Primary metabolism in flowers sustains a plenitude of physiological and ecological functions related to floral development and plant reproduction. Carbohydrates and amino acids provide energy and precursors for the reactions of floral secondary metabolism, such as the molecules for color and scent, and constitute an important resource of food for the pollinators. Recent discoveries have advanced our understanding of the cycles of carbohydrate hydrolysis and resynthesis that regulate pollen development, pollen tube growth, and pollination as well as the composition of nectar. Pathways of de novo amino acid biosynthesis have been described in flowers, and the proteins that regulate pollen tube guidance and ultimately control fertilization are being progressively characterized. Finally, a novel field of research is emerging that investigates the chemical modification of sugars and amino acids by colonizing microorganisms and how these affect the pollinators’ preferences for flowers. In this Update article, we provide an overview of the new discoveries and future directions concerning the study of the primary metabolism of flowers.

The chemistry of flowers is unique, as it sustains very diverse physiological functions such as flower development, the transition from flower to fruit, and the initial phases of seed set (O’Neill, 1997; Pélabon et al., 2015). In addition, floral metabolites fulfill relevant ecological roles, such as acting as signaling molecules in the chemical communication with animal pollinators (Borghi et al., 2017), providing protection against pests and colonizing microorganisms (Kessler and Baldwin, 2007; Nepi, 2014). Stunning displays of the metabolic resources of flowers are, for example, their colors and fragrance, which occur following the accumulation and emission of tinted and scented secondary metabolites, respectively (Grotewold, 2006; Tanaka et al., 2008; Khan and Giridhar, 2015). Perhaps less sensational, but equally as important, are the reactions of primary metabolism. Indeed, these sustain the physiology of flowers, provide the chemical precursors, and meet the energy demand of floral secondary metabolism (Muhlemann et al., 2014). Moreover, sugars and amino acids also serve as a nutritional reward for the pollinators that feed on nectar and pollen (Pacini et al., 2006; Heil, 2011; Roy et al., 2017). Therefore, knowing how primary metabolites are imported or de novo synthesized in flowers, and how they are secreted and catabolized, is at the heart of floral biology, being relevant to understand the physiology of plant reproduction and the role that flowers play in the ecosystem. In this article, we aim to provide an overview of floral central metabolism. How primary metabolism sustains flower development, and fruit and seed set, also will be addressed. Finally, given the considerable proportion of primary metabolites that are channeled into nectar, we will discuss the chemical composition of nectar, the modifications that arise from fermentation processes by colonizing yeasts and bacteria, and the impact that these modifications have on pollinators’ preferences for flowers.
THE PATH OF SUGARS TOWARD THE FLOWER

As photosynthesis in flowers is confined to sepal and young petals, floral tissues rely heavily on the source-to-sink flow for the supply of carbon resources (Mueller et al., 2010). Experiments performed in the early 1970s with cut carnation (Dianthus caryophyllus) flowers revealed that Suc is the sugar preferentially transported alongside the flower peduncle across the phloem (Ho and Nichols, 1975). However, it was not until much later that the transporter proteins (and the genes that encode them), regulating phloem loading and unloading, were discovered and described in detail.

It is now known that, in source tissues (mature leaves), Suc is loaded into the phloem by the coordinated activity of SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTER (SWEET) and SUCROSE UPTAKE CARRIER (SUC), the latter alternatively called SUCROSE UPTAKE TRANSPORTER (SUT) proteins; therefore, we will be referring to this family as SUC/SUT. SWEETs are efflux proteins of the plasma membrane, tonoplast, and Golgi that transport Suc and hexoses (Eom et al., 2015; Feng and Frommer, 2015), and SUC/SUTs are plasma membrane-localized proton-Suc symporters of the Major Facilitator Superfamily of cotransporters (Lalonde et al., 2004). In leaves of Arabidopsis (Arabidopsis thalaina), SWEET11 and SWEET12 are the proteins that export Suc from the parenchyma cells and provide it to SUT1 for phloem loading (Chen et al., 2012).

Flowers are strong sinks that draw Suc and nutrients toward them. The gradient that maintains this upward flow is generated in the flower by a series of phloem-unloading events and the postphloem distribution of photoassimilates to developing organs and tissues. Symplasmic and apoplastic retrieval of Suc have both been documented in flowers, and they reflect the pattern of floral development and the physiological needs of the newly formed tissues (Mueller et al., 2010). Indeed, early studies conducted with symplasmic tracers revealed that the trafficking toward the apical meristem decreases after floral induction (Gisel et al., 2002), while the expression and activity of sugar transporters increase progressively while pollen matures and after fertilization has occurred (Gahrtz et al., 1996).

Symplasmic phloem unloading and postphloem transport requires functional plasmodesmata, and it occurs primarily in petals, along the filament that provides nutrients to the connective tissue of the anthers and across the funiculus (Imlau et al., 1999). A wave of symplasmic postphloem transport also has been observed in young flowers during ovule development (bud stages) and in mature flowers shortly after anthesis, and it seemingly mirrors the de novo formation of new plasmodesmata and morphological adjustments of preexisting connections (Werner et al., 2011).

Apoplastic phloem unloading and postphloem transport requires energy and the intervention of protein carriers to transport Suc across the plasma membrane. In flowers, this occurs in symplasmically isolated tissues such as pollen grains and tubes as well as in developing embryos. The longstanding model of apoplastic phloem transport describes this flow as a two-step process in which Suc is initially unloaded from the sieve elements into the apoplasm and subsequently transported inside the sink cells. Proteins of the SWEET and SUC/SUT families that facilitate the unload of Suc in specific floral tissues have been characterized (see below), while carriers acting in the floral receptacle to export Suc from the cells of terminal phloem have not yet been identified. In this regard, SWEET efflux transporters, whose expression in floral tissues is well documented, are putative candidates (Lin et al., 2014; Eom et al., 2015; Fig. 1A).

