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REVIEW

Arbuscular mycorrhiza and plant chromium tolerance

Songlin Wu[1,2], Xin Zhang[1], Longbin Huang[2], Baodong Chen[1,3,*]

1 State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China
2 Environment Centres (CMLR), Sustainable Minerals Institute, The University of Queensland, Brisbane, Queensland 4072, Australia
3 University of Chinese Academy of Sciences, Beijing 100049, China

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ABSTRACT

Arbuscular mycorrhizal (AM) fungi are ubiquitous soil fungi that form symbiotic associations with most terrestrial plants. The growth and functions of AM fungi depend on carbohydrates supplied by the plants, in return, the fungi assist the plants to acquire mineral nutrients (e.g., phosphorus) from soil. The AM symbiosis also improves plant survival in various unfavorable environments, such as metal (loid) contaminated soil. It has been well demonstrated that AM symbiosis improved plant adaptation to Cr contamination, which would have a great potential in phytoremediation and ecological restoration of Cr contaminated soils. In this paper, we have reviewed the role of AM fungi in alleviation of Cr phytotoxicity and associated factors influencing plant Cr tolerance. AM symbiosis improves plant Cr tolerance through its direct roles in Cr stabilization and transformation and indirect roles via AM symbiosis mediated nutrient acquisition and physiological regulation. Future research on physiological and molecular mechanisms underlying Cr behavior and detoxification in AM symbiosis, as well as potential use of AM fungi in ecological restoration and agriculture production in Cr contaminated soils were also proposed.

1 Introduction

Chromium (Cr) is a common element widely used in electroplating, steel plating, dyeing, tanning, and leather production etc. However, Cr pollution has recently become a serious environmental problem in many regions and countries, because of excessive discharge of Cr-containing effluents resulting from industrial activities (Zayed et al., 1998). Chromium usually exists in oxidation status as Cr(III) and Cr(VI). Chromium(III) is chemically very stable with a low mobility. In contrast, Cr(VI) is highly mobile, much toxic and carcinogenic. At low concentrations, Cr(III) is beneficial to animal and human health as an essential component of glucose tolerance factor (GTF), whereas Cr(VI) is highly toxic and carcinogenic in human and animals (Losi et al., 1994).

In higher plants, Cr is not essential to plant growth and function. Exposure to Cr may cause tissue necrosis and limit chlorophyll production (Sharma et al., 2003; Singh et al., 2013). In particular, Cr is usually involved in electron transfer and induce production of reactive oxygen species (ROS) (e.g., hydroxyl radicals and superoxide radicals), resulting in oxidative stresses and damages to plant cells and tissues (Appenroth et al., 2000; Shanker and Pathmanabhan, 2004; Kováčik et al., 2013).

In natural environments, plant roots are usually associated with various soil microbes, such as arbuscular mycorrhizal (AM) fungi. AM fungi are ubiquitous soil fungi that form

* Corresponding author
E-mail address: bdchen@rcees.ac.cn (B.D. Chen)

symbiotic partnership with most terrestrial plants (Smith and Read, 2008). AM fungi may enhance root's ability and capacity to acquire mineral nutrients (e.g., phosphorus), while in return, they require carbohydrates from the host plants (Smith and Read, 2008; Jiang et al., 2017). In addition, the beneficial effects of AM symbiosis have also been reported on improving plant tolerance to various environmental stresses, such as drought, salinity and soil pollution (Lenoir et al., 2016; Wang, 2017). AM symbiosis was found to improve plant tolerance to heavy metal (e.g., Zn, Cu, Cd, As, Pb) contaminations (Leyval et al., 1997; Wu et al., 2013; Ferrol et al., 2016). However, the role of AM fungi in plant Cr tolerance and the underlying mechanism have not been investigated in detail. Recent studies showed that plant grew better in Cr contaminated soils when roots were colonized by AM fungi (Davies et al., 2002; Gardezi et al., 2003; Arias et al., 2010a, 2010b; Wu et al., 2014). This review has focused on the role of AM fungi in plant Cr tolerance, with the aim to elucidate direct and indirect involvements of AM fungi in Cr translocation and transformation in the plant–soil continuum.

2 AM symbiosis development in Cr contaminated soils

2.1 Reports on AM fungi in the natural Cr contaminated soils

Many studies showed that AM fungi were present in soils contaminated with heavy metal(loid)s, such as As (Sun et al., 2016), Cu (Chen et al., 2005a), Pb (Long et al., 2010; Zarei et al., 2010), Zn (Zarei et al., 2010) and Cd (González-Chávez et al., 2009). In Cr contaminated soils, AM fungi were found in the rhizosphere of *Ricinus communis* and *Conium maculatum* (Gil-Cardeza et al., 2014). Many AM fungal species were found to colonize soils contaminated by tannery waste (containing high concentrations of Cr), which belonged to six genera (*Acaulospora*, *Glomus*, *Gigaspora*, *Scutellospora*, *Paraglomus*, and *Ambispora*) (Nakatani et al. 2011). Besides, in some multi-metal (including Cr) contaminated soils, 59%–79% of the roots were reported to be colonized by AM fungi (Al-Ghamdi and Jais, 2012). These studies have suggested that various AM fungal species are capable of surviving and proliferating in Cr contaminated soil.

