

三酮类除草剂微生物降解的研究进展

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摘要: 三酮类除草剂是一类高效、广谱、高选择性的除草剂, 能够有效地防除玉米地多种阔叶杂草和禾本科杂草。该类除草剂在土壤、水体中残留, 易造成地表和地下水污染。有关研究表明, 微生物降解有望成为解决该类除草剂残留的有效措施。本文分析了 2 种三酮类除草剂带来的生态效应, 总结了已报道的微生物降解资源, 简述了降解基因/酶的研究进展及可能的降解途径, 为深入研究三酮类除草剂的生物降解提供一定的信息支撑。

关键词: 三酮类除草剂; 对羟基苯基丙酮酸双氧化酶; 生态效应; 微生物降解

Research progress in microbial degradation of triketone herbicides

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Abstract: Triketone herbicides with high efficiency, broad spectrum, and high selectivity can effectively control a variety of broadleaf weeds and gramineous weeds in maize fields. The

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residues of the herbicides in soil and water are easy to cause surface and ground water pollution. Studies have indicated that microbial degradation is expected to be an effective measure to solve herbicide residues. In this paper, we analyzed the ecological effects of two triketone herbicides, summarized the reported microbial resources for residue degradation, and briefed the research progress in the degradation genes/enzymes and possible degradation ways, aiming to provide information support for further research on the biodegradation of triketone herbicides.

Keywords: triketone herbicides; *p*-hydroxyphenylpyruvate dioxygenase; ecological effect; microbial degradation

除草剂的应用降低了人工除草的成本,同时有效地减少了因杂草导致的作物生产损失。近年来,我国化学除草面积以每年 200 hm² 的速度递增,除草剂市场潜力巨大,但是长期、广泛、大量地施用除草剂,导致抗性杂草数量不断增加,截至目前共有 514 种抗除草剂的杂草,其中仅抗乙酰乳酸合成酶(acetyl lactate synthase, ALS)抑制剂类除草剂的杂草数量就达到了 170 种之多^[1],给农业生产带来了很大损失^[2],而三酮类除草剂的应用大大降低了这种损失。三酮类除草剂最早是由先正达公司开发,起源于一种挥发性油类植物毒素纤精酮,该物质被敏感杂草吸收后,经由木质部和韧皮部被运输至叶片部位,通过抑制对羟基苯基丙酮酸双氧化酶(*p*-hydroxyphenylpyruvate dioxygenase, HPPD)活性,阻碍叶绿素合成,使杂草出现白化症状后缓慢死亡^[3-4],一经上市广受好评,其中硝磺草酮 2016 年的销售额达到了 6.50 亿美元,占据全球除草剂销售额的第 4 位^[5]。三酮类除草剂是继磺酰脲类、二硝基苯胺类除草剂等后出现的新兴除草剂,主要应用于玉米生产,因其抗性杂草少、杀草谱广,正在成为一类高效的“明星”除草剂,包括硝磺草酮、磺草酮、环磺酮、双环磺草酮等(表 1)。

1 三酮类除草剂的生态效应

尽管三酮类除草剂除草效果良好,对玉米

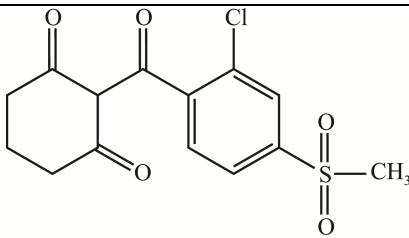
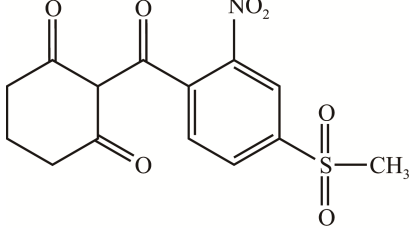
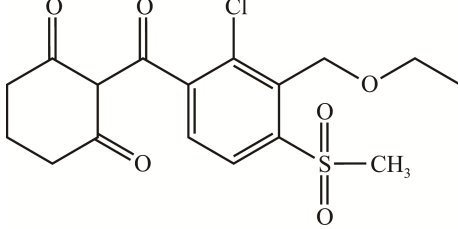
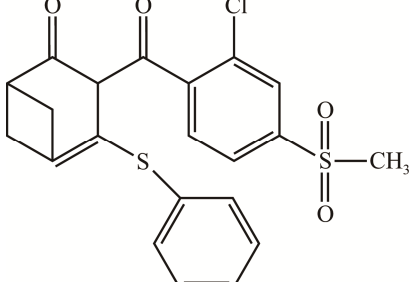
安全性高^[8-9],但由于其广泛、大量的施用,不可避免地造成了该类除草剂在土壤^[10-11]、水体^[12]中的残留积累,对环境造成的污染仍然需要持续关注。已有研究表明,残留在土壤、水体中的三酮类除草剂对生态环境会产生显著的影响。