Carbon is unloaded in target cells in the form of Suc or, alternatively, following its hydrolysis, as Fru and Glc. In the apoplastic space, the hydrolysis of Suc is catalyzed by invertases (INVs) ionically bound to the wall of the surrounding cells and, for this reason, named cwINVs (Ruan et al., 2010). These are enzymes of the β-fructofuranosidase family that catalyze the hydrolysis of terminal units of Fru from molecules of disaccharides and polysaccharides and contribute to creating the concentration gradient that allows Suc to be unloaded from the phloem and effectively partitioned among target floral tissues. In addition to cwINVs, flowers also express vacuolar invertases (VINs) and cytoplasmic invertases, the latter being sensu stricto Suc invertases (Ruan et al., 2010). Finally, plasma membrane SUGAR TRANSPORTER PROTEINs (STPs) also are expressed in flowers and mediate the uptake of the hexoses released in the apoplastic space (Büttner, 2010).

A high rate of sugar import is required to meet the respiratory demand of floral tissues, and indeed, high rates of respiration have commonly been documented in floral organs (Dickinson, 1965; Hew and Yip, 1991; Karapanos et al., 2010). Rates of respiration are exceptionally high in flowers of plants that carry out thermogenesis, such as the Araceae family including skunk cabbage (Symplocarpus foetidus) and voodoo lily (Amorphophallus spp.), which produce a raceme type of unbranched inflorescence known as the spadix (Plaxton and Podestá, 2006). On anthesis, the plenitude of mitochondria of the spadix contributes to enormous respiration rates via the alternative oxidase pathway (Seymour, 1999), which releases free energy as heat, being equivalent to a 10°C to 25°C increase in tissue temperature. This process serves two functions. First, it supports the extreme growth rates of the spadix (Dancer and ap Rees, 1989). Second, it is thought that the temperature aids in the production and volatilization of floral scents (Seymour, 1999), a process that also is aided by the high content of organic acids of the spadix. This striking specific example aside, little is known concerning the relative activities of organic acid metabolism in these tissues (Borghesi et al., 2017); hence, the sections below focus on sugars and amino acids for which our spatial understanding is far more developed.
CARBOHYDRATE PARTITIONING AND METABOLISM IN FLORAL ORGANS

The paragraphs that follow provide the description of primary metabolism organized by floral organs. Sepals that are similar to leaves in their anatomy and metabolism are not discussed, and we refer to reviews on leaf metabolism instead (Plaxton and Podestá, 2006; Smith and Stitt, 2007).

All floral organs, with the exception of sepals, depend upon sugar import in a measure that correlates with their growth and stage of development and are sustained mainly by postphloem Suc delivery and only to a minor extent by carbohydrates produced via floral carbon fixation (Aschan and Pfanz, 2003). With regard to metabolism, petals are mixotrophic: young green petals are able to perform photosynthesis, but they...
progressively lose the ability to fix carbon as they mature and ultimately become fully heterotrophic (Thomas et al., 2003). For example, the corolla of young Nicotiana tabacum flowers contains chlorophylls and an active Rubisco enzyme, which both contribute to carbon acquisition. However, at the onset of anthesis, the rate of photosynthesis decreases progressively while pigments accumulate gradually from the distal part of the perianth inward (Müller et al., 2010). Indeed, a biochemical reprogramming occurring at (or around) anthesis has been documented in numerous plant species. For example, in petals of Antirrhinum majus (snapdragon), chlorophyll content decreases at anthesis (Mühlmann et al., 2012), and similarly, in Arabidopsis, the dismantling of the photosynthetic apparatus, which follows the conversion of chloroplasts to chromoplasts, starts soon after the flowers open (Wagstaff et al., 2009). This shift from autotrophic to heterotrophic metabolism is transcriptionally regulated and marks the moment when flower secondary metabolism becomes predominant (Mühlmann et al., 2012; Tsanakas et al., 2014). As glycolysis and the pentose phosphate pathway are transcriptionally down-regulated and floral secondary metabolic pathways are up-regulated, the concentrations of metabolic intermediates of the tricarboxylic acid cycle, such as fumarate and malate, also decline, while the content of volatile organic compound precursors, such as the aromatic amino acids Phe and Tyr, increases progressively (Mühlmann et al., 2012). Indeed, the physiological function of petals is to attract animal pollinators to flowers, for which pigments and scented molecules are synthesized. Therefore, the transcriptional coregulation of primary and secondary metabolism ensures that the energy requirements and precursors for the biosynthesis of secondary metabolites are in place when this switch occurs.

Petals also store carbohydrates that serve an important function during flower opening. For this, reserve polysaccharides (starch and/or fructans) are accumulated gradually during petal development but degraded rapidly at the onset of anthesis to generate the osmotic potential that leads to cellular water influx and, finally, to flower opening (Bieslki, 1993; Collier, 1997; van Doorn and van Meeteren, 2003; van Doorn and Kamdee, 2014). As plasmodesmata are functional in young petals, symplasmic postphloem Suc is arguably the prime supplier of these reserves, although Suc carriers also may contribute. In this regard, it is worth mentioning that the proton-monosaccharide symporter SUT13 that transports Glc, Fru, and other D-hexoses is highly expressed in the vasculature of young emerging petals (Nørholm et al., 2006) and, therefore, also may participate in hexose unloading in target cells.

Androecium and gynoecium are fully heterotrophic; that is, their metabolism and growth are entirely supported by the carbon resources synthesized in source tissues.

