

特 约 稿 件

Invited Paper

草地贪夜蛾对 Bt 玉米的抗性与治理对策思考

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摘要 Bt 玉米已在美洲广泛种植 20 多年, 成功控制了欧洲玉米螟 *Ostrinia nubilalis*、草地贪夜蛾 *Spodoptera frugiperda* 等玉米重大害虫为害。然而, 近年来相继报道在波多黎各、巴西、阿根廷因草地贪夜蛾产生抗性而导致一些 Bt 玉米抗性丧失。尤其是在热带和亚热带地区, 多数 Bt 玉米品种商业化种植仅 3 年就丧失了对草地贪夜蛾的抗性。本文分析了草地贪夜蛾的生物学和生态学、对 Bt 杀虫蛋白抗性遗传特征和交互抗性特性、种群抗性基因频率等内因对抗性演化的影响, 以及 Bt 玉米种植的生态环境、耕作栽培制度、Bt 玉米种类、抗性治理策略实施情况等外部环境因素对抗性演化的影响。根据我国玉米种植的生态格局, 提出了“整体布局, 源头治理”的抗性治理对策。即在草地贪夜蛾周年繁殖区要谨慎种植 Bt 玉米, 尤其是避免种植表达 Cry1Ab 杀虫蛋白的 Bt 玉米, 以避免源头产生抗性而危及温带玉米主产区。遵循差异化(不同杀虫作用机理)选择 Bt 玉米品种原则, 制定精准抗性监测计划, 以高剂量-庇护所为抗性治理基本策略, 在 Bt 玉米资源有限的情况下, 落实好庇护所尤为为重要。

关键词 草地贪夜蛾; Bt 玉米; 害虫抗性演化; 抗性治理; 对策

中图分类号: S 435.132 **文献标识码:** A **DOI:** 10.16688/j.zwbh.2020224

Resistance evolution to Bt maize in the fall armyworm and consideration on IRM strategy in China

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Abstract Bt maize has been commercialized for over 20 years in the American countries, which was successfully used to control a number of economically important insect pests such as the European corn borer, *Ostrinia nubilalis*, fall armyworm (FAW), *Spodoptera frugiperda*, etc. However, a couple of resistance cases have threatened their efficacy and resulted in the failure of field control. What's worse, most Bt maize events/stacks varieties lost their ability to control FAW in just 3 years after their release in the tropical and subtropical agricultural ecosystems. In this paper, we reviewed the internal and external factors which drove/facilitated the rapid evolution of FAW resistance, including the biology and ecology of FAW, its inheritance of resistance, cross resistance to different Bt proteins, initial allele frequency of resistance in the field populations, agroecosystem landscape of Bt maize planting, cropping systems, Bt maize events, adaptation of insect resistance management (IRM) practices, etc. Furthermore, we suggested a “Natal Source IRM” strategy based on the integral scenario of maize cropping landscape throughout the country, i.e., careful consideration should be taken in deploying Bt maize in the tropical and subtropical regions of China (winter maize region) where FAW reproduced year-round and is the source of adults to migrate to the Yangtze River Basin, Huanghuaihai summer maize region, even up to the northern spring maize region. If the resistance evolved in the Natal Source of FAW population, it will diminish the Bt maize efficacy in the rest regions of the country. Even more care should be taken in deploying Bt maize expressing Cry1Ab protein in the winter maize region. At least, different Bt maize varieties (without cross resistance) should be used between tropical and temperate regions. In addition, IRM plans should be designed to ensure a reliable resistance monitoring program, ensure refuge compliance to make high dose refuge as a corner stone tactics under limited Bt maize resources.

Key words *Spodoptera frugiperda*; Bt maize; evolution of insect resistance; IRM; strategy

草地贪夜蛾 *Spodoptera frugiperda*, 又名秋黏虫 (fall armyworm, FAW), 2018 年末入侵我国^[1], 2019 年随着季节变暖及玉米等作物播种由热带亚热带向温带依次推进, 寄主的可觅性由南向北也相应增加, 草地贪夜蛾入侵逐渐向长江流域、黄淮海及西北地区蔓延, 到 10 月份已迁移扩散至除黑、吉、辽、青、新外的 26 个省(市、区)1 518 县(区、市), 查见幼虫的省份 22 个, 其中玉米草地贪夜蛾发生面积达到 106.5 万 hm^2 ^[2], 对我国玉米生产构成严重威胁。与此同时, 科学工作者积极应对, 在入侵路径^[3]、迁飞扩散轨迹^[4]、化学防控^[5-6]、生物防治^[7]、玉米品种抗性利用等测报和防控技术方面开展了广泛的研究。及时提出了“分区治理、联防联控、综合治理”策略^[8], 有效地遏制了这一危险性害虫可能造成的重大灾害发生。

由于草地贪夜蛾繁殖潜力大^[9], 飞行与扩散能力极强^[10], 易引起异地突发和暴发。因此, 化学防控因其速效、高效和易于实施是应急防控预案必不可少的手段。在其原产地美洲大陆草地贪夜蛾的防治已有悠久的历史。对全球 1910 年—2019 年文献大数据分析表明, 美洲防控草地贪夜蛾以 Bt 玉米商业化应用为标志, 可划分为化学防治和绿色综合防控两个时期。20 世纪末之前是以化学杀虫剂为主的化学防治时期^[11]。即使在其近年侵入的国家如南非、印度以及我国, 亦多首选化学防治遏制其扩散为害。因而不可避免地会面临环境污染和抗药性发展等问题。李永平等分析总结了草地贪夜蛾抗药性的演化史, 提出了化学防治策略^[12]。

