Advances in the Oxidative Stress Response of Plants Under Herbicide Stress

Hui JIANG[1,2], Zhenxian CHEN[2], Ziyuan CHEN[2], Liangji LU[2], Yunxuan OUYANG[2], Chunxing LI[2], Yaping HU[1,2], Qianhua JI[1,2]*

1. Institute of Pomology, Zhaoqing University, Zhaoqing 526061, China; 2. College of Life Sciences, Zhaoqing University, Zhaoqing 526061, China

Abstract This paper summarizes the impact of herbicides on plant antioxidant enzyme systems and malondialdehyde (MDA) activity, and the role of glutathione (GSH) in response to abiotic stresses. Additionally, it provides a perspective on future research regarding the effects of soil herbicide stress on fruit trees.

Key words Herbicide; Oxidative stress; Antioxidant enzyme; Stress

1 Introduction

Weed control is a critical component of agricultural production. Among the various methods available, chemical weed control has emerged as the preferred approach for fruit farmers due to its rapid implementation, easy use, and efficiency. Soil herbicides are extensively utilized globally, with glufosinate ammonium being applied at rates approaching 100% in citrus orchards located in Huizhou, Shaoguan, and Meizhou within Guangdong Province[1]. However, during the weeding process, the potential hazards associated with herbicides on crops are increasingly evident. Residual herbicides in the soil can adversely affect the normal growth of crops, as they may directly or indirectly penetrate the soil and persist at varying depths[2]. This contamination can subsequently impact crop production, yield, and quality, ultimately influencing economic returns. This paper summarizes the impact of herbicides on plant antioxidant enzyme systems and malondialdehyde (MDA) activity, and the function of glutathione (GSH) in response to abiotic stresses. Additionally, it offers a perspective on future research regarding the effects of soil herbicide stress on fruit trees.

2 Impact of herbicides on plant antioxidant enzyme systems

As illustrated in Table 1, the oxidative stress responses of various plant groups, including grains, vegetables, tobacco, medicinal herbs, fruit trees, and others, were summarized following exposure to different herbicide stresses at varying concentrations and types of herbicides. The regulation of antioxidant enzyme systems in these plants varied in response to herbicide stress, influenced by factors such as concentration, species, and duration of treatment.

2.1 Regulatory mechanisms and effects on ROS in plants

Reactive oxygen species (ROS) are signaling molecules that play a crucial role in plant defense mechanisms against external threats. These molecules are chemically active and exhibit high oxidative properties. Under typical growth conditions, the production and scavenging of ROS, including O_2, OH, O^{2-}, and H_2O_2, in plants maintain a stable equilibrium. However, this equilibrium is disrupted by stress, which impairs the antioxidant mechanisms in plants. Consequently, the imbalance between the production and scavenging of ROS results in the accumulation of excessive ROS. This accumulation can subsequently react with biomolecules, leading to oxidative damage and, in more severe instances, necrosis[17]. There are two primary mechanisms through which ROS are generated in response to abiotic stress: metabolic ROS, which arise from the disruption of metabolic processes, and signaling ROS, which are produced as part of the signaling network activated in response to abiotic stress[18]. In the context of abiotic stresses, ROS do not directly mitigate the effects of these stresses. Instead, they assist plants in managing abiotic stressors through indirect mechanisms. Metabolic ROS can directly modify the redox state of enzymes, restrict reaction rates, and regulate intracellular metabolic pathways, thereby influencing various metabolic responses to alleviate the impacts of abiotic stresses on the organism[19]. Furthermore, ROS have the capacity to oxidatively modify essential regulatory proteins, thereby enhancing plant adaptation to abiotic stresses via signaling mechanisms[20]. The attack of ROS on cell membranes results in the accumulation of lipid oxidative damage products, such as thiobarbituric acid reactive substances (TBARS). These substances can serve as indicators of plant susceptibility to abiotic stress injuries[21]. Under abiotic stress conditions, the accumulation of excess ROS results in increased fluidity and permeability of cell membranes, enhanced disintegration of the lipid bilayer, and significant disruption of normal cellular functions. Wang Jian[22] demonstrated that the application of a high concentration of quinclorac at 0.5 g/L significantly elevated ROS levels in rice during an experimental study. To mitigate damage caused by external environmental stresses, plants utilize their antioxidant enzyme system to scavenge excess ROS[23-24]. The herbicide paraquat exerts its effects on photosystem I located with-

