DOI: 10.11829/j.issn.1001-0629.2020-0716
张嘉城，方香玲，南志标. 植物病原镰刀菌产生的毒素种类及其危害. 草业科学, 2021, 38(8): 1513-1524.
ZHANG J C, FANG X L, NAN Z B. Types and effects of toxins produced by plant pathogenic fungi *Fusarium* . Pratacultural Science, 2021, 38(8): 1513-1524.

植物病原镰刀菌产生的毒素种类及其危害

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摘要：镰刀菌 (*Fusarium* spp.) 是多种重要农作物的病原体，不仅可造成农作物产量和品质的严重损失还可在离体培养条件下或植物寄主体内产生一系列被称为镰刀菌毒素的次生代谢产物。这些毒素一方面作为致病因子与镰刀菌对宿主植物的致病力密切相关，另一方面可导致家畜生产性能下降和相关病症的出现，进而影响农业生态系统并对人类健康造成威胁。鉴于镰刀菌毒素对农作物生产的影响及其对家畜和人类的毒性作用，目前已有较多关于镰刀菌侵染粮食作物后产生毒素种类的研究，但关于镰刀菌侵染豆科牧草后产生的毒素种类以及毒素在镰刀菌对豆科牧草致病力方面作用的研究则较少。本文对引起主要粮食和饲料作物病害的常见镰刀菌物种产生的主要毒素，以及这些毒素对植物、家畜和人类的危害进行了综述，并对豆科牧草中镰刀菌毒素的研究前景及意义进行了展望。

关键词：镰刀菌；毒素种类；毒性作用；粮食作物；饲料作物；家畜

文献标志码：A **文章编号：**1001-0629(2021)08-1513-12

Types and effects of toxins produced by plant pathogenic fungi *Fusarium*

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Abstract: As a pathogen of many important crops, *Fusarium* spp. can not only cause serious loss of crop yield and quality, but also produce a series of toxic secondary metabolites *in vitro* and in host plants, which called *Fusarium* toxins. On the one hand, *Fusarium* toxins are closely related to the pathogenicity of *Fusarium* to host plants as virulence factors, on the other hand, *Fusarium* toxins cause the decline of livestock production performance and the emergence of related diseases, which in turn affects the agricultural ecosystem and poses a threat to human health. In view of the influence of *Fusarium* toxins on crop production and their toxicity to livestock and human, there has been considerable studies on the types of toxin in cereal crop after infection caused by *Fusarium*, nevertheless, there are few studies on the types of toxin in legume forage after infection caused by *Fusarium* and the role of toxins in the pathogenicity of *Fusarium* to legume forage. This study reviewed the main toxins produced by *Fusarium* species which commonly cause the diseases of main food and feed crops, and the effects of these toxins on plants, livestock and humans. The prospect and significance of research on *Fusarium* toxins in legume forage were examined.

Keywords: *Fusarium* spp.; toxin types; toxic effects; food crops; feed crops; livestock

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收稿日期：2020-12-30 **接受日期：**2021-04-06
基金项目：国家自然科学基金项目 (31802126)；青海省科技厅基础研究计划创新团队项目 (2021-ZJ-901)；国家绿肥产业技术体系 (CARS-22)
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镰刀菌 (*Fusarium* spp.) 是一类重要的植物病原真菌，能够侵染多种重要的粮食和饲料作物，从而引起根腐、穗腐和茎腐等病害，严重影响粮食和饲料作物的产量和品质。例如，禾谷镰刀菌 (*F. graminearum*)、黄色镰刀菌 (*F. culmorum*) 和燕麦镰刀菌 (*F. avenaceum*) 引起的小麦赤霉病普遍发生于我国西北、西南、黄淮和长江中下游的小麦 (*Triticum aestivum*) 产区，可造成小麦产量损失 10%～50%[1]。拟枝孢镰刀菌 (*F. sporotrichioides*)、禾谷镰刀菌、层出镰刀菌 (*F. proliferatum*) 和亚粘团镰刀菌 (*F. subglutinans*) 等引起的玉米穗腐病普遍发生于我国山西、河北、吉林、黑龙江、内蒙古、辽宁和陕西等玉米 (*Zea mays*) 产区[2]。尖孢镰刀菌 (*F. oxysporum*)、茄病镰刀菌 (*F. solani*)、燕麦镰刀菌、木贼镰刀菌 (*F. equiseti*)、半裸镰刀菌 (*F. semitectum*)、轮枝样镰刀菌 (*F. verticillioides*)、禾谷镰刀菌和三线镰刀菌 (*F. tricinctum*) 等引起的大豆根腐病在我国东北、华北和黄淮海的大豆 (*Glycine max*) 产区均有发生，可导致大豆产量损失 20%～60%[3]。尖孢镰刀菌、锐顶镰刀菌 (*F. acuminatum*)、木贼镰刀菌、半裸镰刀菌、燕麦镰刀菌、层出镰刀菌和三线镰刀菌等引起的苜蓿根腐病普遍发生于我国西北、华北和东北的苜蓿 (*Medicago sativa*) 种植区，严重发病地块苜蓿产量损失在 60% 以上[4]。

