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Influences of leaf-mining insects on their host plants: A review

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Abstract

Influences of leaf-mining insects on their host plants: A review.— Leaf-mining insects are an herbivore group whose larvae live and feed inside plant leaves. Leaf mines are distinct marks on leaves and can provide much information on insect-plant relationships. Most leaf miners are monophagous or oligophagous. Therefore ecologists and paleontologists use them to study interactions and coevolution among plants, insects and natural enemies. There are many different types of leaf-mining patterns on plant leaves, which may have different impacts on host plants. Compared with ectophagous herbivores, leaf-mining insects should have unique influences on host plant characteristics, such as leaf morphology, leaf chemistry, plant physiology, plant growth and production. Obvious impacts include leaf asymmetry, callus formation, photosynthesis, and green islands. Types and degrees of such influences are varied for different leaf miner species or different host plant species. In turn, the change of plant features may have positive or negative impacts on oviposition and feeding of leaf-mining insects. Studies on plant responses to leaf-mining and the defensive mechanisms of plants are helpful in understanding the coevolution between leaf miners and their food plants.

Key words: chemical ecology; interspecific interactions; pest resistance.

Resumen

Revisión de las influencias de los insectos minadores de hojas en sus plantas huésped.— Los insectos minadores de hojas son un grupo de herbívoros cuyas larvas viven y se alimentan del interior de las hojas. Lo que denominamos minas son las diferentes marcas que quedan en las hojas y que pueden proporcionar valiosa información acerca de las relaciones planta-insecto. La mayoría de minadores son monófagos u oligófagos. Los ecólogos y paleontólogos los usan para estudiar las interacciones y la coevolución entre plantas, insectos y sus enemigos naturales. Existen numerosos tipos de patrones de minas en las hojas, que pueden producir diferentes impactos en la planta hospedadora. Si los comparamos con los insectos ectófagos, los minadores de hojas pueden tener una influencia muy característica en numerosos aspectos de la planta hospedadora, como por ejemplo la morfología y la química foliar, la fisiología de la planta y su crecimiento y producción. Entre los impactos más evidentes, podemos nombrar asimetría foliar, formación de callos, fotosíntesis e «islas verdes». La tipología y el gravedad de estos impactos varían según en tipo de insecto minador y de planta hospedadora. Además, los cambios funcionales que se producen en la planta hospedadora pueden a su vez tener efectos positivos o negativos en la oviposición y la alimentación de los minadores. El estudio de los mecanismos de defensa de la planta hospedadora para combatir a los minadores puede resultar de gran utilidad para entender la coevolución entre ambos organismos

Palabras clave: ecología química; interacciones interespecíficas; resistencia a plagas.

摘要
潜叶昆虫对寄主植物的影响：综述。— 潜叶昆虫是一类植食性昆虫，以幼虫在叶片组织内取食并生活，不破坏叶表皮或至少不破坏外壁。潜道（潜叶幼虫在植物薄壁组织或表皮内部形成的取食道）为学者研究昆虫—植物关系提供了大量的信息。大部分潜叶昆虫为单食性或寡食性。因此，生态学家和古生物学家可将其作为模式生物，用于研究植物、昆虫和天敌三者的种间关系与协同进化。潜叶昆虫在植物叶片上形成许多不同类型的潜道，因而对植物造成的影响也不尽相同。与外食性昆虫相比，潜叶昆虫对植物形状有独特的影响，这些性状包括叶片形态、化学成分、植物生理、生长和产量。比较明显的影响包括叶片的不对称性、形成愈伤组织、降低光合作用以及形成“绿岛效应”。不同潜叶昆虫对不同植物的作用方式及影响程度不同。与此相反，植物特性的改变可能会促进或抑制潜叶昆虫的取食和产卵。因此，研究寄主植物对潜叶为害的应对措施及防御机制，有利于了解潜叶昆虫和寄主植物之间的协同进化。

