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Basis for the Breeding of Low-Cd Wheat Varieties

Abstract

Cadmium is a non-essential element for plant growth and has a strong toxicity, which seriously affects plant growth and development.Compared with other heavy metals, cadmium is more easily absorbed and accumulated by wheat, which poses a serious threat to human health. The paper reviewed the effects of cadmium on the growth and development of wheat, the absorption, transport and distribution of cadmium in wheat, the tolerance mechanism and the molecular biological level of cadmium in wheat. To provide strategies and possible schemes for breeding wheat varieties with low cadmium accumulation.

Keywords: Wheat; Cadmium toxicity; Absorption; Transport; Distribution; Tolerance mechanism; molecular mechanisms.

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Introduction

Heavy metal polluted soils have been a serious problem to crop production worldwide [1-4]. Among heavy metals, cadmium (Cd) is highly toxic to plants and even Cd is considered as one of the most toxic elements released into environments even at very low concentrations due to its non-essentiality nutrient element in living organisms [5].The development of industry and agriculture have led to the increase of Cd content in agricultural soil environment [6]. Cd is released into the soil environment through application of phosphate fertilizer, animal manures, waste water and garbage from metal industry and cement industry, Cd-contaminated sludge and fertilizer [7,8]. Due to the high mobility of Cd in soil, the concentration of Cd above the critical level can seriously hinder the growth of plants and may cause cell death by interfering with various biochemical and physiological processes, such as decreased the intracellular space and chloroplasts, stimulated the production of reactive oxygen species (ROS), leading to cell membrane damage and destruction of cell organelles [9-11]. Plants growing in Cd-contaminated soil Cd-contaminated food is the main source of Cd entry to humans via the food chain, Thus Cd may be an element with high residue, difficult to degrade and easy to accumulate, which may seriously threaten the health of human beings and animals [12-15].

Cereal crops such as wheat, rice and maize are the main food crops in the world. Among them, wheat is the source of staple food for more than half of the world's population, and the annual world output is about 650 million tons, Therefore, wheat products are the main source of Cd intake by human. Compared with other cereals, wheat mainly accumulates Cd through the root system, and migrates to the above-ground part, and finally accumulates in the wheat grain [16,17]. Lopez-Luna reported that Cd is more toxic to wheat than other toxic metals. Cd toxicity reduces the absorption and transport of essential elements in wheat. The root growth and morphology of wheat is seriously affected, resulting in the decrease of plant growth, biomass and grain yield [18,19].

The problem must be confronted with reducing Cd-contaminated to be solved urgently. In recent years, agronomic management practices including plant growth regulators (PGRs), mineral nutrients, biochar, fertilizers, compost, crop rotation, cropping patterns, and microorganisms have been used to reduce Cd uptake and toxicity in wheat. However, these measures could pose some problems, such as large investment, high energy consumption, difficult operation and easy to produce secondary pollution [20]. Therefore, it is of great significance to study the molecular mechanism of Cd absorption, transport and efflux of wheat and the creation of wheat varieties with low Cd accumulation for ensuring food security and food safety. The objective of the present review is to discuss the Cd on wheat growth and development, Cd toxicity and tolerance mechanisms and some possible breeding strategies to alleviate Cd toxicity in wheat.

Methods

Effects of Cd on Growth and Development of Winter Wheat

Effects on seed germination and seedling growth of winter wheat : The seed germination and seedling stage are the beginning of plant life cycle. The first organ that comes into contact with Cd in soil is the seed. Therefore, seed germination is the earliest stage to perceive Cd toxicity. In general, low concentration of Cd has little inhibitory effect on seed germination, and even promotes germination of some wheat varieties. With the increase of treatment concentration, Cd had a very strong inhibitory effect on seed germination, which is significantly inhibiting the growth of shoot and root system of wheat seedlings, and the accumulation of dry matter also decreased. The study showed that the treatment concentration of 0.03 mg/kg Cd promoted the growth and dry matter accumulation of wheat. When the concentration of Cd was over 0.03 mg/kg, the growth and dry matter accumulation of wheat were significantly inhibited [21]. The accumulation of Cd near the growing point of radicle leads to the inhibition of amylase activity and starch hydrolysis in wheat cotyledon. As a result, the nutrients required for the growth of radicle and hypocotyl are not satisfied and the elongation is inhibited. Sfaxi-Boushbih A reported that the transport of mineral elements and carbohydrates from cotyledon to cotyledon and radicle of soybean was inhibited, which affected the germination and growth of seeds [22].

