# 中国转基因抗虫玉米的商业化策略

李国平[1] 吴孔明[2*]

（1. 河南省农业科学院植物保护研究所，河南省农作物病虫害防治重点实验室，农业农村部华北南部作物有害生物综合治理重点实验室，郑州 450002；2. 中国农业科学院植物保护研究所，植物病虫害生物学国家重点实验室，北京 100193）

**摘要：**玉米是全球播种面积最大的粮食作物，事关世界粮食安全。鳞翅目和鞘翅目害虫是影响玉米产量和品质的重要因素，长期以来多数国家采取以喷施化学农药为主的防控策略，但存在较高的使用成本和环境风险等问题。作为新一代的害虫防控技术，转基因抗虫玉米于1996年开始在美国商业化种植，并迅速推广到巴西等主要玉米生产国家，成为防控草地贪夜蛾*Spodoptera frugiperda*和欧洲玉米螟*Ostrinia nubilalis*等重大害虫的核心技术。该文综述了全球转基因抗虫玉米商业化的历史和防控害虫的作用，分析了美国对欧洲玉米螟和草地贪夜蛾等靶标害虫抗性治理的成功经验以及巴西等南美国家草地贪夜蛾对多种转基因抗虫玉米产生抗性的成因与教训。基于中国转基因抗虫玉米转化事件的研发现状、玉米生产模式、玉米害虫的区域发生特点和迁飞生物学等特性，提出在南方和西南山地丘陵玉米区种植包含*Vip3A*的多基因叠加抗虫玉米从源头防控草地贪夜蛾，在黄淮海夏玉米区种植包含*Cry2A*的多基因叠加抗虫玉米从源头防控棉铃虫*Helicoverpa armigera*，在北方春玉米区种植包含*Cry1A*的多基因叠加抗虫玉米从源头防控亚洲玉米螟*Ostrinia furnacalis*，以及在双斑长跗萤叶甲*Monolepta hieroglyphica*发生严重的地区种植包含*Cry3B*、*Cry34/35A*的多基因叠加抗虫玉米的区域性布局模式。要实施适合中国国情的高剂量–庇护所抗性治理措施，应基于转化事件是否对害虫达到高剂量要求而注册其对应的靶标害虫种类。在当前产品的庇护所设置上，对防控草地贪夜蛾的抗虫玉米和单基因抗虫玉米应采用10%~20%结构性庇护所进行抗性治理，对防控亚洲玉米螟等害虫的多基因抗虫玉米可采用5%种子混合庇护所进行抗性治理。

**关键词：**转基因抗虫玉米；靶标害虫；抗性治理；种植策略

## Commercial strategy of transgenic insect-resistant maize in China

Li Guoping[1] Wu Kongming[2*]

（1. Henan Key Laboratory of Crop Pest Control; Key Laboratory of Integrated Pest Management on Crops in Southern Part of Northern China, Ministry of Agriculture and Rural Affairs; Institute of Plant Protection, Henan Academy of Agricultural Sciences, Zhengzhou 450002, Henan Province, China 2. State Key Laboratory of Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China）

**Abstract:** Corn is the world's largest sown food crop, which is related to world food security. Lepidoptera and Coleoptera pests are important factors affecting maize yield and quality. Chemical pesticide spraying has been adopted by most countries for a long time, but it has high cost and environmental risk. As a new generation of pest control technology, transgenic insect-resistant corn was commercially planted in the United States in 1996, and quickly spread to major corn producing countries such as Brazil and other areas, becoming a core technology for the control of major pests such as fall armyworm *Spodoptera frugiperda* and European corn borer *Ostrinia nubilalis*. In this paper, the commercial history

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* 通信作者（Author for correspondence），E-mail：wukongming@caas.cn

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of transgenic insect-resistant maize and its role in pest control in the world were reviewed, and the successful experiences of the United States in the management of resistance to target pests such as corn borer and fall armyworm were analyzed, as well as the causes and lessons of resistance of fall armyworm to various transgenic insect-resistant maizes in Brazil and other South American countries. Based on the research and development status of transgenic insect-resistant maize transformation events in China, maize production patterns, regional occurrence characteristics and migratory biology of maize pests, it was proposed to plant multi-gene stacked insect-resistant maize cultivars containing *Vip3A* at the source for prevention and control of fall armyworm in mountainous and hilly maize areas of southern and southwestern China. In the Huang-Huai-Hai summer maize region, multi-gene stacked resistant maize containing *Cry2A* should be planted for the prevention and control of cotton bollworm *Helicoverpa armigera* at the source; in the northern spring maize region, multi-gene stacked resistant maize containing *Cry1A* should be planted for the prevention and control of Asian corn borer *O. furnacalis* at the source, and planting *Cry3b*- and *Cry34*/*35A*-resistant corn in the areas with serious occurrence of two-spotted leaf beetle *Monolepta hieroglyphica*, was proposed. To implement the high dose/refuge resistance management strategy in China, it is necessary to register the target pest species based on whether the transformation event meets the high dose criterion for pests. In terms of the refuge setting for current products, 10%–20% structured refuge should be applied to the resistant corn for management of fall armyworm *S. frugiperda* and the single Bt gene resistant corn, while 5% seed mixed refuge should be applied to the multi-gene resistant corn for pest control, such as Asian corn borer *O. furnacalis*.

**Key words:** transgenic insect-resistant maize; target pest; resistance management; planting strategy

玉米是世界上种植最广泛和产量最高的粮食作物。玉米不仅可以作为粮食食用，也是畜牧和水产养殖业的饲料来源以及医药化工原料。随着人民生活水平的不断提高，中国对玉米的需求量不断增加，种植面积已位于中国三大粮食作物之首。2020年，中国玉米种植面积为4.13×10$^7$ hm$^2$，总产量为2.6×10$^8$ t（国家统计局，https://data.stats.gov.cn/）。玉米虫害一直是影响玉米生产的重要因素。中国玉米害虫有200多种，能够造成严重减产的有10多种，每年引起的产量损失占玉米总产量的10%~20%（中国农业科学院植物保护研究所和中国植物保护学会，2014；吴兰花和郑丽霞，2018）。进入21世纪以来，随着气候变化和农业种植结构调整，玉米虫害发生呈现持续加重趋势（石洁等，2005；张社梅和赵芝俊，2009；王振营和王晓鸣，2019）。特别是重大迁飞性害虫草地贪夜蛾*Spodoptera frugiperda*的入侵对中国玉米安全生产构成了严重威胁（郭井菲等，2018；吴孔明，2020）。

中国当前对玉米害虫的防控主要采取以农业防治为基础、种子包衣为核心、生长期施药防治的对策（王振营和王晓鸣，2019）。这些措施在防控玉米虫害方面发挥了重要作用，但也存在较大问题。玉米苗期施用化学农药易造成环境污染，玉米抽雄后植株高大导致药剂喷洒困难。总体来讲，相对于发达国家，中国玉米虫害的防控手段和技术仍然较为落后，生产成本投入较高，不能适应农业绿色高质量发展的需要。

