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Non-nutritive Mineral Effects on Rice

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ABSTRACT

The study of the responses of rice (*Oryza sativa* L.) to non-nutritive minerals has numerous benefits. With the sequencing of the rice genome, rice is the current model plant for genomic studies of crops and changes in genetic regulation in rice may reflect changes in other plants. The growth of rice is largely determined by the presence or absence of nutritive elements. Some of these are macronutrients while others are required in such small amounts as to be called micronutrients. However, the presence or absence of other, non-nutritive minerals can also influence rice growth. Their presence tends to be by human intervention and a selected few have been studied. Studies on the uptake and transport of non-nutritive elements can often provide correlative information on the nutritive minerals. Genetic information regarding mineral transport proteins in rice has been particularly valuable in understanding transport in other organisms. This paper presents an overview of the following minerals that have been studied and for which a physiological response in rice has been observed: aluminum, arsenic, cadmium, cesium, chlorine, chromium, germanium, mercury, iodine, lanthanum, nickel, lead, selenium, strontium, and vanadium.

Keywords: heavy metals, *Oryza*, rare earth, transporters

Abbreviations: ABA, abscisic acid; **CLC**, chloride protein channels; **GA**, gibberellic acid; **GST**, glutathione *S*-transferase; **HMAs**, heavy metal ATPases; **HSP**, heat shock proteins; **IAA**, indoleacetic acid; **NIP**, nodulin 26-like intrinsic membrane protein; **QTL**, quantitative trait locus; **ROS**, reactive oxygen species; **SOD**, superoxide dismutase

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INTRODUCTION

Rice has a long history of cultivation and study so that information and plant material are available on cultivars that vary in their responses to specific elements, both nutritive (required for growth) and non-nutritive. There are numerous advantages to understanding the relationships between non-nutritive elements and rice. Low levels of these minerals have been found to improve plant growth and/or yield even though the mineral has no known function. Examples are vanadium (Shibuya and Saeki 1934) and lanthanum (Hong *et al*. 2000). Natural concentrations of non-nutritive minerals in soil are seldom high enough to alter plant growth. However, in the case of aluminum where high concentrations can occur naturally, rice is resistant to levels that are toxic to many other crops. This trait of rice is valuable for cultivation in soils affected by acid rain where a low pH ionizes aluminum to a toxic form (Zhang *et al.* 2007). High levels of non-nutritive minerals are far more likely to be a result of human activities such as mining and smelting operations (e.g., cadmium, lead, and mercury), auto exhaust (lead and cadmium), pesticides (arsenic and mercury), electronics industry (germanium), coal-fired power plants (mercury, lead, and vanadium), and atomic fallout (strontium and cesium).

Rice has the promise of providing even greater benefit to humans than simply as a carbohydrate source by increasing its ability to be a source of important minerals such as selenium (Liu *et al.* 2004) and iodine (Mackowiak and Grossl 1999). Iodine is taken up into the stems and leaves

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of rice and so may provide iodine indirectly to humans through meat and milk products from livestock fed these plants (Mackowiak and Grossl 1999).

The non-nutritive minerals are not usually a natural part of the rice plant's environment but their ever-increasing presence indicates a need to understand the responses of rice to these minerals. At high concentrations, minerals may either be toxic to the plant or toxic to animals and humans when consumed, though they may cause relatively little damage to the plant itself. Direct benefits are gained for rice farming from an understanding of responses to toxic minerals and from studying their uptake and transport in rice. It may be possible to utilize the ability of rice plants to accumulate certain toxic compounds, such as arsenic (Wang *et al.* 2006), into the plant without transferring significant amounts into the kernel. In this way, the rice can be harvested for food while the rest of the plant, after it has depleted the soil of the toxic element, is removed.

