinin-synthesizing enzyme, isopentenyl transferase (*IPT*), was expressed under the control of senescence-induced promoters. *SARK-IPT* rice transgenic lines showed higher amounts of shoot dry matter production and seed yield per plant under water stress [33]. Similar strategies resulted in significant yield and salt tolerance increases in cotton [34] and peanut [35]. Delayed leaf senescence has also been approached by down-regulating senescence induction transcription factors that belong to the *NAC* (*NAM/ATAF1/2/CUC2*) gene family [36]. Interestingly, depending on the crop species, the impact of the stay-green phenotype on yield was different. In maize and rice, the down-regulation of *NAC* genes resulted in significant gains in grain weight and number [32]. By contrast, wheat plants silenced for all *NAM* copies showed reduced concentration of grain protein, zinc and iron, with no significant differences in grain size, thus indicating that the extended photosynthetic activity did not compensate for the reduced nutrient translocation from leaves [37]. However, results from a recent study showed a negative correlation between the onset of senescence and grain yield and a positive one with grain protein content [38]. Even the partitioning processes of N and C should be further explored; senescence control thus appears to be a promising target for yield improvement.

## Sink strength as determinant of crop yield

Sink harvestable organs constitute approximately 75% of global crop food production. Sink strength is the major driving force for maintaining source activity, carbon partitioning and, therefore, yield. Its improvement has been approached by two main lines: by altering the expression of enzyme encoding genes related to sugar metabolism or plastid differentiation regulators (Figures 1 and 2), which are reviewed below.

Invertases, the major sucrolytic plant enzymes, are recognized to play a central role in determining sink strength in many crops species. Ectopic expression of a yeast invertase in the cytosol led to large changes in metabolic profile: reduced starch content in potato tubers, increased respiration rate and accelerated starch degradation during storage. On the other hand, apoplasmic expression resulted in increased tuber size and yield due to an increase in water content. These effects could be explained by a reduced glucose-6-phosphate (G6P) availability in the plastid due to the lower expression of the G6P transporter [39]. This mechanism indicates that assimilate utilization is regulated at the level of sucrose degradation controlling energy versus storage metabolism. Cell wall invertases (CWINs) determine the C partitioning during early grain filling [40•] and constitute functional markers associated with kernel weight in wheat [41]. Moreover, under drought stress conditions the heterologous expression of a CWIN gene *CIN1* from *Chenopodium rubrum* in tomato increased fruit yield due to an induced sink metabolism in the leaves [42]. On the other hand, even when vacuolar invertases (VINs) have not been associated directly with yield, it has been hypothesized that they promote cell expansion by an osmotic-independent mechanism stimulating phloem unloading and, thus, sink strength by maintaining the gradient of sucrose from phloem to parenchyma cells [43]. In this regard, VINs are an attractive focus of attention as targets for yield improvement. Overall, however, invertase activities are mostly regulated at post-translational levels, especially by their pH-dependent interaction with inhibitors [44] and examples in tomato and potato have been described with impacts on yield and quality [45,46].

As well as invertases, sucrose synthase (SUS) has been largely studied as a biochemical marker for sink strength, due to its contribution to starch, protein biosynthesis and energy production [47–49]. The enhancement of SUS activity represents a useful strategy for increasing starch accumulation and yield in heterotrophic organs. Despite conflicting results reported for *Arabidopsis* [50,51], in cotton, seed and fiber growth correlate well with SUS activities [49,52], and the ectopic expression of *StSUS4* in maize resulted in seeds with both higher starch content and amylose/amylopectin balance [53].

The enhancement of starch accumulation in harvestable organs was achieved by the increase of the net balance between starch synthesis and breakdown [28••]. Thus, enzymes related to these two processes are good targets for the production of genetically engineered 'high-starch' plants. Endosperm-specific expression of either the *BT2* or *SH2* gene encoding the maize AGPase small and large subunits, respectively, resulted in enhanced seed weight and starch content [54]. In tomato, it has been reported that malate metabolism affects AGPase activity through an effect on the cellular redox balance determining sugar content [55]. Downregulation of starch phosphorylation by silencing of a glucan water dikinase enzyme resulted in an increase in the final yield in wheat [56]. Furthermore, suppression of α-amylase genes improves rice grain quality when plants are grown under high temperature conditions [57].