关键词：化学生态；种间相互作用；抗虫性。

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INTRODUCTION

Leaf miners are a special insect group whose larvae feed and live on leaf tissues lying between the upper and lower epidermis, with the epidermis or at least the outer wall remaining undamaged (Hering, 1951; Kang, 1996; Dai *et al*., 2011*b*). Most leaf-mining insects are monophagous or oligophagous. Their distinct species-specific feeding marks (that is, leaf mines) usually persist for a long time. Therefore, an ecologist or a paleontologist may easily reconstruct the life histories of leaf miners, identify their taxonomic group, evaluate the influences of leaf miners on host plants, and clarify the relationship between leaf miners and plants (Hespenheide, 1991; Labandeira *et al*., 1994; Lopez-Vaamonde *et al*., 2006; Dai *et al*., 2011*b*). Thus, leaf-mining insects can be used as model organisms to study plant–insect–environment interactions (Hirowatari, 2009; Kang *et al*., 2009). Systematic research on leaf-mining insects has been performed in Europe, America and Australia (Needham *et al*., 1928; Hering, 1951, 1957; Spencer, 1990; Hespenheide, 1991). For example, the UK, the Netherlands and Australia have constructed websites on leaf miners and their host plants.

Compared with ectophagous insects, endophagous leaf miners are small; each individual consumes only a small quantity of leaves during the whole life history, generally not causing a large loss on plant biomass. They are more difficult to control due to their hiding habits; more importantly, leaf-mining might not damage the integrity of leaf surface so the impact of leaf-mining on plant physiology should be lower than expected (Pincebourde *et al*., 2006). However, a few mining species are considered as economic pests of agricultural crops and garden plants, e.g. coffee leaf miner (*Leucoptera coffeella*), apple blotch leaf miner (*Phyllonorycter crataegella*), Citrus leaf miner (*Phyllocnistis citrella*) and serpentine leaf miners (*Liriomyza* spp.). Their serious outbreaks may cause considerable damage. Leaf-mining insects have several direct effects on host plants, such as leaf morphology, leaf chemistry, plant physiology, plant growth and production. Plant responses to leaf-mining may vary depending on the leaf miner species and the plant species. Changing plant characteristics would have either negative or even positive impacts on the behavior, growth, or survival of leaf-mining herbivores. In comparison with ectophagous insects, there are fewer studies on the influence of leaf miners on host plants, especially in China. Therefore, it is necessary to summarize the effects of leaf-mining insects on their host plants, which may provide a basis for further studies on leaf miner-plant interactions and sustainable ecological control of leaf-mining pests.