Although AM fungi are found to be present in Cr contaminated soils, their association with plants and their species diversity may depend on the magnitudes of Cr stress in the fungi-plant system. For example, Khan (2001) found that *Dalbergia sissoo*, *Acacia arabica*, and *Populus euro-americana* were colonized by a wide variety of AM fungal species from *Glomus*, *Scutellospora*, and *Araulospora* on the non-contaminated (reference) sites, whereas plants on the contaminated sites formed symbiosis only with *Gigaspora* spp. Besides, high Cr contents also decreased the species richness and diversity of AM fungi as indicated by decreased Shannon-Weiner index upon Cr contamination (Khan, 2001). Nakatani et al. (2011) also found that tannery waste with high Cr concentration decreased AM fungal spore density and influenced the mycorrhizal colonization of native plants. These studies showed that Cr contamination resulted in a selection pressure on AM fungal community in the soils.

2.2 Effects of Cr stress on AM symbiosis formation and development

Our previous study (Wu et al., 2014) found that 20 mg kg^{-1} Cr(VI) amendment decreased mycorrhizal colonization intensity in roots (M%) of dandelion (*Taraxacum platypecidum* Diels.) from 75% to 50%, and decreased M% of bermudagrass (*Cynodon dactylon* Linn.) from 30% to 16%. However, some studies also found that AM fungal colonization was unaffected by Cr contamination (Nakatani et al., 2011). The influence of metal stress on AM colonization depends on both contamination level and metal(loid) speciation in the soil. Low heavy metal level may stimulate AM symbiosis development, but high concentrations of metal(loid)s limit AM symbiosis development (Chen et al., 2005c; Zhang et al., 2005). In our study on dandelion, Cr addition below 10 mg kg^{-1} Cr(VI) had no influence on mycorrhizal colonization (or even increased M% value), while Cr level above 20 mg kg^{-1} significantly decreased M% value (Wu et al., 2014). Estaun et al. (2010) also found that moderate Cr contamination stimulated *mycorrhizal* colonization and performance of *Plantago lanceolata* (Estaun et al., 2010). In addition, Cr(III) and Cr(VI) affect AM symbiosis development in different manners (Davies et al., 2001; Arias et al., 2010a; Arias et al., 2010b). For example, Davies et al. (2010) found that mycorrhizal colonization and arbuscule abundance were more affected by Cr(VI) than Cr(III) in a soil trial, in which spiking 10 mg kg^{-1} Cr(III) only decreased arbuscular abundance (A%) from 97.3% to 81.3%, but 1 mg kg^{-1} Cr(VI) decreased it from 92% to 12.3%. It is no doubt that the toxicity of Cr(VI) in AM symbiosis development is much higher than Cr(III), because Cr(VI) causes much stronger oxidative stress (Shanker et al., 2005). These were consistent with our own experimental findings (Wu et al., 2014). Apart from oxidation status, different metal speciation results in differences in the activity and bioavailability of metal(loid)s, thus differently influencing AM colonization. For instance, Weissenhorn et al. (1995) found that ethylenediaminetetraacetic acid (EDTA)-NH_4OAc and $Ca(NO_3)_2$ extractable heavy metal did not influence mycorrhizal colonization, while Leyval et al. (1995) found that NH_4NO_3 extractable Cd and Zn showed negative effects on AM colonization. The same trends may also work for Cr.

3 AM effects on plant growth, Cr uptake and partitioning

3.1 Effects of AM symbiosis on plant growth and physiology under Cr contamination

Many studies showed that AM symbiosis improved plant growth in Cr contaminated soils. For instance, AM symbiosis dramatically enhanced plant growth of dandelion (Cr-sensitive

plant species) and bermudagrass (Cr-tolerant plant species) in soil contaminated with elevated levels of Cr(VI), and mycorrhizal dependence increased with increasing Cr levels of addition (Fig. 1) (Wu et al., 2014). The same type of responses was also found in *Helianthus annuus* L. in association with *Glomus intraradices* (Davies et al., 2001), *Cannabis sativa* in association with *G. mosseae* (Citterio et al., 2005), *P. lanceolata* in association with *Glomus intraradices* (Estaun et al., 2010) and Mesquite plants (*Prosopis* sp.) in association with *Glomus deserticola* (Arias et al., 2010a). Besides, AM fungi colonized plants exhibited better physiological traits than those non-mycorrhizal plants, when both exposed to Cr stress. For instance, mycorrhizal dandelion exhibited higher chlorophyll content in leaves than that of non-mycorrhizal dandelion under Cr(VI) contamination (Wu et al., 2014), while amylase activity in leaves of plants exposed to Cr stress decreased upon AM fungal colonization (Arias et al., 2010a). Some studies also showed that mycorrhizal plants had higher chlorophyll content, lower malondialdehyde (MDA) content, lower guaiacol peroxidase (GPX) and ascorbate peroxidase (APX) activity than the non-mycorrhizal plants under Cr contamination (Davies et al., 2001; Rahmaty and Khara, 2011). The interpretation of Cr effects on plant physiological traits is closely dependent on Cr speciation in contaminated soil. AM symbiosis was found to improve *A. prolifera* growth and gas exchange in Cr(III) - treated plants, but not Cr(VI)-treated plants (Singh et al., 2014).

