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封面图说:植物生命演进石——这不是一块普通的火山岩,而是一块集中展示植物“原生演替”过程最有价值的石头。火山熔岩冷却后的玄武岩是无生命无土壤的真正“裸石”,风力使地衣的孢子传入,在一定温湿度环境下,开始出现了壳状地衣,壳状地衣尸体混合了自然风化的岩石碎屑提供的条件使叶状、枝状地衣能够侵入,接着苔藓侵入,是它们启动了土壤的形成,保持了土壤的湿度,并使营养物质反复循环。于是蕨类定居,草丛长了起来,小灌木出现,直到树木生长,最终形成森林。

彩图提供:陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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李志毅,隋贺,徐艳博,韩兰芝,陈法军.转Cry1Ab和Cry1Ac融合基因型抗虫水稻对田间二化螟和大螟种群发生动态的影响.生态学报,2012,32(6):1783-1789.

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转Cry1Ab和Cry1Ac融合基因型抗虫水稻对田间二化螟和大螟种群发生动态的影响

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摘要:以Bt水稻华恢1号(Cry1Ac和CryAb融合基因;简称HH1)及其对照亲本明恢63(简称MH63)稻田靶标害虫二化螟*Chilo suppressalis*和次靶标害虫大螟*Sesamia inferens*为研究对象,研究了转基因抗虫水稻大田螟虫发生规律及其靶标和次靶标害虫致害力差异。结果表明,Bt水稻及其对照亲本上二化螟或大螟的卵块数量差异不显著,同时,对照亲本上二化螟与大螟的落卵量差异不显著,但Bt水稻上二化螟的落卵量显著大于大螟。与对照亲本相比,Bt水稻上二化螟幼虫发生量显著降低,降幅高达84.9%—100%,但大螟发生量差异不显著;此外,对照亲本上二化螟幼虫发生量显著高于大螟,但Bt水稻上两者差异不显著。同时,Bt水稻上二化螟导致的枯心/白穗率和受害丛率都显著低于其在对照亲本上的致害程度,降幅分别为30.8%—98.3%和11.4%—96.6%,而大螟差异不显著。可见,Bt水稻对靶标害虫二化螟具有较高抗性,而对次靶标害虫大螟的抗性不明显。另一方面,Bt水稻和对照亲本上二化螟导致的枯心/白穗率和受害丛率都显著高于大螟。可见,二化螟仍是当前非转基因水稻上的主要害虫,而Bt水稻对二化螟幼虫发生的显著抑制作用以及对大螟幼虫发生的不显著影响,使得其大面积商业化种植下靶标害虫二化螟和次靶标害虫大螟间的竞争替代成为可能。

关键词:Bt水稻;靶标/次靶标抗性;二化螟;大螟;种群发生;生态风险

Effects of insect-resistant transgenic *Bt* rice with a fused *Cry1Ab+Cry1Ac* gene on population dynamics of the stem borers, *Chilo suppressalis* and *Sesamia inferens*, occurring in paddyfield

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Abstract: The approval of transgenic *Bacillus thuringiensis* rice (ab., *Bt* rice) with double-stacked traits (including a rice restorer line of cv. *Bt* Huahui-1 and a hybrid rice line of cv. *Bt* Shanyou-63, both expressing a fused *Cry1Ab+Cry1Ac* gene) by China's Ministry of Agriculture (MOA) on 27 November 2009 was a momentous day for biotech crops worldwide. To date, some experiments have been carried out in labs or under controlled environmental conditions, which indicate that *Bt* rice can perform remarkably well against two targeted lepidopteran pests (e.g., the stem borer, *Chilo suppressalis*, and

