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FOCUSED REVIEW

Outstanding questions in flower metabolism

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SUMMARY

The great diversity of flowers, their color, odor, taste, and shape, is mostly a result of the metabolic processes that occur in this reproductive organ when the flower and its tissues develop, grow, and finally die. Some of these metabolites serve to advertise flowers to animal pollinators, other confer protection towards abiotic stresses, and a large proportion of the molecules of the central metabolic pathways have bioenergetic and signaling functions that support growth and the transition to fruits and seeds. Although recent studies have advanced our general understanding of flower metabolism, several questions still await an answer. Here, we have compiled a list of open questions on flower metabolism encompassing molecular aspects, as well as topics of relevance for agriculture and the ecosystem. These questions include the study of flower metabolism through development, the biochemistry of nectar and its relevance to promoting plant-pollinator interaction, recycling of metabolic resources after flowers whiter and die, as well as the manipulation of flower metabolism by pathogens. We hope with this review to stimulate discussion on the topic of flower metabolism and set a reference point to return to in the future when assessing progress in the field.

Keywords: flower metabolism, nectar, pollination, flower development, canalization, *Fusarium*, nitrogen.

INTRODUCTION

Plants are autotrophic organisms that synthesize complex organic molecules starting from simple inorganic elements. In plants of the Angiosperm clade, organs and tissues usually specialize in carrying out a subset of these biosynthetic reactions, as for example, leaves which have the primary function of fixing CO_2 via photosynthesis. However, flowers are essentially heterotrophic as they heavily rely on organic molecules synthesized in leaves and roots. Still, flowers do not merely consume carbohydrate and amino acid resources but also utilize them as a substrate for the synthesis of more complex molecules that sustain plant interactions with animal pollinators (Borghi *et al.*, 2017), as well as playing roles in plant fertilization, embryo development, and the initial stages of fruit and seed set (Ruan *et al.*, 2012; Borghi and Fernie, 2017). Given their ephemeral nature, the metabolism of flowers is dynamic, compartmentalized, and highly intertwined. Indeed, secondary metabolic pathways are rapidly activated in pre-anthesis and just as quickly halted in post-anthesis when pathways of the central metabolism promptly intervene to sustain embryo development and seed set.

We recently witnessed a renaissance in the field of flower metabolism due, among others, to the discovery of a novel route for the biosynthesis of the terpenoid geraniol in rose flowers (Magnard *et al.*, 2015), the identification of the first transporter of volatile organic compounds (VOCs) in petunia (Adebesin *et al.*, 2017), the demonstrated role of the sucrose efflux transporter in nectaries of tobacco and Arabidopsis (Lin *et al.*, 2014), the metabolic cross-talk between Phe biosynthesis and Trp-dependent auxin biosynthesis in petunia (Lynch *et al.*, 2020), and, finally, the molecular mechanism controlling color spots formation in mimulus (Ding *et al.*, 2020). These studies notwithstanding, several questions still await an answer. Here, we have compiled a list of open questions in flower metabolism organized in four sections, encompassing molecular aspects, metabolism and flower development, the relevance of floral metabolites for the interaction with pollinators, and finally, we discuss how pathogens manipulate metabolic pathways of flowers to their advantage. We discuss both the value of these questions and strategies to address them.

MOLECULAR ASPECTS OF FLOWER METABOLISM

This section discusses molecular aspects of flower metabolism. These include the floral demand for chemical energy, uptake and redistribution of amino acids, the metabolic complexity of nectar, metabolic aspect of pollination, and finally recycling of metabolites as flowers whither.

Why so many mitochondria?

Floral tissues are long known to contain very high numbers of mitochondria (Figure 1a). In many instances, the reason for this is likely trivial in that they exhibit very low to negligible rates of photosynthesis but have high needs for ATP due to the high energetic demands of the reproductive process. By analogy, stomatal guard cells are also characterized by very high mitochondrial numbers and low rates of photosynthesis, as well as a need for ATP to energize the ion channels required to mediate control of stomatal movement (Daloso *et al.*, 2017). Research on the mitochondrial NAD^+ transporters which are crucial for import of NAD^+ into the organelle - and thereby for redox aspects of mitochondrial function - revealed that deficiency in their expression resulted in lower pollen viability, shorter siliques, and higher rate of seed abortion (de Souza Chaves *et al.*, 2019), again underlining the importance of the mitochondria for plant reproduction. A further specific process that warrants discussion is that of thermogenesis. The role of mitochondria in thermogenesis has recently been pinpointed to be largely driven by the alternative oxidase (AOX), that is the alternate respiratory pathway known to ameliorate the production of reactive oxygen species without producing ATP (Del-Saz *et al.*, 2018). In cones of *Cycas revoluta*, huge mitochondria were observed that harbored much higher content of AOX protein (Ito-Inaba *et al.*, 2019). Even more convincingly, *in vivo* AOX measurements in *Philodendron bipinnatifidum* inflorescences (which, similar to *Cycas revoluta*, heats up above 40°C) revealed that this pathway contributed to approximately 90% of the respiratory flux. The role of AOX in flowers from non-thermogenic plants has not been fully elucidated, although their correct functioning is deemed essential for the proper fertilization and embryo development. Indeed, pollen grains from *AOX2b* antisense soybean lines have reduced rates of germination, so that fertilization is notably compromised when these lines are used as pollen donor (Chai *et al.*, 2010). The same antisense plants show incomplete development of the embryo sac, although whether this is due to the improper turnover of the tricarboxylic acid cycle (TCA) cycle or the induction of programmed cell death (PCD) caused by elevated levels of hydrogen peroxide has not been investigated. In maize, for example, when high levels of reactive oxygen species (ROS) develop during floral induction, mitochondria switch to the alternative oxidase pathway. This phenomenon, if prolonged in time, may lead to altered inflorescence architecture as in the case of *needle 1* mutant (Liu *et al.*, 2019). The role of AOX during flower anthesis is also not fully known, although a spike in *AOX1* and *AOX2* gene expression has been observed in tobacco petals and sepals as flowers open (Müller *et al.*, 2010). To summarize, whilst we are partially able to address this question, few studies to date have directly targeted the mitochondria of floral tissues. Identifying suitable promoters to drive floral specific expression or to mediate floral specific gene editing (Ali *et al.*, 2020) is a clear research priority because, if successful, this would facilitate a far more in-depth characterization of the role of mitochondria within cellular metabolism and other processes within individual floral tissues.