3.2 Effects of AM symbiosis on plant Cr uptake and partitioning

Besides the effects on plant growth and physiology under Cr stress, AM symbiosis can also influence plant Cr uptake, accumulation and partitioning. Previous studies indicated that AM symbiosis decreased Cr concentrations in plants (Davies et al., 2001; Gardezi et al., 2005; Arias et al., 2010a; Arias et al., 2010b; Wu et al., 2014). This effect may be attributed to "growth dilution," as AM symbiosis increased plant biomass. This is similar to AM symbiosis effects on concentrations of other heavy metals in plants, such as Cu, Zn, As and Cd (Malcová et al., 2003; Ma et al., 2006; Chen et al., 2007a; Dong et al., 2008). However, in most cases, AM symbiosis increased total plant Cr uptake, because that AM plants had much higher biomass than nonmycorrhizal plants.

AM symbiosis also influences Cr partitioning in plants. In a recent study, it was found that AM symbiosis increased root Cr concentrations, but decreased shoot Cr concentrations in *Medicago truncatula* (Wu et al., 2018a). Thus AM symbiosis decreased Cr translocation from roots to shoots, and lowered Cr toxicity in plant shoots (Wu et al., 2014). Similarly, many studies with other heavy metals (such as Cu, Zn, Pb, As) have also showed that AM symbiosis enhanced metal stabilization in roots and limited metal translocation into shoots (Leyval et al., 1997; Christie et al., 2004; Bothe et al., 2010; Wu et al., 2013). The immobilization of heavy metals by AM roots limits Cr accumulation in shoots, thus relieving Cr toxicity in leaves. However, in some cases, AM symbiosis was found to have enhanced translocation of metals (including Cr) from roots to shoots (Davies et al., 2001, 2002; Citterio et al., 2005), indicating AM functions toward Cr partitioning may vary among plant and fungal species.

3.3 Factors that influence AM functions toward plant Cr uptake and tolerance

Many factors influence the roles of AM symbiosis in plant Cr tolerance and uptake, such as plant P nutrition status, Cr contamination level, plant and AM fungal species, and soil physicochemical properties. One of the key functions of AM symbiosis is to improve plant phosphorus (P) acquisition, while soil P supply in return significantly influences mycorrhizal formation and development (Karandashov and Bucher, 2005; Chu et al., 2013; Carbonnel and Gutjahr, 2014). Our recent study showed that the effects of AM symbiosis on Cr tolerance of *Medicago truncatula* was suppressed by P addition (Wu et al., 2018a). This pattern was also found with As in a study by Zhang et al. (2015), who reported that AM benefits on plant As tolerance became more pronounced under low P level. In these studies, the improved plant P nutrition suppresses the development of symbiotic structures (i.e., arbuscules) and associated mycorrhizal functions. Besides, improved P nutrition in plants may also improve plant resistance to metal(loid)s through direct interactions of P

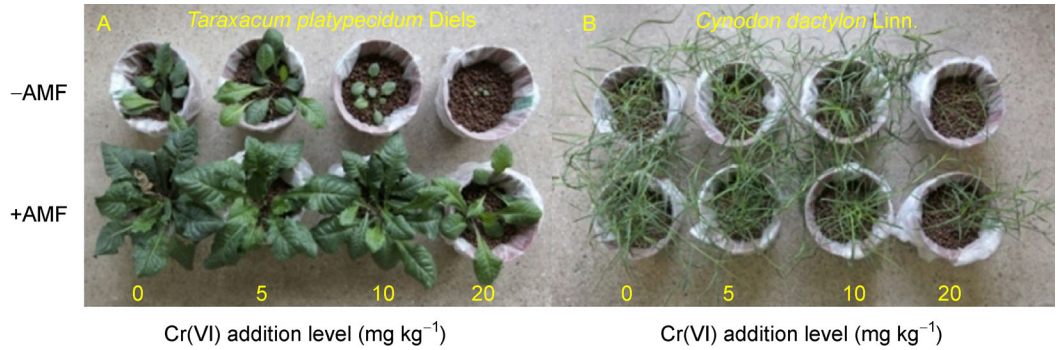

Fig. 1 Pictures of dandelion (*Taraxacum platypecidum*) (A) and bermudagrass (*Cynodon dactylon*) (B) grown in soils amended with different Cr(VI) levels with/without AMF inoculation. "+ AMF" represents inoculation treatment; "-AMF" represents non-inoculation control.

with metal(loid)s (Du et al., 2014; Singh et al., 2015; Arshad et al., 2016), leading to the reduced dependence of plants on AM symbiosis for surviving the metal contaminated environments.

