寄主挥发物、叶色和表皮毛在美洲斑潜蝇寄主选择中的作用

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摘要：在室内条件下，初步研究了寄主挥发物、叶色和表皮毛在美洲斑潜蝇寄主选择中的作用。在嗅觉仪试验中，寄主叶片挥发物对美洲斑潜蝇雌成虫没有明显的引诱作用；在叶色反应试验中，美洲斑潜蝇雌成虫在叶子圆片上停留的时间明显大于在滤纸圆片上停留的时间（$p<0.01$），其在有叶片区域分布的数量明显多于空白对照（$p<0.01$）；在表皮毛试验中，美洲斑潜蝇在无毛叶片上的产卵量明显大于在有毛叶片上的产卵量（$p<0.01$）。上述结果表明，在对寄主的定向和定位过程中，美洲斑潜蝇的视觉起着重要的作用，而嗅觉不起作用；叶片表皮毛有抑制产卵的作用。

关键词：美洲斑潜蝇；寄主选择性；寄主挥发物；叶色；表皮毛

Effects of host volatiles, leaf color, and cuticular trichomes on host selection by *Liriomyza sativae* Blanchard

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Abstract: The serpentine leafminer, *Liriomyza sativae* Blanchard, is one of the most serious worldwide pests of a great variety of vegetables and ornamental crops. It was first recorded in China in the Hainan province in 1993. Since then it has spread to the most regions of China, and it has attacked a wide variety of crops causing great economic losses. Previous studies have shown that the leafminer has different preferences for host plants. The mechanism on its host selection, however, is so far unknown. In this paper, the role of host volatiles, leaf color, and cuticular trichomes of host plants for host preference of the leafminer were studied in the laboratory.

A four-armed olfactometer was used to test the role of volatiles from host plants in host selection by the leafminer. One of the four arms was connected to the odor source of kidney bean leaves and the other three arms were connected to blank controls. The time spent by *L. sativae* adult females in the different areas of the olfactometer; each corresponding to one of the four odor sources was recorded and 30 females were tested in total. The results showed that although the time of the females in each of areas was significantly different ($p<0.05$), the time spent by the females in the area linked to the arm with the odor of kidney bean leaves was not always the longest. In another experiment, ten females were introduced into the olfactometer chamber simultaneously and the of the females remaining in each area of olfactometer was recorded once every 5 minutes for 30 minutes, and totally 100 females were tested. The number of females recorded in the different areas did not differ significantly ($p>0.05$). These results indicate that the volatile compounds emitted from kidney bean leaves do not play an important role in host selection by the leafminer.

To test the role of leaf color in host preference of the leafminer, a Petri dish (15 cm in diameter) was used in which a kidney bean leaf disc (4 cm in diameter) sealed with transparent film to prevent odor release was placed on one side and the

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other side was a piece of filter paper with the same size as the leaf disc. One female leafminer was released into the container and the time spent by the leafminer on the leaf disc or the paper was recorded continuously for 10 minutes, and 30 leafminers were tested. The results showed that the time spent by the leafminer on the kidney leaf disc was much longer ($p<0.01$) than that on the filter paper. In another experiment, four small flasks, one with a kidney bean leaf and the others with nothing in them as blank controls, were put into one of four corners of a square container ($80\times80\times15$ cm^3). Ten females were introduced into the container each time and the number of the females in each corner of the container was recorded every 5 minutes for 20 minutes. One hundred females were tested. It was found that the number of the females present in the corner with bean leaves was much more ($p<0.01$) than that in the other three corners with empty flasks.

A cucumber variety with hairy leaves was chosen to test the role of cuticular trichome of host plants in host preference of the leafminer. Three pairs of cucumber leaves (one normal leaf with cuticular trichomes and the other a control leaf from which the cuticular trichomes had been carefully removed with a forceps) were placed into a container (15 cm in diameter) and two pairs of the female and male were introduced. The number of eggs laid by the leafminer on the normal cucumber leaves and the control leaves was recorded after 24h, respectively. The results revealed that the number of the eggs was much less ($p<0.01$) on the normal leaves than on the control leaves.

