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Current Opinion in Plant Biology

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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Current Opinion in Plant Biology 2015, **25**:79–89

This review comes from a themed issue on **Physiology and metabolism**

Edited by **Steven Smith** and **Sam Zeeman**

http://dx.doi.org/10.1016/j.pbi.2015.05.004

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