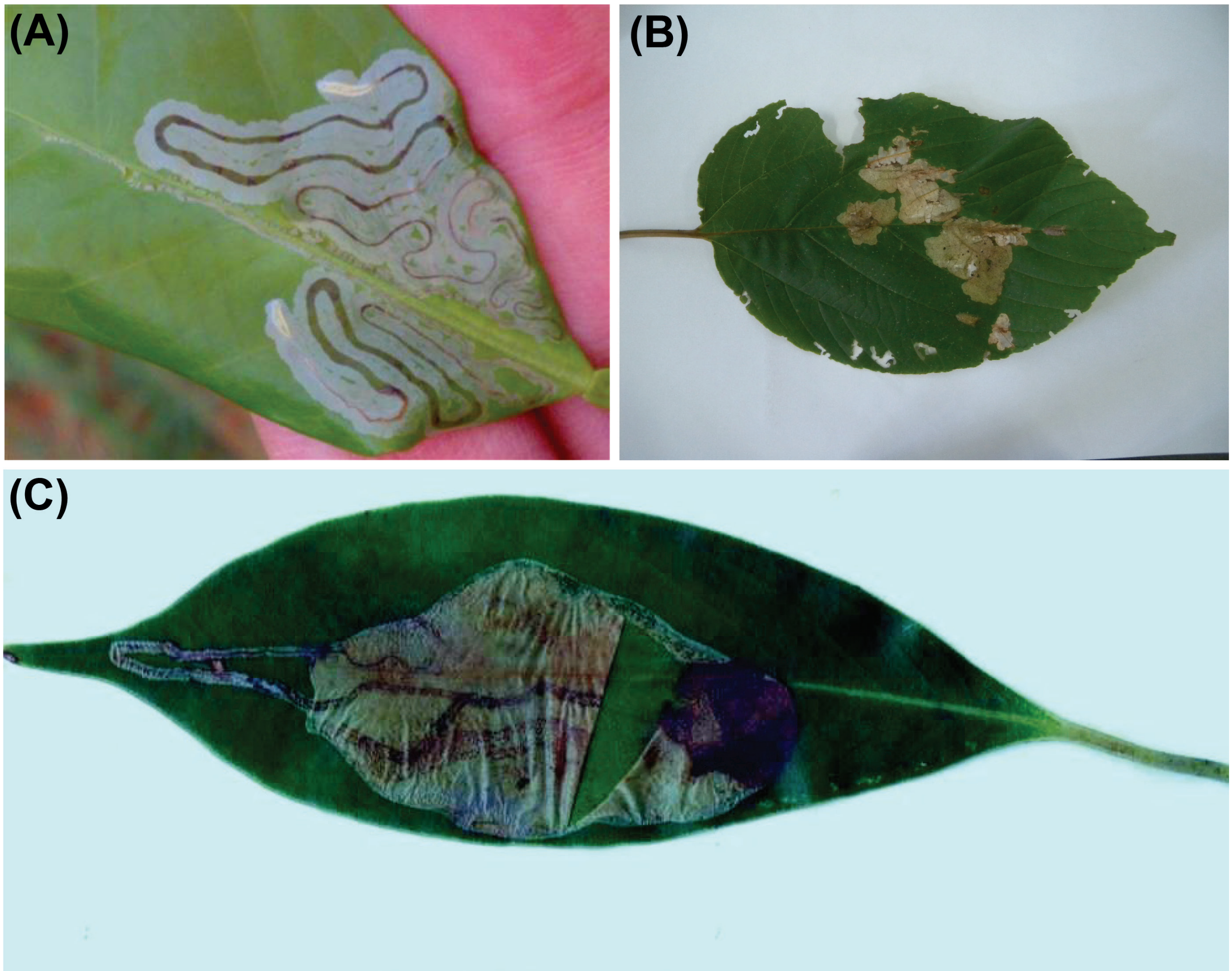

Figure 1. Three typical leaf mine shapes found in Ganzhou City, Jiangxi Province, China: (A), linear: citrus leaf miner (*Phyllocnistis citrella*) on navel orange; (B), blotch: a leaf-mining hispine beetle (*Platypria melli*) on *Hovenia acerba* Lindl.; (C), linear-blotch: a leaf-mining gracillariid moth (*Gibbovalva kobus*) on *Michelia maudiae* Dunn.

DIVERSE LEAF-MINING PATTERNS ON PLANT LEAVES

There are about 10,000 described species of leaf miners in more than 50 families and four orders: moths (Lepidoptera), flies (Diptera), beetles (Coleoptera) and sawflies (Hymenoptera) (Csóka, 2003). However, many more leaf-mining species remain undiscovered (Csóka, 2003; Hirowatari, 2009). For example, most nepticulid moths are leaf miners, with 804 described species but the estimated species number may be about 2500 (E. J. van Nieukerken, pers. comm.). After a long-period of coevolution and interspecific competition, there are diverse leaf-mining patterns (Fig. 1), even on the same plant species (Dai *et al*., 2013, 2014). Leaf-mine diversity shows niche differentiation of leaf-mining insects on host plant leaves, and the trade-off between seeking favorable microhabitats and nutrients and avoiding leaf defensive structures and competition.

The diversity of leaf-mining patterns may refer to different leaf mine shapes and different leaf-mining depths (Table 1; Hering, 1951; Dai *et al*., 2013). The types of leaf mine shapes could be classified as linear mines, blotch mines, and linear-blotch mines (Fig. 1; Hering, 1951). Linear mines occur when the leaf-mining larvae keep feeding forward and have subtypes such as serpentine, spiral and branched (Kato, 1984). Blotch mines made by leaf miners have several feeding directions, with subtypes of circular, oval, rectangular, tentiform, ameba

Table 1. Effects of different vertical leaf-mining patterns on plant photosynthesis.