It was concluded that the physical characteristics of the host plants, leaf color and trichomes, play an important role in the host preference of *L. sativae*, while the volatile compounds emitted from host plants do not.

Key words: *Liriomyza sativae* Blanchard; host selection; host volatiles; leaf color; cuticular trichomes

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植物与昆虫的关系是一个非常重要的生物学问题,对人类的农林生产和生活环境有很大的影响[1]。因此,关于植物与昆虫关系的研究一直是生态学研究的热点之一,特别是近20a来取得了很大的进展,已成为化学生态学研究的核心内容。美洲斑潜蝇(*Liriomyza sativae* Blanchard)是世界上最危险的检疫性害虫之一,自从1993年传入我国海南省以来,目前已至少蔓延到全国25个省、市和自治区,给农业生产造成了严重损失[2]。由于该虫生活史短、繁殖力强及易产生抗药性,因此选用抗虫品种是持续控制其危害的有效途径之一。寄主植物选择性的研究是选育和利用抗虫品种的基础。然而,关于美洲斑潜蝇寄主选择性的研究,国内外并不多见。Carolina等曾研究了美洲斑潜蝇在利马豆和洋葱上的选择性差异[3],邓望喜等在室内比较研究了美洲斑潜蝇对豆科与葫芦科主要蔬菜品种的选择性差异[4],张慧杰等评价了美洲斑潜蝇在田间的寄主选择性[5]。关于美洲斑潜蝇的寄主选择机制方面,Parrella认为美洲斑潜蝇对寄主的嗜好与表面茸毛的分布和密度有关[6],张慧杰等[7]和戴小华等[8]分别探讨了美洲斑潜蝇寄主选择性与叶片结构和叶片营养含量的关系。但是关于寄主挥发物和颜色在美洲斑潜蝇寄主选择中作用的研究未见有过报道,而目前普遍认为昆虫视觉和嗅觉等在寄主选择中起着重要的作用[1]。为此本文对寄主植物叶片挥发物、叶色和表皮毛在寄主选择中的作用进行了初步研究,以其为深入探讨植物与植食性昆虫的相互关系及利用作物布局和抗虫品种防治美洲斑潜蝇的危害提供必要的基础。

1 材料与方法

1.1 试验材料

1.1.1 供试虫源及预处理 供试美洲斑潜蝇成虫来自养虫室,试验前作如下处理:将200对刚羽化的成虫接入养虫笼($35\times35\times61$cm^3)内24h,任其交尾;前12h提供长豇豆作为食物源,后12h任其饥饿。

1.1.2 嗅觉仪 参考Pell和Vet(1983)的装置设计制作,材料为无色无味的有机玻璃。四臂的气流量控制在250ml/min,室内温度控制在25℃左右。将嗅觉仪放置于四周安装有日光灯的装置内,以使反应室各方向的光照强度均匀一致。

1.1.3 气味源 用一真空泵从嗅觉仪中心抽气,气味源(约5g四季豆新鲜叶片,叶片无破损)放置于嗅觉仪其中一臂部的三角烧瓶内,其它臂的三角瓶内放入湿润的滤纸作为对照。

1.2 试验方法

1.2.1 寄主挥发物对美洲斑潜蝇的影响

(1)**单虫试验** 选择活泼的美洲斑潜蝇雌成虫30头,每次接入1头于嗅觉仪反应室内,连续观察20min后更换气味源,每臂轮换一次,当四臂各轮换一次后,更换新的雌成虫。观察时,用秒表连续记录雌成虫在每臂区域停留的时间。臂间更换一次气味源,间隔5min后再观察。

(2)**多虫试验** 选择活泼的美洲斑潜蝇雌成虫100头,每次接入10头于嗅觉仪反应室内,观察30min后更换气味源,每臂轮换一次,当四臂各轮换一次后,更换新的雌成虫10头。观察时,每间隔5min记录在各臂区域停留的雌成虫数。臂间更换一次