20 世纪 90 年代后期, 国外草地贪夜蛾防控进入了以 Bt 玉米为主, 兼有天敌释放、生物农药使用等措施的绿色防控时期^[11]。我国则经历了入侵风险分析预警, 侵入后的监测、应急阻击防控, 到目前以生态控制和农业防治为基础, 生物防治和理化诱控为重点的持续治理探索。在天敌资源鉴定与应用^[7,13], 白僵菌等微生物农药应用, 物理防控技术等方面取得进展, 同时还明确了几个国产 Bt 玉米对草地贪夜蛾具有良好的杀虫效果^[14]。2020 年 1 月 20 日, 随着北京大北农生物技术有限公司和瑞丰公司的两个国产转基因抗虫玉米获得生产应用安全证书, 预示在我国玉米生产中应用这一现代生物技术产品防控草地贪夜蛾指日可待。然而值得注意的是, 在美洲、南非等大面积商业化种植 Bt 玉米的国家, 相继报道了草地贪夜蛾对不同类型的 Bt 玉米产生了抗性。本文就美洲 Bt 玉米的应用与草地贪夜蛾抗性演化、

抗性产生的内外因进行了分析, 结合草地贪夜蛾在我国的迁移扩散情况、玉米产区的生态环境、耕作栽培制度和种植的季节性规律、已获生产应用安全证书的国产 Bt 玉米资源等, 针对未来生产中应用 Bt 玉米防治草地贪夜蛾, 初步提出了抗性治理策略。

1 Bt 玉米应用与草地贪夜蛾抗性的演化

20 世纪 90 年代初, Koziel 等^[15]首次报道了表达 Cry1Ab 蛋白的 Bt 玉米田间高效杀虫效果。1996 年, 以欧洲玉米螟 *Ostrinia nubilalis* 和巨座玉米螟 *Diatraea grandiosella* 等为靶标害虫的 Bt 玉米在北美商业化种植, 包括不同公司研发的‘176’‘MON810’和‘Bt11’(表达 Cry1Ab 杀虫蛋白), ‘DBT-418’(表达 Cry1Ac 杀虫蛋白), ‘CBH-351’(表达 Cry9C 杀虫蛋白)等产品, 且‘MON810’和‘Bt11’持续种植或与后续新的转化事件聚合使用至今。这些 Bt 玉米对既定靶标害虫的防治效果可达 99% 以上^[16-21]。虽然草地贪夜蛾和玉米穗夜蛾(CEW), 即美洲棉铃虫 *Helicoverpa zea* 等鳞翅目夜蛾科害虫没有被列为主要防治靶标对象, 但在田间对这两种害虫亦有显著的防治效果, 心叶期被害率降低 90% 以上, 穗期被害率降低 50%~80%^[22-27]。表达 Cry1F 杀虫蛋白的玉米‘TC1507’于 2001 年在美国获得种植批准^[28], 2003 年商业化种植, 主要防治对象包括欧洲玉米螟^[29], 同时对晚播玉米上草地贪夜蛾有更好的防治效果^[30-32]。2013 年, 美国玉米带种植表达 1 种 Bt 杀虫蛋白的 Bt 玉米面积达到 76%^[33], 美国玉米带的主要害虫欧洲玉米螟已得到有效控制^[34], 而草地贪夜蛾、美洲棉铃虫等害虫在美国南部各州偶发严重为害^[24]。为了扩大杀虫谱以及实施多基因抗性治理策略, 叠加多基因抗虫玉米‘MON89034’(表达 Cry2Aba+Cry1A. 105, 2009 年)和聚合多基因抗虫玉米(如‘Bt11 × MIR162’, 2009 年; ‘MON89034 × TC1507’‘MON89034 × TC1507 × MON88017 × DAS-59122’, 2010 年)在美国和加拿大种植, 尤其是后者不仅能防治多种鳞翅目害虫, 还能防治鞘翅目玉米切根叶甲 *Diabrotica*^[35-36]。目前, 全球商业化的 Bt 玉米多数都是叠加/聚合多个基因^[37]。

波多黎各岛具有独特的热带农业生态系统, 玉米周年连续种植, 尤其是大面积错期月播青贮饲料玉米。草地贪夜蛾是当地最重要的害虫, 周年发生且世代重叠, 频繁造成严重为害损失。表达 Cry1F 杀虫蛋白的 Bt 玉米‘TC1507’于 2003 年开始大面积商业化

种植,2005 年和 2006 年种植面积占整个玉米种植面积的 80%。然而,2006 年田间出现‘TC1507’玉米受草地贪夜蛾为害严重的情况,表明草地贪夜蛾已对‘TC1507’玉米产生了田间抗性,抗性倍数超过 1 000 倍^[38-39]。抗性丧失的主要原因归结为岛屿热带农业生态环境、玉米周年持续播种、草地贪夜蛾周年繁殖和世代重叠,其次还与 2006 年草地贪夜蛾大暴发,以及当年天气干旱导致其他寄主植物源减少有关。靶标害虫田间产生抗性直接导致了‘TC1507’玉米在当地退市停用^[39]。随后数年持续监测数据表明,这一地区的草地贪夜蛾对‘TC1507’持续呈高水平抗性,而同期监测美国南部各州草地贪夜蛾种群对‘Cry1F’杀虫蛋白和‘TC1507’玉米依然敏感^[36,38,40-41]。直到 2013 年,美国东南部的佛罗里达州和北卡罗来纳州田间草地贪夜蛾种群 Cry1F 抗性基因频率增高,田间出现非预期的存活幼虫^[42],可能是由于波多黎各岛及巴西田间抗性草地贪夜蛾迁飞到美国东南部所致^[43-46]。