Received: October 9, 2024 Accepted: November 19, 2024
Supported by Earmarked Fund for China Agriculture Research System (CARS-26); Undergraduate Innovation and Entrepreneurship Training Program (202310580006).
* Corresponding author. E-mail: qhgee@163.com

in the thylakoid membranes of plant chloroplasts, and further induces the generation of a substantial quantity of ROS as a byproduct of the energy conversion processes associated with photosynthesis. This accumulation of ROS results in the degradation of cellular structures, ultimately culminating in the demise of the plant[25-27]. Faisal Islam's research conducted in 2017 demonstrated that the treatment with 2,4-D alone resulted in a significant increase in ROS content[28]. The herbicide prometryne has a significant impact on corals and isolated algae. When the stress level does not surpass the organism's defense capacity, the organism regulates the expression of antioxidant-related proteins through gene regulation, thereby enhancing its defense mechanisms. However, when the stress level exceeds the organism's defense capacity, the defense system becomes compromised, prompting the coral host to engage alternative pathways to mitigate self-damage[29]. A substantial body of experimental evidence indicates that herbicide treatments can elevate the levels of ROS in plants. However, there is a paucity of research examining the impact of soil treatment with herbicides on ROS levels[13].

Table 1 Studies on plant responses to herbicide-induced oxidative stress

Group	Species	Herbicide	Dosage	Oxidative stress response of plants	Reference
Grains	Broom corn millet	50% 2,4-D isooctyl ester	1 000 mL/hm^2	The SOD activity, MDA content, and Pro content in all treatment groups were significantly higher than those in the control group (CK) at 7-21 d post treatment. However, both SOD activity and the content of MDA and Pro in the broom corn millet samples exhibited a decline after 21 d of application, indicating a reduction in herbicide stress on the millets.	[3]
		15% Thifensulfuron-methyl	1 000 mL/hm^2		
		38% Atrazine	1 000 mL/hm^2		
		48% Bentazone	1 000 mL/hm^2		
	Peanut	N-(phosphonomethyl) glycine	48.00 L/hm^2	After 5 d of treatment, the POD activity initially increased and subsequently decreased. The POD activity reached its maximum value after 15 d of treatment, after which it began to return to baseline levels.	[4]
		Butachlor	40.80 L/hm^2	The MDA content in the experimental group was significantly higher than that of the control group within 20 d. This consistent increase in MDA levels suggests that the peanut plants exhibit a defensive response to the stress induced by the herbicide.	
	Sorghum	50% Quinclorac WP	750 g/hm^2	The application of the three herbicides at the maximum safe dosage resulted in an increase in MDA levels in sorghum seedlings, as well as enhanced activities of SOD and POD in sorghum plants within one month. The physiological effects reached their peaks 5 d post herbicide treatment, followed by a recovery observed at 20 d.	[5]
		56% Sodium dimethyltetrachloride DP	1 800 g/hm^2		
		57% 2,4-D butyl ester EC	1 050 g/hm^2		
	Oats	48% Butralin	1 875, 3 750, 5 625 mL/hm^2	The MDA content in oat leaves was significantly higher than that observed in the control group following exposure to multiple concentrations of herbicide stress. Additionally, the activities of SOD, CAT, and POD in oat leaves were elevated to varying degrees in comparison to the control. Notably, these activities exhibited a gradual recovery after one month.	[6]
		96% S-Metolachlor	450, 900, 1 350 mL/hm^2		
Vegetables	Chinese cabbage	Benazolin	1 : 65 mL/667 m^2	At 3 d post treatment, the activities of SOD and POD, as well as the MDA content, exhibited an initial decrease followed by an increase. This pattern suggests that Chinese cabbage is capable of adapting to stress through the regulation of enzyme activities.	[7]
		Triclopyr	1 : 0.04 mL/667 m^2	The CAT activity in Chinese cabbage was significantly elevated compared to the control group following treatment. Additionally, the MDA content was notably higher than that of the control during the pretreatment phase, exhibiting a trend of initial increase followed by a subsequent decrease.	
		Fluroxypyr	1 : 50 mL/667 m^2	The CAT activity and MDA content in Chinese cabbage exhibited an initial increase followed by a subsequent decrease following treatment. Additionally, the activities of POD and SOD were significantly elevated compared to the control group.	
	Carrot	Benazolin	1 : 65 mL/667 m^2	Following treatment, the short-term activity of CAT in carrots exhibited an initial increase followed by a subsequent decrease. Conversely, the activities of SOD and POD, along with the MDA content, demonstrated a pattern of decrease followed by an increase.	