How and in which form is N transported into flowers?

Amino acids find great utility in flowers being the building blocks for the synthesis of enzymes and structural proteins, as well as the precursors of N-rich secondary metabolites and signaling molecules (Borghi and Fernie, 2017). Considerable evidence has accumulated showing that biosynthesis of several amino acids including phenylalanine (Widhalm *et al.*, 2015), asparagine (Gaufichon *et al.*, 2017), and proline (Kishor *et al.*, 2015) can occur *de novo* in flowers. However, even in these cases, given that the assimilation of inorganic nitrogen into organic compounds takes place primarily in the root (Näsholm *et al.*, 2009), nitrogen must be transported into the flower in some form (Figure 1b). Our current knowledge concerning the transport of nitrates, amino acids, and indeed dipeptides into flowers largely originates from work carried out in the laboratories of Tegeder, Rentsch, and Frommer (Fischer *et al.*, 1995; Lee and Tegeder, 2004; Hammes *et al.*, 2006; Komarova *et al.*, 2008; Yuan *et al.*, 2009; Tegeder, 2012; Tegeder and Hammes, 2018). These studies have begun to unravel the complexity and redundancy of N transport in plants, and have started to provide information concerning their hierarchical importance. The approach taken in these works generally aimed to define the biochemical capabilities of the transporters, as well as their expression patterns and importance via transgenic approaches that modulate their expression. We have previously provided a detailed overview of the transporters expressed in the floral receptacle and between the various tissue types of flowers (Borghi and Fernie, 2017). Several other studies that took different routes to investigate transfer of nitrogenous compounds recently documented an extensive long-range nutrient transfer by hoverflies between flowers (Wotton *et al.*, 2019). However, a more exact spatial analysis of the metabolic fate of these nutrients and the extent of their redistribution is currently lacking. The floral levels of many amino acids also increase in response to a short-term heat stress (Borghi *et al.*, 2019). This could either be a result of increased import or

