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# 生态学报

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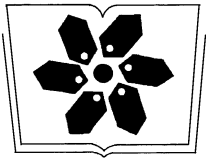
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# 生态学报

(SHENGTAI XUEBAO)

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## 寄主植物叶片物理性状对潜叶昆虫的影响

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**摘要:** 潜叶昆虫广泛分布于鳞翅目、双翅目、鞘翅目和膜翅目中, 其幼虫潜入叶片内部生活和取食, 是一类用于研究植物-昆虫-天敌种间关系和协同进化的重要模式生物。有些潜叶昆虫是重要农林害虫。相比外食性昆虫, 在叶内取食的潜叶昆虫幼虫更易受到叶片物理性状的直接影响。叶片的着生位置、朝向、大小、颜色和表皮毛等直接决定潜叶虫成虫的取食和产卵选择, 从而影响幼虫的空间分布和寄主适应。叶片的某些物理性状也会直接影响幼虫的取食行为、生长发育和被寄生率。研究叶片物理性状的防御作用以及潜叶昆虫对这些防御的适应, 有助于了解潜叶昆虫-寄主植物的协同进化。另一方面, 外界环境和遗传育种都有可能改变植物叶片的物理特性, 而对潜叶害虫产生抗性, 从而实现潜叶害虫的可持续生态控制。

**关键词:** 潜叶虫; 寄主植物; 叶片物理性状; 寄主选择性; 昆虫-植物关系

## Effects of physical leaf features of host plants on leaf-mining insects

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**Abstract:** Leaf-mining insects, belonging to Lepidoptera, Diptera, Coleoptera, or Hymenoptera, have larvae that live and forage inside leaves. The mines remain visible for a long time and the life time of most leafmining larvae is spent inside the mine. Ecologists and even paleontologists can without much difficulty reconstruct the living conditions of these insects and evaluate their influences on host plants. Most leafminers are monophagous or oligophagous and many leaf mines are species-specific. Therefore, leafminers are often used as model organisms to study plant-insect-natural enemy interactions and co-evolution. Although leafminer outbreaks do not occur often in natural habitats, some leafminers are prevalent pests in agriculture and forestry. Due to their small body size, short life history, high reproductive ability and endophagous habit, leafmining pests are not easily discovered during their early stages of development. Once they break out, they damage the leaves and thus degrade photosynthesis and production.

Compared to ectophagous insects, endophagous leafminers should depend more on leaf characteristics. There are many reports on relationship between leaf miners and chemical composition of host plant leaves, whereas few reviews on physical leaf features. Thence we summarize the effects of physical leaf properties on the feeding, survival, distribution, reproduction and behavior of leafminers. For example, the location, directional position, size, color and trichome of leaves have direct impacts on feeding behavior and oviposition site selection of adult leafminers; and therefore also on where larva live and quality of their food. Some physical features of the leaves also act directly on the feeding behavior, parasitism and development of leafmining larvae.

(1) Leaf location and direction: The oviposition and feeding of adults are generally located at the middle to lower parts of plant individuals and thus the eggs and larvae often occur in the same parts. The light conditions of leaves in different

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positions vary and this will indirectly affect the development, survival and parasitism of leafmining larvae via leaf features, nutrient contents, secondary compounds and mine temperatures. However, some leafmining larvae can avoid adverse light effects through selective foraging. (2) Leaf size: Leaf size has a positive relationship with optimal oviposition choices for adults and the developmental success of larvae. (3) Leaf thickness: There is no distinct relationship between leaf thickness and leaf mining. (4) Leaf color: The influence of leaf color on leafmining varies with insect species. (5) Leaf trichomes: Leaf trichomes can disturb the oviposition and feeding of leafminers, but some leafminers select leaves with more denser trichomes since trichomes can also disturb the searching behavior of parasitic wasps and reduce the feeding competition of ectophagous insects. (6) Leaf veins: Many leafminers avoid indigestible vascular bundles while some specialized leafminers prefer leaf veins because leaf veins can provide shelter against natural enemies.

Combining both physical and chemical information of leaves leafminers can form identifying patterns on host plants. The oviposition choices of leafminer adults determine larvae location and thus have a large influence on leafminer population dynamics. However, if polyphagous leafminers oviposit eggs on non-host plants and if they manage to complete their life history their host range can be extended. Studies on the defenses of leaf physical structure and the adaptations of leafminers to these structural defenses are helpful in understanding the co-evolution between leafminers and their host plants. Physical characteristics of plant leaves can be altered by environmental factors and genetic breeding. In this way, leaves can become resistant and the sustainable ecological control of leafmining pests may be achieved.