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Group	Species	Herbicide	Dosage	Oxidative stress response of plants	Reference
		Triclopyr	1∶0.04 mL/667 m^2	The activities of CAT, SOD, POD, and the content of MDA in carrots exhibited a pattern of initial decrease followed by an increase in the short term following treatment.	
		Fluroxypyr	1∶50 mL/667 m^2	Following treatment, the activity of CAT and POD in carrots exhibited an initial increase followed by a subsequent decrease. Conversely, the SOD activity demonstrated a trend of decreasing initially, followed by an increase. Additionally, the MDA content displayed an overall decreasing trend in the short term.	
Tobacco	Tobacco	50% Quinclorac WP	5.0×10^{-2} mg/kg	The MDA content in tobacco leaves subjected to quinclorac stress was significantly elevated compared to the control group. Additionally, the activities of POD and CAT in the tobacco leaves were both reduced and exhibited significant differences from those observed in the control group. Furthermore, the extent of damage to the tobacco leaves was more pronounced at this concentration.	[8]
Medicinal herbs	Woad seedling	17.5% Quizalofop-p-ethyl · benazolin EC	1 500 mL/hm^2	The herbicides selected were all systemic in nature. The activity of POD was observed to be higher than that of the control (CK), reaching its maximum at 5 d post treatment. As the duration of growth increased, the herbicidal activity exhibited a gradual decline, accompanied by a decrease in POD content. Additionally, the MDA content in woad seedlings peaked at 15 d and subsequently showed a gradual recovery by day 20, indicating a relief of plant stress.	[9]
		20% Picloram · clopyralid · clethodim OD	1 500 mL/hm^2		
		50% Benazolin 10 mL + 24% clethodim 20 mL + 30% clopyralid 20 mL + 10% pyribambenz-propyl 5 mL	1 500 mL/hm^2		
Fruit trees	Grape	40% Acetochlor	0.27 mL/m^2	During the treatment period, the activities of POD and CAT in grape leaves exhibited a significant increase in response to herbicide application, while the MDA content was notably higher compared to the control group.	[10]
		10% Fluoroglycofen-ethyl	0.024 mL/m^2		
		10% Gramoxone	0.12 mL/m^2		
		41% Glyphosate	Treatment 1 (1∶160), treatment 2 (1∶140), treatment 3 (1∶120), treatment 4 (1∶100), treatment 5 (1∶80)	At low concentrations (treatments 1, 2, and 3), the POD activity exhibited an initial decrease followed by an increase, while the CAT activity demonstrated an initial increase followed by a decrease. In contrast, the SOD activity consistently increased. At high concentrations (treatments 4 and 5), the SOD activity initially increased before subsequently decreasing, whereas both POD and CAT activities exhibited a continuous decline.	[11]
			0, 1, 5, 10, 20, 50 mg/kg	In grape leaves, the duration of glyphosate treatment resulted in an initial increase followed by a decrease in SOD activity. The POD activity exhibited minimal variation, while the CAT activity consistently increased in leaves subjected to low concentrations of glyphosate (treatments 1 and 2). Conversely, the CAT activity in leaves treated with high concentrations of glyphosate (treatments 4 and 5) demonstrated an increase followed by a decrease.	
	Peach tree	20% Paraquat		Following treatment with paraquat, the activities of CAT and POD in peach leaves exhibited a significant increase in comparison to the control group. In contrast, the activities of CAT and POD following glyphosate treatment showed variable changes, with some exhibiting increases and others decreases; however, none of these changes were statistically significant when compared to the control.	[12]
		41% Glyphosate			
Others	Cotton	240.0 g/L Oxyfluorfen	120, 180, 240, 300, 360 g/hm^2	The activity of SOD was significantly lower in the high concentration treatment compared to the control group. Conversely, the POD activity increased in response to low concentrations of oxyfluorfen; however, it was inhibited as the concentration increased. After 30 d of application, the ascorbic acid (ASA) content in cotton treated with 120 g/hm^2 was significantly higher than that of the control. Additionally, the MDA content in cotton subjected to higher concentrations (240, 300, and 360 g/hm^2) was significantly elevated compared to the control group.	[13]