In the androecium (stamen), photoassimilates are delivered to the anthers through the filament, a duct of vascular tissue that symplasmically connects the anthers to the flower (Mascarenhas, 1989). Carbon unloaded from the filament is stored as granules of starch and soluble sugars (primarily Suc) in the tapetum, a layer of nutritive cells that develops between the anther wall and the sporogenous tissue (Goldberg et al., 1993). In certain plant species, such as tomato (Solanum lycopersicum), Suc is partially hydrolyzed to Glc and Fru while being transported along the filament, so that hexoses are readily available as they reach the anther wall (Pressman et al., 2012; Fig. 1B). Otherwise, Suc synthase in the tapetum cleaves Suc before uptake, while in the cytoplasm of the same cells, Suc phosphate synthase and Suc phosphate phosphatase resynthesize it once again (Fig. 1C; Pacini et al., 1985; Hedhly et al., 2016). Due to the presence of this futile cycle of Suc breakdown and resynthesis (Geigenberger and Stitt, 1991; Nguyen-Quoc and Foyer, 2001), it has been proposed that the tapetum has a buffering function that regulates sugar availability in the whole anther (Castro and Clément, 2007). As anthers develop, sugar resources are mobilized and exported to the locular fluid that surrounds and nourishes the pollen grains while the tapetum slowly degenerates (Pacini et al., 1985). Pollen grains are symplasmically isolated from the surrounding tissues and rely upon plasma membrane transporters for sugar intake. During the course of evolution, this complete dependence on apoplastic transport gave rise to myriad pollen-specific sugar carriers that mediate pollen sugar uptake during development, germination, and pollen tube growth (Table I provides an overview of sugar transporters characterized in Arabidopsis and their site[s] of floral expression). Immature pollen grains utilize sugars for cell wall synthesis as well as to build up the carbon reserves that will be utilized during germination (Hafidh et al., 2016).

In the initial phase of development, cwINVs bound to the wall of pollen grains and Suc synthase enzymes hydrolyze Suc from the locular fluid (Goetz et al., 2001; Persia et al., 2008; Hirsche et al., 2009; Le Roy et al., 2013; Carrizo García et al., 2015), while STP transporters facilitate the uptake of the units of Glc that are released in these reactions (Truernit et al., 1996). Fru, which is also released from the breakdown of Suc, is internalized primarily by POLYOL/MONOSACCHARIDE TRANSPORTERS1 (PMT1; Klepek et al., 2010) and, to a minor extent, by STPs (Hedhly et al., 2016). However, the Fru-to-Glc ratio in the apoplastic space that surrounds the wall of pollen grains is above 2, implying a preferential uptake of Glc (Pressman et al., 2012). Nonhydrolyzed Suc is most probably internalized by SWÉET8 (Fig. 1D; Chen et al., 2012). During pollen maturation, the GLUCOSE PHOSPHATE TRANSPORTER1 transports Glc-6-P across the outer membrane of amyloplasts for starch biosynthesis (Pacini et al., 1985; Niewiadomski et al., 2005; Castro and Clément, 2007). Alternatively, carbohydrates are utilized for the synthesis of the pollen cell wall. At the beginning of their development, pollen grains of all plant species accumulate starch in amyloplasts, which is later
Table 1. Overview of the sugar transporters expressed in flowers of Arabidopsis, organ and tissue of expression, transported substrate, and associated mutant phenotype

