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Responses of Nonprotein Thiols to Stress of Vanadium and Mercury in Maize (*Zea mays* L.) Seedlings

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Abstract

The heavy metal pollution in ecosystems is of increasing global concern. This study investigated firstly the responses of phytochelatins (PCs), glutathione (GSH) and other nonprotein thiols (NPT) in maize seedlings under vanadium (V), mercury (Hg) or their combined stress. With V or V–Hg combined stress, the contents of PCs, GSH and NPT in shoots and roots both increased with increasing the V stress level, and reached the maximum when the V stress level was 5 mg/L. Accumulation of V in all organs of maize seedlings was in sequence as follows: roots ≫ shoots, while Hg inhibited the accumulation of V. Results show that the root of plant has stronger tolerance to V, and the low V stress level can promote the synthesis of thiol groups to reduce the toxicity of Hg for plants.

Keywords Maize seedlings · Accumulation · Nonprotein thiol · Glutathione · Phytochelatins

Pollution of agricultural ecosystems with heavy metal is of increasing global concern. Plants can reduce toxicity of heavy metals through a series of physiological and biochemical reactions, such as reducing the utilization of heavy metals, heavy metal compartmentalization, limiting the entry of heavy metals into cells, forming chelates with heavy metals, antioxidant enzymes detoxification (Sarwar et al. 2015; Verbruggen et al. 2009). Formation of heavy metals complex with thiol-containing species, such as glutathione (GSH), phytochelatins (PCs), cysteine (Cys), nonprotein thiols (NPT), et al. is one of the tolerance mechanism of plant response to heavy metal stress (Song et al. 2014). The chelates formed in the cytosol, or transported to the vacuole, can reduce the toxicity of heavy metals, and block the transfer of heavy metals to other organelles (Li et al. 2011; Sarwar et al. 2015). With increasing the Pb press level, the contents of NPT in *Sedum alfredii* H. increased, while the mass synthesis of GSH could lead to the decrease of Cys content with increasing stress time (Gupta et al. 2010). PCs was induced by heavy metal and synthesized by precursor GSH. It could be detected in roots and stems of wheat after Cd stress for 1 day (Sun et al. 2005). But there were also studies showing that the content of GSH in *Arabidopsis* decreased significantly with increasing the Cu press level, but did not induce the synthesis of PCs (Wójcik et al. 2009).

Vanadium (V) is considered as a potentially harmful pollutant just like mercury (Hg), lead and arsenic (Lazaridis et al. 2003). V is not considered as an essential trace element for plant growth, but excessive V will have toxic effects on plants, humans and animals (Boulassel et al. 2011; Kraepiel et al. 2009). For example, V will lead to lower shoot and root biomass of soybean seedlings, corn yield reduction, and plant height reduction (Olness et al. 2002; Wang and Liu 1999; Yang et al. 2017a). V distribution in plant were in sequences as follows: roots > leaves > stems, while plants can reduce the free heavy metals in the cell by immobilization of heavy metals to the cell wall, thereby reducing the toxicity of heavy metals (Hou et al. 2013). Hg is a highly toxic heavy metal. Because of its special physical and chemical properties, it is particularly easy to migrate and transform, thus diffusing into the environment and causing toxic effects on plants. Numerous studies have shown that after Hg enters the plant, it can affect plant absorption of mineral elements (Patra and Sharma 2000) and plant photosynthesis (Lu et al. 2000), and induce plants to produce large amounts of reactive oxygen free radicals, which cause lipid peroxidation damage to plants (Cho and Park 2000).

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Previous studies showed that, due to the drastically increased mining and smelting activities, 26.49% of soils were contaminated by V scattered in southwest of China, and V in the soil in Guangxi reaches up to 1338.6 mg/kg, with an average of 131.5 mg/kg (Yang et al. 2017b). Therefore, the absorption of V by plants is considered to be the major route from soil to biology (Tian et al. 2014). Sweet corn is a kind of food crop with high nutritional value and economic value, which is widely planted in southern China. The investigation of impact of V pollution on the growth and development of sweet corn in Guangxi can provide scientific basis for the risk assessment and prevention of V pollution in the environment. The responses of PCs, GSH and other NPT in maize seedlings under V, Hg or their combined stress, and accumulation of V, Hg in different organs of maize seedlings were investigated firstly, and the relation between low V stress level and the synthesis of thiol groups were also studied.