Effects of Cd on the growth of wheat organs: Cd toxicity increases with the increase of concentration. Within a certain range of concentration, Cd can promote the growth of some plants. However, with the increase of Cd concentration, the growth and development of plants are significantly inhibited by Cd, which is generally manifested as short stature of plants, dechlorination of leaves, slow growth and decline of biomass. Cd affects plant photosynthesis, membrane system, enzyme system *in vivo* and metabolism related to the physiological activities, which eventually show a decline in growth and yield. Under Cd toxicity, the reoperation amount and reoperation rate of pre-flowering storage substances in wheat leaves and other vegetative organs were significantly reduced, and the thousand seed weight also decreased with the increase of treatment concentration. Sun Dan [23] reported that the root, stem and leaf growth, spike length and yield of wheat were significantly reduced after treated with tailings. Cd toxicity inhibited the differentiation of reproductive organs during the period from young spike differentiation to heading, resulting in the caryatization and abortion. After heading stage, Cd toxicity interferes with and inhibits the synthesis and accumulation of chlorophyll, soluble sugar, soluble protein and starch in wheat flag leaves, and interferes with the migration and redistribution of nutrients in the wheat.

Cd Uptake, Transport and Distribution by Wheat

Cd uptake by wheat: In general, Cd is absorbed into plants through the root system the absorption of Cd by wheat roots at low Cd concentration was an active absorption process, and the energy required for transport was provided by the hydrolysis of ATP produced in the metabolic process, which was mainly reflected in the highly selective absorption of ions and the energy consumption mechanism [24]. There are various carrier proteins in plant root system, and each ion combines with its corresponding carrier protein (transporter) to form ions. Carrier complexes that transport ions into cells by means of metabolic energy. At high Cd concentrations, Cd absorption is a passive process involving diffusion, ion exchange, and chelation. Cation exchange is Cd between the plant root growth medium and the surface of a reversible migration process. This part of the absorption of Cd can be without Cd solution desorption from the epidermal cell walls come down. The other part is combined into irreversible macromolecules, and then Cd is absorbed in the root surface. The longer combined into irreversible the higher the proportion of large molecules [25]. The diffusion process is the process of Cd entering the cell through the cell wall and cell membrane, which is independent of energy and depends on the concentration difference between the medium. Root exudates and a series of changes induced by root exudates also affect the uptake of Cd in wheat. Root exudates affect the uptake of Cd in wheat by influencing PH and Cd availability.

In addition, it has been reported that the variation of Cd uptake in overground part of wheat at different growth stages was as follows: the late growth period was larger than the early growth period, the growth flourishing period was larger than the slow growth period, and the reproductive growth period was larger than the vegetative growth period. The Cd absorption amount and rate in grouting stage, jointing stage and heading stage were significantly higher than those in other periods. Cd absorption was significantly positively correlated with dry matter weight gain (r=0.91633), and absorption rate was significantly positively correlated with dry matter weight gain (r=0.8003) [26].

Cd transport by wheat: The accumulation of Cd in wheat depends on the transport of Cd from root to stem, while the accumulation of Cd in seeds depends on the transport of Cd from root to stem and the direct transport of Cd from root to stem to grain through the transport of lignin and phloem [27]. Transpiration and root pressure provide the impetus for this process. Erren and Feller [28] reported that the concentration of Cd in wheat grains is not determined by the concentration of Cd in xylem fluid, but mainly by the ability of Cd to be transported from xylem fluid to the phloem of the spike. Cakmak and Welch [29,30] found that Cd could be transported from the applied leaves to other phloem reservoir organs, such as new leaves. Cataldo et al. found that Cd was transported in the soybean xylem in the form of cationic complex [31]. This may be because xylem has a large number of amino acids and organic acids, and the metal complex formed by its combination with metal ions can avoid the obstacles to the transport of positively charged metal caused by the strong cation exchange ability of xylem cells, thus making it easier to transport. Citric acid, low molecular weight dicarboxylic anions and inorganic cations in xylem fluid flow can also affect the transport of Cd. Citric acid can promote the transport of Cd in xylem and reduce the transport of Cd out of xylem [32,33].