**Key Words:** leafminer; host plant; physical leaf features; host selection; insect-plant relationship

潜叶昆虫广泛分布于鳞翅目(Lepidoptera)、双翅目(Diptera)、鞘翅目(Coleoptera)、膜翅目(Hymenoptera)等类群中,其幼虫在植物叶片内部生活并取食<sup>[1-4]</sup>。潜叶昆虫潜食造成的潜道可保留较长时间,而且大多数潜叶幼虫的生活史在潜道内完成。因此,生态学家可方便地通过潜道来重建潜叶昆虫的生活情况、衡量潜叶昆虫对寄主植物的影响,以及潜叶昆虫与其它动物如天敌之间的相互作用<sup>[5]</sup>。多数潜叶昆虫为单食性或者寡食性,而且它们的潜道特征通常具备物种特异性,成为分类学家和古生物学家鉴定潜叶昆虫的重要依据。古生物学家可通过叶片化石上的潜道痕迹分析昆虫-植物关系的演化<sup>[6-7]</sup>。因此,潜叶昆虫是一类可用于研究种间关系、协同进化和环境适应性的模式生物<sup>[8]</sup>。

自然生境中潜叶昆虫的大规模发生较不常见,而且很多植物可耐受轻微的潜食。但是,一些潜叶昆虫为重要农林害虫,在大规模单一种植作物上易爆发,导致植物叶面虫道密布,造成叶片早期枯死或脱落,并可能诱发各种病害,影响光合作用、产量与商品价值,给农林业带来重大损失。因此,研究潜叶昆虫也具有相应的经济意义<sup>[3]</sup>。

全世界已描述的潜叶昆虫物种数量超过 10000 种<sup>[4]</sup>,但这些已描述的潜叶种类可能仅占实际数量的一小部分<sup>[4,8]</sup>。国外对潜叶昆虫种类及其寄主植物种类进行了诸多系统研究<sup>[1-5, 9-10]</sup>。例如,英国、荷兰和澳大利亚已经建立了有关潜叶昆虫及其寄主植物的专门网站。国内的研究主要集中在有重要经济意义的潜叶害虫如斑潜蝇(*Liriomyza* spp)、柑橘潜叶蛾(*Phyllocnistis citrella*)、桃潜叶蛾(*Lyonetia clerkella*)、金纹细蛾(*Lithocolletis ringoniella*)等的生物学、生态学及其防治方面<sup>[3,11]</sup>,但潜叶昆虫物种多样性方面的研究工作还相对较少。

植物叶片的物理性状,包括形状、颜色、硬度、毛茸、表面的蜡质、矿物积累和分泌物等,会影响昆虫的取食和产卵行为<sup>[12]</sup>。与外食性昆虫相比,潜叶昆虫的幼虫在叶片内部取食和生活,其生存、分布、繁殖与行为更易受到叶片物理性状的直接作用。叶片物理性状与潜叶昆虫的寄主选择及协同进化密切相关,并在一定程度上影响潜叶害虫的发生与防治。目前,叶片化学成分与潜叶昆虫关系的总结颇多<sup>[5,11]</sup>,但叶片物理性状的影响方面的文献则相对零散。因此有必要归纳总结寄主植物叶片物理性状对潜叶昆虫的影响及机制,以期作为深入研究潜叶昆虫物种进化及生态控制的前期基础。

## 1 叶片着生位置和朝向

### 1.1 叶片位置和朝向对潜叶昆虫成虫分布的影响

潜叶昆虫成虫的活动主要位于植株的中下层,部分双翅目潜叶虫虽然分布在植株上层,但这些植株相对不高(表1)。这可能有下列几种原因:(1)潜叶昆虫成虫的运动能力相对较弱,可能不易到达植株上层;(2)植株中下层的微生境如温度、湿度等有利于成虫的活动;(3)植株中下层的叶片营养物质含量高,或者植物上层叶片有毒次生代谢物含量更高,导致成虫偏嗜中下层叶片。