Materials and Methods

The maize seeds Xincaitian No.1, were obtained from Hubei Vegetable and Rice Agricultural Science and Technology Co. Ltd. All the agents used in Hoagland nutrient solution were analytically pure, and the water was super pure water (Ω = 18.25). The full and uniform maize seeds were selected after disinfection for 20 min with 3% H_2O_2, then washed repeatedly with water. The clean seeds were germinated in an oven at 28°C, then sowed in river sand that had been pre-treated. They were transferred to a plastic cup (8 cm × 4.5 cm) after the seedlings grew two leaves, and cultured with Hoagland nutrient solution. The solution was stressed with V and Hg (V was added as NH_4VO_3, AR, 99%, Macklin; Hg as $HgCl_2$, AR, 99.5%, Beijing Chemical Works) after the seedlings grew the third leaf. The solution was replaced every 3 days for 6 days. The experiment was set to 15 different dose levels, and three repeat tests were set up for each dose level (Table 1).

Approximately 1 g fresh tissue was added in a mortar, with 3 mL pre-cooled sulfosalicylic acid (SSA) of 50 g/L (SSA, 6.3 mmol/L diethylenetriaminepentaacetic acid, pH < 1) and a small amount of quartz sand, ground in ice bath until homogenized, then centrifuged at 10,000×*g* for 15 min at 4°C. The supernatant was collected and its volume was set to 5 mL, then refrigerated at 4°C. Contents of NPT was determined based on Keltjens and van Beusichem (1998). Each experiment result was the average of three repetitions. For determination of GSH, 1 g fresh tissue was added in a mortar, with 3 mL pre-cooled trichloroacetic acid of 50 g/L and a small amount of quartz sand, ground in ice bath until homogenized, then centrifuged at 10,000×*g* for 15 min at 4°C. The supernatant was collected and its volume was set to 5 mL, then refrigerated at 4°C. Contents of GSH was determined by DTNB colorimetric method (Keltjens and van Beusichem 1998). Each test result was the average of three repetitions. PCs content can be got from the relation: $PCs = NPT - GSH$.

Table 1 Different dose levels of V and Hg

Hg (mg/L)	V (mg/L)				
	0	1	5	10	20
0	0 + 0	1 + 0	5 + 0	10 + 0	20 + 0
5	0 + 5	1 + 5	5 + 5	10 + 5	20 + 5
10	0 + 10	1 + 10	5 + 10	10 + 10	20 + 10

Contents of V and Hg in plant were determined by ICP-MS (1288090 iCAP Qc, Thermo Fisher Scientific) after wet digestion with nitric acid and hydrogen peroxide. The analytical limits of detection and quantitation of V and Hg are 0.05 and 0.0035 ng/mL respectively. The percent recoveries from standards is 91.2–101.8. The determination results of V and Hg in samples were monitored by GB W10020 (GSB-11) and GBW10015 (GSB-6). All experiments were accomplished in three independent replicates. One-way ANOVA was performed on the test data to examine the difference between multiple means to determine whether the control factors had a significant effect on the test results. Statistical analysis was performed with DPS data processing system and Microsoft Excel 2010, and significant differences were compared by Duncan multiple comparison method ($p \leq 0.05$).

Results and Discussion

V and Hg concentrations in different parts of maize seedlings are shown in Table 2.

In Table 2, it showed that when the Hg stress level was 0 mg/L, there was still a small amount of Hg in maize seedlings, but it was significantly lower than that under Hg stress. A small amount of Hg in plants may come from maize seeds or hydroponic environment.

Under V, Hg or their combined stress, the accumulation of V and Hg in all organs of maize seedlings were in sequence as follows: roots ≫ shoots. With increasing the V stress level, the accumulation of V in shoots and roots increased, and the increase in the roots was much greater than that in the shoots. In condition of V–Hg combined stress, when the Hg stress level was constant, V content in roots showed a change trend that was first increased and then decreased with increasing the V stress level. With fixed Hg concentration of 10 mg/L and V concentration of 5 mg/L, V content in the roots reached the maximum value 20.02 µg/g, increased by 105.3% compared with that by V

Table 2 V and Hg concentration in different parts of maize seedlings (μg/g, FW)

