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Influences of plants and soil microbes on antibiotics in the rhizosphere: a review

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Abstract: The rhizosphere plays an important role in both farmland and urban areas, affecting water quantity and quality during surface water infiltration by increasing the heterogeneity of the aeration zone. The extensive application of antibiotics, their recalcitrance to degradation, and the resultant accumulation of antibiotics in soil-microbe-plant systems represent significant threats to the rhizosphere system, thereby threatening ecological stability and environmental and human health. This review synthesises recent findings on the migration and transformation of typical and common antibiotics within the rhizosphere. The main findings include that the absorption of antibiotics by plants is influenced by their molecular weight (MW) and octanol-water partition coefficient (log K_{ow}), allowing antibiotics to be divided into three classes: (1) antibiotics with high lipophilicity (log K_{ow} > 2) are mostly adsorbed by root lipids and rarely participate in the soil-plant transport process; (2) antibiotics with log K_{ow} < 2 and high MWs (MW > 700) are blocked outside the plant roots; and (3) antibiotics with log K_{ow} < 2 and low MWs (MW < 700) can enter plants through the roots and are transported *via* transpiration flow in plants. Antibiotics with log K_{ow} < 1 are more easily transported into plant tissues, including leaves. The rhizospheric microorganisms capable of participating in antibiotic migration and transformation are concentrated in *Actinobacteria*, *Firmicutes*, *Proteobacteria*, and *Bacteroidetes*. The inhibitory effect of antibiotics on dehydrogenase, sucrase, urease, catalase, and alkaline phosphatase activities surpasses their promoting effect, reducing these enzyme activities by 6–35% on average. However, the promoting effect of antibiotics on peroxidase, acidic phosphatase, and manganese peroxidase outweighs the inhibitory effect, increasing enzyme activity by 2–23%. Furthermore, it is essential to consider the effects of plant age and root characteristics on antibiotic migration and transformation. The results of this review contribute to a better understanding of the migration and transformation of antibiotics within the rhizosphere.

Keywords: woody plants; herbaceous plants; emerging pollutants; environmental contamination; soil and water pollution; root exudates

Antibiotics, which are chemically derived from the metabolites of plants, animals, or microorganisms, particularly bacteria, are increasingly prevalent in soil-microbe-plant systems, posing significant environmental and human health risks (Homem and Santos 2011, Li et al. 2011, Xu et al. 2015). As a major global pollutant, the widespread use of antibiotics has led to substantial environmental contamination, with the annual global antibiotic production exceeding 100 000 tons in 2009 (Nikaido et al. 2009,

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Cerqueira et al. 2020). In China alone, the 2020 antibiotic output reached 231 400 tons, primarily for use in animal husbandry. Unfortunately, only 10–30% of these antibiotics are metabolised by animals, with the remainder entering ecosystems *via* excretion, leading to significant soil and water pollution (Massé et al. 2014, Ngigi et al. 2019). Antibiotic residues, including sulfonamides, macrolides, fluoroquinolones (FQs), and tetracyclines (TCs), have been detected in various environments at concentrations ranging from nanograms to micrograms per liter or kilogram (Chang et al. 2010, Wang et al. 2014, Wu et al. 2022, Zhao et al. 2023).

Plants play important roles in both farmland and urban areas. Chen et al. (2019) found that global vegetation coverage has increased by 5% since 2000, with China contributing up to 25% of this expansion in green areas. Plants, particularly through their rhizosphere interactions, can affect the water quantity and quality during the surface water infiltration process. The growth of plant roots can enhance the heterogeneity of the aeration zone and affect the infiltration water quantity by altering the soil porosity and increasing the soil preferential flow (Lu et al. 2020). According to Scanlan (2009), root growth causes the division of macropores into smaller pores, and root decay creates biological macropores and root-induced small pores that are highly connected and can increase soil moisture conductivity and provide channels for preferential soil flow (Cheng et al. 2011). Coarse root systems can increase the number of soil macropores by up to 30% (Bodner et al. 2014). Compared with unplanted compacted soil, black oak and red maple root systems can penetrate geotextiles and soil, boosting soil infiltration rates by up to 27 times (Bartens et al. 2008). Allison and Hughes (1983) found that rainwater in eucalyptus forests could percolate up to 12 m along root canals, whereas in wheat fields, precipitation only percolated up to 2.5 m. In addition, plant metabolism, root exudates, and rhizosphere microorganisms can influence the infiltration water quality by affecting the degradation and transformation of some pollutants (Zhang et al. 2022). For example, Hoang et al. (2012) studied the degradation of ciprofloxacin (CIP) and norfloxacin (NOR) in a coastal wetland system and found that both antibiotics were mainly degraded through plant uptake, whereas photodegradation rates were slower than plant uptake rates, and microbial degradation was negligible.

Upon entering the soil, antibiotics undergo adsorption, migration, and degradation, processes that are crucial to the ecological balance. The fate of antibiotics is influenced by soil bonding, adsorption properties, and degradation rates, which in turn depend on the soil pH, moisture, temperature, and structure (Zhao et al. 2014, 2017, Li et al. 2019, Wang 2022). However, comprehensive investigations of antibiotic degradation factors remain limited (Zhang 2022). In addition, enhancing the ability of plants to absorb, migrate, and degrade antibiotics presents a viable solution for reducing environmental antibiotic levels. Plants not only directly affect the transport of antibiotics in soil by taking up and accumulating antibiotics but also rely on rhizosphere microorganisms, enzymes, and root exudates that modify antibiotic behaviour to influence antibiotic migration (Norvill et al. 2017, Tang et al. 2017, Hu et al. 2019, Chen et al. 2021a). The "rhizosphere effect" significantly influences antibiotic dynamics, in addition to altering soil characteristics and microbial diversity, warranting further research into its mechanisms and effects on antibiotic behaviour in soil-microbe-plant systems (Wang et al. 2022, Xiao et al. 2023). These findings highlight the urgent need to understand the interactions and effects of antibiotics within soil-microbe-plant systems. Therefore, this review aimed to elucidate (1) the effect of the rhizosphere on antibiotics migration and transformation and (2) the effect of antibiotics on the rhizosphere microorganisms, enzymes and root exudates. This study can guide future research and strategies to mitigate environmental issues associated with antibiotics.

EFFECT OF DIRECT RHIZOSPHERE UPTAKE ON ANTIBIOTIC MIGRATION AND TRANSFORMATION

Plant uptake significantly influences the physical, chemical, and biological responses of antibiotics entering the soil, leading to their absorption, transformation, or enrichment by vegetation (Zhang et al. 2017). The plant species itself is a crucial determinant of this absorption (Tadić et al. 2021). Plant uptake efficiency is notably influenced by the transpiration stream concentration factor, which encompasses factors such as the leaf number and length, along with root characteristics. For example, previous reports have demonstrated that oxytetracycline (OTC) shows higher accumulation in radishes than in lettuce, highlighting species-specific uptake (Youssef et al. 2020, Matamoros et al. 2022). Research indicates that antibiotics exhibit a higher propensity to con-

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centrate in roots over stems and leaves, with the root system acting as a conduit for transferring various antibiotic classes to edible plant tissues (Tang 2017, Christou et al. 2019). Consequently, plants with extensive root systems and superior transport capabilities display an enhanced potential for antibiotic absorption. For example, solanaceous fruits, which have robust root systems, tend to accumulate more antibiotics than leafy vegetables. The accumulation factor (AF), a metric used to compare the ability of different vegetables to accumulate antibiotics from the soil, has been found to range from 6.20 to 8.44 for solanaceous fruits and from 1.47 to 1.58 for leafy vegetables. Comparatively, *Cyperus alternifolius* L., with fibril roots, was reported to remove 44.70% of sulfamethoxazole (SMX), outperforming the rhizomatic *Gladiolus hybrids*, which removed 40.38% (Li et al. 2014, Hu et al. 2022).

The octanol-water partition coefficient (log K_{ow}) describes the partitioning of organic compounds between water and octanol and indicates the antibiotic adsorption affinity onto solids (Kümmerer 2008). The uptake of antibiotics by plant roots is influenced by their molecular weight (MW) and log K_{ow} (Boonsaner and Hawker 2010, Herklotz et al. 2010), and the detailed mechanism and data are shown in Figure 1 and Table 1. Antibiotics dissolved in soil pore water are introduced into the plant system from a water source. According to their MW and log K_{ow} values, antibiotics can be divided into three classes: (1) antibiotics with high lipophilicity (log K_{ow} > 2) are mostly adsorbed by root lipids and rarely participate in the transport process; (2) antibiotics with log K_{ow} < 2 and a high MW (MW > 700) are blocked outside the plant roots; and (3) antibiotics with log K_{ow} < 2 and a low MW (MW < 700) enter the plant