表1 潜叶昆虫成虫在寄主植物植株各层的分布

Table 1 The distribution of leafminer adults among different plant layers

潜叶昆虫 Leafmining insects	寄主植物 Host plants	成虫在植株上的主要分布 Main distribution layers of adults	参考文献 References
潜叶蛾、潜叶象甲	山毛榉	下层	[13]
山楂潜叶蛾 <i>Phyllonorycter crataegella</i>	苹果	下层	[14]
美洲斑潜蝇 <i>Liriomyza sativae</i>	番茄	中层	[15]
	矮生菜豆	下层	[16]
三叶草斑潜蝇 <i>Liriomyza trifolii</i>	番茄	下层	[15]
	茄子	下层	[17]
南美斑潜蝇 <i>Liriomyza huidobrensis</i>	土豆	上层	[18]
	芹菜	中上层	[19]

叶片朝向也影响一些潜叶昆虫的选择性。例如,水平和45°角的粘板引诱到的三叶草斑潜蝇数量要比垂直的粘板少;自由悬挂的垂直粘板诱蝇数要多于固定南北向的垂直粘板<sup>[20]</sup>。同等面积的黄板诱到三叶草斑潜蝇的效果可以相差4倍,因黄板相对于植株的位置以及水平、垂直角度而异<sup>[21]</sup>。但是,粘板的朝向(水平或垂直)对引诱南美斑潜蝇的效果却没有影响<sup>[18]</sup>。三叶草斑潜蝇和南美斑潜蝇的这种差异,可能要结合两个物种的行为特性进一步研究。

### 1.2 叶片位置和朝向对潜叶昆虫卵、幼虫分布的影响

由于多数种类潜叶昆虫的成虫在植株中下层产卵,因此卵和幼虫主要也分布在这些区域(表2)。但是,

表2 潜叶昆虫卵或幼虫在寄主植物植株各层的分布

Table 2 The distribution of leafminer eggs and larvae among different plant layers

潜叶昆虫 Leafmining insects	寄主植物 Host plants	卵或幼虫在植株上的主要分布 Main distribution layers of eggs or larvae	参考文献 References
穿孔蛾 <i>Paraclemensia acerifoliella</i>	糖槭	下层	[22]
烟草潜叶蛾 <i>Phthorimaea operculella</i>	烟草	下层	[23]
细蛾 <i>Cameraria hamadryadella</i>	橡树	下层	[24]
金纹细蛾 <i>Lithocolletis ringoniella</i>	苹果	下层	[25]
姬果蝇 <i>Scaptomyza nigrita</i>	碎米荠	中下层	[26]
美洲斑潜蝇 <i>Liriomyza sativae</i>	多种作物	下层	[27]
	番茄	中下层	[16]
	矮生菜豆	下层	[28]
	棉花	下层	[29]
	黄瓜	中层	[30]
南美斑潜蝇 <i>Liriomyza huidobrensis</i>	烟草	下层	[31]
	彩椒	中下层	[32]
	黄瓜	下层	[33]
	茄子	下层	[33]
	番茄	下层	[33]
潜叶虫群落	澳洲热带雨林	下层	[34]
山毛榉跳象 <i>Rhynchaenus fagi</i>	山毛榉	上层	[13]
桃潜叶蛾 <i>Lyonetia clerkella</i>	桃树	上层	[35]

也有一部分潜叶昆虫成虫偏嗜在植株上层产卵。例如,山毛榉跳象(*Rhynchaenus fagi*)的潜道主要分布在上部冠层的顶端或林地的边缘<sup>[13]</sup>,它们产卵和取食的植株部位偏好性刚好相反。

叶片朝向对卵或者幼虫的影响也存在物种差异。总的来说,柑橘潜叶蛾在垂直叶片上的卵数要比水平叶片上的高 50%;但在长度小于 8mm 的叶片中只有 20% 的卵产在叶片的远轴面,水平叶片朝上的远轴面的卵量仅占 33%;而当每叶仅有 1—2 个卵时,远轴面卵量占 40%;温度低于 18℃ 时,远轴面卵量占 45%;柑橘杂交种 *Ortanique* 上,64% 的卵位于远轴面<sup>[36]</sup>。然而,金纹细蛾幼虫在东、南、西、北、内膛 5 个水平方位上差异不明显<sup>[25]</sup>。