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leaf-folder, *Cnaphalocrocis medinalis*), and simultaneously offers: 1) the potential to generate economic benefits due to yield increases, and 2) overall decreases in insecticide use in China. In this study, the field experiments were conducted in order to examine the population dynamics and damage characteristics of two stem borers (i. e., target pest, *C. suppressalis* and a sub-target pest, *Sesamia inferens*) feeding on the *Bt* rice with a fused *Cry1Ab+Cry1Ac* gene (cv., *Bt* Huahui-1) and its parent line of nontransgenic rice (cv., Minghui-63). The results indicate that no significant differences were found in the number of egg masses per 100 plants for *C. suppressalis* or *S. inferens* occurring on *Bt* rice in contrast to nontransgenic rice. In addition, no significant differences in egg mass densities between *C. suppressalis* and *S. inferens* were found when fed on nontransgenic rice, whereas a significant increase in egg mass were observed for *C. suppressalis* relative to *S. inferens* fed on *Bt* rice. Compared with nontransgenic rice, *Bt* rice significantly reduced the population density (i. e., individuals per 100 plants; 84.9%—100%) of *C. suppressalis* larvae, while the transgenicity did not significantly influence the population abundance for *S. inferens*. Moreover, *C. suppressalis* had significantly higher larval abundances than *S. inferens* when they fed on nontransgenic rice, while no significant differences were observed when fed on *Bt* rice. Simultaneously, significantly lower percentages of dead heart or white head plants (30.8%—98.3%), and damaged plants (11.4%—96.6%) resulted from *C. suppressalis*, while no significant differences were detected in the damage percentages for *S. inferens*, as they fed on the *Bt* rice relative to the nontransgenic rice cultivar. Therefore, *Bt* rice appears to have a higher resistance to the targeted pest, *C. suppressalis*, while lower resistance was observed for the sub-target pest, *S. inferens*. Furthermore, significantly higher damage percentages were caused by *C. suppressalis* relative to *S. inferens*, regardless of the transgenicity of the rice cultivar. Thus, the stem borer, *C. suppressalis*, remains the key insect pest in the paddyfield. While it is presumed, owing to the significant inhibition of *Bt* rice on the occurrence of *C. suppressalis* relative to *S. inferens* under the commercialization usage of *Bt* rice, the inter-species competition and population succession may be occurring between the target and sub-target pests of stem borers. Furthermore, additional field research work needs to be conducted, especially during the rice growing season when high densities of *C. suppressalis* and *S. inferens* are both available on *Bt* rice to assess ecological risks of the inter-species competition and population successions between the target and sub-target insect pests.

Key Words: *Bt* rice; target/non-target resistance; *Chilo suppressalis*; *Sesamia inferens*; population dynamics; ecological risk

水稻是世界上主要的粮食作物之一,尤其对广大发展中国家而言^[1]。而长期以来,螟虫一直是我国水稻生产上的常发性害虫,尤其自20世纪90年代以来,其种群发生量持续上升,为害不断加剧,对水稻生产构成了严重威胁。其中,优势种二化螟 *Chilo suppressalis* 年发生面积在1666.7万hm²以上,大螟 *Sesamia inferens* 的年发生面积亦超过166.7万hm²^[2]。由于水稻螟虫具有钻蛀为害习性,给防治带来极大困难^[3]。过去对螟虫的控制主要依赖化学农药,进而导致严重的害虫抗药性问题^[4-5]。此外,长期使用化学农药还会带来农药残留和环境污染等问题^[6]。为了改变水稻依赖化学防治这一现状,进行抗虫品种选育是一条简便、经济、安全、有效的途径^[7]。近年来,随着转基因技术的快速发展,多种转基因作物相继培育成功,其中 *Bt* 抗虫育种取得了极大成功,如 *Bt* 抗虫棉花、水稻、烟草、玉米、大豆和甜菜等。

目前,我国转基因抗虫水稻(如转 *Cry1Ab/Cry1Ac* 融合基因型恢复系华恢1号和同样转 *Cry1Ab/Cry1Ac* 融合基因杂交系 *Bt* 汕优63)已获取安全证书,向商业化种植迈出了一大步,这也成为了引发国内外广泛关注的热点问题^[8]。目前,我国产业化前景较好的抗虫水稻主要以转 *Cry1A* 基因为主。研究表明, *Cry1A* 蛋白对螟蛾科害虫如二化螟、三化螟和稻纵卷叶螟均具有较好防效,控制效率均在90%以上^[9-14],但对大螟的防效较低,晚稻上的控制效率仅为44%—64%^[15]。此外,转基因水稻稻茬残存螟虫中,大螟所占比例明显上升,导致转基因稻田存在主要害虫种群竞争演替的生态风险^[15]。这在商业化种植历史已达10余年的 *Bt* 棉花上得以