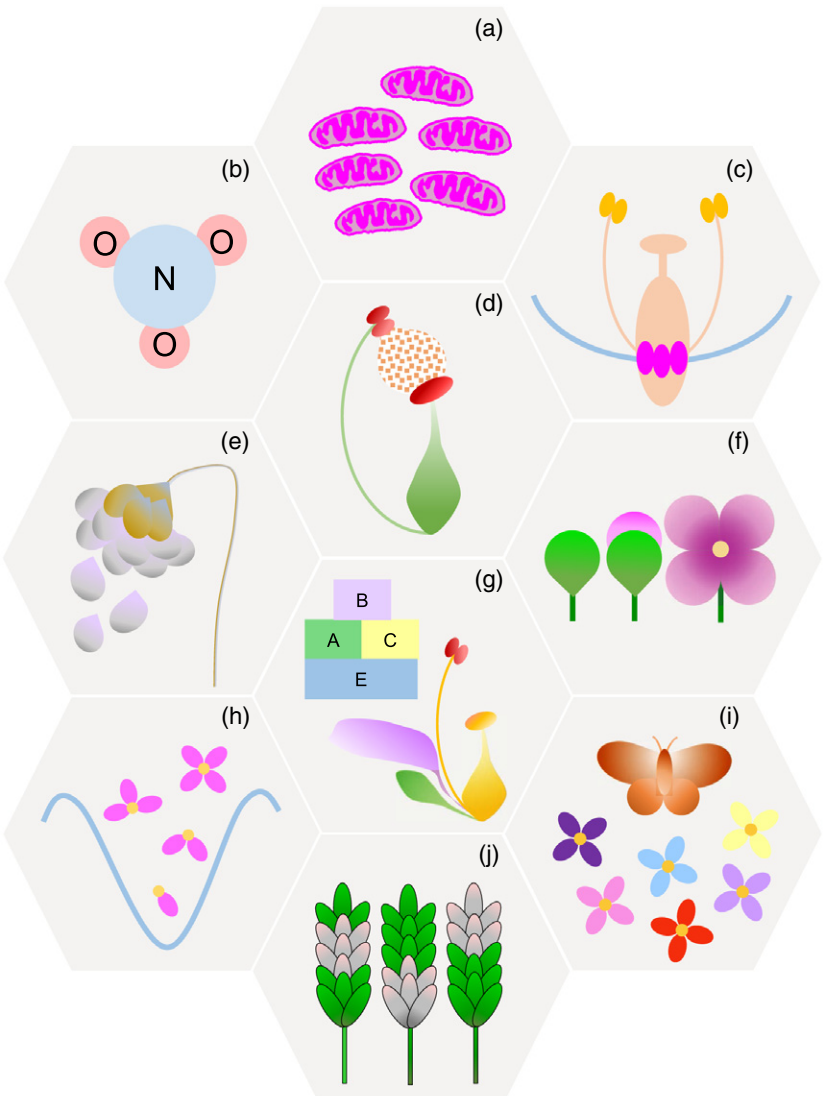

Figure 1. Schematic representation of the questions discussed in the text. (a) Mitochondria. Floral tissues have a higher number of mitochondria than other plant tissues. Since flowers have low rates of photosynthesis, these organelles provide ATP to meet the high energetic demand of flowers. They also contribute the thermal energy allowing the rapid release of volatile compounds over long distances to attract pollinators. (b) Three-dimensional model of nitrate (NO_3). Root absorb N in the form of NO_3. The conversion of NO_3 to ammonium (NH_4^+) and its final incorporation into amino acids takes place in roots and leaves. Flowers receive N from leaves in the form of NO_3 or amino acids. Usually, amino acids with high N:C ratios, such as Asn or Gln, are delivered to the floral calyx via the phloem, from which they are later distributed to floral organs and eventually further converted to other amino acids and metabolites. (c) Schematic representation of a flower with nectaries shown in magenta. Nectaries secrete a water-based solution rich in sugars, amino acids, and other metabolites. Recent metabolomic approaches have started to reveal the metabolic richness and diversity of nectar produced by different plant species. From an ecological perspective, the chemical composition of nectar accounts for plant-pollinator interactions since the animals collect nectar from flowers as a source of nutrients and other relevant molecules. (d) Schematic representation of pollen transfer from anthers to the stigma during pollination. Water and carbohydrate-based exudates secreted from the stigma allow for pollen rehydration and the emergency of the pollen tube. Pollen tube elongation along the style is also supported by exudates produced by the female tissues, which also confer directionality to pollen growth. (e) Flower senescence. At the end of their life cycle, flowers shed petals and anthers, while the carpels develop into fruits and seeds. During flower senescence, which commences soon after pollination, metabolic recourses are mobilized and recycled to support embryo development and growth. (f) Schematic representation of flower development: flower development occurs in four stages named initiation, determination, morphogenesis, and maturation, during which processes flowers acquire their final shape and chemical signature. Our knowledge of floral metabolism mostly pertains to the maturation phase, when flowers acquire their final color and scent. (g) Schematic representation of floral organs and ABCE model of floral organ identity. Genes of class A promote the initiation of sepals; A + B, petals; B + C, anthers; C, carpel. Genes of class E further specify these classes. (h) Simplified representation of John Piper's drawing of the 'epigenetic landscape' underlying the Waddington's theory of canalization. The flowers in the 'canal' with a variable number of petals represent the loss of phenotypic constancy as it occurs in a 'decanalized' trait. Metabolic canalization of flowers is a mostly unexplored area of research. (i) The phenotypic diversity of flowers is represented here by different petal pigmentation. Floral traits that shape plant–pollinator interactions and bear sufficient genetic variance could be exploited to enhance pollination and enhance the yield of outcrossing crop species. (j) Drawing of Fusarium head blight in wheat. Spikelets of wheat become infected at anthesis when fungal spores germinate and penetrate the floral tissues. Infected spikelets develop a silver pink color as a result of the accumulation of fungal spores inside developing seeds.

enhanced *de novo* biosynthesis; however, even in the latter case, an increase import of N into the flower will be required to fuel this biosynthesis. Similarly, the study of Babst *et al*. (2019) administered $^{13}NH_3$ gas to Arabidopsis leaves and followed its accumulation in the flower stalks of three independent mutants deficient in nitrate/peptide transporter family genes. As such, they were able to assign an important role to these transporters with respect to mediating the flow of N from the leaf to the flower. Experiments using stably labelled ^{15}N have additionally recently revealed that root hydraulic lift (e.g. the transfer of water from wetter to drier layers of soil) positively impacts on the quantities of N delivered to the inflorescences of sagebrush (Cardon *et al*., 2013). Although the nitrogen economy of plants has been extensively modelled in crop species (e.g. the NEMA model in wheat; Bertheloot *et al*., 2011), many of these models are restricted to post-flowering. Therefore, construction of multi-tissue models such as that developed by Grafahrend-Belau *et al*. (2013) but encompassing different floral tissues is an obvious priority in addressing this question. It additionally seems likely that an expansion of the isotope labelling approach, utilizing a range of labelled nitrogen sources in combination with a greater number of transporter mutants, would be able to address the above question for Arabidopsis. The tiny size of organs of Arabidopsis flowers represents a real challenge for feeding experiments. Arabidopsis is the species where the largest body of knowledge has been so far developed on the transport of amino acids and for which the existence of knockout lines would considerably facilitate the investigations. Most likely, the need of specific amino acids, or group of amino acids, also change throughout organ development (see also '*How do floral organs acquire their tissue-specific metabolic signature?*'), so that identifying time-specific requirements is also challenging. With this said, different plant species may have different requirements, as seen in petunia, where aromatic amino acids serve as precursors for the biosynthesis of VOCs (Schnepp and Dudareva, 2018). However, gene-editing approaches recently developed for elaborate spiral flowers (Wang *et al*., 2015) hold the promise that testing hypotheses of specific amino acid transport in floral organs and tissues, as well as throughout flower development, may soon be feasible.

How is the metabolic complexity of nectar obtained?

By definition nectar is a water solution of sucrose, glucose, and fructose, of which the relative ratio is used to discriminate hexose-rich from sucrose-rich nectar secreting flowers (Figure 1c). However, metabolomic and proteomic approaches applied to the study of nectar have revealed the presence of multiple classes of compounds including amino acids, proteins, lipids, and several specialized metabolites (Roy *et al*., 2017; Stevenson, 2019). Despite this chemical richness, it was not until recently that the molecular mechanisms governing secretion and the relative concentration of sugars in nectar were uncovered to be a result of the function of the sugar efflux transporter *SUGAR WILL EVENTUALLY BE EXPORTED TRANSPORTER 9* (*SWEET9*) (Lin *et al*., 2014) and the concurrent activity of the cell wall invertase 4 enzyme (cwINV4) (Ruhlmann *et al*., 2010). However, how the remaining classes of compounds are secreted and synthesized still remains elusive. Recent work comparing the metabolomes of floral and extrafloral nectars of cotton supports an eccrine model of secretion where new metabolites are synthesized in the nectary parenchyma and are subsequently secreted by a battery of transporters acting downstream of an H^+ gradient generated by plasma membrane H^+-ATPases (Chatt *et al*., 2019). Given the abundance of transcripts of the pathways of nitrogen assimilation, such work suggests that the novel synthesis of amino acids may also occur in the nectary cells. After sugars, amino acids represent the largest class of compounds found in nectar and one of the most critical chemical traits shaping plant–pollinator interactions (Fornoff *et al*., 2017). Therefore, elucidating the mechanisms of amino acid synthesis and secretion from the cell of the nectary parenchyma would represent a breakthrough discovery for the biology of nectar and flowers. Experiments examining the nectar metabolomes of transporter mutants, ecotypes, and sequenced species will be of high value in addressing these questions (see also *'How and in which form is N transported into flowers*?'). The observation that male and female flowers from monoecious *Cucurbita* plants secrete specific proteins and amino acids in the nectar of one of two sexes suggests a coregulation of organ developmental specificity and nectary's functionality (Chatt *et al*., 2018). A handful of transcription factors (TFs) currently awaiting experimental characterization have been proposed to take part in the regulation of nectar secretion from female flowers of *Cucurbita pepo* (Solhaug *et al*., 2019a). Moreover, progress has been made in elucidating the regulatory roles of auxins (IAA), jasmonic acid (JA), gibberellins (GAs), and trehalose-6P in coordinating nectar secretion (Roy *et al*., 2017; Schmitt *et al*., 2018; Solhaug *et al*., 2019b). Partially understudied remain the cytological and molecular mechanisms involved in the reabsorption of nectar and its regulatory mechanisms (Nepi and Stpiczynska, 2008). Pedersen showed that alfalfa flowers can reabsorb ^{14}C-labeled sucrose through the nectaries and redistribute it to all of the active sink tissues of the plant (Pedersen *et al*., 1958). However, this early observation has only been followed by a handful of studies (Luyt and Johnson, 2002; Cardoso-Gustavson and Davis, 2015). Southwick, who measured photosynthetic assimilation, nectar production, and the amortization of nectar and seed costs over the lifetime of alfalfa and milkweed, reported that nectar is an extraordinarily and powerful sink. In alfalfa, for