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Group	Species	Herbicide	Dosage	Oxidative stress response of plants	Reference
		25.0 g/L Penoxsulam	7.5, 15.0, 22.5, 30.0, 37.5 g/hm^2	After 30 d of application, the inhibition of SOD activity in cotton was most pronounced, while the POD activity exhibited a significant increase at various concentrations, demonstrating a positive correlation with the concentration of the chemicals used. Additionally, the ascorbic acid content in cotton decreased significantly at concentrations of 30.0 and 37.5 g/hm^2, whereas the MDA content increased in response to the escalating amounts of chemicals applied.	
		330.0 g/L Pendimethalin	619, 742, 866, 990, 1 113 g/hm^2	The activity of POD was observed to increase in the low concentration treatments; however, it was inhibited as the concentration increased. Additionally, the activity of SOD was significantly lower than that of the control group at higher concentrations (pendimethalin: 990 g/hm^2, butralin: 1 584 g/hm^2). In contrast, at low concentrations (pendimethalin: 619 g/hm^2, butralin: 1 008 g/hm^2), no significant differences were noted in MDA content when compared to the control. Furthermore, the MDA content in the other treatments was significantly higher than that of the control and exhibited an increasing trend with the rise in application rate.	
		48.0% Butralin	1 008, 1 152, 1 296, 1 440, 1 584 g/hm^2		
	Chinese pennisetum	Atrazine	0, 5, 10, 20, 50, 100, 200 mg/kg	The content of MDA and the activity of SOD in the roots of Chinese pennisetum exhibited an initial increase followed by a subsequent decrease as the concentration of atrazine increased. Conversely, the activity of glutathione reductase (GR) diminished at elevated herbicide concentrations. These findings suggest that oxidative stress is induced in the roots of Chinese pennisetum when exposed to varying concentrations of atrazine.	[14]
	China fir	Glyphosate		As the concentration of glyphosate increased, the POD activity in Chinese fir seedlings exhibited an upward trend. Conversely, the SOD activity initially decreased before subsequently increasing. Notably, both SOD and POD activities in Chinese fir seedlings remained elevated under high glyphosate concentration treatment.	[15]
	Cattail root	≥97% Atrazine		As the concentration of the herbicide increased, the activity of SOD in plants was significantly inhibited. Conversely, the activity of CAT exhibited an initial increase followed by a subsequent decrease. Additionally, the MDA content peaked at high concentrations of herbicide treatment.	[16]