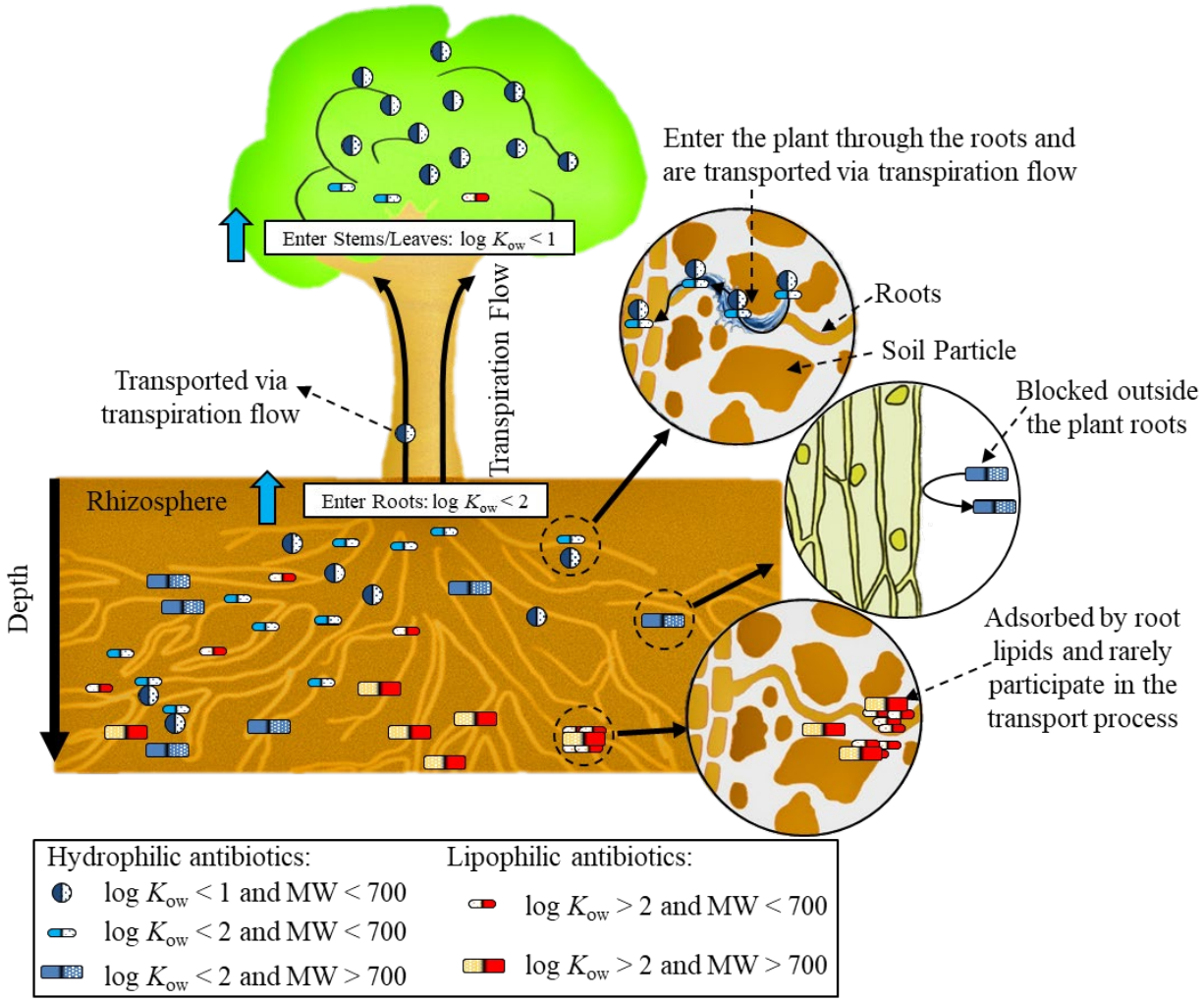

Figure 1. Mechanism of plant uptake of antibiotics with different molecular weights (MWs) and octanol-water partition coefficients (log K_{ow})

Table 1. Plant uptake of antibiotics with different molecular weights (MWs) and octanol-water partition coefficients (log K_{ow})

Class	Anti-biotics	Molecular weight (g/mol)	Water solubility (mg/L, T = 25 °C)[a]	log K_{ow} most reported value (n)[b]	Plant	Antibiotic concentration	Plant uptake (μg/kg) root	stem	leave	fruit	Reference
FQs	CIP[c]	331.34	1 148	0.28 (n = 13)	*Pak choi*	2 mg/L in nutrient solution	7.26×10^4 FW[d]	56.5 FW		not listed	Yu et al. (2022)
					Eichhornia crassipes	0.01–1 mg/L in water	2.23×10^4–1.65×10^6 FW	$1.08–2.01 \times 10^4$ FW			Yan et al. (2020)
					peach orchard	193.36 μg/kg FW in manure	3.2 DW[e]	0.86 DW	0 DW	not listed	Zhao et al. (2020)
					Rhizophora stylosa *Avicennia marina*	not listed	161.6 ± 50.1 DW 304.7 ± 55.4 DW	142.5 ± 10.8 DW 1001.6 ± 273.2 DW	72.8 ± 6.3 DW ND[f]		Sun et al. (2017)
	ENR	359.39	3 397	1.1 (n = 11)	*Pak choi*	2 mg/L in nutrient solution	8.18×10^4 FW	611 FW		not listed	Yu et al. (2022)
					peach orchard	216.06 μg/kg FW in manure	1.77 DW	1.06 DW	not listed		Zhao et al. (2020)
					carrot lettuce	1 000 μg/kg DW in soil	2.8 FW not listed	not listed	not listed < 1.6 fw		Boxall et al. (2006)
					Cucumis sativus *Lactuca sativa* *Phaseolus vulgaris* *Raphanus sativus*	0.05–5 mg/L added in sterile solid medium	111–8 079 DW 31–3 906 DW 1 233 DW 34–7 757 DW				Migliore and Cozzolino (2003)
	NOR	319.33	177 900	−1.03 (n = 13)	*Pak choi*	2 mg/L in nutrient solution	7.87×10^4 FW	60.7 FW		not listed	Yu et al. (2022)
					peach orchard	238.04 μg/kg FW in manure	0.72 DW	0.39 DW	0 DW		Zhao et al. (2020)
					tomato, cucumber, pepper, spinach, eggplant, eggplant	0.4–288.3 μg/kg DW in soil	18.2–658.3 DW				Li et al. (2014)
					spinach	20.5–66.7 μg/kg DW in the irrigated soils	4.6–16.9 DW	not listed	8.6–21.8 DW	not listed	Pan et al. (2014)
	OFL	361.37	676 200	−0.39 (n = 7)	*Pak choi*	2 mg/L in nutrient solution	7.47×10^4 FW	332 FW		not listed	Yu et al. (2022)
					peach orchard	286.03 μg/kg FW in manure	1.07 DW	0.32 DW	0.2 DW		Zhao et al. (2020)
	DANO	357.39	5 818	1.85 (n = 3)	peach orchard	187.91 μg/kg FW in manure	2.09 DW	0.97 DW	0 DW	not listed	Zhao et al. (2020)

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Continued Table 1. Plant uptake of antibiotics with different molecular weights (MWs) and octanol-water partition coefficients (log K_{ow})

Class	Anti-biotics	Molecular weight (g/mol)[a]	Water solubility (mg/L, T = 25 °C)	log K_{ow} most reported value (n)[b]	Plant	Antibiotic concentration	Plant uptake (µg/kg) root	stem	leave	fruit	Reference
SAs	SMX	253.28	3 942	0.89 (n = 16)	*Vallisneria natans* (Lour.) Hara	10–50 mg/L in 10% Hoagland solution	6.68×10^5–1.07×10^6 FW	not listed	6.55–7.85×10^5 FW	not listed	Zhu (2020)
					peach orchard	616.97 µg/kg FW in manure	2.51 DW	0.15 DW	0.61 DW		Zhao et al. (2020)
					Zea mays L.	10 mg/L in Hoagland nutrient solution	156–283 DW	111–244 DW	not listed		Zhang et al. (2019)
					tomato	2.87×10^{-5}–5.52×10^{-5} mg/L in reuse wastewater, 0.43–0.98 µg/kg DW in soil	not listed			0.26–5.26 DW	Christou et al. (2017)
					pepper	0.0005 or 0.005 mg/L in nutrient solution	0.50–6.50 DW	0.10–0.50 DW		not listed	Wu et al. (2013)
	SFD	250.28	28 140	–0.09 (n = 5)	*Vallisneria natans* (Lour.) Hara	10–50 mg/L in 10% Hoagland solution	0.01–0.19 $\times 10^{-3}$ FW	not listed	0.01–0.05 $\times 10^{-3}$ FW	not listed	Zhu (2020)
					carrot lettuce	1 000 µg/kg DW in soil	< 6.1 FW not listed	not listed	not listed < 17 FW		Boxall et al. (2006)
					winter wheat	90 µg/kg DW in soil	487 ± 92 DW	44 ± 5 DW		ND	Grote et al. (2007)
	STZ	255.32	20 030	0.05 (n = 8)	*Zea mays* L.	10 mg/L in Hoagland nutrient solution	34–51 DW	33–106 DW	not listed	not listed	Zhang et al. (2019)
	SPD	249.29	11 990	0.35 (n = 3)	*Cyperus papyrus*	0.05 mg/L in 1/2 Hoagland nutrient solution	7.01–15.8 DW	2.62–5.37 DW	not listed	not listed	Chen et al. (2021b)
	SM1	264.30	14 940	0.14 (n = 5)	*Vallisneria natans* (Lour.) Hara	10–50 mg/L in 10% Hoagland solution	2.16–4.36 FW	not listed	1.76–4.57 FW	not listed	Zhu (2020)
					peach orchard	343.25 µg/kg FW in manure	2.58 DW	0.73 DW	0.54 DW		Zhao et al. (2020)
	SM2	278.33	–	0.89 (n = 16)	*Vallisneria natans* (Lour.) Hara	10–50 mg/L in 10% Hoagland solution	0.73–1.23 FW	not listed	0.61–1.11 FW	not listed	Zhu (2020)
					peach orchard	18 509.03 µg/kg FW in manure	12.17 DW	4.12 DW	0.22 DW		Zhao et al. (2020)
					lettuce, carrot and tomato	0.002 and 0.02 mg/L in wastewater, 200 and2 000 µg/kg DW in animal manure	ND–0.54 DW	ND–0.31 DW		ND	Pan and Chu (2017a)
	TMP[g]	290.32	2 334	0.91 (n = 11)	carrot lettuce	1 000 µg/kg DW in soils	5.3 FW not listed	not listed	not listed 6 FW	not listed	Boxall et al. (2006)
					tomato	2.21×10^{-5}–7.32×10^{-5} mg/L in reuse waste water, 0.15–0.62 µg/kg DW in soil	not listed			0.11–3.40 DW	Christou et al. (2017)
					cucumber, lettuce, pepper, spinach	0.0005 or 0.005 mg/L in nutrient solution	11–270 DW	1.1–120 DW		not listed	Wu et al. (2013)

