Roles of Thermal Adaptation and Chemical Ecology in *Liriomyza* Distribution and Control

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Abstract

Many *Liriomyza* species are pests of agricultural and ornamental plants. In the past two decades, the occurrence and distribution of certain *Liriomyza* species have changed dramatically, leading to an extensive body of research papers. First, we review the association of thermal tolerance with population dynamics, geographic distribution, and species displacement. Differences in thermal tolerances between species result in their differential geographic locations and overwintering ranges. Displacements among *Liriomyza* species are associated with their temperature adaptation. We examine the chemical linkage of plants, *Liriomyza*, and their parasitoids. Chemical compounds from host and nonhost plants mediate the behavior of *Liriomyza* and their parasitoids. *Liriomyza* and their parasitoids use chemical cues to locate their hosts. Induced compounds can be used as attractants of parasitoids or repellents of *Liriomyza*. Thus, understanding the thermal tolerances and chemical ecology of *Liriomyza* may enable researchers to predict geographic distribution and to develop novel control strategies.

INTRODUCTION

Leafminers: insects that mine inside plant tissues

Thermal stress: reaction of organisms to temperature that falls outside their normal living conditions

More than 330 *Liriomyza* species have been described to date, and many polyphagous species are important pests of agricultural and ornamental plants. It has been more than twenty years since Parrella (65) published a review article on the biology of *Liriomyza* species. In the past two decades, the occurrence and distribution of certain *Liriomyza* species have changed dramatically. Numerous research projects have been conducted worldwide owing to the economic importance of some *Liriomyza* species, and an extensive body of research papers has been published. Here we review two key aspects, *Liriomyza* biology and ecology. Thermal tolerance and chemical ecology are directly related to the forecast and management of *Liriomyza* pests, and studies in these areas have not been reviewed to date.

ADAPTATION OF *LIRIOMYZA* TO THERMAL STRESS

Among the economically important *Liriomyza* species, *L. sativae* Blanchard, *L. trifolii* (Burgess), and *L. huidobrensis* (Blanchard) have the most cosmopolitan distributions (63, 65, 78, 89, 99). All three are tropical or temperate species native to South and North America (73, 76). They have a history of rapid dispersal and colonization of new environments, often in association with global trade and transportation (16, 49, 63, 70, 73). Several events of species displacement between these leafminers have been reported during the history of their expansion (19, 69, 70). Generally, the distribution and abundance of many polyphagous insect species appear to be directly restricted by their own ecophysiological adaptation to climatic stresses, largely independent of their host plant (5, 38).

Thermal stress tolerance, particularly cold stress tolerance, is essential for the completion of the life cycle, successful overwintering, and habitat exploration of insects (40, 57). This appears to be the case for *Liriomyza* species, as several studies have shown that commonly sympatric *Liriomyza* species have locally variable distributions that are strongly influenced within a given region by temperature extremes (14, 68, 99). Furthermore, population abundance of the coexisting *Liriomyza* species alternates with seasons (typically between cold springs and hot summers) (14, 99). On the other hand, recent comparative studies between *L. sativae* and *L. huidobrensis* revealed a close correlation between their ability to adapt to thermal stresses and the described phenomenon of species distribution and abundance (13, 18). Therefore, we first review the characteristics of thermal stress tolerance of key *Liriomyza* species in an effort to describe the diverse alternative cold survival strategies they have evolved to adapt to various climatic conditions for dispersal and colonization. Molecular mechanisms for the development of thermal stress tolerance are then discussed, followed by potential practical applications of this knowledge.

Thermal Stress Tolerance

In nature, insects may be subject to injury due to low temperature and freezing. In response, insects evolved several ways to cope with altered temperature conditions, including processes related to the regulation of supercooling, ice nucleation, freezing, cold hardening, and cryoprotection.

Extreme temperature survival and the supercooling point. Thermal stress tolerance of the leafminers without any induction pretreatment (basal thermal stress tolerance) varies in different developmental stages. The ability of eggs and larvae of *L. sativae* to survive in chrysanthemum was examined during cold storage (95). The larvae are more susceptible to cold injury than eggs are. However, *Liriomyza* usually overwinter in the puparial stage (65). Survival data of laboratory-reared populations of *L. sativae* and *L. huidobrensis* indicate that most puparia can survive long-term exposures to temperatures above 0°C (13, 101). However, some puparia can develop normally even after exposure to subzero temperatures for a few days

(13, 83, 101). The lethal time leading to 50% survival (LT_{50}) during cold exposure increases with age of puparia for *L. chinensis* (83). Puparia of *L. huidobrensis* and *L. sativae* can tolerate high temperatures up to 43°C and 45°C for 4 h, respectively (12). However, 1-day-old adults of *L. huidobrensis* had only about 50% survival when exposed to 41°C for 1 h, and 45% survival when exposed to –12°C for 4 h (43). Obviously, the puparial stage is the most resistant to cold and heat stress. This is considered an adaptive life cycle strategy because the pupae are frequently exposed to ambient temperature extremes outside leaves in summer or during overwintering, whereas eggs and larvae inhabit and feed inside leaves (65).

Basal thermal stress tolerance varies greatly among *Liriomyza* species. The LT_{50} for 4-day-old puparia of *L. chinensis* exposed to 0°C is 52 days, compared with ≈9 days for both *L. sativae* and *L. huidobrensis*, indicating that *L. chinensis* is the most cold-tolerant species examined so far (13, 83, 101). The LT_{50} of *L. sativae* puparia is 2 days at –5°C and <1 h at –10°C (101). *L. huidobrensis* is substantially more cold tolerant than *L. sativae*, with an LT_{50} of 5 days at –5°C and 5 h at –10°C (13).

The supercooling point (SCP) is the crystallization temperature of cells, and it has been used as a measurement of low lethal temperature for many insects (55). Puparia from a laboratory-reared population of *L. sativae* have an average SCP of –11°C (14). Puparia of *L. huidobrensis* have a SCP of –20.9°C, much lower than that of *L. sativae* (13). Therefore, the puparia may tolerate subzero temperatures by supercooling or other related physiological mechanisms to keep their body fluids at temperatures well below their melting point (14).

