

小麦产毒病原菌及其毒素防控的研究进展

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摘 要: 小麦是全球第二大粮食作物, 每年因病害造成小麦严重减产, 品质下降。一些病原菌还能够产生真菌毒素, 进一步危害小麦及其制品的质量安全, 对人畜健康造成巨大危害。由镰刀菌引起的小麦赤霉病是我国最主要的小麦病害之一, 由交链孢引起的小麦黑胚病也备受关注。这 2 种真菌既能引起小麦病害, 又能产生真菌毒素, 故称之为产毒病害。镰刀菌产生的脱氧雪腐镰刀菌烯醇(deoxynivalenol, DON)、玉米赤霉烯酮(zearelenone, ZEN)、伏马菌素等和交链孢产生的交链孢酚(alternariol, AOH)、交链孢酚单甲醚(alternariol monomethyl ether, AME)和细交链格孢酮酸(tenuazonic acid, TeA)等是 2 类病原菌产生的主要真菌毒素。本文综述了能引起小麦产毒病害的镰刀菌和交链孢的特点、真菌毒素以及病害和毒素的防控技术, 尤其是 2 类病原菌引起的小麦病害和真菌毒素的防控。这将为后期防治小麦产毒病害及控制毒素产生的研究提供有利参考。

关键词: 小麦; 镰刀菌; 交链孢; 真菌毒素; 防控

Advances on the prevention and control of mycotoxin-producing pathogens and their mycotoxins in wheat

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ABSTRACT: Wheat (*Triticum* spp.) is the second largest food crops in the world. However, annual yields and quality of wheat are severely reduced due to plant diseases. Furthermore, some pathogens can produce mycotoxins threatening the quality and safety of wheat and its products. These mycotoxins are great detrimental to human and animal health. Wheat head blight caused by *Fusarium* spp. is one of the most important wheat diseases in China. More attention has also been paid to wheat black embryo disease caused by *Alternaria* spp. These fungi are regarded as mycotoxin-producing pathogens in that they can not only cause wheat diseases, but also produce mycotoxins. *Fusarium* toxins, especially deoxynivalenol (DON), zearelenone (ZEN), *Fumonisin*s, etc, and *Alternaria* toxins, especially alternariol (AOH), alternariol monomethyl ether (AME) and tenuazonic acid (TeA) etc, are the major mycotoxins produced by the pathogens. In this review, the characteristics, mycotoxins, and especially the prevention

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and control of the diseases and mycotoxins brought about by pathogenic *Fusarium* and *Alternaria* in wheat were summarized. This will provide favorable references for the prevention of the mycotoxin-producing pathogenic diseases and the control of the mycotoxins in wheat.

KEY WORDS: wheat (*Triticum* spp.); *Fusarium*; *Alternaria*; mycotoxin; prevention and control

1 引言

小麦(*Triticum* spp.)是仅次于水稻的第二大粮食作物,全球种植面积约 2.2 亿亩。由于人口增长和经济发展,全球对小麦的需求以每年 1.6%的速度递增。据预测,2050 年,每公顷小麦产量从当前的 3 t 增加至 5 t 左右才能够满足全球需要^[1]。然而,多种病害严重破坏作物生产,造成巨大的产量和经济损失。在现有病害防控条件下,粮食产量损失约有 13%是由作物病害引起的。另外,有些病原菌还能够小麦收获后,在转运、储藏和加工过程中产生严重危害人类健康的真菌毒素,严重影响小麦的品质和安全,造成二次损失。能够引起小麦病害并产生真菌毒素的病原菌主要是镰刀菌和交链孢。由镰刀菌引起的小麦赤霉病是我国最主要的小麦病害之一,由交链孢引起的小麦黑胚病也备受关注。由于这 2 种真菌既能引起小麦病害,又能产生真菌毒素,故称之为产毒病害。

本文以镰刀菌和交链孢为出发点,主要从其病原菌特点、真菌毒素以及产毒病害和毒素防控 3 个方面的研究展开综述,旨在深入认识和理解 2 类小麦病原菌及其产生的真菌毒素,为其病害和真菌毒素防控研究提供有利参考。