example, the energy utilized to produce the total nectar of a plant blossom is almost twice the energy stored into seeds (Southwick, 1984). While this process has not, to our knowledge, been investigated in other crops, the foreseen benefits of unraveling the molecular mechanisms of nectar reabsorption are in the possibility to redirect soluble sugars back towards the production of plant biomass, seeds, and fruits.

Will the intricate puzzle of chemical signals governing plant fertilization be solved?

Pollination and fertilization are characterized by an intense exchange of chemical signals triggered by the recognition of compatible pollen grains landing on stigma and culminating with the fusion of gametes. Studies primarily conducted on mutants of Arabidopsis have helped to identify the nature of these signals and the cascade of molecular events that they trigger (Johnson *et al.*, 2019; Lopes *et al.*, 2019; Zhou and Dresselhaus, 2019). The energy for pollen tube growth, for example, is mainly provided by sugars mobilized from the carpel to the elongating pollen tube, as cell wall invertases (cwINV) and vacuolar INV in the transmitting tissue break down sucrose to free monosaccharides for pollen uptake and growth (Goetz *et al.*, 2017; Rottmann *et al.*, 2018; Kim *et al.*, 2019). Similarly, small peptides (e.g. LUREs) and arabinogalactans (AGPs) are released from female tissues to guide the growth of the pollen tube towards the ovule (Higashiyama and Yang, 2017; Jiao *et al.*, 2017; Zhong *et al.*, 2019). These chemical signals, which are produced and released by the female tissues of carpel and ovule, are crucial for proper fertilization because they provide chemical energy and directionality for the growth of the pollen tube. Except for germination, which is a process energized by carbohydrate and lipid resources stored in pollen grains as they mature inside the anthers, a large proportion of the processes leading to fertilization are supervised by signals produced in the carpel. Although the pollen tube quickly rushes toward the ovule, the sperm cells seem to behave like a passive cargo inside the tube (Zhang *et al.*, 2017). Once the pollen tube reaches the micropyle, a burst of ROS production, mediated by NADPH oxidase in response to a wave of Ca^{2+}, promotes the rupture of the tip of the tube and the release of the sperm cells (Duan *et al.*, 2014). While new tiles of knowledge have recently been added to the puzzling communication between pollen and pistil, the redundancy of molecules that contribute to this conversation makes it hard to decipher their individual contribution. Moreover, the receptors on the pollen tubes that are in charge of receiving the signals delivered from the ovule, as well as the downstream cascade of molecular and chemical responses that they trigger, have only partially been characterized (Johnson *et al.*, 2019). The level of complexity in the communication between pollen and pistil renders pollination a process exceptionally susceptible to abiotic stresses (Borghi *et al.*, 2019). In this regard, the role of metabolism and hormonal signaling in conferring tolerance to heat and drought, and the extent of tolerance that can be achieved if these traits would be engineered, is also not fully understood. Along this same line, research on metabolic priming, which is the persistence of metabolites that last beyond a period of stress to confer tolerance to a second exposure, has only recently emerged (Schwachtje *et al.*, 2019). Given recent technological developments, including single-cell sequencing and tissue-specific knockouts, as well as the advantages afforded by considerably more sensitive mass spectrometers enabling access to proteomic and metabolomic data from decreasing sample volumes, we feel the answer to the above question will be a resounding yes and hope that this will be achieved relatively soon.

What is the quantitative contribution of metabolite recycling into fruits and seeds when flowers wither?

Flower senescence is the process of gradual deterioration of organs and tissues that is induced by pollination, or it occurs naturally (developmental senescence) when the stigma is no longer receptive (Figure 1e). In both instances, senescence is accompanied by the removal of costly tissues such as petals and anthers, which are now surplus to requirements, and nutrient recycling to developing embryos and other organs. Therefore, during senescence, flowers transition from a status of biochemical sink to source organs. Nutrient mobilization and recycling pertain to macromolecules as well as minerals (Bieleski, 1995; Jones, 2013). In daylily, 95% of sugar content corresponding to 65% of the flower's dry weight is lost in the first 24 h following the onset senescence, with non-sugar compounds contributing the remaining 30% (Bieleski, 1995). The underlying mechanisms of sugar and amino acid recycling in senescing daylily have been only recently revealed via proteomic studies. These recent analyses showed enrichment of metabolic pathways associated with the mobilization of sugars and amino acids promoted by invertases and proteases (Ma *et al.*, 2018). Cysteine proteases and components of the ubiquitin–proteasome are also central actors in nutrient recycling, and these are often transcriptionally triggered by the onset of senescence and pollination (Shahri and Tahir, 2014). Indeed, pollination, although not deemed strictly part of the process of flower senesce, greatly accelerates the process as it has been shown in Petunia (Shibuya *et al.*, 2013), and other species including carnation, *Brunfelsia calicina* (Vaknin *et al.*, 2005), and also Arabidopsis (Stead, 1992; Xu and Hanson, 2000). Plant growth regulators also promote flower senescence, with ethylene having a central role and abscisic acid, which instead acts in flowers insensitive to ethylene (van Doorn and Woltering, 2008). Electron microscopy