The interspecific differences in thermal stress tolerance between the *L. sativae* and *L. huidobrensis* are consistent with the field observations that *L. huidobrensis* is more adapted to cool climates than *L. sativae* is, thereby explaining (at least in part) their differential distributions in China (13, 14). Because both *Liriomyza* species originally evolved as tropical or temperate species (77), we speculate that their ancestors probably had relatively high heat resistance and that the subsequent evolution of differential resistance to colder temperatures occurred more recently with their spread to higher-latitude, colder regions. This hypothesis is consistent with proposed explanations of cold tolerance development in *Drosophila* (40).

Supercooling point (SCP): the crystallization temperature of cells; used as a measurement of low lethal temperature for many organisms

Cold tolerance: the survival ability of organisms under low temperature

Inducible thermal tolerance: acclimation and rapid cold hardening. In China, as in many countries, greenhouses are opened during the day but closed at night. As a result, leafminers in greenhouses are frequently exposed to cold air in the spring and fall. Thus, the insects could acquire enhanced resistance to cold exposure by cold acclimation (23) or rapid cold hardening (20). Leafminers reared under both laboratory and field conditions have demonstrated enhanced cold tolerance in response to prechilling at 5°C and 10°C (15, 16). van der Linden (88) investigated the ability of *L. bryoniae* and *L. huidobrensis* puparia to overwinter outdoors and found that the survival of overwintering puparia was lower than the survival of the laboratory-reared puparia. However, an acclimation regime including prechilling field populations of *L. sativae* increased their survival much more than that observed for laboratory populations, suggesting a more active mechanism triggering cold resistance in field populations (17).

Both rapid cold hardening and temperature acclimation are responses to low temperature stress, reflecting processes likely associated with different underlying mechanisms (22, 40). Whereas cold acclimation induces cold hardening by prolonged exposure to low temperature for days, weeks, or even months (54, 55), rapid cold hardening can be induced by a brief exposure (even minutes) to more moderate temperatures (20, 93). The inducible heat resistance of *L. huidobrensis* adults was greatly elevated by a 4-h exposure to 32°C or 35°C. However, this high-temperature acclimation did not improve cold tolerance. Thus, there does not appear to be cross-resistance in the thermal tolerance of this species (44). However, puparia from field populations of *L. sativae* demonstrated enhanced cold tolerance after pretreatment at 39°C for 1 h (16), suggesting a range of rather plastic responses in this species.

Cold survival strategies. Generally, insects respond to low temperature in one of two ways. They either enter into a dormant state (diapause) or remain active (54). *Liriomyza* species usually survive winter in diapause, with the exception of *L. trifolii* in Italy (65), which tolerates cold or freezing by physiologically developing cold resistance or the supercooling of body fluids. A low supercooling capacity enables puparia to tolerate subzero temperatures. For example, a 1-day-old puparium of *L. huidobrensis* has an LT_{50} of 4.8 days at −5°C and survives only for a few hours at −10°C (13). However, no puparia of *L. sativae* and *L. huidobrensis* survive temperatures below their SCPs (13, 101). Therefore, both *L. sativae* and *L. huidobrensis* are freeze susceptible and cannot survive intracellular ice formation. This cold tolerance strategy involving their supercooling capacity has played an important role in their long-term cold stress survival and overwintering in a wide range of climatic zones (13, 18).

Most *Liriomyza* overwinter outdoors in southern tropical or subtropical regions (77). It is also commonly believed that freeze-susceptible insects cannot expand northward or overwinter successfully in the field beyond their northern overwintering range limit because they cannot survive harsh winters (14, 48, 58). However, *Liriomyza* species have dispersed far beyond their apparent overwintering range limit, and in much higher-latitude regions with severe winter conditions, by opportunistic exploitation of protected microhabitats (15, 83, 101). In fact, *Liriomyza* have become established in protected environments year round (16, 17).

Studies on *L. sativae* and *L. huidobrensis* showed that, although some field populations in greenhouses were less cold resistant than other field or laboratory-reared populations, they have developed a more active response to the same prechilling stimulus that triggers their cryo-protecting physiology. This characteristic may function as an important mechanism to ensure their maximum survival under sudden, severe cold stress in the field (15, 16).

Species Adaptations to Natural Thermal Stress

Geographic comparisons can provide information where trait patterns are adapative. However, the different patterns among populations also depend on several factors, including stress resistance assays, seasons, and local habitats occupied by populations.

Geographic variation in supercooling capacity and cold survival ability. *L. sativae* and *L. huidobrensis* are adapted to environments ranging from temperate to tropical (70, 77). This adaptation is reflected by variation in their cold tolerance along a latitudinal gradient within their range of distribution. Working with geographically distinct populations of *L. sativae* and *L. huidobrensis*, Chen & Kang (15) found that low-temperature survival increased significantly with increasing latitude. For populations of *L. huidobrensis* overwintering in fields, cold tolerance increased substantially with latitude as measured by the LT_{50} at −5°C; a similar increase was observed for populations of *L. sativae* (16).

Field populations of *Liriomyza* appear to enhance their cold tolerance by depressing the SCP of the puparial stage. For instance, the SCP of the puparia of *L. huidobrensis* from the southernmost population (latitude 18°N) was 3.6°C higher than that from the northernmost population (latitude 34°N) within their overwintering range (15). For the southern populations of *L. sativae*, the mean SCP of puparia was substantially depressed with decreasing latitude (16). These results also suggest that latitudinal variation in SCPs of puparia matched the variation patterns for cold resistance in the southern populations. Further investigation into SCP variation of *L. huidobrensis* populations revealed that the SCP values exhibit a bimodal distribution in the geographic populations and the distribution was divided into high-group individuals and low-group individuals based on the observed breaking point of –17.5°C; the mean SCP of a population reflected the frequency ratio of individuals with high-group SCPs to individuals with low-group SCPs (16). The same pattern of geographic variation in cold tolerance was observed in cold-susceptible *L. huidobrensis* and *L. sativae* in China (15), although *L. huidobrensis* is a more cold-hardy vegetable and flower pest and therefore has a more northern overwintering limit than *L. sativae* does. According to the results by Chen & Kang (16), the two groups of individuals were divided based on the SCP of puparium. The SCP of the high group is significantly higher than that of the low group. Presumably, the variation in SCP of individuals may result from physiological regulations. SCP is a character typical of and varying among different species. But SCP is plastic and changes after acclimation.