巴西玉米种植面积 120 万~150 万 hm^2 ^[47-48],从南部的亚热带到中、北部的热带环境,年种植 2~3 季^[49-50],传统的第一季(夏)玉米面积占比由 61.5%(2009 年)下降到 34.5%(2015 年),而第二季(冬)玉米面积占比已由 38.5%增加到 65.5%^[51-52],且冬玉米播种时间由当年 12 月持续到翌年 2 月。草地贪夜蛾是当地最主要的害虫^[53],发生高峰通常在夏玉米季节,减产可达 17%~38%^[54]。连续两季玉米,为草地贪夜蛾搭起了发生多代、世代重叠的寄主“绿色桥梁”^[38,55-57],且其发生种群密度高^[58-59]。表达 Cry1Ab(‘Bt11’和‘MON810’)、Cry1F(‘TC1507’)、Cry2Aba+Cry1A.105(‘MON89034’)杀虫蛋白 Bt 玉米先后于 2008/2009、2009/2010、2010/2011 生长季在巴西商业化种植^[52,60-61],能高效控制草地贪夜蛾、美洲棉铃虫、小蔗螟 *Diatraea saccharalis* 等多种鳞翅目害虫的为害^[48,62-63]。然而同样由于热带、亚热带生态环境下连续种植多季玉米^[49],害虫连续多世代重叠,且庇护所面积实施率低^[50]等,仅在商业化种植 1 年后,发现田间草地贪夜蛾已对表达 Cry1F 的 Bt 玉米产生了抗性^[50,64-65],对表达 Cry1Ab 的 Bt 玉米的抗性也逐年上升^[66]。草地贪夜蛾在 Bt 玉米和 Bt 棉花田转移为害^[67],使选择压增加。

阿根廷玉米面积约 300 万 hm^2 。先后商业化种植表达单基因 *cry1Ab*(‘Bt11’‘MON810’和‘176’,1998 年),*cry1F*(‘TC1507’,2005 年),*vip3Aa20*

(‘MIR162’,2011 年)玉米以及多基因‘MON89034’(2010 年),‘MON88017’(‘TC1507×MON810’,2010 年),‘MON89034×MON88017’(2010 年)玉米、‘Bt11×MIR162’(2011 年)^[68],主要防治草地贪夜蛾、小蔗螟等鳞翅目害虫^[69-71]。由于在其北部大量种植晚季玉米,且庇护所有限,以及草地贪夜蛾发生多代且世代重叠等因素,增加了选择压和年选择世代数^[72-73]。2013 年,在阿根廷多地田间发现草地贪夜蛾抗表达 Cry1F 的 Bt 玉米^[74-75],并对表达 Cry1Ab 的玉米有交互抗性^[76]。

2 抗性产生的内因

2.1 草地贪夜蛾生物学、生态学及其对抗性演化的影响

害虫抗性演化与其生物学、生态学密切相关,如寄主范围、繁殖期和繁殖力、性比、迁移扩散行为等^[77],尤其是年发生世代数^[78]。草地贪夜蛾寄主植物广泛,多种主要农作物如玉米、棉花、大豆、高粱等都是其适宜寄主^[56,67,79],草地贪夜蛾在这些作物上的生活史接近^[80],在表达某一杀虫蛋白的一种作物(如 Cry1F 玉米)上产生的抗性个体,在表达相同蛋白的其他作物(如 Cry1F 棉花)上不会产生适合度劣势^[81]。草地贪夜蛾在 28℃时代历期约 30 d,在热带和亚热带地区可年发生 10 代^[82]。美属波多黎各岛,地理环境相对隔离,属热带生态系统,草地贪夜蛾是当地玉米上的最主要害虫,适宜的其他寄主植物少。玉米周年种植,因而对草地贪夜蛾形成了多世代周年汰选。从商业化种植表达 Cry1F 的 Bt 玉米到监测出抗性产生的 3~4 年间,田间汰选已有 30~40 代^[38]。中南美洲的巴西、阿根廷与波多黎各情况相似,草地贪夜蛾是当地最主要的玉米害虫,年平均发生 8 代以上^[64,83]。加上草地贪夜蛾超强的繁殖力^[9,82,84],极易形成高密度种群。如若出现对 Bt 玉米产生抗性的个体,就会在短时间产生大量的后代,且因其没有或很低的抗性适合度劣势^[81,85],使群体的抗性基因频率大量繁衍扩充,促使抗性快速产生。

害虫的迁移能力直接影响其在不同生态系统种群间的基因交流,尤其是不同生产力管理水平下,如用药水平与绿色防控水平等,无疑会导致种群内的遗传结构如抗药性出现空间上的差异分化,如果害虫迁移能力弱,生境相对隔离,这种分化的长期存在就可能演化出特性差异显著的品系/生态型等。相反,如果害虫迁移能力强,个体在不同生境间迁移,使得不同管理水平生境下的抗性差异种群实现基因

交流,其结果一方面迁移个体携带抗性基因在不同生境间得以传播扩散,另一方面,迁入的非抗性个体可以使迁入区域内的汰选富集基因得到稀释。可见,迁移能力直接影响害虫抗性的时空演化^[77]。草地贪夜蛾成虫具有超强的迁移能力,在不同区域、洲际间入侵蔓延^[86-89],携带抗性基因传播扩散^[42,44]。