2 产毒病害的致病菌

2.1 镰刀菌

镰刀菌(*Fusarium*)无性期属于半知菌亚门,有性期属于子囊菌亚门赤霉属(*Gillerella*)、丛赤壳属(*Nectria*)等。镰刀菌属包括禾谷镰刀菌、尖孢镰刀菌、燕麦镰刀菌等。有超过 17 种镰刀菌能够引起赤霉病,其中禾谷镰刀菌是最主要的致病菌。小麦赤霉病是危害我国小麦生产最重要的病害之一,我国常年有大面积麦田受到赤霉病的危害(图 1)。温暖湿润的环境有利于镰刀菌在扬花期产生小麦赤霉病,小麦在扬花期受到赤霉病菌侵染往往引起小花不育等,导致小麦产量损失。另外,镰刀菌等还能够引起小麦镰刀菌根腐病和穗腐病^[2,3]。

2.2 交链孢

交链孢最早描述的历史追溯到 1816 年 Nees 描述细交链孢。交链孢包括互隔交链孢、细极交链孢、芸苔交链孢等,其中互隔交链孢最普遍。交链孢一直存在着分类的问题,近年来,学者逐渐形成了依据形态特征、次生代谢产物、致病性、分子等相结合的分类方法^[5]。

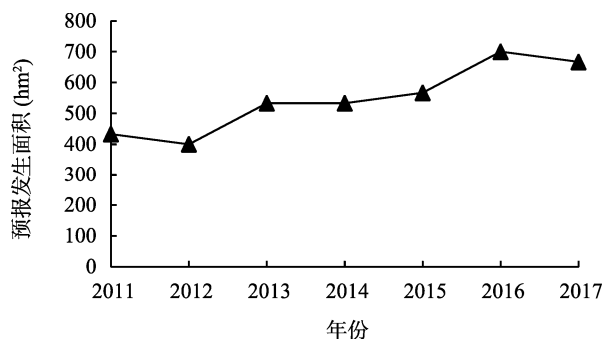


图 1 2011~2017 年全国小麦赤霉病害发生面积趋势预报^[4]

Fig. 1 Forecast of the area trend of wheat head blight in China from 2011 to 2017^[4]

多种交链孢能够引起小麦黑胚病,尤其是互隔交链孢,菌丝和孢子的积累造成胚芽和种子变色。持续降雨、露水或灌溉环境条件下,在小麦籽粒发育过程中,该病害发生概率比较大而严重。小麦交链孢叶枯病是由小麦交链孢等引起的另一种小麦病害。在我国对引起小麦叶枯病的交链孢缺乏深入认识,而在阿根廷它是小麦叶枯病的主要病原菌^[5]。

3 致病菌引起的真菌毒素

镰刀菌和交链孢不仅能够引起小麦病害,而且能够产生多种危害人畜健康的真菌毒素。表 1 列出了镰刀菌和交链孢产生的主要真菌毒素。

3.1 镰刀菌毒素

镰刀菌毒素不仅包括聚酮类毒素,如玉米赤霉烯酮(zearalenone, ZEN)、伏马菌素、镰刀菌酸等,而且还有 A-型和 B-型单端孢霉烯族毒素。A-型单端孢霉烯族毒素包括 T-2、HT-2 毒素、二醋酸蔗草镰刀菌烯醇(diacetoxyscirpenol, DAS)等, B-型单端孢霉烯族毒素包括脱氧雪腐镰刀菌烯醇(deoxynivalenol, DON)、雪腐镰刀菌烯醇(nivalenol, NIV)、3-乙酰基脱氧雪腐镰刀菌烯醇(3-acetyl deoxynivalenol; 3-ADON)、15-乙酰基脱氧雪腐镰刀菌烯醇(15-acetyl deoxynivalenol; 15-ADON)等。

ZEN 主要由禾谷镰刀菌、黄色镰刀菌等代谢产生,主要污染谷物、饲料、食用油等。ZEN 能够引起动物雌激素紊乱,造成动物繁殖机能异常。伏马菌素主要由串珠镰刀菌产生,其结构与神经鞘氨醇类似,能够干扰鞘脂代谢,对神经系统具有显著的毒性。