Factors affecting the variation pattern of cold tolerance. Cold acclimation is an important factor contributing to enhanced survival ability of *Liriomyza* populations. Acclimation of *L. sativae* and *L. huidobrensis* greatly enhances cold resistance. Although the chronic and acute assays of cold resistance may have different physiological mechanisms (58), the pattern of variation in cold resistance for the southern populations has been consistent and appears to be physiologically stable and independent of the form of exposure (15, 16). Furthermore, *L. huidobrensis* populations show a consistent latitudinal pattern of cold tolerance over multiple seasons (in spring/postwinter, summer, and autumn/prewinter) during several years of investigations (15). Studies of the two species also suggested that the patterns of variation in cold tolerance are seasonally independent for populations within their natural range (16, 17). Another important ecological factor, the availability of greenhouse habitats, has considerable impact on the development of cold tolerance, but this has been largely ignored by most researchers (16).

Greenhouse habitats and elimination of development of cold tolerance. Leafminer populations have survived harsh winter conditions and have caused significant economic losses beyond their northern overwintering limit by inhabiting and developing in sheltered places such as thermally buffered greenhouses (19, 83). The mild microhabitats provided by the greenhouses may limit and even eliminate the development of cold resistance of *Liriomyza* (16). For *L. sativae* and *L. huidobrensis* populations, these northern greenhouse populations are always intermediate in cold hardiness between the southernmost outdoor populations and the marginal populations immediately adjacent to the northernmost overwintering border (15, 16). Furthermore, the relative cold resistance of the northern greenhouse populations fluctuates with seasons. Therefore, the pattern of variation in cold tolerance with latitude differs for *Liriomyza* populations on different sides of the northern overwintering boundary (15–17). Because leafminers have a high rate of fecundity and overlapping generations, they have the potential to quickly colonize the surrounding plants, resulting in high-density infestations as well as a fairly rapid increase in frequency of alleles for cold-susceptible genes (33, 39). Thus, greenhouse habitats can limit gene flow between cold-tolerant and cold-susceptible individuals and reduce cold tolerance even at high latitudes (16, 17, 39).

Hsp: heat shock protein

Molecular Mechanisms for Adaptation to Thermal Stress Tolerance

Hardening to high or low temperatures induces the heat shock or stress response, leading to the expression of molecular chaperones (heat shock proteins, Hsps) and antioxidants (31, 40). Hsps may be one of the most conserved and important proteins involved in temperature responses in *Drosophila* and many other organisms (31).

***hsp* gene expression and its role in thermal stress tolerance.** A number of candidate genes have been related to variation in thermal tolerance. Huang & Kang (44) identified and cloned *hsp90*, *hsp70*, *hsp60*, and *hsp40* and small *hsps* in *L. huidobrensis* and *L. sativae*. The coding regions of *Liriomyza hsps* are highly conserved. *hsp90*, *hsp70*, *hsp60*, and *hsp40* amino acid sequences had >90% identity between the two species and 60%–85% identity to *D. melanogaster*. The amino acid identity of small Hsps is 73% between the two species and is higher than those between leafminers and other insects. This high level of conservation of genes suggests that heat shock genes have been important throughout evolutionary time. However, the 5′ UTRs (untranslated regions) of these heat shock genes are variable except for *hsp90*, in which only two nucleic acids differ between the two species. Generally, the numbers of TATA-box-like elements and A/T-rich insertion/deletions are different between the two species. For example, the TATA-box-like elements are more abundant in *L. huidobrensis* than in *L. sativae* (44). Considering the functional importance of these regulatory elements in other organisms, such variation in the regulatory region may be responsible for shaping specific patterns of gene expression between the two leafminers (44, 80).

The expression profiles of Hsps of *L. huidobrensis* and *L. sativa* at the mRNA level were in agreement with expression profiles found at the protein level (44). The five *hsps* in puparia could not be induced by 1 h pretreatment at temperatures ranging from 2.5°C to 27.5°C. Most *hsps* were significantly upregulated when puparia were exposed to either higher or lower temperature stress, with the exception of *hsp60*, which did not respond to cold stress. The temperatures for onset (T_{on}) or maximal (T_{max}) induction of *hsp* expression in *L. huidobrensis* were generally 2.5°C–10°C lower than those in *L. sativae* whenever they were induced by cold or heat stress. These studies suggest that the T_{on} (or T_{max}) of *hsps* can explain the differences in temperature tolerances of the two species (44).

Trade-offs between thermal hardening, gene expression, and fitness. Thermal hardening has no lethal impact on insects but does induce changes in gene expression and in physiological response (43). Mild temperature hardening of adult *L. huidobrensis* when exposed to 10°C, 32°C, and 35°C has a beneficial impact on survival. These exposures increased adult heat resistance but did not improve cold tolerance of adults. However, such hardening processes dramatically reduced both adult feeding and fecundity. The deleterious effect on fecundity was likely the result of direct cessation of oviposition during the period of stress, and no extensional effect was observed on egg hatching, larva viability, eclosion of puparia, or sex ratio (43).

hsp gene expression may underlie the trade-offs between thermal tolerances and fitness costs in *L. huidobrensis*. The mRNA levels of *hsp70* and *hsp20* significantly increased upon thermal hardening. Studies on *D. melanogaster* showed that high levels of *hsp70* decrease or even retard growth and cell division and reduce reproduction (31, 40). Therefore, mild temperature hardening improves the thermotolerance of *L. huidobrensis* at the cost of impairment of fecundity, and the induced expression of *hsp70* and *hsp20* may be one of the important reasons for this consequence (43).

Practical Applications

Research on thermal stress tolerance has led to many practical applications around the world in areas of pest management, quarantine treatment, and cryopreservation, as well as implications for natural enemy introduction and beneficial insect culture.

