Plants in nature are subject to attack by a wide variety of phytophagous insects. Nevertheless, the world is green, and most plants are resistant to most individual species of insect herbivores. To a large extent, this resistance is due to an array of toxic and deterrent small molecules and proteins that can prevent nonadapted insects from feeding. Although many plant defenses are produced constitutively, others are inducible (i.e. defense-related metabolites and proteins that are normally present at low levels become more abundant in response to insect feeding). Inducible defense systems, which allow more energy to be directed toward growth and reproduction in the absence of insect herbivory, represent a form of resource conservation. Well-studied examples of inducible plant defenses include the production of nicotine in tobacco (Nicotiana tabacum; Baldwin et al., 1998), protease inhibitors in tomato (Solanum lycopersicum; Ryan, 2000), benzoxazinoids in maize (Zea mays; Oikawa et al., 2004), and glucosinolates in Arabidopsis (Arabidopsis thaliana; Mewis et al., 2005). Additionally, herbivore-induced plant responses can include the production of physical defenses such as trichomes or thickened cell walls that can make insect feeding more difficult. Some plant defensive metabolites are highly abundant, suggesting that their biosynthesis can have a significant effect on overall plant metabolism. For instance, benzoxazinoids can constitute 1% to 2% of the total dry matter of some Poaceae (Zúñiga et al., 1983), and up to 6% of the nitrogen in herbivore-induced Nicotiana attenuata can be devoted to nicotine production (Baldwin et al., 1998).

In addition to the herbivore-induced production of physical and chemical defenses, numerous changes in plant primary metabolism occur in response to insect herbivory. Among other observed effects, these can include either elevated or suppressed photosynthetic efficiency, remobilization of carbon and nitrogen resources, and altered plant growth rate. However, although the defensive value of induced toxins such as nicotine, terpenes, benzoxazinoids, and glucosinolates is clear, it is sometimes more difficult to elucidate the function of herbivore-induced changes in plant primary metabolism. Insects may also manipulate plant primary metabolism for their own benefit, making it challenging to determine whether the observed changes are actually a plant defensive response.

Here, we describe commonly observed changes in plant primary metabolism, focusing on carbohydrates and nitrogen, and discuss their possible functions in plant defense against insect herbivory. There are large differences among published studies involving different plant-herbivore combinations, and no universal patterns in the herbivory-induced changes in plant primary metabolism. Therefore, we also discuss how the potential benefits can depend on the tissue that is being attacked, the extent of the tissue damage, and the type of insect herbivore that is involved in the interaction.

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BIOSYNTHESIS AND MOVEMENT OF PRIMARY METABOLITES

Research on changes in primary metabolism associated with insect feeding has been focused largely on the
role of carbohydrates and amino acids. Carbohydrates, as products of photosynthesis, are the major source of stored energy for both host plants and insect herbivores. Amino acids, the major form of nitrogen found in plants, are not only growth limiting for insect herbivores but also serve as precursors for many defense-related plant metabolites. Thus, regulation of amino acid biosynthesis represents an important control mechanism in plant defense against herbivory. Both local responses at the site of insect feeding and systemic responses that can involve resource reallocation are important components of plant-herbivore interactions.

Carbohydrate Metabolism

Photosynthesis, which is the source of almost all carbohydrates in green plants, is central to any discussion of carbon allocation in response to herbivory. There are divergent theories as to how plants should alter photosynthesis, and thereby carbon fixation, to optimize defense. On the one hand, photosynthetic activity might be promoted because (1) synthesis of defensive metabolites requires carbon fixation, (2) plants may compensate for the loss of leaf area by increasing photosynthetic activity in the remaining tissue, or (3) insects could manipulate plant metabolism to increase carbon fixation and thereby obtain more resources. On the other hand, photosynthetic activity could be reduced because (1) production of the photosynthetic apparatus itself is energy intensive and, as a trade-off for the production of increased defensive metabolites, photosynthesis would be compromised; (2) if insect feeding is localized, senescence and eventual abscession of the affected foliar tissue could involve a reduction in photosynthesis; or (3) less carbon assimilation could make fewer carbohydrates available for the insect herbivores.