证实,即 *Bt* 棉花的种植有效地控制了大田棉铃虫和棉红铃虫的暴发为害^[16]。但对 *Bt* 毒素耐受性较高的次靶标害虫甜菜夜蛾的种群数量却呈上升趋势^[17],上升为棉田的主要害虫^[18-20]。*Bt* 抗虫水稻的种植是否也会引起田间不同螟虫种群间的竞争演替?进而面临次要害虫上升为主要害虫的生态风险?这是 *Bt* 抗虫水稻大面积商业化推广种植前,其生态风险评价中亟待明确的重要问题之一。本文通过 *Bt* 抗虫水稻华恢 1 号的大田试验,开展主要靶标害虫二化螟和次靶标害虫大螟的种群动态调查和致害力差异比较研究,为进一步明确 *Bt* 抗虫水稻种植下大田螟虫的种群发生规律及其种间竞争演替提供试验依据,同时服务于转基因抗虫水稻的生态安全评价和生态风险评估。

1 材料与方法

1.1 供试转基因水稻

试验所用转基因水稻为华恢 1 号(*Cry1Ac* 和 *Cry1Ab* 融合基因型,简称 HH1),及其对照亲本水稻明恢 63(简称 MH63)。两种水稻种子均由华中农业大学提供。

1.2 试验地布局

试验地设在广西兴安县湘漓镇——中国农业科学院植物保护研究所野外观测基地。*Bt* 水稻 HH1 与其对照亲本 MH63 播种小区间隔交替排列,每个品种各设置 3 个重复,共计 6 个小区,每个小区面积为 5 m×20 m,小区间设置 1 m 空白隔离带,以防止不同品种水稻间螟虫幼虫的转株为害。

1.3 试验地农事管理:

2010 年 5 月 23 日秧田育秧,6 月 28 日大田移栽插秧,秧苗定植尺寸行间距为 18 cm × 18 cm。水稻插秧时,按每 666.7 m² 5 kg 尿素和 5 kg N:P:K(18:15:12)复合肥的标准撒施基肥,并在大田插秧后,按照每 666.7 m² 65% 五氯酚钠粉剂 200 g 拌土 15 kg 的标准均匀撒施于水田表面,用于防治福寿螺对秧苗的为害。此外,水稻整个生育期内不施用农药,以确保稻田昆虫自然消长。自 7 月 7 日起,每隔 4 d 人工补水 1 次。7 月 15 日,按每 666.7 m² 10 kg 尿素和 10 kg N:P:K(18:15:12)复合肥的标准追肥一次,并于水稻分蘖前期集中人工除草一次,其它的农事操作均同当地常规田。

1.4 二化螟和大螟发生与为害调查

为了明确 *Bt* 水稻种植对靶标害虫二化螟和次靶标害虫大螟的种群发生规律及两种螟虫对水稻的致害力差异,于 7 月 29 日—9 月 30 日,每 7 d 调查一次,每品种各 3 个小区,每小区按“双平行线”取样法随机抽检 50 丛水稻进行调查,分别记录二化螟和大螟的落卵量和幼虫量,后转化为百丛落卵量和百丛幼虫量,用来作为表示两种螟虫发生量差异的指标;另外,详细记录二化螟和大螟分别导致的水稻枯心数(包含前期的枯鞘数)、白穗数(包含孕穗期的枯孕穗数)、受害丛数(若被调查的稻丛有其中一个分蘖为枯心或者白穗,则此丛即算为受害丛)及总分蘖数,最终转化为枯心/白穗率(在抽穗前和抽穗后分别用枯心率和白穗率来表示水稻的受害程度)、受害丛率,用以上两个指标来表示两种螟虫对水稻的致害力差异。

1.6 统计分析

数据分析采用 SAS6.12 统计软件(SAS Institute, USA, 1996)进行。采用 Excel 2003 软件计算枯心/白穗率和受害丛率,计算方法根据中华人民共和国国家标准——水稻二化螟测报调查规范(GB/T15792—1995)进行:枯心/白穗率=(枯心数或白穗数/总分蘖数)×100%,受害丛率=(有枯心或白穗丛数/调查丛数)×100%。其中,二化螟和大螟的种群发生动态(包括百丛落卵量和百丛虫量)及其致害力指标(即枯心白穗率和受害丛率)采用成对 *T* 检验(Paired-*T* test)进行统计分析(*P*<0.05)。数据分析前,分别对绝对值和百分比数据进行对数转换和反正弦平方根转化,以符合正态分布假设。