Distribution prediction and phenological modeling. Different *Liriomyza* species can exist in a habitat or on the same cultivated host. For example, in Japan *L. sativae* can coexist with *L. trifolii* and *L. bryoniae* on tomato plants (3). However, the perpetuation of coexistence will change as new congeneric species invade and compete with existing species or after species disperse to new habitats (69, 70). *L. huidobrensis* is indigenous to the cooler, mostly highland areas of Latin America (77). *L. huidobrensis* became most widely distributed, particularly serious in highland vegetables, compared with *L. sativae* in Indonesia. *L. sativae* caused extensive damage in lowland areas on the north coast of West Java (68). These two species also have had distinctive distributions in southern and central China since their first outbreak in the early 1990s (14, 49). All *L. huidobrensis* populations are predominant in the southwest region, where the climate is cool, but *L. sativae* populations were seasonally abundant prior to the invasion of *L. huidobrensis*. In contrast, *L. sativae* is found only in the southeast region, where the climate is warm or hot in most seasons, and no *L. huidobrensis* is found in southern coastal provinces (14). Thus, *L. huidobrensis* is a more temperate species than *L. sativae* is (77). Similar events of species displacement were also reported in other countries and habitats (3, 14, 68, 70). For example, displacement of *L. sativae* by other vegetable leafminers such as *L. huidobrensis*, *L. trifolii*, or *L. bryoniae* was increasingly recognized and reported in Asia and South America. Comparative studies on *L. sativae* and *L. huidobrensis* showed that these two species had developed differential thermal stress tolerance in the history of their expansion, which is an adaptive trait to cope with varied local climatic stress (18). The differential thermal tolerance of the two species explained the present status of distribution and species replacement in investigated regions (68–70).

The correlation between thermal stress tolerance and species distribution also suggested that the ability to survive at low temperatures is a critical factor determining the range of distribution of *Liriomyza* and particularly their successful overwintering in high latitudes. This range boundary is important for *Liriomyza* because populations of the more temperate species will risk freezing to death while expanding north beyond their thermal limit (17). For instance, although *L. munda* occurs on vegetable and ornamental plants throughout the southern United States, it does not normally overwinter as far north as Maryland (95).

On the basis of low-temperature survival ability, the cold acclimation effect on survival, and field investigations, Chen & Kang (15–17) have proposed that the overwintering range limits under natural conditions are the isotherms of the minimum mean temperature in the coldest month of the year, i.e., –2°C isotherm for *L. sativae* and –5°C isotherm for *L. huidobrensis* in January in China. Populations of *Liriomyza* species could not survive the cold extremes in open fields beyond the northern overwintering boundary solely by enhancing their cold survival ability. The induction temperature, T_{on}, for *hsp* gene expression was highly consistent with the temperature limits of the northern boundary of the two species. These results also suggest the ecological and biological significance of the overwintering boundary for cold-susceptible leafminers (16–18) and predict a northward expansion of the distribution boundaries with global warming (5). The rapid rise in minimum winter temperatures, milder winters due to regional warming, and increased resistance to cold, along with the availability of protected microhabitats, have likely contributed to the recent expansion of several leafminer species (14, 17).

High or low temperatures influence not only the survivorship and overwintering activity of *Liriomyza*, but also the developmental rate/time and fecundity (53, 65). The impact of variable temperatures has been incorporated into several phenological models to predict population dynamics of *Liriomyza* species (13, 36, 53, 65). Although currently used primarily by researchers, these models may have practical applications if adopted by growers, cooperatives, extension personnel, and others who measure initial population densities to provide a biofix.

Quarantine treatments. Cold tolerance limits the distribution of leafminers in the temperate areas under natural conditions; however, they could be pests in greenhouse conditions. Therefore, quarantine is an effective method to prevent *Liriomyza* species from establishing in new areas (49). Cold storage of infested plants has been recommended for killing *Liriomyza* eggs and larvae (94). This method has been used to prevent leafminers from dispersal through trade and transportation. Recent studies on SCPs and mortality under cold conditions of *Liriomyza* species provide reliable information that can be used in quarantine (13, 15, 17, 101).

Natural enemy introduction. Temperature not only affects the development of *Liriomyza*, but also influences performance of their parasitoids (49, 65). Generally, *Liriomyza* species cannot successfully overwinter under natural conditions in the temperate areas (49). The natural enemies should coincide with the distribution of their prey or hosts, and those under consideration should have thermal requirements similar to that of their host. The natural enemies could be introduced from a wide range of sources if they are used as biological control agents under greenhouse conditions.

Greenhouse management strategies. Management strategies can be employed specifically against *Liriomyza* pests under greenhouse conditions that act as reservoirs in areas above the northernmost overwintering latitude for field populations (57). The inability of greenhouse populations of some *Liriomyza* species to adjust their SCPs, and their comparative intolerance of cold temperatures, suggests that opening greenhouses between crops during cold temperatures (–5°C to –10°C for as few as 5 days) would likely eliminate populations of *L. sativae*. Populations of *L. huidobrensis* would require a longer duration. This approach has the advantage of providing suppression without pesticides, but it may be problematic for those greenhouse operations that stagger plantings within individual greenhouse units. Nonetheless, eliminating the populations serving as reservoirs would result in substantial savings not just for the subsequent greenhouse plantings, but for warm-season plantings in adjacent fields.

CHEMICAL ECOLOGY OF *LIRIOMYZA* SPECIES, HOST PLANTS, AND PARASITOIDS

Studies of the chemical ecology of host-leafminer-parasitoid interactions have made significant progress in recent years (97). This work has been based on the concept that to locate host plants successfully, insects use signals from plants, including visual, chemical, acoustic, gustatory, and touch signals (8, 91). In this process, insects exhibit a sequence of behavioral responses to a variety of cues associated with host and nonhost plants. To date, the literature indicates that chemical information from plants plays a critical role in host selection (11, 25, 82, 87, 90, 97, 98, 102, 103).

The chemical compounds produced by plants can be classified according to their effect on the host-location behavior of insects into categories such as attractants, repellents, feeding and oviposition stimulants, and deterrents (8). These chemicals can be either constitutive or inducible. They play important roles in host selection by leafminers and at the same time in host plant defense against the leafminers.

Chemically Mediated Behavior of the Adult *Liriomyza*

Host selection by *Liriomyza* species differs from many other herbivorous insects because the larvae of leafminers are unable to move between plants, and the choice of host is made solely by adult females (65). This fact has resulted in numerous studies on the chemicals that play important roles in mediating the behavior of the adult leafminers.