Hg	V	V (μg/g, FW)		$(BF)_V$	$(TF)_V$	Hg (μg/g, FW)		$(BF)_{Hg}$	$(TF)_{Hg}$
		Shoots	Roots			Shoots	Roots		
0	0	0.04 ± 0.00e	0.37 ± 0.04d	–	0.12	0.30 ± 0.01b	0.65 ± 0.02b	–	0.46
	1	0.51 ± 0.03d	2.55 ± 0.24d	3.05	0.20	2.60 ± 0.47a	4.69 ± 0.21a	–	0.55
	5	0.90 ± 0.04c	9.75 ± 0.52c	2.13	0.09	2.74 ± 0.05a	4.63 ± 0.07a	–	0.59
	10	1.27 ± 0.08b	14.01 ± 0.23b	1.53	0.09	2.19 ± 0.03b	4.56 ± 0.08a	–	0.48
	20	2.43 ± 0.16a	19.89 ± 0.41a	1.12	0.12	2.83 ± 0.05a	4.60 ± 0.02a	–	0.62
5	0	0.31 ± 0.03d	1.53 ± 0.18d	0.37	0.20	4.39 ± 0.04c	19.84 ± 0.04c	4.85	0.22
	1	0.53 ± 0.03d	3.80 ± 0.31c	0.72	0.14	4.42 ± 0.12c	22.15 ± 1.07b	4.43	0.20
	5	1.14 ± 0.20c	17.85 ± 0.78a	1.90	0.06	18.97 ± 0.02a	132.15 ± 0.19a	15.11	0.14
	10	1.56 ± 0.16b	19.47 ± 0.58a	1.40	0.08	4.60 ± 0.05b	16.00 ± 0.10d	1.37	0.29
	20	1.95 ± 0.17a	16.82 ± 1.54ab	0.75	0.12	4.24 ± 0.00d	4.86 ± 0.12e	0.36	0.87
10	0	0.30 ± 0.01b	1.84 ± 0.08d	0.21	0.16	5.73 ± 0.08d	44.83 ± 0.03c	5.06	0.13
	1	0.46 ± 0.07b	4.96 ± 0.39c	0.49	0.09	6.50 ± 0.16c	45.34 ± 0.98c	4.71	0.14
	5	1.62 ± 0.19a	20.02 ± 0.15a	1.44	0.08	22.54 ± 0.32a	298.53 ± 1.03a	21.40	0.08
	10	1.66 ± 0.03a	19.78 ± 0.54a	1.07	0.08	8.41 ± 0.07b	63.31 ± 0.30b	3.59	0.13
	20	1.70 ± 0.05a	9.79 ± 0.42b	0.38	0.17	6.63 ± 0.03c	11.34 ± 0.08d	0.60	0.58

Values are means ± SD (n = 3). Different letters in the same column indicate a significant difference at the 5% level

Hg, V extraneous mercury and vanadium mg/L, *BF* bioconcentration factor, *TF* translocation factor

single stress. When V concentration was at 20 mg/L, the content of V in roots decreased to 9.79 μg/g, 50.8% lower than that under V single stress. The V content of maize shoots increased always with increasing the metal stress level, however, with fixed V level of 20 mg/L and Hg levels of 5 and 10 mg/L, the V contents in shoots decreased by 19.6% and 30.1%, respectively, than that with V single stress. When Hg stress level was constant, the Hg contents in roots and shoots increased first and then decreased with increasing the V stress level. With fixed Hg level of 10 mg/L and V level of 20 mg/L, the Hg content in roots decreased by 74.7% than that with single Hg stress. With single Hg stress, the bioconcentration factor of V ($(BF)_V$ in Table 2) in maize seedlings decreased with increasing the V stress level, while BF of V and Hg increased first and then decreased with V–Hg combined stress. In contrast, the transport coefficient (TF) of V showed a decreasing trend, while the TF of Hg decreased first and then increased.

NPT contents in shoots and roots all increased firstly and then decreased with increasing the V stress level (Fig. 1). They reached the maximum 4.00 and 4.62 μmol/g, increased by 27.9% and 38.8%, respectively, compared with the control when V stress level was at 5 mg/L. Then the NPT content decreased by 5.85% and 3.41%, respectively, with a fixed V level of 20 mg/L. When the Hg stress levels were at 5 and 10 mg/L, NPT contents in shoots and roots decreased with increasing the single Hg stress level. It decreased by 9.5% and 12.1% in the shoots, respectively, compared with the control.

