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封面图说: 遗鸥群飞来——遗鸥意即“遗落之鸥”(几乎是最后才被发现的新鸥种,因此得名)。1931年,瑞典动物学家隆伯格撰文记述在中国额济纳采到了标本。1987年,中国的鸟类学家在鄂尔多斯的桃力庙获得了一对遗鸥的标本。1990年春夏之交,发现了湖心各岛上大量的遗鸥种群。近年来的每年夏季,大约全球90%以上的遗鸥都会到陕西省神木县境内的沙漠淡水湖-红碱淖上聚集。遗鸥——国家一级重点保护、CITES附录一物种。

彩图提供: 陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

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曹宇, 郅军锐, 孔译贤. 西花蓟马在6种蔬菜寄主上的实验种群生命表. 生态学报, 2012, 32(4): 1249-1256.

Cao Y, Zhi J R, Kong Y X. Life tables for experimental populations of *Frankliniella occidentalis* on 6 vegetable host plants. Acta Ecologica Sinica, 2012, 32(4): 1249-1256.

西花蓟马在6种蔬菜寄主上的实验种群生命表

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摘要:自西花蓟马 *Frankliniella occidentalis* 传入我国后, 该虫对蔬菜寄主的危害趋于严重, 组建了 25 ℃ 条件下, 西花蓟马在黄瓜、甘蓝、莴苣、茄子、芹菜和大蒜叶片的实验种群生命表, 以研究西花蓟马的危害差异性, 为西花蓟马的防治提供基础数据。结果表明西花蓟马的生长发育、繁殖和生命表参数等在不同寄主之间有明显差异。西花蓟马在黄瓜上发育最快, 其未成熟期为 11.43 d, 同时在黄瓜上最先开始产卵, 产卵前期为 1.22 d, 在芹菜上发育最慢, 为 16.11 d。其每雌每天在甘蓝上和莴苣上产卵量最大, 分别为 2.88 粒和 2.48 粒, 在大蒜上最小, 为 0.77 粒; 每雌每天产雌率、子代雌性比在甘蓝和莴苣上都大于其他寄主。雌虫寿命在甘蓝上最长(29.06 d)、雄虫寿命在莴苣上最长(13.22 d)。西花蓟马在黄瓜、莴苣、茄子、甘蓝、芹菜和大蒜上的内禀增长力 r_m 值分别为 0.1318、0.1228、0.1154、0.1197、0.0860 和 0.0791; 净增殖率 R_0 分别为 19.1248、30.8523、17.9322、34.5322、8.9491 和 8.3536。种群趋势预测指数(I)在甘蓝(34.17)、莴苣(30.09)上明显高于其它寄主, 在芹菜(8.00)和大蒜(8.22)上最低。

关键词:西花蓟马; 蔬菜寄主; 实验种群; 生命表

Life tables for experimental populations of *Frankliniella occidentalis* on 6 vegetable host plants

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Abstract: Western flower thrips, *Frankliniella occidentalis* (Pergande), has become one of the most important agricultural pests worldwide, because of its extensive host range, reproductive capacity, invasion potential, plant viruses transmission ability and insecticide resistance. All of these interrelating factors are related to the basic life cycle and life history of the species, making western flower thrips the significant, difficult pest to manage. More than 500 kinds of host plants of western flower thrips have been reported. Notably, more and more serious damage to vegetables by *F. occidentalis* has been observed in recent years and the levels of damages were different with vegetable species. In order to know the differences and offer basis data for control, the life tables for experimental populations of *F. occidentalis* were established at constant temperature of 25 ℃, relative humidity of 70% and photoperiod of 16L:8D, on cucumber, lettuce, eggplant, cabbage, celery and garlic leaves, respectively. The results showed that the thrip could develop and reproduce on all tested host plants, and there were significantly differences in the developmental periods, survival rates and fecundities on the 6 vegetable hosts. The shortest time for *F. occidentalis* to complete one generation was 11.43 days on cucumber, and the longest was 16.11 days on celery. The survival rates of *F. occidentalis* at different stages were different on different host