In most cases, the latter hypothesis, reduced photosynthesis in response to herbivory, is supported by actual measurements of changes in photosynthesis rate, photosynthesis-related gene expression, or production of proteins that are part of the photosynthetic apparatus (Reymond et al., 2004; Giri et al., 2006; Wei et al., 2009; Bilgin et al., 2010; Coppola et al., 2013; Appel et al., 2014). Reduced photosynthetic capacity can exceed what would be expected from the observed amount of foliar tissue that is removed (Zangerl et al., 2002). However, actual insect damage is not a prerequisite for reduced photosynthetic activity. Feeding by both chewing herbivores that remove leaf material (Reymond et al., 2004; Lawrence et al., 2008) and phloem-feeding insects that do not (Zhu-Salzman et al., 2004; Botha et al., 2006) resulted in lower levels of photosynthesis-related gene expression. Even plant-perceived evidence of insect attack that does not lead to any actual damage (e.g. insect oviposition [Little et al., 2007; Velikova et al., 2010] or exposure to volatiles from infested plants [Arimura et al., 2000]) can reduce photosynthetic capacity. Together, these observations indicate that reduction in photosynthetic activity is an active plant response, rather than just a side effect of metabolic limitation during insect herbivory.

A regulated plant response is also indicated by the fact that the jasmonic acid signaling pathway, which influences many aspects of plant defense against insect herbivory, is required for the observed suppression of photosynthesis and growth (Wasternack and Hause, 2013). Treatment of Arabidopsis with coronatine, which induces defenses as a molecular mimic of jasmonate-Ile conjugate, reduced photosynthesis-related gene expression within 2 h (Attaran et al., 2014). However, actual photosynthetic output was not reduced until the following day in this experiment. Thus, it may be possible for plants to increase the production of defensive metabolites without having an immediate deficit in photosynthesis and carbon fixation.

Despite the general pattern of decreased photosynthesis in response to insect feeding, there are also well-documented exceptions. When mirid bugs (Tupiocoris notatus) are feeding from N. attenuata (Halitschke et al., 2011), increases in CO₂ fixation that occurred in response to components of mirid bug saliva compensated for the loss of functional leaf tissue during insect feeding. Thus, there was no observed decrease in plant fitness due to mirid bug feeding. Similar increases in photosynthetic capacity have been observed in other plant species that are tolerant of herbivory (i.e. growth and reproductive fitness are not significantly impacted by insect damage). For instance, wheat (Triticum aestivum) and barley (Hordeum vulgare) resistance to Russian wheat aphids (Diuraphis noxia) has been associated with increased expression of photosynthesis-related genes after attack (Botha et al., 2006; Gutsche et al., 2009).

In the more common case, where there is reduced photosynthetic activity in response to insect feeding, plants nevertheless face increased energetic and carbon demands to support production of inducible defenses. With reduced carbohydrate supply from photosynthesis, cells in herbivore-attacked plant tissues may need other sources of carbon and energy to produce defense-related metabolites. To cope with this challenge, many plants respond to herbivore attack by promoting local catabolism of energy storage compounds (e.g. Suc or starch). For instance, a transcriptomic study involving Arabidopsis and four different insect herbivores showed increased expression of invertases and genes encoding enzymes involved in degrading complex carbohydrates (Appel et al., 2014; Fig. 1A). Similarly, in grain amaranth (Amaranthus cruentus), foliar herbivory induced a local increase in cytoplasmic invertase and amylolytic enzyme activities (Castrillon-Arbelaez et al., 2012). Furthermore, this study showed lower concentrations of monosaccharides, Suc, and starch in local tissues in the days after herbivore infestation.

As in the case of altered photosynthetic activity, not all studies show the same pattern of local, herbivore-induced carbohydrate catabolism. For example, tomato leaves that were fed upon by two caterpillar species (Helicoverpa zea and Manduca sexta) exhibited few or no changes in sugar content (Steinbrenner et al., 2011).
Figure 1. Overview of Arabidopsis primary metabolism gene expression changes. Gene expression data from Appel et al. (2014) were analyzed using MapMan (http://mapman.gabipd.org/web/guest/mapman), identifying 178 genes of primary metabolism that showed significantly altered expression in response to at least one herbivore treatment. A, Overrepresentation analyses of the primary metabolism pathways induced in response to feeding by two chewing herbivores (cabbage butterfly [Pieris rapae] and...
Instead, monosaccharide levels were significantly depleted in the shoot apex and root, tissues that were not directly attacked, whereas Suc and raffinose concentrations were not affected.