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TCs	TC	444.43	3 877	–1.1 (n = 6)	*Pak choi*	2 mg/L in nutrient solution	2.46 × 10^4 FW	32.4 FW			Yu et al. (2022)
					Pontederia cordata	0–0.4 mg/L in sewage	46.63–102.2 DW	5.01–39.55 DW	114.2–164.6 DW		Xu et al. (2022)
					lettuce	50–1 350 µg/kg in soil	1 329–24 578 DW	406–1 498 DW		not listed	Wang et al. (2021a)
					Myriophyllum aquaticum	0.3–30 mg/L in hydroponic microcosms	16–1 228 mg FW	4–154 mg FW	2–26 mg FW		Guo et al. (2020)
					peach orchard	6 865.01 µg/kg FW in manure	13.65 DW	4.84 DW	15.58 DW		Zhao et al. (2020)
					carrot lettuce	0.1–15 mg/L in irrigation water		12.0–36.8 FW 4.4–28.3 FW			Azanu et al. (2016)
					Chinese white cabbage	5–21.9 µg/kg DW in the irrigated soil	< 5.90 DW	4.00–10.1 DW		not listed	Pan et al. (2014)
					coriander	20.9–105 µg/kg in soil	1.20–4.10 DW	1.90–5.60 DW			Hu et al. (2010)
	CTC	478.88	616	–0.62 (n = 3)	*Pontederia cordata*	0–0.4 mg/L in sewage	98.79–329.3 DW	ND–242.7 DW	48.03–250.0 DW		Xu et al. (2022)
					lettuce	50–1 350 µg/kg in soil	2 761–30 535 DW	807–3 947 DW			Wang et al. (2021a)
					Myriophyllum aquaticum	0.3–30 mg/L in hydro ponic microcosm	16–1 215 mg FW	3–168 mg FW	1–51 mg FW	not listed	Guo et al. (2020)
					peach orchard	31 464.42 µg/kg FW in manure	159.54 DW	43.21 DW	121.14 DW		Zhao et al. (2020)
					Zea mays L.	10 mg/L in Hoagland nutrient solution	54–118 DW	104–231 DW	not listed		Zhang et al. (2019)
					winter wheat	240 µg/kg DW in soil	1 104 ± 176 DW	822 ± 213 DW		43 ± 13 FW	Grote et al. (2007)
					Allium cepa L.	50 mL, 0.02 mg/L CTC, 1-L Hubbard soil		14.4 ± 2.3 FW			Kumar et al. (2005)
					Brassica oleracea L. Capitata group	50 mL, 0.02 mg/L CTC, 1-L Hubbard soil		11.4 ± 2.1 FW			
	OTC	460.43	1 399	–1.22 (n = 5)	*Pontederia cordata*	0–0.4 mg/L in sewage	32.05–163.1 DW	ND–181.8 DW	67.28–232.1 DW		Xu et al. (2022)
					lettuce	50–1 350 µg/kg in soil	1 459–20 617 DW	431–1 143 DW			Wang et al. (2021a)
					Myriophyllum aquaticum	0.3–30 mg/L in hydroponic microcosm	12–1 039 mg FW	2–133 mg FW	1–16 mg FW	not listed	Guo et al. (2020)
					peach orchard	2 488.32 µg/kg FW in manure	8.87 DW	4.54 DW	0.23 DW		Zhao et al. (2020)
					carrot lettuce	1 000 µg/kg DW in soil	< 23 FW not listed	not listed	not listed < 7.2 FW		Boxall et al. (2006)

Continued Table 1. Plant uptake of antibiotics with different molecular weights (MWs) and octanol-water partition coefficients (log K_{ow})

Class	Anti-biotics	Molecular weight (g/mol)	Water solubility (mg/L, T = 25 °C)[a]	log K_{ow} most reported value (n)[b]	Plant	Antibiotic concentration	Plant uptake (µg/kg) root	stem	leave	fruit	Reference
	DOC	444.43	313	–1.14 (n = 3)	*Pontederia cordata*	0–0.4 mg/L in sewage	ND–233.7 DW	ND–295.5 DW	38.89–283.4 DW	not listed	Xu et al. (2022)
					peach orchard	2 573.61 µg/kg FW in manure	17.73 DW	9.78 DW	11.20 DW		Zhao et al. (2020)
MLs	TYL	916.10	–	3.5 (n = 3)	peach orchard	96.32 µg/kg FW in manure	0 DW	0 DW	0 DW	not listed	Zhao et al. (2020)
					carrot lettuce	1 000 µg/kg DW in soil	< 0.5 FW not listed	not listed	not listed < 1.5 FW		Boxall et al. (2006)
					Zea mays L., *Allium cepa* L., *Brassica oleracea* L. Capitata group	50 mL, 0.02 mg/L TYL, 1-L Hubbard soil	ND				Kumar et al (2005)
	ERY	733.93	–	3.06 (n = 4)	peach orchard	21.04 µg/kg fw in manure	0 DW	0 DW	0 DW	not listed	Zhao et al. (2020)
					lettuce, carrot and tomato	0.002 and 0.02 mg/L in wastewater, 200 and 2 000 µg/kg DW in animal manure	ND–9.66 DW	ND–2.04 DW		ND	Pan and Chu (2017a)
					cucumber, Chinese white cabbage, corn, radish and rice	1.1–4.4 µg/kg DW in the irrigated soil	ND–2.20 DW	ND			Pan et al. (2014)
	RTM	837.05	–	2.75 (n = 4)	lettuce, spinach, and carrots	0–0.001 mg/L in Colorado River water	ND–115 DW	ND		not listed	Jones-Lepp et al. (2010)
	AZI	748.98	–	4.00 (n = 1)				ND		not listed	
BLs	FFC	358.21	5 936	–0.04 (n = 3)	carrot lettuce	1 000 µg/kg DW in soil	5 FW not listed	not listed	not listed 15 FW	not listed	Boxall et al. (2006)
	CAP	323.13	389	0.92 (n = 5)	lettuce, carrot and tomato	0.002 and 0.02 mg/L in wastewater, 200 and 2 000 µg/kg DW in animal manure	0.78–12.7 DW	0.99–14.1 DW		0.76–17.7 DW	Pan and Chu (2017a)
					spinach	3.2–22.3 µg/kg DW in the irrigated soil	ND–3.00 DW	not listed	ND–10.1 DW	not listed	Pan et al. (2014)
	AMX	365.40	3 433	0.87 (n = 2)	carrot lettuce	0.1–15 mg/L in irrigation water		14.3–45.2 FW 13.7–33.6 FW			Azanu et al. (2016)

[a]Water solubility calculated using Episuite v4.11 (http://www.epa.gov/opptintr/exposure/pubs/episuite.htm); [b]Data obtained from the following studies: Boxall et al. 2006; Babić et al. 2010; Choi et al. 2008; Gao et al. 2012; Hansch et al. 1995; Howard and Mwylan 1997; Hu et al. 2007; Huang et al. 2017; Lissemore et al. 2006; Leal et al. 2013; Muñoz et al. 2009; Ngigi et al. 2019; Picó and Andreu 2007; Pan et al. 2014; Pan and Chu 2017b; Ratola et al. 2012; Schmitt-Kopplin et al. 1999; Senta et al. 2013; Tolls 2001; Tadič et al. 2021; Wu et al. 2013; Yang et al. 2011; Yan et al. 2013; Zhao et al. 2015, 2020; Zhang et al. 2019, 2021; [c]FQs – fluoroquinolones, SAs – sulfonamides, TCs – tetracyclines, MLs – macrolides, BLs – beta–lactams, CIP – ciprofloxacin, ENR – enrofloxacin, NOR – norfloxacin, OFL – ofloxacin, DANO – danofloxacin, SMX – sulfamethoxa-zole, SFD – sulfadiazine, STZ – sulfathiazole, SPD – sulfapyridine, SM1 – sulfamerazine, SM2 – sulfamethazine, TMP – trimethoprim, TC – tetracycline, CTC – chlortetracycline, OTC – oxytetracycline, DOC – doxycycline, TYL – tylosin, ERY – erythromycin, RTM – roxithromycin, AZI – azithromycin, FFC – florfenicol, CAP – chloramphenicol, AMX – amoxicillin; FW[d] – fresh weight; DW[e] – dry weight; ND[f] – not detected; [g]Used with SAs

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through the roots and are transported *via* transpiration flow. Antibiotics with log K_{ow} < 1 are more easily transported to plant tissues, such as stems, leaves, and fruits.

Yan et al. (2020) concluded that CIP (log K_{owCIP} = 0.28) is easily absorbed and accumulated by the roots of the large plant *Eichhornia crassipes*, with approximately 1 645.2 μg/g of CIP absorbed by the roots when the initial concentration of CIP in water was 1 000 μg/L. *Eichhornia crassipes* (Mart.) Solms has the ability to transport CIP from the roots to the above-ground portion of the plant with an average leaf bioconcentration factor = 0.34 and a transfer factor (TF) of up to 23.34. After prolonged irrigation with wastewater containing antibiotics, SMX (log K_{owSMX} = 0.89) and trimethoprim (TMP, log K_{owTMP} = 0.91) exhibited high bioconcentration capacities in tomato fruits, with bioconcentration factor values for SMX and TMP ranging from 0.471 to 5.419 and from 0.178 to 6.441, respectively (Christou et al. 2017). The uptake of ofloxacin (OFL, log K_{owOFL} = −0.39) has been reported in several plant tissues (Marsoni et al. 2014). Neither *Allium cepa* L. nor *Brassica oleracea* L. var. *capitata* can absorb the large and lipophilic antibiotic tylosin (TYL, log K_{owTYL} = 3.50). However, these plants can take up nearly 50% of the smaller hydrophilic antibiotic chlortetracycline (CTC, log K_{owCTC} = −0.62) (Kumar et al. 2005). Both CTC and sulfadiazine (SFD, log K_{owSFD} = −0.09) can be transferred from the roots of growing wheat to its stems and leaves. The initial CTC of 1.1 mg/kg DW absorbed by the roots and the initial absorption of SFD of 0.5 mg/kg DW decreased to 0.1 mg/kg DW and below the detection limit at maturity, respectively (Grote et al. 2007).