植物病原镰刀菌不仅可以影响重要农作物的产量和品质，还可产生一系列对人类和家畜具有毒性和致癌作用的毒素。家畜摄入被镰刀菌毒素污染的饲料会产生诸多不利影响，如采食量减少、拒食、饲料转化率降低、体重增量减少、疾病发生率增加和生殖能力下降[5]，从而造成家畜产业的经济损失。此外，镰刀菌毒素还可作为致病因子在促进镰刀菌对作物的侵染以及相关病害发展过程中发挥重要作用[6]。本文总结了镰刀菌毒素的来源、种类及其对作物、家畜和人类的危害 5 个方面的研究进展，阐明了镰刀菌毒素对农业生态系统的危害；指出了迄今为止国内外关于豆科牧草中镰刀菌毒素研究较少的问题，并对此类研究的前景及其在实际农业生产中的应用进行了展望，旨在促进牧草中镰刀菌毒素的研究并为草牧业的发展提供理论依据。

1 镰刀菌毒素的产生

镰刀菌毒素可由多种植物病原镰刀菌在人工培养基或宿主体内合成 (表 1 和表 2)。与镰刀菌在人工培养条件下产生毒素的过程相比，镰刀菌在侵染植物时产生毒素的过程受到病原体和宿主植物相互作用的调节，由植物产生的信号分子或次生代谢产物能够起到促进或抑制镰刀菌产毒的作用[25]。因此，同一种镰刀菌在人工培养基和植物体内的产毒种类可能存在差异。此外，镰刀菌在人工培养条件下的产毒能力也受到培养基成分、温度、湿度等人工环境条件的影响[7, 26-27]。由此可见，实际农业生产中镰刀菌毒素对农作物的影响同时受到温度、湿度等多种非生物因子以及作物种类和病原镰刀菌种类等生物因子的调控。镰刀菌属真菌既能够产生 3 类最重要的真菌毒素 (单端孢霉烯族毒素、伏马菌素和玉米赤霉烯酮)，也能够产生包括白僵菌素、恩镰孢菌素和串珠镰刀菌素在内的新型真菌毒素，其中多数毒素化学性质稳定，通过高温或食品和饲料的储存、加工和烹饪过程很难将其彻底清除[5]，因此可对人类和家畜的健康构成严重威胁。

此外，由于多种植物病原镰刀菌在植物宿主体内和人工离体培养条件下均可产生多种镰刀菌毒素，而在实际农业生产中作物又通常被多种镰刀菌共同侵染，因此作物在收获和贮藏过程中可被多种镰刀菌毒素污染。2007－2008 年间，对安徽、河北、四川、河南、重庆、江苏和广西 7 个省 (市) 小麦和玉米样品中镰刀菌毒素的检测结果显示 7 个省 (市) 的小麦和玉米样品均受到多种单端孢霉烯族毒素和玉米赤霉烯酮的污染[28]；刘凤芝等[29] 对 2017 年采自山东、江苏、辽宁、内蒙古、江西、河南、安徽、四川和河北 9 省 (区) 的配合饲料和青贮饲料样品中镰刀菌毒素的检测结果表明两种饲料均受到脱氧雪腐镰刀菌烯醇和玉米赤霉烯酮的污染。现有研究显示不同种类的镰刀菌毒素之间存在协同和加性的毒性互作效应，其中协同作用的存在可使多种镰刀菌毒素共存时的复合毒性大于各毒素单独作用时毒性的总和，而毒素间的加性作用导致以低浓度出现在食品和饲料中的镰刀菌毒素同样对家畜和人类健康构成威胁[30]。因此基于单一镰刀菌毒素的检测和危害评价程序并不能确切地反映食品和饲料中镰刀菌毒素的实际危害等级。