单端孢霉烯族毒素一般都能够引起动物呕吐。T-2、HT-2 毒素主要由拟枝孢镰刀菌代谢产生,具有细胞毒性和基因毒性等,能够引起食欲不振、体重下降、食道病变等。DON 又称呕吐毒素,主要由禾谷镰刀菌、尖孢镰刀菌等产生,具有细胞毒性、免疫毒性,大多数学者认为其具有致畸和胚胎毒性,可能还具有遗传毒性,引起人畜腹泻、拒食、神经紊乱等。另外,单端孢霉烯族毒素有助于增强镰刀菌的毒力^[14]。然而,不同的单端孢霉烯族毒素以一种宿主各异的方式影响病原菌的毒力^[15]。

3.2 交链孢毒素

交链孢中发现超过 120 多种次生代谢产物,大多是植物毒性物质,仅约 1/4 是危害人畜健康的真菌毒素^[16],其中互隔交链孢是最重要的产毒菌。交链孢毒素包括 3 类主要真菌毒素,分别是苯并吡喃酮类、吡咯烷类和二萜嵌苯类。苯并吡喃酮类主要包括交链孢酚(alternariol, AOH)、交链孢酚单甲醚(alternariol monomethyl ether, AME)和交链孢

烯(altenuene, ALT)。吡咯烷类主要指细交链孢菌酮酸(tenuazonic acid, TeA)。二萜嵌苯衍生物,主要包括交链孢毒素-I、-II、-III(altertoxins I, II, III; ATX-I、-II、-III)。AOH、AME、TeA 等是小麦污染产生的最主要真菌毒素。

AOH、AME 或 ALT 的急性毒性相对较轻^[17]。AOH 和 AME 均具有基因毒性能够致突变。利用人体结肠癌细胞进行试验发现,AOH 基因毒性强于 AME^[18]。沙门氏菌 Ames 试验表明, ATX 也具有致突变活性,甚至试验研究发现其致突变的毒性要高于 AOH 和 AME。ATX-I 具有急性毒性,在动物细胞系试验中发现 ATX-I 具有很高的致突变性^[19]。ATX-I 和 ATX-III 似乎还具有潜在的细胞转化作用^[20]。中国仓鼠 V79 细胞毒性试验表明, ATX-II 的致突变性远强于 AOH 和 AME^[21]。AAL 毒素(*Alternaria alternata* f. sp. *lycopersici* toxin, AAL toxin)结构上和伏马菌素类似,均是鞘氨醇类似物,能够抑制神经酰胺合酶的活性,影响鞘脂的合成;它还是一种植物毒素,以内质网为靶位点促进细胞损伤^[22]。

表 1 镰刀菌和交链孢产生的主要真菌毒素
Table 1 Main mycotoxins produced by *Fusarium* spp. and *Alternaria* spp.

种类			分子式	分子量	参考文献
	中文名	英文(缩写)			
镰刀菌毒素	T-2 毒素	T-2 toxin	C ₂₄ H ₃₄ O ₉	466	[6]
	HT-2 毒素	HT-2 toxin	C ₂₂ H ₃₂ O ₈	424	[6]
	二醋酸蔗草镰刀菌烯醇	DAS	C ₁₉ H ₂₆ O ₇	366	[7]
	脱氧雪腐镰刀菌烯醇	DON	C ₁₅ H ₂₀ O ₆	296	[8]
	3-乙酰脱氧雪腐镰刀菌烯醇	3-ADON	C ₁₇ H ₂₂ O ₆	322	[8]
	15-乙酰脱氧雪腐镰刀菌烯醇	15-ADON	C ₁₇ H ₂₂ O ₇	338	[8]
	雪腐镰刀菌烯醇	NIV	C ₁₅ H ₂₀ O ₇	312	[9]
	玉米赤霉烯酮	ZEN	C ₁₈ H ₂₂ O ₅	318	[10]
	伏马菌素 B ₁	fumonisin B ₁	C ₃₄ H ₅₉ NO ₁₅	721	[10]
	镰刀菌素 C	fusarin C	C ₂₃ H ₂₉ NO ₇	431	[11]
	镰刀菌酸	fusaric acid	C ₁₀ H ₁₃ NO ₂	179	[11]
交链孢毒素		apicidin F*	C ₃₅ H ₄₃ N ₅ O ₇	645	[11]
	交链孢酚	AOH	C ₁₄ H ₁₀ O ₅	258	[5]
	交链孢酚单甲醚	AME	C ₁₅ H ₁₂ O ₅	272	[5]
	交链孢烯	ALT	C ₁₅ H ₁₆ O ₆	292	[5]
	细交链格孢酮酸	TeA	C ₁₀ H ₁₅ NO ₃	197	[5]
	赈毒素	TEN	C ₂₂ H ₃₀ O ₄ N ₄	414	[5]
	交链孢毒素-I	ATX-I	C ₂₀ H ₁₆ O ₆	352	[5]
	交链孢毒素- II	ATX-II	C ₂₀ H ₁₄ O ₆	350	[5]
	交链孢毒素- III	ATX-III	C ₂₀ H ₁₂ O ₆	348	[5]
	AAL 毒素	AAL toxins	C ₂₅ H ₄₇ O ₁₀ N	521	[12,13]