Low-MW antibiotics with log K_{ow} < 1 show stronger mobility through the xylem *via* transpiration flow in various tissues of the plant body than high-MW antibiotics with log K_{ow} > 1. Tetracycline (TC, log K_{owTC} = −1.19), NOR (log K_{owNOR} = −1.03), and chloramphenicol (CAP, log K_{owCAP} = 0.92) accumulate the most in the fruit, followed by the stems and leaves, with the least distribution in the roots (Pan and Chu 2017a). The high MW of macrolides prevents their uptake by many plants. The lipophilic TYL, erythromycin (ERY, log K_{owERY} = 3.06), roxithromycin (RTM, log K_{owRTM} = 2.75) and the azithromycin (AZI, log K_{owAZI} = 4.00) are absorbed by the roots in trace amounts (Jones-Lepp et al. 2010).

The concentration of enrofloxacin (ENR, log K_{owENR} = 1.10) was previously found to be higher on the outer layer of carrot roots (8.5 μg/kg) than inside the roots (2.8 μg/kg). In comparison, the concentration of OTC (log K_{owOTC} = −1.22), which has a MW similar to that of ENR, was higher inside the roots (Boxall et al. 2006). NOR and CIP both have MWs of more than 300 g/mol (Li et al. 2014), but NOR (vegetable detection frequency = 100%) shows a stronger transfer capacity in soil-vegetable systems than CIP (vegetable detection frequency = 25%). Yu et al. (2022) measured the maximum uptake rate (V_{max}) of FQs in pak choi roots using the Michaelis-Menten equation and determined that $V_{max\ NOR}$ (142.34 mg/kg/h) > $V_{max\ OFL}$ (102.12 mg/kg/h) > $V_{max\ CIP}$ (50.86 mg/kg/h); that is, for antibiotics with similar MWs, the smaller the log K_{ow}, the higher the root absorption rate.

In addition to herbaceous plants, woody plants have the ability to absorb antibiotics and exhibit a higher uptake potential. This was confirmed through quantitative analysis by Sun et al. (2017), who showed that *Rhizophora stylosa* Griff. and *Avicennia marina* (Forssk.) Vierh. could accumulate 366.6 μg/kg and 1 306.3 μg/kg of CIP through root uptake to achieve an environmental cleanup of TF_{CIP} 1.4 and 3.5, respectively. Direct rhizosphere absorption by woody plants is the main factor interfering with antibiotic migration and transformation. For example, the FQ content in the rhizosphere soil of *Aegiceras corniculatum* (L.) Blanco and *Kandelia candel* (L.) Druce was found to be approximately twice the FQ content in non-rhizosphere soil. In other words, the rhizosphere effect promoted the migration of antibiotics to the roots of woody plants for absorption and degradation (Ren et al. 2017). In addition, relative to the total antibiotic mass accumulated in plant compartments (1.66 mg), the enrichment of antibiotics in the various zones of peach trees (*Amygdalus persica* L.) was found to be as follows: root (percentage of antibiotic accumulation = 0.031%) > stem (0.021%) > leaf (0.013%) > shoot (0.007%) (Zhao et al. 2020).

In conclusion, multiple plant organs, mainly the roots, can absorb different kinds of antibiotics. The uptake capacity of plants varies with the plant species and the type of antibiotics. Plants with well-developed roots, stems, and branches exhibit greater uptake potential for antibiotic treatment because they have a larger contact area, which enhances their ability to reduce antibiotic contamination in soil. However, most of the plants used in current antibiotic translocation studies are shallow-rooted herbaceous plants instead of woody plants with well-

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developed root systems and longer root lengths. Thus, specific scientific questions, such as the relationship between antibiotic migration and transformation in the rhizosphere system of woody plants as well as soil, roots, and root microorganisms, remain to be addressed.

MECHANISM OF INTERACTION BETWEEN RHIZOSPHERE MICROORGANISMS, ENZYMES, AND ANTIBIOTICS

Influence of rhizosphere microorganisms and enzymes on antibiotics

Changes in the rhizosphere microbial community and associated rhizosphere enzymes are the key to understanding antibiotic migration and transformation (Kumar and Dubey 2020, Chen et al. 2023). The interaction between rhizosphere enzymes and antibiotics is presented in Table 2. Antibiotics can undergo biosorption, bioaccumulation, biodegradation, or biotransformation through the action of soil and rhizosphere microorganisms, which have the ability to absorb, use, and transform antibiotics in the soil environment (Huang et al. 2021). The degradation/transformation of antibiotics by selected rhizosphere microorganisms is shown in Table 3.

Existing studies have shown that the species capable of participating in the migration and transformation of antibiotics are concentrated in *Actinobacteria*, *Firmicutes*, *Proteobacteria*, and *Bacteroidetes*. Most rhizosphere microorganisms are important for plant growth and development (Zhan et al. 2005). The effect of rhizosphere microorganisms on antibiotics is displayed in Figure 2. Beneficial rhizosphere microorganisms produce metabolites or secretions, including antibiotics that promote plant colonisation. For example, *Streptomyces* species distributed in the rhizosphere of *Cupressus gigantean* W.C.Cheng & L.K.Fu and *Myrica rubra* Siebold & Zucc. (Wang et al. 2023a,b) prevent the growth of pathogens by secreting a variety of antibiotics, such as streptomycin and TC, in the root system of plants (Kelly and Wolfson 2020).

Rhizosphere microorganisms can selectively degrade antibiotics through intracellular and extracellular enzymes or other metabolites. *Mycobacterium* spp., a sub-set of *Actinobacteria*, can grow and propagate on the surface and rhizosphere of plants. Intracellular N-acetyltransferase and nitrate reductase from *Mycobacterium* spp. biodegrade quinolone antibiotics through acetylation and nitrification (Adjei et al. 2006, 2007). Chen et al. (2021b) found that rhizosphere biodegradation was dominant (90.2–92.2%) in the wetland phytoremediation pathway of sulfonamide contamination. Some strains of the *Bacillus* genus in the phylum *Firmicutes* are widespread in the rhizosphere of crops and promote plant growth (Yang et al. 2023). *Bacillus* can biodegrade up to 83.58% of chlortetracycline by breaking amino and hydrogen groups (Zhang and Wang 2022) and can effectively degrade 66.2% of OFL through the oxidation and hydroxylation of the piperazine ring (Zhang et al. 2022). *Pseudomonas*, *Thauera*, *Azoarcus*, and *Flavobacterium* (sub-sets of *Proteobacteria*) are all highly effective antibiotic-degrading bacteria. *Pseudomonas* sp. F2 was shown to degrade 100% of 5 μg/L OFL through defluorination and dealkylation (Li et al. 2021b). A sludge system harboring the latter three bacterial genera demonstrated a removal efficiency of 95% for SFD and 70% for ERY (Fu 2020). The cytochrome P450 complex in various fungi can degrade 85–100% of FQs and sulfonamides (García-Galán et al. 2011, Gao et al. 2018).

Plants with more complex rhizosphere systems have more abundant microbial community structures that can degrade antibiotics. For large, rooted woody plants, antibiotic degradation by microorganisms exceeds 90% (Hoang et al. 2013). Increasing antibiotic concentrations enhance the overall tolerance and degradation efficiency of these rhizosphere antibiotic-degrading microorganisms, producing a negative feedback effect and weakening the toxicity of antibiotics. As the level of CIP contamination increased, the proportion of *Alphaproteobacteria* and *Betaproteobacteria* in the rhizosphere of high and low CIP-accumulating cultivars of *Brassica campestris* L. increased from 9.8–15.3% to 16.3–18.4% (*Alphaproteobacteria*) and from 5.3–15.3% to 7.4–13.1% (*Betaproteobacteria*) (Huang et al. 2017). Some rhizosphere microorganisms affect the migration and transformation of antibiotics through bioadsorption or bioenrichment. Biological adsorption or bioenrichment methods proceed as follows: first, lipophilic antibiotics are persistent and ($\log K_{ow} > 2$) overcome the biofilm restriction of rhizosphere microorganisms through hydrophobic distribution between aliphatic and aromatic groups and lipid-soluble cell membranes. Second, the electrostatic interaction between charged groups and soil, hydrogen bonding between molecular structures, surface complexation, and the ion exchange of antibiotics affect the adsorp-

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Table 2. Interactions between common rhizosphere enzymes and antibiotics