The accumulation of Cd in the grain was mainly transported into the grain by the phloem of flag leaves. The Cd in the leaves and stems can be redistributed to the seeds and the Cd in the seeds hardly transports to other parts. It can be speculated that the transport of Cd may be related to the transport of photosynthetic products. The re-transport of Cd into grains is also related to other metal ions. For example, zinc inhibits the phloem loading and transport of Cd, thus reducing the transfer of Cd from phloem transport to grains.

Cd distribution in wheat: In general, Cd is accumulated in roots or transported to stems, leaves, fruits and other organs after being absorbed by plant roots. However, the accumulation of Cd in plants varies with different parts, varieties, ecotypes and species of the same species. In the same planting object, Cd accumulation is usually caused by roots higher than stems, leaves, and grain. Cd is mainly distributed in the plastid and cell wall, and some of it forms carbonate and phosphate precipitation. Cd is absorbed by plant roots and usually accumulates in the roots or transports to stems, leaves and fruits. Leaf, root and waste were easily enriched with Cd in wheat plants, while lower Cd in seeds was an immovable element, which accumulated more in senescent parts and could not be reused by other non-senescent organs. Cd uptake was significantly positively correlated with dry matter weight gain (r=0.916), and Cd uptake rate was significantly positively correlated with dry matter weight gain (r=0.800)[25]. The filling period and jointing-heading period are the key periods for the control of Cd pollution. The Cd content of wheat root was higher than that of leaf, stem and grain. At the early stage of filling, the accumulation of Cd in different organs of wheat was mainly higher in leaves than in stems, leaf sheaths and grains. The accumulated content of leaf in mature stage was higher than that of leaf sheath, grain and stem.

Cd Tolerance Mechanisms in Wheat

Under the stress of Cd, it can stimulate the antioxidant defense system of plants, remove O2- and H2O2 generated under the stress of Cd, maintain the balance of reactive oxygen metabolism, and protect the membrane structure, so as to enable plants to endure, reduce or resist stress injury to a certain extent. Therefore, increasing antioxidant enzyme activity is one of the main mechanisms of tolerance to Cd in plants, including wheat [34-37]. Antioxidant defense systems include enzymes such as Superoxide Dismutase (SOD), Catalase (CAT), Peroxidase (POD), and non-enzymes such as Ascorbic Acid (AsA) and Glutathione (GSH). Zhang lihong et al. used the method of direct stress of Cd on wheat seeds during germination to study that the activities of Superoxide Dismutase (SOD) and Peroxidase (POD) increased with the increase of concentration, and Malondialdehyde (MDA) content and cell membrane permeability also showed an increasing trend [38]. The activity of POD and CAT increased with the increase of stress intensity, which indicated that the protective enzyme system in wheat was changed, which was also the protective response of plants to the adverse environment [39]. Under the stress of Cd, the function of reactive oxygen radical scavenging system in wheat was reduced, resulting in the accumulation of H2O2 in cells and the decrease of APX and GR activity. Wu extended their research showed that Cd stress lead to the sharp decline in barley seedling GSH content, this may be a GSH Cd detoxification in great quantities, such as GSH for plant chelating peptide (PC) synthetic substrates, or act as antioxidants in the body by removal of biological active oxygen free radicals and generate oxidized glutathione (GSSG), to show the content [40]. Malondialdehyde (MDA) is one of the main products of membrane lipid peroxidation, and its content is an important indicator of the degree or strength of membrane lipid peroxidation. Wu showed that MDA content in functional leaves of barley increased sharply under the treatment of 5 μm Cd, and increased with the extension of the treatment time of Cd [41]. In addition, when the concentration of Cd was higher than 0.1 μm, the stress of Cd would cause the lipid peroxidation in the leaves of barley overground, while the lipid peroxidation was alleviated after a certain period of treatment under the stress of low concentration Cd. Wu found that AsA can avoid the deficiency of nutrients caused by Cd poisoning [40]. By scavenging free radicals, the function of membrane, enzyme and DNA can be restored, thus detoxifying effect can be achieved. The addition of AsA into Cd stress solution had a certain alleviating effect on the growth of Cd poisoned barley seedlings, and the existence of AsA increased the accumulation of dry matter in wheat crops.