首先,三酮类除草剂会影响土壤酶活和微生物群落的丰富度。土壤酶活和微生物群落是表征土壤健康非常重要的指标,对维持土壤生态系统稳定、植物健康生长具有至关重要的作用^[13-14]。磺草酮和硝磺草酮均会对土壤的微生物群落产生一定的扰动,改变土壤物种丰富度,显著降低土壤中固氮根瘤菌的末端限制性片段(*terminal restriction fragment*, T-RF)丰度,减弱土壤固氮能力^[15-16]。孙约兵等^[17]发现在实验浓度(0–100 mg/kg)范围内,硝磺草酮对土壤中的过氧化氢酶和蔗糖酶活性存在一定的激活作用,且随浓度的增加呈现先增加后降低的趋势,而土壤中脲酶在硝磺草酮浓度>20 mg/kg 时活性受到抑制,低浓度(5.0 g/kg)时相对稳定, β -葡萄糖苷酶活性等也受到一定程度的影响^[16]。

其次,硝磺草酮、磺草酮及其降解产物在环境中性质稳定,对土壤造成污染,影响后茬作物的健康生长。磺草酮的喷施导致蚕豆、洋葱等敏感作物有丝分裂异常,死亡率随剂量的增加而增加,呈现剂量依赖性,表明该除草剂原药可能有强大的诱变效应^[18],磺草酮的商业产品 Mikado® 显示出比原药更大的细胞毒性^[19-20]。

表 1 常见三酮类除草剂的结构式和理化性质

Table 1 Structural formula and physical and chemical properties of common triketone herbicides

除草剂类型 Type of herbicides	结构式 Structure	物质特性 Characteristics	来源 References
磺草酮 Sulcotrione		褐灰色固体, 25 °C时溶解度为 0.2 g/L, CAS: 99105-77-8 Gray solid with solubility of 0.2 g/L at 25 °C, CAS: 99105-77-8	[6]
硝磺草酮 Mesotrione		浅黄色固体, 20 °C时溶解度为 2.2–22.0 g/L, CAS: 104206-82-8 Pale yellow solid with solubility of 2.2–22.0 g/L at 20 °C, CAS: 104206-82-8	[6]
环磺酮 Tembotrione		无臭固体, 20 °C时溶解度为 0.2–29.7 g/L, CAS: 335104-84-2 Odorless solid with solubility of 0.2–29.7 g/L at 20 °C, CAS: 335104-84-2	[6]
双环磺草酮 Benzobicyclon		浅黄色结晶, 20 °C时溶解度为 0.1 mg/L, CAS: 156963-66-5 Light yellow crystal with solubility of 0.1 mg/L at 20 °C, CAS: 156963-66-5	[7]

停用推荐剂量的硝磺草酮一年后的土壤仍会导致后茬作物金鱼草、卷心菜、甜椒、蔓越莓、芸豆出现发育迟缓、组织坏死、整体生长减少等损伤, 造成产量下降^[21-22]。土壤中残留的磺草酮和硝磺草酮在土壤微生物的作用下部分被转化为各自的降解产物, 磺草酮的 2 种主要光解产物也会使洋葱有丝分裂指数显著降低, 染色异常呈现剂量依赖性^[23-24]。