Enzyme	The role of rhizosphere enzymes in the antibiotic-rhizosphere system	The effect of antibiotics on rhizosphere enzymes	Reference
Urease (UE)	Catalyze the decomposition of urea, providing available nitrogen for plants; promote the metabolism of rhizosphere microorganisms, hindering the inhibitory effect of antibiotics on microorganisms; Participate in the nitrogen cycle and its activity is used to analyze the ability of nitrogenous antibiotics to be converted by rhizosphere microorganisms; degrade antibiotics such as BLs.	Affect the expression and activity of urease; bind to urease and inhibit its decomposition of urea.	Yao et al. (2010)
Phosphatase	Key enzyme of phosphorus cycle, catalyzing phosphate hydrolysis; degrade antibiotics, change antibiotic diffusion and transmission.	Decrease phosphatase activity; bind to phosphatase and inhibit its hydrolysis of phosphoric acid.	Wang et al. (2020), Xiao (2021)
Sucrase (SC)	Hydrolyze sucrose, decompose organic matter, participate in carbon cycle, and provide nutrients and energy for plants and rhizosphere microorganisms; degrade antibiotics.	Promote or inhibit sucrose decomposition, enhance or reduce enzyme activity; bind to sucrase and inhibit it from catalyzing sucrose decomposition	Ren et al. (2017), Yao et al. (2010)
Laccase (Lac)	Destroy glycoside bond and lipid bond in antibiotic molecules; oxidative degradation of lignin benzene ring structure antibiotics; bind to antibiotics to change the distribution of antibiotics.	Bind to laccase substrate or enzyme protein, interfering with catalysis; bind to laccase, changing its function and distribution	Huang and Yang (2022), Solano and Lucas-Elio (2000)
Dehydrogenase (DHA)	Catalyze the redox reaction of organic matter to degrade antibiotics; catalyze the oxidation of aliphatic group of antibiotics to reduce the water solubility of antibiotics; catalyze cleavage of carboxyl group to enhance the water solubility.	Interfere indirectly with dehydrogenase function in the process of destroying cell wall, membrane and protein synthesis.	Lin et al. (2022), Xiao (2021)
Peroxidase (POD)	Catalyze the peroxidation reaction to convert antibiotics containing benzofuran structures into products containing hydroxyl or carboxyl groups, which can be easily decomposed.	Kill the rhizosphere microorganisms secreting peroxidase and reduce peroxidase activity.	Wen et al. (2010), Yao and Qing (2022)
Catalase (CAT)	Catalyze the decomposition of hydrogen peroxide and protect rhizosphere microorganisms from peroxide damage; catalyze hydrogen peroxide to bind to antibiotics and destroy the structure of antibiotics.	Indirectly Influence enzyme activity by affecting the growth and metabolism of rhizosphere microorganisms.	Huang et al. (2017), Li et al. (2021a)
Manganese peroxidase (Mnp)	Oxidize organic molecules to inorganic molecules to regulate the growth of plants and rhizosphere microorganisms; bind to antibiotics; degrade antibiotics such as TCs.	Inhibit Mnp expression and activity by inhibiting protein shearing; promote manganese ion solubilization to increase enzyme activity; bind to enzymes and affect antioxidant effect.	Wen et al. (2010)

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Table 3. Removal of antibiotics by rhizosphere microorganisms and rhizosphere enzymes

Phylum	Genus	Enzyme	Plant	Antibiotic	Concentration	Removal rate	Changes in microbial structure	Changes in enzyme activity	Reference
Phanerochaet chrysosporium		manganese peroxidase (Mnp)	not listed	SMX CIP NOR	10 mg/L	63.30–73.20%	not listed	decreased by 70–80% on 6th day	Gao et al. (2018)
Pycnoporus sanguineus		laccase (Lac)	not listed	SMX CIP NOR	10 mg/L	96.4–100%	not listed	increase from 0–40 U/L to 160 U/L on 4th day, and decrease by 10–20% on 6th day, then increase by 100–105% on 8th day.	Gao et al. (2018)
Proteobacteria, Actinobacteria, Patescibacteria., et al	*Arthrobacter, Gemmatimonas, Arthrobacter, Gemmatimonas, Massilia, and Sphingomonas*	peroxidase (POD)	wheat	OTC	0–150.0 mg/kg	not listed	Sobs index: decreased by 5–7%, Chao1 index: decreased by 8–10%, operational taxonomic units (OUTs): decreased by 2.35%.	increased by 60–70%	Guo et al. (2022)
		dehydrogenase (DHA)						decreased by 12–16% with antibiotic concentration from 0–5 mg/kg, increased by 20–23% with antibiotic concentration form 5–50 mg/kg, increased by 12–15% with antibiotic concentration form 50–150 mg/kg.	
		urease (UE)						increased by 40–46% with antibiotic concentration from 0–5 mg/kg, decreased by 8–13% with antibiotic concentration from 5–50 mg/kg, increased by 13–15% with antibiotic concentration from 50–150 mg/kg.	
		sucrase (SC)						increased by 3–4% with antibiotic concentration from 0–5 mg/kg, decreased by 14–16% with antibiotic concentration from 5–50 mg/kg, increased by 7–9% with antibiotic concentration from 50–150 mg/kg.	

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Continued Table 3. Removal of antibiotics by rhizosphere microorganisms and rhizosphere enzymes

Phylum	Genus	Enzyme	Plant	Antibiotic	Concentration	Removal rate	Changes in microbial structure	Changes in enzyme activity	Reference
Proteobacteria, *Actinobacteria*, *Bacteroidetes*, *Patescibacteria*,. *Firmicutes*., et al	*unclassified_f _Burkholderiaceae, Thermomonas, Asticcacaulis, Citrobacter*	catalase (CAT)	*Gladiolus hybridus*	SMX	0–100 mg/L	40.38%	Shannon-Weiner index: decreased from 4.26 to 2.98.	Increased by 20%–30% with antibiotic concentration from 0–1 mg/L, decreased by 30%–40% with antibiotic concentration from 1–100 mg/L.	Hu et al. (2022)
	Devosia, Rhodanobacter, Thiomonas, Sphingomonas		*Cyperus alternifolius*			44.70%	Shannon-Weiner index: increased from 4.83 to 5.14 with antibiotic concentration from 0–1 mg/kg and then decreased to 2.98 with antibiotic concentration from 1–50 mg/kg.	increased by 10–20% with antibiotic concentration from 0–1 mg/L, decreased by 20–30% with antibiotic concentration from 1–100 mg/L.	
	unclassified_f_ Burkholderiaceae, Thermomonas, Asticcacaulis, Citrobacter	peroxidase (POD)	*Gladiolus hybridus*		0–100 mg/L	40.38%	Shannon-Weiner index: from 4.26 to 2.98.	increased by 95–100% with antibiotic concentration from 0–1 mg/L, decreased by 30–40% with antibiotic concentration from 1–100 mg/L.	
	Devosia, Rhodanobacter, Thiomonas, Sphingomonas		*Cyperus alternifolius*			44.70%	Shannon-Weiner index: decreased from 4.26 to 2.98.	increased by 35–45% with antibiotic concentration from 0–1 mg/L, decreased by 50–60% with antibiotic concentration from 1–100 mg/L.	
Proteobacteria, *Actinobacteria*., et al.	*Granulibacter bethesdensis, Azospirillum brasilense, Dechloromonas aromatica, Haliangium ochraceum, Helicobacter heilmanii, Streptomyces scabiei*	CAT UE	high CIP accumulation cultivars of *Brassica campestris* L.	CIP	2.94, 10.84, 67.11 mg/kg	48.70%	The diversity index H decreased from 3.37 to 3.02. The richness index (number of bands) decreased from 27 to 24. The evenness index E decreased from 0.91 to 0.85.	The correlation coefficient between enzyme activity and CIP contamination level was –0.474 for catalase and –0.740 for urease.	Huang et al. (2017)
			low CIP accumulation cultivars of *Brassica campestris* L.			39.40%	The diversity index H decreased from 3.38 to 3. The richness index(number of bands) decreased from 29 to 22. The evenness index E decreased from 0.90 to 0.84.		

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Continued Table 3. Removal of antibiotics by rhizosphere microorganisms and rhizosphere enzymes

Phylum	Genus	Enzyme	Plant	Antibiotic	Concentration	Removal rate	Changes in microbial structure	Changes in enzyme activity	Reference
			low CIP accumulation cultivars of *Brassica campestris* L.			39.40%	The diversity index H decreased from 3.38 to 3. The richness index (number of bands) decreased from 29 to 22. The evenness index E decreased from 0.90 to 0.84.		
Funneliformis mosseae, Serendipita indica		UE DHA	*Lactuca sativa*	TC CTC	100 mg/kg	not listed	The root colonisation with F. mosseae decreased by 15.6–50.9%, the root colonisation with S. indica decreased by 10–40%.	UE: TC decreased by 39.1%, CTC decreased by 35.8%; DHA: TC decreased by 40.5%, CTC decreased by 46.1%.	Narges et al. (2023)
Phanerochaete chrysosporium		MnP	not listed	TC	10 mg/L	80%	not listed	increased from 80–90 U/L to 142 U/L.	Qing et al. (2018)
Trametes versicolor		Lac	not listed	SMZ	9 mg/L	100%	not listed	increased from 0 to 126 U/L.	Rodríguez et al. (2011)
not listed	*Sphingomonas*	CAT	not listed	TC	20 mg/kg	86.70%	Shannon-Weiner index: decreased by 59.2% on 90th day	decreased by up to 50–60% (7–35 days), increased by up to 30–40% (35–50 days) and leveled off after 50 days	Shen et al. (2016)
Pleurotus ostreatus		MnP	not listed	CIP	500 mg/L	95%	increased by 27% in the radial growth	increased from 13.779 μm/min/mg to 23.864 μm/min/mg.	Singh et al. (2017)
Actinobacteria., et al.	not listed	acidic phosphatase (ACP)	wheat	OTC	0–70 mg/kg	not listed	an 8–9-fold increase in quantity	The activity increased by more than 50% on 5th day, and then decreased by more than 60% on 20th day at the maximum. After 30 days, the activity exceeded that of the control group by 80%.	Tang and Tang (2009)
		alkaline phosphatase (ALP)						Decrease by up to 80% on 5th day.	
		UE						Decrease by up to 20% on 5th day, then returned to normal 10 days later.	
		DHA						Decrease by 40% on 5th day, the enzyme activity increased by 50% at 10 mg/kg after 10 days, and the remaining concentrations returned to normal.	