20世纪90年代中期以来，转Bt（*Bacillus thuringinesis*）抗虫基因玉米在美国得到了广泛的种植，高效防控了欧洲玉米螟*Ostrinia nubilalis*和草地贪夜蛾等害虫的发生为害（Koziel et al.，1993；Mason et al.，1996），取得了十分显著的经济、社会和生态效益（Hutchison et al.，2010；Dively et al.，2018；ISAAA，2019）。中国一直高度重视作物转基因技术的研究，已培育了一批转基因玉米新品系（沈平等，2016）。2020年中央经济工作会议提出要尊重科学、严格监管，有序推进生物育种产业化应用。2021年农业农村部开展了转基因玉米的产业化试点工作，结果表明转基因抗虫玉米不仅可高效防控害虫，还提高了玉米产量和品质，也减少了化学杀虫剂的应用，保护了生态环境（https://xhpfmapi.xinhuaxmt.com/vh512/share/10482302?channel=weixin）。本文综述了转基因抗虫玉米的研发历史、发展趋势、国外商业化种植的经验和教训，并结合中国实际情况提出了抗虫玉米的商业化种植策略。

## 1 国外转基因抗虫玉米的研发历史和发展趋势

转基因抗虫玉米主要用于防控鳞翅目害虫和鞘翅目害虫。防控鳞翅目害虫的基因可分为3类，第1类是Cry1类，包括*Cry1Ab*、*Cry1Ac*、*Cry1A.105*和*Cry1F*等基因；第2类是Cry2类，包括*Cry2Ab*和*Cry2Ae*等基因；第3类是Vip类，包括*Vip3A19*和*Vip3A20*等基因（Huang，2021）。用于防控鞘翅目害虫的基因有*Cry3B1*、*Cry34/35Ab1*、*mCry3A*、*eCry3.1Ab*及*V-ATPase* dsRNA和*DvSnf7* dsRNA等（Frank et al.，2013；Head et al.，2017）。自1996年到现在，转基因抗虫玉米的研发和应用大致经历了3个阶段（表1）。

**表1 转基因抗虫玉米的发展阶段**

Table 1 Developmental stages of transgenic insect-resistant maize

| 阶段<br>Stage | 基因类型<br>Genetic type | 注册年份<br>Year registered | 基因<br>Gene | 靶标害虫<br>Target pest |
|---|---|---|---|---|
| 第1阶段（1996—2009年）<br>The first stage（1996—2009） | 单个Cry基因<br>Single Cry gene | 1996 | *Cry1Ab* | 鳞翅目 Lepidoptera |
| | | 2003 | *Cry3B1* | 鞘翅目 Coleoptera |
| | | 2003 | *Cry1F* | 鳞翅目 Lepidoptera |
| | | 2005 | *Cry34/35Ab1* | 鞘翅目 Coleoptera |
| | | 2006 | *mCry3A* | 鞘翅目 Coleoptera |
| 第2阶段（2010—2016年）<br>The second stage（2010—2016） | 多个Cry基因叠加<br>Multiple Cry genes | 2010 | *Cry1A.105+Cry2Ab*, *Cry1F+Cry1A.105+Cry2Ab*, *Cry1Ab+Cry1F* | 鳞翅目 Lepidoptera |
| | | 2013 | *eCry3.1Ab+mCry3A*, *Cry3Bb1+Cry34/35Ab1*, *mCry3A+Cry34/35Ab1* | 鞘翅目 Coleoptera |
| 第3阶段（2017年至今）<br>The third stage（2017—Now） | Cry基因、Vip基因和RNAi等叠加<br>Cry gene, Vip gene and RNAi stacked | 2017—2018 | *Cry1A.105+Cry2Ab+Vip3A*, *Cry1A.105+Cry2Ab2+Cry1F+DvSnf7+Cry3Bb1+Cry34/35Ab1* | 鳞翅目和鞘翅目<br>Lepidoptera and Coleoptera |

第1阶段（1996—2009年）：种植单个Cry基因的抗虫玉米（表1）。1995—1996年登记的玉米品种以表达Cry1Ab为主，包括先正达、孟山都等公司登记的“176”、“MON810”和“Bt11”等转化事件，以欧洲玉米螟和西南玉米秆草螟*Diatraea grandiosella*为主要靶标害虫，主要在美国和加拿大商业化种植。由于表达Cry1Ab玉米对草地贪夜蛾的防效不高，未将草地贪夜蛾列为靶标害虫（Graeber et al.，1999；Lauer & Wedberg，1999；Archer et al.，2000；2001）。2001年，表达Cry1F的“TC1507”在美国登记并于2003年开始商业化种植，表达Cry1F玉米对欧洲玉米螟和草地贪夜蛾都有极好的防控效果，因此草地贪夜蛾被列为了表达Cry1F玉米的主要靶标害虫。除此之外，表达Cry1F玉米对西南玉米秆草螟、小蔗秆草螟*Diatraea saccharalis*和小地老虎*Agrotis ipsilon*等鳞翅目害虫也有较好的防控效果（Buntin，2008；Siebert et al.，2008a）。2003年，表达Cry3Bb1的“MON863”和“MON88017”转化事件也在美国登记和商业化种植，用于防控鞘翅目害虫玉米切根叶甲*Diabrotica virgifera*；2005年表达Cry34/35Ab的“DAS-591227-7”和2006年表达mCry3A的“MIR604”转化事件被批准用于防控玉米切根叶甲（Frank et al.，2013）。到2010年，美国种植的表达单一Bt基因抗虫、耐除草剂玉米面积达到0.36亿$hm^2$，占该国玉米总种植面积的86%（James，2010）。

第2阶段（2010—2016年）：种植具有不同作用方式的多个Cry基因抗虫玉米。由于防控美洲棉铃虫*Heliocoverpa zea*和草地贪夜蛾等害虫和实施多基因抗性治理策略的需要（Storer et al.，2012a），2010年，孟山都公司研发的表达Cry1A.105+Cry2Ab2的“MON89034”转化事件在美国和加拿大商业化种植。Cry1A.105蛋白提高了玉米对草地贪夜蛾和小地老虎的抗性，Cry2Ab2能够高效防控美洲棉铃虫，且这2种蛋白之间没有明显的交互抗性（Niu et al.，2016a，b）。2013年，表达eCry3.1Ab+mCry3A、Cry34/35Ab1+mCry3A、Cry34/35Ab1+3Bb1蛋白以防控玉米切根叶甲的转化事件开始商业化种植（US EPA，2020）。此后，通过传统的育种方法，将“MON89034”、“TC1507”、“MON863”和“MON88017”等多个抗虫转化事件聚合，扩大了转基因玉米的杀虫谱并延缓了害虫的抗性发展（Storer et al.，2012b；Siebert et al.，2012b）。

第3阶段（2017年至今）：种植Cry抗虫基因、Vip抗虫基因和RAN干扰技术（RNA interference， RNAi)叠加防控多个靶标害虫的抗虫玉米。由于草地贪夜蛾和玉米切根叶甲对Cry1类和Cry3类蛋白、美洲棉铃虫对Cry1/Cry2类蛋白均产生了抗性,生物技术公司研发了不同于Cry类作用方式的新基因,如*Vip3A*抗虫基因和RNAi等。Vip是伴胞晶体形成过程中产生的一种营养期杀虫蛋白(vegetative insecticidal protein,Vip),与Cry类蛋白无交互抗性,对草地贪夜蛾和美洲棉铃虫表现良好的抗虫效果(Gilreath et al.,2021)。表达Vip3A玉米以先正达公司登记的"MIR162"转化事件为主,当前北美洲大多通过种植"MON89034"×"TC1507"×"MIR162"、"Bt11"×"MIR162"等多基因聚合的抗虫玉米品种来防控鳞翅目害虫,在一些地区还与抗鞘翅目害虫玉米切根叶甲的*mCry3A*、*Cry3Bb1*和*Cry34Ab1*/*Cry35Ab1*基因进行叠加(US EPA,2020)。