2 镰刀菌毒素的种类

2.1 单端孢霉烯族毒素

Freeman 和 Morrison 于 1948 年从粉红单端孢

表 1　镰刀菌在人工培养条件下的代谢毒素种类

Table 1　Types of toxins produced by *Fusarium* species *in vivo*

镰刀菌 *Fusarium* species	培养基类型[a] Culture medium	毒素[b] Toxins
层出镰刀菌 *F. proliferatum*	玉米 Maize	FB_1, MON, BEA
黄色镰刀菌 *F. culmorum*	小麦，玉米 Wheat, maize	DON, 3-ADON, NIV, ZEA, MON
梨孢镰刀菌 *F. poae*	玉米，稻米，小米 Maize, rice, millet, PSA	T-2, HT-2, NEO, DAS, NIV, FX, BEA, ENN-B
拟枝孢镰刀菌 *F. sporotrichioides*	玉米，稻米 Maize, rice, PSA	T-2, HT-2, T-2 triol, T-2 tetraol, NEO DAS, DON, ZEA, MON, BEA
三线镰刀菌 *F. tricinctum*	稻米 Rice	ENN-A, ENN-A_1, ENN-B, ENN-B_1, MON, BEA
木贼镰刀菌 *F. equiseti*	玉米 Maize	DON, ZEA, BEA
轮枝样镰刀菌 *F. verticillioides*	玉米，稻米 Maize, rice	FB_1, FB_2, MON, BEA, FA
亚粘团镰刀菌 *F. subglutinans*	玉米，稻米 Maize, rice	FB_1, FB_2, ZEA, MON, BEA, FA
茄病镰刀菌 *F. solani*	玉米，稻米 Maize, rice, PDA	FB_1, FB_2, MON, FA
尖孢镰刀菌 *F. oxysporum*	玉米，稻米 Maize, rice	DON, ENN-A, ENN-A_1, ENN-B_1, MON, BEA, FA
燕麦镰刀菌 *F. avenaceum*	玉米，稻米 Maize, rice	MON, BEA, ENN-A_1, ENN-B, ENN-B_1
半裸镰刀菌 *F. semitectum*	玉米，稻米 Maize, rice	T-2, DAS, ZEA, MON, BEA
禾谷镰刀菌 *F. graminearum*	玉米 Maize	DAS, DON, 3-ADON, ZEA
藤仓镰刀菌 *F. fujikuroi*	玉米，稻米 Maize, rice, PDA	FB_1, FB_2, MON, BEA, FA
锐顶镰刀菌 *F. acuminatum*	稻米 Rice	T-2, HT-2, NEO, MON, ENN-B

表1根据参考文献[7-13] 汇总。[a] PDA：马铃薯葡萄糖琼脂培养基；PSA：马铃薯蔗糖琼脂培养基。[b] T-2，T-2毒素；HT-2，HT-2毒素；T-2 triol，T-2三醇；T-2 tetraol，T-2四醇；NEO，新茄病镰刀菌烯醇；DON，脱氧雪腐镰刀菌烯醇；3-ADON，3-乙酰脱氧雪腐镰刀菌烯醇；15-ADON，15-乙酰脱氧雪腐镰刀菌烯醇；NIV，雪腐镰刀菌烯醇；FX，镰刀菌烯酮；DAS，蛇形毒素；FB: 伏马菌素；FB_1，伏马菌素B_1；FB_2，伏马菌素B_2；MON，串珠镰刀菌素；BEA，白僵菌素；ZEA，玉米赤霉烯酮；ENN-A，恩镰孢菌素A；ENNs: 恩镰孢菌素；ENN-A_1，恩镰孢菌素A_1；ENN-B，恩镰孢菌素B；ENN-B_1，恩镰孢菌素B_1；FA，镰刀菌酸；下同。

Table 1 was summarized based on references [7-13] . [a] PDA: potato dextrose agar medium; PSA: potato sucrose agar medium. [b] T-2: T-2 toxin; HT-2: HT-2 toxin; T-2 triol; T-2 tetraol; NEO: neosolaniol; DON: deoxynivalenol; 3-ADON: 3-acetyldeoxynivalenol; 15-ADON: 15-acetyldeoxynivalenol; NIV: nivalenol; DAS: diacetoxyscirpenol; FX: fusarenon-X; FB: fumonisins; FB_1: fumonisin B_1; FB_2: fumonisin B_2; MON: moniliformin; BEA: beauvericin; ZEN: zearalenone; ENNs: enniatins; ENN-A: enniatin A; ENN-A_1: enniatin A_1; ENN-B: enniatin B; ENN-B_1: enniatin B_1; FA: fusaric acid; this is applicable for the following tables as well.