在美国本土,草地贪夜蛾冬季一般仅能在佛罗里达和得克萨斯南端越冬,暖冬可在墨西哥湾沿岸地区过冬,夏季世代发育历期 28~30 d,冬季可长达 3 个月^[90]。4 月—5 月佛罗里达种群(FP)北迁到佛罗里达北部及佐治亚南部;得克萨斯种群(TP)向东北迁入路易斯安那、密西西比、亚拉巴马^[45-46,91];得克萨斯种群沿密西西比河流域北上到美国北部的宾夕法尼亚州等地,而佛罗里达种群则沿东海岸经南/北卡罗来纳、弗吉尼亚、宾夕法尼亚州,一般在夏末或秋初扩散至北部^[92]。美国玉米主要分布在中北部玉米带,南部尤其是佛罗里达州玉米种植面积很小^[91]。由于冬春季(1 月—5 月)在佛罗里达种植大面积(>12 万 hm²)的马铃薯 *Solanum tuberosum* L.、甘蓝 *Brassica oleracea* L. var. *capitata* 等蔬菜,后续种植绿肥作物高粱苏丹草(高粱和苏丹草的杂交种) *Sorghum bicolor* (L.)^[93],因此,在佛罗里达有大量的非玉米庇护所。南部极小面积玉米上越冬种群北迁到佛罗里达北部非玉米绿肥寄主时的死亡率高。由于草地贪夜蛾在美国温带玉米带不能越冬,而在美国本土,尤其是玉米带,玉米为单季种植,玉米生长期草地贪夜蛾仅能繁殖 1~2 代,仅在局地零星重发生,不会出现周年多世代频繁汰选。即使出现抗性个体,在冬季到来时不能完成下一世代,因而不能在种群中遗传。

值得注意的是,在巴西报道了草地贪夜蛾抗性问题上,很快在阿根廷、巴拉圭、乌拉圭、哥伦比亚等也发现田间 Bt 作物防治失效问题^[53]。除当地热带环境、庇护所不足的高压频繁汰选外,外来携带抗性基因成虫迁入可能也是原因之一^[94]。

害虫幼虫的转移扩散规律会显著影响其对 Bt 玉米抗性演化,尤其是在采用“种子混合”庇护所法的情景下。幼虫在 Bt 与非 Bt 植株间的转移为害将有利于其抗性产生^[95]。一方面幼虫由非 Bt 玉米植株转移至 Bt 玉米植株,导致死亡率显著增加,从而减少了庇护所种群密度^[96-97];另一方面,抗性杂合个体或携带微小抗性基因的个体由 Bt 植株转移到非 Bt 植株,将导致其没有摄食足够的 Bt 蛋白,不能满

足高剂量-庇护所抗性治理策略的“高剂量”先决条件而存活^[98-99],从而富集种群中的抗性基因,加剧抗性演化^[100]。此外,Bt 蛋白在玉米组织的时空表达存在差异^[101],幼虫在植株上的不同部位间的转移,尤其是对植株不同生长发育时期的器官组织有选择性时,亦会影响其存活率^[102],以及在非 Bt 植株上的抗性杂合体(尤其是不完全隐性遗传)或携带微小抗性基因的大龄幼虫转移到 Bt 植株(即使对初孵幼虫是“高剂量”)也能存活,提高抗性基因频率^[103]。由此可见,幼虫的迁移扩散行为将直接影响庇护所设置策略。草地贪夜蛾有显著的株间转移习性,但多数发生在同行(50%)及邻近(1.1 m)植株间(91.4%)^[104]。

草地贪夜蛾对一些 Bt 蛋白的抗性间不存在交互抗性,如 Cry1F、Cry1Ab 与 Vip3Aa20, Cry1F 与 Cry2Ab 等,因此在多个不同 Bt 玉米同时商业化种植的景观生态下,其难以克服不同杀虫蛋白在时/空叠加(轮换)。这可能是美国玉米带转基因玉米防治草地贪夜蛾依然有效的原因之一^[39,105-106]。

2.2 抗性遗传特征

抗性遗传学特征直接关系到抗性演化速率,是抗性治理的基础。在田间出现抗性之前,有关草地贪夜蛾对 Bt 玉米表达的主要杀虫蛋白 Cry1Ab、Cry1Ac、Cry1F、Vip3Aa、Cry2Ab 等的抗性遗传特征几乎没有报道。自从 Storer 等^[39]首次报道草地贪夜蛾在波多黎各田间对 Cry1F 玉米产生抗性以来,已有多分离自巴西、阿根廷、美国本土东南部州及波多黎各岛等地的 Cry1F 抗性种群的遗传特征报道(表 1)。总的来看,草地贪夜蛾对 Cry1F 玉米的抗性为常染色体、隐性或不完全隐性遗传,仅在美国北卡罗来纳州普利茅斯分离的种群为显性或不完全显性。无母系效应。抗性由单基因或 1 簇紧密连锁的基因控制。抗性产生较快,且田间抗性产生后,即使消除选择压,抗性依然能稳定遗传^[39,81]。多地 Cry1F 抗性草地贪夜蛾种群没有抗性相关的适合度劣势。对 Cry1Ab、Cry1Ac 存在低水平交互抗性,对 Cry1Aa、Vip3Aa、Cry2Ab、Cry2Aa、Cry1Ba 没有交互抗性^[107]。相比之下,对表达 Cry1Ab 的 Bt 玉米的抗性报道较少,该抗性为常染色体 1 个以上基因控制的隐性遗传,有抗性适合度劣势。对‘MON89034’玉米抗性为常染色体多基因控制的隐性遗传,存在抗性相关的适合度劣势。对表达 Vip3Aa20 玉米的抗性为常染色体单基因或 1 簇紧密连锁基因控制的隐性遗传,显著的抗性相关适合度劣势。

表 1 草地贪夜蛾对 Bt 玉米/蛋白抗性遗传特征

Table 1 Inheritance of *Spodoptera frugiperda* resistance to Bt maize and/or insecticidal proteins