RNAi是应用外源双链RNA(double-strand RNA,dsRNA)干扰真核生物特定基因表达的一种基因沉默技术,特定基因的沉默可导致靶标害虫生长发育受阻、繁殖力降低和死亡(Fire et al.,1998)。为了延缓美国玉米切根叶甲对Cry3类基因的抗性,农业生物技术公司积极研发RNAi技术与Cry3类基因叠加来防控玉米切根叶甲,目前成熟应用的基因包括*vATPase-A* dsRNA和*Snf7* dsRNA等(Baum et al.,2007;Fishilevich et al.,2019)。2017年,美国环境保护局批准了孟山都公司申请的表达Cry3Bb1+DvSnf7的"MON87411"抗虫玉米转化事件。同年,孟山都和陶氏益农公司合作获批了表达Cry1A.105+Cry2Ab + Cry1F + Cry3Bb1 + Cry34Ab1/Cry35Ab1 + DvSnf7的SmartStax Pro®转基因玉米新产品(Head et al.,2017)。RNAi技术增加了抗虫新机制,提高了Bt玉米对玉米切根叶甲防控的持久性。因此,采用常规杂交手段聚合优势抗虫基因获取兼抗鳞翅目和鞘翅目害虫的玉米,或与耐除草剂基因*EPSPS-CP4*或*Pat*叠加培育兼抗多种害虫和耐除草剂的复合性状玉米已成为转基因玉米发展的方向。

# 2 转基因抗虫玉米商业化种植历史与经验教训

## 2.1 全球转基因抗虫玉米商业化种植情况

1996年,美国首次批准转*Cry1Ab*基因玉米("Bt176"、"MON810"和"Bt11")商业化种植,在随后的25年里,转基因作物在全球范围内得到了快速的推广和应用。2019年,全球已经有29个国家种植了转基因作物,种植面积由1996年的$1.7\times10^6$ $hm^2$增加到2019年的$1.904\times10^8$ $hm^2$,提高了112倍。其中,转基因玉米种植面积为$6.09\times10^7$ $hm^2$,占转基因作物总种植面积的32%(ISAAA,2019)。兼具抗虫和耐除草剂复合性状的玉米种植面积为$5.59\times10^7$ $hm^2$,占转基因玉米总种植面积的91.2%,包括北美洲、中美洲、南美洲、欧盟、非洲和亚太地区的14个国家,其中美国种植面积为$3.317\times10^7$ $hm^2$、巴西为$1.63\times10^7$ $hm^2$、阿根廷为$5.9\times10^6$ $hm^2$、加拿大为$1.6\times10^6$ $hm^2$(ISAAA,2019)。

当前,全球种植的抗虫玉米转化事件如表2所示。在北美洲、中美洲和南美洲,主要靶标害虫是欧洲玉米螟、草地贪夜蛾、美洲棉铃虫和玉米切根叶甲等。在非洲,南非是唯一种植Bt玉米的国家。1998年,南非开始种植表达Cry1Ab的"MON810"玉米,主要用来防控玉米蛀茎害虫,包括斑禾草螟*Chilo partellus*、亚澳白裙夜蛾*Busseola fusca*、枚蛀茎夜蛾*Sesamia calamistis*和非洲甘蔗茎螟*Eldana saccharina*(Gouse et al.,2005)。但在2007年,亚澳白裙夜蛾对"MON810"中表达的Cry1Ab蛋白产生了抗性(van Rensburg,2007;Kruger et al.,2014)。为了解决亚澳白裙夜蛾的抗性问题,2010年开始种植表达Cry1A. 105+Cry2Ab2的"MON89034"玉米(Kruger et al.,2014)。草地贪夜蛾入侵后,"MON89034"对其起到了较好的防控作用(Botha et al.,2019)。亚洲国家菲律宾和越南已商业化种植"MON810"玉米,主要用于防控以亚洲玉米螟*Ostrinia furnacalis*为主的鳞翅目害虫(Afidchao et al.,2013)。

## 2.2 种植转基因抗虫玉米对靶标害虫的防控作用

北美洲种植表达Cry1Ab的"Bt176"、"Bt11"和"MON810"等转化事件对欧洲玉米螟和西南玉米杆草螟有极高的防控效果(Castro et al.,2004;Huang et al.,2006),田间防控效率达到99%以上(Lauer & Wedberg,1999;Graeber et al.,1999;Siegfried & Hellmich,2012),而对豆纹缘夜蛾*Striacosta albicosta*的防控效率较低(Catangui & Berg 2006;Eichenseer et al.,2008),表达Cry1Ab玉米对草地贪夜蛾有一定的防控效果,使玉米心叶期被害率降低90%,穗期被害率降低50%~80%(Buntin et al.,2001;Buntin,2010);表达Cry1Ab玉米对美洲棉铃虫的防控效率为75%~80%(Storer et al.,2001)。表达Cry1F的"TC1507"玉米对欧洲玉米螟、西南玉米杆草螟、小蔗杆草螟和草地贪夜蛾具有极好的防控效果,田间防控效率达到99%以上(Graeber et al.,1999;Siebert et al.,2008b),对豆纹缘夜蛾有中等水平抗性(Eichenseer et al.,

2008）。表达Vip3A的“MIR162”玉米对草地贪夜蛾和美洲棉铃虫的防控效率均在99%以上（Burkness et al.，2010）。表达Cry3Bb1的“MON863”和“MON88017”转化事件对玉米切根叶甲的防控效率为89%~95%（Oyediran et al.，2007），表达mCry3A的“MIR604”转化事件对玉米切根叶甲的防控效率达96.88%~98.86%（Hibbard et al.，2010a；2011），而表达Cry34Ab1/Cry35Ab1的“DAS-59122-7”转化事件对玉米切根叶甲的防控效率为95.96%~99.44%（Storer et al.，2006；Binning et al.，2010；Hibbard et al.，2010b）。

**表2 全球转基因抗虫玉米商业化概况**（https://www.isaaa.org/gmapprovaldatabase/default.asp）

Table 2 An overview of commercializtion of transgenic insect-resistant maizes in the world (https://www.isaaa.org/gmapprovaldatabase/default.asp)

