

烟粉虱种内及种间竞争取代机制

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摘要: B型烟粉虱(*Bemisia tabaci*)是烟粉虱复合种下危害最为严重的一个生物型, 现已成为一种世界性的害虫, 被称为“超级害虫”。近年来, 在许多地区发现B型烟粉虱竞争取代非B型烟粉虱和其他害虫的现象。综合相关报道, B型烟粉虱竞争取代机制包括资源利用竞争和相互干扰竞争, 可能涉及的因素包括: 生态位竞争、寄主适应能力的差异、非对称交配互作、高温逆境适应能力差异、药剂敏感性差异及其与双生病毒的互作等, 且B型烟粉虱可能含有的独特的内共生菌对增强其竞争能力也具有一定作用。此外, 本文还就目前Q型烟粉虱在局部区域严重危害的相关机制进行了探讨。

关键词: 烟粉虱, 生物型, 入侵物种, 种内/种间竞争, 竞争机制

Mechanisms of inter- and intra-specific competitive replacement by the *Bemisia tabaci* B biotype (Homoptera: Aleyrodidae)

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Abstract: The B biotype of *Bemisia tabaci*, sometimes called a “super bug”, has been one of this species complex’s most harmful biotypes because of the tremendous damage it inflicts worldwide. Recently, competitive displacement of pre-existent biotypes and other herbivores by the *B. tabaci* B biotype has been observed in many regions worldwide. Based on literature review, the mechanisms responsible for competitive replacement by *B. tabaci* may include exploitation or interference competition, which involve niche competition, differential abilities in resource acquisition, asymmetric mating interactions, heat shock adaptation, pesticide susceptibility, and interactions between *B. tabaci* B biotype, host plants, and viruses. Moreover, the B biotype likely has unique endosymbionts, which may be important in enhancing its competitive ability. We also discuss related mechanisms involved with serious damage caused by the *B. tabaci* Q biotype.

Key words: *Bemisia tabaci*, biotype, invasive alien species, inter- and intra-specific competition, competitive mechanism

20世纪80年代末, 烟粉虱(*Bemisia tabaci*)在美国及其他国家相继暴发, 据推测这些地区的烟粉虱可能是一个新的生物型(Schuster *et al.*, 1990)。之后, Costa和Brown (1991)证实了烟粉虱新的生物型即B型烟粉虱的出现。Bellows等(1994)认为B型烟粉虱是一个新种, 并命名为银叶粉虱(*Bemisia argentifol-*

lii)。然而, 多数学者认为烟粉虱是一个正在处于快速进化过程的复合种(species complex), 而B型烟粉虱只是其中的一个生物型(De Barro *et al.*, 2000; Kirk *et al.*, 2000; Perring, 2001; 柯俊成等, 2002)。在过去的近20年间, B型烟粉虱借助一品红(*Euphorbia pulcherrima*)或其他花卉的贸易活动在世界范围内

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扩散(Brown *et al.*, 1995; De Barro *et al.*, 1998), 并暴发成灾, 已成为一种世界性的重要害虫, 被称为“超级害虫”(super bug) (Barinaga, 1993)。

烟粉虱造成的危害主要包括: 其成虫和若虫直接吸取植物汁液, 分泌的蜜露招致霉污病而影响植物光合作用、污染植物产品, 传播植物病毒以及引起植物生理异常等, 给农业生产造成了巨大的经济损失(Perring *et al.*, 1993)。如在美国的佛罗里达州、德克萨斯州、亚利桑那州和加利福尼亚州, 1991年和1992年B型烟粉虱危害造成的损失分别为2亿和5亿美元(Henneberry & Toscano, 1996); 加利福尼亚州的Imperial County仅1996年对B型烟粉虱的防治费用就高达1,200万美元(White, 1998)。在澳大利亚, B型烟粉虱已成为园艺产业的重要害虫(Gunning *et al.*, 1995)。目前, 在南非(Bedford *et al.*, 1992)、以色列(Horowitz *et al.*, 2002)、韩国(Lee & De Barro, 2000)、巴西(Lima *et al.*, 2002)等许多国家也有B型烟粉虱危害的报道。在我国, 烟粉虱最早记载于1949年(周尧, 1949), 但在20世纪90年代中期以前危害并不严重。自1997年在广东省局部地区发生烟粉虱危害以来, 逐年加重, 且在南方和北方地区均大面积发生, 现已成为我国蔬菜、花卉、棉花等的重要害虫(罗晨等, 2000; 张芝利和罗晨, 2001)。分子标记(mtDNA COI)鉴定结果显示, 我国至少存在6个烟粉虱单倍型(B、Q、ZHJ-1、ZHJ-2、ZHJ-3和FJ-1) (Li, 2006; 万方浩和郭建英, 2007), 其中外来的B型烟粉虱已在我国大部分地区发生(罗晨等, 2002; Wu *et al.*, 2002, 2003; Qiu *et al.*, 2003)。