(*Trichothecium roseum*) 上分离得到的单端孢菌素 (trichothecin) 是首个被发现的单端孢霉烯族类物质[31]。目前已发现超过 200 种单端孢霉烯族毒素，根据其化学结构可以分为 A、B、C、D 4 类，其中 A 类和 B 类单端孢霉烯族毒素因其在饲料和食品中的广泛分布以及有较强的动物毒性而备受关注[32]。A 类单端孢霉烯族毒素主要包括蛇形毒素 (diacetoxyscirpenol, DAS)、T-2 毒素和 T-2 毒素的代谢衍生物 [HT-2 毒素、T-2 三醇、T-2 四醇和新茄病镰刀菌烯醇 (neosolaniol, NEO)][33]; B 类单端孢霉烯族毒素主要包括雪腐镰刀菌烯醇 (nivalenol, NIV)、镰刀菌烯酮 (fusarenon-X, FX) 和脱氧雪腐镰刀菌烯醇 (deoxynivalenol, DON) 及其乙酰化代谢衍生物 [3-乙酰脱氧雪腐镰刀菌烯醇 (3-acetyldeoxynivalenol, 3-ADON) 和 15-乙酰脱氧雪腐镰刀菌烯醇 (15-acetyldeoxynivalenol, 15-ADON)][34]。2014 年采自中国 8 个省份的玉米饲料原料中可检测到 A 类和 B 类单端孢霉烯族毒素，其中蛇形毒素和脱氧雪腐镰刀菌烯醇是样品中检出率最高的 A 类和 B 类单端孢霉烯族毒素，检出率分别为 58.5% 和 100%[35]。

2.2　伏马菌素

伏马菌素在 1988 年首次由 Gelderblom 等人从轮枝样镰刀菌培养基中分离得到，已知其对人类具有高致癌性[36]。伏马毒素是一组非荧光、水溶性的真菌毒素，迄今已鉴定出至少 15 种伏马毒素类化合物。伏马菌素主要分为 A (A_1、A_2、A_3)、B (B_1、B_2、B_3)、C (C_1、C_2、C_3)、P (P_1、P_2、P_3) 4 个类别。其中 B 类伏马菌素 (fumonisin B_1, FB_1; fumonisin B_2, FB_2; fumonisin B_3, FB_3) 在食品和饲料中最为常见[37]。FB_1 是毒性最强的伏马菌素，大约占到镰刀菌属真菌合成伏马菌素总量的 75%。玉米、小麦和水稻 (*Oryza*

表 2 镰刀菌在植物体内的代谢毒素种类

Table 2 Types of toxins produced by *Fusarium* species *in planta*

镰刀菌 *Fusarium* species	寄主植物 Host plant	毒素 Toxins
层出镰刀菌 *F. proliferatum*	玉米 Maize	FB_1, FB_2, BEA
黄色镰刀菌 *F. culmorum*	小麦，大麦 Wheat, barley	HT-2, DON, 3-ADON, NIV, ZEA, BEA, ENN-A ENN-A_1, ENNB, $ENNB_1$
梨孢镰刀菌 *F. poae*	燕麦，大麦，玉米，小麦 Oat, barley, maize, wheat	HT-2, DAS, DON, NIV, BEA, ENN-A, ENN-A_1 ENN-B, ENN-B_1
拟枝孢镰刀菌 *F. sporotrichioides*	小麦，大麦 Wheat, barley	T-2, HT-2, T-2 tetraol, NEO, DON, 3-ADON, NIV BEA, ENN-A_1, ENN-B, ENN-B_1
三线镰刀菌 *F. tricinctum*	小麦，大麦 Wheat, barley	DON, NIV, BEA, ENN-A, ENN-A_1, ENN-B, ENN-B_1
木贼镰刀菌 *F. equiseti*	小麦，大麦，燕麦, 豌豆, 苜蓿 Wheat, barley oat, pea, alfalfa	NIV, ZEA
轮枝样镰刀菌 *F. verticillioides*	玉米 Maize	DON, FB_1, FB_2, ZEA
亚粘团镰刀菌 *F. subglutinans*	玉米 Maize	DON, MON, BEA, ZEA
茄病镰刀菌 *F. solani*	–	–
尖孢镰刀菌 *F. oxysporum*	香蕉，黄瓜 Banana, cucumber	BEA, FA
燕麦镰刀菌 *F. avenaceum*	小麦，大麦，小黑麦 Wheat, barley, triticale	HT-2, DON, NIV, MON, BEA, ENN-A, ENN-B ENN-B_1
半裸镰刀菌 *F. semitectum*	–	–
禾谷镰刀菌 *F. graminearum*	小麦，大麦 Wheat, barley	HT-2, DON, 3-ADON, 15-ADON, NIV, ZEA, BEA ENN-A_1, ENN-B, ENN-B_1
藤仓镰刀菌 *F. fujikuroi*	–	–
锐顶镰刀菌 *F. acuminatum*	小麦 Wheat	T-2, HT-2

表2根据参考文献[10-11, 14-24] 汇总。

Table 2 was summarized based on references [10-11, 14-24].