| 商品名<br>Trade name | 登记单位<br>Registered company | 转化事件名称<br>Event name | 抗虫基因<br>Insect-resistant gene | 商业化批准时间<br>Approval time for commercialization | 靶标害虫<br>Target pest |
|---|---|---|---|---|---|
| NaturGard KnockOu™, Maximizer™ | Syngenta | Bt176 (176) | *Cry1Ab* | 美国（1995）、加拿大（1996）、阿根廷（1998）、西班牙（1998）、葡萄牙（1999）<br>USA (1995), Canada (1996), Argentina (1998), Spain (1998), Portugal (1999) | 鳞翅目<br>Lepidoptera |
| Agrisure™ CB/LL | Syngenta | Bt11 | *Cry1Ab* | 美国和加拿大（1996）、阿根廷（2001）、巴西(2008)、巴拉圭(2012)、菲律宾(2010)、南非(2003)、乌拉圭(2004)、越南(2015)<br>USA and Canada (1996), Argentina (2001), Brazil (2008), Paraguay (2012), Philippines (2010), South Africa (2003), Uruguay (2004), Vietnam (2015) | 鳞翅目<br>Lepidoptera |
| YieldGard™, MaizeGard™ | Monsanto | MON810 | *Cry1Ab* | 美国（1996）、加拿大和南非（1997）、阿根廷（1998）、洪都拉斯（2001）、菲律宾（2002）、乌拉圭（2003）、巴西和哥伦比亚（2007）、巴拉圭（2012）<br>USA (1996), Canada and South Africa (1997), Argentina (1998), Honduras (2001), Philippines (2002), Uruguay (2003), Brazil and Colombia (2007), Paraguay (2012) | 鳞翅目<br>Lepidoptera |
| Herculex™ I, Herculex™ CB | Dow AgroSciences/ DuPont | TC1507 | *Cry1Fa2* | 美国（2001）、阿根廷（2005）、巴西（2008）、加拿大（2002）、哥伦比亚（2007）、洪都拉斯（2009）、乌拉圭（2011）、巴拿马（2012）、巴拉圭（2012）、菲律宾（2013）、南非（2012）<br>USA (2001), Argentina (2005), Brazil (2008), Canada (2002), Colombia (2007), Honduras (2009), Uruguay (2011), Panama (2012), Paraguay (2012), Philippines (2013), South Africa (2012) | 鳞翅目<br>Lepidoptera |
| YieldGard™ Rootworm RW, MaxGard™ | Monsanto | MON863 | *Cry3Bb1* | 美国（2002）、加拿大（2003）<br>USA (2002), Canada (2003) | 鞘翅目<br>Coleoptera |
| YieldGard VT RW | Monsanto | MON88017 | *Cry3Bb1* | 美国（2005）、加拿大（2006）、阿根廷（2010）、巴西（2010）、洪都拉斯（2013）<br>USA (2005), Canada (2006), Argentina (2012), Brazil (2014), Honduras (2013) | 鞘翅目<br>Coleoptera |
| Agrisure™ RW | Syngenta | MIR604 | *mCry3A* | 美国(2007)、阿根廷(2012)、巴西(2014)、加拿大(2007)<br>USA (2007), Argentina (2012), Brazil (2014), Canada (2007) | 鞘翅目<br>Coleoptera |
| Agrisure™ Viptera | Syngenta | MIR162 | *Vip3Aa20* | 巴西(2009)、美国、加拿大和阿根廷（2011）、哥伦比亚和巴拉圭（2014）、菲律宾（2018）<br>Brazil (2009), USA, Canada and Argentina (2011), Colombia and Paraguay (2014), Philippines (2018) | 鳞翅目<br>Lepidoptera |

**续表2 Continued**

| 商品名 Trade name | 登记单位 Registered company | 转化事件名称 Event name | 抗虫基因 Insect-resistant gene | 商业化批准时间 Approval time for commercialization | 靶标害虫 Target pest |
|---|---|---|---|---|---|
| YieldGard™ VT Pro™ | Monsanto | MON89034 | *Cry1A.105+CryAb2* | 美国和加拿大(2008)、阿根廷(2010)、巴西(2009)、洪都拉斯(2012)、葡萄牙(2014)、菲律宾(2009)、南非(2010) USA and Canada (2008), Argentina (2010), Brazil (2009), Honduras (2012), Portugal (2014), Philippines (2009), South Africa (2010) | 鳞翅目 Lepidoptera |
| Herculex™ RW | Dow AgroSciences/ DuPont | DAS-59122-7 | *Cry34Ab1/Cry35Ab1* | 美国(2005)、加拿大(2005) USA (2005), Canada (2005) | 鞘翅目 Coleoptera |
| Agrisure® Viptera™ 2100 | Syngenta | Bt11×MIR162 | *Cry1Ab+Vip3Aa20* | 阿根廷(2014)、巴西(2015) Argentina (2014), Brazil (2015) | 鳞翅目 Lepidoptera |
| YieldGard Plus | Monsanto | MON863× MON810 | *Cry3Bb1+Cry1Ab* | 菲律宾(2004) Philippines (2004) | 鳞翅目和鞘翅目 Lepidoptera and Coleoptera |
| Herculex XTRA™ | Dow AgroSciences/ DuPont | TC1507× DAS-59122-7 | *Cry1Fa2+Cry34Ab1/ Cry35Ab1* | 巴西(2013)、加拿大(2006) Brazil (2013), Canada (2006) | 鳞翅目和鞘翅目 Lepidoptera and Coleoptera |
| Yieldgard® | Dow AgroSciences/ DuPont | TC1507× MON810 | *Cry1Fa2+Cry1Ab* | 阿根廷(2013)、巴西(2011)、哥伦比亚(2011)、巴拉圭(2015)、菲律宾(2014)、南非(2014) Argentina (2013), Brazil (2011), Colombia (2011), Paraguay (2015), Philippines (2014), South Africa (2014) | 鳞翅目 Lepidoptera |
| Agrisure® Viptera™ 3100 | Syngenta | Bt11×IR162× MIR604 | *Cry1Ab+Vip3Aa20+ mCry3A* | 美国(2009)、巴西(2019) USA (2009), Brazil (2019) | 鳞翅目和鞘翅目 Lepidoptera and Coleoptera |
| Genuity® SmartStax™ | Monsanto/Mycogen/ Dow AgroScience | MON89034× TC1507× MON88017× DAS-59122-7 | *Cry1A.105+ Cry2Ab2+Cry1F+ Cry3Bb1+Cry34Ab1/ Cry35Ab1* | 加拿大(2009)、巴西(2016) Canada (2009), Brazil (2016) | 鳞翅目和鞘翅目 Lepidoptera and Coleoptera |
| SmartStax Pro | Monsanto/Dow AgroScience | MON89034× TC1507× MON87411× DAS-59122-7 | *Cry1A.105+Cry2Ab2+ Cry1F+DvSnf7+ Cry3Bb1+Cry34Ab1/ 35Ab1* | 美国(2017) USA (2017) | 鳞翅目和鞘翅目 Lepidoptera and Coleoptera |

南美国家转基因抗虫玉米的主要靶标害虫为草地贪夜蛾(Burtet et al., 2017; Signorini et al., 2018)、美洲棉铃虫和小蔗杆草螟(Blanco et al., 2016; Grimi et al., 2018);菲律宾和越南等亚太地区抗虫玉米的靶标害虫为亚洲玉米螟,抗性效率在99%以上(Afidchao et al., 2013; Liem, 2016)。在南非,种植表达Cry1Ab的"MON810"对斑禾草螟、亚澳白裙夜蛾、枚蛀茎夜蛾和非洲甘蔗茎螟的田间防控效率达99%以上(Gouse et al., 2005)。2016年1月草地贪夜蛾入侵非洲后,表达Cry1A. 105+Cry2Ab2的"MON89034"玉米对草地贪夜蛾的抗性效率在99%以上(Botha et al., 2019)。欧洲的西班牙、葡萄牙等国家种植的表达Cry1Ab的"Bt176"主要用于防控欧洲玉米螟和中东蛀茎夜蛾 *Sesamia nonagrioides*,防控效率大于99%(Shelton et al., 2002; Farinós et al., 2004; Brookes, 2019)。

### 2.3 不同国家对靶标害虫的抗性治理模式及经验教训

害虫对抗虫作物抗性的定义为靶标害虫种群暴露于抗虫作物选择压下而引起种群以遗传为基础的敏感性降低(Tabashnik, 1994; Tabashnik et al., 2009)。转基因抗虫玉米可持续种植的主要威胁是靶标害虫的抗性问题。因此,多数国家在批准转基因抗虫玉米商业化时,要求执行抗性治理措施。抗性治理的理论依据是高剂量/庇护所,有3个要点:一是抗虫玉米要表达高剂量的杀虫蛋白;二是靶标害虫种群的抗性基因起始频率处于很低的水平;三是源自抗虫玉米田块和非抗虫玉米田块(庇护所)的成虫在田间能随机混合交配(Gould, 1998)。