目前, 在许多国家和地区发现B型烟粉虱竞争取代非B型烟粉虱的现象。在美国, B型烟粉虱在很短时间内取代了土著A型烟粉虱(Perring *et al.*, 1993; Bellows *et al.*, 1994); 在墨西哥(Costa *et al.*, 1993)、澳大利亚(De Barro & Hart, 2000)、巴西(Lima *et al.*, 2002)和我国浙江的杭州、温州、宁波等地(臧连生等, 2005), 也相继发现B型取代本地非B型烟粉虱的现象。同时, 研究还表明B型烟粉虱能竞争取代其他植食性害虫如叶蝉、蚜虫等(Patil, 1996; Inbar *et al.*, 1999a; McKenzie *et al.*, 2002; Pascual & Callejas, 2004)。

竞争取代是种间竞争中最残酷的结果, 一般是指一种生物通过直接或间接的竞争作用将一个原来已经建立种群的生物替代的现象, 并随着人类对

环境影响的增加如外来入侵物种增多(Niemela & Mattson, 1996)和气候变化(Gryj, 1998)而日益频繁(Reitz & Trumble, 2002)。多数竞争取代是由多个竞争机制引起的, 而B型烟粉虱竞争取代的机制包括资源利用竞争和干扰竞争(Perring, 1996; Mayer *et al.*, 2002; McKenzie *et al.*, 2002), 其中所涉及的因素主要包括: 生态位竞争、寄主适应能力的差异、非对称交配互作、高温逆境适应能力的差异、药剂敏感性差异、烟粉虱与双生病毒的互作(Reitz & Trumble, 2002; 褚栋等, 2004; 万方浩等, 2005; Jiu *et al.*, 2007; Liu *et al.*, 2007)等。另外, B型烟粉虱可能含有独特的内共生菌(褚栋等, 2006), 对增强其竞争能力具有一定作用。

1 生态位竞争

B型烟粉虱与非B型烟粉虱和温室粉虱(*Trialeurodes vaporariorum*)由于生态位相同而发生竞争取代。竞争排斥原理(principle of competition exclusion)认为, 生态位相同的两个物种, 由于食物、空间等环境资源的限制, 大多不能长期共存于同一空间。Perring (1996)在分析B型取代A型烟粉虱的因素时发现, 两者的许多生态位相同, 包括相同的寄主植物、相似的季节活动规律以及相同的小生境。两者的寄主范围多有重叠, 但B型寄主植物范围更广, 并涵盖A型的寄主(Byrne & Miller, 1990; Bellows *et al.*, 1994)。这对于B型的生存尤其是越冬有利, 也进一步加大了它对春季瓜类作物和棉花的危害(Perring, 1996)。B型和A型具有相似的季节活动节律, 如在美国加利福尼亚州, 越冬的B型烟粉虱于1-2月份迁至葫芦科植物上; 而A型1月末孵化, 3月底迁至葫芦科植物上(Perring, 1996)。B型与A型具有相同的小生境, 如A型主要在远轴的叶子背面取食, B型在棉花(Naranjo & Flint, 1994)和瓜类作物(Tonhasca *et al.*, 1994)上也有相似的取食分布方式。另外, A、B型的雌性均喜欢在幼嫩的叶片上产卵(Chu *et al.*, 2002)。

在我国北方一些地区, B型烟粉虱正在逐渐取代温室粉虱(张芝利, 2000)。研究表明, B型烟粉虱和温室粉虱也有相似的生态位, 它们生活史相近, 均以成虫和若虫群集于寄主叶片背面刺吸植物汁液, 且有很多共同的寄主。如在北京地区, 7-8月份是温室粉虱的发生盛期, 而B型烟粉虱的盛发期稍晚,