Non-nutritive elements are useful in science by their ability to "stand-in" for nutritive elements in biochemical studies. Their location and activity can be used to trace the activity of nutritive compounds that are more difficult to study such as screening for silicon-uptake mutants using germanium (Ma *et al.* 2002). Some elements such as lanthanum are useful as tools for studies of particular biochemical and molecular systems where it can be used to inhibit ion channels and to mimic the effects of the abscisic acid on gene expression (Hagenbeek *et al.* 2000). In other cases, an element, e.g. mercury (Lu and Neumann 1999), may affect the activity of specific channels and transporters which can provide means for the study of those channels. Transport and uptake proteins function primarily for nutrients but generally more than one mineral, nutritive or non-nutritive, can be transported by each protein because of structural similarities. Thus, understanding transport of non-nutritive elements can increase understanding of nutrient transport mechanism and its specificity.

ALUMINUM

Rice plants growing in excess levels of aluminum (Al) exhibit poor growth, i.e., stunted leaves, and orange-yellow interveinal chlorosis on the leaves. The leaf interveinal areas become yellow to white and the leaf tips as well as the leaf margins die (Dobermann and Fairhurst 2000). The most important symptom of Al-toxicity is inhibition of root growth. Al is one of the most abundant components of soil and generally exists in forms that are harmless to plants. However, at acid pHs Al is ionized to the form of Al^{+3} which can inhibit root elongation, resulting in lowered nutrient and water uptake and results in poor growth and productivity (Ma and Furukawa 2003). Overall, rice is one of the most Al-resistant crops, but Al-toxicity is a primary cause of low productivity of rice in acid soils (Mishra and Dubey 2008; Yang *et al.* 2008).

A mechanism utilized by other plants for Al-resistance is to increase root surface pH, which does not appear to be used by rice (Ma *et al.* 2005; Chen and Shen 2008; Yang *et al.* 2008). Al-resistance in other cereal species involves secretion of organic acid anions, another mechanism that does not seem to be employed by certain cultivars of rice (Ma *et al.* 2003; Ma *et al.* 2005; Yang *et al.* 2008; Khan *et al.* 2009). Nonetheless, exudation of organic acids by rice roots was shown to be a mechanism for detoxification of Al using transgenic rice and other plants containing rice genes that altered organic acid exudation (Begum *et al.* 2009; Han *et al.* 2009). Indeed, different rice genotypes have a large range of tolerance to Al and employ different mechanisms, probably a result of the high abundance of Al in soil.

Other methods of stress avoidance include the exclusion of Al from sensitive sites and the decrease of Al activity in the rhizosphere (Dobermann and Fairhurst 2000). Al uptake and transport to the shoot is reduced in Al-resistant cultivars (Macêdo and Jan 2008; Yang *et al.* 2008). Two ATP binding cassette transporters were found to be responsible for Al tolerance by using RNA interference and a mutagenized rice (Huang *et al.* 2009b). Pectin methylesterase activity, which increases the ability of pectins in the cell wall to bind Al, is increased by Al treatment. The cell wall polysaccharides in the root apex of Al-sensitive cultivar 'Zhefu802' bind more Al than the Al-resistant 'Nipponbare', resulting in the sensitive plant having more Al present in the highly Al-sensitive portion of the root (Yang *et al.* 2008), though resistance may also occur by having more Al bound up in the iron plaque covering the root surface (Chen and Shen 2008). Reactive oxygen species (ROS) appears to have an Al-tolerance role in another study (Xie *et al.* 2009).

The levels of reducing sugars (primarily monosaccharides) is notably increased in roots and shoots during Al treatment in conjunction with increases in sucrose hydrolyzing enzymes (Mishra and Dubey 2008). Rice Al-sensitivity is altered by changes in root permeability resulting from alterations in sterol composition of plasma membranes (Khan *et al.* 2009) or disorder in the structure of the root outer cells (Huang *et al.* 2009c).

Over 20 quantitative trait loci (QTLs) important for Al-tolerance in rice are found across a number of studies, with very little commonality of chromosomal location among them (Ma and Furukawa 2003; Xue *et al.* 2006). Since Al-resistance can be inducible, alterations in gene expression could indicate the mechanism(s) for Al-resistance. Thirty-seven genes in rice are identified as being differentially expressed in the presence of Al, including four ion transporter genes. Also, genes involved in cysteine and metallothionein synthesis, and hence sulfur metabolism, are upregulated. The downregulated genes are associated with cytoskeletal dynamics (Zhang *et al.* 2007).