高剂量指抗虫玉米植株表达的杀虫蛋白量能杀死靶标害虫种群中100%的敏感纯合子个体(ss)

和95%的敏感杂合子个体(sr)(Gould,1998)。在抗性产生前,该量化指标实际上无法准确测定。因此美国转基因作物科学顾问小组提出以表达量高于杀死敏感幼虫浓度25倍的剂量作为可操作的高剂量标准。常用的测定方法是将抗虫玉米冻干组织用人工饲料稀释25倍进行生物测定,如果校正死亡率达到100%,则认为达到高剂量的要求(US EPA,1998)。

庇护所是指所有能让靶标害虫正常生长发育的非抗虫植物。庇护所设有3种形式,一是结构庇护所,即在种植抗虫玉米时专门种植非抗虫作物来降低害虫的抗性进化速度,结构庇护所的比例一般在10%~50%之间;二是种子混合庇护所,即抗虫玉米种子在销售的时候已经将一定比例的非抗虫种子混入到抗虫种子中,比例一般为5%~10%;三是自然庇护所,指的是可以提供敏感害虫的杂草或者其他栽培植物(US EPA,1998)。

美国和加拿大主要采取结构庇护所和种子混合庇护所治理靶标害虫的抗性(Matten et al.,2012)。转单基因玉米防控鳞翅目害虫要求种植20%的结构庇护所,而防控鞘翅目时可以种植20%的结构庇护所或者10%的种子混合庇护所;多基因玉米防控欧洲玉米螟要求种植5%的结构庇护所或5%的种子混合庇护所,但对草地贪夜蛾和美洲棉铃虫等则基于种植地区提出不同的结构庇护所要求。在美国南部地区由于害虫发生世代多,庇护所面积的设定比例高于北部地区;多基因抗虫玉米防控鞘翅目害虫要求种植5%的结构庇护所或5%种子混合庇护所。鳞翅目害虫的结构庇护所一般要求与抗虫玉米的间隔距离小于0.8 km,鞘翅目害虫庇护所要求与抗虫玉米相邻种植,以保障敏感害虫与抗性个体可随机交配(https://www.epa.gov/regulation-biotechnology-under-tsca-and-fifra/insect-resistance-management-bt-plant-incorporated)。在南美洲的阿根廷和巴西等国家,统一要求设置10%的结构庇护所(IRAC,2017)。在菲律宾等国家,单基因抗虫玉米要求种植20%的结构庇护或10%的种子混合庇护所,多基因抗虫玉米要求设置5%的种子混合庇护所(Prooeso,2014;Alcantara et al.,2021)。

高剂量/庇护所的抗性治理模式已在全球应用了20多年,但不同国家实施的效果存在较大差别。美国等发达国家农场化生产模式执行程度高,靶标害虫抗性发展慢,而发展中国家的小农生产方式执行难度大,靶标害虫抗性演化速度快(Huang et al.,2011)。靶标害虫的抗性水平可分为3类,第1类是产生实质抗性,即田间抗性个体的数量大于50%,显著降低了抗虫玉米的田间防控效果(Tabashnik et al.,2014);第2类是产生了早期抗性,指的是种群敏感性虽然下降但田间防控效率并没有明显降低(Tabashnik & Carrière,2017);第3类是田间种群的敏感性没有明显下降。

草地贪夜蛾是对转基因抗虫玉米产生实质抗性最快的害虫。2003年,"TC1507"开始在波多黎各商业化种植,但2006年田间就发现有草地贪夜蛾为害。Storer et al.(2010)从田间采样进行生物测定证实草地贪夜蛾对Cry1F蛋白产生大于1 000倍的高水平抗性(Storer et al.,2010;2012a)。巴西于2009年开始商业化种植表达Cry1F玉米,2011年草地贪夜蛾就对其产生了抗性(Farias et al.,2014;2016),随后对Cry1Ab蛋白也产生了实质抗性(Omoto et al.,2016);2018年,阿根廷的草地贪夜蛾对Cry1F蛋白产生了抗性(Chandrasena et al.,2018)。此后,美国东南部佛罗里达州和北卡罗莱纳州的草地贪夜蛾对Cry1F蛋白产生了抗性(Huang et al.,2014;Li et al.,2016),这可能与中美洲的抗性个体迁入有关。

到2021年,还有12种靶标害虫对表达不同杀虫蛋白的转基因玉米也产生了实质抗性,主要有南非亚澳白裙夜蛾对"MON810"玉米(van Rensburg,2007),阿根廷小蔗杆草螟对"TC1507"和表达Cry1A.105玉米(Blanco et al.,2016;Grimi et al.,2018),美国玉米切根叶甲对"MON863"、"DAS-591227-7"、"MIR604"和"5307"玉米(Gassmann et al.,2011;2014;2016;Andow et al.,2016),美国美洲棉铃虫对"Bt11"和"M89034"玉米(Storer et al.,2001;Dively et al.,2016),加拿大豆纹缘夜蛾对"TC1507"玉米(Smith et al.,2017),美国豆纹缘夜蛾对"TC1507"玉米(Eichenseer et al.,2008;Ostrem et al.,2016),以及加拿大欧洲玉米螟对"TC1507"玉米(Smith et al.,2019)等都产生了实质抗性。此外,美国小蔗杆草螟对表达Cry1Ab玉米(Huang et al.,2012)、菲律宾亚洲玉米螟对表达Cry1Ab玉米(Alcantara et al.,2011)和美国美洲棉铃虫对表达Vip3A玉米(Yang et al.,2019)的抗性已达到早期预警水平(表3)。

对靶标害虫产生实质抗性案例的分析表明,大多数原因是高剂量/庇护所的抗性治理技术无法有效落实。首先,一些转基因抗虫玉米产品对害虫没有达到高剂量,如表达Cry1Ab的"MON810"玉米对南非的玉米蛀茎夜蛾,表达Cry3Bb1的"MON863"、表达Cry34/35Ab的"DAS-591227-7"、表达mCry3A的"MIR604"和表达eCry3.1Ab的转化事件对美国的玉米切根叶甲,表达Cry1Ab的"Bt11"和表达

Cry1A.105+Cry2Ab的"M89034"对美国的美洲棉铃虫,表达Cry1F的"TC1507"对加拿大和美国的豆纹缘夜蛾,表达Cry1F的"TC1507"对美国、巴西和阿根廷等国家的草地贪夜蛾以及表达Cry1Ab的"MON810"对巴西的草地贪夜蛾等(Tabashnik & Carrière,2017)均未达到高剂量(表3);其次,尽管法规规定了种植庇护所,但在一些国家和地区,如波多黎各、巴西、阿根廷等国家的种植者没有切实履行种植庇护所的规定。在美国本土,虽然抗虫玉米对草地贪夜蛾没有达到高剂量的要求,但庇护所得到了较好的落实,种植20年后仍然没有产生明显的抗性,这是一个十分成功的抗性治理案例(Huang, 2021)。在波多黎各,岛内单一的热带生态系统以及周年循环种植转基因玉米,在缺乏庇护所的情况下种群快速产生了抗性(Storer et al., 2012a)。在巴西,玉米、棉花和大豆都是转Bt作物,尤其是在同一地区连续种植同一转基因玉米或相似的Bt作物,如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,庇护所缺乏是导致产生抗性的一个重要原因(Santos-Amaya et al., 2017)。在加拿大,尽管法规要求种植20%的结构庇护所,但由于种植者不遵守规定,导致欧洲玉米螟对Cry1F产生了实质抗性(Smith et al., 2019)。