约在8–9月份; B型烟粉虱和温室粉虱均可危害黄瓜、番茄、茄子等温室作物及一些观赏植物(罗晨等, 2007)。

2 寄主适应能力

许多研究表明, B型烟粉虱在不同寄主植物上所具有的某些生物学特性, 使之在与其他生物型烟粉虱或其他种昆虫的竞争中占据优势。首先, B型烟粉虱具有较强的寄主适应与利用能力, 从而具有更强的种群增长能力。例如, Bedford等(1994)在比较B、B₂、L、D、E和K型烟粉虱成虫在不同寄主上的适应性时发现, B型成虫的存活率均高于其他生物型。在墨西哥南瓜、西葫芦、黑籽南瓜以及中国南瓜上, B型比A型烟粉虱定居速度快(Quintero *et al.*, 1998); 在一品红和棉花上, B型较A型产卵量高(Bethke *et al.*, 1991)。Zang等(2006)比较了B型和ZHJ-1型烟粉虱的棉花种群在棉花、烟草、西葫芦、甘蓝和菜豆上的生物学特性, 发现B型雌性在5种寄主上的寿命均显著长于ZHJ-1型, 其中在棉花上为ZHJ-1型的2倍; 在甘蓝、蚕豆和南瓜上, B型的产卵量分别约为ZHJ-1型的130、6和3倍; 在甘蓝、蚕豆和烟草上, B型若虫期的存活率为55–79%, 而ZHJ-1型的若虫却不能发育为成虫; 在两者均能完成世代发育的南瓜上, B型的若虫期存活率(62%)也显著高于ZHJ-1型(26%)。在甘蓝上的刺吸电波图技术研究显示, B型烟粉虱有7种波形, 而温室粉虱只记录到刺探波形(高庆刚等, 2006)。

其次, B型烟粉虱具有较强的寄主转换适应能力。雷芳等(2006)以番茄为对照寄主, 以甘蓝、棉花和玉米为转换寄主, 对B型烟粉虱和温室粉虱寄主转换过程中海藻糖含量和海藻糖酶活性的动态变化进行了比较研究, 结果表明, 在非寄主玉米上, 与温室粉虱相比, B型烟粉虱海藻糖含量和海藻糖酶比活力的恢复能力强、稳定性好, 表明B型烟粉虱对潜在寄主植物的适应能力更强、反应更为及时有效。这一特性对加快其竞争取代非B型烟粉虱和温室粉虱具有重要作用。

3 非对称交配互动

异域物种间交配信号的相似程度大于同域物种(Butlin, 1995), 生物入侵使得异域物种共存, 而它们之间相似的交配识别机制可能导致种间非对

称交配互动(asymmetric mating interactions)的产生(Liu *et al.*, 2007)。非对称交配互动机制是入侵生物B型烟粉虱一种重要的内在潜能, 在其与新栖息地共存的土著生物发生互动时被激发并迅速发挥作用, 刺激B型烟粉虱交配, 并对土著烟粉虱的交配行为产生干扰, 使得后者被取代(Liu *et al.*, 2007)。通过非对称交配互动, B型烟粉虱能在3–5年内取代本地危害并不严重的土著烟粉虱。B型烟粉虱的这种竞争能力与其种群性比的调节能力及其对土著烟粉虱交配行为的干扰有关(Liu *et al.*, 2007)。

3.1 种群性比调节能力和交配能力

无论是单独生存还是与其他生物型混合发生, B型烟粉虱均具有调节种群雌性比例的能力, 使雌性比例增加(Liu *et al.*, 2007; Zang & Liu, 2007), 从而增强自身的竞争能力。田间笼罩实验表明, 当在棉花上将B型与ZHJ-1型混合种群(B型:ZHJ-1型为13:87)、B型单独种群以及ZHJ-1型单独种群(两种群雌雄性比均为1:1)分别饲养时, 随着时间的延长, 各烟粉虱种群的雌性比例会发生不同的改变: ZHJ-1型单独种群的雌性比例始终保持在50–60%; 50 d后, B型单独种群的雌性比例则增加为60–70%, 随后保持稳定。在混合种群中, 当两生物型共存50–150 d时, B型的雌性比例增加为70–80%, 而ZHJ-1型雌性比例则下降为30–40%; 225 d后, B型完全取代ZHJ-1型(Liu *et al.*, 2007)。B型烟粉虱较高的后代雌性比例显示其具有较强的繁殖潜能(臧连生, 2005), 这也许是导致其取代ZHJ-1型烟粉虱的主要机制之一。