Leaf-mining depth	Damaged leaf tissues	Leaf miner and host plant	Effects on photosynthesis	Author (year)
Full depth mining	Both palisade and spongy parenchyma	*Platypria melli* on *Hovenia acerba* Lindl.	Very significant reduction	Liao *et al*. (2014), C. Liao *et al*. (unpubl. data)
Upper surface mining	Palisade parenchyma	*Liriomyza sativa* on tomato	Significant reduction	Johnson *et al*. (1983)
		Liriomyza trifolii on *Chrysanthemum morifolium* Ramat., lima bean, and potato	No or slight reduction	Parrella *et al*. (1985), Martens & Trumble (1987), Bueno *et al*. (2007)
		Liriomyza trifolii on celery	Significant reduction	Trumble *et al*. (1985)
		Cameraria ohridella on *Aesculus hippocastanum* L.	Slight reduction	Raimondo *et al*. (2003)
Lower surface mining	Spongy parenchyma	*Liriomyza huidobrensis* on *Chrysanthemum morifolium* Ramat.	Significant reduction	Parrella *et al*. (1985)
		Phyllonorycter blancardella on apple	Significant reduction	Kappel (1986)
Epidermal mining	Upper and lower epidermis	*Phyllocnistis populiella* on quaking aspen	Upper epidermis: no reduction; lower epidermis: significant reduction	Wagner *et al*. (2008)
		Phyllocnistis citrella on *Citrus* × *aurantium* L., *C.* × *limon* L. (Osbeck), and *C. paradisi* Macfad.	No reduction in the green areas of mined leaves; significant reduction in mined area only (especially in old and broken mines)	Raimondo *et al*. (2013)

shape, etc. Among linear and blotch leaf mines, there are a series of transitional types. For example, linear mines could suddenly become much wider, or blotch mines may extend a narrow mine. Both are called “linear-blotch mines” (Hering, 1951; Kang, 1996; Csóka, 2003), which may be due to a change on feeding habitats in different larval stages (Hering, 1951). The vertical feeding sites of leaf miners may be epidermal cells, palisade tissues, spongy tissues or whole leaf tissues, which are called epidermal mines, upper surface mines, lower surface mines, and full depth mines, respectively (Hering, 1951; Kang, 1996). One special case is interparenchymal mines when leaf miners forage among the lower layer of palisade tissues and the upper layer of spongy tissues (Hering, 1951). Depending on the different leaf-mining pattern, we can divide leaf-mining insects into different functional groups, and study the ecological effects of different functional groups on host plants.

IMPACTS ON LEAF MORPHOLOGY

The feeding or oviposition of leaf miners often contributes to deformities and cracks in plant leaves (Hering, 1951; Kang, 1996). Due to the presence of insect larvae inside leaves, the leaves become asymmetrical, holes appear or parts are missing from the mined leaves (Hering, 1951). The tunnel of some leaf-mining weevils ends as a circular blotch from which an exit is cut leaving a round hole. Some infested leaves are crumpled because the cuticular layer is damaged (Raimondo *et al*., 2013). As for leaf asymmetry, the injured side of a birch leaf damaged by *Phylloporia bistrigella* is often smaller than the other (Hering, 1951); the width of each half and between side-ribs is variable in the leaves of elm (*Ulmus glabra* Huds.) mined by a leaf-mining weevil (*Rhynchaenus rufus*) (Møller, 1995). The abundance of leaf mines is associated with increasing leaf asymmetry in stone oak (*Quercus rotundifolia* Lam.)

(Møller & Lope, 1998). In unpolluted forests, the mined leaves are smaller and more asymmetric than the intact ones (Kozlov, 2005). There are a couple of factors responsible for the above growth abnormalities. If a new leaf has been oviposited in, young leaf cells are damaged and striking deformities occur during later growth (Hering, 1951). A disproportionate distribution in nutrients between damaged and normal areas of a leaf may lead to leaf asymmetry. The level of leaf asymmetry was higher when elm was provided with fertilizer. Besides, there is a positive relationship between leaf asymmetry and leaf size. That is, large-sized leaves infested by a leaf miner result in greater asymmetry than infested small ones (Møller, 1995). Oak trees with higher levels of asymmetry are more likely to die than those with lower levels (Møller & Lope, 1998). However, some researchers have argued that leaf asymmetry is induced by other environmental factors, which also result in higher leaf miner numbers (Møller, 1995). Not all miners have impacts on leaf external morphology. For example, *Liriomyza strigata* mines the main vein of leaves, and has minor effects on leaf distortion (Kang, 1996). In the other way, leaf anatomy such as vein patterns can also dictate the shape of leaf mines (Scheirs *et al*., 1997).