Chemotactile and olfactory cues: attractants and repellents. To date, no sex pheromone used by *Liriomyza* for intraspecific communication has been reported (65). Therefore, it appears likely that these leafminers employ plant volatiles for host location and mating. For example, both sexes of *L. sativae* positively respond to the odors of bean leaves (103, 104). Moreover, adult *L. sativae* respond positively to headspace odors from host plants (kidney beans, cucumbers, and tomatoes) but negatively to odors from nonhost plants (creeper and Chinese rose) (104). Although a large number of volatile compounds have been identified from various host and nonhost plants of leafminers (97), the behavioral responses of leafminers to key blends of compounds, and even some specific chemicals induced by insect damage, are not well understood. However, there is evidence that specific ratios of ubiquitous plant compounds play important roles in the host selection process (11). Adult leafminers (across species) provide an excellent system for studying behavioral responses to host volatiles, and the opportunity exists for using these insects to investigate the underlying physiological mechanisms responsible for host location behaviors.

Feeding and oviposition stimulants and deterrents. Although feeding and oviposition stimulants of leafminers have not been studied in detail, chemicals acting as deterrents have been identified from several host plants. Hawthorne et al. (37) observed that oviposition and adult feeding of *L. trifolii* on wild tomato [*Lycopersicon pennellii* Corr. (D'Arcy)] and its F_1 hybrid with tomato (*L. esculentum* Mill.) were significantly less than that on tomato. They isolated and identified trichome-borne acylsugars from wild tomatoes and reported that application of purified acylglucoses on leaflets of the wild tomato plant deterred adult feeding and oviposition. Recently, several similar studies identified oviposition deterrents of leafminers from various plants. Dekebo et al. (24) isolated three nitrogenous compounds from the leaves of sweet pepper (*Capsicum annuum* L.) and demonstrated that these compounds had significant oviposition inhibition for adult *L. trifolii*. Mekuria et al. (60, 61) identified cucurbitane glucosides and triterpenoids from the cucurbitaceous plant *Momordica charantia* L. and observed significant oviposition deterrence to adult *L. trifolii* when these compounds were applied on kidney bean (*Phaseolus vulgaris* L.) leaves. They also identified oviposition deterrents from peppers, including phytol and luteolin (50, 51). These deterrents were identified exclusively from studies with *L. trifolii*, and examination of the materials for deterrence effects on other *Liriomyza* species should be the subject of future research. Additional research should investigate the potential inclusion of these deterrent compounds in integrated pest management programs for leafminers.

Nutrition. Nutritional components in plants are important indicators of host plant quality for phytophagous insects, which demonstrably affect feeding, survival, and fecundity (4). For example, fertilizers generally increase foliar nutrients, and in turn those nutrients affect leafminers (30, 52, 56, 62). Most studies have concluded that leafminers perform better on leaves with higher nutrient contents, with a few exceptions. For instance, application of fertilizers that increased nitrogen in potato leaves increased survival of immature stages of *L. trifolii*, but survival decreased with increasing concentrations of potassium and phosphorus (30). However, Letourneau et al. (56) compared crop nitrogen and insect damage in organic versus conventional tomato fields and demonstrated that damage to tomato foliage did not increase with increased nitrogen content of the crop, and a weak negative correlation between tissue nitrogen and herbivores was detected. To date, most studies have focused on the effect of nutrients on immature development of leafminers. Minkenberg & Ottenheim (62) hypothesized that plant preference for leafminers was related to better performance of adult females on high-nitrogen plants than on low-nitrogen plants. Their research indicated that *L. trifolii* females responded to increased leaf nitrogen with significantly increased feeding and fecundity, longer oviposition periods, and higher feeding and oviposition rates. In leafminers, the behavioral responses of adults to different levels of foliar nutrients are important, and the responses of adult leafminers of other species to a wide range of foliar nutrients should be the subjects of additional research.

Plant defensive chemicals. Constitutive and induced plant defensive chemicals are critically important determinants of leafminer fitness. Constitutive chemicals are compounds expressed by plants regardless of insect presence. Induced chemicals are compounds that increase

JA: jasmonic acid

following plant stress resulting from insect, bacterial, or fungal attack. Constitutive chemicals have been used as indicators of resistance to leafminers in various plants or different cultivars. For instance, eight cruciferous vegetables could be classified as resistant, tolerant, or susceptible to *L. brassicae* on the basis of total glucosinolate content in general and sinigrin content in particular (2). This study showed that glucosinolate and sinigrin repelled adults, whereas gluconapin was an attractant.

Recently, induced plant resistance to leafminers has received much more attention because of both local and systemic plant effects (47, 79). For example, different subsets of the four proteins, proteinase inhibitor, polyphenol oxidase, peroxidase, and lipoxygenase, can be induced by *L. trifolii* (79). Moreover, feeding by *L. trifolii* induced local and systemic production of putative defensive proteins, i.e., chitinases, peroxidases, β-1,3-glucanases, and lysozymes, from tomato plants (46). Early infestations by other herbivores had negative systemic effects on leafminers owing to the defense provided by these chemicals in tomato foliage (46). However, not all induced compounds are toxic to leafminers. The linear furanocoumarins, which are toxic to most insects, bacteria, and fungi (26), are tolerated by *L. trifolii* adults and immatures even at high concentrations (84).

Plant resistance to herbivores can be induced by application of elicitors such as BTH [benzo (*1*,*2*,*3*) thiadiazole-7-carbothioic acid (*S*)-methyl ester], jasmonic acid (JA), or salicylic acid (SA). For example, BTH provided cross-resistance and significantly reduced the incidence of bacterial spot, early blight, leaf mold, and *Liriomyza* larval densities (46). Moreover, in a two-choice experiment, adult leafminers preferred untreated plants to BTH-treated plants, suggesting an induced chemistry that reduced feeding and oviposition of leafminers (46). An additional study demonstrated a significant control effect of JA application on celery in a field situation (10). Application of the elicitor apparently altered the volatile emissions from these plants, thereby affecting the preferences of adults.