Under V–Hg combined stress, the NPT contents in shoots and roots decreased with increasing the Hg stress level for each V stress level. With a fixed V level of 5 mg/L, NPT contents in shoots and roots reached the maximum under V–Hg

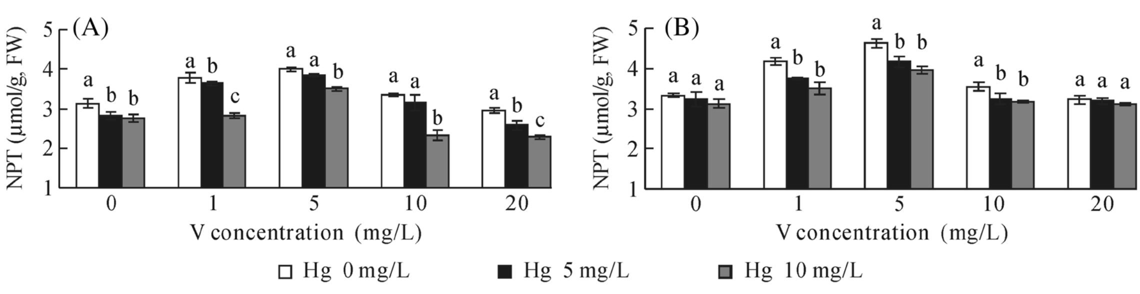

Fig. 1 Effects of different V and Hg stress levels on the contents of NPT in the shoots (**A**) and roots (**B**) of maize seedlings. Different letters in each individual experiment indicate significant difference between different Hg concentrations ($p < 0.05$)

combined stress, while Hg levels were at 5 and 10 mg/L, NPT contents decreased by 3.9% and 12.6% in shoots, 9.9% and 14.3% in roots, respectively, compared with that of the single V press. Moreover, with fixed V level of 20 mg/L and Hg levels of 5 and 10 mg/L, the NPT contents in shoots decreased significantly by 12.7% and 22.8%, respectively, compared with that of the V single stress.

The change of GSH content in maize seedlings (Fig. 2) was similar to that of NPT. The contents of GSH in shoots and roots both increased firstly and then decreased with increasing the single V stress level, and they reached the maximum 3.26 and 3.50 μmol/g, respectively, when the V stress level was at 5 mg/L, which were 19.6% and 25.1% higher than that of the control. However, the contents of GSH in shoots and roots changed little with increasing the single Hg stress level. Under V–Hg combined stress, the contents of GSH in the shoots and roots decreased with increasing the Hg stress level for each V stress level. Moreover, when the V stress level was at 5 mg/L, with fixed Hg levels of 5 and 10 mg/L, the GSH contents decreased by 3.8% and 7.5% in shoots, 4.1% and 6.7% in roots, respectively. However, the GSH content of maize seedlings was still higher than that of the control (with V, Hg stress level of 0 mg/L) at low V stress levels (1 and 5 mg/L).

Figure 3 shows PCs contents in maize seedlings under different V and Hg press levels. Regardless of V or V–Hg combined press, the contents of PCs in maize seedlings increased first and then decreased with increasing the V stress level, and reached the maximum with V level of 5 mg/L. With single V stress, PCs contents reached the maximum 0.74 and 1.14 μmol/g in shoots and roots, increased by 101.3% and 114.1%, respectively, compared with the control when V level was at 5 mg/L. Except the V level at 20 mg/L, PCs contents were significantly higher than that of the control at all V stress levels. Under the single Hg stress, the content of PCs in plant decreased significantly with increasing the Hg stress level. It decreased by 58.3% and 66.1% in shoots respectively, with fixed Hg levels of 5 and 10 mg/L. Under V–Hg combined stress, for each V press level, the contents of PCs decreased with increasing the Hg stress level. With fixed V level of 5 mg/L, Hg levels of 5 and 10 mg/L, the contents of PCs decreased by 4.8% and 24.8% in shoots, 22.1% and 38.9% in roots, respectively, in comparison with that of the single V stress.