IMPACTS ON LEAF CHEMISTRY

Leaf-mining may alter host plant chemical composition especially for secondary substances. Trees with leaf miners have less root carbohydrate and twig starch than healthy ones (Percival *et al*., 2011). The midrib damaged by leaf-mining moths (Lepidoptera: Eriocranniidae) has slighty higher nitrogen concentration in tunnels than those in which the midrib was intact (Johnson *et al*., 2002). The injured midrib would restrict water supply to the xylem, speed up protein degradation, and increase available nitrogen compounds (White, 1984). On the contrary, the alfalfa blotch leaf miner decreased the yield of protein and digestible dry matter in the field (Byers & Valley, 1981). Leaf nutritional quality changed by leaf miners may indirectly affect other insects (Johnson *et al*., 2002). Plant secondary chemicals induced by leaf-mining larvae includes alkaloids, phenolic, benzaldehydes, methyl salicylates, benzyl alcohols, jasmonic acid, salicylic acid and so on (Mopper *et al*., 2004; Johne *et al*., 2006; Magalhães *et al*., 2010). The production of secondary metabolites may have either positive or negative impacts on the oviposition and feeding of conspecific or heterospecific herbivores (Johne *et al*., 2006; Magalhães *et al*., 2010). Mined leaves can induce chemical, physical and even visual defensive signals to herbivores (Yamazaki, 2010). Leaf-mining impacts are not the same for different leaf-mining behaviors. For example, apple leaves injured by the tissue-mining stages of the spotted tentiform leaf miner (*Phyllonorycter blancardella*) contain higher levels of ethylene and 1-aminocyclopropane-1-carboxylic acid (ACC) than intact leaves or leaves injured by the sap-feeding stages of the same leaf miner (Kappel *et al*., 1987).

Another reaction by the plant to leaf-mining is to form callus tissue in the damaged mine tunnels. A callus is a loose layer of parenchymal tissue formed by not only meristems but also in fully developed tissues (Hering, 1951). The function of callus tissue remains unclear. One reasonable guess is that callus might help to repair the leaf mines and compensate for leaf damage in photosynthesis (Hering, 1951). The main mortality factor of *Phytomyza ilicis* is the increasing quantities of callus which may squeeze the larvae to death (Ellis, 2000). On the other hand, *Liriomyza strigata* sometimes feeds on callus tissues (Kang, 1996).

Cytokinins are phytohormones with significant roles in plant growth and development (Naseem *et al*., 2014), such as maintenance of chlorophyll (Engelbrecht *et al*., 1969) and inhibition of leaf senescence (Pritchard & James, 1984*b*). Leaf miners could make "green islands" around leaf mines in autumn leaves, and leaf-mining larvae manage to complete their life history inside green islands. This phenomenon is attributed to high concentrations of cytokinins in the mined leaf area to keep living green tissues functional for photosynthetic activity (Giron *et al*., 2007). It is amazing that insect bacterial symbionts are found to manipulate cytokinin levels to induce green islands (Kaiser *et al*., 2010).

IMPACTS ON PLANT PHYSIOLOGY

The activities of leaf miners such as oviposition and feeding have negative effects on plant photosynthesis, which varies with different leaf-mining depths.

Generally, the impacts on photosynthesis from large to small should be: full depth mining > lower surface mining > interparenchymal mining > upper surface mining > epidermal mining (Table 1; Johnson *et al*., 1983; Parrella *et al*., 1985; Trumble *et al*., 1985; Kappel, 1986; Martens & Trumble, 1987; Raimondo *et al*., 2003; Bueno *et al*., 2007; Wagner *et al*., 2008; Liao *et al*., 2014). The possible explanation should be that different leaf tissues play different roles in photosynthesis. For example, stomata are mainly distributed on the lower epidermis and mining in the spongy tissue and the lower epidermis may lead to the close of stomata (Parrella *et al*., 1985; Wagner *et al*., 2008). Different leaf-mining depths thus have different impacts on leaf hydraulics, gas exchange, water use and chlorophyll fluorescence (Johnson *et al*., 1983; Parrella *et al*., 1985; Trumble *et al*., 1985; Kappel, 1986; Raimondo *et al*., 2003, 2013; Pincebourde *et al*., 2006; Bueno *et al*., 2007; Wagner *et al*., 2008; Lombardini *et al*., 2013). However, the whole-plant photosynthetic loss from most leaf miners is slight because insect populations are small in natural vegetation (Hileman & Lieto, 1981; Nardini *et al*., 2004) and the photosynthetic loss does not extend beyond the mined leaf area (Lombardini *et al*., 2013; Raimondo *et al*., 2013). While in some economic plants, photosynthesis is negatively correlated with leaf miner density and injury leaf area (Fujiie, 1982; Johnson *et al*., 1983; Lombardini *et al*., 2013).