<table>
<thead>
<tr>
<th>Name</th>
<th>Gene No.</th>
<th>Organ (or Tissue) of Expression</th>
<th>Substrate</th>
<th>Mutant Phenotype</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>SUC1</td>
<td>At1g71880</td>
<td>Stamen, pollen, funiculus (ecotype specific)</td>
<td>Suc</td>
<td>No germination of pollen in the absence of Suc, lower anthocyanin accumulation</td>
<td>Sauer and Stolz (1994); Stadler et al. (1999); Sivitz et al. (2008); Feuerstein et al. (2010)</td>
</tr>
<tr>
<td>SUC2/SUT1</td>
<td>At1g22710</td>
<td>Sepals, filament</td>
<td>Suc, maltose, α- and β-phenylglucoside</td>
<td>Plants are smaller than the WT when grown without Suc</td>
<td>Truernit and Sauer (1995)</td>
</tr>
<tr>
<td>SUC3/SUT2</td>
<td>At2g02860</td>
<td>Carpels, pollen grain, and pollen tube</td>
<td>Suc, maltose</td>
<td>n/a</td>
<td>Meyer et al. (2000, 2004)</td>
</tr>
<tr>
<td>SUC4/SUT4</td>
<td>At1g09960</td>
<td>Anthers, pistil, tonoplast</td>
<td>Suc (low-affinity transporter)</td>
<td>WT</td>
<td>Weise et al. (2000); Schneider et al. (2012)</td>
</tr>
<tr>
<td>SUC7/SUT7</td>
<td>At1g66570</td>
<td>Pollen tube growth</td>
<td>Suc</td>
<td>Shorter pollen tube growth (ecotype-dependent phenotype)</td>
<td>Johnson et al. (2004); Sauer et al. (2004)</td>
</tr>
<tr>
<td>SUC8/SUT8</td>
<td>At2g14670</td>
<td>Transmitting tissue</td>
<td>High-affinity Suc; maltose</td>
<td>n/a</td>
<td>Sauer et al. (2004)</td>
</tr>
<tr>
<td>SUC9/SUT9</td>
<td>At5g06170</td>
<td>Transmitting tissue</td>
<td>High-affinity Suc; α- and β-glucosides, maltose</td>
<td>Early flowering in short days</td>
<td>Sauer et al. (2004); Sivitz et al. (2008)</td>
</tr>
<tr>
<td>STP1</td>
<td>At1g11260</td>
<td>Whole flower</td>
<td>Glc, Gal, Man, Xyl, 3-O-methylglucose, Fru (traces)</td>
<td>n/a</td>
<td>Sauer et al. (1990)</td>
</tr>
<tr>
<td>STP4</td>
<td>At3g19930</td>
<td>Anthers and pollen (expression increases during pollen development)</td>
<td>Glc, Gal, Man, Xyl, 3-O-methylglucose</td>
<td>n/a</td>
<td>Truernit et al. (1996)</td>
</tr>
<tr>
<td>STP2</td>
<td>At1g07340</td>
<td>Pollen grains</td>
<td>Glc, Gal, Man, Xyl, 3-O-methylglucose, Fru (traces)</td>
<td>n/a</td>
<td>Truernit et al. (1999)</td>
</tr>
<tr>
<td>STP6</td>
<td>At3g05960</td>
<td>Pollen (late stages of development)</td>
<td>Glc, Gal, Man, Xyl, 3-O-methylglucose, Fru, ribose</td>
<td>WT</td>
<td>Schneiderereit et al. (2003)</td>
</tr>
<tr>
<td>STP9</td>
<td>At1g50310</td>
<td>Mature pollen, pollen tube</td>
<td>Glc, Gal, Man, Xyl</td>
<td>n/a</td>
<td>Schneiderereit et al. (2003)</td>
</tr>
<tr>
<td>STP10</td>
<td>At3g19940</td>
<td>Pollen tube</td>
<td>Gal, Man, Glc</td>
<td>WT</td>
<td>Rottmann et al. (2016)</td>
</tr>
<tr>
<td>STP11</td>
<td>At5g23270</td>
<td>Pollen tube</td>
<td>Glc, Gal, Man, Xyl, 3-O-methylglucose, Fru, ribose</td>
<td>n/a</td>
<td>Schneiderereit et al. (2005)</td>
</tr>
<tr>
<td>STP13</td>
<td>At5g26340</td>
<td>Sepals, vasculature of emerging petals</td>
<td>Glc, Fr, Gal, Man</td>
<td>WT</td>
<td>Bi et al. (2005); Nørholm et al. (2006)</td>
</tr>
<tr>
<td>SWEET1</td>
<td>At1g21460</td>
<td>Pollen grain, pollen tube, petels, sepalas</td>
<td>Glc, Gal</td>
<td>n/a</td>
<td>Chen et al. (2010)</td>
</tr>
<tr>
<td>SWEET2</td>
<td>At3g14770</td>
<td>Sepal, petals, stamen</td>
<td>2-Deoxyxylucose</td>
<td>n/a</td>
<td>Chen et al. (2015a)</td>
</tr>
<tr>
<td>SWEET3</td>
<td>At5g33190</td>
<td>Stamen</td>
<td>2-Deoxyxylucose</td>
<td>n/a</td>
<td>Chen et al. (2015a)</td>
</tr>
<tr>
<td>SWEET4</td>
<td>At3g28007</td>
<td>Whole flower, stamen</td>
<td>2-Deoxyxylucose</td>
<td>n/a</td>
<td>Chen et al. (2015a)</td>
</tr>
<tr>
<td>SWEET5/VEX</td>
<td>At5g62850</td>
<td>Pollen (vegetative cells)</td>
<td>Glc</td>
<td>n/a</td>
<td>Engel et al. (2005)</td>
</tr>
<tr>
<td>SWEET7</td>
<td>At4g10850</td>
<td>Stamen</td>
<td>Glc</td>
<td>Male sterility, abnormal microspore membrane, defective exine pattern formation</td>
<td>Chen et al. (2015a)</td>
</tr>
<tr>
<td>SWEET8/RPG1</td>
<td>At5g40260</td>
<td>Pollen grain, pollen tube, tapetum</td>
<td>Glc</td>
<td>Male sterility, abnormal microspore membrane, defective exine pattern formation</td>
<td>Chen et al. (2015a)</td>
</tr>
<tr>
<td>SWEET9</td>
<td>At2g39060</td>
<td>Nectary</td>
<td>Suc</td>
<td>No nectar secretion</td>
<td>Ge et al. (2000); Lin et al. (2014)</td>
</tr>
<tr>
<td>SWEET13/RPG2</td>
<td>At5g50800</td>
<td>Tapetum, tetrad</td>
<td>Suc</td>
<td>Male sterility, abnormal microspore membrane, defective exine pattern formation</td>
<td>Sun et al. (2013)</td>
</tr>
<tr>
<td>SWEET14</td>
<td>At4g25010</td>
<td>Stamen</td>
<td>Suc</td>
<td>n/a</td>
<td>Chen et al. (2015a)</td>
</tr>
</tbody>
</table>
Pollination is characterized by an intense sugar turnover. In fact, once the pollen grain reaches the stigma and rehydrates, sugar resources are mobilized and the pollen tube emerges and starts to elongate inside the transmitting tissue of the style (Rounds et al., 2011). As ovules are usually borne at the base of the carpel, frequently one to a few centimeters from the stigma, rehydrated pollen grains rapidly grow a long tube to deliver sperm for the process of fertilization. Tube elongation is supported by a rapid and intense deposition of plasma membrane and new cell wall material at the tip of the tube, for which sugars provide building blocks (Konar and Linskens, 1966) and energy (Ylstra et al., 1998). Pollen germinates in a sugar-rich environment (Labarca et al., 1970) that boosts glycolysis (Carrizo García et al., 2015) to produce abundant pyruvate to be flown through the tricarboxylic acid cycle for ATP production. It has been discovered that aerobic fermentation also supports pollen tube growth. For this, a series of cytosolic reactions collectively referred to as the pyruvate dehydrogenase (PDH) bypass convert pyruvate to acetyl-CoA, which is then transported to mitochondria (tricarboxylic acid cycle) and glycosomes (glyoxylate pathway) or utilized for the synthesis of lipids (Gass et al., 2005; Rounds et al., 2011). The PDH bypass confers the evolutionary advantage of fast growth to pollen grains that germinate onto permissive stigmas so that wild-type pollen outcompetes PDH bypass-defective mutants. This extensive uptake of sugars in elongating pollen tubes is mediated by SUC/SUT transporters and the activity of STPs, PMTs, and cwINVs (Mascarenhas, 1970; Singh and Knox, 1984; Truernit et al., 1996; Ylstra et al., 1998; Stadler et al., 1999; Schneidereit et al., 2003, 2005; Scholz-Starke et al., 2005; Büttner, 2010; Klepek et al., 2010). Recently, it was found that the combined activities of cwINVs on the cell wall of pollen tubes and VINs in the cells of the transmitting tissue of the style also promote proper tube elongation (Fig. 1E). Indeed, VINs in the female tissues show a wave of activation that follows closely the growth of the pollen tube, so that sugar resources are rapidly made available as the tip of the tube moves forward along the style (Goetz et al., 2017). The discovery of this mutual interaction adds one more tile to the mosaic of molecular mechanisms that regulate the long-known phenomenon of the appearance of random elongation trajectories and slow growth rates observed in pollen grains germinated in vitro.