2 结果

2.1 *Bt* 水稻及其对照亲本上二化螟和大螟的落卵量

图 1 显示,*Bt* 水稻及其对照亲本上二化螟和大螟的卵块数量均不大(≤2 块/百丛),*Bt* 水稻 HH1 上大螟的落卵量甚至为零。成对 *T* 检验表明,大螟和二化螟在 *Bt* 水稻及其对照亲本上的卵块数量差异不显著,且对

照亲本上二化螟与大螟的落卵量差异不显著,但 *Bt* 水稻 HH1 上二化螟的卵块数量显著高于大螟的卵块数($P<0.05$; 图 1)。

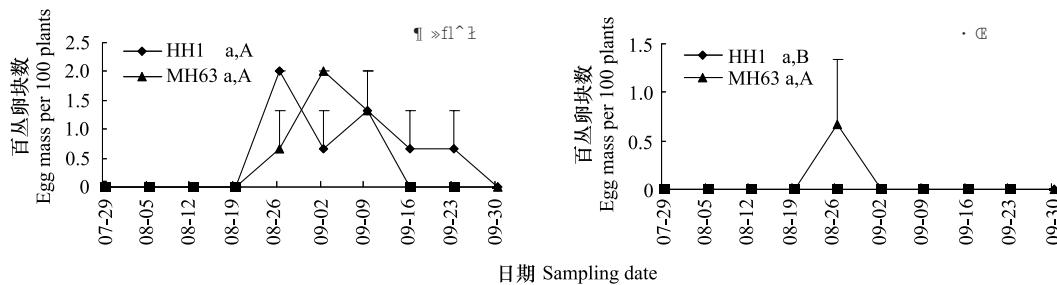


图 1 *Bt* 水稻(Cry1Ab 和 Cry1Ac 融合基因型;华恢 1 号)及其对照亲本(明恢 63)上二化螟和大螟的落卵量

Fig. 1 The egg masses of stem borers *Chilo suppressalis* and *Sesamia inferens* fed *Bt* rice (cv. HH1 with fused *Cry1Ab* and *Cry1Ac*) and nontransgenic rice (cv. MH63, the parent line)

不同小写字母表示在 *Bt* 水稻及其对照亲本上二化螟或大螟的落卵量差异显著;不同大写字母表示同一水稻品种上,大螟和二化螟的落卵量差异显著;成对 *T* 检验, $P<0.05$

2.2 *Bt* 水稻及其对照亲本上二化螟和大螟幼虫发生量

图 2 显示, *Bt* 水稻及其亲本上二化螟和大螟的幼虫发生量存在极大差异,且两者之间存在近 2 个数量级($\times 100$)的差异;其中, *Bt* 水稻及其亲本上二化螟和大螟的高峰期虫量分别为百丛 43 头和 287 头、0 头和 3.3 头。与对照亲本相比, *Bt* 水稻上二化螟种群发生量显著降低($P<0.05$; 图 2), 降幅高达 84.9%—100%,而大螟发生量差异不显著($P>0.05$; 图 2)。此外, 对照亲本水稻上二化螟种群发生量显著高于大螟种群($P<0.05$),而 *Bt* 水稻上两者种群发生量都很小,且差异不显著($P>0.05$; 图 2)。