Although increased photosynthesis and/or local carbohydrate catabolism can serve as energy sources for the production of plant defenses in many plant-herbivore interactions, the observed exceptions suggest that there are also other mechanisms of defense induction. As discussed below, herbivore-attacked tissue could draw energy from systemic tissues through carbon reallocation. Or, alternatively, there are other potential energy sources (e.g., protein degradation to release free amino acids, which is observed in response to a variety of plant stress treatments [Caldana et al., 2011]).

Nitrogen Metabolism

Plant amino acids play a central role in plant-herbivore interactions, both as major growth-limiting nutrients and as precursors for the production of many plant defense compounds. Given this dual function of amino acids, herbivore-infested plants are hypothesized to enhance their amino acid production for the synthesis of defensive metabolites, while striving to limit the herbivores’ access to free amino acids. For instance, genes involved in both amino acid biosynthesis and sulfur assimilation, which is required for Cys and Met biosynthesis, are overrepresented among those that are induced by caterpillar feeding on Arabidopsis (Appel et al., 2014; Fig. 1A). Increased expression of genes related to Met and Trp biosynthesis (Appel et al., 2014) can lead to greater accumulation of defense-related glucosinolates, which are largely derived from Met and Trp in Arabidopsis (Halkier and Gershenzon, 2006). Similarly, foliar insect herbivory induced strong accumulation of Trp, which can serve as a precursor for defensive metabolites, in systemic stem and apex tissue of tomatoes (Steinbrenner et al., 2011). Hence, in some scenarios, herbivore-induced amino acid biosynthesis likely serves as a response to support inducible production of defense metabolites.

In other cases, herbivore-induced changes in amino acid metabolism may be related to subsequent amino acid movement between attacked and systemic tissues. Phloem transport of nitrogen in many plant species, including Arabidopsis, is dominated by Gln, Glu, Asn, and Asp, the four main amino acids involved in nitrogen assimilation (Coruzzi and Last, 2000). Indeed, transcript profiling experiments generally show herbivory-induced changes in the expression of genes related to the production of these amino acids. For instance, herbivory on sorghum induced expression of nitrate and nitrite reductases that are required for nitrogen assimilation into Gln and Glu (Zhu-Salzman et al., 2004); expression of Glu synthase (also known as Gln oxoglutarate amino-transferase, or GOGAT) was induced by aphid feeding on N. attenuata (Voelckel et al., 2004); and aphid feeding induced Gln synthetase, which acts together with GOGAT in the Gln synthetase/GOGAT cycle, in celery (Apium graveolens; Divol et al., 2005). However, examination of multiple such data sets shows that either production or degradation amino acids can be preferred, depending on the specific plant-herbivore system being investigated and the type of tissue (local or systemic) being analyzed (Dorschner et al., 1987; Sandström et al., 2000; Arnold et al., 2004; Koyama et al., 2004; Caldana et al., 2011; Appel et al., 2012).

Since nitrogen is a key nutrient for most insect herbivores, transcriptional changes of genes involved in amino acid metabolism also may result from insect manipulation of plant gene expression. Particularly in the case of some aphids, there is good evidence of increased free amino acids levels being the direct result of insect feeding. For instance, chlorosis-inducing greenbugs (Schizaphis graminum) enhance the content of essential amino acids in the phloem sap of wheat (Dorschner et al., 1987; Sandström et al., 2000). A similar scenario has been reported in Japanese rowan (Sorbus commixta) leaves infested with apple-grass aphids (Rhopalosiprum insertum), such that the amount of amino acids exuded from galled leaves was 4-fold higher than from ungalled ones (Koyama et al., 2004). Yet, the exact physiological events underlying these ecological observations are not fully elucidated. It is likely that these herbivores enrich the amino acid content of their diet by some combination of (1) increasing free amino acid biosynthesis, (2) inducing early senescence and proteolysis to release free amino acids into the phloem, or (3) manipulating the sink-source relationship to allow more transport of nitrogen into infested leaves.