### 1.3 光照的间接影响

光照条件会导致不同位置叶片的各种性状如表皮角质层厚度、叶片大小、叶片形状、营养物质、次生代谢物、温度等出现差异,从而间接影响到潜叶昆虫的寄主选择、生长发育及其被寄生率。例如,潜蝇(*Chromatomyia milii*)只受害浓密树冠下的花叶根茎绒毛草(*Holcus mollis*)受荫蔽的叶子,这些叶子要比阳光下更长更黑;实验室条件下,潜蝇在阴叶上要产更多的卵<sup>[37]</sup>。黑蚜蝇(*Cheilisia semifasciata*)的潜道主要出现在岩生脐景天(*Umbilicus rupestris*)的阴叶上<sup>[38]</sup>。在向阳环境中,光化学过程会降低美国白栎(*Quercus alba*)叶片质量,从而导致潜叶蛾(*Cameraria hamadryadella*)幼虫存活率的下降<sup>[39]</sup>。晴天的时候,向阳叶片中的潜道温度要比荫蔽叶片中的高几度,从而影响到潜叶虫的生长发育<sup>[40]</sup>。

光照对潜叶昆虫的影响在不同空间尺度上会发生变化。例如,人工荫蔽的艾氏栎(*Quercus emoryi*)叶片更大,而且具备更少的蛋白质和水解单宁,但对 4 种主要潜叶虫在植株尺度上的选择影响有所不同;其中 2 种潜叶虫(*Stigmella* sp. 和 *Stilbosis juvantis*)喜欢荫蔽植株,而另 2 种(*Cameraria* sp. 和 *Tischeria* sp.)更喜欢向阳植株,然而这种偏好性跟潜叶虫存活率之间的关系可以是正相关、负相关或者中性,因潜叶虫种类而异<sup>[41]</sup>。但在叶片尺度上,同一棵艾氏栎阴面叶片上的潜蛾(*Cameraria* sp.)密度却高于阳面叶片<sup>[42]</sup>。同样,自然生长的碎米荠(*Cardamine cordifolia*)向阳植株上的姬果蝇(*Scaptomyza nigrita*)成虫密度和幼虫取食为害都要比自然背阴植株多<sup>[26]</sup>;但是,开阔地中人工遮蔽的碎米荠上姬果蝇的潜叶为害却显著高于开阔地中未遮蔽的植株<sup>[43]</sup>。3 种环境中光照强度、光谱成分和小气候的不同可能影响了碎米荠叶片的化学成分和碎米荠姬果蝇成虫的产卵行为,从而导致了碎米荠姬果蝇的为害差异<sup>[43]</sup>。

有时候潜叶幼虫可以通过选择性的取食避开光照的不利影响。例如,受荫蔽的美洲冬青(*Ilex opaca*)树上的植潜蝇(*Phytomyza ilicicola*)多度、发育速率、到蛹期的存活率、潜道面积、蛹重等参数与未荫蔽树相比,差异很小甚至没有差异<sup>[44]</sup>。美洲冬青的阴生叶更大更薄,只有两层栅栏细胞;在叶子的远轴面细胞层中的晶体更多,可能是阻碍潜叶幼虫取食的机械限制;而潜叶虫可以选择性地取食阳生叶的没有机械限制但水分和蛋白质含量很高的中部栅栏组织,然而中部栅栏组织的不利之处在于皂甙含量也很高<sup>[45]</sup>。在更薄的阴生叶片中,潜叶虫可以通过取食部分的近轴面或者远轴面的栅栏层并留下更薄的潜道壁来加以补偿<sup>[44]</sup>。当然,虽然两种处理的植株上的植潜蝇幼虫存活率没有差异,但成虫在向阳开阔地中的植株上有更高的取食率和产卵率,从而导致阳叶上出现更多的潜道和 1 龄幼虫<sup>[46]</sup>。