Potential of Transgenic Plants for *Liriomyza* Suppression

Novel developments in molecular biology and genetic engineering provide opportunities for modifying plants for defense against *Liriomyza* species. Abdeen et al. (1) reported that leaf-specific overexpression of the potato PI-II (protease inhibitor I and protease inhibitor II) and carboxypeptidase inhibitors resulted in increased resistance to *Heliothis obsoleta* (F.) and *L. trifolii* larvae in homozygous tomato lines expressing high levels (>1% of the total soluble proteins) of the transgenes. Combined expression of defensive genes with different mechanisms of action, rather than combinations of inhibitors, may be more effective in overcoming the general adaptive responses in the insects (1). Codon-optimized *cry* genes encoding *Bacillus thuringiensis* (Bt) toxins from various *Bacillus* isolates have been transferred into several crops, including corn, rice, cotton, potato, tomato, soybean, and *Brassica* species, for control of agricultural insect pests (74). Because *L. trifolii* is a nontarget pest, it is not surprising that no difference in leaf damage has been found between the nontransgenic hybrid and the transgenic hybrid with the Bt *cry1Ac* gene (74). With the increased ease of creating transgenic plants, the opportunity now exists to determine the potential for dipteran-active Bt on the immature stages of *Liriomyza* species. Given the damage caused by these species, the potential is substantial for a pest management strategy that could replace foliar insecticide applications.

Tritrophic Interactions of Plants, *Liriomyza*, and Natural Enemies

The interactions between herbivores and their host plants, and between herbivores and their natural enemies, are best understood when considered within a tritrophic context (67). Vet & Dicke (90) and most studies afterward (25, 27, 82, 75, 87, 96, 97, 103) have revealed that among the various sources of chemical cues, plant volatiles play a vital role in host location of herbivores and their natural enemies. Recently, herbivore-induced plant volatiles (HIPVs) have received increasing attention because of their roles in plant indirect defenses as well as direct defenses. New developments in the interdisciplinary fields of biochemistry, physiology, and behavioral ecology have resulted in a growing knowledge of the chemical ecology of plants, *Liriomyza* species, and their associated parasitoids.

HIPV: herbivore-induced plant volatile

GLV: green leaf volatile

***Liriomyza* spp.–induced plant volatiles.** Dicke & Hilker (28) demonstrated that different types of attackers can evoke different plant responses owing to specific elicitors. Furthermore, these HIPVs can vary with plant species, plant genotype, and even with plant part (34, 71, 85). Induction of these chemicals also can vary with herbivore species or instar and potentially with environmental conditions (34, 35). At the same time, HIPVs are found in a wide range of plant taxa, induced by numerous herbivorous arthropods (85, 87). As a result, these compounds have been the focus of considerable research related to *Liriomyza* species.

Finidori-Logli et al. (32) identified 15 volatile components emitted from kidney bean damaged by *L. trifolii*. Of these compounds, only (*Z*)-3-hexen-1-ol, a common green leaf volatile (GLV), was induced by *Liriomyza* species (98). Dicke (27) suggested that differences between volatile blends are largest between plant species and smallest between plants of one species infested by different herbivores.

Subsequently, Wei et al. (98) identified a large number of volatiles in headspace samples from mechanically damaged beans and compared these with volatiles from plants damaged by *L. huidobrensis* or *L. sativae*. In a separate study, these authors investigated plant volatiles in headspace samples from other hosts and JA-treated nonhosts from seven plant families that were mechanically damaged or subjected to feeding by *L. huidobrensis* (97). The resulting volatiles could be divided into three major categories: GLVs, terpenoids, and oximes (**Figure 1**). The GLVs always refer to six-carbon chain length alcohols, aldehydes, and esters. Terpenoids include monoterpenes [e.g., linalool, (*E*)-β-ocimene], sesquiterpenes [e.g., (*E*,*E*)-α-farnesene, β-caryophyllene], and homoterpenes [(3*E*)-4,8-dimethyl-1,3,7-nonatriene and (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene]. Oximes are three- to four-carbon, nitrogen-containing compounds (**Figure 1**). In addition, there are many other volatile compounds, such as short-chain alkanes, alcohols, ketones, aldehydes, and methyl salicylate, in the headspace samples of these plants (7, 97, 98). No qualitative differences in volatile emissions were found between bean plants damaged by the two fly species; however, the amounts of several major compounds induced by *L. huidobrensis* damage were significantly higher than those from plants damaged by *L. sativae* (98). The differences in volatile emissions were related to the variable feeding habits of the two agromyzid species (98).

In a large-scale study on plant volatiles from various plant families, Wei et al. (97) demonstrated that undamaged plants released a few volatile compounds in relatively low concentrations in most plant families (including Fabaceae and Cucurbitaceae), whereas undamaged plants from Asteraceae and Solanaceae (species *Solanum lycopersicum* L.) produced many monoterpenes and sesquiterpenes in relatively high concentrations. A hierarchical cluster analysis with the association of the total amount of volatile compounds and the numbers of volatile compounds emitted from either mechanically damaged plants, *L. huidobrensis*–damaged host plants, or JA-treated nonhost plants showed that volatile profiles from mechanically damaged plants had a partly phylogenetic signal, whereas the inducible compounds of the insect-infested plants did not, even though the induced plant volatiles dominated most of the volatile blends of the host and nonhost plants of the leafminer pests (97). This is the first report to use volatile chemistry for a phylogenetic analysis of an angiosperm. These data suggest that the complex volatile chemistry present following *Liriomyza* feeding can provide important signals (cues) regarding