气味源后,间隔5min再观察。每更换一次成虫,各臂记录6次,统计总虫量。

1.2.2 寄主叶色对美洲斑潜蝇的影响

(1)单虫试验　将四季豆叶片用打孔器打出直径为4cm的圆片,并将滤纸剪成同样大小的圆片作为对照。将直径15cm的培养皿底部垫上滤纸并分成两半,一半放上叶子圆片,另一半放上滤纸圆片,用透明的食物保鲜膜密封圆片,以防叶片气味散出产生干扰作用。选择活泼的美洲斑潜蝇雌成虫30头,每次在培养皿中接入1头雌虫,连续观察10min,用秒表分别记录雌虫在叶子圆片和滤纸圆片上停留的时间。10min后将培养皿水平旋转90°,间隔2min后继续观察。每头雌虫共观察4个方向,然后换用另一头雌虫、叶片、保鲜膜和滤纸等,并用75%酒精擦洗培养皿3遍,待干后再用。

(2)多虫试验　将嗅觉仪平板装置的通气口密封后,将一三角瓶放置于平板的一角,瓶内放有四季豆叶片并密封,另取3个同样的空三角瓶放置于平板另外三角作对照。注意放置时以便于平板内供试的成虫能充分发现瓶内叶片。选择活泼的美洲斑潜蝇雌成虫100头,每次将10头雌虫接入平板内,连续观察20min,每隔5min记录各区域分布的虫数。20min后在嗅觉仪平板的四角间轮流更换一次装有叶片的三角瓶,然后换用另外的10头雌虫,并对平板用75%酒精擦洗3遍,待干后使用。

1.2.3 寄主叶片表皮毛对美洲斑潜蝇寄主选择行为的影响　选择表皮毛较多的黄瓜(夏丰一号)叶片作为供试材料,用打孔器打出直径为2.3cm的小圆片。将另外同一叶龄的黄瓜叶片在解剖镜下小心地用眼科镊子夹除表皮毛,注意不要损伤叶片,也同样打出直径为2.3cm的圆片。取直径为15cm的养虫缸,内铺有约1cm厚的植物营养培养基,将成对的有毛、无毛叶子圆片紧贴于培养基上。每个培养缸内贴有3组成对的叶子圆片,接入两对经预处理的美洲斑潜蝇成虫,然后盖上纱布,用橡皮筋扎紧。24h后用解剖镜观察记录叶子圆片上的产卵数。试验共设15个养虫缸,即15个重复。

所用数据处理及分析均采用DPS软件进行。

2 结果与分析

2.1 寄主挥发物对美洲斑潜蝇寄主选择行为的影响

将单虫试验和多虫试验结果分别列于表1和表2。从表1可以看出,在单虫试验中雌虫在各臂区域停留的时间在总体上存在显著的差异($p<0.05$),但无一定的规律性,雌虫不一定在气味源所在臂区域停留的时间最长,有时甚至最短。例如,当气味源位于嗅觉仪的Ⅱ臂时,雌虫在其区域内停留的时间反而最短。在多虫试验中,当气味源分别位于Ⅰ臂和Ⅱ臂时,各臂区域分布的虫量差异不明显($p>0.05$);当气味源分别位于嗅觉仪的Ⅲ臂和Ⅳ臂时,各臂区域分布的虫量在总体上存在显著差异($p<0.05$),但与单虫试验一样也无一定的规律性。这说明供试寄主挥发物在美洲斑潜蝇寄主选择行为中作用不明显。

表1　单虫实验中美洲斑潜蝇在嗅觉仪各臂停留的时间

Table 1　Time of *Liriomyza sativae* adult female staying in the arms of olfactometer in single adult test