Chromium is nonessential to plant growth. AM symbiosis lowers Cr uptake by plants even at very low Cr concentration in soil. This is contrary to plant uptake of essential metal elements such as Cu and Zn to AM symbiosis. AM symbiosis usually increases plant uptake of Cu and Zn under low concentrations, but decreases their uptake at high concentrations in contaminated soil, which has been confirmed by meta analysis (Audet and Charest, 2007).

The functions of AM symbiosis in plant uptake of metals vary among different plant species with different heavy metal tolerance. Our study indicated that AM symbiosis significantly decreased Cr concentrations in both shoots and roots of dandelion, while showed no influence on that of bermudagrass (Wu et al., 2014). In comparison, AM symbiosis increased Pb translocation factor in *Kummerowia striata*, *Ixeris denticulate* L. and *Ecrusgallivar mitis*, while had no effects on that of *Lolium perenne* L. and *Trifolium repens* (Chen et al., 2005c). Plant species have no strict specificity for AM fungi, and one plant species may form symbiosis with several AM fungal species (Smith and Read, 2008). However, this does not mean that these AM fungi would have the same functions in the symbiosis with plant roots. Different AM fungal strains may function differently in plant metal uptake and partitioning. For example, in As contaminated soil, *Glomus mosseae* and *Glomus etunicatum* decreased shoot As concentrations, while *Glomus constrictum* had no influence on shoot As concentrations (Yu et al., 2010). Besides, different isolates of the same AM fungal strains may also influence plant metal uptake and tolerance differently. For instance, *G. mosseae* isolated from Cd contaminated soils increased shoot Cd concentration in *Trifolium repens*, while *G. mosseae* isolated from non-polluted soils had no influence on plant Cd uptake (Biro et al., 2009). Based on the above studies on As and Cd, it is expected that different AM fungal species influence plant Cr uptake and tolerance differently.

Soil physicochemical characteristics can also influence AM functions. For instance, soil pH influences AM functions through influencing AM symbiosis development, as AM fungi and their association with plants may vary with different soil pH (Coughlan et al., 2000). For example, *Glomus* spp. prefer pH 5-9, while *Acaulospora, Gigaspora, Scutellospora* spp. are more active at pH < 7 (Yu and Zhao, 2008).

4 Mechanisms underlying the enhanced plant Cr tolerance by AM symbiosis

AM symbiosis can improve plant performance under Cr contamination through direct and indirect pathways. In the direct way, AM symbiosis influences Cr behavior in the rhizosphere or plant roots and thus influences its uptake and toxicity; in the indirect way, AM symbiosis indirectly enhances plant resistance to Cr stress through improvement of plant nutrition or regulation of Cr defense system in host plants.

4.1 Direct involvements of AM fungi in Cr translocation and transformation

4.1.1 Cr bioavailability changes in the mycorrhizosphere

AM fungi influence rhizosphere micro-environment through exudation of low molecular weight acids (LMWA) or glomalin related soil protein (GRSP–a glycoprotein with repeated monomeric structures), altering metal bioavailability. In addition, exudates (e.g., GRSP) may also complex with metals, thus influencing metal speciation. For example, acid-extractable Cr concentration in the rhizosphere decreased in soils with AM fungal inoculation (Wu et al., 2014). Similarly, studies on Pb and Zn showed that AM symbiosis increased organic combined Zn concentration, while decreased crystalline and residue Zn concentrations (Subramanian et al., 2009), increased exchangeable Pb and organic Pb but decreased Fe/Mn oxidized Pb and cabonate Pb in soils (Zhang et al., 2012).

GRSP has a great potential in complexation of heavy metals, such as Cr, Cu, Pb and Zn (Nichols, 2003; González-Chávez et al., 2004). For example, Gil-Cardeza et al. (2014) investigated GRSP concentrations and their relationship with Cr in a Cr contaminated industrial and urban soil and found that much Cr(III) was complexed with total glomalin related protein (T-GRSP), indicating the possible role of GRSP in stabilization of Cr in the soil. Cornejo et al. (2008) found that GRSP in the rhizosphere showed a positive relationship with Cu and Zn concentrations in the soil. Besides, GRSP-Cu in the soils accounted for 1.4%–27.5% of the total Cu (Cornejo et al., 2008). Vodnik et al. (2008) found that GRSP-complexed pool contained 690–23400 mg kg^{-1} Pb, accounting for 0.8%–15.5% of the total Pb in the soil.