Reallocation of Primary Metabolites

Insect attack frequently induces mobilization of existing and newly assimilated primary metabolites...
between attacked and systemic tissues. Movement of primary metabolites toward herbivore-attacked tissue can be interpreted as (1) providing substrates for the reinforcement of local defenses, or (2) manipulation of plant metabolism by the insects, as described above. In contrast, movement of primary metabolites away from insect feeding sites has been hypothesized to (1) directly starve herbivores, (2) promote tolerance of herbivore damage by preserving resources for later regrowth, or (3) recruit beneficial soil microbes as an indirect defense response. Numerous studies examining carbon and nitrogen movement in response to insect feeding have been conducted, and specific examples fitting all of these scenarios can be found in nature.

Consistent with the hypothesis that import of systemic resources promotes plant defense, treatment with volatile defense signal methyl jasmonate, mechanical damage, and actual insect feeding all can increase movement of carbohydrates toward treatment sites in many plant species (Sturm and Chrispeels, 1990; Zhang et al., 1996; Ehness et al., 1997; Ohyama and Hirai, 1999; Allison and Schultz, 2005; Schultz et al., 2013). In methyl jasmonate-treated or wounded Arabidopsis, radioactively labeled carbohydrates were imported into sink leaves within hours after treatment, and were incorporated into defense-related compounds such as cinnamic acid and phenolic glycosides (Ferrieri et al., 2012). When carbohydrate import was disrupted by removing source leaves or cutting vascular connections, hybrid poplar (Populus deltoides × Populus nigra) defenses were induced less efficiently (Arnold and Schultz, 2002; Arnold et al., 2004). In contrast to carbohydrate transport, labeled nitrogen tracking studies have shown little evidence of jasmonic acid-induced nitrogen transport to elicited leaves in poplar (Arnold et al., 2004; Appel et al., 2012). Nevertheless, it is well established that defense-related nitrogenous compounds such as nicotine and other alkaloids are transported from roots to leaves upon insect attack (Baldwin et al., 1994; Hartmann and Ober, 2000; Ziegler and Facchini, 2008). Hence, it may be a common theme that plants deliver nitrogen as premanufactured resistance compounds but carbon as free carbohydrates for local production of defensive metabolites. Possible explanations for this dichotomy are that (1) carbohydrates are relatively inexpensive in plants growing under full sunlight, and (2) given that nitrogen is often the growth-limiting nutrient for herbivores, direct delivery of nitrogen in the form of phloem-transported amino acids could inadvertently lead to improved nutrition of the herbivores, rather than the production of defensive metabolites.

In support of contrasting hypotheses, herbivore attack or chemical elicitation of plant defenses can redirect primary metabolites away from treated tissues (Holland et al., 1996; Lu et al., 2015). Such reallocation of primary metabolites may hamper herbivore performance by reducing the nutritive value of plant tissue. For example, both the generalist cucumber beetle (Diabrotica balteata) and the specialist rice water weevil (Lissorhoptrus oryzophilus) grew significantly slower on a jasmonate-deficient rice (Oryza sativa) mutant, despite the fact that these plants suffered greater loss of biomass than wild-type controls (Lu et al., 2015). This observation was correlated with herbivore-induced depletion of Suc in the infested tissue of the mutant rice line. In an example that indicates nitrogen transport away from insect feeding sites, foliar feeding by monarch caterpillars (Danaus plexippus) decreased nitrogen allocation to the leaves of common milkweed (Asclepias syriaca), whereas a below-ground herbivore, larvae of red milkweed beetle (Tetraopes tetrophthalmus), significantly induced nitrogen movement away from roots to stems and leaves (Tao and Hunter, 2013).