气味源所在臂 Arm with leaf volatile	停留的时间(min)Staying time in minutes				F值
	Ⅰ	Ⅱ	Ⅲ	Ⅳ	
Ⅰ	5.32±0.10a	4.34±0.09b	5.65±0.11a	4.45±0.09b	3.72*
Ⅱ	5.46±0.06a	3.98±0.12b	4.79±0.11c	5.56±0.09a	4.01*
Ⅲ	4.26±0.12a	5.42±0.10b	5.82±0.12b	4.37±0.08a	3.90*
Ⅳ	5.11±0.10a	5.76±0.09a	4.29±0.12b	4.54±0.07b	3.75*

* 表中数据为平均数±标准误差;同一行数据后标有相同字母表示无显著性差异($df=3,116$;$p>0.05$) Data are mean±standard error; Means in the same line followed by the same letter do not differ significantly($df=3,116$;$p>0.05$),by Duncan's multiple range test

表2　多虫试验中美洲斑潜蝇在嗅觉仪各臂停留的虫量

Table 2　Number of *Liriomyza sativae* adult female staying in the arms of olfactometer in multiple adults test

气味源所在臂 Arm with leaf volatile	停留的虫量(头)Number of female staying				F值
	Ⅰ	Ⅱ	Ⅲ	Ⅳ	
Ⅰ	15.60±0.55a	14.70±0.70a	14.70±0.77a	15.10±0.64a	1.22
Ⅱ	14.80±0.68a	14.80±0.55a	15.70±0.75a	14.70±0.60a	1.23
Ⅲ	15.11±0.69a	15.40±0.64a	13.60±0.48b	15.90±0.38a	4.26*
Ⅳ	15.30±0.63a	14.70±0.58b	14.20±0.87b	15.80±0.39a	3.41*

* 表中数据为平均数±标准误差;同一行数据后标有相同字母表示无显著性差异($df=3,36$;$p>0.05$) Data are mean±standard error; Means in the same line followed by the same letter do not differ significantly ($df=3,36$;$p>0.05$), by Duncan's multiple range test

2.2 寄主植物叶色对美洲斑潜蝇寄主选择行为的影响

u检验结果表明,在单虫试验中美洲斑潜蝇在滤纸圆片上与在叶子圆片上停留的时间存在着极显著的差异($p<0.01$)(表3),其在叶子圆片上停留的时间明显多于在滤纸上停留的时间。同时,在试验中观察到,每当美洲斑潜蝇雌成虫停留在叶子圆片

上时，会不停地在上面爬动，有伺机取食或产卵的迹象。这说明寄主植物叶片的绿色对美洲斑潜蝇雌成虫有明显的吸引力。

方差分析表明，在多虫试验中美洲斑潜蝇雌虫在嗅觉仪各臂区域分布的虫量存在极显著的差异($p<0.01$)(表 4)，其在有叶片区域停留的数量均在 30 头以上，而在其它 3 个无叶片区域停留的数量均在 4 头以下。这进一步说明寄主植物叶色在美洲斑潜蝇寄主选择中起着重要的作用。

表 3 美洲斑潜蝇在叶色反应中不同处理上停留的时间(min)

Table 3 Time of *Liriomyza sativae* adult female staying in different treatments of leaf color test

方向 Direction	东 East	南 South	西 West	北 North
叶子 Leaf	6.57±0.06	6.69±0.05	6.63±0.06	6.67±0.04
滤纸 Filter paper	3.20±0.04	3.07±0.05	3.11±0.04	3.11±0.03
u 值	40.77	50.97	38.95	71.20

* 表中数据为平均数±标准误 Data are mean±standard error; $u_{0.05}=1.96$，$u_{0.01}=2.58$

表 4 美洲斑潜蝇在叶色反应中嗅觉仪各臂停留的虫量

Table 4 Number of *Liriomyza sativae* adult female staying in the arms of olfactometer in leaf color test