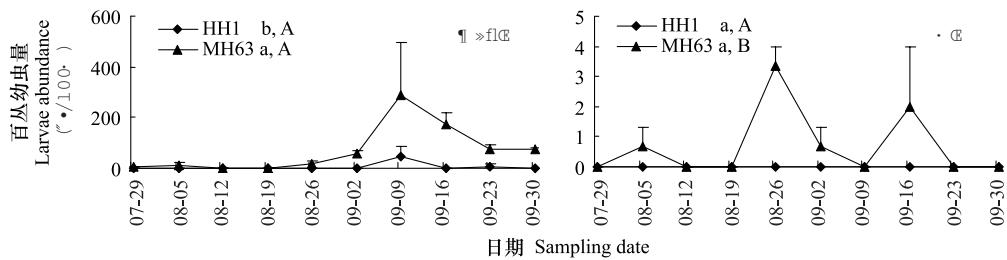


图 2 *Bt* 水稻(Cry1Ab 和 Cry1Ac 融合基因型;华恢 1 号)及其对照亲本(明恢 63)上二化螟和大螟的幼虫发生量

Fig. 2 Population dynamics of the larvae of stem borers *C. suppressalis* and *S. inferens* fed *Bt* rice (cv. HH1 with fused *Cry1Ab* and *Cry1Ac*) and nontransgenic rice (cv. MH63, the parent line)

不同小写字母表示二化螟或大螟在 *Bt* 水稻及其对照亲本上的虫量差异显著;不同大写字母表示同一水稻品种上,大螟和二化螟的虫量差异显著;成对 *T* 检验, $P<0.05$

2.3 *Bt* 水稻及其对照亲本上二化螟和大螟导致的枯心/白穗率和受害丛率差异分析

Bt 水稻及其对照亲本上二化螟导致的枯心/白穗率和受害丛率都显著高于大螟的危害($P<0.05$),且在 *Bt* 水稻上二化螟导致的枯心/白穗率和受害丛率都显著低于其在对照亲本水稻上的危害程度($P<0.05$),降幅分别为 30.8%—98.3% 和 11.4%—96.6%,但在 *Bt* 水稻及其对照亲本上大螟的危害程度间差异不显著($P>0.05$)(图 3)。

3 讨论

转基因抗虫水稻对农田生态系统中生物群落多样性和稳定性的影响是其生态安全性评价的重要内容,以往研究多集中于对非靶标害虫、天敌及其生物多样性等方面^[21-23]。有关转基因抗虫水稻引起的鳞翅目害虫种群演替方面却少有报道。本研究结果表明,在产卵选择性方面,对于靶标害虫二化螟和次靶标害虫大螟来说,在 *Bt* 水稻及其对照亲本上的落卵量都不大(≤ 2 块/百丛),且落卵量差异不显著;而在 *Bt* 水稻上二化螟

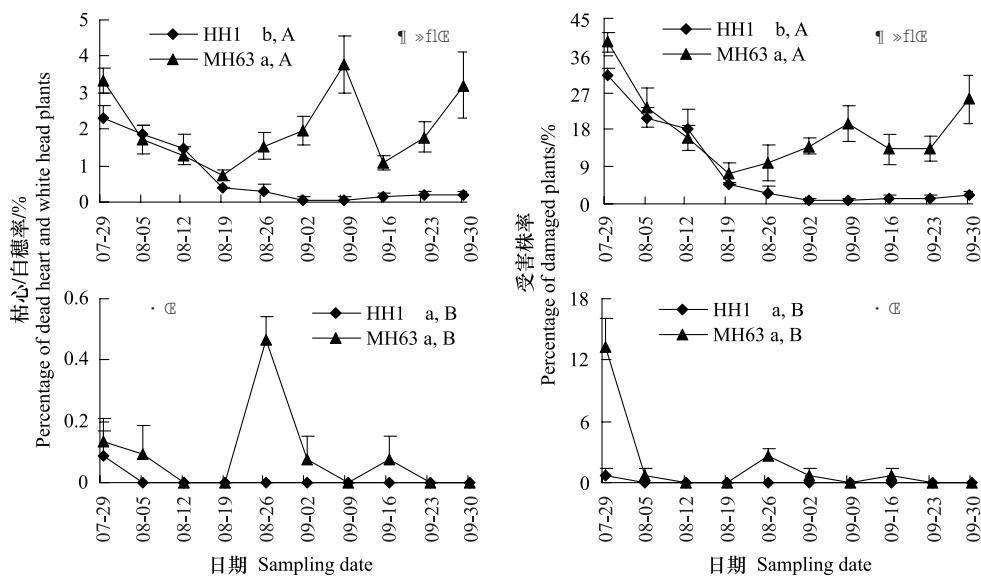


图3 Bt 水稻(Cry1Ab 和 Cry1Ac 融合基因型;华恢1号)及其对照亲本(明恢63)上二化螟和大螟发生导致的枯心/白穗率和受害丛率

Fig. 3 Percentage of dead heart or white head plants, and percentage of damaged plants by stem borers *C. suppressalis* and *S. inferens* fed Bt rice (cv. HH1 with fused Cry1Ab and Cry1Ac) and nontransgenic rice (cv. MH63, the parent line)