In addition to making plant tissue less nutritious, herbivore-induced reallocation of primary metabolites could be a tolerance strategy that allows later regrowth after the threat of herbivory has passed (Millard and Grelet, 2010). For instance, carbohydrate was transported away from maize roots infested with western corn rootworm (Diatracta virgifera) into stem tissue, thereby allowing better regrowth of crown roots after herbivory (Robert et al., 2014). In the opposite phenomenon, simulated herbivory of N. attenuata promoted carbon movement to the roots, which provided reserves to subsequently delay senescence and prolong the reproductive phase of the plants (Schwachtje et al., 2006).

Finally, metabolites that are transported in response to herbivore attack may be exuded rather than stored within the plants themselves (Holland et al., 1996; Lee et al., 2012). Lee et al. (2012) suggested that increased root exudation by pepper (Capsicum annuum) upon foliar aphid herbivory can attract beneficial rhizospheric microbes that are known to promote plant health, and hence should be considered a means of indirect defense. Similarly, grasshopper feeding on maize leaves caused increased carbon release and respiration in the root system (Holland et al., 1996).

Although physiological experiments have provided evidence describing the pattern of herbivore-induced primary metabolite reallocation, and some studies have gone further to test particular hypotheses, the signaling and molecular mechanisms that control resource reallocation remain further to be investigated. Reallocation of carbohydrates is thought to be primarily driven by differential sink strength of tissues, which is in turn heavily influenced by activities of cell wall-bound invertases (Sturm and Tang, 1999; Schultz et al., 2013). In congruence with this framework, herbivore-induced carbohydrate depletion has coincided with decreased invertase activities in the same tissues (Machado et al., 2013; Robert et al., 2014). Carbohydrate movement in source tissues is facilitated by sets of membrane transporters (Burkle et al., 1998; Gottwald et al., 2000; Ayre, 2011; Chen et al., 2012). Although expression of these transporters is required for herbivore-induced carbohydrate reallocation (Ferrieri et al., 2012), there is so far little evidence showing that their expression is directly influenced by herbivore attack. In contrast, genes
encoding transporters for both inorganic nitrogen and specific amino acids have been shown to be differentially expressed in response to wounding (Grallath et al., 2005; Meyer et al., 2006), jasmonic acid treatment (Okamoto et al., 2006; Camarés et al., 2012), and insect herbivory (Voelckel et al., 2004; Coppola et al., 2013). Thus, these herbivore-induced changes in gene expression could provide a gateway for future efforts to incorporate resource reallocation into the current signaling and molecular framework of herbivore-induced responses.

### OPTIMAL PLANT RESPONSES IN PRIMARY METABOLISM DEPEND ON THE SPECIFIC NATURE OF THE PLANT-HERBIVORE INTERACTION

Although there are some recurring themes, there are by no means universal patterns in the observed herbivore-induced changes in plant primary metabolism. For instance, whereas photosynthetic activity is generally reduced upon herbivore attack, some studies show the exact opposite. Although many publications show reallocation of carbohydrates toward herbivore-attacked plant tissues, others support resource sequestration. Together, this sometimes contradictory experimental evidence suggests that herbivore-attacked plants are genetically programmed to adopt different responses in primary metabolism based on the nature of a specific plant-herbivore interaction. Therefore, in addition to testing functional hypotheses of herbivore-induced primary metabolic changes on a case-by-case basis, it is necessary to establish a theoretical framework to address the many variables that will influence the reconfiguration of primary metabolism. Recent reviews have addressed aspects of this challenging question (Schwachtje and Baldwin, 2008; Orians et al., 2011; Massad, 2013). For instance, Orians et al. (2011) proposed a fulcrum model containing several intrinsic and extrinsic factors that may shift plants between resource reallocation toward and away from herbivore-attacked tissues. In contrast, Massad (2013) discussed how plant ontogeny affects broader herbivore-induced plant responses. Here, we focus on the effects that specific herbivore characteristics, including (1) the feeding guild, (2) dietary specialization, (3) the extent and type of damage that is caused, and (4) the composition of insect secretions, can have on plant primary metabolism during responses to insect herbivory.