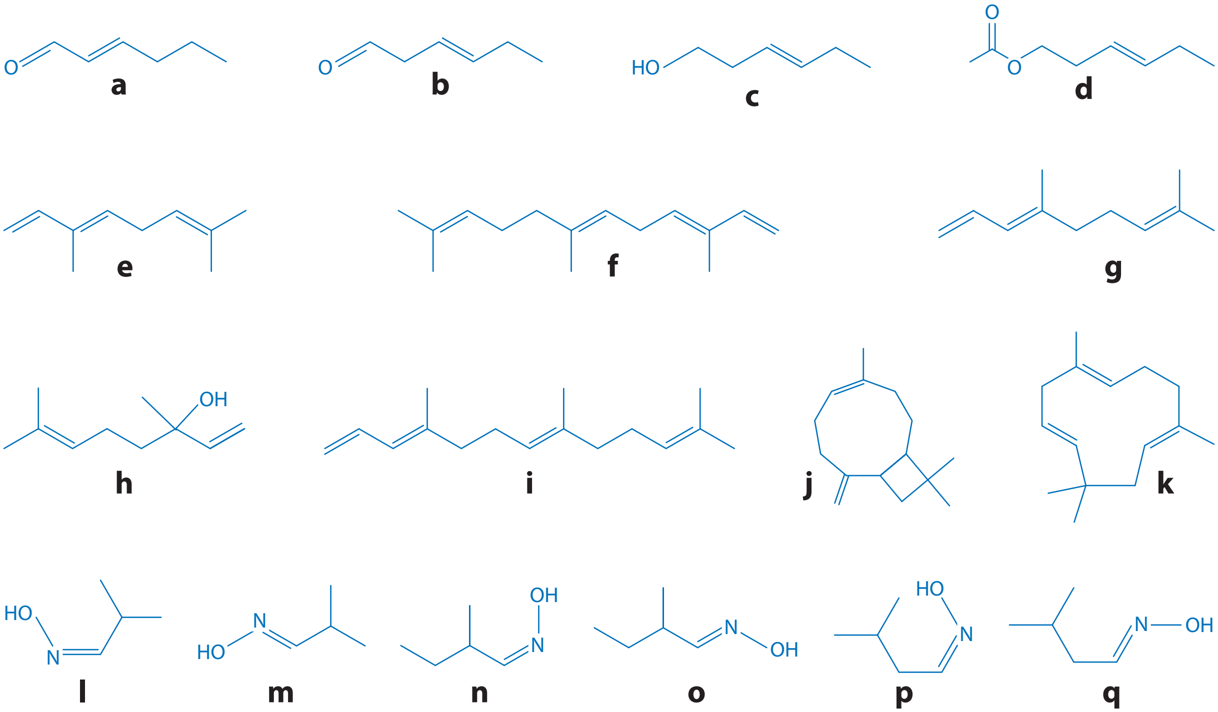

Figure 1

Chemical structures of the major inducible volatile compounds collected from headspace samples of plants either damaged mechanically or damaged by leafminers. Green leaf volatiles: (*a*) (*E*)-2-hexen-1-al; (*b*) (*Z*)-3-hexen-1-al; (*c*) (*Z*)-3-hexen-1-ol; (*d*) (*Z*)-3-hexenyl acetate. Terpenoids: (*e*) (*E*)-β-ocimene; (*f*) (*E*,*E*)-α-farnesene; (*g*) (3*E*)-4,8-dimethyl-1,3,7-nonatriene; (*h*) linalool; (*i*) (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene; (*j*) β-caryophyllene; (*k*) α-humulene. Oximes: (*l*) (*syn*)-2-methylpropanal oxime; (*m*) (*anti*)-2-methylpropanal oxime; (*n*) (*syn*)-2-methylbutanal oxime; (*o*) (*anti*)-2-methylbutanal oxime; (*p*) (*syn*)-3-methylbutanal oxime; (*q*) (*anti*)-3-methylbutanal oxime.

host location to their natural enemies and to other leafminers.

***Liriomyza* responses to plant odors.** Host-produced volatile cues play an important role in enabling phytophagous insects to recognize host plants at a distance (91). Olfactory receptor neurons on the insect antenna are the major receptors that perceive these volatile signals. The antenna ultrastructure of *L. sativae* has been studied using scanning electron microscopy, and four types of antennal sensilla (trichoid, basiconic, clavate, and grooved) have been discovered and measured on the funiculus (no sensilla were detected on arista) (102). The authors indicated that the sensilla diversity and distribution are similar between males and females. In addition, the types and distribution of sensilla in *L. sativae* proved highly consistent with those of other phytophagous flies, such as *Delia radicum* L. (72), *Hylemya antiqua* (Meigen) (41), and *Ceratitis capitata* (Wiedemann) (59). Therefore, there is a reasonable likelihood that other species of *Liriomyza* have similar sensilla.

Although the specific function of each type of sensillum is not known, their summed reactions to chemical stimuli can be measured by electroantennograms (EAGs) (92). The most distinct EAG responses of adult *L. sativae* were to plant odors from the most-suitable host plants (kidney bean and tomato) and to synthetic 6-C alcohols [hexan-1-ol and (*E*)-2-hexen-1-ol] (102–104). Intermediate responses were to less-suitable plants (cucumber, celery, and chrysanthemum) and to 6-C esters and aldehydes. Weak responses were to the odors of nonhost plants (tobacco and morning glory) and to most synthetic terpenoids except the compound limonene, which is a dominant volatile of tomatoes. Whatever the host or nonhost plants of leafminer tested, the volatiles from mechanically damaged plants always elicited higher EAG responses than did volatiles from healthy plants (102). Although electrophysiological techniques have the ability to identify the most electrophysiologically active components of volatile blends, these compounds are not always behaviorally active for insects (9). Therefore, EAG studies can provide important data, but the results should be verified using behavior of whole organisms. Subsequent research indicated that the behavioral responses of adult *L. sativae* to the volatiles from various plants were consistent with the observed EAG responses (103). For instance, adult leafminers spent more time searching in the presence of volatiles from host plants such as beans, tomatoes, and cucumbers, whereas little time was spent searching in the presence of odors from nonhost plants (103). When the EAG and whole-organism results are considered in combination with the headspace chemistry from the various plant families examined by Wei et al. (97), the key role in host location of GLVs produced by damaged plants becomes obvious.

Parasitoid responses to plant odors. Although host location cues of parasitic wasps include visual, chemical, acoustic, contact, and taste cues, there is substantial evidence that chemical information plays the most important role in this process for leafminer parasitoids. Dicke & Minkenberg (29) found that the volatile blend from leafminer-infested tomato leaves affected the behavior of *Dacnusa sibirica* Telenga in the absence of visual cues. Similarly, Petitt et al. (66) reported that *Opius dissitus* Muesebeck preferentially landed on leafminer-infested, rather than noninfested, lima bean plants. This preference was confirmed by choice experiments in a four-armed olfactometer without any visual cues. Evidence to support the use of alternative cues is scarce in the literature on parasites of Agromyzidae. In the only example found, *Dapsilarthra rufiventris* (Nees) females appeared to require visual cues to locate their host, *Phytomyza ranunculi* Schrank (81).