注: *apicidin F 属环四肽化合物,是一种组蛋白脱乙酰酶抑制剂,由 L-苯丙氨酸、L-2-氨基辛二酸、N-甲氧-L-酪氨酸和 D-哌啶酸缩合成环四肽。

4 产毒病害及其毒素的防控

对于既能引起小麦病害而又在能够致使小麦及其制品产生真菌毒素的镰刀菌和交链孢的防控,要从病害和真菌毒素2方面入手。小麦产毒病害的防控能够有效抑制镰刀菌和交链孢的侵染,控制小麦发病;而镰刀菌毒素和交链孢毒素的防控以及脱毒能够有效地保障小麦在转运、储藏、加工等环节保持安全。

4.1 产毒病害防控

4.1.1 传统防控措施

传统防控措施防治小麦产毒病害一般具有普适性,遵循相似的防控措施。小麦赤霉病的传统防控措施旨在花期和早期谷粒形成时避免谷穗暴露,防止镰刀菌孢子侵染。作物轮作是一种重要的传统防控措施,即在小麦收获后种植非宿主作物^[23]。此外,通过耕种将感染的谷物残留埋于土表之下能够降低孢子和谷穗的接触^[24]。焚烧感染的残留秸秆以杀死在上面生长的孢子也是一种重要的传统防控措施^[25]。

4.1.2 化学防控

施用杀真菌剂对小麦病原真菌进行抑杀,能够有效地防治病原真菌的侵害。防治赤霉病时农药的施用一般是在扬花期或扬花期之前,效果比较理想。苯菌灵、丙硫菌唑、戊唑醇、代森锰锌、咯菌腈等农药用于防控赤霉病或镰刀菌穗腐病的发生^[2,26-28]。啉酰菌胺、嘧菌酯、苯醚甲环唑能够高效地控制茄交链孢的侵染^[29]。应用杀真菌剂控制小麦病害的发生有诸多挑战,病原菌的耐药性和农药残留问题一直是长期存在的巨大困扰。

植物提取物包括植物精油等用于真菌病害防控的研究由来已久。Zaker等^[30]研究5种植物提取物拮抗互隔交链孢,发现薄荷、桉树和薰衣草的甲醇提取物的抗真菌潜能巨大。牛角瓜等植物提取物与代森锰锌相比,也有较好的防控交链孢的效果^[31]。Dellavalle等^[32]分析了10种乌拉圭传统药用植物提取物对交链孢的抑杀效果,发现欧鼠尾草、熏衣草、迷迭香的植物提取物效果和化学杀真菌剂相当,作为重要抗真菌物质应用潜力巨大。

4.1.3 抗病育种

虽然传统防控措施、杀真菌剂的使用可能会降低病害的严重性,但是这些防控措施很难长期有效。抗性品种的培育是理想的防控病原菌侵害的重要措施。小麦育种遵循2种抗性育种途径:(1)引入抗性基因,如被广泛应用的QTL位点*Fhb1*; (2)从天然的具有抗性的小麦的种质资源来选育。抗性基因的研究中,位于染色体3BS上的QTL位点*Fhb1*广泛应用于赤霉病抗性育种,另外还有位于染色体6BS上的*Fhb2*^[33,34]。