抗性种群 R population	Bt 玉米/蛋白 Bt maize/Protein	虫源采集地/室内汰选法 FAW collection site/ Laboratory selection method	抗性遗传规律 Inheritance of resistance	适合度劣势 Fitness cost	交互抗性 Cross resistance	文献 Reference
SI	TC1507	波多黎南部沿海地区,2007 年‘TC1507’玉米植株	常染色体、高度隐性遗传	—	低水平: Cry1Ab, Cry1Ac	[39]
456	TC1507	波多黎各 Juana Diaz 区玉米植株	—	无	低水平: Cry1Ab, Cry1Ac 无: XenTari WG 和 Dipel ES Bt 杀虫剂	[81,108]
rr	Cry1F	波多黎各	常染色体、隐性遗传,单基因,无母系效应	无	低水平: Cry1Ab,Cry1Ac 无:Cry1Aa, Cry1Ba, Cry2Aa, Vip3Aa	[107]
RR-PR RR-FR	TC1507/Cry1F	波多黎各 美国佛罗里达	常染色体、隐性或不完全隐性遗传 PR-与 FR 共同的抗性基因及另外微小基因 FR-单基因或 1 簇紧密连锁基因	非隐性 劣势		[40,109 - 110]
Pooled F ₃	TC1507/Cry1F	美国北卡罗来纳州灯诱成虫	显性或不完全显性,主效基因	—	Cry1A. 105 无:Cry2Ab, Vip3Aa20	[111]
IrmaF IrmaD	TC1507	巴西米纳斯杰拉斯州马托津霍斯和伊雷德米纳斯室内幼虫期‘TC1507’叶片连续汰选 1~4 代,‘TC1507’叶片汰选 3、6、8、10 d,第 5 代幼虫期汰选	常染色体、不完全隐性遗传,单基因,无母系效应	无		[85,112]
MRH	TC1507	巴西 Morrinhos ‘TC1507’田	常染色体、隐性遗传,单基因/或 1 簇紧密连锁基因,无母系效应	不明显		[85,113]
TC1507 MTH		巴西巴拉那州,马托格罗索,戈亚斯州,巴西利亚 4 地混合种群,非 Bt 玉米田		不明显		[85,113]
R-Cry1F BA25R	TC1507/Cry1F TC1507/Cry1F	巴西巴伊亚巴雷拉斯 巴西巴伊亚巴雷拉斯	常染色体遗传 不完全隐性遗传	无 —		[50,114 - 115] [116]
R	Cry1F/TC1507	阿根廷,‘TC1507’玉米田室内再汰选	常染色体、不完全隐性遗传,与巴西相似			[75]
— 玉米型 Corn strain	MON810 Cry1Ab, Cry1Ac	巴西 哥伦比亚,玉米田		有 —		[66] [117]
水稻型 Rice strain RR	MON89034	巴西巴伊亚,‘TC1507’玉米田,F ₂ 分离的近等基因系(MON89034 汰选)	常染色体、隐性遗传,非性别连锁,无母系效应	一定的 劣势	Cry1F, Cry1A. 105, Cry1Ab, 低水平或不显著: Cry2Ab2	[118]
VT-R	MON89034	巴西,F ₂ 汰选法	常染色体、隐性遗传,多基因控制	一定的 劣势	Cry1F, Cry1A. 105, Cry1Ab 低水平:Cry2Ab2	[114,118]
PW-R	MON89034× TC1507× NK603	巴西,F ₂ 汰选法	常染色体、隐性遗传,多基因控制	一定的 劣势		[114,118 - 119]
Vip-R	MIR162 MIR162×Bt11	巴西巴伊亚室内表达 Vip3Aa20 蛋白玉米叶 F ₂ 汰选法	常染色体、隐性遗传,单基因控制	显著		[114,120 - 121]

续表 1 Table 1(Continued)

抗性种群 R strain	Bt 玉米/蛋白 Bt maize/Protein	虫源采集地/室内汰选法 FAW collection site/ Laboratory selection method	抗性遗传规律 Inheritance of resistance	适合度劣势 Fitness cost	交互抗性 Cross resistance	文献 Reference
RR	MIR162	美国路易斯安那州高粱田和 Bollgard II 棉田。用 ‘MIR162’,F ₂ 汰选法。	常染色体、隐性遗传,单基因或 1 簇紧密连锁基因	—	无;Cry1F, Cry2Aba, Cry2Ae	[122]
RR	Cry2Ab 玉米	美国佐治亚 2013	常染色体、隐性/不完全隐性遗传,单基因控制	无		[84]
RR32, RR67	Cry1A. 105 玉米/蛋白	2011 年美国佛罗里达州种群与 SS(德州种群)回交,F ₂ 汰选法。	常染色体、单基因,不完全隐性-不完全显性	无		[123]

2.3 抗性基因频率

在草地贪夜蛾对‘TC1507’玉米田间产生抗性被报道之前,自然种群的抗性基因频率并没有相关监测数据报道。自报道田间出现抗性之后,在巴西、美国多地对抗性基因频率进行了检测。虽然商业化种植前,草地贪夜蛾田间种群对 Cry1F 抗性的基因频率未知,但从后来各国多年监测数据可以看出,草地贪夜

蛾对 Cry1F 抗性基因频率上升有明显的地理差异,在热带亚热带生态系统的波多黎各、巴西、阿根廷抗性基因频率上升非常快,其次是美国南部的佛罗里达等,而在美国北卡罗来纳则相对慢(表 2)。这与年发生世代数相关。虽然草地贪夜蛾对 Vip3Aa20 的抗性基因频率监测数据较少,但可以看出其上升相对较慢。说明不同杀虫蛋白之间抗性基因频率有一定差异。

表 2 田间草地贪夜蛾种群对 Bt 玉米/蛋白抗性基因频率

Table 2 Frequencies of Bt maize/protein resistance alleles in field populations of *Spodoptera frugiperda*