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plants. In short, the highest generation survival rates were on eggplant and garlic, and the lowest were on celery and cucumber. The fecundities per female per day were 2.88 on cabbage and 2.48 on lettuce, which were much bigger than those on other hosts, and the least was 0.77 on garlic. From all the life history of *F. occidentalis*, the number of female offspring increased at beginning and then declined, with the obvious oviposition peaks varying with different hosts as time increased. The rates of *F. occidentalis* female offspring on cabbage 1.9694 and lettuce 1.7649 per female per day were significantly higher than on other host plants. In addition, the sex ratio of offspring was also the highest on the two hosts, 0.72 and 0.76, respectively. The innate capacity of increase (r_m) of experimental population of *F. occidentalis* on cucumber, lettuce, eggplant, cabbage, celery and garlic was 0.1318, 0.1228, 0.1154, 0.1197, 0.0860 and 0.0791, respectively, and the net reproductive rate (R_0) was 19.1248, 30.8523, 17.9322, 34.5322, 8.9491 and 8.3536, respectively. There were no significant differences in the mean generation time (T), and the trend indexes of experimental population (I) of *F. occidentalis* were similar to R_0 . Based on the parameters of the life tables on different hosts, the most suitable host plants for the development and reproduction of *F. occidentalis* were cabbage and lettuce, followed by cucumber and eggplant, the least celery and garlic. It could be concluded that host was an important factor influencing the development and fecundity of *F. occidentalis* populations. A lot of studies pointed out that there were many factors influencing the feeding, growth, development and oviposition of insects, such as flower, nutritional status, secondary substances and so on. So much more work needed to do for further understanding the differences and mechanism of *F. occidentalis* on different hosts.

Key Words: *Frankliniella occidentalis*; vegetable host; experimental population; life table

近30年来,西花蓟马 *Frankliniella occidentalis* 由于其强大的繁殖能力和入侵能力^[1-3],被视为重要的检疫性害虫;其寄主范围广、传播番茄斑萎病毒 Tomato spotted wilt virus (TSWV)等多种病毒造成巨大的危害^[4-7],被认为是世界范围最重要的农业经济作物害虫之一;其抗药性强,是防治上的难题^[8-10]。因此,在超过5000种类的蓟马研究中,每年对西花蓟马的研究报道达到三分之一^[11]。

西花蓟马于2003年传入我国,调查发现西花蓟马的寄主几乎包括了所有的露天蔬菜^[12-14],且危害程度不同。Mound^[15]指出找到引起寄主之间不同危害的因素非常关键,有助于找出植物的抗性机制。鉴于西花蓟马对露天蔬菜的危害日趋严重^[16],本文选取了不同科的6种常见蔬菜为寄主研究西花蓟马取食它们时的实验种群生命表,以期为掌握西花蓟马在蔬菜寄主上的种群变化规律,探讨其与寄主植物的相互关系及其对植物的适应性,选育抗性品种、调整作物布局,以及为西花蓟马的防治和预测预报等提供一定的理论依据。

1 材料与方法

1.1 供试虫源

西花蓟马采自贵州省贵阳市花溪区附近各类蔬菜上,带回实验室在人工气候室分别以黄瓜、甘蓝、莴苣、茄子、大蒜和芹菜叶片饲养3代纯化备用。

1.2 饲养条件

本实验在贵州大学昆虫研究所人工气候箱(RXZ系列多段可编程智能人工气候箱)中进行,温度设定为(25±1)℃,湿度(70±1)%,光照L:D(14:10)。

1.3 供试寄主

黄瓜、莴苣、芹菜、茄子、大蒜、甘蓝均种植在温室中且未喷洒农药,以获取无蓟马及其它害虫污染的干净寄主植物,其叶片作为供试材料。

1.4 实验方法

将若干西花蓟马雌、雄成虫分别置于食料为黄瓜、甘蓝、莴苣、茄子、大蒜和芹菜叶片的养虫盒内,任其产卵,12 h后移去成虫,每日8:00和20:00在镜下观察养虫盒内植物组织中卵的孵化情况,直到没有若虫孵化