The gynoecium (pistil) is composed of one or more carpels, each consisting of a stigma, style, and ovary. The metabolic activity of each part of the pistil specifies its physiological function, correlates with flower development, and is subject to transcriptional regulation. Indeed, an analysis of transcript levels in pollinated and

<table>
<thead>
<tr>
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<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>VGT1</td>
<td>At3g03090</td>
<td>Pollen (vacuolar transporter)</td>
<td>Glc, Fru</td>
<td>Late bolting and flowering</td>
<td>Aluri and Büttner (2007)</td>
</tr>
<tr>
<td>INT2</td>
<td>At1g30220</td>
<td>Tapetum</td>
<td>Myo ninositol and several inositol epimers</td>
<td>WT</td>
<td>Schneider et al. (2007)</td>
</tr>
<tr>
<td>INT4</td>
<td>At4g16480</td>
<td>Pollen, pollen tube, transmitting tissue</td>
<td>Myo ninositol and several inositol epimers</td>
<td>n/a</td>
<td>Schneider et al. (2006)</td>
</tr>
<tr>
<td>PMT1</td>
<td>At2g16120</td>
<td>Germinating pollen grains, pollen tube</td>
<td>Xylitol, Fru</td>
<td>WT</td>
<td>Klepek et al. (2010)</td>
</tr>
<tr>
<td>PMT2</td>
<td>At2g16130</td>
<td>Mature pollen grains, pollen tube</td>
<td>Xylitol, Fru</td>
<td>WT</td>
<td>Klepek et al. (2010)</td>
</tr>
<tr>
<td>PMT5/PLT5</td>
<td>At3g18830</td>
<td>Peduncle, sepals, stigma, anthers, abscission zone</td>
<td>Ribose, arabinose, Xyl, Glc, Man, Gal, Fru, rhamnose, Fuc, sorbotol, erythiol, xylitol, inositol</td>
<td>n/a</td>
<td>Klepek et al. (2005); Reinders et al. (2005)</td>
</tr>
</tbody>
</table>
unpollinated pistils of Arabidopsis revealed that pollination, precisely the transfer of pollen grains to a compatible stigma, triggers the metabolic switch that assists flower fertilization (Boavida et al., 2011). While flowers develop, the pistil symplasmically receives Suc from source tissues and stores it as transitory starch at the base of the carpel and alongside the style up to the base of the stigma (Hedhly et al., 2016). It is accepted that Glc-6-P/phosphate antiporter is responsible for carrying Glc across the outer membrane of plastids to support the progressive enlargement of starch granules (Dresselhaus and Franklin-Tong, 2013).

At the onset of anthesis, when flowers open, the starch that had accumulated at the base of the stigma is mobilized gradually to support the metabolic activity of the papillae. The papillae are cells with finger-like projections located atop the stigma whose function is to secrete the enzyme expansins that loosen the cell wall of the grain and facilitate adhesion, hydration, and germination of pollen grains. Flowers with dry stigmas still secrete polymers of the papillae. The papillae are cells with dense cytoplasm, numerous mitochondria, endoplasmic reticulum, and Golgi vesicles, which are notable signs of an intense metabolic activity (Rosen and Thomas, 1970; Labarca and Loewus, 1972; Elleman et al., 1992). Direct evidence of stigma active metabolism has been provided by experiments performed with radioactively labeled sugars and amino acids. Indeed, when detached styles of lily (Lilium longiflorum) flowers were provided with labeled Glc, inositol, and Pro, radioactivity was revealed in the sugars (Gal, rhamnose, and arabinose) secreted by the stigmatic pollen tubes growth also has been documented (Lee et al., 2009).