IMPACTS ON PLANT GROWTH AND PRODUCTION

Plant growth may be significantly subjected to leaf miner activities such as oviposition and feeding (Wagner *et al*., 2008). One interesting phenomenon is that mined leaves fall earlier than unmined leaves (Owen, 1978; Fujiie, 1982; Maier, 1983, 1989; Nagasaki, 2004; Nardini *et al*., 2004; Bueno *et al*., 2007; Wagner *et al*., 2008). The effects of leaf-mining on leaf life span are stronger than other herbivore guilds (Kozlov & Zvereva, 2014). Some researchers argued that premature leaf abscission is simply a response to herbivore damage (Pritchard & James, 1984*b*; Stiling & Simberloff, 1989). While others suggested that early leaf fall is an evolutionary adaptation, which is beneficial to host plants themselves (Owen, 1978; Pritchard & James, 1984*b*). First, premature leaf fall stops the further development of young leaf miner larvae lessening leaf miner numbers in the next generation. The falling of mined leaves earlier than unmined leaves may attribute high mortality of some leaf miners (Faeth *et al*., 1981; Simberloff & Stiling, 1987; Stiling *et al*., 1987, 1991; Auerbach & Simberloff, 1989; Preszler & Price, 1993; Connor *et al*., 1994; Waddell *et al*., 2001), since the development of most leaf miner larvae is restricted to a single leaf (Zvereva & Kozlov, 2014). Second, leaf miners could make leaves fall year-round and return the nutrients back to the tree in a more even way (Owen, 1978). Premature leaf abscission is positively correlated with the densities of the mines (Shinozaki *et al*., 2012). Infested cranberry leaves by *Coptodisca negligens*, those with two mines drop earlier than those with only one mine (Maier, 1989). Leaf-mining (and other herbivorous feeding) damage to young leaves and to plants with a higher specific leaf area reduce more in leaf life span than damage to old leaves and to plants with a lower specific leaf area (Zvereva & Kozlov, 2014). Premature abscission due to leaf-mining is lower for deciduous trees than for evergreen ones (Bultman & Faeth, 1986). Impacts of mining on plant leaves differ from season to season or from insect generation to generation (Pritchard & James, 1984*b*).

However, early leaf drop is not a characteristic of all plants infested with leaf miners and appears to be a relatively minor ecological factor. For example, <40% of mined leaves drop early (Kahn & Cornell, 1983); less than 3% of leaf miner larvae in dropped leaves suffer mortality (Pritchard & James, 1984*a*; Oishi & Sato, 2007; Gripenberg & Roslin, 2008; Shinozaki *et al*., 2012); and photosynthesis is not reduced enough to severely damage the host plant (Parrella *et al*., 1985; Martens & Trumble, 1987; Raimondo *et al*., 2003; Bueno *et al*., 2007). Moreover, early leaf abscission has no influence on holly leaf miner survivorship (Kahn & Cornell, 1989). Possible reasons are that fallen leaves onto the forest floor would escape searching by parasitoids and the maggots are already in the pupal stage (Kahn & Cornell, 1989). *Coptotriche japoniella* can prevent premature leaf abscission to make sure the sucessful emergence of the imago before leaf falls (Oishi & Sato, 2007). Some plants retain and change the visibility of leaf mines to deter other herbivores and to attract natural enemies (Yamazaki, 2010).