3.2 生殖干扰

生殖干扰是竞争取代的重要机制, 这种竞争取代不是通过资源竞争, 而是通过竞争对方雌性个体实现的, 是一种不直接导致死亡的干扰方式(Reitz & Trumble, 2002)。生殖干扰的发生必须具备以下条件之一: 参与竞争的两个物种的雄性均缺乏辨别同种雌性的能力; 或者一方雌性比另一方雌性具有更强的种间识别能力。无论是哪种情况, 一个物种因此与另一物种竞争配偶。当种间求偶和交配行为失衡时, 一方雌性的生殖力降低, 最终导致被取代(Reitz & Trumble, 2002)。

生殖干扰可能是B型烟粉虱竞争取代的重要机制。研究表明, 当B型和非B型烟粉虱共存时, B型雄性对非B型雌雄个体间的交配行为具有明显的干扰

作用(Perring *et al.*, 1993; Perring, 1996; De Barro & Hart, 2000; Pascual & Callejas, 2004; 臧连生, 2005; Liu *et al.*, 2007; Zang & Liu, 2007), 导致非B型雌雄个体间的求偶和交配失衡、雌性繁殖力降低、后代雌性比例下降。Perring (1996)用2个A型烟粉虱种群(A1, A2)分别和B型烟粉虱进行杂交实验时发现, B型雌雄个体间的交配时间比A型的短, 且B型雄性对A型雌性的求偶能力比A型的雄性更强。因此, 在混合种群中B型的雄性能更长时间地占据A型雌性, 使能够成功交配的A型雌性个体减少, 进而使其生殖力降低。Liu等(2007)研究表明, 入侵的B型烟粉虱与土著生物型雌雄个体间互作而导致的非对称交配可能与种群性比的改变有关。B型与ZHJ-1型和澳大利亚AN型烟粉虱之间存在生殖干扰(De Barro & Hart, 2000; Zang & Liu, 2007), B型烟粉虱雄性更倾向与ZHJ-1型和AN型的雌性为伴, 使ZHJ-1型雄性搜索雌性的效率下降、求偶时间延长, 首次交配时间明显滞后(臧连生, 2005), 进而使ZHJ-1型的交配频率降低了46.2%, 后代雌性比例减少; 而ZHJ-1型雄虫的存在却反而能刺激B型烟粉虱雌雄个体交配, 使交配频率增加了45.9%, 后代雌性比例升高, 从而有利于其取代ZHJ-1型烟粉虱(Liu *et al.*, 2007)。

B型烟粉虱具有较快的发育速率和较强的生殖能力(Pascual & Callejas, 2004), 亦有利于增强其竞争力。实验室条件下, B型烟粉虱日产卵量(6.6粒/♀)显著高于Q型(2.8粒/♀), 且发育速率较快(较Q型快1.2 d)、若虫死亡率较低(较Q型低14.5%)、产生的F1代雌性比例较高(分别为2.9和1.4), 表明B型烟粉虱具有较强的种群增长潜能; 两生物型共存1代时, B型烟粉虱比例即由50%上升到79% (Pascual & Callejas, 2004)。与温室粉虱相比, B型烟粉虱在黄瓜、番茄和茄子上的发育历期短1.8–2.5 d; 在黄瓜和番茄上的寿命长5.2–7.2 d; 在黄瓜上的存活率高10.6%; 而且在棉花、黄瓜和番茄上, 其单雌产卵量较温室粉虱增加了18.0–35.2% (罗晨等, 2007)。较快的发育速度和较强的繁殖能力使B型烟粉虱种群数量迅速增加, 进而利于其在混合种群中占据优势。

4 高温逆境适应能力

B型烟粉虱对高温胁迫的适应能力较温室粉虱强。研究表明, 高温胁迫下, B型烟粉虱的卵、拟蛹和成虫的存活能力显著高于温室粉虱, 而随着胁迫

时间的延长和胁迫温度的升高, 温室粉虱各虫态的存活率迅速降低。如在 $\geq 43^{\circ}\text{C}$ 下4 h, B型烟粉虱成虫存活率约为30%, 而温室粉虱低于10%; 在 37°C 下1–6 h, B型烟粉虱羽化率仅下降25.3%, 而温室粉虱则下降34.2%。高温胁迫对两种粉虱的生殖特性(产卵量、若虫孵化率、后代存活率)亦会产生不利影响, 但对温室粉虱的影响更为强烈。如 43°C 下1 h, B型烟粉虱成虫产卵量为67.2粒, 若虫孵化率为60.8%, 成虫羽化率为25.1%; 而温室粉虱几乎完全丧失繁殖能力(崔旭红等, 2007, 2008)。