studies in *Petunia*, common morning glory (Matile and Winkenbach, 1971) and carnation (Smith *et al.*, 1992) suggest that nutrient recycling in post-pollination flower petals occurs via autophagy. Consistent with this, the application of an autophagy inhibitor to petals constrains ovary growth (Shibuya *et al.*, 2013). Similarly, autophagy has been demonstrated to play an important role in nitrogen mobilization to the seeds of Arabidopsis (Guiboileau *et al.*, 2013). Quantifying the autophagy induced protein degradative fluxes, as has already been achieved in Arabidopsis (Avin-Wittenberg *et al.*, 2015; Ishihara *et al.*, 2017), but extending the scope to assess the metabolic fate of the breakdown products at a tissue-specific level would allow us to gain a handle on the quantitative importance of this recycling. Such studies would thereby complete our temporal understanding from the birth to the death of the flower.

FLOWER METABOLISM AND DEVELOPMENT

This section discusses metabolic requirements of flowers during development, as well as aspects of flower metabolic resilience towards genetic and environmental perturbations.

How do floral organs acquire their tissue-specific metabolic signature?

The metabolism of organs and tissues is compartmentalized in space and time as it defines the trajectories of organ development and the acquisition of organ identity (Miyazawa and Aulehla, 2018). Therefore, at the completion of morphogenesis and maturation, individual organs acquire their structure-specific metabolic signature (Figure 1f). Individual floral organs differ in their degree of metabolic specialization, to such an extent that qualitative and quantitative annotations of secondary metabolites (otherwise known as specialized metabolites) can be used to draw clusters representative of single organs (or groups of organs) with similar physiological and ecological functions. For example, computational metabolomics of floral tissues of *Nicotiana attenuata* predicted associations of metabolites with organs directly related to reproduction, such as anthers and ovaries, as well as with tissues not immediately associated with a reproductive function, such as petals, sepals, and filaments (Li *et al.*, 2016b). The acquisition of tissue-specific pigmentation during the maturation phase of petal development is undeniable evidence that metabolism and development are coregulated. Three classes of pigments are responsible for the color of petals: flavonoids, carotenoids, and betalains (Borghi *et al.*, 2017). The pathways of flavonoid biosynthesis and their transcriptional regulators are well characterized (Xu *et al.*, 2015). Recently, research on carotenoid biosynthesis in mimulus flowers identified a master regulator of the entire carotenoid pathway in petals (Stanley *et al.*, 2020), as well as the activator-inhibitor system controlling spot pigmentation (Ding *et al.*, 2020). Surprisingly, an R2R3-MYB TF, notably known to control anthocyanin biosynthesis, has recently been shown to co-regulate carotenoid biosynthesis and anthocyanin-based venation in flowers of *Medicago truncatula* (Meng *et al.*, 2019). Differently from carotenoids and flavonoids, much less known about betalain biosynthesis and regulation in flowers (Polturak and Aharoni, 2018; Guerrero-Rubio *et al.*, 2019). As for pigments, biosynthesis and emission of floral VOCs are also developmentally regulated. Scent emission usually occurs at the end of the maturation stage, when flowers have obtained their final shape and size, and it synchronizes with flower anthesis, as well as with cycles of corolla opening and closure. A handful of TFs have been identified that control these processes (Verdonk *et al.*, 2005; Cna'ani *et al.*, 2015; Fenske *et al.*, 2015). Among these, the clock gene *CHANEL*, a *ZEITLUPE* ortholog in petunia, and its chaperone *GIGANTEA 1*, control size of flowers and qualitative and quantitative emission of VOCs (Terry *et al.*, 2019; Brandoli *et al.*, 2020). However, our current knowledge of organ- and tissue-specific metabolism in flowers mostly pertains to the steady-state levels of specialized metabolites at the completion of the maturation phase, which is when all floral structures have already obtained their final metabolic signature. A few studies have addressed the question how floral tissues attain their metabolic specialization throughout development, for which petals were often chosen as preferred organs for the investigations. It emerged from these researches that sepals provide bioenergetic carbohydrates for the proper development and expansion of the corolla limb (Kwak *et al.*, 2007), as well as precursors for the biosynthesis of VOCs (Muhlemann *et al.*, 2012). Indeed, tobacco plants deficient in the sepal-specific ADP-glucose pyrophosphorylase isozyme also develop smaller flowers with reduced length of the areas between corolla lobes, a phenotype that is reverted to the wild-type when sucrose is supplemented to the flowers (Kwak *et al.*, 2007). Since ovaries and anthers maintain their canonical shape and dimensions, it has been speculated that their strength as sink tissues is stronger. However, how flowers coordinately allocate resourses to different organs and across development, only feeding experiments with labeled carbon sources can reveal. A JA-Ile-dependent signal triggers changes in the content of primary and specialized metabolites during maturation of limb tissue (Stitz *et al.*, 2014). However, the cascade of events between the perception of JA-Ile signal and induction of metabolite changes is not known. Additionally, a comprehensive analysis of primary and secondary metabolites and transcripts of whole flowers across the maturation phase is also missing, which, when implemented with feeding experiments with stably labeled C and N sources, could provide great insight to the source-sink distribution of metabolites in flowers (see also '*How and in which form is N transported into flowers?*').

Maturation phase aside, how floral tissues achieve specialization during morphogenesis is a mostly unexplored area. During this phase, cells proliferate, expand, and differentiate in final units that characterize each organ, so that disruption of morphogenesis profoundly impacts the final appearance and function of flowers (Shan *et al.*, 2019). Attempts to investigate metabolism in these early stages of development have employed entire inflorescences of inducible homeotic mutants of Arabidopsis (Bellaire *et al.*, 2014; Nakamura *et al.*, 2014), and, as such, the contribution of single tissues to the metabolism of the whole flower did not emerge. Nevertheless, substantial changes of primary metabolite and lipid contents were measured between the initial stages of flower development (which also included morphogenesis) and the later stages (which also included maturation), which further supports the hypothesis that morphogenesis and maturation are driven by different metabolic requirements. To address this question, species with instable merosity (i.e. number of floral organs within whorls) offer convenient models of study. For example, *Cardamine hirsuta*, a species where the number of petals, stamens, and sepal trichomes shows a high degree of variation between early versus late-developing flowers, as well as among natural accessions, is emerging as a suitable model for implementing metabolomic-assisted transcriptomic and genomic studies (Hay *et al.*, 2014; Shan *et al.*, 2019).