在研究交链孢病害时也发现了一些抗性基因,为小

麦选育抗性品种提供了有力的基因参考。Spassieva等^[35]证实*Asc-1*能够阻止AAL毒素对宿主鞘脂代谢的破坏,使宿主对AAL毒素不敏感,拮抗互隔交链孢。Mora等^[36]发现携带哈茨木霉内切几丁质酶基因的转基因西兰花能够拮抗甘蓝交链孢。橡胶蛋白具有抗真菌活性,将其基因转入印度芥菜中,能够拮抗芸苔交链孢的侵染^[37]。

然而,现阶段仅有很少的抗性分子资源问世。此外,这些抗性形状多是由多基因联合作用以一种非常复杂的方式才能发挥其抗性效果^[38]。这使后续的小麦抗性品种的开发困难重重。随着基因组测序技术的不断进步,基于全基因组的育种策略逐渐被采用,为育种打下良好的分子基础,避免转基因分子育种的不周之处。结合转录组学和蛋白质组学技术,能够更加深入理解小麦抗性基因,挖掘潜在的抗性遗传要素。这将为获得持久、高效的防控病害的小麦新品种打下更坚实的基础。

4.1.4 诱导小麦抗病性

诱导植物的抗病性也是防治小麦镰刀菌和交链孢病害的一个重要防治策略。植物激素能够诱导增强小麦的抗病性。水杨酸是一种重要的信号分子,能够诱导小麦等不同植物的抗病性,拮抗镰刀菌、交链孢等多种病原菌^[39-42]。甲基茉莉酸能够诱导抗性抑制黄色镰刀菌对小麦植株的侵害^[43]。

除植物激素外,还有多种材料能够有效地诱导小麦抗病性。铝离子处理能够致使小麦中谷胱甘肽积累,从而提高其抗病性,防止镰刀菌侵染^[44]。印度苦楝树等植物叶片提取物能够诱导茶树的抗病性,防治互隔交链孢引起的病害^[45]。微生物也能够诱导植物的抗病性,甚至有研究表明灭菌后的真菌也能够诱导抗病性,用以防治小麦赤霉病^[46]。

4.1.5 生物防控

生物防控以其无残留、环境友好等优点备受青睐。从自然界中筛选出有潜在生防价值的微生物,是未来开发生物菌剂的关键。高效的筛选策略往往能够带来事半功倍的效果。Palazzini等^[47]通过优势指数试验,从小麦花粉中最终筛选出诸如链霉菌、短芽孢杆菌、芽孢杆菌等多株有效防控小麦赤霉病的菌株。Wang等^[3]利用抑菌试验、分泌胞外水解酶能力和PCR技术进行筛选,结合温室和田间防控小麦赤霉病和镰刀菌根腐病的试验,筛选出10株潜在的生防菌剂,尤其一株荧光假单胞菌效果最佳。荧光假单胞菌也能够有效的防控交链孢对宿主的侵害^[31]。

除链霉菌、芽孢杆菌、荧光假单胞菌等细菌能够有效防控小麦镰刀菌和交链孢病害外,诸如酵母、木霉和菌根真菌中也存在重要的小麦生防菌种资源。Schisler等^[48]浅黄隐球酵母和丙硫菌唑结合能够极大地降低赤霉病的发生。Matarese等^[49]找到一株木霉*Trichoderma gamsii* 6085能够抑制黄色镰刀菌和禾谷镰刀菌的生长,然而在贫营养环境,该菌无法防控2种病原菌的侵染。

4.2 真菌毒素防控与脱毒

4.2.1 物理防控与脱毒

物理方法主要包括清洗、机械分选、高温、射线、超声和溶剂萃取等过程。热处理是防控真菌毒素的常用方法,包括干热处理、蒸汽消毒等,能够用以杀灭毒素产生菌,进而控制真菌毒素的产生,但对热稳定的真菌毒素的消除效果较差,不能完全脱除毒素^[50]。日照晾晒能够使收获的粮食快速干燥,使其保持在相对安全的水分活度,从而有效地抑制产毒真菌的活动,防控真菌毒素的产生^[51]。⁶⁰Co- γ 射线处理能够很好地降解小麦中的 DON,而小麦形态、籽粒的含水量和赤霉病感染程度不影响⁶⁰Co- γ 射线对毒素的降解^[52,53]。荧光和紫外线能够抑制轮枝镰刀菌等真菌生长繁殖,进而防控镰刀菌毒素 ZEN、DON、T-2 毒素的产生,而且轮枝镰刀菌对紫外短波长和荧光照射较敏感,对紫外长波长不敏感^[54]。紫外线也能够降解面粉中的 DON 毒素,降解率在 30%以上,不影响面粉品质,而且降解产物毒性下降^[55]。