2.2 Regulatory mechanisms and effects on SOD activity in plants By inducing and activating the activities of antioxidant enzymes, as well as regulating their maintenance within the body, plants can effectively mitigate or eliminate the damage to membrane lipids caused by oxidative stress. Superoxide dismutase (SOD) is a class of metalloenzymes that are prevalent in a diverse range of organisms, including plants, animals, and microorganisms[30]. These enzymes play a crucial role in regulating oxygen radicals within the organism, thereby mitigating the toxic effects associated with elevated concentrations of superoxide anion radicals. To facilitate the elimination of superoxide anion radicals, these radicals undergo disproportionation to form hydrogen peroxide (H_2O_2) and oxygen (O_2), thereby effectively scavenging superoxide radicals from the organism[31]. Plants subjected to adverse conditions generate free radical reactions that lead to the denaturation of proteins and biomolecules. Research demonstrated that China fir seedlings intensified the extent of damage to cell membrane lipid oxidation when exposed to glyphosate. This exposure subsequently induced an increase in SOD activity, which serves to mitigate the excessive production of superoxide anion radicals resulting from oxidative damage to the cells[15]. Herbicides can induce a phenomenon known as enzyme system collapse in plants within a relatively short timeframe. Chen Ying *et al.*[32] observed that following the application of herbicide on a *Ligustrum quihoui* hedgerow heavily infested by *Cuscuta japonica*, the enzyme system collapse was evident in glufosinate ammonium-treated *L. quihoui* by the 10th day post treatment. Furthermore, the activity of SOD in *L. quihoui* was significantly lower than that observed in the control group. This finding suggests that the plants may adapt to herbicide-induced stress by modulating SOD enzyme activity. Research demonstrated that following herbicide treatment, carrot seedlings activated their resistance mechanisms in response to environmental stressors, thereby eliminating excessive free radicals within their systems[33]. As the concentration of herbicide increased, the activity of SOD initially rose before subsequently declining. This phenomenon can be attributed to the generation of elevated levels of free radicals in

carrots subjected to low concentrations of herbicide. In response, the physiological mechanisms in carrots enhanced SOD activity, which in turn improved their capacity to scavenge free radicals and mitigated the damage inflicted by herbicides on the plants. Over time, the carrot seedlings demonstrated the capacity to adapt to elevated concentrations of herbicides and to scavenge excess reactive oxygen species from its system. In this context, the activity of SOD decreased, indicating that carrots were capable of activating the body's resistance mechanisms in response to varying herbicide concentrations. This adaptation serves to protect the biofilm by inducing SOD activity. Ma Chunying[34] demonstrated that the application of the herbicides monosulfuron and prometryne on cereal crops resulted in an increase in SOD activity. This observation suggests that the plants may be employing a protective mechanism by enhancing enzyme activity in response to stress. Furthermore, it has been proposed that following glyphosate treatment, the herbicide penetrates plant cells, causing cellular damage, which subsequently leads to an elevation in SOD enzyme activity[35].