Do flowers with different ABCE model of development have different metabolic requirements?

Despite their great diversity, flowers are composed of units, or 'identities' with similar structure and function (Shan *et al.*, 2019). Homeotic genes belonging to the classes described by the ABCE model of flower developmental patterning specify these floral organ identities by determining the initiation of sepals (A function), petals (A+B), anthers (B+C), and carpels (C). Finally, genes of class E are further needed for the developmental specification of these functions (Thomson and Wellmer, 2019) (Figure 1g). Homeotic genes recruit TFs to targeting DNA sites that promote, or silence, transcription. Studies on the gene regulatory networks acting downstream of the primary floral homeotic TFs have revealed activation of hormone signaling genes, as well as genes involved in carbon and nitrogen assimilation and photosynthesis (Wils and Kaufmann, 2017; Chen *et al.*, 2018). However, the molecular mechanisms by which homeotic TFs promote the metabolic responses that give rise to organ shape and size are far from being understood. Since larger floral meristems give rise to flowers with a larger number of organs (Wang *et al.*, 2015), the bioenergetic function of metabolism, which provides building blocks and high energy molecules to sustain cell divisions and growth, is intuitively involved in the process (see also '*How do floral organs acquire their tissue-specific metabolic signature?*'). However, how metabolism is dynamically regulated thought the process of organ initiation, so as to sustain the spatiotemporal rate and number of floral organs that are formed, has hardly ever been addressed. The majority of studies on flower homeotic genes and their downstream targets have, once again, been primarily conducted in Arabidopsis. However, orthologs of Arabidopsis homeotic TFs have already been identified in many plant species, in which expansion or silencing of one of the ABCE functional classes gives rise to flowers with a peculiar shape, size, orientation, and fusion of organs of which ornamentals and orchids offer a vast array of examples (Kanno, 2015, Specht and Howarth, 2015). Studies that aim to shed light on the coordination between metabolism and floral architecture should look in the direction of comparative phylogenetic research where metabolite and transcript levels are assessed in parallel throughout organ initiation and growth. Fully-sequenced genomes of plant species with different model of flower development are available, for which homeotic TFs have been computationally annotated. In these species, CRISPR-Cas9 and virus-induced gene silencing (VIGS) offer great opportunities for silencing regulatory genes of flower organ initiation (Wang *et al.*, 2015), in which not only the appearance of new phenotypes, but also the downstream gene regulatory networks (Chen *et al.*, 2018) and metabolite levels could be assessed and measured.

Is the metabolism of flowers canalized?

Flowers, as organs directly related to reproduction and Darwinian fitness, are under a strong stabilizing selection, which warrants phenotypic constancy in circumstances of environmental and genetic perturbation (Givnish, 2002) (Figure 1h). Stabilizing selection canalizes flower phenotypes by making them 'free from undesirable correlation' with vegetative traits (Berg, 1960; Conner and Lande, 2014). Hence, although vegetative traits are 'free' to vary in response to environmental and genetic perturbation, flower traits show a higher degree of phenotypic constancy. This phenomenon extends to intra-floral traits, for which characters related to the mechanics of pollen transfer and retrieval from animal pollinators (e.g. length of staminate and pistillate column) vary less than traits associated with the attraction of pollinators (e.g. size of petals) (Armbruster and Wege, 2019). Therefore, the degree of specialization of flowers such as symmetry and orientation, rather than the type of specialization in the plant–pollinator interaction (generalist versus specialist plants), appears to drive differences in trait variance (Armbruster and Wege, 2019). Different organs of flowers have their specific metabolic signature that is acquired during development as the metabolic requirements of cells and tissues are met (see also '*How do floral organs acquire their tissue-specific metabolic signature?*'). Therefore, it is expected that the

central metabolism of flowers, which supports growth and development of floral organs, is at least partly, canalized. Unfortunately, the study of canalization in flowers has so far focused on traits related to morphology and development, with canalization of metabolism thus far being restricted to tomato fruits (Alseekh *et al.*, 2017) and Arabidopsis rosettes (Joseph *et al.*, 2015; Li *et al.*, 2016a). Thus, whether metabolic phenotypes are canalized and covary with morphology and size of flowers and floral organs is currently not known. Concerning canalization of metabolism to environmental perturbation, we have recently shown that the metabolic traits of flowers respond to high temperature and drought (Borghi *et al.*, 2019), although still little is known about the loci controlling the variance of these metabolic traits. In sunflower, where the study of the phenotypic variation of floral traits such as size and color is of relevance for farmers and end consumers, large phenotypic plasticity was measured in plants grown in a greenhouse setting and in the field, which was further associated with several genetic markers (Dowell *et al.*, 2019). However, to ascertain the contribution of these quantitative trait loci (QTL) to stochastic variance in flower morphology, as well as carotenoid and anthocyanin contents, validation experiments are demanded. Yet, these experiments show the power of genome-wide association and QTL mapping applied to the study of flower traits, which, so far, have been applied primarily to fruits, seeds, and biomass. Metabolomics studies of mutants of hub genes of flower plasticity (Laitinen and Nikoloski, 2019), as well as of species with unstable flower merosity such as *Cardamine* (McKim *et al.*, 2017) and *Borrago* (Descamps *et al.*, 2018), will also offer excellent opportunities to identify loci controlling floral metabolic constancy.

FLOWER METABOLISM, POLLINATORS, AND AGRICULTURE

Insights into breeding approaches of flower metabolism to increase animal mediated pollination are discussed in this section.

Can we breed flowers to enhance pollination services for better yields?