ARSENIC

Shoot growth in rice is reduced by arsenic (As) to a greater extent than root growth. Arsenic treatment, in the form of either organic or inorganic As compounds, decreases plant height, leaf number, tiller number, and leaf width and causes curled leaves, chlorotic young leaves, and a slippery, reddish color along the root (Shaibur *et al.* 2006; Wang *et al.* 2006). Application of As can cause plants to exhibit symptoms similar to that found in the physiological disease straighthead, so called because of the upright panicles that result from lack of grain filling. The hulls on individual kernels have a distinctive parrot beak. Otherwise, leaves appear healthy, sometimes even a darker green (Yan *et al.* 2005).

Accumulation of As in the rice plant is not uniform, with the highest amounts in the root and successively less in the stem, leaves, and panicle, suggest that As is carried in the transpiration stream (Frans *et al.* 1988). Levels of As rise in the leaf, stem, and root with increasing application of organic As, regardless of the developmental stage at application from tillering to maturing stage. Spikelets, however, tend to accumulate As more readily when application is at the boot stage rather than at later stages (Wang *et al.* 2006). More than three-quarters of the As associated with a rice plant occurs in the Fe plaque surrounding the roots. The Fe plaque seems to function as a buffer to prevent As uptake into the plant. The more Fe plaque present on the roots, the more As is contained in the plaque, without any increase in the As concentration in the rice shoot (Liu *et al.* 2004). Once the plaque's storage capacity is exceeded, then As is absorbed and translocated to the shoot. Stems and leaves accumulate nearly an order of magnitude less As than roots, and seed hulls can be another order of magnitude lower. The grain itself is a further order lower if either inorganic As (Abedin *et al.* 2002a) or organic As (Wang *et a*l. 2006) is applied. Straighthead does not result in a distinctive distribution of minerals (including As) throughout a rice plant, making it difficult to associate any specific mineral with the appearance of straighthead (Belefant-Miller and Beaty 2007).

Starch and sugar metabolism are adversely affected in plants growing under stressful conditions which may result in the accumulation of soluble sugars. Arsenic treatment causes an increase in soluble sugars in rice roots and shoots. Based on the changes in the activities of several enzymes involved in sugar and starch metabolism caused by As treatment, it appears that sucrose synthase and acid invertase are responsible for the increase in sugars (Jha and Dubey 2004).

Arsenate (As^{+5}) is the predominant form of As in aerobic, upland soil. In anaerobic, flooded soil, the predominate form of As is arsenite (As^{+3}). The most phytotoxic forms of As are As^{+3} and mono-methyl arsenic acid possibly because these two forms are also taken up to the greatest extent by rice (Marin *et al*. 1992). The presence of the iron plaque on excised rice roots enhances As^{+3} uptake while decreasing As^{+5} uptake (Chen *et al*. 2005). Organoarsenic compounds are taken up by rice roots but at a slow rate (Abedin *et al*. 2002b). Uptake of As^{+5} and As^{+3} is similar at low concentrations, while at high levels As^{+5} and As^{+3} are taken up into cells by different mechanisms and As^{+3} is taken up more quickly than As^{+5}. Rice genotypes with high root porosities or high rates of oxygen loss from the roots into the soil accumulated less As, possibly resulting from oxidative changes in the root plaque (Mei *et al*. 2009).

Zhang *et al*. (2008) found four genes associated with As accumulation in different parts of the rice plant. Norton *et al*. (2008b) found three different major genes, the presence of any two of which confers tolerance to As^{+5} in one cultivar of rice. Microarray results using the same cultivar set showed that the classic oxidative stress response genes are not differentially regulated with As treatment, except for glutathione *S*-transferase (GST) and arsenate methylation genes (Norton *et al*. 2008a). Several GST proteins are upregulated in 2-D gels in response to As treatment (Ahsan *et al*. 2008). Various stresses, in addition to heat, can result in the expression of heat shock proteins (HSP). Arsenic induces the expression of a number of HSP located on chromosomes 1 and 3 (Guan *et al*. 2004). A microarray study showed that As exposure led to large changes in DNA expression in rice seedlings. Comparisons were made with changes induced by other heavy metals. Most were similar except for a cytochrome P450 gene was singularly induced by As^{+5} in the root and a glutaredoxin was singularly induced by As^{+3} in the shoot (Chakrabarty *et al*. 2009).