## 2 叶片大小

叶片的大小主要影响潜叶虫成虫的取食、产卵选择性和幼虫的生长发育。一般说来,成虫将卵产在足够大的叶片上才能保证幼虫完成生活史。例如,一种日蛾(*Coptodisca kalmiella*)成虫对甸杜(*Chamaedaphne calyculata*)的叶片大小可能存在产卵选择性:较大的营养叶上有 18% 出现潜道,较小的花叶上只有 8% 出现潜道,而最小的叶片上则不出现虫道<sup>[47]</sup>。与大叶枝条相比,艾氏栎的小叶枝条上潜蛾(*Cameraria* sp.)密度更低,聚集度更大,而聚集度过大则会降低潜蛾幼虫的存活率;潜蛾较少为害小叶的枝条或者小叶的植株,因为成虫在上面产卵较少<sup>[42]</sup>。柑橘潜叶蛾的卵在长度为 15—25mm 的叶片上最多,叶片过大或者过小时卵密度都不高<sup>[36]</sup>。叶面积也同样影响了美洲斑潜蝇对寄主植物种类的选择性<sup>[48]</sup>。美洲斑潜蝇的取食、产卵的选择性强弱与叶片面积呈正相关;随着叶龄的增长,叶片面积增大,美洲斑潜蝇的取食、产卵选择性增强<sup>[49]</sup>。

虽然美国白栎的阴生叶要比阳生叶长 30%,但由于潜叶蛾 (*Cameraria hamadryadella*) 成虫在夜间产卵,所以两种叶片上面的潜道密度并没有差异<sup>[39]</sup>。这个特例充分说明潜叶昆虫的产卵选择性决定了其幼虫的生长发育及种内竞争状况,可见潜叶昆虫选取较大的叶片是一种进化上的适应。

### 3 叶片厚度

不同寄主植物对美洲斑潜蝇的适合度与叶片上表皮厚度、栅栏组织厚度和叶片厚度之间均不存在显著相关性,而叶片上的虫道面积与栅栏组织细胞的宽度之间则显著相关<sup>[50]</sup>。在更薄的叶片中,潜叶虫或可通过取食更上部或者更下部的组织并留下更薄的潜道壁来加以补偿<sup>[44]</sup>。有关叶片厚度与潜叶虫关系的文献不多,需要进一步研究确定。

### 4 叶片颜色

叶色主要由叶绿素和有色色素等决定,其对潜叶昆虫的影响可能因昆虫种类而异。例如,斑潜蝇具有趋向黄色、避开蓝色<sup>[51]</sup>的习性,因此多在叶色黄绿的植株上取食和产卵。寄主植物叶色在美洲斑潜蝇寄主选择中起着重要的作用<sup>[52]</sup>,叶色越浓绿,对美洲斑潜蝇的吸引越大<sup>[16]</sup>。对于三叶草斑潜蝇,绿叶型的蓖麻是高感品种,而紫叶型的蓖麻则是抗性品种<sup>[53]</sup>。黄色不透明或半透明的粘板则对南美斑潜蝇的诱杀效果最好<sup>[54]</sup>。但是,叶色对潜叶蛾的作用较为复杂。例如,红色粘板诱到的山楂潜叶蛾要多于其它颜色的粘板<sup>[14]</sup>,这可能与苹果属植物叶片多含有有色色素有关。然而,粘板对斑幕潜叶蛾 (*Phyllonorycter blancardella*) 成虫的引诱效果不明显,并且斑幕潜叶蛾对粘板的颜色并无偏好性<sup>[55]</sup>。寄主植物的叶片色调同样对柑橘潜叶蛾的产卵没有影响<sup>[36, 56]</sup>。

### 5 表皮毛

表皮毛常干扰昆虫的产卵、取食和吞咽<sup>[3, 5]</sup>。一般说来,表皮毛密度越大,越不利于潜叶昆虫成虫的活动。美洲斑潜蝇对寄主植物种类的选择性受到叶片表皮毛的影响<sup>[48, 52]</sup>。叶片表皮毛的密度大则抗性强,表皮毛长度大则受害轻,叶片不光滑则受害轻<sup>[57]</sup>。同一个品种的番茄中,长茸毛的植株对美洲斑潜蝇的抗性明显强于短茸毛的植株<sup>[58]</sup>。四季豆叶片表皮毛可以抑制美洲斑潜蝇的产卵<sup>[52]</sup>。矮生菜豆的表皮毛长度和密度越大,美洲斑潜蝇就越不趋向于取食<sup>[16]</sup>。美洲斑潜蝇的取食、产卵的选择性强弱与菜豆叶片表皮毛的密度、长度呈负相关。随着叶龄的增长,叶片表皮毛密度减少,美洲斑潜蝇的取食、产卵选择性增强,取食痕与产卵痕数增多<sup>[49]</sup>。黄瓜叶片表皮毛的密度和长度与美洲斑潜蝇对其选择性强弱呈负相关<sup>[59]</sup>。菊科植物腺毛密度会影响三叶草斑潜蝇的取食和产卵位置<sup>[60]</sup>。高密度的腺毛会从物理上驱除三叶草斑潜蝇<sup>[61]</sup>。苜蓿潜蝇 (*Agromyza frontella*) 更喜欢在没有腺毛的苜蓿属植物上产卵,腺毛密度对苜蓿潜蝇的产卵影响最大<sup>[62]</sup>。多毛番茄 (*Lycopersicon hirsutum*) 株龄越大,腺毛密度也增加,可能导致正十三烷-2-酮水平的增加,从而减缓了番茄潜叶蛾 (*Tuta absoluta*) 幼虫的发育<sup>[63-64]</sup>。