**表3 不同国家转基因抗虫玉米庇护所法规要求及靶标害虫的抗性发展**

Table 3 Regulatory requirements for resistance management of transgenic insect-resistant maize in different countries and resistance levels of main target pests

| 靶标害虫 Target pest | 国家或地区 Country or region | 抗虫蛋白(抗虫玉米转化事件) Insect-resistant protein (transformation event) | 当前抗性水平 Resistance level | 商业化初田间防控效率 Field efficancy | 高剂量 High dose | 庇护所设置法规要求 Refuge | 参考文献 Reference |
|---|---|---|---|---|---|---|---|
| 草地贪夜蛾 *Spodoptera frugiperda* | 美国波多黎各 Puerto Rico, USA | Cry1F (TC1507) | 实质抗性 Practical resistance | ≥99% | 接近 Near | 20%结构庇护所 20% structured refuge | Storer et al., 2010; 2012a |
| | 巴西 Brazil | Cry1F (TC1507) | 实质抗性 Practical resistance | ≥99% | 接近 Near | 10%结构庇护所 10% structured refuge | Farias et al., 2014; 2016 |
| | | Cry1Ab (MON810) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 10%结构庇护所 10% structured refuge | Omoto et al., 2016 |
| | 阿根廷 Argentina | Cry1F (TC1507) | 实质抗性 Practical resistance | ≥99% | 接近 Near | 10%结构庇护所 10% structured refuge | Blanco et al., 2016; Chandrasena et al., 2018 |
| | 美国佛罗里达和北卡罗莱纳地区 Florida and North Carolina, USA | Cry1F (TC1507) | 实质抗性 Practical resistance | ≥99% | 接近 Near | 20%结构庇护所 20% structured refuge | Huang et al., 2014; Li et al., 2016 |
| | 巴西 Brazil | Vip3A (MIR162) | 敏感性未下降 No decrease in susceptibility | ≥99% | 是 Yes | 10%结构庇护所 10% structured refuge | Leite et al., 2018 |
| 亚澳白裙夜蛾 *Busseola fusca* | 南非 South Africa | Cry1Ab (MON810) | 实质抗性 Practical resistance | ≥99% | 否 No | 20%结构庇护所 20% structured refuge | van Rensburg, 2007; Kruger et al. 2014 |
| 小蔗杆草螟 *Diatraea saccharalis* | 阿根廷 Argentina | Cry1F (TC1507) | 实质抗性 Practical resistance | ≥99% | 否 No | 10%种子混合庇护所 10% seed mixed refuge | Blanco et al., 2016; Grimi et al., 2018 |
| | 美国 USA | Cry1Ab (MON810, Bt11) | 早期预警水平 Early warning of resistance | ≥99% | 否 No | 20%结构庇护所 20% structured refuge | Huang et al., 2012 |
| 玉米切根叶甲 *Diabrotica virgifera* | 美国 USA | Cry3Bb1 (MON863, MON88017) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 20%结构庇护所 20% structured refuge | Gassmann et al., 2011; 2014 |

**续表3 Continued**

| 靶标害虫<br>Target pest | 国家或地区<br>Country or region | 抗虫蛋白（抗虫玉米转化事件）<br>Insect-resistant protein (transformation event) | 当前抗性水平<br>Resistance level | 商业化初田间防控效率<br>Field efficacy | 高剂量<br>High dose | 庇护所设置法规要求<br>Refuge | 参考文献<br>Reference |
|---|---|---|---|---|---|---|---|
| | | Cry34/35Ab (DAS-591227-7) | 实质抗性 Practical resistance | ≥99% | 否 No | 5%结构庇护所、10%种子混合庇护所、5%种子混合庇护所 5% structured refuge, 10% seed mixed refuge and 5% seed mixed refuge | Ludwick et al., 2017 |
| | | mCry3A (MIR604) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 20%结构庇护所 20% structured refuge | Andow et al., 2016 |
| | | eCry3.1Ab (5307) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 20%结构庇护所 20% structured refuge | Gassmann et al., 2016 |
| | | mCry3A+Cry34/35Ab1 MIR604× DAS-591227-7) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 5%种子混合庇护所 5% seed mixed refuge | Andow et al., 2016 |
| 美洲棉铃虫 *Helicoverpa zea* | 美国 USA | Cry1Ab (Bt11, MON810) | 实质抗性 Practical resistance | 75%–80% | 否 No | 20%结构庇护所 20% structured refuge | Dively et al., 2016 |
| | | Cry1A.105+ Cry2Ab (M89034) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 5%种子混合庇护所 5% seed mixed refuge | Kaur et al., 2019 |
| | | Vip3A (MIR162) | 早期预警水平 Early warning of resistance | ≥99% | 接近 Near | 5%种子混合庇护所 5% seed mixed refuge | Yang et al., 2019 |
| | 巴西 Brazil | Vip3A (MIR162) | 敏感性未下降 No decrease in susceptibility | ≥99% | 接近 Near | 10%结构庇护所 10% structured refuge | Leite et al., 2018 |
| 豆纹缘夜蛾 *Striacosta albicosta* | 加拿大 Canada | Cry1F (TC1507) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 20%结构庇护所 20% structured refuge | Smith et al., 2017 |
| | 美国 USA | Cry1F (TC1507) | 实质抗性 Practical resistance | 中等抗性 Moderate reistance | 否 No | 20%结构庇护所 20% structured refuge | Eichenseer et al., 2008; Ostrem et al., 2016 |
| 欧洲玉米螟 *Ostrinia nubilalis* | 美国 USA | Cry1Ab (MON810, Bt11) | 敏感性未下降 No decrease in susceptibility | ≥99% | 是 Yes | 20%结构庇护所 20% structured refuge | Siegfried & Hellmich, 2012 |
| | 美国 USA | Cry1F (TC1507) | 敏感性未下降 No decrease in susceptibility | ≥99% | 是 Yes | 20%结构庇护所 20% structured refuge | Siegfried et al., 2014 |
| | 加拿大 Canada | Cry1F (TC1507) | 实质抗性 Practical resistance | ≥99% | 是 Yes | 20%结构庇护所 20% structured refuge | Smith et al., 2019 |
| | 西班牙 Spain | Cry1Ab (MON810, Bt11) | 敏感性未下降 No decrease in susceptibility | ≥99% | 是 Yes | 20%结构庇护所 20% structured refuge | EFSA, 2015 |
| 亚洲玉米螟 *Ostrinia furnacalis* | 菲律宾 Philippines | Cry1Ab (MON810) | 早期预警水平 Early warning of resistance | ≥99% | 否 No | 20%结构庇护所 20% structured refuge | Alcantara et al., 2011 |
| 中东蛀茎夜蛾 *Sesamia nonagrioides* | 西班牙 Spain | Cry1Ab (MON810) | 敏感性未下降 No decrease in susceptibility | ≥99% | 是 Yes | 20%结构庇护所 20% structured refuge | Camargo et al., 2018; Castañera et al., 2016 |
| 西南玉米杆草螟 *Diatraea grandiosella* | 美国 USA | Cry1Ab (MON810) | 敏感性未下降 No decrease in susceptibility | ≥99% | 不知 Unknown | 20%结构庇护所 20% structured refuge | Huang et al., 2007 |