Continued Table 3. Removal of antibiotics by rhizosphere microorganisms and rhizosphere enzymes

Phylum	Genus	Enzyme	Plant	Antibiotic	Concentration	Removal rate	Changes in microbial structure	Changes in enzyme activity	Reference
		CAT UE	Lettuce	OTC	0–1 350 mg/kg	not listed	Bacterial count: increased by 44% with antibiotic concentration from 0–50 mg/kg, decreased by 85% with antibiotic concentration from 50–1 350 mg/kg; fungi count: increased by 13% with antibiotic concentration from 0–50 mg/kg, decreased by 29% with antibiotic concentration from 50–150 mg/kg, increased by 150% with antibiotic concentration from 150–450 mg/kg, increased by 40% with antibiotic concentration from 450–1 350 mg/kg; Actinomycete count: increased by 46% with antibiotic concentration from 0–50 mg/kg) decreased by 63% with antibiotic concentration from 50–150 mg/kg, increased by 155% with antibiotic concentration from 150–1 350 mg/kg.	CAT: decreased by 10–15% with antibiotic concentration from 0–50 mg/kg, increased by 10–20% with antibiotic concentration form 50–450 mg/kg, decreased by 20–30% with antibiotic concentration from 450–1 350 mg/kg. UE: decreased by 35–45% (0–450 mg/kg), increased by 10–20% (450–1 350 mg/kg).	Wang et al. (2021a)
not listed				TC			Bacterial count: decreased by 21% with antibiotic concentration from 0–50 mg/kg, increased by 20% (50–150 mg/kg), decreased by 68% with antibiotic concentration from 150–1 350 mg/kg; Fungal count: decreased by 20% with antibiotic concentration from 0–50 mg/kg, unchanged with antibiotic concentration from 50–150 mg/kg, increased by 33% with antibiotic concentration from 150–450 mg/kg, decreased by 19% with antibiotic concentration from 450–1 350 mg/kg; Actinomycetes count: increase by 5% with antibiotic concentration from 0–50 mg/kg, decrease by 46% with antibiotic concentration from 50–150 mg/kg, increase by 271% with antibiotic concentration from 150–1 350 mg/kg.	There was no significant difference in CAT activity. UE: decreased by 15–20% with antibiotic concentration from 0–50 mg/kg, increased by 3–5% with antibiotic concentration from 50–150 mg/kg, decreased by 25–30% with antibiotic concentration from 150–1 350 mg/kg.	
				CTC			Bacterial count: decreased by 68% with antibiotic concentration from 0–1 351 mg/kg; Fungal count: decreased by 13% with antibiotic concentration from 0–50 mg/kg, increased by 54% with antibiotic concentration from 50–150 mg/kg, decreased by 25% with antibiotic concentration from 150–450 mg/kg, increased by 13% with antibiotic concentration from 450–1 350 mg/kg; Actinomycete count: decreased by 30% with antibiotic concentration from 0–50 mg/kg, increased by 192% with antibiotic concentration from 50–1 351 mg/kg.	CAT: increased by 10–20% with antibiotic concentration from 0–50 mg/kg, decreased by 30–40% with antibiotic concentration from 50–150 mg/kg, increased by 5–15% with antibiotic concentration from 150–1 350 mg/kg; UE: decreased by 25–35% with antibiotic concentration from 0–150 mg/kg, increased by 10–20% with antibiotic concentration from 150–450 mg/kg, decreased by 15–25% with antibiotic concentration from 450–1 350 mg/kg.	

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Continued Table 3. Removal of antibiotics by rhizosphere microorganisms and rhizosphere enzymes

Phylum	Genus	Enzyme	Plant	Antibiotic	Concentration	Removal rate	Changes in microbial structure	Changes in enzyme activity	Reference
not listed	not listed	UE	wheat	OTC	100 mg/kg	not listed	not listed	decreased by 0.1–50%.	Yao et al. (2010)
		SC phosphatase						decreased by 0.1–47%.	
		CAT						decreased by 0.1–80%.	
		CAT						decreased by 27–46%.	
		UE phosphatase	*Sedum plumbizincicola*	TCs SAs FQs	0.6–12.74 µg/kg	35.8 –76%	increased by 18.8–73.1%.	increased by 65.4%.	Zhou et al. (2019)
								increased by 16.5%.	
								increased by 20.5%	

tion process of rhizosphere microorganisms (Wang and Zhou 2012). For example, Tan et al. (2021) found that *Sphingobacterium changzhouense* TC931 could remove nearly 90% of TCs through the combined effect of biological adsorption and biological and abiotic degradation.

Rhizosphere microorganisms secrete a significant number of enzymes. The effect of rhizosphere enzymes on antibiotics is illustrated in Figure 2. Rhizosphere enzymes can degrade different classes of antibiotics to form both inactive and more active metabolites through catalysis. This process involves breaking the molecular structure of antibiotics, introducing new structures, and reducing or enhancing their inhibitory effect on rhizosphere microorganisms. For example, β-lactamase and urease produced by *Pseudomonas aeruginosa* can destroy the structure of β-lactams and promote rhizosphere microorganism tolerance. Laccase can destroy glycoside and ester bonds in antibiotic molecules or oxidize and acylate antibiotic molecules to degrade antibiotics and reduce their toxicity (Song et al. 2021, Han et al. 2022). The alkaline laccase from *Bacillus amyloliquefaciens* degrades 70–90% of FQs containing benzene ring structures into smaller molecules through hydroxylation reactions. This laccase is a highly efficient enzyme for degrading FQs (Blanquez et al. 2016) that is found in the rhizosphere soil of the coniferous woody plant *Taxus* (Song 2015). Laccase from the white rot fungus *Trametes versicolor* (L.: Fr.) Lloyd was shown to degrade 16% of TC, 48% of CTC, 34% of doxycycline, and 14% of OTC by oxidizing phenolic hydroxyl groups in the molecular structure of TCs (Suda et al. 2012). Peroxidase in the rhizosphere soil catalyses the conversion of benzofurans and other structures in TCs into easily decomposable products containing hydroxyl or carboxyl groups, effectively catalysing the degradation of 72.5–84.3% of TCs (Wen et al. 2010, Yao and Qing 2022). Some rhizosphere enzymes alter the chemical structure of antibiotic molecules to change properties such as water solubility. Dehydrogenase (DHA) can catalyse the oxidation of aliphatic groups in antibiotic molecules to reduce the water solubility of antibiotics. In addition, DHA may enhance the water solubility of antibiotics by introducing or exposing hydrophilic groups (Wei 2020). Rhizosphere enzymes can also regulate the migration and transformation of antibiotics by influencing the growth and reproduction of microorganisms or through synergistic interactions. Microorganisms use sucrase *in vivo* to hydrolyse

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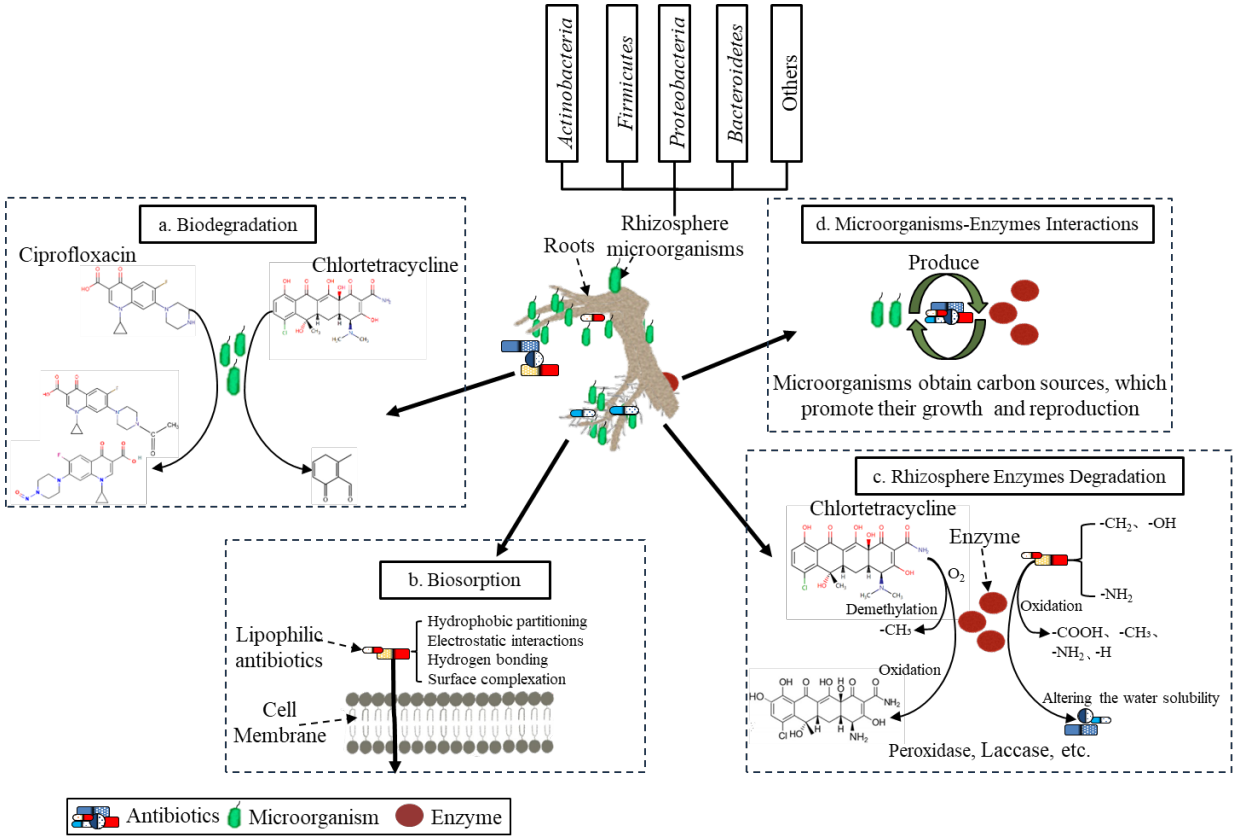

Figure 2. Action mechanism of rhizosphere microorganisms and enzymes on antibiotics

sucrose secreted by plant roots and obtain carbon sources. Rhizosphere microorganisms whose growth and reproduction are promoted proximally influence the migration and transformation of antibiotics. The ammonia-oxidizing bacteria *Nitrosomonas* and *Nitrospiracea* secrete ammonia monooxygenase (AMO), which degrades nearly 86% of antibiotics by co-metabolizing β-lactam cycles in the molecular structure, thus reducing the interference effect of antibiotics on ammonia-oxidizing bacteria (Kassotakie et al. 2016, Wang et al. 2019).

