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Next-generation strategies for understanding and influencing source–sink relations in crop plants

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Whether plants are source or sink limited, that is, whether carbon assimilation or rather assimilate usage is ultimately responsible for crop yield, has been the subject of intense debate over several decades. Here we provide a short review of this debate before focusing on the use of transgenic intervention as a means to influence yield by modifying either source or sink function (or both). Given the relatively low success rates of strategies targeting single genes we highlight the success of multi-target transformations. The emergence of whole plant models and the potential impact that these will have in aiding yield improvement strategies are then discussed. We end by providing our perspective for next generation strategies for improving crop plants by means of manipulating their source–sink relations.

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The concepts of source and sinks

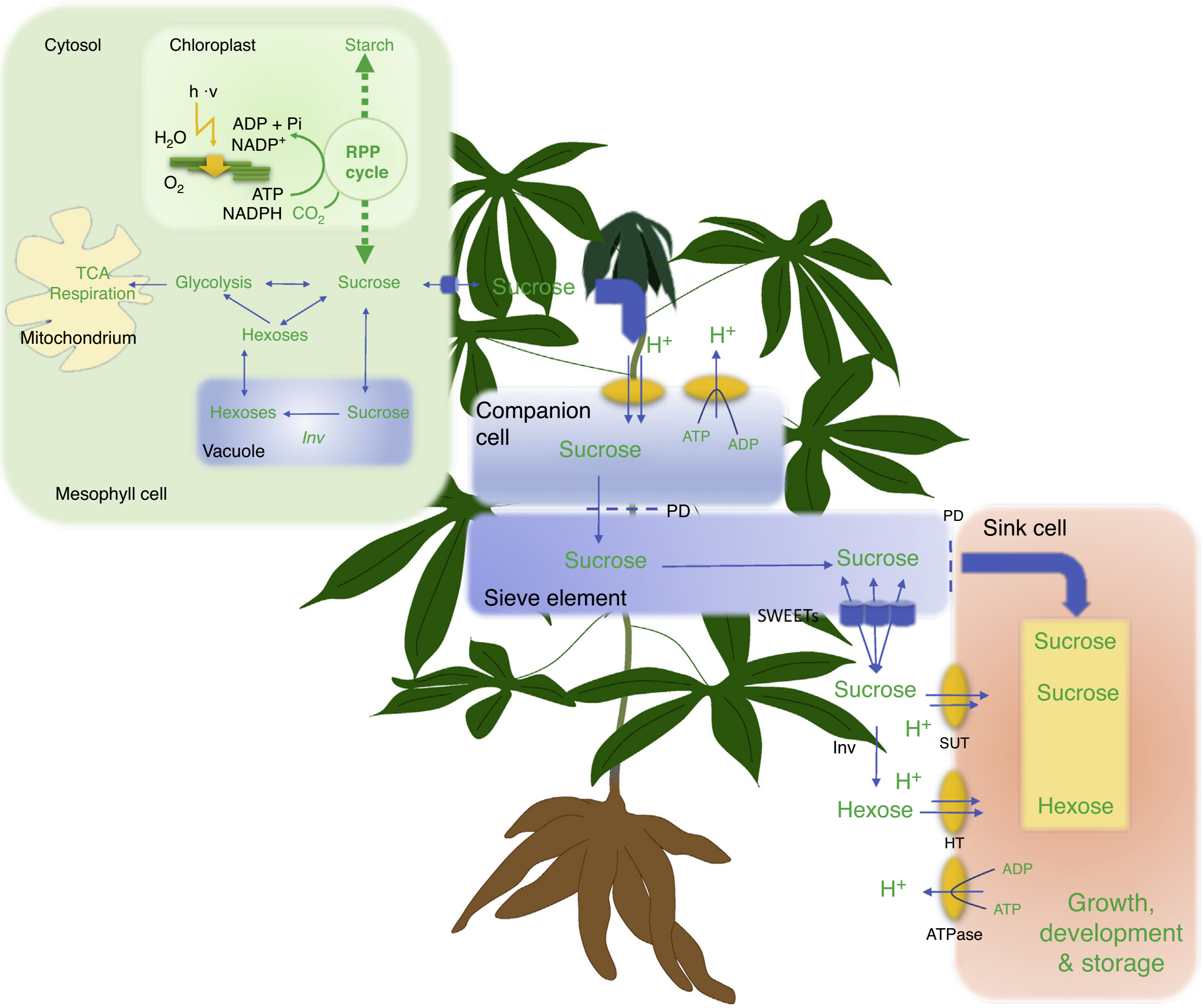
Given the burgeoning human population [1], the corresponding ever-increasing per capita calorific consumption (http://faostat3.fao.org/home/E), and the simultaneous erosion of arable land [2], the need for improvement of plant yield is more acute than ever. The cardinal question is, therefore, how best to do so. Whilst huge efforts have been made to address adverse environmental conditions, bad agronomy and the effects of all manner of disease plant intrinsic features such as the allocation of nutrients within a plant have been far less considered [3•]. Within the study of plant resource allocation the terms ‘source production’ and ‘sink utilization’ of photoassimilates are commonly used wherein a source tissue is defined as a net producer of photoassimilates whilst a sink tissue is a net importer of photosynthetic products [4]. All subterranean organs of plants are carbon sinks during plant growth since they cannot perform photosynthesis, additionally certain above-ground organs including flowers and petioles are sinks [3•]. Others transition from sink to source such as leaves [5], or from storage sink to source as is the case for seeds, tubers, roots and stems [3•], on maturation. The transferability of information from one crop to another is, however, rendered more complex by the fact that sinks can become sources. This transition normally only occurs after death or a period of dormancy. However, in some species, such as the tropical crop cassava, leaves are sacrificed in times of water-scarcity and carbon is mobilized from the root to enable the generation of new leaves when the prevailing conditions are more favorable [3•,6]. Despite the long-history of studies on source–sink interaction there is still a controversy on which processes mainly control plant growth and hence final crop yield. Indeed, one school of thought maintains that photosynthetic carbon dioxide assimilation ranks above any other driver of plant growth [7•,8], whilst another strongly argues that source and sink effects co-limit plant growth [9–11,12••]. Part of this controversy may be explained by the different growth strategies of plants as recently highlighted by studying fast growing annual and slow growing perennial barley plants [13].