Heavy metals in soil are harmful to the growth and development of crops. NPT is one of the main substances that alleviates or eliminates heavy metal stress in plants. It can form chelates with heavy metal ions.The chelates can be transferred to vacuoles and cell walls, which reduces free metal ions in the cells and blocks the migration of heavy metals between different tissues (Li et al. 2011). In addition, a large number of thiol groups in NPT are also important

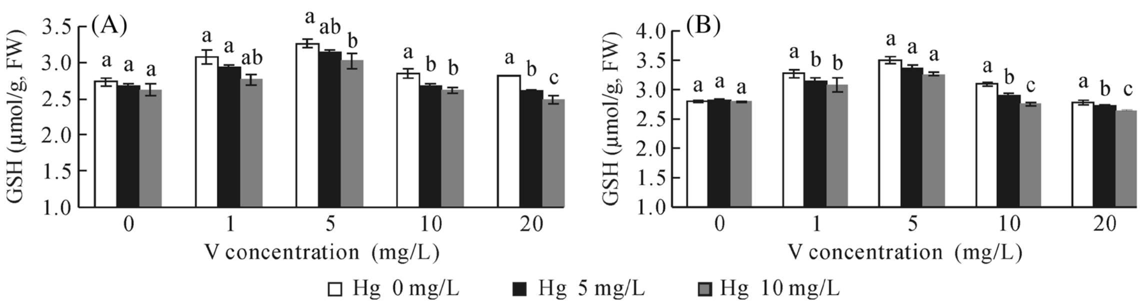

Fig. 2 Effects of different press levels of V and Hg on the contents of GSH in the shoots (**A**) and roots (**B**) of maize seedlings. Different letters indicate significant difference between different Hg concentrations ($p<0.05$)

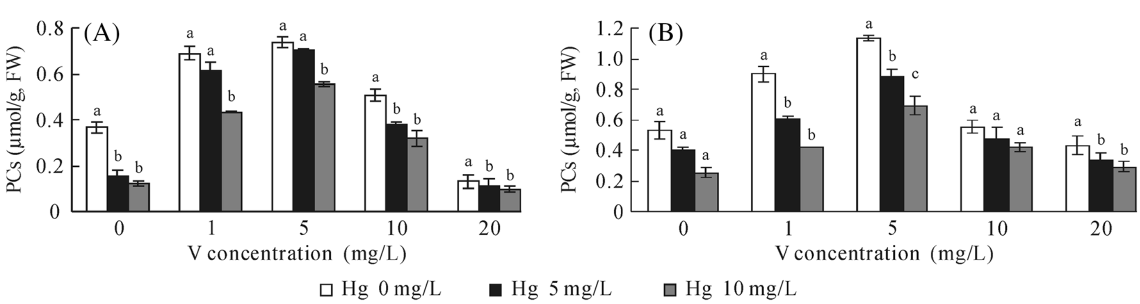

Fig. 3 Effects of different press levels of V and Hg on the contents of PCs in the shoots (**A**) and roots (**B**) of maize seedlings. Different letters indicate significant difference between different Hg concentrations ($p<0.05$)

antioxidants and signaling substances in plants. They can make antioxidant enzymes play a role in the detoxification of heavy metals (Jozefczak et al. 2012). Under single Hg press, the shoots of maize seedlings were sensitive to the change of Hg concentration, showing obvious Hg-poisoned effect. While there are more thiol groups combined with heavy metal ions in the roots, which makes the roots more tolerant to metal poisoning. The results showed that treatment with low V stress level could significantly promote the synthesis of NPT in maize seedlings. Whereas excessive V would have a toxic effect on seedlings and inhibit the synthesis of NPT, hindering the absorption of the necessary elements, such as magnesium, calcium and phosphorus, from soil or nutrient solution (Olness et al. 2000, 2001).

GSH is a low molecular weight peptide and an important precursor of plant for chelating heavy metals. The content of GSH is closely related to the tolerance of plants to various environmental stress. However, there was no significant difference in GSH contents between shoots and roots of maize seedlings under Hg single stress, which was consistent with the results of Majid et al. (2017). It may be due to the operation of GSH redox system in plants controls the decrease of GSH content in a certain range. Under V–Hg combined stress, the content of GSH in shoots and roots of maize seedlings decreased with increasing Hg stress level, indicating that the toxicity of metal to maize seedlings was enhanced, and the synthesis of GSH in plants was inhibited. It was found that, at certain low stress levels, content of GSH in maize seedlings increased with increasing metal stress level, suggesting that low stress levels of V and Hg could promote the synthesis of GSH in maize seedlings. It may be due to the chelates formed by the combination of thiol groups and heavy metals in maize seedlings were immobilized in vacuoles, and a new chelate was formed by amino acid cycle, thus the content of thiol groups was not significantly changed. This phenomenon was also found in lettuce and carnation plants, such as *Lactuca sativa* L. and *Dianthus chinensis* L. (Arnetoli et al. 2008). As shown in Figs. 1, 2 and 3, the contents of NPT, GSH and PCs in the shoots and roots of maize seedlings showed a downward trend with increasing single Hg stress level (V concentration was 0 mg/L). However, with different Hg concentrations (showed as blank, black or gray column in figures), the contents of NPT, GSH and PCs showed an upward trend with increasing V concentration (≤ 5 mg/L), and their contents were higher, in comparision with that by single Hg stress. It suggested that low concentration V could stimulate the defense mechanism of maize seedlings, and promote the synthesis of thiols compounds, so as to remove heavy metal ions and reduce the toxicity of Hg to plants.