sativa) 等食品和饲料原料中均可检测到 FB_1[38]。孙武长等[39] 对 2003 年采自吉林省 3 个地区 (四平、通化和长春) 的玉米、小麦、水稻样品中镰刀菌毒素的检测结果显示 3 种粮食样品中 FB_1 的检出率在 30%～100%。

2.3 玉米赤霉烯酮

玉米赤霉烯酮 (zearalenone，ZEA)，又称 F-2 毒素，于 1962 年由 Stob 等人从被禾谷镰刀菌侵染的玉米中首次分离得到，1966 年，Urry 采用核磁共振和质谱技术确定了玉米赤霉烯酮的分子式和化学结构，玉米赤霉烯酮的分子式为 $C_{18}H_{22}O_5$，白色晶体，微溶于水[40]。玉米赤霉烯酮广泛存在于谷物及谷物制品中。陈丽媛[41] 对全国 2018 年 1 月－6 月玉米、小麦和麸皮等饲料原料样品中真菌毒素的分析显示饲料原料中 ZEA 检出率为 99.7%; 李丹迪等[42] 对 2019 年采自济南市的谷物制品中镰刀菌毒素的检测结果显示参试样品中 ZEA 的检出率为 76%。ZEA 的代谢衍生物包括玉米赤霉酮 (zearalanone, ZAN)、α-玉米赤霉烯醇 (α-zearalenol, α-ZEL)、β-玉米赤霉烯醇 (β-zearalenol, β-ZEL)、α-玉米赤霉醇 (α-zearalanol, α-ZAL) 和 β-玉米赤霉醇 (β-zearalanol, β-ZAL); α-ZEL、β-ZEL、α-ZAL 和 β-ZAL 是 ZEA 在哺乳动物中的主要代谢产物[43]，其中，α-ZEL、β-ZEL 也是 ZEA 在植物体内的代谢产物[44]。

2.4 串珠镰刀菌素

串珠镰刀菌素 (moniliformin，MON) 在 1973 年由 Cole 等人从感染叶枯病的玉米种子中首次分离得到[45]，起初串珠镰刀菌素被认为由轮枝样镰刀菌产生，但随后被证明是层出镰刀菌的次生代谢产物[46]。MON 为淡黄色针状结晶，易溶于水，分子式为 C_4HO_3R (R 为 H 或 Na 或 K)，在自然界中通常以钠盐或钾盐的形式存在[47]。采自中国、欧洲和美洲的玉米、小麦、水稻和大麦 (*Hordeum vulgare*) 等谷物样品中均可检测到串珠镰刀菌素，检出率最高可达 100%[46]。

2.5 恩镰孢菌素和白僵菌素

恩镰孢菌素 (enniatins, ENNs) 和白僵菌素

(beauvericin, BEA) 均为由 D-α-羟基-异戊酰基 (2-羟基-3-甲基丁酸) 和氨基酸单元交替组成的环状六肽[46]。恩镰孢菌素首次由 Gaumann 等人在 1947 年通过 *Fusarium orthoceras* var. *enniatinum* 分离得到，该菌种之后被命名为尖孢镰刀菌[46]。目前已发现 29 种恩镰孢菌素[48]，其中，在食物和饲料中含量最高的恩镰孢菌素是 ENN-A、ENN-A_1、ENN-B 和 ENN-B_1[49]，恩镰孢菌素因其离子载体的性质可促进阳离子 (K^+和 Ca^{2+}) 的跨细胞膜流动，从而破坏这些离子在细胞内的正常生理浓度[50]，低浓度的恩镰孢菌素已被证明对不同的细胞系均具有细胞毒性[48]。现有研究表明恩镰孢菌素可存在于谷物、植物油、豆干、干果、坚果和咖啡等多种食物中[49]。

白僵菌素首次于 1969 年由 Hamill 等人从一种昆虫病原真菌——球孢白僵菌 (*Beauveria bassiana*) 的培养基中分离得到[51]，白僵菌素的分子式为 $C_{45}H_{57}N_3O_9$，白色针状晶体，微溶于水。白僵菌素具有与恩镰孢菌素相同的离子载体特性，因此也具有一定的细胞毒性，白僵菌素可使生物膜对钙离子的渗透性快速增加，进而导致钙依赖性核酸内切酶活化和 DNA 片段化，最终介导细胞凋亡[46]。白僵菌素还具有其他多种生物活性，包括抗菌性 (真菌和细菌)、杀虫性和抗癌性等[52]。白僵菌素广泛存在于欧洲、美洲和亚洲生产的谷物及谷物制品中[49, 53]，韩小敏等[54] 对 2017 年采自山东省东部、西部、南部和中部的玉米及其制品中白僵菌素污染的调查结果显示样品中白僵菌素的检出率最高可达 87%。