种群采集地 Population location	采集时间 Collection time	Bt 玉米/蛋白 Bt maize/Protein	抗性等位基因频率(95%置信区间) Frequency of resistance alleles (95% CI)	文献 Reference
波多黎各胡安娜迪亚兹 Juana Diaz, Puerto Rico	2011 年—2013 年	Cry1F	0.85~0.925	[81,107]
美国佛罗里达州 得克萨斯州 Florida, Texas, USA	2011 年—2012 年	Cry1F	0.132 2(0.079 9~0.172 9) 0.020 0(0.005 5~0.042 6)	[107]
美国路易斯安那州 佛罗里达州 Louisiana, Florida, USA	2011 年	Cry1F	0.103(0.070~0.141) 0.293(0.242~0.347)	[42]
美国北卡罗来纳州 North Carolina, USA	2014 年	Cry1F Cry1A. 105+Cry2Ab Cry1F+Cry1A. 105+Cry2Ab Cry1F+Cry1Ab+Vip3Aa20	0.009 35(0.004 05~0.016 79) 0.001 17(0.000 03~0.004 30) 0.001 17(0.000 03~0.004 30) 0.001 17(0.000 03~0.004 30)	[111]
美国路易斯安那州 佛罗里达州 Louisiana, Florida, USA	2011 年	Cry1A. 105	0.015 8(0.005 2~0.032 3) 0.055 9(0.031 9~0.086 8)	[124]
巴西 7 个主要玉米种植州 8 个地理种群 Eight populations from 7 major states of Brazilian maize production	2011 年—2012 年	Cry1F	0.07(0.02~0.13)~0.6 平均:0.24(0.17~0.25)	[125]
巴西 5 个主要玉米种植州 12 个地理种群 Twelve populations from 5 major states of Brazilian maize production	2012 年	Cry1F	0.009(0.000~0.027)~ 0.277(0.222~0.327) 平均:0.088(0.077~0.100)	[65]
巴西 6 个主要玉米种植州 11 个地理种群 Eleven populations from 6 major states of Brazilian maize production	2013 年—2014 年 2013 年—2015 年	Vip3Aa20 诊断剂量:3 600 ng/cm ²	平均:0.000 9(0~0.002 1) 其中 3 个种群幼虫存活率 0.87%~0.97% 0.001 2(0~0.003 3) 0.001 1(0~0.003 1)	[121]

续表 2 Table 2(Continued)

种群采集地 Population location	采集时间 Collection time	Bt 玉米/蛋白 Bt maize/Protein	抗性等位基因频率(95%置信区间) Frequency of resistance alleles (95% CI)	文献 Reference
巴西 Brazil	2010 年—2011 年,第二季 2011 年—2012 年,第一季 第二季 2012 年—2013 年,第一季 第二季	Cry1F 诊断剂量: 2 000 ng/cm ²	0.000 0(0.000 0~0.003 7)~ 0.006 9(0.003 2~0.014 1) 0.001 0(0.000 1~0.006 0)~ 0.087 6(0.071 4~0.106 4) 0.001 0(0.000 1~0.006 0)~ 0.813 3(0.787 9~0.836 8) 0.000 0(0.000 0~0.003 7)~ 0.780 8(0.754 4~0.805 4) 0.224 4(0.198 2~0.252 5)~ 0.971 6(95.95~0.980 5)	[50]
巴西中南部 6 个州 7 个地理种群 Seven populations from 6 states in Mid-South Brazil	2012 年	Cry1F 诊断剂量:2 000 ng/cm ²	1	[64]
阿根廷 Argentina	2009 年—2012 年 2012 年—2013 年 2013 年—2014 年 2014 年—2015 年	Cry1F 诊断剂量:10 μg/mL 或 2 000 ng/cm ²	0.00~0.02 >0.02(15 个种群中的 8 个) 0.052~0.915(17 个种群,平均 0.415) 0.166~0.979(25 个种群,平均 0.629)	[75]
阿根廷图库曼省 Tucumán, Argentina	2017 年	Cry1F 玉米	0.479	[76]

3 抗性产生的外因

3.1 热带亚热带农田生态系统有利于抗性产生

热带亚热带地区,一般降水丰富,温度适宜作物周年生长,复种指数高,常出现“反季”作物种植,如我国玉米等南繁育/制种、冬季种植鲜食甜糯玉米就是利用热带周年可种植的生态条件,在温带地区不能应季生产时的反季种植。由于制/育种、鲜食、饲用等不同目的需要,同一地区存在多个播期/生育期田块的景观格局,为草地贪夜蛾的周年连续繁殖提供了丰富的易觅寄主^[126]。在巴西,不同作物组成嵌合周年生长农田景观,包括大豆、玉米、小麦、棉花等,其中玉米、棉花和大豆都是 Bt 作物^[58]。尤其在同一地区不同播期连续种植同一转基因玉米或转相同或相似 Bt 基因作物,如表达 Cry1Ab 玉米、Cry1Ac 棉花、Cry1Ac 大豆、Cry1F 玉米、Cry1Ac+Cry1F 棉花、Vip3Aa20 玉米以及 Vip3Aa19 棉花等^[58,64,67,79],必然出现连续多代汰选,提高抗性演化风险。

3.2 表达蛋白种类及表达量

高剂量-庇护所是目前应用最广、最有效的抗性治理策略。庇护所起作用的关键前提之一是产品表达的 Bt 蛋白达到“高剂量”,即表达的剂量能够杀死隐性敏感纯合(ss)个体和杂合(sr)个体,仅有抗性纯合个体可能存活^[100]。这一措施有效延缓了多种害虫抗性产生,如烟芽夜蛾 *Heliothis virescens*、棉红铃虫 *Pectinophora gossypiella*^[127-128]、欧洲玉米螟等^[34]。