Effects of antibiotics on rhizosphere microorganisms and enzymes

Antibiotics, in turn, affect the composition and properties of rhizosphere microorganisms and enzymes. The mechanism is illustrated in Figure 3. Antibiotics alter the growth and metabolism of rhizosphere microorganisms and the structure of microflora (Liu et al. 2012, Li et al. 2023). Antibiotics may reduce microbial activity through several mechanisms, including interfering with protein function; inhibiting nucleic acid synthesis; altering the microbial internal environment, cell wall, and cell membrane structure; and disrupting microbial energy metabolism and the material exchange system (Yang et al. 2022). Some rhizosphere microorganisms adapt to antibiotic stress, allowing them to become dominant strains that participate in the degradation of antibiotics and promote growth in certain microorganisms (Cerqueira et al. 2020). Furthermore, antibiotics can affect plant or microbial enzymes, resulting in the promotion or inhibition of certain enzymatic activities, such as those that occur in the root domain (Zhou et al. 2022).

Rhizosphere microorganisms are highly sensitive to antibiotics, even at low concentrations (Yang et al. 2010). Some antibiotics inhibit the structure and function of the cell wall and cell membrane of rhizosphere microorganisms. For example, penicillin, which is in the β-lactam family, binds to the penicillin enzyme in the cell wall synthesis pathway, thereby inhibiting cell wall synthesis (Herren et al. 2022). Penicillin and streptomycin (aminoglycosides) can bind to specific receptors on the cell membrane and change its permeability (Kim et al. 2023, Wang and Blount 2023). TCs can block cell wall formation by

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inhibiting methyl methacrylate, which is required for cell wall synthesis (Ledger and Edwards 2023). ERY destroys the integrity of the cell wall, causing cell death. Both TC and ERY can interfere with ion channels on the cell membrane, promoting changes in membrane permeability and affecting rhizosphere microbial diversity (Liu et al. 2011). Some antibiotics harm rhizosphere microorganisms by hindering the synthesis and expression of nucleic acids and proteins. Macrolides can suppress cell protein synthesis and subsequently affect cell proliferation (Fu 2020). Streptomycin and OTC affect protein synthesis by interfering with ribosome function (Tang and Tang 2009). CAP inhibits the formation of tRNA, which blocks the protein synthesis process.

Additionally, antibiotics can change the structure of the rhizosphere microbial community by interfering with microbial energy metabolism and the material exchange system. Huang et al. (2017) found that with the increase in the CIP concentration, the community diversity index of *Brassica campestris* L. with high (CT) and low (SJ) CIP accumulation decreased from 3.38 to 3 and from 3.37 to 3.02, respectively; the richness index (number of bands) decreased from 29 to 22 and from 27 to 24, respectively; and the evenness index decreased from 0.90 to 0.84 and from 0.91 to 0.85, respectively. Liu et al. (2022) found that high SMX concentrations resulted in reduced microbial activity, the inability of microorganisms to adapt to antibiotic stress, and declines in biomass and diversity. The degree of tolerance and response of rhizosphere microorganisms to antibiotics varies depending on the type of antibiotic, content, exposure time, and microbial type. For example, Zhang et al. (2009) examined the sensitivity of six different wheat rhizosphere strains to aureomycin and penicillin at different concentrations. The tolerance concentration of *Actinomyces* F1 to aureomycin was 1 000 μg/L, while 500 μg/L CTC could inhibit the growth of *Actinomyces* F2. Moreover, the relative abundance of *Proteobacteria* decreased at a TC concentration of 300 μg/L, but the relative abundance increased at TC concentrations ranging from 300 to 30 000 μg/L (Guo et al. 2020).

The activity of some rhizosphere enzymes is inhibited or promoted under antibiotic stress, thereby affecting the growth conditions of microorganisms. Huang et al. (2017) found that CIP contamination

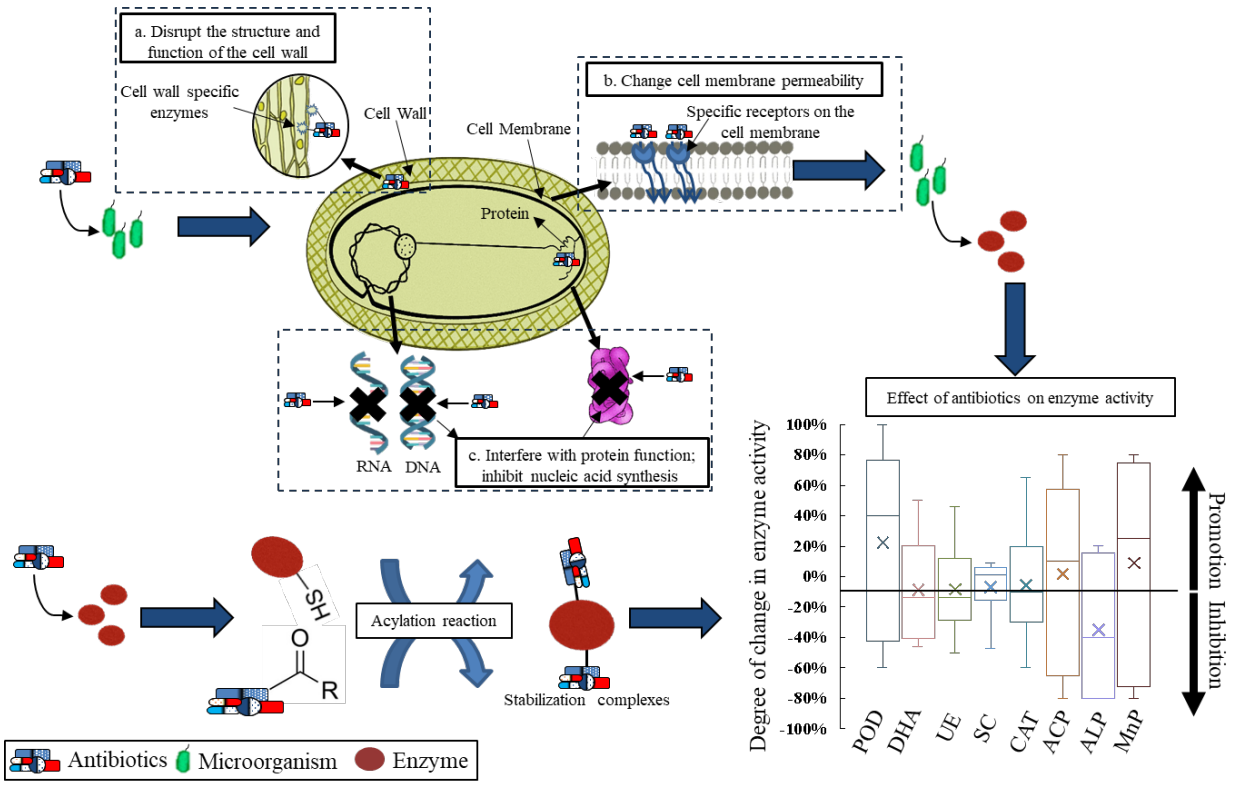

Figure 3. Mechanism and effect of antibiotics on rhizosphere microorganisms and enzymes (some of the data in the figure are adopted from Table 3)

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levels were negatively correlated with catalase (correlation coefficient = –0.474) and urease activity (correlation coefficient = –0.740) in the rhizosphere of high and low CIP-accumulating cultivars of *Brassica campestris* L. Penicillin, TC, ERY, and streptomycin can affect the function and expression of urease, hinder its decomposition into ammonia and carbon dioxide, and suppress the growth and metabolism of rhizosphere microorganisms. Low concentrations of antibiotics can enhance the activity of plant antioxidant enzymes, thereby removing reactive oxygen species to protect the growth of plants and rhizosphere microorganisms (Wang et al. 2021b). However, studies have shown that the inhibitory effect of antibiotics on the activities of most enzymes surpasses the promoting effect (Figure 3), such as those on DHA, sucrase, urease, catalase, and alkaline phosphatase, which exhibit average decreases in activity of 6–35% when exposed to antibiotics. In contrast, the promoting effect of antibiotics on peroxidase, acidic phosphatase, and manganese peroxidase outweighs the inhibitory effect, resulting in average increases of enzyme activity of 2–23%.

Antibiotics can affect the normal function of rhizosphere enzymes by directly binding with them or binding with their substrates or ligands. During acylation, TCs bind to sulfhydryl groups in urease molecular structures to form stable complexes, disrupting urease function (Schnappinger and Hillen 1996). OTC binds to specific parts of various rhizosphere enzymes. A previous study found that the activity of urease decreased by 0.1–50%, the activity of sucrase decreased by 0.1–47%, phosphatase activity decreased by 0.1–80%, and catalase activity decreased by 27–46% under OTC (100 mg/kg) exposure (Yao et al. 2010). Additionally, the promoting or inhibitory effect of antibiotics on rhizosphere microorganisms can also lead to changes in the activity, functions, or structures of specific enzymes. TC interferes with the function of ribosomes, hindering the function of sucrase, while ERY and streptomycin can promote the synthesis and activity of sucrase. Yi et al. (2017) found that CIP inhibited the activity of nitrite reductase and polyphosphate kinase by blocking the conversion of intracellular polyhydroxyalkanoates and glycogen by rhizosphere microorganisms.