As^{+3} (Meharg and Jardine 2003) and methylated As (Li *et al*. 2009) are transported into rice roots via the nodulin 26-like intrinsic membrane protein (NIP) subset of aquaporins. Aquaporins transport neutral molecules and are highly expressed in rice roots, moving water into the root using six membrane-spanning domains. The molecular sizes of As^{+3} and silicic acid are similar and both are neutral at normal soil pHs so a silicic acid transporter also transports As^{+3}. The silicic acid transporter with the highest expression in rice roots is Lsi1 (OsNIP2:1), which is also responsible for the uptake of As^{+3} (Ma *et al*. 2008). Both Lsi1 and Lsi2 are needed for these elements to cross the root Casparian strip, Lsi1 for influx and Lsi2 for efflux. Lsi2 controls the xylem deposition of As that ultimately gets to the grain (Bienert *et al*. 2008; Ma *et al*. 2008).

CADMIUM

Cadmium (Cd) decreases photosynthesis and the most common symptom of its toxicity in rice is chlorosis (Moya *et al*. 1993). With Cd treatment, chloroplasts have less chlorophyll and fewer thylakoids, while photosynthetic activity in terms of oxygen release and CO_2 assimilation is decreased (Rascio *et al*. 2008). Cd decreases the lengths and weights of roots and shoots (Rubio *et al*. 1994; Shah and Dubey 1995; Cheng *et al*. 2008; Huang *et al*. 2009c) and results in broad and discolored leaves (Shah and Dubey 1995). Cd reduces yield by reducing the number of grains per panicle and grain weight in an indica variety (Hassan *et al*. 2008) but variably decreases or has no effect on yield components in four different cultivars (Huang *et al*. 2008b). Low levels of Cd inhibit root growth of germinating seeds but have no effect on the average seed germination rate (Zeng *et al*. 2007) and, in a different test, even increase the germination percentages of most of the japonica cultivars tested (Cheng *et al*. 2008). Very low levels of Cd increase both shoot and root growth (Aina *et al*. 2007).

Cd is phytotoxic, interfering with photosynthetic and respiratory activities by acting as an uncoupler of oxidative phosphorylation (Chino 1981a). Other detrimental effects of Cd include a decrease in the plant content of essential minerals such as K, Ca, or Mg because of the competition among these divalent cations for transport across membranes (Llamas *et al*. 2000). In other plant species, Cd can adversely alter the transmembrane electrical potential. In rice, however, Cd does not sustainably directly cause a depression of the electrical potential (Llamas *et al*. 2000). Cd decreases the transpiration rate in rice seedlings, which may serve to reduce toxic Cd levels in the shoot (Moya *et al*. 1995; Hsu and Kao 2005).

During germination and early development, Cd can temporarily inhibit the transport of carbohydrate reserves from the seed to the developing seedling but the effect is largely gone by 10 days of treatment (Moya *et al*. 1993). In rice roots and shoots, Cd treatment results in changes in sugar metabolism and content. A Cd-induced decrease in sucrose phosphate synthase activity accompanies a decrease in sucrose levels, increases in invertase and sucrose synthase accompany increases in reducing sugars, and decreases in α-amylase accompany increases in starch (Verma and Dubey 2001). Additionally, Cd inhibits nitrate reductase activity in rice seedling leaves (Hemalatha *et al*. 1997).

A toxic mechanism of Cd in rice is overproduction of reactive oxygen species (ROS) such as hydrogen peroxide, which is normally countered by ROS-scavenging pathways (e.g., superoxide dismutase (SOD), peroxidase, and catalase). Cd treated rice plants have higher levels of glutathione, an antioxidant (Hassan *et al*. 2008). Roots of Cd treated seedlings have higher hydrogen peroxide levels (Guo *et al*. 2009) and release phytometallophores in the root exudate (Adhikari *et al*. 2006). Cd provided to detached rice leaves induces NADPH oxidase to generate hydrogen peroxide, which damages cells by reducing chlorophyll content (Hsu and Kao 2007).