2.3 Regulatory mechanisms and effects on POD activity in plants Under adverse conditions, peroxidase (POD), a critical enzyme within the antioxidant defense system, functions synergistically with catalase (CAT) and SOD[36] to eliminate excess free radicals in the organism and reduce their impact on lipid peroxidation in plant biofilms. Concurrently, POD facilitates the oxidative degradation of indole acetic acid (IAA) and plays a crucial role in the biosynthesis of lignin as well as the development of corky layers[37]. Furthermore, POD promotes lignification and may therefore function as a physiological marker for tissue senescence. The increased activity of POD correlates with enhanced plant defense mechanisms against ROS-induced damage[38]. In their investigation of the effects of atrazine and sethoxydim on watermelon seed germination and associated enzyme activities, Lu Shuangxue *et al.*[39] reported that the application of both herbicides at varying concentrations enhanced the expression of POD activity in watermelon seeds. The increase in POD activity was influenced by elevated concentrations of glyphosate. Zhou Chuifang *et al.*[15] demonstrated that China fir seedlings could adapt to stress responses, effectively scavenging free radicals, preventing membrane lipid peroxidation, and mitigating cellular damage under low concentrations of herbicide stress. Furthermore, China fir seedlings exposed to high glyphosate concentrations (20 mg/kg) exhibited significantly elevated POD activity, surpassing that of the control treatment by as much as 66.2%. Song Xudong *et al.*[40] investigated the effects of various types of herbicides on the physiological and biochemical indices of oat seedlings. Their findings indicated that the POD activity in the plants increased with higher concentrations of herbicides, suggesting that these herbicides have a stimulatory effect on POD activity in plants. Guo Lei *et al.*[12] investigated the impact of herbicides on the physiological characteristics and runoff of peach trees. Their findings indicated that the POD activity in the leaves of peach trees treated with the herbicide paraquat was more than double that of the control group. Qian Lanjuan *et al.*[41] conducted a study on the antioxidant properties of clodinafop-propargyl in young wheat leaves, demonstrating a significant increase in POD activity in wheat seedlings treated with clodinafop-propargyl compared to the control group. These findings indicate that various herbicide treatments can enhance POD activity in plants.

2.4 Regulatory mechanisms and effects on CAT activity in plants H_2O_2 is classified as a harmful ROS that can be reduced to various types of detrimental free radicals. Additionally, it has the capacity to oxidize numerous cellular components, thereby leading to cellular damage[42]. CAT catalyzes the decomposition of H_2O_2 into molecular O_2 and H_2O, thereby facilitating the removal of H_2O_2 from biological systems and protecting cells from hydrogen peroxide-induced toxicity. This enzymatic activity also inhibits the conversion of H_2O_2 and O_2 into the highly reactive hydroxyl radical ($\cdot OH$), which is a potent oxidant[43]. Furthermore, CAT contributes to the maintenance of cellular homeostasis in plants and mitigates the detrimental effects of oxidative stress on plant tissues. The plant possesses the ability to defend itself against environmental stress by modulating CAT levels in response to stress conditions[43]. CAT functions as a negative regulator of plant immunity, and its activity is regulated in an antagonistic manner to facilitate either defense mechanisms or susceptibility to invasion by pathogens. Programmed cell death (PCD) represents a crucial strategy employed by plants to defend against the invasion of pathogenic bacteria. Plants can initiate the PCD process as a defensive mechanism against pathogen invasion by modulating the function of CAT to promote the accumulation of ROS. Alternatively, plants may directly eliminate pathogens through the action of the accumulated ROS[44]. Hao Hongdan[7] demonstrated that the CAT activity in herbicide-treated Chinese cabbage, as well as in the clear water control, initially increased before subsequently decreasing. Furthermore, it was noted that the CAT activity in *Echinochloa crus-galli* exhibited a similar pattern, with an initial increase followed by a sharp decline following herbicide treatment. This observation suggests that the integrity of the cell membrane system was compromised, leading to the stimulation of antioxidant enzyme activity within the rice plant. This response appears to be a mechanism employed by the rice plant to enhance its resistance to stress and to mitigate the toxic effects of hydroxyl radicals (OH^-) generated by free radicals[45]. Guo Lei *et al.*[12] reported that the treatment of peach leaves with paraquat resulted in a 66.50% increase in CAT activity compared to the control group. This finding suggests that paraquat significantly enhances the antioxidant activity of peach leaves. The CAT enzyme family plays a crucial role in maintaining the redox balance within plant cells and regulating the levels of H_2O_2. The diminished activity of the CAT family results in elevated concentrations of H_2O_2, the oxidation of GSH to its oxidized form (GSSG), and a disruption of the equilibrium between GSH and GSSG. Additionally, there is a reduction in ascorbic acid levels, which impedes the plant's ability to produce sufficient reducing power necessary for the maintenance of ascorbate-glutathione recirculation, thereby disrupting the intracellular redox balance. Plants exhibiting low activity of the CAT family are particularly vulnerable to environmental stresses, including herbicide exposure and salinity. These stresses can result in membrane lipid peroxida-