That the world population relies substantially on animal pollination for crop production has been known for more than a decade (Klein *et al.*, 2007). However, this issue only recently received due attention as the market demand for pollination-dependent produce and nuts has consistently been rising and, in parallel, a large body of bibliometric data has been published on the threat of the global decline of pollinators (van der Sluijs and Vaage, 2016; Christmann, 2019; Decourtye *et al.*, 2019). In the effort of confronting this global issue, attention turned towards breeding strategies for floral traits with the hope of promoting pollination services by enticing the animals with tasty nutritional resources and other cues (Bailes *et al.*, 2015; Prasifka *et al.*, 2018). But, is 'breeding for pollinators' realistically attainable? While we are still waiting for experimental results that will prove - or disprove - this approach, a discussion has been raised about suitable floral traits for breeding, for which any character that enhances plant-pollinator interactions and concurrently bears high genetic variance is a potential target (Bailes *et al.*, 2015) (Figure 1i). Given the poor resolution of insect eyes, color probably has a negligible impact on flower attractiveness (de Ibarra *et al.*, 2015), unless large patches of brightness are created (e.g. by reshaping plant architecture so to change floral arrangement and display), which would offer wider visual cues to inform insect navigation decisions. So far, scent has not received much attention in the discussion of breeding programs for pollinators, despite it is a powerful cue for attracting insects to flowers. Indeed, manipulating volatile emission bears the hidden risk of rendering flowers more attractive to undesired florivores (Theis and Adler, 2012). Given that bees quickly learn to associate honest cues to rewards, programs that aim to breed the chemical traits of nectar and pollen bear the promise of having a positive impact on plant-pollinator interaction (Prasifka *et al.*, 2018). Still, altering the chemical composition of pollen carries the risk of compromising pollination during pollen germination and pollen tube elongation, not to mention that insects do not always seek pollen with a high amino acid or lipid content (Roulston *et al.*, 2000). Since it has recently been shown that breeding may alter the chemical composition of pollen and nectar, programs that assess the quality of flowers and floral rewards should be implemented. Likewise, the influence that the environment and agricultural practices have on the chemistry of flowers is often overlooked (Borghi *et al.*, 2019; Dowell *et al.*, 2019; Prado *et al.*, 2019); thus, breeding programs targeting floral rewards should also focus on stable metabolic traits in order to ensure that constant resources are provided to pollinators. For this, metabolomics-assisted breeding (Fernie and Schauer, 2009) with a focus on flowers and flower rewards holds great potential to inform decisions that will benefit both, pollinators and end consumers.

FLOWER METABOLISM AND PATHOGENS

This section provides an overview of modification of flower metabolism by fungi and bacteria.

How is the metabolism of flowers manipulated by pathogens?

As flowers secrete exudates rich in carbohydrates, amino acids, and lipids, they offer an ideal environment for the proliferation of microorganisms, many of which thrive on floral tissues. Pathogenic microorganisms and fungal spores are transported to flowers by pollinators, wind, and

water, after which they preferentially colonize wet pistils and nectaries and cause necrosis and malformations (Ngugi and Scherm, 2006). Petals and pollen are not immune to pathogen colonization (Steiner *et al.*, 2019). That said, since the infection of the gynoecium entails severe grain losses, research has preferentially focused on the mechanisms of carpel infection by fungi of the genera *Fusarium* and *Ustilago*, the etiological agents of scar of wheat and barley (Figure 1j), and smut of maize.

The necrotrophic fungus *Fusarium graminearum* infects the florets of small grain crops at the onset of anthesis and manipulates the basal metabolism of flowers by releasing lethal mycotoxins. One of the most potent of these toxins, deoxynivalenol (DON), binds to the peptidyl transferase of ribosomes and inhibits protein synthesis (Rocha *et al.*, 2005; Abolmaali *et al.*, 2008; Walter *et al.*, 2010; Knutsen *et al.*, 2017). The ribosomes subsequently release incomplete proteins and the ubiquitin–proteasome complex degrades them to dipeptides and amino acids (Doppler *et al.*, 2019). Fungi derive all their nitrogen from plants, and many prefer amino acids to nitrate as a source of nitrogen (Seifi *et al.*, 2013). Therefore, by stopping protein synthesis at its start, the fungus repurposes nitrogen resources to its advantage. Since flowers are sink tissues, one could assume that pathogenic fungi act on flowers by simply draining nutrients. However, evidence shows that the content of flower metabolites differentially decreases - or increases - upon fungal infection (Cuperlovic-Culf *et al.*, 2019; Doppler *et al.*, 2019), an indication that *Fusarium* may sense the nutritional status of the host (Bolton and Thomma, 2008) and reconfigure the metabolism of the infected tissues accordingly (Seifi *et al.*, 2013). In the initial stage of infection, the fungus takes advantage of the glyoxylate cycle for the conversion of fatty acids to glucose by depleting the cytosolic pool of citrate. As less citrate flows from glyoxysomes to mitochondria, plant gluconeogenesis slows down and finally stalls. Concurrently, the transcriptional activation of fungal invertases and glucose transporters further sustains the energy metabolism of the fungus which starts growing aggressively. As the authors discussed, they performed this study in wheat coleoptiles, and whether this model of infection holds true also in flowers, it has not yet been confirmed (Zhang *et al.*, 2012). Flower peroxisomes, rather than glyoxysomes, contribute to the energy requirements for the elongation of the pollen tube (Goto-Yamada *et al.*, 2014). However, depending on the plant species, flower peroxisomes may or may not have a functional malate synthase (Zhang *et al.*, 1994; Mellema *et al.*, 2002) and therefore a functional glyoxylate cycle that the fungus can successfully exploit. A metabolic trade-off between the peroxisomal β-oxidative pathway and the cytosolic pathway of phenylpropanoid synthesis has recently been identified in *Petunia* flowers (Adebesin *et al.*, 2018). Following the hypothesis that *Fusarium* can take advantage of the β-oxidative pathway, the draining of metabolic precursors common to both pathways would make the infected florets more susceptible to fungal infection also because less lignin will be available for thickening the cell wall. Despite the insight from the above studies, the question how *Fusarium* can selectively alter the content of amino acids is far from being understood. It has been proposed that the fungus interferes with the metabolism of glutamate in multiple steps along the processes of nitrogen assimilation, remobilization, and transport, but these hypotheses have not been thoroughly tested (Seifi *et al.*, 2013; Fagard *et al.*, 2014). The ability of *Fusarium* to take advantage of the floral metabolome depends on the physiological status of the plant (Mur *et al.*, 2017). Under elevated CO_2, when the rate of photorespiration decreases and the translocation of photoassimilates to flowers usually increases, susceptible varieties of wheat seem to become more resistant to fungal infection (Noctor and Mhamdi, 2017). In spikelets of wheat exposed to both *Fusarium* and elevated CO_2, a full reprogramming of the floral metabolome was also reported (Cuperlovic-Culf *et al.*, 2019). However, as the Authors clarified in that study, the host and the fungus synthesize similar pools of primary metabolites, and only feeding experiments could help to identify whether fungal metabolites are synthesized *de novo* or imported as are from the flower. Still, given that fungal hyphae grow inside the cells of the host, separating these tissues is not easy. To investigate flower metabolic reprogramming in response to *Fusarium* infection, ^{13}C-labelled Phe and DON mycotoxin were sprayed on spikelets of two representative resistant and susceptible near-isogenic lines of wheat (Doppler *et al.*, 2019). Although this experiment was informative in unambiguously highlighting the flow of metabolites towards the synthesis of lignin in wheat tissues, it is not representative of a true fungal infection. In the previously described experiment performed in wheat coleoptiles, a laser capture microdissection technique was employed to separate fungal hyphae from the tissue of the host (Zhang *et al.*, 2012). We think that when combined, these two techniques could provide the spatio-temporal resolution required to uncover the metabolic reprogramming occurring in flowers during a pathogenic infection.