亚致死高温驯化可以明显提高B型烟粉虱成虫对极端高温胁迫的抵抗能力, 但对温室粉虱的耐热性能没有明显改善。如在 37°C 驯化30 min后B型烟粉虱成虫存活率提高了19.9%, 而温室粉虱仅提高了6.1% (崔旭红等, 2007, 2008; Cui *et al.*, 2008)。较强的耐热能力有利于B型烟粉虱种群在炎热夏季的大发生, 并成为优势种群。

5 药剂敏感性

药剂敏感性的差异可能也是B型竞争取代本地非B型烟粉虱的重要原因之一(Costa *et al.*, 1993; 臧连生等, 2006)。已有报道表明, 烟粉虱生物型间抗药性各异, 其中尤以B型烟粉虱的抗药性较强, 已对广泛使用的有机磷、有机氯、氨基甲酸酯、拟除虫菊酯、新烟碱类和生长抑制剂类杀虫剂产生了抗药性(Cahill *et al.*, 1995, 1996; Tan & Riley, 2000; Horowitz *et al.*, 2002)。Costa等(1993)报道, A、B型烟粉虱对有机磷类杀虫剂具有相同的敏感性, 但B型对菊酯类的抗性更强。Byrne和Devonshire (1993)对古北区烟粉虱的研究表明, B型烟粉虱的多数个体携带有对氨基甲酸酯类和有机磷类杀虫剂不敏感的乙酰胆碱酯酶。Byrne等(2000)研究发现, B型烟粉虱对拟除虫菊酯的抗性主要是由于增强了酯的水解作用。臧连生等(2006)研究表明, 浙江非B型ZHJ-1烟粉虱的卵、若虫和成虫对吡虫啉和吡丙醚的敏感性均高于B型烟粉虱。此外, 具有较高氟氯菊酯抗性的B型烟粉虱种群与敏感种群杂交后可以增强种群的生殖能力, 使母系种群和F1雄性回交种群的净生殖力增加约2倍(Riley & Tan, 2002)。

另外, B型和非B型烟粉虱对杀虫剂的反应也存在差异。如Toscano等(1997)研究发现, 与对照相比, 在印楝素处理的寄主上, 非B型烟粉虱雌性成虫和

若虫数量以及成虫产卵量明显减少, 而B型烟粉虱却未受到不良影响。此外, 杀虫剂的使用也可能是导致B型烟粉虱竞争取代其他刺吸式害虫(如叶蝉、蚜虫)的主要原因(Patil, 1996)。

综上所述, 抗药性的形成增强了B型烟粉虱与其他生物型或其他生物间的竞争能力, 使其在竞争取代中处于优势。

6 诱导植物防御反应和传播双生病毒

通常, 在B型烟粉虱为害的植株上很少发现其他植食性昆虫, 这可能与B型烟粉虱取食诱导所产生的寄主防御反应及其所携带的病毒密切相关(Mayer *et al.*, 2002; McKenzie *et al.*, 2002)。B型烟粉虱取食能对寄主植物、植食性昆虫和病原菌产生影响(Mayer *et al.*, 1996; Inbar *et al.*, 1999a, b; Walling, 2000), 这种影响可以是直接的, 如传播双生病毒(Oliveria *et al.*, 2001)和引起植物生理异常, 包括西葫芦的银叶反应(Maynard & Cantliffe, 1989; Jiménez *et al.*, 1995)、莴苣叶的黄化、青椒叶上的白色条斑、甘蓝茎干的白化(Hoelmer *et al.*, 1991)和番茄的不规则成熟(Schuster *et al.*, 1996)等。B型烟粉虱的取食还能直接影响其他植食性昆虫的取食行为, 如使拟尺蠖(*Trichoplusia ni*)从在羽衣甘蓝叶片背面转向叶片正面取食, 并偏好取食未受B型烟粉虱危害的叶片(Inbar *et al.*, 1999a; Mayer *et al.*, 2002)。