再次, 三酮类除草剂对动物和水生生物也会造成不同程度的毒伤。磺草酮显著增加了大

鼠肝脏酪氨酸水平, 5 mg/kg 的磺草酮对大鼠的角膜造成 18% 以上的伤害, 并呈现剂量依赖性^[25]。Piancini 等^[26]研究发现, 硝磺草酮增加了 *Oreochorimis niloticus* 和 *Geophagus brasiliensis* 的 DNA 损伤和氧化应激水平。另外, 10 mg/L 硝磺草酮能增加微囊藻的相对丰度, 增加水华发生的风险^[27]; 同时还能降低小球藻的叶绿素含量和光合作用相关基因转录水平, 破坏小球藻的细胞膜和叶绿体结构的完整性, 影响其光合作用能力, 减少小球藻的生长量^[28]。

此外, Bonnet 等^[29]发现这 2 种除草剂的降解中间产物相较于母体分子, 对 2 种代表性环境微生物 *Tetrahymena pyriformis* 和 *Vibrio fischeri* 表现出更强的毒性。

2 磺草酮和硝磺草酮的生物降解

许多研究表明, 三酮类除草剂在土壤中的降解受到多种因素的影响。例如, 土壤水分、pH、微生物、土壤类型等, 其中微生物是其降解的主要驱动力^[30-31]。三酮类除草剂在玉米土壤中较为稳定^[32-33], 淋溶性强, 其除草剂分子及降解产物易对后茬敏感作物产生毒害, 对土壤、地下水有一定的污染风险。因此, 研究三酮类除草剂的微生物降解、彻底矿化显得非常有必要^[12]。

2.1 微生物降解资源

生物降解是指微生物(包括一些其他生物)对物质(特别是环境污染物)的分解作用^[34]。自然界中的微生物数量大、种类繁多、适应性强、繁殖速度快, 修复环境污染时具有绿色、经济、效率高等优点。目前已有研究者从土壤、水体等环境中筛选出了部分以芽孢杆菌属(*Bacillus*)为主的三酮类除草剂降解微生物资源(表 2)。

2.2 微生物降解硝磺草酮和磺草酮的特性

Romdhane 等^[35]发现了一株能够降解 2 种三酮类除草剂的慢生根瘤菌(*Bradyrhizobium* sp. SR1), 在 48 h 内能够将 35 mg/L 的磺草酮完全降解, 并且检测到一种代谢物 2-氯-4-甲磺酰基苯甲酸(2-chloro-4-methylsulfonyl benzoic acid, CMBA); 该菌株完全降解相同浓度的硝磺草酮需要 20 d, 同时在降解液中检测到了 2 种常见产物, 即 2-氨基-4-甲磺酰基苯甲酸(2-amino-4-methylsulfonylbenzoic acid, AMBA)和 2-硝基-4-甲磺酰基苯甲酸(4-methylsulfonyl-2-nitrobenzoic acid, MNBA), 并且随着时间的延长, 可以观察到 MNBA 向 AMBA 的 1:1 定量转化。Calvayrac 等^[36]分离筛选出 8 株耐受磺草酮的菌株, 其中一株假单胞菌(*Pseudomonas* sp. 1OP)能够以磺草酮为唯一碳源, 以 $(\text{NH}_4)_2\text{SO}_4$ 为氮源, 在 30 d 内将 34 mg/L 的磺草酮降解 80% 以上, 并且生成主要代谢产物 CMBA, 其 3 种主要中间产物的结构式见图 1。

Durand 等^[37]于 2006 年从云水里首次分离出了一株能够降解硝磺草酮的菌株芽孢杆菌(*Bacillus* sp.) 3B6, 其能够在 10 h 内将 1 700 mg/L 的硝磺草酮完全降解, 生成 2 种代谢产物 AMBA 和 MNBA。Batisson 等^[38]发现未灭菌的

表 2 三酮类除草剂微生物降解资源统计

Table 2 Statistics of microbial degradation resources of triketone herbicides

除草剂类型	降解菌株	浓度	降解率	来源
Type of herbicides	Degrading strains	Concentration (mg/L)	Degradation rate (%)	References
磺草酮	<i>Bradyrhizobium</i> sp. SR1	35	100 (48 h)	[35]
Sulcotrione	<i>Pseudomonas</i> sp. 1OP	34	>80 (30 d)	[36]
硝磺草酮	<i>Bacillus</i> sp. 3B6	1 700	100 (10 h)	[37]
Mesotrione	<i>Bacillus</i> sp. Mes11	34	100 (50 h)	[38]
	<i>Bacillus pumilus</i> HZ-2	200	100 (5 d)	[39]
	<i>Pantoea ananatis</i>	13.6	100 (24 h)	[40]
	<i>Escherichia coli</i> DH5 α	136	100 (3 h)	[41]
	<i>Bradyrhizobium</i> sp. SR1	35	100 (20 d)	[35]