### Insect Feeding Guilds

The diverse mouthparts of insects, ranging from mandibles to stylets, vary in the amount of damage that they inflict on plant tissue (Fig. 2). Chewing herbivores such as caterpillars and beetle larvae cause extensive tissue damage. In contrast, piercing/sucking Hemiptera, including whiteflies, aphids, and psyllids, remove phloem sap and cause relatively little visible damage. Other arthropods such as mites (Tetranychidae) and thrips (Thysanoptera) feed on cell contents, damaging the surface without macerating the entire leaf. These diverse feeding habits lead to highly differentiated metabolic changes in plants.

Correlation of changes in primary metabolism gene expression that are induced by caterpillars and aphids, respectively, indicates that the feeding guild (chewing versus piercing/sucking) has an important effect on the metabolic pathways that are induced or repressed (Appel et al., 2014; Fig. 1B). Arabidopsis gene expression induced by two caterpillar species, cabbage butterfly and beet armyworm, is highly correlated, but different from that induced by two aphid species, green peach aphid and cabbage aphid. A variety of factors, ranging from the amount of physical tissue damage to manipulation of plant defenses by insect salivary components, could influence these differences in the gene expression induced by different feeding guilds.

Intuitively, chewing herbivores would cause greater loss of photosynthetic capacity due to greater tissue damage. Although this hypothesis has received some experimental support (Duceppe et al., 2012), there are also examples showing photosynthesis reduction in the absence of extensive tissue damage, as we have discussed above. Because herbivore-induced reduction in photosynthesis is an active plant response, one cannot simply assume that chewing herbivores tend to cause a more drastic decrease in photosynthetic activity than phloem and cell content feeders.

Less is known about how carbohydrate breakdown, amino acid metabolism, and resource reallocation are differentially affected in plants when challenged by herbivores from different feeding guilds. Orians et al. (2011) hypothesized that greater tissue damage would make resource sequestration a preferred strategy. In support of this hypothesis, the chewing herbivore Egyptian cotton worm (Spodoptera littoralis) feeding on cotton reduced leaf growth, whereas leaf growth was not affected by a cell content feeder, the red spider mite (Tetranychus urticae; Schmidt et al., 2009). Similarly, caterpillar feeding on young turnip (Brassica rapa) increased the mass of storage bulbs, whereas aphid infestation promoted leaf growth (Sotelo et al., 2014).
These changes, however, were not observed on older plants, suggesting that plant ontogeny was more influential in this particular system.

**Dietary Specialization**

Although there is obviously a continuum in the degree of host plant specialization, for convenience, individual species of insect herbivores are often classified as being specialists or generalists (Fox, 1981; Berenbaum et al., 1989; Ali and Agrawal, 2012). Specialist herbivores are generally limited to feeding from plants in a specific family or even genus, and are typically able to tolerate the characteristic defensive metabolites (Agrawal and Kurashige, 2003; Gols et al., 2008). In contrast, generalist herbivores have a wider host range, typically show a lower tolerance of specialized plant toxins, and tend to feed from less-defended parts of the host plant (Ballhorn et al., 2010; e.g., senescing leaves). By themselves, such divergent feeding preferences could influence the type of changes in plant primary metabolism that are induced by insect feeding.

As specialist herbivores are often highly resistant to the toxins of their host plants, there may be greater benefits resulting from sequestering primary metabolites rather than increasing the production of specialized defenses. Steinbrenner et al. (2011) supported this hypothesis by showing that feeding by the generalist *H. zea* induced more phenolics, amino acids, and other defense-related compounds, whereas the specialist *M. sexta* primarily caused accumulation of metabolites such as Glu and Gln that associated with carbon and nitrogen transport. As the sample size consists of only two species, there clearly are other possible explanations for this observation (e.g. differing amounts of leaf area consumed by the two herbivores). Nevertheless, these results are consistent with the hypothesis that, in response to specialist herbivores, plants should modify their growth rate and change resource allocation instead of increasing chemical defenses that are predicted to have less impact. In another study on tomato, *M. sexta* regurgitant treatment was shown to decrease plant growth and chlorophyll content, but accelerate regrowth after defoliation, a collection of responses resembling a resource sequestration and herbivore tolerance strategy (Korpita et al., 2014).