Symplasmic connections with the ovule are present in the bundle sheath of funiculus and chalaza (Imlau et al., 1999; Werner et al., 2011), where transitory starch also accumulates (Hedhly et al., 2016). However, after fertilization, the developing embryo remains symplasmically isolated from the mother tissues, and further transport of photoassimilates is attained with specific transporters and carriers (Stadler et al., 2005; Werner et al., 2011; Chen et al., 2015b). Here, the expression of SUC1, SUC8, and SUC9 genes has been detected (Sauer et al., 2004; Feuerstein et al., 2010), although the differential expression of the SUC1 transporter observed in Arabidopsis ecotypes suggests functional redundancy. In the ovule, the synergid cells that surround the egg also are metabolically very active. Analysis of transcripts isolated from the synergids of Torenia fournieri revealed that 30% of the transcripts encode Cys-rich proteins of the secretory pathway. These include short-distance signaling peptides involved in sporophytic guidance, such as LURE and LORELEI that guide the pollen tube out the transmitting tissue inside the micropyle to fertilize the ovule (Jones-Rhoades et al., 2007; Capron et al., 2008; Okuda et al., 2009; Higashiyama and Yang, 2017). After double fertilization, large amounts of sugars are transported to the endosperm, where they accumulate as storage reserves for the embryo and are converted to starch, lipids, or proteins. As double fertilization marks the beginning of seed and fruit development, we refer to the numerous reviews that have been written on the topic (Weber et al., 1997; Chen et al., 2015b; Sosso et al., 2015). Nevertheless, the energy resources still present in the flower (petals, carpel, and filament) are promptly mobilized and repurposed. Indeed, experiments performed with radioactively labeled Suc applied to sensing daylily (Hemerocallis spp.) flowers revealed that up to 50% of the total Suc is rapidly and extensively retrotranslocated to young developing buds at a rate of 25 cm per hour (Bieleski, 1995; Sklensky and Davies, 2011). Reabsorption of unutilized nectar also has been observed; however, further research on this topic is clearly warranted.

Finally, it must be remembered that most of the transporters mediating sugar partitioning in flowers made of a short chain of dipeptide motifs and a large carbohydrate component that constitutes up to 90% of the total AGP molecule (Ellis et al., 2010; Knoch et al., 2014). Given that transitory starch stored along the style also is mobilized at anthesis, it most probably provides the backbones for the synthesis of the carbohydrate component of the AGP proteins, although this has not been proven directly. The sugar moiety of the AGPs triggers signaling responses that guide the pollen tube toward the ovule (Dresselhaus and Franklin-Tong, 2013; Jiao et al., 2017). Internalization of AGP carbohydrates by the pollen tube followed by carbohydrate relocation in the callus that pushes the nuclei forward in the direction of pollen tube growth also has been documented (Lee et al., 2009).
have been identified and characterized in studies conducted in model plants such as Arabidopsis, *N. tabacum*, and *Petunia hybrida*. While these studies provide a general understanding of the processes occurring in model flowers, different taxa may have evolved slightly different sets of transporters and enzymes to distribute sugars among tissues and cells.

**FLORAL AMINO ACIDS: SYNTHESIS AND FUNCTION**

The assimilation of inorganic nitrogen (N) into organic compounds takes place primarily in the root, where ammonium is initially incorporated into Gln, Asn, Glu, and Asp (Coruzzi, 2003; Näsholm et al., 2009). Then, amino acids and small peptides are loaded into the vascular system of xylem and phloem and transported to sink organs. In flowers, symplasmic and apoplasmic partitioning of organic N follows the routes described previously for sugar distribution. Similarly, the transport of amino acids and small peptides across the plasma membrane of symplasmically isolated tissue requires the assistance of protein carriers. In fact, numerous amino acid transporters are expressed in pollen, which is symplasmically isolated from the remaining part of the flower (Foster et al., 2008). Current knowledge on amino acid transporters (Rentsch et al., 2007; Tegeder, 2012) and their expression and function in flowers (Tegeder and Rentsch, 2010) has been compiled in recent reviews. Therefore, we refer to these for a detailed description of floral transporters and provide an overview of the sites of their expression in Figure 2. In this section, we focus on the more recent discoveries regarding the synthesis and physiological functions of amino acids that take place in flowers.

In flowers, amino acids are utilized as building blocks for the synthesis of enzymes and structural proteins as well as precursors of N-containing secondary metabolites and signaling molecules. Despite the common belief that amino acids are transported exclusively to flowers from roots and leaves, evidence has emerged that their de novo synthesis also occurs in floral tissues. For example, studies conducted in petals of *P. hybrida* initially aimed to characterize the enzymatic reactions for the production of benzoinoid volatile compounds brought about the identification of the enzymes prephenate amino transferase and arogenate dehydratase of the Phe biosynthetic pathway. The plastidial CATION AMINOCACID PHENYLALANINE TRANSPORTER also was identified in these studies (Maeda et al., 2010, 2011; Maeda and Dudareva, 2012; Widhalm et al., 2015), as well as the cytosolic Phe biosynthetic pathway (Yoo et al., 2013). Phylogenetic studies revealed that these enzymes and transporters also are present in plants that produce negligible amounts of aromatic volatile compounds, where they may provide the Phe that is incorporated into floral enzymes and structural proteins.

Recently, it was shown that the Asn biosynthetic pathway also is active in flowers. Indeed, ASPARAGINE SYNTHETASE1 (ASN1), encoding for the enzyme that transfers amide N from Gln to Asn, releasing Asn and Glu, displays a high level of expression in flowers. ASN1 transcription increases throughout the lifespan of Arabidopsis flowers, starting from the stages that precede anthesis up to pollination and early embryo growth (Le et al., 2010). Concomitantly, genes of the Asn metabolism also are up-regulated and floral Asn content also rises (Gaufichon et al., 2017). Having a high N:C ratio (2:4), Asn is an efficient carrier and storage compound of N. Thus, enhancing the supply of Asn during flower development is an effective strategy to store reserves that will be used to generate energy during ovule maturation and embryo growth (Gaufichon et al., 2017). In developing pollen grains, hydrolysis of Asn by asparaginase A1 and B1 (ASPAG1 and ASPGB1) releases ammonium, which is later reassimilated into Gln, the precursor for the synthesis of other amino acids (Ivanov et al., 2012; Guan et al., 2015).