2.6　镰刀菌酸

镰刀菌酸 (fusaric acid, FA) 又称萎蔫酸，由 Yabuta 等于 1934 年培养异孢镰刀菌 (*F. hetersporum*) 时首次分离得到[55]。镰刀菌酸分子式为 $C_{10}H_{13}NO_2$，易溶于水。镰刀菌酸在加速香蕉 (*Musa nana*) 和番茄 (*Lycopersicon esculentum*) 等许多植物枯萎病的发展中起到至关重要的作用[56-57]，目前关于镰刀菌酸的动物毒性及其在食品和饲料中分布的研究较为有限，已有研究表明玉米、小麦、大麦等多种谷物和畜禽饲料中含有镰刀菌酸[48]。

3　镰刀菌毒素的植物毒性

主要的镰刀菌毒素诸如单端孢霉烯族毒素、伏马菌素、恩镰孢菌素、镰刀菌酸均可作为致病因子与镰刀菌对植物的致病力密切相关。单端孢霉烯族毒素合成必需基因 *Tri5* 的敲除导致禾谷镰刀菌对田间小麦的致病力显著降低[58]；接种产生伏马菌素的轮枝样镰刀菌菌株的玉米种子的出苗率和幼苗枝条长度均显著低于接种不产生伏马菌素的轮枝样镰刀菌菌株的玉米种子[59]；尖孢镰刀菌中镰刀菌酸合成基因 *fub1* 的敲除使其对番茄幼苗的致病力显著降低[60]；燕麦镰刀菌中恩镰孢菌素合成基因 *esyn1* 的敲除显著降低了其对马铃薯 (*Solanum tuberosum*) 块茎组织的致病力[61]。现有研究表明镰刀菌毒素作用于植物后所产生的毒性效应包括生长抑制、萎蔫和坏死 (表 3)，其中，DON 和 3-ADON 可显著抑制小麦胚芽鞘的生长[62]；NIV 可抑制小麦幼苗根和枝条的发育[63]；T-2 毒素可显著抑制小麦幼苗和玉米愈伤组织的生长[64-65]。关于伏马菌素的植物毒性，FB_1 可导致番茄叶片坏死、玉米幼苗和番茄幼苗的生长受到抑制[66]、黄瓜 (*Cucumis sativus*) 叶片黄化以及大豆和棉花 (*Gossypium* spp.) 幼苗叶片的坏死斑[67]。恩镰孢菌素可导致番茄枝条萎蔫、小麦幼苗生长受到抑制和马铃薯块茎组织坏死[68-69]。镰刀菌酸可导致香蕉苗根茎和假茎的维管变色、叶片萎蔫[70]、棉花叶片坏死[71]；黄瓜和番茄幼苗的萎蔫[60, 72]。玉米赤霉烯酮可抑制玉米胚的萌发和生长[73]。串珠镰刀菌素可显著抑制玉米愈伤组织的生长[65]。

4　镰刀菌毒素对家畜的毒性作用

动物因摄入真菌毒素而导致的疾病被称为真菌毒素中毒症[74]。中毒症状的类型和严重程度取决于动物摄入毒性种类与剂量、毒素作用时间以及动物个体所属的物种 (表 4)。目前仅有关于家畜在摄入单端孢霉烯族毒素、伏马菌素、玉米赤霉烯酮、串珠镰刀菌素和镰刀菌酸这 5 种镰刀菌毒素后表现病症和生产力下降的报道。

T-2 毒素可导致猪摄食减少、增重下降、拒食和皮炎[75]；也会造成牛的肠炎、胃部溃疡和羊腹泻[76]；摄入 T-2 毒素后肉鸡增重减少、母鸡产蛋量和蛋壳厚度均显著减少[77]。NIV 可导致猪的采食量大幅下降并且使得进食时间延长[75]；还会造成肉鸡饲料消耗和增重减少[77]。DON 可导致猪摄食减少、完全拒食和呕吐[78]。摄入被 FB_1 和 FB_2 污染的饲料可导致猪的急性肺水肿综合症 (呼吸窘迫、皮肤青紫、急性肺水肿和胸膜积水)、羊死亡 (伴随着严重的肾脏损