出来为止。统计从产卵至孵出若虫的时间,作为卵的发育历期。另将初孵若虫单头挑取在25.4 mm×76.2 mm,凹面直径为18 mm的两片凹玻片形成的饲养小室内^[17]。凹玻片内事先分别放入6种寄主植物约1 cm²的叶片小块,每种寄主植物下供试若虫为100头。每日8:00和20:00各观察1次,记录各虫态的发育和存活情况,每隔1—2 d更换1次新鲜寄主植物。羽化为成虫后,马上把西花蓟马雌雄成虫配对在直径3 cm,高2.5 cm的透明塑料小瓶中,小瓶底部铺上滤纸,滴上适量蒸馏水,滤纸上再各放上稍小于小瓶直径的6种植物叶片。每种蔬菜供试成虫25对。每天记录成虫的存活情况,且每天更换植物叶片,并将更换的叶片保留至8 d以上,保证所有的卵均能孵化,记录孵化出的若虫数,以若虫数作为产卵量的估计^[18],直到雌虫自然死亡。孵化出的若虫继续饲养至成虫,鉴别雌雄并进行计数,统计后代的雌雄比例和存活率。

1.5 西花蓟马实验种群生命表的主要指标

生命表中参数的计算公式如下:净增殖率 $R_0 = \sum l_x m_x$; 平均世代周期 $T = \frac{\sum l_x m_x x}{R_0}$; 内禀增长率 $r_m = \frac{\ln R_0}{T}$; 周限增长率 $\lambda = e^{r_m}$; 种群加倍时间 $t = \frac{\ln 2}{r_m}$ 。式中 x 为按年龄划分的单位时间间距; l_x 表示任一个体在 x 期间的存活率; m_x 表示在 x 期间平均每雌产雌数。

1.6 数据处理

实验数据用SPSS18.0程序进行统计分析,采用Duncan氏新复极差检测法比较不同寄主上西花蓟马的未成熟期、产卵前期、产卵历期、产卵量和寿命等之间的差异显著性。

2 结果与分析

2.1 西花蓟马在不同寄主上的生长发育和繁殖情况

西花蓟马取食不同蔬菜时,生长发育和产卵量明显不同(表1)。在所选6种蔬菜寄主上,西花蓟马在芹菜上发育速度最慢,其未成熟期为16.11 d,在黄瓜上发育速度最快,为11.43 d,稍快于甘蓝、莴苣。西花蓟马在黄瓜上最先开始产卵,产卵前期为1.22 d,在大蒜上最慢,为3.28 d;在甘蓝上的产卵期最长,为24.83 d,但和莴苣上没有显著差异;产卵期在芹菜上最短,为14.94 d。西花蓟马的产卵量在不同寄主之间有明显的差

表1 25℃下西花蓟马在6种寄主上的发育、繁殖参数和寿命

Table 1 Life-span of adult and parameters about development and oviposition of *Frankliniella occidentalis* on 6 hosts at 25℃

寄主 Host	黄瓜 Cucumber	莴苣 Lettuce	茄子 Eggplant	甘蓝 Cabbage	芹菜 Celery	大蒜 Garlic
未成熟期 Immature	11.43±0.21e	12.15±0.16d	13.54±0.19b	12.23±0.21d	16.11±0.28a	12.96±0.17c
产卵前期/d Pre-oviposition of imago	1.22±0.17d	1.78±0.28cd	1.94±0.21bcd	2.12±0.27bc	2.72±0.32ab	3.28±0.38a
产卵后期/d Post-spawning	3.28±0.32bc	1.72±0.27e	2.89±0.31cd	2.06±0.26de	4.72±0.27a	3.94±0.37ab
产卵历期/d Oviposition of imago	21.44±1.46a	23.67±2.16a	20.00±1.20a	24.83±1.12a	14.94±1.76b	21.11±2.25a
每雌每天产卵量/粒 Oviposition amount per day	1.91±0.08c	2.48±0.17b	1.68±0.05cd	2.88±0.09a	1.47±0.07d	0.77±0.04e
每雌总产卵量/粒 Oviposition amount per female	40.39±2.68c	58.11±6.63b	33.39±2.14c	70.83±3.23a	20.50±1.81d	15.50±1.48d
每天每雌产雌量/粒 Female offspring per day per female	1.10±0.02b	1.75±0.01a	0.97±0.01bc	1.97±0.03a	0.72±0.02c	0.40±0.01d
雌虫成虫寿命/d Life-span of female	25.94±1.68ab	27.28±2.38ab	23.94±1.09ab	29.06±1.08a	22.50±1.87b	28.50±2.48a
雄虫成虫寿命/d Life-span of male	12.33±0.64ab	13.22±0.75a	12.22±0.75ab	12.56±0.69ab	10.67±0.63b	12.67±0.86ab