EAG: electroantennogram

The chemical cues for parasitoid attraction are often composed of complex blends of leafminer-induced volatiles (97), thus making it difficult to understand the role of specific compounds in host location by parasitoids (98). However, several studies have revealed that the olfactory sensilla of parasitoids only respond to a limited number of compounds released by insect-damaged plants, thereby substantially reducing the number of compounds that require testing (64, 75, 96). Electrophysiological techniques have been used successfully to understand the underlying mechanism of odor perception by parasitoids of *Liriomyza* spp. For example, in a study involving *L. sativae* and *Diglyphus isaea*, Zhao & Kang (103) found that neither the healthy host nor nonhost plants of the leafminer elicited distinctive EAG responses in the parasitoid. However, odors of physically damaged leaves, whether from host or nonhost plants, elicited strong EAG responses from both the leafminer and the parasitoid. Wei & Kang (96) showed that 6-C alcohols and esters from mechanically damaged plants elicited strong EAG responses of parasitoids. The authors also identified nine EAD-active volatiles in the headspace extracts from bean leaves damaged by second instars of both *L. huidobrensis* and *L. sativae* (96).

Behavioral responses to leafminer-induced volatiles. Behavioral studies have demonstrated that odors and headspace volatiles from leafminer-damaged plants play an important role in host location by leafminer parasitoids (29, 32, 66, 96, 103). However, our knowledge of leafminer-induced volatiles was incomplete before the study by Wei et al. (98). Using gas chromatography–mass spectrometry, gas chromatography–electroantennographic detection, and Y-olfactometers, Wei et al. (96) demonstrated that synthetic versions of (*Z*)-3-hexen-1-ol, 2-methylpropanal oxime, 2-methylbutanal oxime, 3-methylbutanal oxime, linalool, (*E*,*E*)-α-farnesene, and TMTT [(3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene] were attractive individually, whereas (*Z*)-3-hexenyl acetate and DMNT [(3*E*)-4,8-dimethyl-1,3,7-nonatriene] were unattractive at concentrations similar to those obtained from headspace collections (96). Moreover, *O. dissitus* responses to (*Z*)-3-hexen-1-ol, TMTT, or 3-methylbutanal oxime at four dosages from 10 to 10,000 ng 10 μL^{-1} showed significant differences (97). This dosage effect adds another level of complexity to the research required to understand behaviors responsible for host location. Experiments designed to compare responses to individual compounds versus a blend of mixtures showed that the parasitoids responded preferably to (*Z*)-3-hexen-1-ol regardless of how the chemical was presented. However, TMTT and 3-methylbutanal oxime were also important semiochemicals for the parasitoid to distinguish host from nonhost plants of *L. huidobrensis* (97).

Tritrophic interactions: plant-herbivore-natural enemy interactions

Parasitoids have a level of behavioral plasticity in host selection that involves learning and the context-dependent analysis of chemical cues (86, 90). *Liriomyza* parasitoids exhibit associative learning in response to plant odors. Petitt et al. (66) demonstrated that female *O. dissitus* exposed to lima bean plants preferred the odors of infested lima bean plants to those of infested eggplants or cotton plants. However, an oviposition experience on these plant species caused a considerable change in preference that the authors believed was due, at least in part, to learning. Clearly, there is an opportunity for future research to better define the patterns and processes involved in these interactions.

Can Chemical Ecology Yield New Control Tactics?

Biologically active chemicals identified from the studies of tritrophic interactions of plants, phytophagous insects, and their natural enemies have potential for the development of novel control strategies. The push-pull strategy is a behavioral manipulation method that uses repellent/deterrent (push) and attractant/stimulant (pull) stimuli to direct the movement of pests or beneficial insects for pest management (21). Chemical ecology studies on plants, leafminers, and parasitoids have yielded some promising control tactics. Host and nonhost plant extracts (e.g., neem, chinaberry tree extracts, and essential oils), botanical insecticides (e.g., neem-based insecticides and rotenone), and elicitors (e.g., JA) that act as repellents/deterrents have been used to push adult leafminers away from crops (6, 10, 42, 45, 100). Leafminer-induced volatile blends or individual compounds can be used to attract natural enemies of leafminers. Several compounds were identified that attracted the parasitoids but not the leafminers (96, 97). However, these chemicals have not been tested under field conditions. These studies provide opportunities to explore the potential of transgenic crops that overexpress induced defensive chemicals (1, 74) for suppression of leafminers. Although transgenic plants are important in pest management, any negative effect on nontarget insects, yields, the environment, and human health will need to be documented and alerted. Again, the opportunities for additional research designed to answer important fundamental and applied questions on these leafminer systems appear to be nearly unlimited.

SUMMARY POINTS

1. *Liriomyza* species differ in their thermal stress tolerances and have evolved diverse cold survival strategies that enable them to use various habitats that affect their distribution, dispersal potential, and control strategies.

2. Most *Liriomyza* species have a high supercooling capacity but are susceptible to freezing. Acclimation and rapid cold hardening are two effective ways to survive short exposure to cold environments.
3. Expression of some Hsps is apparently involved in tolerance of thermal stress. Trade-offs between *hsp* gene expression and fitness costs appear to determine the limitations of cold tolerance, heat tolerance, and important aspects of population dynamics. A cross-disciplinary approach will further our understanding of adaptation to temperature extremes and stress response mechanisms by *Liriomyza* species.
4. The chemical ecology studies of tritrophic interactions have made remarkable progress. Attractants and repellents from host and nonhost plants of leafminers have been isolated and identified. Although intact plants from different families release different volatiles, they produce similar compounds following leafminer damage.
5. Infochemical-mediated behaviors of leafminers and their parasitoids have been well documented. *Liriomyza* species use the cues of host plants, including GLVs and characteristic chemical compounds. (*Z*)-3-hexen-1-ol is the most important chemical that attracts leafminer parasitoids, and TMTT and 3-methylbutanal oxime play important roles in distinguishing host from nonhost plants of *Liriomyza* species.
6. Infochemicals induced by leafminers from host and nonhost plants could be employed as repellents to push leafminers away from crops and as attractants to pull in natural enemies. More research is essential before any of these strategies can replace the current reliance on pesticides.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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