Marker-Quantitative Trait Loci (QTL) Analysis for Cd Tolerance in Wheat

The application of molecular marker-assisted selection in breeding has been paid more and more attention. Early in 1999, it was feasible to identify soybean germplasm using marker-quantitative trait loci (QTL). Lai yong et al. analyzed the genetic information of 113 barley materials by using QTL method [42]. The development of molecular markers related to Cd accumulation capacity also has a certain basis. Major genes associated with Cd uptake and transport in arabidopsis thaliana have been identified as ABC family [43], HMA family [44-46], Nramp family [47], ZIP family [48]. Understanding the genetic basis and gene composition of Cd absorption of wheat varieties can provide theoretical basis for breeding low Cd absorption varieties. ScOpc20 gene is a dominant marker associated with high Cd content, which is restricted in backcross breeding [49]. Developed an EST derived marker (XBF474090) co-isolated from a gene variant of a Cd absorbing trait in crops, which has been successfully transformed into a co-dominant CAPS marker, usw47. After digestion of PCR amplification products with restriction enzyme Hpyl88 I, electrophoresis analysis showed that the marker could be used to detect two alleles of Cd absorption trait genes. 96 wheat strains were successfully divided into low Cd absorption type or high Cd absorption type. KIM et al. isolated a TM20 gene from the CDNA library of a wheat root, which produced specific Cd(Cd (II)) tolerance [50]. These genes potentially related to Cd accumulation in wheat, which could be further developed to match molecular markers. It is a new idea to use molecular marker technology to screen germplasm resources. Molecular markers are developed based on the presence of abundant polymorphisms in genomic DNA, is a new and reliable genetic marker that directly reflects the differences of biological individuals at the level of DNA. DNA molecular markers are not affected by the environment and development stage, and a large number of markers can greatly improve the effectiveness and reliability of cross breeding.

Breeding Strategies and Possible Schemes for Cd Low-accumulation Winter Wheat Varieties

At present, the treatment of Cd pollution is mainly in three aspects: first, starting from soil treatment, the development of soil improver and Cd inhibitor [51]. The second is to select and breed cultivars with low accumulation of Cd and adjust the overall planting structure [52]. Cd pollution hazards can also be controlled through rational management of fields, control of contaminated areas and restricted planting and production. However, these measures could pose some problems, such as large investment, high energy consumption, difficult operation and easy to produce secondary pollution. Molecular breeding is a new way to select germplasm resources. Compared with conventional chemical analysis methods, molecular breeding does not produce secondary pollution and is the most effective and important mode to reduce the accumulation of Cd in agricultural products. Using molecular breeding technology to select crop varieties with low accumulation of Cd has important practical significance for ensuring safe agricultural production of Cd contaminated soil.