tion, increased ion leakage, and degradation of photosynthetic pigments, ultimately leading to a reduction in photosystem II (PSII) efficiency and overall photosynthetic activity. Consequently, elevated levels of CAT family activity are crucial for enhancing the antioxidant defense mechanisms in plants[46].

3 Regulatory mechanisms and effects on MDA content in plants

During senescence or when plants are subjected to stress, membrane lipid peroxidation occurs in various plant organs. Malondialdehyde (MDA), a product of lipid peroxidation, serves as an indicator of the degree of peroxidation and reflects the strength of the plant organism's response to stress[7]. To assess the extent of membrane lipid peroxidation, the measurement of MDA content serves as an indirect indicator of damage to the membrane system[47]. Free radicals generated within the organism initiate lipid peroxidation by targeting unsaturated fatty acids present in biological membranes. This process can yield various catabolic ester products, some of which may be detrimental to the organism's cells and can potentially lead to cell death. MDA can induce functional impairment through its interactions with macromolecules, including proteins and nucleic acids. It has been shown to inhibit protein synthesis and to weaken the bridging bonds between cellulose molecules[45]. Additionally, MDA exhibits cytotoxic properties, disrupting both the structure and function of cell membranes[48-49]. It was observed that the MDA content in *E. crusgalli* increased following treatment with the florpyrauxifen-benzyl herbicide, in comparison to the control group treated with clear water[45]. This finding suggests that the peroxidation of the plasma membrane in the plant was exacerbated after herbicide application, indicating that *E. crusgalli* experienced significant physiological stress. Hao Hongdan[7] conducted a study on the phytotoxic effects of commonly used herbicides on carrot and Chinese cabbage. The findings indicated that Chinese cabbage exhibited a significant increase in MDA content following treatment with herbicides such as metamifop, asulam, and pendimethalin. Shi Shenkui *et al.*[50] administered a lethal dose of imazethapyr to Jigu 25 seedlings and observed a statistically significant difference in MDA content when compared to the control group. Chu Hangjian[51] investigated the MDA content in the leaves of Jimai 22 following exposure to varying concentrations of isoproturon. The results indicated that the increase in MDA content was largely proportional to the concentration of the herbicide. Furthermore, significant differences were observed in MDA levels between the different herbicide treatment groups and the control group after 48 h. Liu Qian[52] conducted a study on peach trees treated with glyphosate and paraquat, observing that the MDA content in the new roots exhibited an initial increase followed by a subsequent decrease. This pattern suggests that the impact of herbicides on the new roots of peach trees diminishes over time as the duration of treatment extends.