但是也有表皮毛不影响甚至有利于潜叶昆虫的例子。例如,美洲斑潜蝇在不同种寄主植物的适合度与叶片上表皮毛数、毛长度无关<sup>[50]</sup>。苜蓿的不同腺毛品系对苜蓿潜蝇的抗性并不强<sup>[65]</sup>。而橡树的表皮毛密度与一些潜叶昆虫(主要为潜叶蛾属 *Phyllonorycter* 和微蛾属 *Stigmella*) 的密度显著正相关,原因可能是表皮毛会阻碍寄生蜂的搜寻行为、减少外食性昆虫的取食竞争及降低寄生蜂的寄生率<sup>[66]</sup>。

据推测,叶刺应该也不利于潜叶成虫的取食和产卵。

### 6 叶脉

叶片维管束特别是叶脉中的维管束,对潜叶昆虫的生活相当重要。嫩叶叶脉含果胶、糖类和纤维素等,尚具较多可食部分;但老叶叶脉主要含纤维和木纤维,很难消化和吸收。因此,多数潜叶虫都避开维管束<sup>[2]</sup>。例如,一种微蛾 (*Stigmella lemniscella*) 沿着叶片的锯齿状边缘形成潜道,是因为叶缘的维管束非常纤细;多数情形下早龄幼虫避免穿越叶脉,但老熟幼虫口器发达,可穿越叶脉<sup>[2]</sup>。但桃潜蛾的早龄幼虫常穿过主脉,说明存在种间差异<sup>[2]</sup>。叶吉丁 (*Brachys tessellatus*) 所产的卵都避开火鸡栎 (*Quercus laevis*) 较大的叶脉并靠近叶缘<sup>[67]</sup>。一种穿孔蛾 (*Pertida glyphopa*) 幼虫会避免潜食红桉 (*Eucalyptus marginata*) 较厚的叶脉和油腺<sup>[68]</sup>。

一种尖蛾(*Stilbosis quadricustatella*)幼虫通常不穿越主脉但沿着侧脉形成斑块—线型的潜道;并且多个潜道通常不分布在主脉的同一侧<sup>[69]</sup>。山楂潜叶蛾主要产卵于苹果叶片的介于叶柄和叶尖之间的中部,而且也是介于主脉和叶缘之间<sup>[70]</sup>。七叶树潜蛾(*Cameraria ohridella*)沿着叶正面的侧脉产卵,但潜道却主要在两条侧脉间延伸<sup>[71]</sup>。芦苇潜蝇(*Agromyza phragmitidis*)将卵堆产于叶片的近端,在相邻的两条叶脉之间;幼虫孵化后向叶尖潜食,每个幼虫在两条叶脉间形成一个单独的虫道;幼虫选择性潜食叶脉间的叶肉,避免取食维管束组织<sup>[72]</sup>。两种彩潜蝇(*Chromatomyia milii*和*C. nigra*)尽量减少取食叶脉组织,取食叶肉的速率明显高于叶脉,取食小叶脉的速率明显高于更大、更硬且更强的叶脉<sup>[73]</sup>;它们的取食和产卵嗜好跟植物的叶脉间距离显著正相关,如果相邻叶脉间的距离太小可能会限制彩潜蝇产卵和生长<sup>[74]</sup>。胡桐(*Vismia guianensis*)的潜道解剖发现,潜叶虫避免取食叶肉中的晶体以及主脉和侧脉中的维管束组织<sup>[75]</sup>。