Cd treatment at heading increases catalase and peroxidase activities (Hassan *et al*. 2008). A Cd-resistant transgenic rice has higher levels of ROS-scavenging enzymes activity upon Cd treatment than the control plant (Zhao *et al*. 2009a). The increase by Cd of SOD and catalase activities and on superoxide radical and peroxide contents is greater at early developmental stages (Huang *et al*. 2008). Salicylic acid alleviates Cd-induced damage by changing the activities of the ROS scavenging enzymes, as mediated by increases in hydrogen peroxide (Guo *et al*. 2008; Chao *et al*. 2010), and resulting in increases in the levels of antioxidants which are able to bind up the Cd (Guo *et al*. 2008).

Rice resistance to Cd is associated with retention of Cd in root cell walls and reduced translocation of Cd from roots to shoots (Zhang *et al*. 2009), although Ueno *et al*. (2009) saw no differences in cell wall binding of Cd between a high- and low-Cd rice accession. However, nitric oxide can increase Cd tolerance in rice, apparently by increasing the pectin and hemicellulose content of root cell walls, enabling more Cd to be sequestered there (Xiong *et al*. 2009a). Nitric oxide levels are reduced by the presence of Cd, and the lower nitric oxide levels decreases the crown root number (Xiong *et al*. 2009b).

Cd uptake by rice plants in culture varies with the Cd concentration and time. At the lowest concentrations, active uptake dominates. As Cd concentrations increase, active exclusion takes over the incorporation and sequentially lower amounts of Cd end up in the above ground plant portions with increasing amounts in the roots. At low concentrations, Cd is transported as an organo-metal complex (Chino 1981b). At higher concentrations, most of the Cd is retained in the root (Chino 1981b; Rubio *et al*. 1994) as inorganic ions where they accumulate at the endodermis (Chino

1981b). After a short (10 min) period of passive uptake of Cd, a longer period of active Cd uptake occurs. The active uptake appears to be primarily via Zn and Ca channels (He *et al.* 2008). Rice can be used for phytoextraction of soil Cd and to reduce Cd levels in the grain of subsequently grown rice by about half (Murakami *et al.* 2009).

The initial transport of Cd through the plant occurs in the xylem (Uraguchi *et al.* 2009). Ueno *et al.* (2009) describe a QTL responsible for root to shoot translocation that explains some of the phenotypic variation in Cd accumulation between two cultivars. Essentially all the Cd found in rice grains is transported through the phloem (Tanaka *et al.* 2007). Cd can be transferred in a split-root test from Cd-exposed roots to the unexposed roots (Guo *et al.* 2009). Cd accumulation in the grain is a result of the accumulation of Cd in leaves and culms before heading. After heading, Cd taken up by the roots ends up in the panicle but not in the brown rice itself (Kashiwagi *et al.* 2009). Cd levels are higher in the xylem exudate than in the phloem sap, indicating that Cd is not concentrated when transferred from xylem to phloem (Tanaka *et al*. 2003).

Both abscisic acid (ABA) and gibberellic acid (GA) reduce Cd uptake (Rubio *et al.* 1994). GA, but not ABA, reverses Cd-induced growth inhibition (Moya *et al.* 1995). The use of a GA synthesis inhibitor ameliorates some of the effects of Cd on rice growth and function (Hsu and Kao 2005). Cd treatment increases ethylene evolution but has no effect on ABA content (Huang *et al*. 2008a).

A number of QTLs are associated with Cd tolerance and accumulation (Xue *et al.* 2009). Cd induces the expression of heat shock proteins but only those located on chromosome 3 (Guan *et al*. 2004). A number of genes in rice seedlings have a unique expression pattern under Cd stress compared with other heavy metal stresses (Chakrabarty *et al.* 2009). Heavy metal ATPases (HMAs) play roles in heavy metal detoxification. *OsHMA5*, *6*, and *9* are induced in shoots by the presence of Cd, and *OsHMA4* and *5* are induced in roots. Their expressions are highest in vascular bundles of roots and shoots and in anthers, where they are localized to the plasma membrane. OsHMA9 itself functions as an efflux pump and without a functioning OsHMA, rice plants accumulate more Cd (Lee *et al.* 2007). The Nramp1 and ABC transporter are transporter proteins whose expression is induced by Cd (Aina *et al*. 2007).