GRSP complexation with metals may be attributed to strong chemical bonding rather than electrostatic adsorption. González-Chávez et al. (2004) found that GRSP was tightly bound with Cu, which could not be broken down by 50 mM citric acids, boric acid or chloride acid. However, the traditional method of extraction has their drawbacks, as extraction process may also cause metal transformation. These limitations of conventional methods can be overcome by *in situ* analysis of metal speciation in the rhizosphere using advanced spectroscopic methods such as synchrotron based X-ray florescence spectroscopy (XRF) and X-ray absorption spectroscopy (XAS).

4.1.2 Cr translocation and transformation in plant roots as influenced by AM symbiosis

AM fungi influence metal distribution and speciation, consequently alleviating metal phytotoxicity. Arias et al. (2010b) found that mycorrhizal inoculation favored Cr accumulation in the vascular system, and reduced Cr translocation into shoots. By using synchrotron based X-ray fluorescence microscopy (micro-XRF), Wu et al. (2016a) revealed that AM symbiosis altered Cr distribution in main roots, resulting in Cr distribution mainly in epidomeris of the mycorrhizal roots, in

contrast to nonmycorrhizal roots in which Cr was mainly distributed in vascular bundles. These suggest that mycorrhizal symbiosis may reduce Cr transport from lateral roots to main roots, and subsequent Cr transport from roots to shoots. Chromium was found to be transported from roots to shoots via vascular bundles (Skeffington et al., 1976). This may explain why AM symbiosis decreased Cr translocation factor (Wu et al., 2016a).

A further study indicated that mycorrhizal fungi compartmented Cr in fungal structures inside the roots by using synchrotron based scanning transmission soft X-ray microscopy (STXM) (Wu et al., 2016b). Chromium may be retained in fungal structures, resulting in reduced amount of Cr transport from fungi to cytoplasm of plant cells and lowered Cr phytotoxicity. Further study showed that Cr was possibly complexed with phosphate or histidine inside the fungal structures as revealed by synchrotron based XAS (Wu et al., 2016b). AM symbioses are well known to be functional in assisting plant P acquisition because mycelium assist P absorption from distance and transport it into arbuscules (the symbiotic interface between plants and AM fungi) (Kuga et al., 2008). As a result, it may be hypothesized that phosphate may precipitate Cr, contributing to the retention of Cr in fungal structures.

Apart from Cr, many cation metals (such as Cu, Cd, Pb and Zn) were also found to be precipitated in fungal structures within plant roots. For instance, as revealed by synchrotron based micro-XRF, Nayuki et al. (2014) and Chen et al. (2018) found that Cd mainly accumulated in fungal structures inside mycorrhizal roots. Some studies even found that U was located in intraradical mycelia or vesicles inside mycorrhizal roots (Weiersbye et al., 1999). By using Particle-induced X-ray emission (PIXE), Orłowska et al. (2011) also found that Ni was accumulated in fungal structures inside AM roots of a Ni hyperaccumulator (*Berkheya coddii* Roessler). A recent study by Wu et al. (2018b) observed that Zn was mainly immobilized by arbuscules in the mycorrhizal maize roots grown in Zn/Pb contaminated soils. These studies collectively revealed that mycorrhizal stabilization of heavy metals may be a common strategy for plants capable of forming AM symbiosis to tolerate heavy metals in soil.

In addition, AM symbiosis also influences Cr transformation in plants through redox changes to reduce Cr(VI) to Cr(III) once being taken up by roots. In most studies, Cr(III) was found to be the main Cr species inside the plant roots, which is present in the form of Cr(III)-carboxyl groups (Aldrich et al., 2003). AM symbiosis may also further influence Cr(III) speciation inside roots by decreasing the percentage of Cr (III)-systeine and Cr(III)-acetate analogs, while increasing the proportions of Cr(III)-phosphate and Cr(III)-histidine (Wu et al., 2018a). The changes in Cr speciation in roots by AM symbiosis may have resulted from direct involvement of fungal structures or the stimulation of root metabolism by AM symbiosis. In summary, Cr in the mycorrhizal roots tended to exist in a more stable form than that in nonmycorrhizal roots, enhancing Cr stabilization in roots and contributing to the enhanced plant Cr tolerance. Similar roles of AM symbiosis in metal transformation in plants were also reported for As. For instance, AM symbiosis can facilitate Dimethylarsinic acid (DMA) formation in plant shoots (Zhang et al., 2015). Yu et al. (2009) also found that AM symbiosis can restrain As(V) reduction to As(III), and reduce As(III) concentrations, which may due to the decreased activity of As reduction enzymes.