B型烟粉虱取食的间接影响主要表现为诱导寄主防御反应, 包括产生致病相关蛋白(pathogenesis-related protein, 以下简称PR, 即能被侵染因子或相似条件诱导产生的植物蛋白, 如几丁质酶、 β -1, 3-葡聚糖酶、过氧化物酶、脱乙酰壳多糖酶等)的积累(Inbar *et al.*, 1999b), 这可能会给其他植食性昆虫的取食和生长发育带来不良影响(Inbar *et al.*, 1999a, b; Mayer *et al.*, 2002)。如在美国佛罗里达州的桑福德地区田间发现, 受B型烟粉虱危害的植株上仅有4%的拟尺蠖可以化蛹, 而在未受危害的植株上其化蛹率为18%。拟尺蠖幼虫在B型烟粉虱危害的羽衣甘蓝上的发育速度比对照降低了20.8%、相对生长速率减缓18.0%, 这些现象表明遭受B型烟粉虱为害的植株对早期的拟尺蠖幼虫具有不利的影响(Inbar *et al.*, 1999a)。然而, PR的出现对B型烟粉虱的影响却很小(Inbar *et al.*, 1999b)。如在B型烟粉虱危害的番茄上, 三叶斑潜蝇

(*Liomyza trifolii*)成虫的取食、产卵刺孔和幼虫存活率分别降低了47.4%、30.7%和26.5%, 而斑潜蝇的危害对B型烟粉虱的产卵却没有明显的影响(Mayer *et al.*, 2002), 这可能与B型烟粉虱取食的是植物的韧皮部有关。无论防御物质是次生代谢物还是蛋白, 通常不在韧皮部表达或产生效应, 而取食植物叶肉组织的昆虫对植物防御物质则较为敏感。B型烟粉虱利用这种保护方式以及诱导植物产生防御物质的能力使它在与其他昆虫的竞争中占据优势(Mayer *et al.*, 2002)。

B型烟粉虱与双生病毒间存在间接的互惠共生关系。B型烟粉虱通过传播双生病毒使寄主植物感病, 而感病植物反过来会对其发育、存活和生殖等产生有利的影响(McKenzie *et al.*, 2002; 褚栋等, 2004; Jiu *et al.*, 2007)。如将携带番茄斑点病毒(tomato mottle virus, ToMoV)的B型烟粉虱转移到健康植株上饲养, 以未携带该病毒的个体为对照, 56 d后其产卵量和若虫数量分别比对照高2.5和4.5倍; 同时, 前者危害的植株比后者产生更多的PR, 且在42 d时PR的差异最为明显, PR的增加必然会影响到其他昆虫的取食(McKenzie *et al.*, 2002)。与取食健康植株相比, B型烟粉虱取食感染烟草曲茎病毒(tobacco curly shoot virus, TbCSV)的烟草植株后, 其种群产卵量和成虫寿命分别增加12和6倍; 取食含中国番茄黄化曲叶病毒(tomato yellow leaf curl China virus, TYLCCNV)的烟草植株后, 其产卵量和寿命分别增加18和7倍; 取食含TbCSV和TYLCCNV的烟草植株56 d后, 其种群密度分别为健康植株上的2和13倍。然而, 感染TbCSV和TYLCCNV病毒的植株对非B型ZHJ-1的生殖力和寿命均无明显影响(Jiu *et al.*, 2007)。

另外, B型烟粉虱传毒所引起的植物病毒病反过来对其有一定的诱食作用。因为B型烟粉虱对黄绿色有较强的偏好, 所以病毒病的症状如黄化、色斑或花叶等能吸引更多的B型烟粉虱(McKenzie *et al.*, 2002)。B型烟粉虱与这些病毒的相互作用, 可能有利于其入侵和竞争取代土著粉虱, 同时传播病毒病(Jiu *et al.*, 2007)。此外, 粉虱取食产生的大量蜜露能导致真菌的滋生(Hendrix *et al.*, 1996), 进而极可能诱发植物产生防御反应(Mayer *et al.*, 2002), 增加PR的积累, 从而影响其他植食性昆虫的取食。