表中数据为平均数±标准误,同一行中小写字母不同,表示西花蓟马在不同寄主之间达到显著水平($P<0.05$; Duncan氏新复极差测验法)

异,产卵较高的为甘蓝和莴苣,分别为70.83粒和58.11粒;在大蒜上最低,为15.5粒。雌虫平均寿命在甘蓝上最长,雄虫寿命在莴苣上最长。雌虫寿命在6种寄主上均是雄虫寿命的2倍多,从危害时间来说,雌虫危害比雄虫要严重得多。综合各项指标,西花蓟马在甘蓝和莴苣上的各项参数优于其他寄主,表1可清楚的反映出这种关系。

2.2 寄主对西花蓟马存活率和产雌率的影响

西花蓟马在6种蔬菜寄主上的存活率与产雌率的关系如图1所示。从图1可以看出,西花蓟马在不同年龄时期的存活率不同,并在各寄主的前期曲线坡度较陡,说明在幼龄时期间的死亡率较高,在芹菜上表现的最突出。西花蓟马进入成熟期后,在各个寄主上有一个相对较长的稳定存活率伴随其产卵,此段时间可产生大量后代个体,到成虫后期死亡率也较高。西花蓟马产雌数在不同寄主上表现出不同的变化曲线,但相同的是中间存在多个峰值。不同寄主上,峰值出现的时间和幅度有着不同程度的差异。从图中可以看出,莴苣和甘蓝上的平均每雌产卵数显著高于其他寄主,说明西花蓟马在莴苣和甘蓝上繁殖最快,种群增长速度最快。