In tomato fruit, photosynthesis affects development and ripening, contributing to final quality and yield. The *GOLDEN 2-LIKE* (*GLK2*) transcription factor is a regulator of chloroplast development in tomato fruit that affects sugars and lycopene contents [58,59], this fact identified this gene as an interesting target to enhance quality traits. Another example is the tomato *auxin response factor 4* (*SlARF4*) that affects fruit chlorophyll contents and controls starch accumulation in fruit by repressing the expression of the *SlAGPase* gene. In this way, *SlARF4*-silenced lines showed denser, firmer, and prolonged shelf-life fruits with reduced water loss [60,61]. Similarly, the tomato *ARR-2 LIKE* gene (*ARABIDOPSIS PSEUDO RESPONSE REGULATOR2-LIKE*) affects plastid number and area in fruit, enhancing the levels of chlorophyll in immature unripe fruit and carotenoids in red ripe fruit [62]. These studies provide insight into the link between hormone signaling, chloroplast activity and sugar metabolism that could be further targets for improving fruit yield and quality, not only in tomato but in other fruit bearing species.

## Source–sink partitioning and its relationship with crop yield

Most of the fixed C not required to support leaf homeostasis is loaded to phloem and partitioned to sink organs. Crop yield depends on the source–sink relationship, which in turns is highly influenced by environmental responses and metabolic demands (Figures 1 and 2). Thus, knowledge about the balance between assimilate production and consumption must be very precise if improvement in crop productivity is desired. An increase in night temperature during the rice reproductive period impacted negatively on grain yield and total dry matter. This is in line with N and non-structural carbohydrate content reductions and decreased 1000-grain weight and grain yield. Increments in the abundance of molecular chaperones and nucleic acid/protein modification proteins at early grain filling stages indicate that the observed source limitation is under genetic control and provides a basis for metabolic engineering approaches [63]. The above described results somehow contrast with the hypothesis postulated for wheat and barley. By removing sink-strength and/or source-strength, these authors proposed that these two crop species do not seem to be source-limited under a range of different production conditions, as the source availability exceeds their sink capacity [64]. On the other hand, removing secondary inflorescences in *Arabidopsis* resulted in a stimulation of elongation of the primary inflorescences and in the development of longer and larger siliques that contained fewer, bigger seeds of higher fatty acid content [65].

Resource allocation in plants is completely dependent on the stage of the plant's life cycle and the reproductive strategy of the species under consideration. So far, with a handful of exceptions, efforts to increase the partitioning of fixed C into harvestable organs have largely been restricted to the manipulation of C fluxes via the modification of individual enzymatic steps (reviewed in [66]). Nevertheless, sugar movement systems across plasma membranes for phloem loading, which ultimately define the total biomass allocated into harvestable organs, are an intense focus of research. Two types of phloem loading can occur in the same vein: apoplastic and symplastic. Once loaded into the phloem, sucrose moves along hydrostatic pressure gradients by bulk flow through the transport phloem. It was not until recently, however, that a 'missing link' of sugar movement systems was identified: the SWEETs sugar efflux carriers. These transport proteins are responsible for the efflux of sucrose from the phloem parenchyma to the sieve element-companion cell complex for translocation toward sink organs where it is loaded actively with the help of a sucrose transporter (SUT1) and energized by $H^+$-ATPases into the actual conduits [67,68••]. These proteins are now starting to be identified in economically important crops and proposed as promising new ways of engineering both crop yield and pathogen resistance [69,70•,71].

Sugars are not the only metabolites that comprise source–sink relationships, but N uptake and transport also sustains development and growth and finally impacts on yield. N can be transported as free amino acids and small peptides. In some tropical and subtropical legumes (i.e. soybean, common bean, chickpea and cowpea), ureides represent the major form for long-distance transport of N. This is mediated by various types of proteins involving different tightly controlled transport mechanisms (reviewed by [72]). A more specialized nitrate and dipeptide and tri-peptide transport system (NRT/PTRs), which distributes nitrogen throughout the vascular system involves a very large transporter family belonging to the ubiquitous proton-dependent oligopeptide transporter family (POT) (reviewed by [73]). This vast protein family is an emerging field for engineering with potential impact on crop yield and quality.