也有部分潜叶昆虫偏嗜叶脉,其大部分的潜道都穿过主脉或者比较大的侧脉,只有比较小的潜道分支通向叶边缘<sup>[2]</sup>。双翅目的裂斑翅实蝇(*Trypeta zoe*)、植潜蝇(*Phytomyza ramosa*和*P. alpiginae*)和潜蝇(*Agromyza apfelbecki*)都会在主脉形成潜道<sup>[2]</sup>。许多斑潜蝇潜食时都会回避叶脉,但有些斑潜蝇种类则专门潜食叶脉,甚至从中脉潜食到侧脉,例如线斑潜蝇(*Liriomyza strigata*)喜食维管束组织,尤其是叶脉<sup>[3]</sup>。潜食叶脉的昆虫停止取食时,绝大多数都会回到叶脉中的潜道,叶脉似乎可以为其提供庇护。因为叶脉中的潜道不易被天敌发现,而且叶脉潜道上面的覆盖层远比其它部位的表皮层更坚固<sup>[2]</sup>。因此潜叶昆虫取食叶脉是一种特化的习性。

## 7 小结和展望

叶片的着生位置、朝向、大小、颜色和表皮毛直接影响潜叶虫成虫的取食和产卵选择,叶片的这些物理性状成了潜叶昆虫识别寄主适合度的可靠参考。叶片的物理性状常常和叶片化学性状相关;结合叶片的物理信息和化学信息,潜叶虫可以形成所谓的寄主识别图谱。由于潜叶虫成虫产卵决定了其幼虫的生活场所和食料,从而影响其种群动态。长期进化的结果使得潜叶虫成虫具备选择适宜寄主植物的能力,从而可以保证后代能够正常生长发育。相反,如果多食性的潜叶虫成虫将卵产在不适宜的寄主上并成功完成生活史,则可能扩大其寄主范围<sup>[76]</sup>。

叶片的大小决定了叶片所能供养的潜叶虫幼虫数;叶片的厚度和叶脉则影响了幼虫的取食行为,也影响了潜道的形状和潜道覆盖层的厚度,从而对跨营养级的天敌也造成了间接影响,例如寄生率的变化。叶片的着生位置和朝向则会影响叶片的营养物质含量和次生物质含量,间接地作用于幼虫的取食。叶片的着生位置、朝向、叶片厚度、潜道覆盖层厚度都与潜道内部温度相关,从而影响潜叶虫的生长发育速率。叶片物理性状与潜叶昆虫的主要关系总结见表3。

表3 叶片物理性状与潜叶昆虫的主要关系

Table 3 The relationship between physical leaf features and leaf-mining insects

选择尺度 Scale of selection	主要叶片物理性状 Main physical features of leaves	多数潜叶昆虫的选择 Selection of most leafminers	可能的原因 Possible causes	关联因素 Related factors
生境	叶色	绿色	叶绿素	化学信息素
植株	叶片位置、朝向	向阳	容易发现	光照
冠层	叶片位置、朝向	中下层或阴生叶	成虫飞行能力、小气候、营养物质和有毒物质含量	光照
叶片	叶片大小、表皮毛	大叶片、叶毛少	大叶片可供养更多虫口、表皮毛少有利于成虫活动	植物品种差异、植物个体和构件差异等
叶片内部	叶脉	避开叶脉	叶脉营养低、难消化	昆虫种类差异

叶片物理性状与潜叶昆虫的关系不但因昆虫和植物种类而异,而且要受到外界环境如光照、气温、降水、土壤等的影响。这些外界因素不但影响寄主植物的生长发育,也影响了叶片结构物质的合成,从而影响叶片的物理性状。叶片的物理性状和叶片的化学特性是紧密联系的,叶片理化性质联合决定了潜叶成虫的寄主选



择性以及潜叶幼虫的生长发育和存活。

植物形态结构的某些细微变异可能对植食性昆虫的适应性产生明显的影响<sup>[12]</sup>。因而,研究叶片物理性状的防御作用以及潜叶昆虫对这些防御的适应,有助于了解潜叶昆虫-寄主植物的协同进化。外界环境和遗传育种都有可能改变植物叶片的物理特性,而对潜叶害虫产生抗性,实现潜叶害虫的可持续生态控制。

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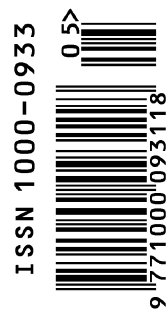
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