Regulatory factors involved in Cd stress response: MicroRNA (miRNA) is an important group of Small RNA, which negatively regulates the expression of target genes after transcription by mediating the degradation or translation of target mRNA, and is a new type of expression regulator [53,54]. Previous studies have found that these Cd-related miRNA can participate in the response to Cd stress through heavy metal transport, sulfur assimilation, antioxidant stress and auxin signal transduction pathways, and play an important role in the response process of plants to heavy metal stress [55-57]. For example, miR 159 and miR 67 exert effects through the A B C (ATP-binding cassette) type transporter and Nramp family (Natural Resistance-associated Macrophage Protein) of important proteins that regulate the transport of heavy metal ions respectively [58]. miR395 is involved in the response to heavy metal A1, Cd and Hg stress by participating in the regulation of sulfate-starved low affinity sulfate transporters and APS1, APS3 and APS4 genes (ATP sulphurylase, APS) [54]; miR398 plays an important role in the stress response of A1, Cd, Hg, Cu and other heavy metals by targeting two kinds of SOD, namely CSD1 and CSD2 in Cu and Zn superoxide dismutase (Cu, Zn superoxide dis-mutase, CSD) [54]. miRNA are at the center of gene expression regulation. In recent years, with the development and application of high-throughput sequencing technology, more and more miRNA related to heavy metals in plants have been cloned and identified.

Genes involved in response to Cd stress in wheat: At present, most of the studies on Cd stress in wheat focus on the selection of varieties resistant to Cd and the physiological and biochemical aspects. In recent years, with the deepening of the study on the mechanism of Cd accumulation, some genes involved in Cd transport have been discovered in arabidopsis, rice and other plants.Natural resistances associated with macrophage protein (OsNARMP5) is a strongly expressed Cd and Mn transporter in the root of rice.The mutant of OsNARMP5 can significantly reduce the absorption of Cd by the root system of rice, thus reducing the content of Cd in the grain to below 3% of the control. OsHMA3 of the p1b-atpase subgroup is a heavy metal ion pump mainly expressed in the root of rice, which is located on the vacuole membrane and mediated the enrichment of Cd in the vacuole of rice root cells. The over-expressed plants can selectively reduce the accumulation of Cd in seeds. Low affinity cationic transport protein (LCT1) is a new transport protein cloned from wheat, which is mainly expressed in the root and leaf of wheat. After RNA interference with OsLCT1 gene in rice, there was no significant change in xylem mediated Cd translocation. However, phloem-mediated Cd translocation decreased significantly, and the content of Cd in seeds was reduced to half of the control, indicating that it may be involved in the process of Cd transport from xylem of large vascular bundles to phloem of dispersed small vascular bundles in stem nodes, as well as the process of phloem-mediated Cd transport to grains. The results showed that the study of the genes related to Cd stress played an important role in the development of new varieties of Cd tolerant crops, which laid a foundation for excavating and functional analysis of Cd stress related genes in wheat. Simultaneously, it opens up a new way of high speed, simple operation and low cost for further breeding high Cd tolerance wheat varieties, which is of great significance to improve the grain safety of wheat and promote the sustainable development of agricultural production.

Author contributions

G.A. Zhatova initiated and designed the research, L.L.W. wrote the paper, G.A. Zhatova also revised and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Conclusion

Cd is one of the major inorganic contaminants in the environment. Its presence in the soil or atmosphere has been recognized as a serious threat to agriculture. It is a practical and feasible way to select wheat varieties with low accumulation of Cd to reduce the absorption and accumulation of Cd in crops and thus reduce the content of Cd in agricultural products. In summary, many important achievements have been reported on the injury of Cd to wheat and the tolerance mechanism of Cd to wheat.

However, the effect of Cd on the growth of wheat is very complex. Multiple benefits could be achieved by future critical research efforts including the following.

• More detailed studies are needed to have a better understanding of Cd toxicity in wheat at the molecular level.

• The process and mechanism of the uptake, transport and accumulation of Cd by plants should be clarified, and some of these processes should be artificially regulated to improve the tolerance of plants to Cd pollution or reduce the absorption of Cd.

• Whether the grain yield of wheat varieties with low Cd absorption is low in the planting process.

• When wheat was subjected to Cd stress, which genes were activated? How these genes work together to synthesize resistant proteins, peptides, amino acids, reducing sugars, and more.

• In many physiological and biochemical reactions, how to define a physiological index as the standard to measure the resistance and non-resistance to Cd in wheat?

If the research in these aspects can achieve breakthrough results, it will be another breakthrough direction of soil pollution treatment and utilization.

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