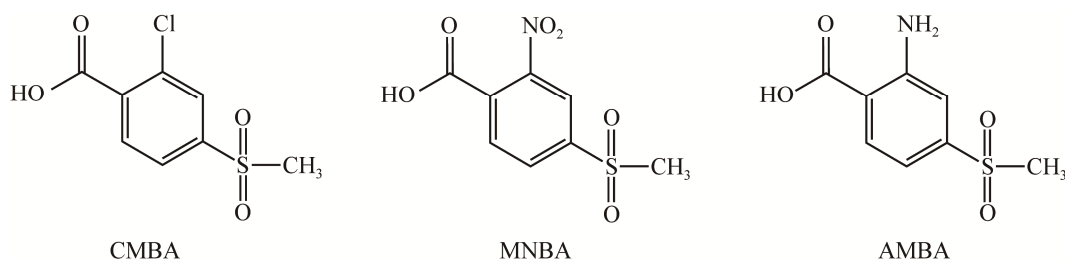


图 1 三种主要中间产物的结构式

Figure 1 Structural formulas of three main intermediates.

土壤 40 d 内对 4.5 mg/kg 硝磺草酮的降解率达 50%，从土壤中分离出耐受硝磺草酮的菌株有芽孢杆菌 (*Bacillus* sp.) Mes11 和节杆菌 (*Arthrobacter* sp.)，仅芽孢杆菌能够快速降解硝磺草酮，24 h 内能完全降解 340 mg/L 的硝磺草酮，产物 AMBA 不能被降解，在培养基中积累。韩海涛等^[39]以广东省惠州市第七污水处理厂厌氧污泥池中的活性污泥为原料，筛选出硝磺草酮降解菌株芽孢杆菌 (*Bacillus* sp.) HZ-2，通过对其 16S rRNA 基因测序分析，鉴定为 *Bacillus pumilus*；该菌株能耐受和降解高浓度硝磺草酮，在适宜的条件下 5 d 内可将 200 mg/L 的硝磺草酮完全降解，当硝磺草酮的初始浓度提高至 400 mg/L 时，菌株 HZ-2 仍能良好生长，降解率仍可达到 98.29%。周亮成^[42]在实验室的硝磺草酮降解菌株 *Bacillus* sp. HZ-2 前期培养基基础上，添加惰性载体和多种助剂研发出能够降解硝磺草酮的 HZ-2 菌剂；在田间试验中，用该菌剂处理 14 d 后，对 3 898 g/hm² 的硝磺草酮的降解率达到 48%，一定程度上减少了硝磺草酮的残留。Pileggi 等^[40]从水环境中筛选出一株高效降解硝磺草酮的菠萝泛菌 (*Pantoea ananatis*)，该菌株能够在 24 h 内将 13.6 mg/L 的硝磺草酮完全降解，通过 2 次液相色谱-质谱联用仪 (liquid chromatograph mass spectrometer/mass spectrometer, LC-MS/MS) 分析检测了硝磺草酮在菌株作用下可能产生的降解中间体。

Olchanheski 等^[41]研究发现大肠杆菌 (*Escherichia coli* DH5 α) 在 3 h 内对 10 倍推荐剂量 (136 mg/L) 硝磺草酮的降解率可达 100%。

还有研究报道，土壤中的环磺酮和双环磺酮的降解有微生物的参与^[43-44]，但降解环磺酮、双环磺酮的微生物尚未见报道^[33]。

2.3 三酮类除草剂生物降解相关的酶

降解三酮类除草剂微生物资源的不断丰富，促进了对其降解分子机制的研究。Carles 等^[45]通过分析硝磺草酮高效降解菌株 *Bacillus* sp. Mes11 的蛋白组学，揭示了 9 个可能降解硝磺草酮的硝基还原酶 (nitroreductase, NR)，分子量在 21.9–29.3 kDa 之间，通过外源表达确定了 *NfsAfrp* 家族中的 2 种硝基还原酶基因 (*NfrA1* 和 *NfrA2/YcnD*) 参与了硝磺草酮生物转化，辅因子分别是 NADPH 和 NADPH/NADH，最适 pH 值和温度为 6.0–6.5 和 23–25 °C，并且证实该 NRs 对其他硝基化合物，如除草剂地乐西、杀虫剂对硫磷等也有一定的降解作用。有学者基于以上 2 种硝基还原酶和相对应的辅因子研发了监测硝磺草酮生物传感器，响应值 (电流大小) 与硝磺草酮浓度成正比^[46]。