不同小写字母表示在 Bt 水稻及其对照亲本上二化螟或大螟导致的枯心/白穗率或受害丛率差异显著;不同大写字母表示同一水稻品种上,大螟和二化螟导致的枯心/白穗率或受害丛率差异显著;成对 T 检验, $P < 0.05$

的落卵量显著大于大螟,这与本年度二化螟为田间优势种群有关。在我国主要水稻螟虫种类中二化螟和三化螟属螟蛾科,为优势种;大螟属夜蛾科,发生相对较轻,为次要害虫^[15]。此外,田间二化螟和大螟的幼虫发生量之间存在极大差异,二化螟的百丛虫量高出大螟近两个数量级($\times 100$)。在对照亲本水稻上,二化螟的幼虫发生量显著高于大螟的发生量,也说明了二化螟是当前稻田的优势种群。在 Bt 水稻对两种螟虫的致死作用上来看,与对照亲本水稻相比,Bt 水稻上二化螟的幼虫发生量显著降低,而大螟的发生量没有显著差异,且在 Bt 水稻上二化螟的幼虫量较低且与大螟差异不显著。此外,在两种螟虫的田间致害力方面,Bt 水稻上二化螟导致的枯心/白穗率和受害丛率都显著低于其在对照亲本水稻上的致害程度,而大螟的致害性差异不显著。从而说明,Bt 水稻对靶标害虫二化螟具有较高抗性,这与已有的研究结果相一致^[11-15];同时,Bt 水稻对次靶标害虫大螟的抗性相对较差,这也与已有的研究结果相吻合^[9-10,15]。进而说明,Bt 水稻极大地降低了二化螟种群的优势度。为将来高虫口密度下大螟在 Bt 水稻上暴发危害、进而演变为优势虫群创造了可能,进而导致 Bt 水稻大面积商业化推广种植下大田螟虫的竞争演替及次要害虫上升为主要害虫的生态风险,这与高玉林等^[15]的研究推测相一致。之前的研究表明,无论是室内离体稻株上试虫的存活情况还是田间自然种群的防治效果,转基因水稻对大螟的抗性均明显弱于对二化螟的防治效果^[24-25]。两种螟虫对转基因抗虫水稻所表达的杀虫蛋白敏感性不同应该是其内在主要原因。

转基因作物的生态风险研究是其大规模商业化推广前所必须开展的一项重要研究,也是一项长期生态科学的研究工作^[26-27]。虽然需要在其大面积商品化生产之前通过室内或田间小范围的模拟试验获得大量的相关资料,评价其生态风险,但对该问题的真正解答还需要在其商业化生产后进行持续有效的监管和监测,采取合理对策,以确保将转基因作物对生态系统的潜在负面影响降至最低。眼下,国内转基因水稻的产业化似已成为必然的发展态势。就转基因抗虫水稻对田间螟虫类群的影响而言,除了在生产性试验及随后的商品化应用过程中进一步监测、研究和评价其种群暴发危害规律及其致害性差异之外,还要探明螟虫对转基因抗虫水稻的抗性发展规律及其生态和遗传因子,最终明确转基因抗虫水稻种植下靶标害虫二化螟和次靶标大螟之间的竞争演替,进而构建两者的种群演替模型,并据此系统评价转基因抗虫水稻所面临的次要害虫上升为主要害虫问题,以指导生产转基因抗虫育种,如筛选对不同螟虫的高效杀虫蛋白基因或培育多抗的新型转基因

抗虫水稻;同时,生产中应积极协调转基因抗虫水稻与化学农药等害虫防治措施优势互补关系,将转基因抗虫水稻作为一种简便、经济、有效、安全、持续的害虫防治手段,并纳入到害虫综合防治体系中,这亦是转基因抗虫水稻产业化过程中值得探索的重要课题。

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