De novo synthesis of Pro also occurs in flowers. Pro is found as a free amino acid in pollen grains and nectar and as a component of proteins of the pollen coat (Lamport et al., 2011; Bianucci et al., 2015). Free Pro in pollen grains is thought to act as an osmotic protectant toward desiccation (Chiang and Dandekar, 1995), while Pro in nectar may serve as a propellant for the lift phase of the flight of insect pollinators (Carter et al., 2006). In addition to the transcriptional activation of the floral Pro transporter (Schwacke et al., 1999), high levels of Pro in flower are obtained via up-regulation of the pyrroline-5-carboxylate synthetase enzyme, which catalyzes the conversion of Glu to pyrroline-5-carboxylate (Kavi Kishor et al., 2015). Interestingly, Pro is the most abundant amino acid in nectar, regardless of the evolutionary distance between plant species (Carter et al., 2006; Nepi et al., 2012). This suggests that Pro may have a relevant ecological role for rewarding animal pollinators (Carter et al., 2006).

As we mentioned briefly above, amino acids and small peptides are synthesized in large amounts by the cells of the transmitting tissue and ovule. These include numerous small secreted proteins of unknown function (Jones-Rhoades et al., 2007) and Cys-rich proteins such as the LUREs, which are involved in the female gametophytic guidance of pollen tube attraction (Okuda et al., 2009; Takeuchi and Higashiyama, 2012; Higashiyama and Yang, 2017). γ-Amino butyric acid (GABA), a nonproteinogenic amino acid that contributes to pollen tube growth and attraction, also is produced in the cells of the transmitting tissue. GABA is synthesized in the cytosol by the activity of GABA Glu decarboxylase and degraded in the mitochondria by the activity of the GABA transaminase (Fait et al., 2008), the latter being encoded by the POLLEN-PISTIL INCOMPATIBILITY2 (POP2) gene. The coordinated activity of Glu decarboxylase and transaminase along the pistil creates a gradient of GABA concentration that guides the pollen tube toward the ovule. The disruption of this gradient observed in the *pop2* mutants negatively influences the success of fertilization (Palanivelu et al., 2003).
CHEMICAL MODIFICATIONS OF NECTAR BY COLONIZING MICROORGANISMS

A large proportion of floral primary metabolites is channeled into the nectar, which is a water-based secretion of sugars, amino acids, lipids, and secondary metabolites including volatile organic compounds. The ecological function of nectar is to reward animal pollinators; therefore, its chemical composition differs among plant species, as it evolved to enhance floral visitation by pollinators and reduce the losses imposed by nectar thieves and florivores (Nicolson and Thornburg, 2007). In the last decade, research on nectar had seen a renaissance brought about by targeted nectary transcriptomics and metabolomics (Kram et al., 2009; Noutsos et al., 2015) and the discovery of the mechanisms regulating nectar secretion, such as transporters (Lin et al., 2014), hormones (Wiesen et al., 2016), and transcription factors (Liu et al., 2009). These recent discoveries on nectar biology have been compiled in exhaustive reviews (Nepi, 2017; Roy et al., 2017). Hence, we exclusively focus discussion here on the chemical modifications of nectar by colonizing microorganisms.
nectar primary metabolites that are induced by floral microbes.

The inoculation of floral nectar with yeasts, bacteria, and fungi takes place during floral visitation by pollinators and florivores (Belisle et al., 2012; Anderson et al., 2013; Aleklett et al., 2014). Given this horizontal transfer from the animals to the flowers, the epiphytic communities of microbes of the anthosphere differ from the microbial species of the rhizosphere and phyllosphere. Moreover, in a single flower, organ-specific species of microbes grow separately on sepalas, petals, and nectaries (Junker et al., 2011; Aleklett et al., 2014). The microbial communities that colonize the anthosphere depend upon the combinatorial effects of plant genotype and the ability of the microbes to competitively exploit the carbon and nitrogen resources present in floral tissues and exudates (Junker and Keller, 2015; Pozo et al., 2016). Without any doubt, nectar offers an ideal habitat to support microbial growth, with sugars providing the substrate for microbial fermentation and amino acids contributing the required nitrogen. That microorganisms can modify the composition of nectar became evident when the uniformity of nectar sugar content from plants grown in a glasshouse was contrasted with the variability of field-grown plants of the same species (Canto et al., 2007).

Yeasts are the most common group of microbes found in flowers, with individuals of the genus Metschnikowia being predominant (Pozo et al., 2016). Following yeast inoculation, Suc-dominant nectar shows a shift toward Fru or Glc that is proportional to the rate of microbial growth (Herrera et al., 2008; de Vega and Herrera, 2013). This implies that yeast cells hydrolyze Suc to Fru and Glc but then preferentially utilize one of the two hexoses. Lastly, highly concentrated Suc-dominant nectar (typically dry nectar) prevents yeast growth (Schaeffer et al., 2015).

Floral bacteria received far less attention than yeasts, until pyrosequencing and culturing techniques made it possible to identify the strains that grow on flowers (Fridman et al., 2012; Junker and Keller, 2015). Similarly to yeast, bacterial growth also correlates negatively with total sugar content and/or Suc content in nectar but usually correlates positively with the proportion of the monosaccharide Fru (Vannette et al., 2012; Lenaerts et al., 2016; Vannette and Fukami, 2016). In addition, bacterial isolates of the genus Acinetobacter can convert Suc into a mucous matrix of polysaccharides (Fridman et al., 2012; Fig. 1F).

Although the chemical modifications of nectar by yeasts and bacteria look very similar, the effects on pollinators’ preferences frequently diverge. The presence of bacterial colonies on floral nectar often has negative effects on pollination success (Vannette et al., 2012) and insect visitation rate (Junker et al., 2014). Conversely, nectar inoculated with yeasts results in increased seed set of bumblebee- and hummingbird-pollinated flowers (Vannette et al., 2012) as well as enhanced pollen donation via an increment in the pollinator foraging rate (Schaeffer and Irwin, 2014). Nectar modifications of the amino acid content represent a small and under-investigated field of research. However, early observations suggest that bacteria may cause a reduction of specific amino acids such as Thr and Val (Lenaerts et al., 2016).