上述研究不仅解释了B型烟粉虱危害后的植物

上其他植食性昆虫较少的原因(Mayer *et al.*, 2002), 还进一步表明产生这一现象的原因是B型烟粉虱危害的直接和间接影响的联合作用。

7 内共生菌

昆虫内共生菌分为初生内共生菌(primary endosymbiont)与次生内共生菌(secondary endosymbiont)。初生内共生菌能为宿主提供必需的营养物质(Koga *et al.*, 2003), 而次生内共生菌可能对宿主的适合度、竞争能力乃至宿主的进化等产生影响(Zchori-Fein & Brown, 2002; Tsuchida *et al.*, 2004)。褚栋等(2006)经过系统发育分析推测, B型烟粉虱可能具有独特的初生、次生内共生菌。这些内共生菌不仅能为B型烟粉虱提供营养(Costa *et al.*, 1997), 而且其产生的GroEL蛋白(属分子伴侣, 是一类保守性相当高的蛋白, 主要作用是保护病毒在进入血淋巴的过程中免遭降解, 同时与昆虫携带病毒的专一性有关(Llorca *et al.*, 1996))对烟粉虱传播病毒起重要的保护作用(Morin *et al.*, 2000; Akad *et al.*, 2004), 进而可能增强B型烟粉虱的竞争能力(褚栋等, 2006)。

另外, 与非B型烟粉虱相比, B型种群的*Wolbachia*感染率极低(褚栋等, 2005a), 且缺乏杀雄菌属(*Arsenophonus*) (阮永明和刘树生, 2005); 与A型、*Jatropha*型烟粉虱相比, B型缺少衣原体纲细菌*Candidatus Fritschea bemisiae*以及类噬胞细菌(cytophaga-like-organism, CLO) (褚栋等, 2006)。这些内共生菌可能给烟粉虱的生长发育和繁殖带来不良影响。如*Wolbachia*共生菌不仅能够引起昆虫宿主的生殖方式异常, 包括细胞质不亲和(cytoplasmic incompatibility)、孤雌生殖、雌性化和雄性致死(Darby *et al.*, 2001; Zchori-Fein & Brown, 2002; Nirgianaki *et al.*, 2003), 还能对宿主的其他生物学特性产生不良的影响(Fleury *et al.*, 2000; Wenseleers *et al.*, 2002), 可能是限制某些入侵性害虫种群增长的决定性因子(Shoemaker *et al.*, 2000; Tsutsui *et al.*, 2003)。CLO也与宿主生殖方式的异常有关(Weeks *et al.*, 2003)。*Wolbachia*和CLO可能是B型与许多非B型烟粉虱产生生殖隔离的重要因素之一(De Barro & Hart, 2000; 褚栋等, 2006)。一般认为, 衣原体细菌对其宿主具有致病作用。Costa等(1995)认为衣原体的存在可能是导致A型烟粉虱繁殖力较低、寄主

范围较窄的主要原因。近期的研究也表明, 缺乏衣原体的B型烟粉虱比A型具有更强的生长发育能力和生殖能力(Everett *et al.*, 2005)。

由此可见, B型烟粉虱所拥有的独特的内共生菌可以增强其传毒能力, 进而对提高其竞争力产生积极作用; 另一方面, 某些内共生菌的缺乏使B型烟粉虱避免受到不良影响, 从而拥有较广的寄主范围、较强的繁殖能力和种群增长能力, 进而增强其竞争能力。此外, 这些共生菌感染所引起的生殖隔离使得B型烟粉虱通过生殖干扰的方式在竞争中占据优势地位。

8 讨论与展望

尽管B型烟粉虱具有较强的竞争取代其他生物型和其他种昆虫的能力, 但在某些环境下这种取代作用会受到一些因素的影响。如田间条件下, 植食性昆虫与寄主植物间的相互作用以及其他生物型烟粉虱的某些生物学特性对B型烟粉虱种群的建立均具有较大的影响。例如草莓叶螨(*Tetranychus turkestani*)取食棉花后诱导产生的植物防御反应对B型烟粉虱的种群建立具有不利影响(Agrawal *et al.*, 2000); 在西班牙东南部的田间调查发现, Q型烟粉虱正在逐渐替代B型(Pascual & Callejas, 2004)。研究表明, Q型对昆虫生长调节剂类农药如吡丙醚的抗性强于B型, 对新烟碱类农药的抗性更稳定(Nauen *et al.*, 2002; Rauch & Nauen, 2003), 这可能是它在一些区域取代B型烟粉虱的主要原因之一(Pascual & Callejas, 2004)。另外, 与B型相比, Q型烟粉虱在一些杂草上的生殖力更强、发育速度更快, 在一些作物上扩散更迅速、危害性更大。如在3种不同的杂草(*Malva parviflora*, *Capsella bursa-pastoris*, *Brassica kaber*)上, Q型烟粉虱的产卵量、化蛹率和成虫羽化率等均明显高于B型; 26℃时, Q型在杂草*Datura stramonium*和*Solanum nigrum*上从卵发育到成虫的历期明显短于B型(Muniz, 2000); 在甜椒(*Capsicum annum*)上, 当温度为17℃、33℃时, Q型烟粉虱的世代历期短于B型(Muniz & Gloria, 2001); 在不同品种的番茄上, Q型烟粉虱的危害性强于B型(Nombela *et al.*, 2001)。因此, Q型烟粉虱具有在短时间内建立高密度种群的能力(Moya *et al.*, 2001), 其潜在危害性较大。