There are, however, counterexamples to the hypothesis that responses of plant primary metabolism to specialist and generalist herbivores should be different. The duration of feeding (6 or 24 h) had a greater effect than the herbivore species when measuring gene expression induced by the specialist cabbage butterfly and the generalist beet armyworm feeding on Arabidopsis (Appel et al., 2014; Fig. 1B). Similarly, comparison of cabbage butterfly with the generalist Egyptian cotton worm showed almost identical induced gene expression patterns, including genes that are involved in primary metabolism (Reymond et al., 2004).

**Duration of Infestation**

The time of exposure to insect infestation, and by extension the amount of tissue damage that occurs during feeding, is another parameter that significantly affects plant metabolic responses (Frost et al., 2008; Bruce, 2015). Metabolites and energy can be allocated more efficiently if there is not only recognition of herbivory, but also reprogramming over time (Mithöfer and Boland, 2012). Within an hour after exposure to herbivore feeding, expression of genes encoding diverse plant metabolic pathways is altered (Fürstenberg-Hägg et al., 2013). However, most published research on plant responses to herbivory has been focused on longer time periods ranging from 6 hours to several days after the start of infestation. Coppola et al. (2013) performed transcriptomic and proteomic analyses of tomato leaves infested with potato aphids (*Macrosiphum euphorbiae*) for 1, 2, and 4 d. Comparison of significantly altered transcripts showed limited overlap; expression of only three genes was significantly altered at all three measurement times. Appel et al. (2014) found that the duration of caterpillar infestation had a greater effect on primary metabolism than the degree of herbivore specialization or even the tissue being assayed (local versus systemic; Fig. 1B). Given the dynamic changes in plant metabolism that occur during insect feeding, any conclusion about changes in plant primary metabolism in response to insect feeding must be tempered with the statement “at this particular time point.”

**Insect Secretions**

Plants can recognize insect herbivores by perceiving so-called herbivore-associated molecular patterns (Heil, 2009), characteristic changes in the plant metabolite profile that can result from the addition of insect-derived compounds, modification of plant metabolites by insect enzymes, or changes in the abundance of endogenous plant metabolites (e.g. the accumulation of cell wall fragments due to damage from chewing herbivores). Specific metabolites that trigger plant defenses have been found in the saliva of both lepidopteran and orthopteran herbivores (Alborn et al., 1997, 2000, 2007). In *N. attenuata*, insect-derived fatty acid-amino acid conjugates are perceived by a protein that acts as a suppressor of abscisic acid catabolism (Dinh et al., 2013). As abscisic acid regulates free amino acid accumulation in plants (Nambara et al., 1998), this provides a direct link between herbivore-derived elicitors and primary metabolism. Species-specific differences in the metabolites secreted by lepidopteran herbivores are thus likely to affect the types of changes that are induced in plant primary metabolism.

In contrast to chewing insects, most of the reported functional molecules in aphid saliva are proteins that are secreted into the phloem (Tjallingii and Esch, 1993; Moreno et al., 2011; Ammar and Hall, 2012). Several proteomic studies have identified potential effectors in aphid saliva (Harmel et al., 2008; Carolan et al., 2009;
Rao et al., 2013), and specific proteins have been reported to affect aphid performance on host plants (Bos et al., 2010; Elzinga et al., 2014). Although there are clearly differences in the salivary proteomes of different aphid species, it is not yet known whether this variation causes differences in plant primary metabolism, such as those that are observed when the specialist cabbage aphid and the generalist green peach aphid are feeding from Arabidopsis (Fig. 1).

In addition to salivary components, waste products that are secreted by insects onto host plant leaves likely influence plant primary metabolism. Aphids and other Hemiptera secrete sugar-rich honeydew that contains abundant trehalose (Hodge et al., 2013). Trehalose and trehalose-6-phosphate are important plant-signaling molecules regulating the relative allocation of carbon into starch and sugar (Cortina and Culiáñez-Macià, 2005), as well as plant growth and development (Satoh-Nagasawa et al., 2006). As the concentration of trehalose in aphid honeydew is higher than what is normally found in plants, it may influence sugar metabolism in the leaves from which the aphids are feeding. Research involving both Arabidopsis and tomato genes suggested that TREHALOSE PHOSPHATE SYNTHASE11 activity regulates host defense during infestation with green peach aphid by providing a threshold level of signaling trehalose (Singh et al., 2011; Singh and Shah, 2012). However, whether plants regulate trehalose signaling through an internal pool or in response to exogenous addition from insect honeydew remains an open question (Lunn et al., 2014).