The biotrophic fungus *Ustilago maydis* infects tassel and ear of maize, as well as leaves, where it forms large tumoral masses of ashy-looking spores from which the name smut disease was coined. The disease *per se* is of marginal relevance for the annual revenue of corn production; however, the fungus represents a very well-established model for studying the molecular mechanisms of fungal infection and plant resistance (Dean *et al.*, 2012). As the hyphae of *U. maydis* grow on the host tissues, they secrete an extensive battery of protein effectors that diffuse in the apoplast or translocate inside the cytoplasm of

a plant cell to steer plant metabolism in favor of tumoral growth. Well-characterized effectors of *U. maydis* include the allosteric regulator Tin2 and the enzyme chorismate mutase 1, which deflect the plant metabolome from the synthesis of protective compounds such as lignin and salicylic acid (Djamei *et al.*, 2011; Tanaka *et al.*, 2014). Then, as tumoral masses grow bigger, they start importing large amounts of sugars and amino acids from source tissues. Fungi are unable to metabolize large polysaccharide molecules (Goulet and Saville, 2017); therefore, they have adopted peculiar strategies to manipulate the carbohydrate metabolism of their hosts. A recent model proposed that the fungus induces leakage of sugars into the apoplast via transcriptional upregulation of *SWEET* transporters and concurrently prevents the reabsorption of sugars by the plant tissues via transcriptional deregulation of sugar importers (Sosso *et al.*, 2019). However, the effectors that control sugar metabolism at a molecular level are not known. Concurrently, feeding experiments with labeled nitrogen have revealed that the growing tumors preferentially import organic nitrogen reallocated from source leaves (Horst *et al.*, 2010). Indeed, by changing the natural metabolic progression of plant tissues, the fungus maintains the tumors in a permanent sink status and the plant tissues in a prolonged source status, which is also attained by delaying the natural progression of plant senescence (Doehlemann *et al.*, 2008; Horst *et al.*, 2010). While changing the physiological state of a tissue and its relation with the remaining organs of the infected plant may require fungal-mediated modulation of hormone signaling (Doehlemann *et al.*, 2008), the molecular mechanisms leading to this metabolic reprogramming are not fully known and understood. Moreover, the majority of the studies with *U. maydis* were conducted in infected seedling or leaf tissues, although it is known that the changes in transcript levels in infected seedling, tassel and ear have different trends (Kretschmer *et al.*, 2017).

Flower visitation by pollinators is key to the spread of diseases in obligatory allogamous species and crops (McArt *et al.*, 2014). The fire blight and the canker of Rosaceae species, which occur when flowers become infected with *Erwinia amylovora* and *Pseudomonas syringae*, respectively, fall into this category as bees and bumblebees are the primary carriers of both diseases to healthy flowers. In flowers, these pathogens are primarily found on wet stigmas. However, as the infection spreads to nectaries, it often becomes systemic, to the extreme that pollen from unopen flowers can also be infected (Donati *et al.*, 2018). Although some of the floral chemical compounds that confer increased resistance to these pathogens have been identified (Farkas *et al.*, 2012), to our knowledge, it is not known whether bacteria can manipulate the metabolism of flowers as fungi do. Interestingly, recent research conducted on apple blossom has revealed that *E. amylovora* is capable of modifying the composition of volatiles emitted by infected flowers and thus increasing the honeybee-mediated dispersal of the pathogen by stirring the preferences of the animals (Cellini *et al.*, 2019). How commonly pathogens deceive pollinators via modification of flower metabolism has also been poorly investigated.

CONCLUSIONS

The different forms of flowers, as well as their color and pollination mechanisms, have inspired poets, artists, and fascinated biologists for centuries (Darwin, 1877). Metabolic processes of flowers are mostly responsible for this enormous phenotypic diversity, as metabolites fuel and regulate the growth and development of different floral forms, as well as mediate the interactions between flowers and other biotas. Although some of these metabolic processes are well studied and known, others have only partially been addressed or have only recently received attention. Here, we have chosen to discuss only a small number of questions that are perceived of primary scientific and economic importance. Additional, but no less important points concerning the metabolic responses of flowers to climate change (Borghi *et al.*, 2019), the central role of primary metabolism in driving critical aspects of floral biology (Borghi and Fernie, 2017), and the photosynthetic activity of reproductive organs (Brazel and Ó'Maoiléidigh, 2019), have been recently and deeply discussed elsewhere and therefore have not been included in this review. We hope that this summary of questions stimulates further discussion on the topic of flower metabolism and offers a reference point to return to in the future when assessing progress in the field.

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CONFLICT OF INTERESTS

The authors declare that they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

MB and ARF wrote the paper.

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