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Review

Post photosynthetic carbon partitioning to sugar alcohols and consequences for plant growth

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ABSTRACT

The occurrence of sugar alcohols is ubiquitous among plants. Physiochemical properties of sugar alcohols suggest numerous primary and secondary functions in plant tissues and are often well documented. In addition to functions arising from physiochemical properties, the synthesis of sugar alcohols may have significant influence over photosynthetic, respiratory, and developmental processes owing to their function as a large sink for photosynthates. Sink strength is demonstrated by the high concentrations of sugar alcohols found in plant tissues and their ability to be readily transported. The plant scale distribution and physiochemical function of these compounds renders them strong candidates for functioning as stress metabolites. Despite this, several aspects of sugar alcohol biosynthesis and function are poorly characterised namely: 1) the quantitative characterisation of carbon flux into the sugar alcohol pool; 2) the molecular control governing sugar alcohol biosynthesis on a quantitative basis; 3) the role of sugar alcohols in plant growth and ecology; and 4) consequences of sugar alcohol synthesis for yield production and yield quality. We highlight the need to adopt new approaches to investigating sugar alcohol biosynthesis using modern technologies in gene expression, metabolic flux analysis and agronomy. Combined, these approaches will elucidate the impact of sugar alcohol biosynthesis on growth, stress tolerance, yield and yield quality.

1. Introduction

Improvements to the resilience of plant growth and yield production are at the forefront of the global research and development agenda (Cavalieri et al., 2011; Godfray et al., 2010). Growth and yield production are undoubtedly a result of complex biochemical networks under multigenic control. Consequently, few higher-level biochemical and molecular markers for plant stress tolerance exist.

The flexibility of carbon partitioning within plants underpins primary productivity and is central to plant responses to environmental change. If we are to understand how plants acclimate to changes in resource availability, we must understand the mechanisms that govern the central conduits of carbon allocation. Partitioning of carbon within plants in response to resource availability and alterations in plant condition has been shown among a range of plant genera including various major crops. However, focus has largely relied on the influence of single metabolite pools, the physiochemical properties of that solute, and their subsequent function as stress metabolites (Chen and Murata, 2002; Hare et al., 1998; Merchant and Richter, 2011; Michell, 2007; Sickler et al., 2007; Valluru and Van den Ende, 2011). A broader view of carbon partitioning among plant tissues and within metabolite networks indicates common physiochemical requirements of metabolite pools to suit the purpose of their synthesis. For example, in leaf tissues, carbon partitioned to pools of metabolites destined for transport must be incorporated into highly reduced (and thus relatively inert) metabolites to avoid damage to cellular infrastructure during that transportation (Turgeon and Wolf, 2009). When viewed at the network scale, patterns and processes of carbon partitioning among metabolite classes may offer insight into the higher-level regulation of downstream growth and biomass partitioning underpinning yield.

The soluble component of leaves contains a complex network of reactions governing processes that underpin growth and offer prime candidates for the development of tools to monitor plant processes. For example, recent studies quantifying starch

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accumulation in leaves of *Arabidopsis* (Sulpice et al., 2009; Thalmann and Santelia, 2017) suggest the role of starch as an indicator of growth. While many existing examples demonstrate allocation of carbon to specific metabolite pools and provide insight on its function in the broader context (see for example: Hare et al., 1998; Stitt et al., 2010), few studies illustrate systematic alterations in allocation of carbon to compound classes across plant genera under a range of conditions.

Sugar alcohols (polyols) are major constituents of plant soluble components yet are often neglected in considerations outside that of their direct physiochemical function. Up to 30% of gross primary production is thought to proceed through polyols in place of carbohydrates (Bieleski, 1982) a figure supported by more recent quantification of sugar alcohols to high concentrations in leaf and phloem tissues (e.g. Dinant, 2008; Reidel et al., 2009). In contrast to carbohydrates, sugar alcohols lack aldehyde and ketone functional groups, making them well suited to a range of cellular functions, transport entities and storage molecules (for review see: Merchant and Richter, 2011). Many sugar alcohols often accumulate to concentrations equal to and exceeding common carbohydrates such as glucose and sucrose, signifying a substantial sink for carbon exported from the photosynthetic cycle. Similar to carbohydrates, many sugar alcohols are synthesized via a small number of metabolic steps away from central metabolism (see Fig. 1) and are commonly found to occur in concentrations comparable to carbohydrates among the soluble fraction of plant tissues. The qualitative and quantitative occurrence of sugar alcohols is widely documented across a range of plant genera (Anderson and Wolter, 1966; Angyal and Anderson, 1959; Bieleski, 1982; Drew, 1984; Lewis and Smith, 1967; Loescher, 1987; Loewus and Dickinson, 1982; Loewus and Murthy, 2000; Merchant et al., 2006a, 2007) with many implications for functions as 'stress metabolites'. Adverse growth conditions have been shown to elicit the accumulation of sugar alcohols (Klages et al., 1999; Merchant and Richter, 2011; Streeter et al., 2001; Wanek and Richter, 1997; Williamson et al., 2002) with correlative patterns also observed across environmental gradients (Streeter et al., 2001). Whilst the sugar alcohol *myo*-inositol is ubiquitous to plants, but rarely accumulated to high concentrations, other sugar alcohols form a major constituent of significant crop species including the majority of legumes (Guo and Oosterhuis, 1997; Merchant, 2012; Murakeozy et al., 2002; Streeter et al., 2001; Wanek and Richter, 1995), horticultural species such as *Malus, Prunus, and Pyrus* (Loescher and Everard, 2000; Teo et al., 2006), *Olea* (Dichio et al., 2009; Rejskova et al., 2007), *Actinidia* (Klages et al., 1998) and in a broad range of dominant trees such as all gymnosperms (Loewus and Dickinson, 1982; Merchant et al., 2006a; Popp et al., 1997), *Quercus* (Popp et al., 1997), *Eucalyptus* (Merchant et al., 2007) and *Acacias* (Merchant et al., 2006a; Seigler, 2003), just to name a few.