**PRIMARY METABOLITES AND POLLINATORS’ PREFERENCES: IMPLICATIONS FOR SEED AND FRUIT SET**

Seeds and fruits develop following a successful process of plant reproduction, which ultimately depends upon the proper development of the stamen and pistil coupled to successful pollination and fertilization events. Since floral primary metabolism is deeply intertwined with flower development, aberrant floral metabolism can form a prezygotic barrier that prevents mating and fertilization. For example, mutations that impair the metabolic processes of pollen and egg maturation, or that interfere with pollen germination, tube growth, and guidance (both in the pollen and in the transmitting tissue), impede pollination and fertilization. As detrimental as these mutations seem to be, they are favorably exploited in agriculture, for example, in the generation of male-sterile plants for hybrid breeding (Goetz et al., 2001; Hirsche et al., 2009). Neither as equally well exploited nor understood is the influence that primary metabolism of nectar and pollen has on pollinators’ preferences. Animal-pollinated plants depend upon insects, birds, and mammals as go-betweens for pollen transfer. Therefore, their flowers produce signals (color and scent) to attract pollinators and nectar and pollen rewards to preserve floral fidelity. However, as animal pollinators display preferences for quality and quantity of the reward, their choice to pollinate, or not pollinate, a flower affects fertilization and ultimately may reduce seed and fruit set (Hanley et al., 2008; Carruthers et al., 2017). Insect preferences for flower color and odor have been largely investigated, and a few studies describe the link between plant genotype and animal behavioral response (Bradshaw and Schnepske, 2003; Hoballah et al., 2007; Klahre et al., 2011; Owen and Bradshaw, 2011; Yuan et al., 2013; Amrad et al., 2016; Sheehan et al., 2016). Instead, traditional single-gene studies to ascertain pollinators’ responses to changes in floral primary metabolism have been delayed by the late discovery of the SWEET9 transporter as a mediator of nectar secretion (Lin et al., 2014), and so far, no transporter has been identified that controls the secretion of amino acids in floral nectar (Zhou et al., 2016).

However, a growing body of evidence shows that primary metabolites of pollen and nectar are shaping the interaction between plants and their pollinators through pollination syndromes (Johnson et al., 2006; Weiner et al., 2010). That pollinators’ choices can affect nectar chemical composition has been evident since the early studies of Baker (1977), who observed that nectars are richer in amino acids if they are the only source of...
protein-building material of the pollinators that feed on those. A similar conclusion was reached in more recent studies, which showed that pollinators’ preference had the most important effect on amino acid content in nectar, while taxonomic plant groups had a weakly significant effect (Petanidou et al., 2006). For example, Phe- and GABA-enriched nectars are commonly represented in plants pollinated by long-tongued bees and flies independently of their taxonomic group. As GABA functions as an inhibitory neurotransmitter of insects’ nervous systems, GABA-rich nectar may be preferred by pollinators for its calming effect (Nepi et al., 2012). The volume of secreted nectar also varies in response to environmental fluctuations (e.g. temperature and rainfall), which, ultimately, also may affect pollination and fertilization success (Gallagher and Campbell, 2017).

CONCLUSION AND PERSPECTIVE

The current knowledge on flower central metabolism is largely inferred from experiments performed in leaves, and it is certainly skewed by the generally accepted prejudice that flowers are entirely heterotrophic. However, we have seen that cycles of carbohydrate hydrolysis and resynthesis are functional and activated in flowers and they are the routes for the biosynthesis of amino acids and peptides. Therefore, there are many unsolved issues concerning floral central metabolism and the implications for flower development, pollinators’ choices, and seed and fruit set (see Outstanding Questions). The investigations on floral metabolism have certainly been made difficult by the redundant number of transporters of sugars and amino acids that, on one side, warrant pollination and fertilization success to the plant but, on the other side, add complexity to a deep understanding of single-gene function. In addition, studies performed on knockout mutants focused on the leaf or root phenotypes and only rarely on flower physiology. Largely underinvestigated is the measure by which floral metabolism depends on de novo biosynthesis versus intake of sugars and amino acids. There also is a lack of knowledge concerning the spatial distribution of metabolites in floral tissues and their physiological and ecological significance. In addition, analysis of metabolites often is conducted on individual flowers (or inflorescences) that are regarded as integral floral units, despite the fact that, in no other plant organ as much as in flowers, tissue compartmentalization underlies function. In addition, floral metabolism dramatically changes multiple times in response to development and, presumably, to environmental cues (Lauxmann et al., 2016). Recent advances in analytical techniques that couple metabolomics with histological imaging can now be employed to shed light on this topic (Dong et al., 2016). Techniques of rapid sequencing coupled with genome-wide association studies and quantitative trait locus analysis promise to speed the discovery rate of genes and the network of genes that control plant-pollinator interactions (Clare et al., 2013; Sedio, 2017). Moreover, with the use of the CRISPR/Cas9 technology, the link between a plant genotype, floral chemotype, and pollinator response will likely be possible in nonmodel organisms.

In conclusion, floral biology has become an intense area of study for scientists with expertise in the most disparate disciplines encompassing plant developmental biology, molecular biology, metabolomics and genomics, entomology, and behavioral biology. As described above, recent advances, in particular in understanding sugar transport and pollen tube growth, and in better characterizing the chemical composition...
of nectar provide a firm foundation to comprehend the link between floral metabolism and function. That said, it is our belief that today, as never before, a more holistic and collaborative approach is demanded to shed light on the mechanisms that control floral metabolism and the implications for flower development and plant-pollinator interactions.

LITERATURE CITED


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