In this review, we will summarize published experimental evidence and highlight current multi-national efforts aimed at understanding and influencing the source–sink relations of crop plants. Figure 1 is a schematic diagram representing the most important steps characterizing the source–sink carbon transfer in cassava, however, it is by-and-large representative of that exhibited by most crop plants. Following the definitions provided above we split our discussion of successful and informative transgenic experiments into those which targeted the source, those which targeted the sink and those which targeted both. We review both single and multi-gene strategies. We then describe nascent modelling approaches which have been initiated in order to afford better understanding of bottlenecks in the conversion of photoassimilate into biomass within a given organ.

Molecular intervention of source–sink interactions

A massive number of transgenic plants have been created in which the activities of enzymes, transporters and other proteins which were anticipated to be likely to have an

Figure 1



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A schematic representation of the source–sink relations using the tropical crop cassava (*Manihot esculentum*) as an example. The source cell is represented in green with the sink cell being a dirty pink color. The companion cells and sieve elements with responsibility for long-distance transport are colored blue as is the vacuole of the source cell. Carbon assimilated in the source cells via the RPP (reductive pentose phosphate pathway) is either converted to starch or sucrose, the latter is either respired via the TCA (tricarboxylic acid) cycle and mitochondrial respiration, transferred to the vacuole or exported to the companion cell via sucrose transporters coupled to ATP-driven proton pumps. It then passes via PD (plasmadesmata) to the companion cells whereafter it is transported to the source cell either via plasmodesmata or the SWEET efflux proteins, followed by uptake by sucrose or hexose transporters that again are energized by ATP-driven proton pumps. Abbreviations; ATP adenosine triphosphate, ADP adenosine diphosphate, Pi inorganic phosphate, NADP+ oxidized nicotinamide diphosphate, NADPH reduced nicotinamide diphosphate, inv, invertase.

impact on source or sink metabolism were either elevated or repressed [3•,14]. Here we will focus mainly, although not exclusively, on approaches that have been carried out in tobacco, potato and tomato which are amongst the most facile to transform. Our intent is not to provide an exhaustive survey, for which readers are rather pointed to other more extensive recent reviews [3•,7•,14,15], but rather to highlight a few major examples and where possible to discuss their findings in a whole plant context. For this purpose we split this section into three subsections covering perturbation of sources, perturbation of sinks and simultaneous perturbation of source and sink. We additionally summarize the rationale behind and the outcomes of these strategies in Table 1.