## 3 中国转基因抗虫玉米的主要靶标害虫和区域性发生特点

中国转基因抗虫玉米的靶标害虫主要有小地老虎、黄地老虎 *Agrotis segetum*、二点委夜蛾 *Athetis lepigone*、甜菜夜蛾 *Spodoptera exigua*、劳氏黏虫 *Leucania loreyi*、东方黏虫 *Mythimna separata*、亚洲玉米螟、桃蛀螟 *Conogethes punctiferalis*、棉铃虫 *Helicoverpa armigera*、双斑长跗萤叶甲 *Monolepta hieroglyphica* 以及新入侵重大害虫草地贪夜蛾等(王晓鸣和王振营,2018;吴孔明,2020;Li et al.,2021)(表4)。根据各地气候、土壤、地理条件及耕作制度等因素的差别,可将中国玉米种植划分为北方春玉米区、黄淮海平原夏玉米区、西南山地丘陵玉米区、南方丘陵玉米区、西北内陆玉米区和青藏高原玉米区(佟屏亚,1992),各地区害虫发生规律存在较大差异。

北方春玉米区为一年一熟制,玉米单种或间作、套作。亚洲玉米螟和黏虫是该区抗虫玉米的主要鳞翅目靶标害虫,此外,鞘翅目害虫双斑长跗萤叶甲在北方春玉米区为害也较重。黄淮海平原夏玉米区为一年两熟制,棉铃虫、玉米螟、桃蛀螟、二点委夜蛾和黏虫是该区常发玉米害虫。西南山地丘陵玉米区和南方丘陵玉米区是中国秋、冬玉米的主要种植地区,以新入侵的草地贪夜蛾为主要害虫;西北内陆玉米区以玉米螟为主要害虫(王振营和王晓鸣,2019)。

**表4 中国转基因抗虫玉米靶标害虫的种类组成、生物学特点和分布地区**

Table 4 Species composition, biological characteristics and distribution areas of transgenic insect-resistant maize target pests in China

| 害虫种类 Pest species | 寄主植物 Host plant | 主要分布区域 Regional distribution | 抗寒能力 Cold hardiness | 迁飞行为 Migratory behaviour |
|---|---|---|---|---|
| 小地老虎 *Agrotis ipsilon* | 玉米、大豆、花生、棉花等 Maize, soybean, peanut, cotton, etc. | 各玉米区均有分布 Distributed in all maize regions | 弱(无滞育特性) Weak (no diapause) | 远距离迁飞 Long-distance migration |
| 黄地老虎 *Agrotis segetum* | 玉米、大豆、花生、棉花等 Maize, soybean, peanut, cotton, etc. | 北方春玉米区 North spring corn region | 弱(无滞育特性) Weak (no diapause) | 远距离迁飞 Long-distance migration |
| 二点委夜蛾 *Athetis lepigone* | 玉米、大豆、花生、棉花等 Maize, soybean, peanut, cotton, etc. | 黄淮海夏玉米区 Huang-Huai-Hai summer corn region | 中等(幼虫滞育越冬) Medium (overwintering as larval diapause) | 中距离迁飞 Medium-distance migration |
| 甜菜夜蛾 *Spodoptera exigua* | 玉米、甜菜、棉花等 Maize, sugarbeet, cotton, etc. | 黄淮海夏玉米区 Huang-Huai-Hai summer corn region | 弱(无滞育习性) Weak (no diapause) | 远距离迁飞 Long-distance migration |
| 东方黏虫 *Mythimna separata* | 玉米、小麦、水稻、谷子等 Maize, wheat, rice, millet, etc | 除新疆外的各省(自治区、直辖市) All provinces (autonomous regions, municipalities) except Xinjiang | 弱(无滞育特性) Weak (no diapause) | 远距离迁飞 Long-distance migration |
| 劳氏黏虫 *Leucania loreyi* | 玉米、小麦、大麦、水稻、甘蔗等 Maize, wheat, barley, rice, sugar cane, etc. | 黄淮海夏玉米区、西南山地丘陵玉米区 Huang-Huai-Hai summer corn region, Southwest hilly corn region | 弱(无滞育特性) Weak (no diapause) | 远距离迁飞 Long-distance migration |
| 草地贪夜蛾 *Spodoptera frugiperda* | 玉米等 Maize, etc. | 除新疆、甘肃、黑龙江、吉林外各省(自治区、直辖市) All provinces (autonomous regions, municipalities) except Xinjiang, Gansu, Heilongjiang and Jilin | 弱(无滞育特性) Weak (no diapause) | 远距离迁飞 Long-distance migration |
| 亚洲玉米螟 *Ostrinia furnacalis* | 玉米、高粱、谷子等 Maize, sorghum, millet, etc. | 除青海、西藏外各省(自治区、直辖市) All provinces (autonomous regions, municipalities) except Qinghai and Tibet | 强(幼虫滞育越冬) Strong (overwintering as larval diapause) | 短距离迁飞 Short-distance migration |
| 桃蛀螟 *Conogethes punctiferalis* | 玉米、高粱、向日葵、桃、板栗等 Maize, sorghum, sunflower, peach, chestnut, etc. | 黄淮海夏玉米区、西南山地丘陵玉米区、南方丘陵玉米区 Huang-Huai-Hai summer corn region, Southwest hilly corn region, South hilly corn region | 强(幼虫滞育越冬) Strong (overwintering as larval diapause) | 短距离迁飞 Short-distance migration |
| 棉铃虫 *Helicoverpa armigera* | 棉花、小麦、玉米、花生、大豆等 Cotton, wheat, maize,peanuts, soybean, etc. | 黄淮海夏玉米区和西北内陆玉米区 Huang-Huai-Hai summer corn region and Northwest inland corn region | 中等(蛹滞育越冬) Medium (overwintering as pupal diapause) | 中距离迁飞 Medium-distance migration |
| 双斑长跗萤叶甲 *Monolepta hieroglyphica* | 玉米、大豆、棉花等 Maize, soybean, cotton, etc. | 北方和西北地区 North and northwest corn region | 强(卵滞育越冬) Strong (overwintering as egg diapause) | 短距离扩散 Short-distance dispersal |

上述玉米害虫最突出的生物学特性就是迁飞扩散行为。害虫的迁飞扩散习性是适应环境变化、保障种群繁衍的季节性转移为害策略。从东北到西南地区，中国玉米种植随季节和纬度变化从北至南递次推移，播期从春到冬，耕作制度由单季到多季，时间和空间上互补，为迁飞性玉米害虫区域性迁移为害提供了丰富和充足的食物资源（何康来和王振营，2020）。亚洲玉米螟和桃蛀螟属于短距离的迁飞害虫，迁飞距离一般小于200 km，具有较强的抗寒能力，亚洲玉米螟能以滞育幼虫在北方春玉米区等高纬度地带安全越冬，桃蛀螟能以滞育幼虫在黄淮海夏玉米区安全越冬（周洪旭等，2004；张洪刚等，2010；周燕等，2020）。棉铃虫和二点委夜蛾是中距离迁飞性害虫，常在越冬区和非越冬区之间迁飞，多采取1~2个夜晚迁飞200~500 km进入北方非越冬区（周燕等，2020）。棉铃虫的越冬北界在1月平均最低温度−15℃等温线左右，其在东北的绝大多数地区不能越冬，一般在春末夏初，1代棉铃虫成虫由华北中北部迁入东北地区，6月底—7月中旬，华北地区的2代棉铃虫成虫可随气流继续迁往东北地区，8月底以后，东北地区繁衍的后代回迁到华北地区（吴孔明和郭予元，2007；Feng et al.，2009）。