在 *E. coli* DH5 α 降解硝磺草酮速率最快的 30 min 内，谷胱甘肽-S-转移酶 (glutathione-S-transferase, GST) 活性显著上升^[41]。Prione 等^[47]研究发现，*P. ananatis* 在硝磺草酮开始降解 (17.5 h) 和降解完成时，GST 的活性最大，说明这两种

菌中可能都有一个 GST 参与硝磺草酮的降解,但是还需要进一步验证其降解效率。此外,已有报道表明植物中存在有硝磺草酮降解能力的基因/酶^[48-51],如细胞色素 P450、单加氧酶、糖基化酶等,这对挖掘降解微生物中降解硝磺草酮的酶有一定的指导意义。

目前尚未见其他三酮类除草剂降解相关酶的报道。

2.4 关于 2 种三酮类除草剂的微生物降解途径

三酮类除草剂最早在 1993 年上市,至今仅二十余年,环境中能够适应和降解该类除草剂的微生物资源较少,因此,关于菌株降解硝磺草酮的机理研究报道相对更少。硝磺草酮的微生物降解主要通过环己二酮和苯磺酰基之间的 β -二酮键断裂及硝基的还原实现,目前公认的降解途径大致分为 2 个途径^[4,52-53]: (1) 硝磺草酮 \rightarrow M2 (游离或环化的羟胺类物质) \rightarrow AMBA,这是硝磺草酮降解的主要途径。在组成型和氧不敏感的硝基还原酶功能下,先产生具有毒性和诱变性的中间体 M2,在氧气存在时通过 β -二酮键的断裂能定量转化为 AMBA,并通过添加内标物证实了戊二酸是硝磺草酮有效的生物转化物,迅速被消耗,戊二酸源于环己二酮部分的氧化裂解。(2) 硝磺草酮 \rightarrow MNBA \rightarrow AMBA,这被认为是一条次要的降解途径。多次研究发现 MNBA 很难被检测到,推测是生成后立即转化为下一个物质。Durand 等对 MNBA 的生物转化反应证明了 MNBA 的消散伴随着 AMBA 的定量积累^[52-53]。*Pantoea ananatis* 降解硝磺草酮有不同的降解途径,产生了不同于 AMBA 和 MNBA 的降解中间产物,主要通过去硝基化($m/z=292$)、去甲基化、环己二酮开环($m/z=334$ 、 $m/z=288$)等步骤完成对硝磺草酮的降解^[40]。水稻中也检测到类似的物质^[48],推测认为是硝磺

草酮在 *Pantoea ananatis* 和水稻中存在相同的代谢途径(图 2)。

磺草酮主要的降解产物为 CMBA 和 1,3-环己二酮(1,3-cyclohexanedione, CHD),也有学者提出了一种新的中间代谢产物羟基磺草酮(hydroxy-sulcotrione)^[35],特殊情况下会转化为苯庚酸衍生物^[30,54]。但是在已经报道的 2 株磺草酮降解菌的降解产物中并未检测到 CHD,可能是和硝磺草酮一样在 $\text{pH}>7.0$ 时 β -二酮键断裂后开环成 5-氧代乙酸,最终生成戊二酸(图 3)^[52]。

3 存在的问题与展望

三酮类除草剂具有除草效果好、杀草谱广、靶标性强等特征,可以在芽前、苗后使用,是替代阿特拉津等三氮苯类除草剂的重要品种之一^[55],但是因其易残留,从而会对生态环境造成一定的危害。微生物降解除草剂技术因其绿色、安全、高效等特点,成为备受关注的消除除草剂残留的重要手段之一。