4.1.3 Cr uptake and stabilization by extraradical mycelium

The formation of AM symbiosis leads to the production of extensive extraradical mycelia in rhizosphere. The mycelium is usually much finer than roots, with a diameter of up to several micrometers, possessing high capacity to absorb nutrients and heavy metals. By using a three-compartment cultivation system, it was demonstrated that extraradical mycelium (ERM) absorbed and transported Cr to mycorrhizal roots from distance, but might not translocate these Cr from roots to shoots, and therefore contributed to Cr stabilization in roots and relieved Cr phytotoxicity (Wu et al., 2016a).

By using a compartmented root-organ cultivation system (Fig. 2A), we found that Cr can be taken up by AM fungal mycelium and transported to mycorrhizal roots (Wu et al., 2015). To further study whether the uptake of Cr by mycelium was active or passive, we inhibited the activity of mycelia by formadehyde or 2,4-dinitrophenol (DNP). Interestingly, we found that the limitation of fungal myceliuim activities resulted lowered Cr uptake and transport by mycelium. These suggest that the uptake and transport of Cr was mainly via an active uptake pathway.

Other studies also found that AM fungal mycelia actively took up and transported Zn (Chen et al., 2003), As (Chen et al., 2007b), and even U (Rufyikiri et al., 2003). The uptake of nonessential heavy metals is mainly through the transporters for essential nutrients. For instance, fungi take up As(V) through P transporters (Catarecha et al., 2007) and Cr(VI) through sulfate transporters (de María Guillén-Jiménez et al., 2008; Holland and Avery, 2011) or phosphate transporters (de Oliveira et al., 2015).

Although AM mycelia take up significant amounts of metals, the absorbed metals may not be completely transported into root cells. This may be due to the compartmentation of metals by fungal structures inside roots, or due to stabilization of metals by extraradical mycelium. In fact, some studies found that mycelium had a great capacity to immobilize heavy metals (e.g., Cu, Zn) (Chen et al., 2001). Similarly, by using root-organ cultivation system, it was found that 70% of Cr taken up by AM fungi was stabilized in extraradical mycelium, leading to reduced Cr transport to roots and alleviated Cr phytotoxicity (Wu et al., 2015).

4.1.4 Cr translocation and transformation by AM fungal mycelium

After absorption by AM fungi, Cr(VI) can be completely reduced to Cr(III), which is catalyzed by chromate enzyme activities or some molecules (such as carboxyl groups, thiols)

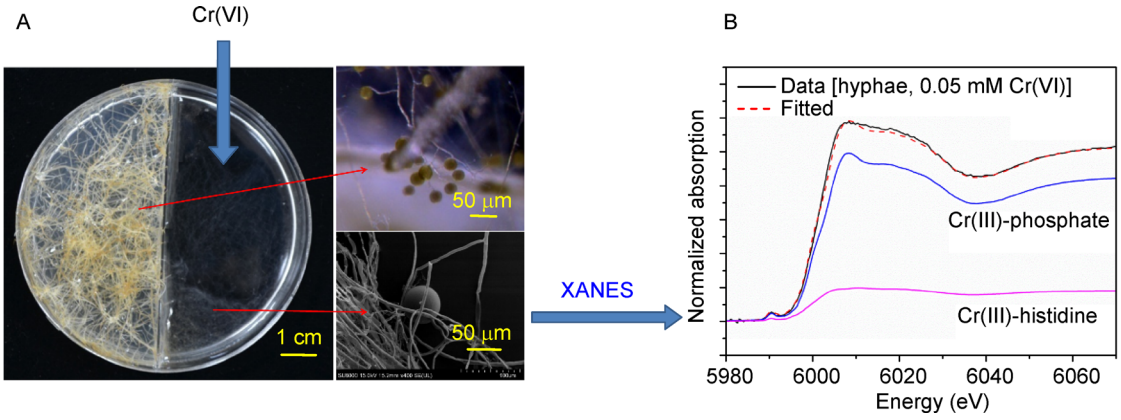

Fig. 2 Diagram showing uptake and transport of Cr by AM fungal mycelium in a root-organ cultivation system (A), as well as the Cr speciation in AM fungal mycelium as revealed by synchrotron based X-ray absorption near edge spectroscopy (XANES) analysis (B).

acting as electron acceptors (Wu et al., 2015). However, when the metabolic activity was limited by DNP or HCHO, Cr(VI) may be completely reduced to Cr(III) in 4 days interaction with mycelium. This indicates that Cr(VI) may also be reduced partially and non-metabolically.