Cry1Ab 蛋白对草地贪夜蛾等夜蛾科害虫毒力相对较低^[129-130],虽然表达 Cry1Ab 玉米(‘MON810’和‘Bt11’)能有效控制草地贪夜蛾的为害,抑制幼虫生长,尤其是在虫口密度高的情况下能显著减少产量损失,但最终幼虫死亡率与对照差异不显著^[22,131-133],即没有达到高剂量,甚或没有将草地贪夜蛾列为转 *cry1Ab* 基因 Bt 玉米的靶标害虫^[134]。巴西 2010 年—2015 年多地监测数据表明,尽管不同地区草地贪夜蛾种群对 Cry1Ab 的敏感性存在显著性差异,但平均敏感性逐年下降^[66]。Cry1F 蛋白对草地贪夜蛾有较高的毒力和更好的防治效果^[30-32],然而其在田间的表现也没有达到高剂量的要求^[116]。聚合 2 个或多个具有不同杀虫谱且作用机理不同基因的 Bt 玉米,如‘MON89034’‘TC1507×MON89034’以及‘TC1507×MON810’等被认为既能扩大杀虫谱,又能延缓抗性产生^[35,135-136],然而有研究结果表明单基因 Cry1F 和 Cry1Ab 玉米与聚合多基因玉米对草地贪夜蛾等的防效并没有显著差异^[36,106]。值得注意的是,有研究报道 Cry1F 抗性草地贪夜蛾对‘MON89034’产生了抗性^[137],且 Cry1F 与 Cry1A.105 间存在交互抗性,将影响聚合多基因的抗性治理作用效果^[118]。

‘MIR162’玉米表达 Vip3Aa20 杀虫蛋白,其与 Cry 类蛋白作用机理不同^[138],且对鳞翅目夜蛾科多种害虫如草地贪夜蛾、美洲棉铃虫有很高的毒力^[139-141],尤其是对 Cry1F、Cry1Ab、Cry1Ac、Cry2Ab 抗性草地贪夜蛾有很高的毒力,即没有交互抗性^[142-144]。

值得关注的是,目前为止,表达单一 Vip3Aa20 或与 Cry 类聚合的玉米产品是唯一没有出现田间草地贪夜蛾产生抗性而防控失效的产品^[58]。

3.3 有效的抗性治理措施缺失

自从 McGaughey 首次报道印度谷螟 *Plodia interpunctella* (Hübner) 对 Bt 制剂产生抗性^[145],尤其是发现小菜蛾 *Plutella xylostella* 在田间对 Bt 制剂产生抗性后^[145],害虫对 Bt 作物的抗性问题的商业化应用伊始就备受重视。有学者曾预测,如若缺乏相应的抗性治理对策,Bt 作物种植 2~4 年靶标害虫将产生抗性^[100,146]。因此,美国在转基因抗虫作物商业化种植的同时,提出实施“高剂量-庇护所”的抗性治理策略^[28,100]。转基因抗虫作物商业化种植初期,抗性治理策略的落实是自愿的,但很快成为美国环保署 (USA-EPA) 颁布的强制性要求,即在种植 Bt 作物的同时,要求种植 5%~20% 的非转基因作物作为庇护所。这一策略在北美的实施,有效地避免或延缓了靶标害虫产生抗性^[147],被各国科学家普遍认同是转基因抗虫作物靶标害虫抗性治理的根本策略^[148-151]。

目前抗性治理策略主要包括高剂量-庇护所策略、聚合多基因策略、IPM 策略等。其中聚合多基因策略依赖于可用的 Bt 基因产品。而高剂量-庇护所策略和 IPM 策略则需要种植者根据生产实际加以落实。高剂量-庇护所策略有效性的前提条件是种植必要面积的庇护所。纵观转 *cry1F* 和 *cry1Ab* 玉米在波多黎各、巴西、阿根廷等中南美洲国家因草地贪夜蛾产生抗性而防治失效,其原因之一就是没有种植足够的庇护所,使得高剂量-庇护所这一抗性治理基本策略得不到落实。虽然巴西生物技术行业协会制定并推广了科学的 IRM 策略^[152],但庇护所在巴西种植业者中难以落实^[58,64]。据巴西种业协会估计,庇护所落实率不到 20%^[58]。

4 我国 Bt 玉米利用与草地贪夜蛾抗性治理策略的思考

种植 Bt 玉米可为农民带来巨大的直接经济效益^[34]。2020 年初 2 个国产转基因抗虫玉米产品“DBN9936”(表达 Cry1Ab 杀虫蛋白)和“瑞丰 125”(表达 Cry1Ab/Cry2Aj 杀虫蛋白)获得在北方春玉米区的生产应用安全证书^[153],将我国转基因玉米的研发应用向前推进了一大步,为亚洲玉米螟 *Ostrinia furnacalis*、黏虫 *Mythimna separata*、草地贪夜蛾等我

国玉米主要鳞翅目害虫提供了可供选择的防治新途径。基于全球种植 Bt 玉米的历史与害虫抗性演化与治理经验,尽早依据我国生产力水平、种植制度、农田景观生态类型以及虫害发生为害规律等,制定适宜的害虫抗性治理策略,是确保这一技术能长期持续有效应用的前提。笔者认为,应用 Bt 玉米防治草地贪夜蛾及其抗性治理策略应重点考虑以下几点。