黏虫、草地贪夜蛾、小地老虎和甜菜夜蛾等不具备滞育特性，抗寒能力弱，一般经过3个以上夜晚超过500 km的连续迁飞从东南亚国家和中国南方向北方迁移，是典型的远距离迁飞性害虫。黏虫在中国主要有2次北迁过程，第1次是3、4月从长江以南的越冬区域进入江淮、黄淮平原，第2次是5、6月继续北迁，进入东北地区（周燕等，2020）。小地老虎的越冬北界与黏虫相似，春夏季节由长江流域向东北区域迁飞，秋季从东北地区向南方越冬区回迁（Liu et al.，2015）。草地贪夜蛾冬季主要在热带、南亚热带地区为害冬秋玉米，夏季迁入黄淮海夏玉米区和北方春玉米区为害（陈辉等，2020）。这就要求针对不同靶标害虫的源头发生地选择抗虫基因的类别，并有针对性的对转基因玉米进行区域性布局。

## 4 基于靶标害虫区域防控和抗性治理的商业化对策

2019年，北京大北农生物技术有限公司转*Cry1Ab*与*epsps*基因的抗虫耐除草剂玉米“DBN9936”和杭州瑞丰生物科技有限公司转*Cry1Ab*/*Cry2Aj*与*G10evo-epsps*基因抗虫耐除草剂玉米“瑞丰125”两个转化事件获得了在北方春玉米区生产应用安全证书（http://www.moa.gov.cn/ztzl/zjyqwgz/spxx/201912/t20191230_6334015.htm）。2020年，“DBN9936”获得了在黄淮海夏玉米区、南方丘陵玉米区、西南山地丘陵玉米区和西北内陆玉米区生产应用的安全证书。此后，大北农公司培育的转*Vip3Aa19*和*pat*基因抗虫耐除草剂玉米“DBN9501”获得了在北方春玉米区生产应用的安全证书（http://www.moa.gov.cn/ztzl/zjyqwgz/spxx/202101/t20210111_6359740.htm）；2021年，“瑞丰125”获得了在黄淮海夏玉米区和西北内陆玉米区生产应用的安全证书（http://www.moa. gov. cn/ztzl/zjyqwgz/spxx/202104/t20210407_6365331.htm）。*Cry1F*、*Vip3A*和*Cry2Ab*等基因叠加的多个转化事件已接近完成研发过程，这些转基因抗虫玉米产品展现了良好的商业化前景（He et al.，2021；Liang et al.，2021）。吸取国外转基因抗虫玉米种植和靶标害虫抗性治理的经验和教训，中国应根据玉米种植区主要害虫发生的区域、寄主为害和迁飞扩散等生物学特点，采取“分区布局，源头管控”的转基因抗虫玉米种植策略和适合中国国情的高剂量/庇护所抗性治理对策。

### 4.1 中国转基因抗虫玉米的区域化布局

对于玉米迁飞性害虫的防控工作，最有效的策略是区域性监测预警和虫源基地种植抗虫玉米（吴孔明，2020；周燕等，2020）。中国西南山地丘陵和南方丘陵秋冬玉米区，是国内草地贪夜蛾、黏虫等害虫的周年繁殖区和国外迁入种群的集中降落地，也是黄淮海夏玉米区和北方春玉米区的重要虫源地。因此，在该区域应种植能高效防控草地贪夜蛾和黏虫且满足高剂量要求的以转*Vip3A*、*Cry1F*等基因为主的多价Bt基因玉米品种，以期达到降低源头地区草地贪夜蛾和黏虫的发生数量，形成国家防控草地贪夜蛾和黏虫阻截带。黄淮海夏玉米种植区是棉铃虫、桃蛀螟和二点委夜蛾的主要发生区，种植以转*Cry2A*、*Vip3A*为主的多基因抗虫品种防控棉铃虫、桃蛀螟和二点委夜蛾，可防控这3种害虫的跨区迁移为害，实现全国性高效管控的战略目标。在东北春玉米区，亚洲玉米螟是该区主要的鳞翅目害虫，种植以转*Cry1A*、*Cry2A*为主的多基因叠加抗虫玉米可实现区域性防控的目标，而在西北内陆玉米区和青藏高原玉米区，由于玉米种植面积较小，靶标害虫发生较轻，可基于局部害虫发生特点，选择适宜的抗虫玉米。在双斑长跗萤叶甲发生严重的地区可以种植转*Cry3B*、*Cry34*/*35A*等多基因叠加抗虫玉米。

### 4.2 中国转基因抗虫玉米的抗性治理策略

总结近20年来美国在欧洲玉米螟、草地贪夜蛾对Bt抗虫玉米和中国在棉铃虫对Bt棉花的抗性治

理过程中积累的经验,发现高剂量/庇护所策略是保障转基因抗虫作物可持续应用的有效措施(Wu,2007;Huang et al.,2011;Wan et al.,2017;Tabashnik & Carrière,2017)。抗性治理策略的选择要考虑抗虫基因类型和杀虫剂量水平、害虫的生物学习性和寄主种类等因素。要建立杀虫剂量水平的评价体系、方法和标准。对于任何一个转化事件的商业化,都要首先评估确定达到高剂量的靶标害虫种类,并注册为防控对象。如用于防控低于高剂量的害虫,则需要加大庇护所的面积。原则上,对于单一抗虫基因的转基因玉米一般采用结构性庇护所;对于扩散能力较弱的靶标害虫则要求庇护所邻近于转基因玉米;对于为害玉米籽粒的靶标害虫一般不宜采用种子混合庇护所;对于寄主植物种类多的靶标害虫可以利用自然庇护所。理论上需要在研究靶标害虫生物学的基础上建立抗性风险评价模型,权衡抗性发展速度与抗性治理成本,提出经济可行且社会能接受的具体措施(Roush,1994)。总体而言,结构庇护所对抗性治理的有效性高于种子混合庇护所,而种子混合庇护所的可操作性和成本显著优于结构庇护所。在中国多数地区,小农生产模式仍然是主体,这样就难以推广结构庇护所。但在科学层面上,对单基因抗虫玉米和取食玉米籽粒的草地贪夜蛾等采用种子混合庇护所将很难实现延缓抗性的目标。因此,就目前的研发产品而言,防控草地贪夜蛾的抗虫玉米和单基因抗虫玉米建议采用10%~20%结构性庇护所进行抗性治理,防控亚洲玉米螟等害虫的多基因抗虫玉米建议采用5%种子混合庇护所进行抗性治理。随着高抗草地贪夜蛾多基因新产品的研发,条件成熟时可全部采取种子混合庇护所进行抗性治理。对于一家一户的小农生产模式,可以以自然村为单位,通过补贴政策鼓励部分农户种植非转基因抗虫玉米,形成结构式庇护所。

抗性监测是转基因作物抗性治理的基础。应针对中国生产上即将推广应用的Bt玉米种类,尽早摸清不同生态区域主要靶标害虫的敏感基线和抗性基因频率,并建立切实可行的抗性监测计划。当前,中国已经建立了北方春玉米区和黄淮海夏玉米区的亚洲玉米螟不同种群对Cry1Ab、Cry1Ac和Cry1F蛋白的敏感基线和初始抗性基因频率(He et al.,2005;Li et al.,2020)。同时,也建立了黏虫、棉铃虫、草地贪夜蛾、桃蛀螟和二点委夜蛾等对Cry1Ab等蛋白的敏感基线和抗性基因频率。这些工作为转基因玉米商业化种植后监测害虫的抗性发展提供了基准对照值。转基因玉米一旦商业化种植,就要及时监测其抗性水平变化情况。当进入早期抗性阶段后,就需要强化抗性治理措施和实施应急管理,防止抗性继续发展而出现实质抗性。

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