近年来, Q型烟粉虱已从其起源地伊比利亚半

岛(Guirao *et al.*, 1997; Moya *et al.*, 2001)逐渐向外扩散和蔓延, 现已在摩洛哥(Moya *et al.*, 2001; Rauch & Nauen, 2003)、意大利、德国(Nauen *et al.*, 2002)、以色列(Horowitz *et al.*, 2003)、中国(Chu *et al.*, 2006)、美国(Brown & Dennehy, 2006)、墨西哥和中美洲等地发现, 并逐渐成为某些地区的重要害虫(Gobbi *et al.*, 2003; Pascual & Callejas, 2004)。如在我国, Q型烟粉虱已成为长江流域部分地区的优势种群(褚栋等, 2005b; Chu *et al.*, 2006; Li, 2006; 徐婧等, 2006)。鉴于Q型烟粉虱抗药性强、可以在多种杂草上建立种群的特点, 为了有效防止其在我国的进一步扩散与危害, 在烟粉虱发生区域应避免滥用杀虫剂; 同时, 要充分发挥我国精耕细作的种植和管理模式的作用, 减少农田杂草, 消灭虫源基地, 使Q型烟粉虱的发生数量维持在较低水平。

较强的竞争力有利于B型烟粉虱的成功入侵, 使其成为世界性害虫。因此, 明确B型与非B型烟粉虱及其他昆虫间的竞争机制, 对揭示B型烟粉虱的入侵机理, 明晰其入侵后种群形成和扩张机制具有重要意义, 并能为B型烟粉虱的可持续治理提供理论依据。此外, Q型烟粉虱作为一种新入侵的生物型, 其潜在危害性较大。了解Q型烟粉虱与其他生物型间的竞争机制, 对预防其传入、控制其进一步扩散危害具有重要的理论指导意义。然而, 要建立烟粉虱预警与预防、检测与可持续控制体系, 还需进一步加强以下各方面的研究:

(1) 尽管越来越多的学者认为烟粉虱是一个正在快速进化的复合种, 但对这一具有一定遗传分化的类群尤其是B型烟粉虱的分类地位, 仍存在不同的观点。现有的生物学、酶谱和分子鉴定方法均存在一些不足, 缺乏公认的标准的鉴定方法。鉴于不同生物型的烟粉虱具有一定的地理分布模式(De Barro *et al.*, 2003), 因此有必要开展烟粉虱的种群系统发育地理格局与演变机制的研究, 明晰各地理群体遗传结构的多态性特征、遗传分化与生物入侵的关系。在此基础上, 完善和发展快速分子鉴定技术, 并应用于监测和检测烟粉虱各生物型的实时动态和扩张趋势, 预测哪种粉虱或何种烟粉虱生物型在长期的适应进化过程中将占据优势地位、成为优势物种或种群, 为建立烟粉虱早期预警和风险评估体系提供关键的技术支持。(2) 由于B型烟粉虱具有较强的逆境胁迫适应能力(Cui *et al.*, 2008; 崔旭红

等, 2007, 2008), 而地理环境、杀虫剂均是诱导其遗传分化的关键因素(张丽萍, 2005; Zhang *et al.*, 2005; 褚栋等, 2006; Chu *et al.*, 2007), 所以需要我们从逆境生物学和分子生物学的层面, 采用功能基因组学等方法(如expressed sequence tags, EST)研究B型烟粉虱对环境胁迫响应的分子生态学机制和逆境生物学机制。(3) 应用分子标记等技术研究烟粉虱不同生物型间杂交与基因交流的模式, 探讨生物型间控制寄主选择适应性等性状基因的交流与分化机制, 从而揭示烟粉虱新类群形成的遗传基础及其对环境生态适应的过程与机理, 探明B型烟粉虱扩张过程中生态对策的调整及其效应, 为构建烟粉虱生物生态可持续控制体系提供基础。

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