当前能够降解三酮类除草剂的微生物资源报道较少,仅有 *Bacillus*、*Pseudomonas*、*Pantoea* 等少数几类菌属,亟待在传统分离菌株的基础上尝试开发更多样的分离培养技术^[56-60],加强对新降解资源的挖掘、鉴定、评价与利用^[61-64],筛选更多潜在的降解菌株。同时,这些已报道的降解菌株主要是聚焦在对除草剂原药的降解上,而针对毒性比原药分子稍强的中间降解产物(如 AMBA、CMBA)的研究尚未开展,导致中间产物积累、除草剂不能完全降解将成为一大隐患。然而合成微生物群落(synthetic microbial community, SMC)的出现有望解决这一问题,SMC 定义为按照功能导向性的需求将已知的 2 个或多个遗传背景清晰的微生物菌株在自定义的培养环境中共培养构建的微生物群落^[65-66],因其对环境有更好的适应性,使微生物彼此配合

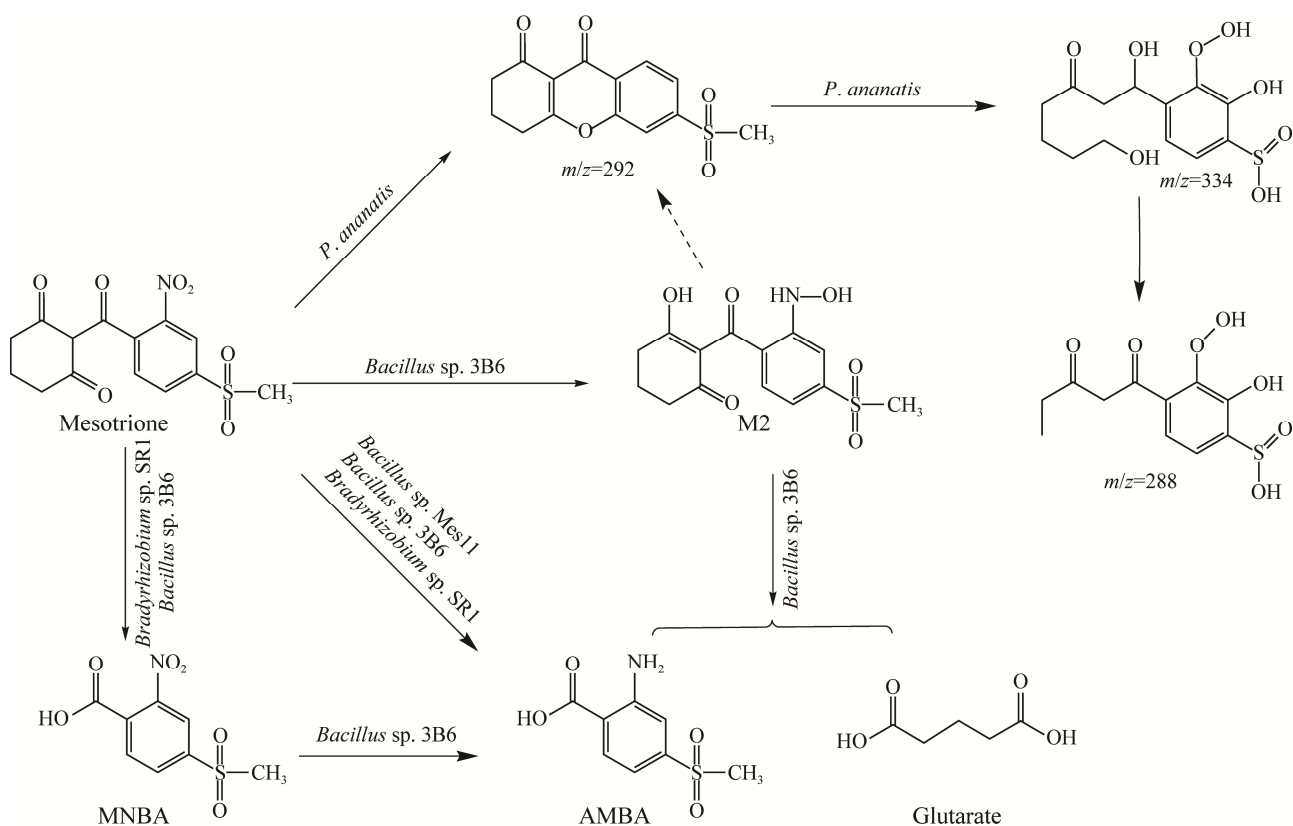


图 2 硝磺草酮微生物降解途径

Figure 2 Degradation pathway of mesotrione by microorganisms.