叶片所在臂 Arm with leaf	停留的虫量(头)Number of female staying				F 值
	Ⅰ	Ⅱ	Ⅲ	Ⅳ	
Ⅰ	32.80±0.44Aa	2.40±0.22Bb	1.60±0.15Bb	3.20±0.33Bb	157.60**
Ⅱ	3.40±0.22Bb	30.40±0.27Aa	3.20±0.17Bb	2.90±0.31Bb	358.57**
Ⅲ	3.60±0.15Bb	3.20±0.26Bb	29.20±0.30Aa	4.00±0.31Bb	337.85**
Ⅳ	2.50±0.16Bb	2.50±0.17Bb	3.20±0.26Bb	30.70±0.31Aa	457.89**

* 表中数据为平均数±标准误差；同一行数据后标有相同小写(大写)字母表示无(极)显著性差异($df=3,36$; $p>0.05$ (0.01)) Data are mean±standard error; Means in the same line followed by the same small or capital letter do not differ significantly or much significantly ($df=3,36$; $p>0.05$ or 0.01), by Duncan's multiple range test

2.3 寄主叶片表皮毛对美洲斑潜蝇寄主选择行为的影响

t 测验结果表明，美洲斑潜蝇在有毛和无毛叶子圆片上的产卵量存在极显著的差异($t=17.95$，$df=14$)，无毛叶子圆片上的平均卵量(5.60±0.14)明显高于有毛叶子圆片上的平均卵量(2.69±0.88)。这说明寄主叶片表皮毛有阻碍美洲斑潜蝇产卵的作用。

3 讨论

植食性昆虫对寄主植物的发现和选择主要包括定向和定位两个行为过程。在对寄主植物及生境的定向反应中，昆虫的视觉和嗅觉起着重要的作用，而在对寄主植物种类和取食、产卵的定位反应中，昆虫的触觉和味觉起着重要的作用。通常认为寄主植物的挥发性物质、颜色和形状等在植食性昆虫对寄主植物的定向过程中起着重要作用[9]。在本研究中，四季豆叶片颜色对美洲斑潜蝇雌成虫具有明显的引诱作用，而四季豆叶片挥发物对美洲斑潜蝇雌成虫行为无明显的影响，这是否是由于挥发物浓度不够，还是美洲斑潜蝇本身既有的特性，有待于进一步深入研究。此外，寄主的形状和颜色种类(波长)在美洲斑潜蝇对寄主定向中起什么作用，也有待于今后补充研究。

美洲斑潜蝇成虫用产卵器在叶片上刺孔产卵和取食，产卵行为和取食行为相一致。美洲斑潜蝇幼虫移动性差，只能在成虫所产的叶片内蛀食，成虫的产卵行为决定了幼虫的生存环境和食料。因此，美洲斑潜蝇成虫的产卵选择行为决定了美洲斑潜蝇的寄主选择性。一般认为植物叶表面毛状体在植食性昆虫对寄主植物的定位过程中起着重要的作用[10]。本研究表明寄主叶片表皮毛有阻碍美洲斑潜蝇产卵的作用。李勇等人在研究美洲斑潜蝇对番茄的选择性行为中发现[11]，番茄叶片表皮毛的密度和长度与选择性强度呈负相关。其它种类的斑潜蝇也有相同的现象[12～15]。但张惠杰等人调查研究了不同寄主植物对美洲斑潜蝇的适合度及其与叶片结构的关系，其结果是适合度与叶片表皮毛的数量无显著的相关性[7]。本文认为张文之所以得到与绝大多数研究相反的结果，是与其选用的研究材料有关。张文所用的寄主材料为不同种的植物，不同种的寄主植物所含的营养物质、特别是次生物质的种类和含量可能存在较大的差异，而后者在植食性昆虫选择寄主植物的过程中可能起着更大的作用[16]。上述绝大多数研究选用的寄主材料为同种植物的不同品种，其所含营养物质和次生化合物的种类和含量的差异小于不同种寄主的差异，特别是本研究使用的材料为同一品种、同一叶龄的黄瓜叶片，其唯一的差别是有毛和无毛。因此，认为寄主叶片表皮毛有阻碍美洲斑潜蝇产卵的作用的结论更符合实际情况。

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