Leaf-mining may have a detrimental effect on whole plant primary productivity (Nardini *et al*., 2004). Leaf miner outbreaks have strong negative influences on plant development and aboveground biomass production: more basal sprout dieback, lower plant height, lower girth, smaller leave size, fewer leaf number, fewer petiole number, and fewer shoot number (Trumble *et al*., 1985; Norris, 1997; Kozlov, 2005; Wagner & Doak, 2013). Leaf-mining injury could cause severe loss of the total leaf area (Hileman & Lieto, 1981; Peña *et al*., 2000; Nardini *et al*., 2004). Leaf miners markedly increased the mortality of floral leaves, but not of vegetative leaves (Hileman & Lieto, 1981). Leaf miners could significantly reduce whole-tree energy, seed weight, seed germination, seedling vigor and stem extension (Percival *et al*., 2011; Straw & Williams, 2013). Serious leaf-mining could also lead to reduction in fruit set, fruit size, fruit weight and fruit quality, and even premature ripening, early fruit fall, and total yield loss (Fujiie, 1982; Reissig *et al*., 1982; Peña *et al*., 2000; Nardini *et al*., 2004; Straw & Williams, 2013). However, leaf-mining does not reduce plant productivity in three *Citrus* L. species (Raimondo *et al*., 2013). Leaf-mining could also mediate the competition between different plant species (Norris, 1997).

LEAF MINERS AS PHYSICAL ECOSYSTEM ENGINEERS FOR OTHER PLANT PARASITES

Leaf miners can change resource availability to other organisms. First, other arthropods such as springtails can use empty leaf mines as feeding and reproductive sites (Kagata & Ohgushi, 2004). We also noticed that many insects and mites overwinter inside abandoned leaf mines in the field. Second, leaf-mining damage to leaf midribs may reduce the survival rate of an aphid (Johnson *et al*., 2002). Third, the feeding galleries of leaf miners can be an entrance for pathogens. For example, the Asian citrus leaf miner (*Phyllocnistis citrella*) has increased the incidence of Asiatic citrus canker (*Xanthomonas axonopodis* pv. *citri*) and changed the spatial distribution type of canker-infested trees (Chagas *et al*., 2001; Christiano *et al*., 2007). Moreover, leaf miners may transmit plant virus as a vector. A leaf-mining beetle (*Dactylispa lenta*) unexpectedly transmits rice yellow mottle virus in Africa (Banwo *et al*., 2001). Another leaf-mining beetle (*Phylloplatypus pandani*) can also transmit diseases among plants (Sugiura & Masuya, 2010).

STUDIES ON LEAF MINERS AND THEIR HOST PLANTS IN CHINA

Leaf miner taxonomy

Researchers have described some major leaf miner groups in China, although some publications have not emphasized much on leaf-mining habit. Well-studied leaf-mining moths (Lepidoptera) included Gracillariidae (Liu & Zeng, 1985, 1989; Yuan, 1986, 1992; Yuan & Robinson, 1993; Bai & Li, 2008, 2009*a*, *b*, 2011*a*, *b*, 2012; Xu *et al*., 2009; Bai, 2011; Kobayashi *et al*., 2011, 2013; Cai, 2013), Lyonetiidae (Wu *et al*., 2006), Nepticulidae (Yang, 1989; Nieukerken & Liu, 2000; Liu & Nieukerken, 2001), and Tischeriidae (Huang & Tan, 2009). Leaf-mining flies (Diptera) included Agromyzidae (Lin, 1983; Feng & Jer, 1989; Gu *et al*., 1991; Shiao *et al*., 1991; Shiao & Wu, 1995, 1996, 1999, 2005; Chen & Wang, 2001, 2003*a*, *b*, *c*, *d*, 2008; Shiao, 2004; Sasakawa, 2006, 2008; Chen *et al*., 2007). Leaf-mining beetles (Coleoptera) included Alticinae (Wang, 1990; Zhang & Yang, 2004), Cassidinae (Gressitt, 1950, 1953; Chen *et al*., 1961, 1962, 1964, 1986; Gressitt & Kimoto, 1963, 1965; Chen & Tan, 1964, 1985; Takizawa, 1978; Yu, 1985; Lee, 2009), and Rhynchaenae (Yang *et al*., 1991, 1996). Leaf-mining sawflies included Tenthredinidae (Wei, 1994, 1997; Nie & Wei, 1998; Wei & Nie, 1998, 1999; Wei *et al*., 2003; Wu *et al*., 2010; Hou *et al*., 2012). However, the reported number of Chinese leaf miner species is much lower than estimated. For example, China hosts much more species in Fagaceae family than North America (7 genera and 294 species vs. 5 genera and 97 species) (Nixon, 1997; Huang *et al*., 1998), but species number of Tischeriidae are 4 vs. 40 (J.-S. Xu *et al*., unpubl. data). There are over 400 leaf-mining species feeding on 600–1000 Fagaceae plant species in the whole world, with only 10% leaf miners with Chinese names (X.-H. Dai *et al*., unpubl. data). Our Leaf Miner Group began to collect and rear leaf miners in 2007, and at present we have built a database on Chinese leaf miners and their host plants collected in 25 provinces. We have got nearly 300 leaf-mining species in over 30 families and four orders, with about 140 described species. We have also obtained 3000 parasitoid specimens (X.-H. Dai *et al*., unpubl. data).