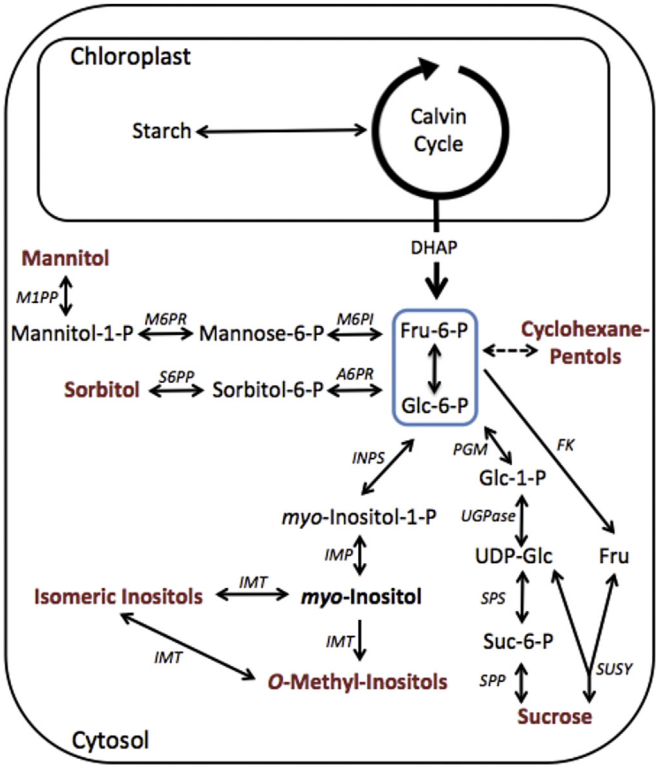

Fig. 1. Pathways for the biosynthesis of selected sugar alcohols in plants illustrate the close proximity to hexose phosphates and central metabolism (Merchant and Richter, 2011). Abbreviations- DHAP: dihydroxyacetone phosphate; Fru-6-P: fructose-6-phosphate; Glc-6-P: glucose-6-phosphate; M6PI: mannose-6-phosphate isomerase; Mannose-6-P: mannose-6-phosphate; M6PR: mannitol-6-phosphate reductase; Mannitol-1-P: mannitol-1-phosphate; M1PP: mannitol-1-phosphate phosphatase; A6PR: Aldose-6-phosphate reductase; Sorbitol-6-P: sorbitol-6-phosphate; S6PP: sorbitol-6-phosphate phosphatase; INPS: *myo*-inositol-1-phosphate synthase; *Myo*-Inositol-1-P: *myo*-inositol-1-phosphate; IMP: inositol monophosphatase; IMT: *myo*-inositol methyltransferase; PGM: phosphoglucomutase; Glc-1-P: glucose-1-phosphate; UGPase: UDP-glucose-pyrophosphorylase; UDP-Glc: uridine diphosphate glucose; SPS: sucrose phosphate synthase; Suc-6-P: sucrose-6-phosphate; SPP: sucrose phosphatase; Fru: fructose; FK: fructokinase; SUSY: sucrose synthase.

Despite their wide distribution across the plant kingdom and abundance, significant gaps remain in our understanding of this important class of compounds, specifically outside the focus of physiochemical properties. Given the magnitude of sugar alcohol accumulation in plant tissues, their role needs to be considered in the context of resource partitioning and homeostatic regulation within the biochemical network of the whole plant. Equally, the molecular control mechanisms that dictate the activity of these biochemical pathways needs to be investigated. This review outlines significant conceptual and methodological challenges to the characterisation of sugar alcohols and suggests several specific ways forward to better characterize the function(s) of these compounds in plant tissues. Namely: 1) the quantitative characterisation of carbon flux into the sugar alcohol pool; 2) the molecular control governing sugar alcohol biosynthesis on a quantitative basis; 3) the role of sugar alcohols in growth and ecology; and 4) consequences for yield production and yield quality.

2. The quantitative flux of carbon into the sugar alcohol pool is poorly characterized

Sugar alcohols constitute a major sink for photosynthetic carbon at the leaf scale demonstrated by both their concentrations in leaf tissues (see: Ford, 1984; Merchant et al., 2009; Richter and Popp, 1992; Streeter et al., 2001) and presence in the phloem mediated transport pool (e.g. Moing et al., 1997; Noiraud et al., 2001b). The distribution of sugar alcohols among plant families and plant tissues has been the focus of several chemotaxonomic reviews (Angyal and Anderson, 1959; Bieleski, 1982; Merchant et al., 2006a) illustrating the ubiquitous presence of these compounds in plant metabolism. Similarly, the physiochemical properties of sugar alcohols has received significant attention (Merchant and Richter, 2011) owing largely to the perceived osmotic and osmoprotectant functions as stress metabolites. Despite this magnitude, metabolite characterisations are commonly limited to quantifying tissue concentration with little regard for flux, offering limited insight into the quantitative allocation of resources to their synthesis.

The biosynthetic pathways of carbon exiting the Calvin cycle are well characterized (for example Stitt et al., 2010). Major sinks for carbon exiting the cycle are starch synthesis in the chloroplast and