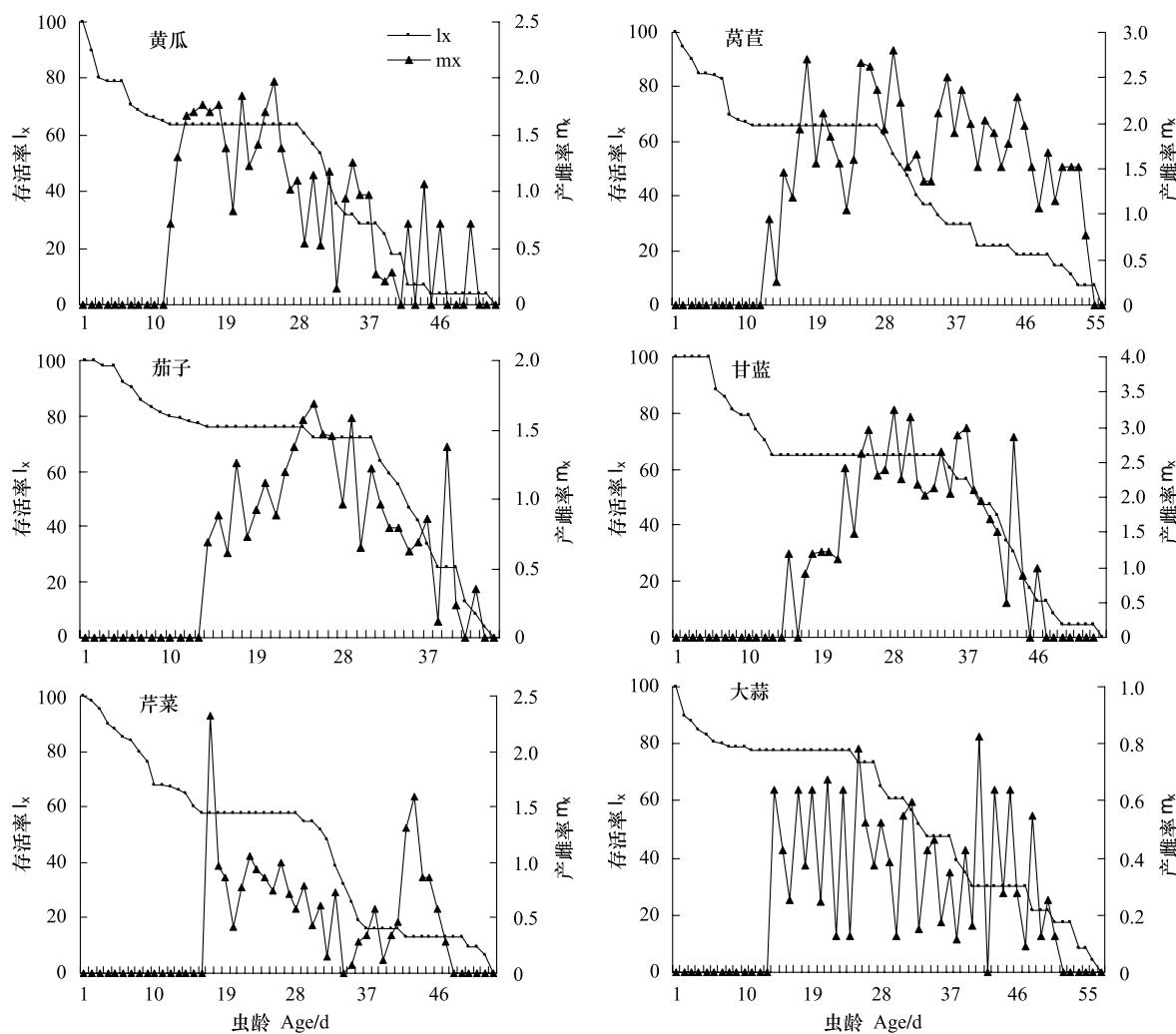


图1 西花蓟马在不同蔬菜上的年龄特征存活率(l_x)和年龄特征产雌数(m_x)

Fig. 1 Age specific survival(l_x) and fecundity(m_x) of *Frankliniella occidentalis* feeding on different vegetables

2.3 西花蓟马在不同寄主上的生命表参数

由表2可见,净增殖率 R_0 (34.5322)在甘蓝上最大,其次为莴苣(30.8523),两者的后代可增长30倍以上,说明西花蓟马在此两种寄主上有爆发的潜能;在芹菜、大蒜上较低,分别为8.9491、8.3536,其后代增长倍数在10以下;在黄瓜和茄子上居中,分别为19.1248、17.9322。西花蓟马在6种寄主上的 r_m 均大于零,说明种

群数量在所选取的寄主植物上都呈上升趋势。内禀增长率 r_m 在甘蓝(0.1197)和莴苣(0.1228)上依然较大,虽然略小于黄瓜(0.1318),但相差不大,且明显高于芹菜(0.0860)和大蒜(0.0791)。种群加倍时间 t 在黄瓜、莴苣、茄子和甘蓝5—6d,而在芹菜、大蒜上需要8d以上,平均世代周期 T 在黄瓜上最小,但6种寄主上世代周期 T 相差不大,所以在不同寄主上发生的世代危害数也不会有明显差异。周限增长率 λ 在甘蓝上最大(1.1272),但6种寄主之间差异也不大。西花蓟马在6种寄主上种群趋势预测指数(I)和净增殖率 R_0 在后代倍数增长的结论基本上是一致的,表明在甘蓝和莴苣上,西花蓟马后代种群数量增加幅度比其他寄主大很多。综合表2中各生命表参数分析,莴苣和甘蓝最适于西花蓟马的生长和繁殖,黄瓜、茄子次之,大蒜、芹菜则不适用于西花蓟马的生长与繁殖。