表 3 镰刀菌毒素的植物毒性

Table 3 Phytotoxic effects of *Fusarium* toxins

毒素 Toxin	植物材料 Plant material	浓度 Concentration/(μg·mL^{-1})	毒性效应 Toxicity effects	参考文献 Reference
DON	小麦胚芽鞘 Wheat coleoptile	0.30～296.00	抑制生长 Inhibition of growth	[62]
3-ADON	小麦胚芽鞘 Wheat coleoptile	0.34～338.00	抑制生长 Inhibition of growth	[62]
NIV	小麦幼苗 Wheat seedling	25.00～150.00	抑制生长 Inhibition of growth	[63]
T-2	小麦幼苗 Wheat seedling	1.00	抑制生长 Inhibition of growth	[64]
	玉米愈伤组织 Corn callus	1.00～100.00	抑制生长 Inhibition of growth	[65]
FB_1	番茄幼苗叶片 Tomato leaf	0.07～72.10	叶片组织坏死 Necrosis of leaf tissue	[66]
	番茄幼苗 Tomato seedling	0.07～72.10	抑制生长 Inhibition of growth	[66]
	玉米幼苗 Corn seeding	0.07～72.10	抑制生长 Inhibition of growth	[66]
	黄瓜幼苗 Cucumber seedling	200.00	叶片黄化 Leaf chlorosis	[67]
	大豆幼苗 Soybean seedling	1 000.00	叶片坏死斑 Necrotic spot of leaf	[67]
	棉花幼苗 Cotton seedling	500.00	叶片坏死斑 Necrotic spot of leaf	[67]
ENN-B	小麦幼苗 Wheat seedling	10.00～80.00	抑制生长 Inhibition of growth	[68]
ENNs	马铃薯块茎 Potato tuber	5.00～100.00[a]	块茎组织坏死 Necrosis of tuber tissue	[69]
FA	香蕉幼苗 Banana plantlet	89.50～179.00	根茎、假茎变色，叶片萎蔫 Rhizome and pseudostems discoloration, leaves wilt	[70]
	棉花幼苗 Cotton seedling	89.50～1 432.00	叶片坏死斑 Leaf necrosis	[71]
	黄瓜幼苗 Cucumber seedling	100.00	幼苗萎蔫 Seedlings wilt	[72]
	番茄幼苗 Tomato seedling	89.50～179.00	幼苗萎蔫 Seedlings wilt	[60]
ZEA	玉米胚 Corn embryo	5.00	抑制生长 Inhibition of growth	[73]
MON	玉米愈伤组织 Corn callus	10.00～100.00	抑制生长 Inhibition of growth	[65]

[a] 施加在每片马铃薯块茎的毒素浓度单位：μg。

[a] The concentration unit of the toxin applied to each potato slice: μg.

伤) 以及肉鸡腹泻、增重减少[79] 和死亡[80]。摄入被玉米赤霉烯酮污染的饲料可导致母猪的高雌激素症 (外阴发炎、肿胀)[81] 和不孕[82]；亦会造成奶牛产奶量降低、不孕[81]；并且使得母绵羊排卵率和生育力降低[83]；导致火鸡产蛋量显著减少[81]。摄入含有串珠镰刀菌素的饲料可导致肉鸡增重显著降低和死亡[80]；造成火鸡摄食量和增重显著降低[84]；使得母鸡增重和产蛋量显著降低[85]。猪在摄入镰刀菌酸后表现出呕吐的症状[86]。

5 镰刀菌毒素对人类的毒性作用

已报道疾病发生地区的谷物中镰刀菌毒素的检测结果表明了该类毒素可能是疾病发生的原因。T-2 毒素可能导致食物中毒性白细胞缺乏症，其主要症状包括恶心、头痛、皮肤坏死、口鼻出血[87]。食用受到 DON 污染的谷物可导致人体出现恶心、腹泻、头