New molecular mechanisms concerning source and sink communicating signals have been recently described. Plant purple acid phosphatases (PAPs) catalyze the hydrolysis of a wide range of phosphomonoester and amide substrates and are considered to mediate phosphorus acquisition and redistribution. Ectopic overexpression of a dual-targeted PAP (plastids and mitochondria — AtPAP2) resulted in earlier bolting and higher seed yield in *Arabidopsis* [74]. These lines presented upregulation of sucrose phosphate synthase (SPS) activity and enhanced sucrose and hexose levels in leaves, with no changes in starch contents. The authors hypothesized that AtPAP2 operates in a novel mechanism, independent of the action of the well-known SnRK kinases, which releases Pi, promoting triose-P production in the chloroplast and subsequently enhances sucrose synthesis. Similarly, in the mitochondria, Pi provision modulates the tricarboxylic acid (TCA) cycle and activates oxidative phosphorylation and ATP synthesis. Overexpression of this enzyme in potato increased tuber number and starch content, and raised the photosynthesis rate by a mechanism also mediated by increments in SPS activity and the sucrose transporter 1 (StSUT1) [75]. Similarly, SnRK1 is proposed as a common player in regulating the source–sink relationship and, although under debate [76], its connection with T6P in improving wheat yield is illustrated (reviewed by [77]). This protein kinase is regulated by T6P, a sensor of sucrose availability [78,79]. Under conditions of low temperature or low N T6P regulation of SnRK1 provides an explanation for the control of growth in response to tissue sucrose availability [11]. However, contrasting results have been reported regarding consequences of modifying T6P on crop productivity. For example, in potato, increased or decreased T6P leads to lower tuber size and yield. Tubers with elevated T6P have lower levels of sucrose and hexose phosphates, decreased starch, higher respiration and more lenticels [80]. Source–sink balance coordination is intimately linked to triose-P metabolism and sensing. In this vein, a recently described plausible regulator of source–sink partitioning with an impact on yield is a small plastidial protein from tomato, named *SPA* (*SUGAR PARTITIONING AFFECTING*), whose role in plastid metabolism limits the rate of sucrose translocation to fruits. Source leaves from *SPA*-silenced plants have **a** lower content of soluble sugars and starch, while ripe fruit accumulates over two-fold more starch but soluble sugars remain unaltered. As a consequence, silenced plants produce more and heavier fruits summing to a considerably higher harvest index [81•]. Surprisingly, the *Arabidopsis* ortholog *LOW QUANTUM YIELD* (LQY) [82] interacts *in vivo* with *HYPERSENSITIVE TO HIGH LIGHT1* (HHL1) [83] and together maintains PSII activity by regulating repair and reassembling of PSII complexes under light stress. These findings are, by no means divergent, and instead suggest that SPA/LQY1 could operate as a bifunctional protein involved in sugar partitioning and PSII stabilization in both species.

Further, sugar-hormone signals and molecular networks have been long implicated in controlling plant growth through modulation of source–sink partitioning (reviewed by [84]) and plausible molecular mechanisms are being revealed. A small DNA-binding protein from the *ASR* (*ABSCICIC ACID*, *STRESS AND RIPENING*) family has been found to act at the convergence of glucose and abscisic acid signaling cascades through *HEXOKINASE1* and *SnRK1* [85]. In potato, ASR1 suppresses the expression of hexose transporters in tubers, in opposition to the observed function of this protein in leaves [86]. Thus, ASR1 could have antagonistic effects on source and sink tissues in sugar metabolism. This duality in the effect of ASR1 could be caused by the interaction of ASR1 with different factors that regulate gene expression. In maize, *ASR1* overexpression has a large impact on vegetative biomass and increases yield and this phenotype correlates with changes in the branched-chain amino acid biosynthesis [87]. More recently, it was shown that ASR1 regulates leaf glucose levels and C partitioning in tobacco through its action in the glucose–ABA and glucose–gibberellin crosstalks [88]. Many genes with a role in abiotic stress tolerance also seem to have a direct or indirect effect on source–sink relations and it has been hypothesized that under stress conditions plants may display adaptive responses to recover functional equilibrium. However, even when this would be attractive from a biotechnological point of view, until the mechanisms behind this link are elucidated their potential application cannot be fully exploited.

## Conclusions and perspectives

The experimental data discussed above make it evident that results produced by individual interventions in the source–sink relationship have had limited success and ‘multiple targeted engineered plants’ may suit the requirement for achieving high yield and elevated fitness of crops. In this sense, a pioneer study has reported a combined ‘pull’ and ‘push’ approach aiming to improve potato tuber yield. Source capacity was increased by mesophyll-specific overexpression of a pyrophosphatase or, alternatively, by antisense expression of the ADP-glucose pyrophosphorylase. In contrast, sink capacity was enhanced by the overexpression of two plastidic transporters in tubers, a glucose 6-phosphate/phosphate and an adenylate translocator. Both combinations of engineered plants resulted in reduced leaf starch accumulation and double the starch yield in tubers [89].

As stressed in this review, many metabolic pathways have direct impacts on crop yield through a plethora of different mechanisms. Whether the plasticity of such mechanisms can overcome yield constraints in a context of global climate change (i.e. higher temperatures and water limitation) should be one of the most important questions for the plant science field in the coming years. Moreover, a current urgent challenge is to transfer these findings to open field trials and demonstrate the effects on yields on a per unit area basis.

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