表2 25℃下西花蓟马取食6种寄主植物生命参数的比较

Table 2 Comparison of life table parameters of *Frankliniella occidentalis* on 6 host plants at 25 ℃

参数 Parameter	黄瓜 Cucumber	莴苣 Lettuce	茄子 Eggplant	甘蓝 Cabbage	芹菜 Celery	大蒜 Garlic
净增殖率(R_0) Net reproductive rate	19.1248	30.8523	17.9322	34.5322	8.9491	8.3536
内禀增长率(r_m) Intrinsic increase rate	0.1318	0.1228	0.1154	0.1197	0.0860	0.0791
平均世代周期(T)/d Mean generation time	22.3948	27.9306	25.0101	29.5911	25.4623	26.8134
周限增长率(λ) Finite increase rate	1.1409	1.1307	1.1223	1.1272	1.0898	1.0823
种群加倍时间(t)/d Population doubling time	5.2590	5.6445	6.0064	5.7907	8.0598	8.7629
种群趋势预测指数(I) Population trend index	18.61	30.09	18.03	34.17	8.00	8.22

3 讨论

生命表是研究昆虫种群数量变动机制的重要方法^[19],其涉及到的参数如净增值率 R_0 、内禀增长率 r_m 、发育速率、存活率、产卵量等可以在不同的侧面评价昆虫对寄主植物的适应性。一般而言,昆虫在较短的发育时间和较大的繁殖能力能够反映出昆虫对特定寄主的适应性^[20-21]。本实验结果表明6种寄主对西花蓟马不同生育阶段影响不同,单从发育速率看,黄瓜、莴苣是西花蓟马的适宜寄主;单从存活率来看,大蒜、莴苣、茄子是西花蓟马的适宜寄主,但莴苣 R_0 、产卵量都远远大于黄瓜、大蒜和茄子,因此,莴苣为西花蓟马的更适宜寄主;而甘蓝上虽然存活率低,但其单雌产卵量高、生殖力强, R_0 和 r_m 值均大,说明甘蓝也是西花蓟马的适宜寄主。同时,西花蓟马在不同寄主上的产卵的差异性在一定程度上可以用来评价其对特定寄主的适应性^[22]。李传明的研究表明,昆虫到达新寄主后,一般经过1—2代就能基本适应新寄主,即产卵量稳定^[23]。本文将田间西花蓟马带回实验室,都是在各寄主上饲养3代以后进行的实验,因此,其产卵量已经稳定,可以根据其产卵量对寄主的适应性进行评价。所以,根据决定种群增长的两个重要参数的 R_0 和 r_m 值,以及其它生命表参数综合分析,从本文的结果可以得出,甘蓝、莴苣为西花蓟马的适宜寄主,黄瓜、莴苣次之,而芹菜、大蒜为其不适宜寄主。这可能也是西花蓟马侵入贵州后,在贵州蔬菜寄主上适应的结果。营养生长期的莴苣、甘蓝植株体积、叶片等大于其他4种寄主,利于提供西花蓟马广阔的生存空间,减小其种内和种间竞争等。生殖生长期的黄瓜植株体积虽然最大,从整个生长期考虑,其提供的有效生态位可能小于甘蓝和莴苣,使得在长期的相互适应过程中,甘蓝和莴苣成为西花蓟马的更适宜寄主,芹菜、大蒜成为其不适宜寄主。另外,大蒜、芹菜自然条件下强烈的刺激性挥发物质可能影响西花蓟马的产卵选择。

西花蓟马自我国首次在辣椒上发现以来,寄主范围逐步扩大,也就是其对不同寄主逐渐适应的过程。这种对不同寄主的适应过程,从西花蓟马在不同寄主上的繁殖力和生命表参数的差异有所体现。例如相同条件下的黄瓜上,Mollema的38.7粒^[24]、Kiers等的38.4粒^[25]与本文研究结果40.39粒接近,而西花蓟马产卵量