4 Role of GSH in plants under herbicide stress

GSH is a crucial antioxidant compound in plants[53]. Under conditions of environmental stress, plants experience an increase in intracellular ROS levels. If the removal of ROS is not adequately managed, their excessive accumulation can result in oxidative damage to essential biological macromolecules, including proteins, nucleic acids, and lipids. In severe cases, this oxidative stress may lead to cell death, ultimately contributing to the senescence of plants. In addition to the antioxidant enzyme system, which includes SOD, POD, and CAT, the GSH antioxidant system plays a crucial role in mitigating excess ROS within plants. This system primarily operates through two pathways: the antioxidant system and direct reactions with free radicals, particularly under adverse conditions[54]. GSH requires catalysis by glutathione transferase (GST) to engage with toxic substances, facilitating their conversion into harmless or low-toxicity compounds. GSH does not independently participate in the detoxification process[55]. GSH undergoes oxidation to form GSSG via an enzymatic reaction. GSSG can serve as a reactant to scavenge ROS or act as a substrate in an antioxidant enzyme-catalyzed reaction that reduces H_2O_2 to H_2O, while itself being oxidized to GSSG. Subsequently, under the influence of glutathione reductase (GR), GSSG can accept electrons to be reduced back to GSH. This cyclical process facilitates the sustained scavenging of reactive oxygen radicals in plants, thereby mitigating the damage inflicted by these radicals on plants[56]. The detoxification of herbicides by maize glutathione S-transferases (GSTs) has been documented since the early 1970s. This suggests that GSTs mitigate the toxic effects of herbicides on maize by catalyzing the conjugation reaction between the herbicide atrazine and GSH[57]. Consequently, GSHs play a crucial role in the plant's response to herbicide stress. Furthermore, Cummins *et al.*[58] discovered that the transgenic system exhibited heightened sensitivity to herbicides when genes isolated from the multi-resistant species *Alopecurus myosuroides* were transferred to *Arabidopsis thaliana* for expression. This finding underscores the significant role that GSHs play in the response of plants to herbicide stress. Numerous years ago, several researchers conducted assays to measure the activity of the GSH enzyme in glyphosate-treated wheat[59], maize[60], pea[61], peanut[62], and various other plant species. Their findings indicated that enzyme activity in these plants increased following glyphosate treatment. In recent years, studies have investigated the effects of mesosulfuron treatment on wheat, revealing an increase in the activity of GSTs *in vivo*[63]. This finding suggests that the activity of GSH or GSTs is elevated in response to herbicide-induced stress, potentially serving to alleviate the toxic effects of herbicides.

Numerous studies have demonstrated that under herbicide stress, the GSH content in plants is increased as a mechanism to alleviate the damage caused by herbicides[64]. Huang Chunyan *et al.*[65] demonstrated that imazethapyr can enhance the GSH content in oilseed rape seedlings. Furthermore, in the presence of GSTs, GSH and herbicides undergo a conjugation reaction, rendering the herbicides non-toxic and facilitating their detoxification. This finding suggests that the plant mitigates the toxic effects of imazethapyr by utilizing GSH as a protective mechanism when subjected to stress from the herbicide. Meanwhile, Ding Wei *et al.*[66] demonstrated in their study on the biochemical mechanisms underlying chlorimuron tolerance in sugar beet that the elevated levels of GSH

in tolerant sugar beet under herbicide stress facilitated the detoxification of chlorimuron absorbed by the plants. This finding underscores the critical role of GSH in the detoxification process of chlorimuron. Andrews *et al.* [55] discovered that following the application of fomesafen in soybean fields, soybeans utilized GSTs to facilitate the reaction between GSH and fomesafen. This process resulted in the substitution of chlorine atoms in the herbicide, thereby rendering it non-toxic.

5 Prospects

The fruit tree industry constitutes a significant sector within China's agricultural economy and plays a crucial role in supporting the livelihoods of fruit farmers. There has been limited research on the oxidative stress response of fruit trees subjected to herbicide stress, particularly in relation to soil herbicides. Future efforts should focus on enhancing the investigation of the oxidative stress response of fruit trees under soil herbicide stress. Additionally, it is essential to further analyze and explore the residual mechanisms of soil herbicides on fruit trees. Such research will provide a scientific theoretical foundation for fruit farmers aiming to maintain both quality and yield. In future research, it is recommended to concentrate on several critical areas: conducting an in-depth investigation into the mechanisms by which herbicide residues affect fruit trees, particularly regarding their impact on plant hormones such as gibberellins and growth hormones; examining the mitigation mechanisms of exogenous Ca, GSH, salicylic acid (SA), and other compounds on plants subjected to abiotic stress; and exploring the mechanisms underlying the remediation of herbicide-contaminated soils through the combined application of plant and microbial remediation technologies.

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