CONCLUSION

Insect herbivory clearly has profound effects on plant primary metabolism. However, the specific costs and benefits are not yet fully defined. Depending on factors such as the host plant species, the tissue being infested, the feeding style of the particular insect herbivore, and the duration of insect feeding, different plant defensive strategies may provide optimal fitness gains. The situation is further complicated by the fact that any observed changes in plant primary metabolism may result from the ability of some insect herbivores to manipulate plant primary metabolism for their own benefit. Thus, it is probably not possible to make universal statements about the regulation of primary metabolism during insect herbivory, but rather one must consider each plant-insect interaction individually to determine how plants are responding in a particular situation and what fitness benefits these responses may provide.

FUTURE PERSPECTIVES

In this review, we have outlined hypotheses regarding changes in plant primary metabolism that should occur in response to insect feeding to promote plant fitness. We have compiled experimental evidence that supports or refutes specific hypotheses. Because herbivore-induced metabolic changes are influenced by a large number of variables, we have emphasized the importance of accounting for these intrinsic and environmental factors in a more comprehensive framework. One of the major challenges for drawing overarching conclusions from these studies was the inconsistency in experimental conditions and the resulting poor comparability of results from different studies. Hence, experiments that are more specifically designed to evaluate how different plant and insect characteristics and environmental factors influence herbivore-induced changes in plant metabolism are required for answering this complex and important question. Additionally, most published studies describe investigation of plant responses to herbivory using either transcriptomic or metabolomic approaches, but rarely both at the same time. Although both approaches generate large amounts of data, they are also inherently limited. For example, Castrillon-Arbelaez et al. (2012) found little correlation between transcript abundance and enzymatic activities when studying herbivore-induced changes in carbohydrate metabolism. Similarly, Coppola et al. (2013), from among a thousand differentially expressed transcripts and 87 differentially abundant proteins, found only three transcript-protein matches in herbivore-attacked tomato leaves. These observations highlight the role of posttranscriptional effects in herbivore-induced responses in plants, especially when sampling after a short period of infestation. On the other hand, metabolite profiling of the static pool in tissues at different time points does not differentiate the dynamics of different metabolic pathways that may result in a similar accumulation or depletion of certain metabolites. An observed accumulation of free amino acids, for example, gives limited information about whether they are a result of reallocation from systemic tissues or local protein degradation. Therefore, it is important to combine transcriptomic, proteomic, and metabolomic approaches to devise testable hypotheses and draw valid conclusions.

There also are notable gaps in our understanding of plant primary metabolism during insect feeding. Lipids, for instance, are an important group of primary metabolites that remain comparatively uninvestigated. Whereas many lipids serve important storage and structural purposes, others are precursors of plant defense signaling molecules such as jasmonic acid. However, little is known about the dynamic changes in the lipid metabolism of plants facing herbivore attack. Pioneering work has shown remarkable diversity in the plant lipidome, which can be restructured during abiotic stress in a genotype-specific manner (Degenkolbe et al., 2012). The relatively few lipidomic studies of herbivore infestation (e.g. measurement of maize lipid responses to Egyptian cotton worm feeding; Marti et al., 2013) demonstrate significant induced responses. Thus, further research is warranted to explore the role of endogenous plant lipids in plant-herbivore interactions.
In another frontier, exciting progress has been made in elucidating the signaling pathways that trigger and regulate herbivore-induced changes in plant primary metabolism. Lu et al. (2015), for example, found that herbivore-induced carbohydrate sequestration can still occur in the roots of jasmonate-signaling-deficient rice mutants, whereas reallocation of carbohydrates toward herbivore-attacked leaves and away from roots in *N. attenuata* is modulated by both jasmonate and auxin signaling (Machado et al., 2013, 2015). Following this same line of investigation, concomitant with the incorporation of less-studied signaling networks, one would expect the eventual union of defense signaling networks that control herbivore-induced changes in both primary and secondary metabolism.

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