The XAFS analysis further showed that Cr(III) was subsequently precipitated mainly by phosphate analogs and Cr(III) histidine (Fig. 2B). Further examination using STXM indicated that those Cr may precipitate on mycelium surface as particles (Wu et al., 2016b), in which Cr correlated with P. Chromium K edge XAFS confirmed that phosphate contributed to Cr stabilization on mycelium surface (Wu et al., 2016b). When the mycelium activity was inhibited by DNP or HCHO, Cr(III)-histidine in mycelia tended to disappear (Wu et al., 2015). This suggests that that Cr(III)-histidine analogs may exist inside the living hyphae or fungal structures in roots (i.e. arbuscules, intraradical mycelium, vesicles etc.). Cr(III) may be transported in the form of Cr(III)-histidine in the mycelium. This is in contrast to Cr(III)-phosphate which precipitates on hyphal surface. This may be due to the functions of extracellular polymeric substances (EPS) exudated by the fungi. In a recent study, we found that AM fungi produced numerous EPS on the mycelium surface upon Cr(VI) stress and Cr mainly existed in these EPS (Wu et al., 2016b). These suggested that EPS potentially contributed to Cr(VI) reduction and immobilization on fungal surface. Taken together the results of STXM and XAFS analysis, it is concluded that AM fungi can adsorb and reduce Cr(VI) to Cr(III), and complex Cr (III) mainly by phosphate groups on mycelium surface resulting from EPS produced by AM fungi in response to Cr (VI) stress. Beside, a small proportion of Cr may be taken up and transported into fungal structures inside roots possibly in the form of Cr(III)-histidine. Other heavy metals can exist in the vesicles and cell walls of the fungi (Weiersbye et al., 1999; González-Guerrero et al., 2008). By using Energy-dispersive X-ray spectroscopy (EDS), González-Guerrero et al. (2008) found that either in spores or mycelium, metal was accumulated in cell walls, but less in cytoplasm (González-Guerrero et al., 2008). Further study should pay more attention to subcellular Cr localization and speciation in the AM symbiosis.

4.2 Indirect involvements of AM fungi in plant Cr tolerance

4.2.1 AM symbiosis improves plant mineral nutrition under Cr contamination

Cr stress may reduce plant nutrient uptake and cause nutrient deficiency, because Cr uptake competes for transporters of essential nutrients, such as sulfate and phosphate transporters (Holland and Avery, 2011). For examples, Cr(VI) exposure may result in S or P deficiencies (Pereira et al., 2008; de Oliveira et al., 2015). However, AM fungi may assist nutrient uptake by plants, such as P (Karandashov and Bucher, 2005), N (Govindarajulu et al., 2005), or S (Allen and Shachar-Hill, 2009), alleviating nutrient deficiency in infertile soil. In fact, we found that AM symbiosis can dramatically increase P and S and N concentrations in plants under Cr(VI) contaminations (Wu et al., 2014). The improvement of nutrition status of plants by AM symbiosis may enhance plant tolerance to Cr toxicity. For example, Chen et al. (2007) found that the mycelium of *G. mosseae* preferred to take up P over As (Chen et al., 2007b). While at the same time, under U contamination AM mycelium improved P uptake by barley plants from phosphate rock containing U (Chen et al., 2005b). In most cases, AM symbiosis enhances plant growth through increasing nutrient uptake, resulting in reduced metal concentrations in plants, generating “growth dilution effects” (Chen et al., 2007a; Dong et al., 2008).

4.2.2 AM symbiosis regulates plant physiological and molecular processes for Cr detoxification

AM symbiosis may regulate molecular or physiological processes in plants to deal with Cr stress. Heavy metals usually cause oxidative stress by producing reactive oxygen species (ROS), while AM symbiosis may stimulate antioxidative processes in plants and thus help plant surviving

heavy metal stress (Yang et al., 2015; Azcón et al., 2009). Our recent study showed that AM symbiosis dramatically upregulated expression of high affinity sulfate transporter genes *MtSULTR1.1* and *MtSULTR1.2* in roots of *Medicago trunctula* plants and improved S uptake by plants under Cr(VI) contamination. Besides, AM symbiosis also systematically regulated S metabolism as one of the mechanisms of Cr detoxification, contributing to the relief of oxidative stress caused by Cr(VI) (Wu et al., 2018a). Similarly, some studies also found that AM symbiosis increased NP-SH, GSH and PCs levels in plants, which complexed with heavy metals and alleviated metal toxicity (Garg and Chandel, 2012). By proteomic analysis, some studies (Repetto et al., 2003; Aloui et al., 2009) also found that AM symbiosis systematically regulated functional proteins (e.g., annexin or cyclophilin etc.) to enhance plant tolerance to Cd through various ways including alleviate oxidative stress. As Cr causes oxidative stress, it is expected that AM symbiosis may also regulate plant metabolisms to alleviate Cr toxicity.

In conclusion, AM fungi play an important role in plant Cr tolerance. On one hand, AM fungi can directly immobilize Cr in the rhizosphere, or stabilize Cr in fungal structures through precipitation of Cr on fungal surface or compartmentation of Cr in fungal structures inside plant roots. Histidine and phosphate may be the main groups that contribute to the mechanisms of AM fungi to detoxify Cr in plants. On the other hand, AM symbiosis can indirectly enhance plant tolerance to Cr through improvement of plant mineral nutrition status or through regulation of physiological and molecular processes of plants to enhance plant capacity to resist Cr (Fig. 3).