PCs, like GSH, can form stable thiopeptide complexes with heavy metal ions, transporting metal ions from transport protein to extracellular, or store them in organelles such as vacuoles to reduce or eliminate heavy metal damage to plants. The results showed that the low V press level could induce plants to synthesize more thiol compounds through various physiological and biochemical pathways, while the high V stress level could inhibit the synthesis of PCs. It was also confirmed that low As press level promoted the synthesis of PCs in rice roots (Lemos Batista et al. 2014).

Under the V–Hg combined stress, the content of PCs in maize seedlings was significantly lower than that under single V stress. It suggested that Hg had a great effect on the content of PCs in maize seedlings. When Hg stress level was constant, the content of PCs increased firstly and then decreased with increasing the V stress level. The content of PCs was always significantly higher than that of single Hg stress (as showed by black or gray column in Fig. 3, $p < 0.05$), except that when V stress level was at 20 mg/L. The toxicity of Hg was alleviated by adding a certain amount of V, thereby enhancing the tolerance of maize seedlings to metal stress. The study also found that, regardless of V, Hg or their combined stress, the content of PCs in roots was always higher than that in the shoots, suggesting that plant roots are more tolerant to metal toxicity.

Regardless of V, Hg or their combined stress, the accumulation of metal in maize seedlings was mainly distributed in the roots of plants. Increase of the single V stress level would raise the absorption of V in maize seedlings, and the enrichment of V in the roots was more obvious. Low level of V–Hg combined stress improved the absorption and accumulation of V or Hg in roots and shoots. The BF and translocation factor (TF) (Arnot and Gobas 2006) can be used to investigate enrichment degree of heavy metals and migration ability of plants. With low V stress level (≤ 5 mg/L), the accumulation of V and the BF value were both increased, with a normal plant growth. However, with high V press level (> 10 mg/L), the BF value decreased, while the plant yellowed and withered, and the accumulation of V decreased. Regardless of single V stress or V–Hg combined stress, the total amount of V accumulation in maize seedlings increased with increasing the metal stress level, but the TF of V showed a downward trend, suggesting that there was a decreased ability of maize to transport V from roots to shoots, and the ability of holding V in maize roots increased, thereby reducing the migration of V from roots to shoots and alleviating the toxic effects of excessive V on plant growth.

In terms of V, Hg tolerance of maize seedlings, the roots of maize play more important role. In order to resist heavy metal stress, plants can inhibit the activity and bioavailability of toxic heavy metal ions by using rhizosphere microorganisms and some organic substances secreted by themselves to change the physical and chemical properties of the environment, such as the pH value, the redox potential and so on (Li et al. 2011). Moreover, vacuolar compartmentalization of the root tissues or suborganelles of plants act as indispensable component of heavy metal detoxification in plants, a large part of the heavy metal absorbed by plants from the environment is trapped in the cell walls of the root epidermal cells (Weng et al. 2012; Lyubenova et al. 2012). The results (Table 2; Figs. 1, 2 and 3b) showed that there were higher contents of heavy metals and sulfhydryl compounds in the roots of maize seedlings. The fixation ability of maize roots to V was stronger, which reduced the migration of V from roots to shoots, and alleviated the toxic effect of excess V on plant growth. So, in terms of V, Hg tolerance of maize seedlings, the roots of maize play more important role (Zhan et al. 2017).

In summary, under V, Hg or their combined stress, V stress in certain levels can promote the synthesis of thiol groups in maize seedlings and inhibit the absorption of Hg by plant, thus reducing the effect of Hg toxicity on plant. Hg inhibits the synthesis of thiol groups in maize seedlings and its toxicity increases with increasing the Hg concentration. The contents of PCs, GSH and NPT in maize increased with increasing the V stress level, and reached the maximum when the V stress level was 5 mg/L. The root of plant has stronger tolerance to V.

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