4.1 整体布局,源头治理

我国玉米主产区分布北起东北(黑龙江)、穿越华北、南至西南(云贵高原南端)地带,由南到北面积递增,播期从春到冬,耕作栽培制度由多季到单季。由此构成了草地贪夜蛾以玉米为寄主的可觅性时空分布路线图。结合 2019 年我国草地贪夜蛾监测数据表明,其发生区可划分为周年繁殖区——北迁过渡区——重点防范区(黄淮海夏玉米区)——潜在为害区(北方玉米区)^[2,4]。以发生时序划分为越冬区(南方冬玉米区)——春末迁入区(江淮)——夏季迁入区(黄淮海夏玉米区)——秋季迁入区(北方玉米区)。这与草地贪夜蛾在美国玉米带发生、迁移扩散为害规律相似^[91-92]。因此,应按照整体布局,源头治理的原则,做好周年繁殖虫源区抗性治理,以达到整体解决草地贪夜蛾对 Bt 玉米的抗性问题的。

南方冬玉米面积约 10 万 hm^2 ^[2],主要种植鲜食玉米,是草地贪夜蛾的周年繁殖区,世代重叠,年发生 6~8 代。如果在此区域种植 Bt 玉米,草地贪夜蛾将会面临连续世代高频汰选抗性,导致抗性演化风险增加。加之境外虫源地越南和菲律宾是 Bt 玉米(‘Bt11’‘MON810’‘MON89034’‘TC1507’)种植国以及缅甸是 Bt 棉(表达 Cry1Ac 杀虫蛋白)种植国^[2,3,37,51],草地贪夜蛾在这些国家可周年繁殖,多代的汰选压容易导致当地草地贪夜蛾对 Bt 玉米产生抗性,携带抗性基因的个体随季风迁入我国南方玉米区,使得春夏季迁移扩散虫源携带抗性基因北上,势必对其他玉米种植区尤其是夏玉米区 Bt 玉米的利用构成严重威胁。因此,在草地贪夜蛾周年繁殖区应谨慎种植 Bt 玉米(尤其是应避免种植表达 Cry1Ab 的 Bt 玉米),以避免源头产生抗性而危及黄淮海夏玉米区乃至北方春玉米主产区。在种植 Bt 玉米的情况下,尽管春、夏、秋迁入区草地贪夜蛾也会面临抗性汰选,但其后代不能越冬,因而抗性基因不能在种群中累积遗传,目前尚未见草地贪夜蛾在秋季回迁到周年繁殖区的文献报道。

如果要在南方冬玉米区应用 Bt 玉米防治草地贪夜蛾等害虫,在 Bt 玉米种类选择上应采取“差异化”原则,即选择与其他种植区没有交互抗性(杀虫作用机理不同)的 Bt 玉米品种(应避免选择表达 Cry1Ab 及其类似的 Cry1 类杀虫蛋白的 Bt 玉米),以使周年繁殖区北迁携带抗性基因的个体,在迁入区的不同 Bt 玉米上成为敏感个体。这与草地贪夜蛾抗药性治理要在不同省份尽量做到“药剂品种、施用时间和空间不同”^[12]类似。

4.2 长期精准的抗性监测计划

技术上应针对生产上即将推广应用的 Bt 玉米种类,尽早摸清草地贪夜蛾自然种群的敏感基线、抗性基因频率(包括基因型检测^[154-156]和表型检测),明确其对不同 Bt 玉米产品表达 Bt 蛋白的抗性和交互抗性,建立抗性监测计划。同时应密切关注境外迁入虫源地 Bt 玉米种植情况,包括 Bt 玉米种类、种植制度、草地贪夜蛾的汰选史,当地监测抗性情况,外来虫源的敏感性测定等。精准的抗性监测将为抗性演化预测、抗性治理措施有效性评价提供及时可靠的科学依据。

4.3 切实落实好庇护所策略

美国 20 多年的成功实践经验证明,高剂量-庇护所是靶标害虫抗性治理的根本性策略^[147,157]。理论上高剂量是指 Bt 作物植株表达的 Bt 杀虫蛋白量能杀死靶标害虫种群中 100% 的 *ss* 个体和 95% 的 *sr* 个体^[100]。在抗性产生前,这一量化指标实际是无法准确得到的。因此,提出以表达量 $\geq 25 \times LC_{99.9}$ 剂量作为可操作高剂量指标^[148,158-160]。评价一个产品是否高剂量,与评价方法有关。Burkness 等报道了田间‘MIR162’及‘MIR162×Bt11’甜玉米上多年多点试验结果,草地贪夜蛾无存活幼虫,转基因玉米杀虫效果达到高剂量水平^[141]。Niu 等报道了 2 个草地贪夜蛾 Cry1A.105 抗性品系在 Cry1A.105 玉米离体叶片上表现为隐性或不完全隐性遗传,然而在整株玉米上表现为中等或不完全显性遗传^[161],甚至在‘MON89034’植株上也一样^[162],说明了田间评价的重要性。目前,国产转基因玉米多以亚洲玉米螟、黏虫为靶标,而草地贪夜蛾作为新入侵害虫没有被列为靶标。张丹丹等报道了‘C0030.3.5’(表达 Cry1Ab 蛋白)玉米离体叶片对草地贪夜蛾 1 龄幼虫的致死率 $< 66\%$,‘DBN3601’和‘DBN5608’(表达 Cry1Ab + Vip3Aa 蛋白)对 1~2 龄幼虫的致死率达到 100%,

3 龄幼虫的死亡率 $84\% \sim 95\%$ ^[14]。是否达到高剂量,有待进一步田间试验评价。

由于有限的可利用 Bt 玉米资源,这一措施的实施重点在于庇护所的落实。我们知道,‘TC1507’‘MON810’‘Bt11’等对于草地贪夜蛾都没有达到高剂量水平。但在美国本土应用已有 20 多年,现在依然有效,其中一个重要的原因是庇护所得到较好的落实^[147]。

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