5 Perspectives

(1) Revealing physiological and molecular mechanisms underlying Cr behavior and detoxification in AM symbiosis

Previous studies have uncovered the processes of Cr translocation and immobilization by AM symbiosis. However, the molecular mechanisms controlling the translocation and transformation of Cr in the symbiotic interface remain unclear. Further investigations are required to unravel the way by which AM fungi take up Cr(VI) or Cr(III) and associated transporters, as well as the physiological and molecular mechanisms underlying the Cr tolerance of AM fungi. In future, the combined use of advanced microspectroscopic methods (such as synchrotron based XRF, XAS, STXM and NanoSIMS etc.) with newly developed physiological and molecular technologies (such as advanced transcriptomics, proteomics and metabolomics) will be of great value for uncovering the mechanisms of Cr behavior at the symbiotic interface, as well as the mechanisms of Cr tolerance of AM fungi.

(2) Potential use of AM fungi in ecological restoration and agriculture production in Cr contaminated soils

Considering the important role of AM symbiosis in plant Cr tolerance (Davies et al., 2001; Wu et al., 2014), AM fungi would be of great value in revegetation or phytostabilization of

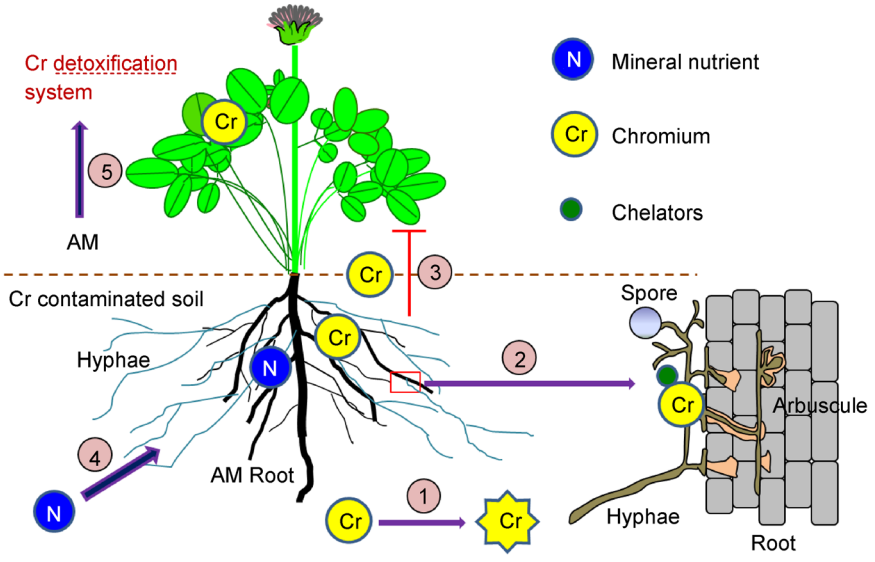

Fig. 3 Schematic representation of mechanisms underlying the enhanced plant tolerance to Cr by AM symbiosis. Key processes controlling Cr transformation and translocation are indicated by numbers. “1” represents the complexation of heavy metal by secretions (such as glomalin, or small acid organic compounds) produced by mycorrhizal roots, or alters metal speciation and bioavailability through influencing chemical characteristics of rhizosphere soils; “2” represents the immobilization of Cr in AM fungal structures including extra- and intraradical fungal structures (e.g. mycelium, arbuscules, vesicles, etc) via complexation with phosphate nitrogenous or carboxylic ligands; “3” represent the reduced Cr translocation from roots to shoots by AM symbiosis; “4” represents that AM symbiosis assists plant nutrient acquisition (such as phosphorus, nitrogen and sulfur uptake); “5” represents the AM regulated molecular or physiological processes in plants for Cr detoxification.

Cr contaminated soils. As AM fungal structures can stabilize Cr in the soils and reduce Cr mobility (Wu et al., 2015; Wu et al., 2016b), therefore AM fungi also has a great potential in assisting phytostabilization of Cr. In addition, AM symbiosis favors rhizosphere microbial communities, accelerating the recovery of rhizosphere ecosystem (Johansson et al. ,2004; Miransari, 2011). From these benefits, AM fungi may be used in improving safe agricultural production in Cr contaminated farmlands, as it can decrease Cr translocation from roots to shoots and reduce Cr accumulation in edible parts of crops (Wu et al., 2014; Wu et al., 2016a). However, most previous studies have been conducted in the laboratory (highly artificial growing conditions), while few studies focused on the AM fungal functions in the field. In fact, due to complex climate and soil chemical/biological conditions in the field, the results of glasshouse work may not be easily extended into the field practices. For example, Dietterich et al. (2017) found in a field experiments that AM colonization had little effects on plant heavy metal uptake, which was much different from many previous laboratory work. Therefore, future studies should further investigate the role of AM fungi in plant surviving Cr contamination under field conditions.

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