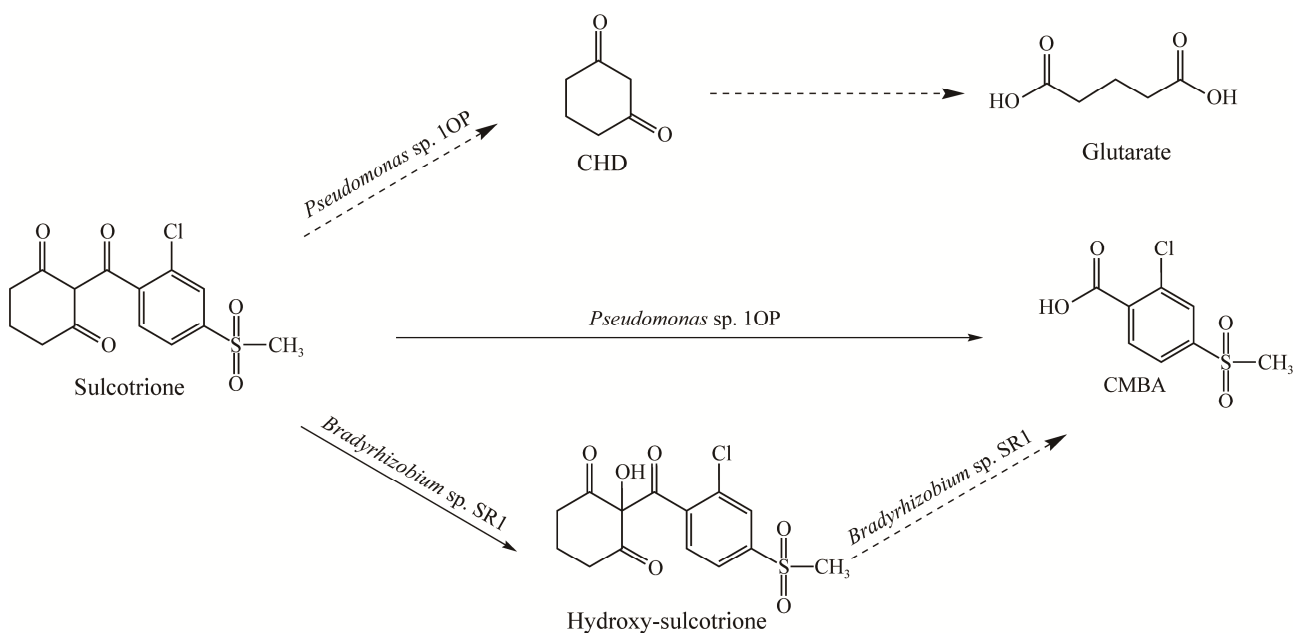


图 3 磺草酮的微生物降解途径

Figure 3 Degradation pathway of sulcotrione by microorganisms.

发挥更大的作用^[67]。SMC 应用于污染物降解的研究已有报道, Yu 等^[68]在研究双酚 A 的微生物群落降解效果时发现, 假单胞菌(*Pseudomonas* sp.)能够加快鞘氨醇单胞菌(*Sphingomonas* sp.)对双酚 A 的完全矿化速度, *Pseudomonas* sp.也有类似于 *Pseudomonas* sp.的中间产物 4-羟基苯甲酸酯(4-hydroxybenzoate, 4-HBZ)转运蛋白, 同样能够促进双酚 A 的快速矿化。Li 等^[69]利用改造过的 *E. coli* BL21 及分离得到的 *Ochrobactrum* sp. LL-1 这 2 种菌对甲基对硫磷(MP)进行了完全矿化。几种关键菌株降解复杂有机物时协同作用, 最终将残留较强的污染物完全降解, 既降低了微生物群落复杂性, 又保留了较好的降解效果, 非常有应用前景。该项研究有望应用在三酮类除草剂的完全矿化上, 以已知降解中间产物为底物筛选合适的降解菌株, 与降解母体分子的菌株组合共同矿化除草剂。

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