表 4　家畜摄入镰刀菌毒素后的症状

Table 4　Livestock symptoms after *Fusarium* toxin intake

毒素 Toxin	家畜 Livestock	毒素来源 Toxin source	剂量 Dosage/(mg·kg^{-1})	时间 Time/d	症状 Symptoms	参考文献 Reference
T-2	猪 Swine	发霉玉米 Moldy corn	3.20	21	摄食减少 Reduced feed intake	[75]
		纯化毒素 Purified toxin	> 4.00	14	皮炎 Dermatitis	[75]
		纯化毒素 Purified toxin	> 2.00	21	增重减少 Reduced weight gain	[75]
		纯化毒素 Purified toxin	> 2.00	21	摄食减少 Reduced feed intake	[75]
	绵羊 Lamb	纯化毒素 Purified toxin	0.60[a]	21	腹泻 Diarrhea	[76]
	牛 Cattle	–	0.64	20	血便、肠炎、皱胃和瘤胃溃疡 Bloody feces, enteritis, abomasal and ruminal ulcers	[76]
NIV	肉鸡 Broiler	纯化毒素 Purified toxin	> 6.00	20	摄食和增重减少 Reduced feed intake and weight gain	[77]
DON	猪 Swine	发霉玉米 Moldy corn	> 1.34	21	摄食和增重显著减少 Reduced feed intake and weight gain	[78]
		发霉玉米 Moldy corn	> 11.90	21	完全拒食 Complete feed refusal	[78]
		发霉玉米 Moldy corn	> 19.70	21	呕吐 Vomiting	[78]
FB_1	猪 Swine	发霉玉米 Moldy corn	166.00	6	急性肺水肿 Pulmonary edema	[79]
	肉鸡 Broiler	轮枝样镰刀菌 *F. verticillioides*	> 100.00	21	腹泻和增重减少 Diarrhea and reduced weight gain	[79]
		纯化毒素 Purified toxin	125.00	14	死亡 Death	[80]
FB	绵羊 Lamb	轮枝样镰刀菌 *F. verticillioides*	45.50[a]	7	死亡 Death	[79]
ZEA	猪 Swine	发霉玉米 Moldy corn	> 3.00	14	高雌性素症 Hyperestrogenism	[81]
		纯化毒素 Purified toxin	> 60.00	42	不孕 Infertility	[82]
	奶牛 Dairy	纯化毒素 Purified toxin	250 mg[b]	–	产奶量减少，不孕 Reduced milk production and infertility	[81]
	绵羊 Lamb	纯化毒素 Purified toxin	12.50	10	排卵率和生育力下降 Reduced ovulation rate and fertility	[83]
	火鸡 Turkey	纯化毒素 Purified toxin	100.00	21	产蛋量减少 Reduced egg production	[81]
MON	肉鸡 Turkey	纯化毒素 Purified toxin	27.00	7	增重减少和死亡 Reduced weight gain and death	[80]
	火鸡 Turkey	藤仓镰刀菌 *F. fujikuroi*	100.00	21	摄食量和增重减少 Reduced feed intake and weight gain	[84]
	母鸡 Hen	藤仓镰刀菌 *F. fujikuroi*	100.00	28	产蛋量和增重减少 Reduced egg production and weight gain	[85]
FA	猪 Swine	纯化毒素 Purified toxin	200 mg[b]	–	呕吐 Vomiting	[86]

[a] 摄入毒素剂量单位(体重基础上)：mg·kg^{-1}。[b] 毒素通过明胶胶囊一次性饲喂家畜。

[a] Intake dosage unit (body weight basis): mg·kg^{-1}. [b] Toxins are fed to livestock at one time via gelatin capsules.

痛、头晕和发烧的症状[88]。此外，食品中 DON、DON 的乙酰化衍生物和 NIV 的含量与人类的大骨节病和食管癌有关[89]。中国和南非关于食管癌的报道显示食管癌的高发病率与 FB_1 有关[90]。ZEA 因其具有的雌激素活性且能够刺激人类乳腺细胞的生长而被推测为人类乳腺癌的病因[87]。

6 问题与展望

植物病原镰刀菌不仅寄主范围广，而且在离体培养条件下或植物寄主体内常产生多种对植物、家畜和人类均具有毒性作用的镰刀菌毒素。因此由镰刀菌导致的植物病害和镰刀菌毒素对饲料和食品的污染可对整个农业生态系统造成较大危害，并可能导致严重的经济损失。就草地生态系统而言，以尖孢镰刀菌为代表的多种镰刀菌能够侵染苜蓿等豆科牧草，而现有研究已证明单端孢霉烯族毒素、伏马菌素、恩镰孢菌素和镰刀菌酸 4 种镰刀菌毒素作为致病因子在镰刀菌对植物的致病力方面发挥着至关重要的作用[58-61]。因此镰刀菌毒素也可能作为致病因子增强镰刀菌对豆科牧草的致病力，进而导致严重的牧草产量损失。此外，被植物病原镰刀菌侵染的牧草产品也可能含有多种镰刀菌毒素，可对家畜和人类的健康构成潜在威胁。虽然目前已有较多关于植物病原镰刀菌在人工培养基上产生毒素种类的报道，但关于其侵染豆科牧草后产生毒素种类的报道较少，且现有关于镰刀菌在豆科牧草体内产生毒素的研究仅对豆科牧草中的毒素进行了定量分析[19]，尚未阐明镰刀菌毒素是否能够增强镰刀菌对豆科牧草的致病力。因此急需开展深入研究，以明确镰刀菌侵染豆科牧草后的产毒种类、影响因素和调控机制以及毒素对牧草生长和病害严重度的影响，进而为减少镰刀菌病害导致的牧草产量和品质损失以及镰刀菌毒素对家畜和人类的健康构成潜在影响提供理论依据。

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