物理吸附剂也是一种降低污染饲料中的真菌毒素方法。活性炭、膨润土、硅藻土、沸石等吸附剂用于 DON、NIV、ZEN 等毒素的脱毒,而且已有多种商品化吸附剂产品用于脱除饲料中镰刀菌毒素,然而其脱毒效果仍待提高^[56,57]。

4.2.2 化学防控与脱毒

除杀真菌农药、植物提取物能够抑制小麦中镰刀菌和交链孢生长和毒素积累外,氨水、双氧水、氢氧化钠等处理也是较常见的化学防控脱毒方法,然而这些化合物可能会严重影响小麦的品质。臭氧处理能够有效抑制小麦及其制品中真菌的生长,去除其中的 DON 毒素。对处理后小麦及其制品的品质指标进行测定,评价臭氧处理对小麦粉蛋白质、氨基酸、淀粉等营养成分,脂质氧化程度以及韧性、色泽等品质指标的影响,发现没有影响小麦粉品质,而且发现臭氧处理能够使面粉增白、提高韧性、降低延展性和发黄^[58]。然而,较长时间在臭氧中的暴露,会影响小麦的发芽率^[59]。另外,谷物和药用植物中的抗氧化物,如丁香酸、没食子酸等酚酸类化合物,能够有效地抑制镰刀菌和交链孢的生长,具有很强的抗真菌活性,进而防控真菌毒素的产生^[60,61]。

4.2.3 生物防控与脱毒

物理、化学防控与脱毒选择性较差,它们在去除毒素的同时可能会造成其他营养成分的流失或破坏。生物法似乎是一种前景广阔的防控脱毒方式,利用微生物或其产生的降解酶通过作用于真菌毒素的致毒基团将真菌毒素降解或转化为低毒或无毒化合物。Fuchs 等^[62]分离出一株能够降解 A-型单端孢霉烯族毒素的细菌 BBSH 797,能够将 DON 转化为去环氧基的无毒 DOM-1。Fonnum 等^[63]发现一种从大鼠肝脏中分离的羧酸酯酶同工酶能够代谢 T-2 毒

素和 HT-2 毒素。

对交链孢毒素的防控和脱毒研究较浅,多是从拮抗交链孢霉的生长和产毒的角度加以阐述。真菌如哈赤木霉、绿色木霉、酵母,细菌如荧光假单胞菌、枯草芽孢杆菌、地衣芽孢杆菌等多种拮抗菌能够有效地抑制交链孢的生长和毒素积累^[31,64-66]。

5 展望

小麦病害一直困扰着小麦生产,加之真菌毒素的污染进一步加剧了小麦损失。镰刀菌和交链孢是 2 种主要的产生真菌毒素的小麦病原菌。它们不仅在田间造成小麦严重减产降质,而且在后续的转运、储藏和加工等阶段因为其产生真菌毒素,仍然严重影响着小麦及其制品的品质和安全,不仅危害我国人民的身体健康,而且严重影响我国小麦产品的进出口贸易,造成巨大的经济损失。

小麦镰刀菌和交链孢引起的病害以及真菌毒素污染问题,至今仍没有比较长期安全有效的防控措施,由小麦赤霉病的发生面积的预报(图 1)也可可见一斑。单一方法很难长期有效地防控产毒病害和真菌毒素污染,将传统方法、理化以及生物防控等方法相结合,开发出安全高效而又持效期长的综合防控措施对小麦产毒病害及其毒素进行防控似乎是更加有效的手段。综合防控措施的开发将为小麦及其制品的安全生产提供良好的保障。

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