Different types of plants, enzymes, and antibiotics; antibiotic contents; and soil regions all affect enzymatic responses to antibiotics. For example, low concentrations of SMX (15 mg/kg) were found to increase the activity of DHA by 4–30% in rhizosphere zones, and DHA activity decreased by 6–40% in bulk soil zones, but high concentrations (45 mg/kg) of SMX decreased DHA activity by 10–90% in all regions. However, under sulfamerazine treatment, the activity of DHA at low and high concentrations near the rhizosphere zones increased by 1–50% overall (Li et al. 2021a). Wang et al. (2021a) concluded that catalase activity in a soil-lettuce system initially decreased by 10–15% with the increase in the OTC concentration from 0 to 50 mg/kg before significantly increasing by 10–20% (from 50 to 450 mg/kg). Catalase activity was reduced by 20–30% at OTC concentrations of 450–1 350 mg/kg. Zhang et al. (2012) confirmed that various soil enzyme activities in the rhizosphere region of wheat cultivars were inhibited by OTC, with soil alkaline phosphatase activity decreasing by 31.7–44.3%. However, there was no significant relationship between acid phosphatase, DHA activity, and the OTC dose effect.

Studies have shown that rhizosphere microorganisms and related enzymes play key roles in pollutant treatment, including antibiotic degradation, pure bacteria and enzyme degradation, and multi-enzyme synergism (Liu et al. 2020). The roles of rhizosphere microorganisms and enzymes in antibiotic migration and transformation can be studied through the combination of modern high-throughput sequencing technology to analyze the microbial community structure, next-generation sequencing, bioinformatics methods, and microbiome techniques with enzyme assay methods. Rhizosphere microorganisms and enzymes not only participate in the antibiotic degradation process but are also closely linked to rhizosphere plant and soil interactions and functions; this is a phenomenon that needs further study.

BEHAVIOUR OF RHIZOSPHERE EXUDATES DURING ANTIBIOTIC MIGRATION AND TRANSFORMATION

Influence of rhizosphere exudates on antibiotics

Rhizosphere exudates play important roles in driving antibiotic migration and transformation (Zhalnina et al. 2018). Exudates can regulate the activity of antibiotics by binding to antibiotics or changing the target. For example, the combination of phenolic acid coumarin with antibiotics reduced the minimum inhibitory concentrations (MICs) of TC and NOR from 64 to 32 μg/mL and from 128 to 16 μg/mL, respectively (De Araujo et al. 2016). *Phellinus baumii*

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ethyl acetate extract (Hong et al. 2016) and cinnamaldehyde (Dhara and Tripathi 2020) changed the target of β-lactam and FQs. As a result, microorganisms were inhibited from producing targets that hindered the binding of antibiotics to the cell wall, and the MIC values of β-lactam and CIP against bacterial targets were reduced by 8 to 128 folds and by 2 to 1 024 folds, respectively, enhancing the antibacterial activity of antibiotics. Lastly, rhizosphere exudates can inhibit degradation or produce less toxic or harmless byproducts in the soil environment. For example, Gujarathi et al. (2005) demonstrated that the process of OTC removal by *Helianthus annuus* was dependent on active oxide rhizosphere exudates. Moreover, phytoactive compounds such as quercetin (Kim et al. 2018) and carvacrol (Miladi et al. 2016) inhibit antibiotic degradation by suppressing β-lactamase activity.

Rhizosphere exudates affect microbial activity and abundance (Wu et al. 2017, McLaughlin et al. 2023). The growth and reproduction of rhizosphere microorganisms further degrade antibiotics or interfere with the migration and transformation of antibiotics in correlation with exudates. Jin et al. (2015) investigated the degradation of sulfonamides in an artificial root exudate tank (T-ARE) and concluded that the presence of rhizosphere exudates, even at the same concentration of antibiotics, enhanced rhizosphere microbe activity and increased the SFD removal rate by 23.8%. Another study found that the removal rate of 5 mg/L CIP by rhizosphere microorganisms was only 5.8%, while the removal rate of antibiotics in synergistic interactions with rhizosphere secretions was as high as 98% (Sodhi et al. 2021). Li (2021) showed that the rhizosphere exudates of four plants, including *Vallisneria natans* (Lour.) Hara, increased the degradation rate of SFD by 39.71–55.85% and that of sulfachloropyridazine by 40.76–54.44%.

Effects of antibiotics on rhizosphere exudates

First, antibiotics can induce changes in the quality of rhizosphere exudates or lead to unstable compositions. Exposure to OFL and TC at 10 μg/L stimulated the oxalic acid content of four wetland plants, including *Cyperus alternifolius* L., and increased its cumulative concentration from 7.512–16.488 mg/g to 22.008–31.944 mg/g over the 24-day experiment (Tong et al. 2019). After exposure to 150 mg/kg OTC, the relative abundance of organic acids such as acetic acid in rhizosphere exudates increased significantly, while the relative abundance of carbohydrates (such as galactose) and fatty acids (such as heptadecanoic acid and 7-hydroxyoctanoic acids) decreased. Therefore, OTC affects amino acid metabolism and carbohydrate metabolism pathways (Guo et al. 2022).

Second, changes in the rhizosphere microbial community structure under antibiotic stress affect the composition and quality of rhizosphere exudates accordingly. At concentrations of 100 mg/kg, TC, CIP, and sulfonamides increased the number of rhizosphere microorganisms related to antibiotic migration and transformation, such as *Proteobacteria*, *Actinobacteria*, and *Firmicutes* (Grenni et al. 2018). As a result, these rhizosphere microorganisms produced more hormone substances that promoted plant growth or improved the absorption of nutrients by plants, thereby releasing more rhizosphere exudates (Zhou et al. 2016).

RESEARCH OPPORTUNITIES

Mechanism of antibiotic migration and transformation in soil-microbe-plant systems

The study of antibiotics within rhizosphere systems remains notably insufficient, and there is a critical need for a more systematic research framework to unify previous fragmented approaches. Future research should prioritise the following areas: (1) investigating the distribution of antibiotics in the rhizosphere systems of plants, focusing on their migration and transformation processes; (2) examining the interconnectivity among different components within rhizosphere systems in relation to antibiotics; (3) assessing the temporal and spatial variations of antibiotics within the plant rhizosphere; and (4) synthesising and applying the mechanisms of interaction between antibiotics and the plant rhizosphere to enhance antibiotic utilisation and mitigate environmental pollution.

Influence of plant age on antibiotic migration and transformation

Plants of different ages exhibit different root characteristics and developmental degrees (including the root density, root length, and root diameter). Root traits can predict the interaction between the rhizosphere and antibiotics in later stages. Under antibiotic stress, the older the plant and the more developed the root system, the stronger its toler-

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ance and adaptability to antibiotics. In addition, the content of soil organic matter and other nutrients can change with plant root age, soil structure, and physical and chemical properties. Soil pores enhance soil permeability and are closely associated with the root structure (Li and Duan 2012, Yan et al. 2016). The uptake and transport of antibiotics by plant roots are dependent on soil penetration. The abundance and composition of microorganisms change with increased plant age, especially in regard to rhizosphere microorganisms such as *Actinomycetes* that are involved in antibiotic migration (Xie et al. 2023). Changes in morphological characteristics caused by root development allow for the increased secretion of substances that promote the growth of microorganisms and affect the activities of enzymes such as urease and protease in soil. This can influence the antibiotic conversion process. Therefore, it is necessary to conduct extended studies with different plant ages to analyse the effect of plant age on antibiotic migration and transformation.

CONCLUSIONS

Interaction mechanisms between the plant rhizosphere system (consisting of soil-plant-microbes) and antibiotics have been reviewed in this article. The effects of plants on antibiotics in the rhizosphere system were divided into two aspects, namely, the direct rhizosphere uptake of antibiotics and the influence of rhizosphere microorganisms, enzymes, and exudates on antibiotics. The main findings include that the absorption of antibiotics by plants is influenced by their MW and log K_{ow}, which can be divided into three classes: (1) antibiotics (including TYL, ERY, and RTM) with high lipophilicity (log $K_{ow} > 2$) are mostly adsorbed by root lipids and rarely participate in the soil-plant transport process; (2) antibiotics (including AZI) with log $K_{ow} < 2$ and high MWs (MW > 700) are blocked outside the plant roots; and (3) antibiotics (including ENR and danofloxacin) with log $K_{ow} < 2$ and low MWs (MW < 700) can enter the plant through the roots and are transported through transpiration flow in plants. Antibiotics (including TC, CTC, and OTC) with log $K_{ow} < 1$ are more easily transported into plant tissues, such as stems, leaves, and fruits. In addition, antibiotics are more readily adsorbed by plants with extensive root systems and superior transport capabilities.

The fate of antibiotics can include biosorption, bioaccumulation, biodegradation, or biotransformation through the action of soil rhizosphere microorganisms and their ability to absorb, use, and transform antibiotics in the soil environment. The microorganisms capable of participating in the antibiotic migration and transformation process are concentrated in *Actinobacteria*, *Firmicutes*, *Proteobacteria*, and *Bacteroidetes*. Rhizosphere enzymes can degrade different classes of antibiotics to form both inactive or more active metabolites through catalysis. This process involves breaking the molecular structure of antibiotics, introducing new structures, and reducing or enhancing their inhibitory effect on rhizosphere microorganisms. The inhibitory effect of antibiotics on DHA, sucrase, urease, catalase, and alkaline phosphatase activities surpasses the promoting effect, reducing the activities of these enzymes by an average of 6–35%. However, the promoting effect of antibiotics on peroxidase, acidic phosphatase, and manganese peroxidase outweighs the inhibitory effect, resulting in a 2–23% increase in enzyme activity. There are still major knowledge gaps in the research regarding the mechanism of antibiotic migration and transformation in soil-microbe-plant systems, as well as the influence of plant age and different root characteristics on the migration and transformation of antibiotics.

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