Host plant diversity

Not much systematic work on host plant diversity has been completed in China (Dai *et al*., 2011*b*), except for some economically important leaf-mining pests such as *Liriomyza* spp. (Kang, 1996; Dai *et al*., 2000, 2001*d*; Zhang *et al*., 2000; He *et al*., 2001) and *Phyllocnistis* spp. (Liu & Zeng, 1980). Host plant records of non-economic leaf miners are still poor in China. At Mt. Jiulianshan in South China, from 2008 to 2011 we have collected 69 families, 155 genera, and 293 species of host plants of leaf miners (Dai et al., 2011*a*), while in 2014 the numbers have increased to 92 families, 232 genera, and 471 species, occupying about 1/5 of total plant species number in the area (X.-H. Dai *et al*., unpubl. data).

Insect-plant relationship

Chinese scholars have done many studies on the interactions between leaf miners and host plants, mainly on *Liriomyza* spp. Topics are as follows: (1) host selection and location by leaf-mining insects (e.g. Wei *et al*., 2000; Dai et al., 2001*c*, 2003; He *et al*., 2001; Zhao & Kang, 2001, 2002*a*, *b*, 2003; Zeng *et al*., 2003; Pang *et al*., 2004, 2006; Zhang *et al*., 2004; Ko, 2006; Yan *et al*., 2008; Yu *et al*., 2008; Zheng *et al*., 2010); (2) plant resistance to leaf miners (e.g. Cheng *et al*., 2006; Zhang *et al*., 2008); (3) influences of different host plants on leaf miners (Zhang *et al*., 1998; Li *et al*., 2002; Wei *et al*., 2004; Pang *et al*., 2005); (4) impacts of leaf miners on plants (Sun *et al*., 2012); (5) effects of environmental factors on insect-plant interactions (e.g. Dai *et al*., 2001*a*, *b*, 2002, 2011*a*, 2013, 2014; Cen *et al*., 2003); (6) coevolution and codiversification (e.g. Du *et al*., 2008; Liao *et al*., 2015).

CONCLUSIONS

Different leaf miners have variable degrees of impact on the morphology, chemistry, physiology and growth of their host plants, while different plant species show inconsistent resistance or tolerance to leaf-mining (Trumble *et al*., 1985; Williams, 1989). The influence of leaf-mining on plants is also affected by other ecological factors such as light, water, soil, temperature and biotic relationship. Such factors not only directly act on plant growth and development, but also on the performance of leaf-mining insects. In turn, the induced changes of plant physical and chemical features may have either positive or negative impacts on oviposition and feeding of leaf-mining insects. Studies on plant responses to leaf-mining and the defensive mechanisms of plants are helpful in understanding the coevolution between leaf miners and their food plants. Plant resistance to leaf-mining may be altered by both the environment and genetics, therefore we could adopt suitable management strategies and genetic breeding technology to control pest leaf miners. Future research trends may include but not be limited to: (1) cophylogeny and cophylogeography between leaf miners and host plants; (2) coexistence and niche differentiation of different leaf-mining species in the same plant; (3) how plant community diversity affect leaf miner abundance and richness, and vice versa.

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