在相同条件下的四季豆叶、四季豆豆荚、萝卜叶、棉花叶等表现出不同程度的差异性^[26-31],本研究表明在西花蓟马的 r_m 值在不同寄主上也有一定差异,类似研究在相同寄主黄瓜上,本实验得出 r_m 值为0.1318,小于同样条件下Wilma的0.3^[32],与Paul的0.166接近^[33],其他报道西花蓟马在相同条件下的菜豆叶、棉花叶、花生叶、四季豆豆荚的 r_m 值都有不同的波动^[28, 31,,34-35]。

昆虫与寄主相互适应的关系非常多,有报道称植物中可溶性蛋白质和可溶性糖的比例会影响植食性昆虫的取食,可溶性蛋白质含量高,昆虫的存活率、生长发育速率和生殖力相对提高,寄主体内各种成分的差异都可能影响着昆虫对寄主的适应性^[36-38]。本文仅从生物学上组建了西花蓟马的生命表,因此,要研究西花蓟马对寄主植物的适应性,还需要进一步对其在不同寄主植物上的取食行为、寄主植物对西花蓟马的抗性因子及寄主植物体内物质等进行分析,同时研究西花蓟马取食不同寄主后各项生理指标的差别。除此之外,文中6种寄主分属于6个不同的科,因此,寄主叶片的物理结构、叶片厚度以及叶毛数等也可能影响西花蓟马的产卵,西花蓟马产卵是将其产在组织内,因此,叶片厚度大、栅栏组织疏松等可以提供相对广阔的产卵空间,而营养状况好利于卵的孵化,叶毛数多则可以更好的保护卵,防止更多的天敌危害等,这都可能是西花蓟马产卵为适应环境的而采取的对策,而且寄主物理性状等对烟粉虱寄主适应性的影响有所报道^[39-40]。

另外,本实验是利用寄主的叶片,并没有考虑到寄主的开花因素。事实上,研究表明花粉对西花蓟马的存活率、产卵等有很大的影响^[41-42],且西花蓟马在棉花上,加入花粉饲养的 r_m (0.22)大于无花粉的 r_m (0.157)^[31],无花寄主比有花寄主对西花蓟马具有更强的抗性^[43]。Mound和Brent等都指出,花中含有高浓度的营养物质,大量蛋白质聚集在花粉中,花可以以花粉的方式提供营养,有利于昆虫的生长繁殖^[44-45],但是这其中起作用的营养物质并不清楚,蛋白质也不一定就是唯一影响物质。实际观察中,短花期植物上,花期阶段的西花蓟马数量明显高于非花期,这可能是花期引起的暂时性爆发;而长花期植物比如一些花卉,其数量相对稳定,但Isobel发现不同种类花上的西花蓟马的种群数量是不同的^[46],虽然不清楚是何种因素引起的差异,但可以肯定花对西花蓟马的取食、危害以及产卵等是有影响的,所以探讨西花蓟马对寄主适应性时考虑花的因素更为全面。在研究寄主影响因素时,应横向比较不同寄主的花、叶、果实之间成分的差异,同时纵向比较同寄主花、叶、果实等成分的差异,尤其花期、非花期及两者共存时的各种因素比较,以发现比较一致的影响因素。当然,这种比较不能仅限于寄主营养物质,寄主的次生物质也是很重要的,Fraenkel指出植食性昆虫的适应性决定于对植物次生物质的适应性^[47-48],Kennedy则认为植物次生物质、营养成分都是决定昆虫适应性的重要因素^[49-50],李典模、钦俊德等也指出昆虫与寄主之间的关系非常复杂,影响两者相互适应的因素非常多^[51-52]。所以,我们在研究西花蓟马对寄主的适应性时,除了上述寄主的物理结构、营养物质的分析外,还应该对寄主次生物质的影响进行探讨,甚至进一步研究西花蓟马取食不同寄主后各项生理指标都是必要的。

本文只研究了各寄主上一代的生命表数据,若研究多代可提供更精细的数据,且温度、光照对西花蓟马的生命表参数也是有影响的^[27, 30, 34],所以从寄主差异、温度、光照、天敌等综合考虑西花蓟马的对寄主的适应性,对于防治西花蓟马可提供更可靠的依据。

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