Numerous microRNAs (miRNAs) are expressed in response to toxic levels of Cd. These miRNAs have sequences complementary to metabolism and stress-related genes. The majority of the miRNAs have no known counterparts in other plants and so may have roles specific to rice (Huang *et al*. 2009a). The protein profile is also altered by Cd stress in rice seedling roots and leaves (Ge *et al.* 2009; Lee *et al.* 2010). Non-specific DNA fragmentation occurs as a result of Cd treatment. At very low levels of Cd which stimulate growth, the damage seems to be repairable by the rice plant. Protein expression is induced with very low Cd treatment while under high Cd a number of these proteins are repressed and some new proteins are induced (Aina *et al.* 2007). A microarray study has also found a large number of changes in gene regulation (Ogawa *et al.* 2009).

CESIUM

The concentration of cesium (Cs) in natural soils is not in sufficient quantity to have a physiological effect, but studies of Cs and its radioactive isotope in rice are useful for assessments of radiation exposure. Cs is more available to rice plants when it is deposited into paddy soil rather than non-flooded soil (Ichikawa *et al.* 1962; Myttenaere and Bourdeau 1968). Radioactive Cs, ^{137}Cs, is more easily absorbed by rice plants than stable Cs (Tsukada *et al.* 2002a). Uptake of ^{137}Cs is higher into both brown rice and straw at 83 days after planting than at 12 days after planting (Choi *et al.* 2009). The maximum uptake of Cs occurs at the boot stage (Asada and Kasai 1960; Kodaira *et al.* 1973) and Cs has an affinity for cell sap (Kodaira *et al.* 1973). However, within the plant the translocation rates for the isotopes are similar to each other but differ from those of K (Tsukada *et al.* 2002b), for which Cs is a toxic analog (Hasegawa 1996). The distribution of Cs, radioactive or stable, is equivalent between roots and shoots for flooded rice. In non-flooded rice, stable Cs accumulates in the root (Myttenaere and Bourdeau 1968).

Rice has a low ratio, compared to other cereals, of Cs activity in the grain relative to that remaining on the leaves (transfer factor) (Colle *et al.* 2009). Almost 10% of the Cs in the above ground rice plant is found in the hulled rice (Tensho *et al.* 1961). Polished rice from plants exposed to airborne Cs have approximately the same amount of Cs as protected plants, indicating that Cs can be translocated easily from leaf to grain (Ichikawa *et al.* 1962). Also, significant portions of the Cs supplied via irrigation water to flooded rice plants are found in the seed (Myttenaere and Bourdeau 1968). Uchida *et al.* (2009) review the transfer factors for ^{137}Cs for rice.

CHLORINE

Chlorine (Cl) is highly available from soil and water and taken up in quantities equivalent to those of a macronutrient. However, Cl has few specific functions in the plant other than in the photolysis of water in photosystem II of photosynthesis (Obata 1995). Most of the roles of Cl in the plant are non-nutritive and Cl is more of a concern for its association with plant osmotic and oxidative characteristics.

Cl is readily mobile within plants. It is absorbed from the soil as the chloride ion, Cl^-. Generally the plant absorbs much more Cl than it requires. Low concentrations of Cl promote rice root growth (Kimura *et al.* 2004). Deficiency symptoms include reduced growth, wilting, and development of chlorotic and necrotic spots, but Cl deficiency is rare because of its high solubility and availability in soil and wind-carried soil. Cl may also be involved in controlling the osmotic pressure of the cells and of the vacuoles within cells (Obata 1995).

Chlorates are an oxidized form of Cl and are phytotoxic. Plant cells do not discriminate between chlorate and nitrate and they are taken up at the same site; absorption can occur through either roots or leaves (Borges *et al*. 2004). Chlorate, as an analogue of nitrate, is used to identify mutants lacking nitrate reductase activity since the mutants don't take up chlorate and thus survive chlorate treatment (Zhao *et al.* 2000).

Chlorate is directly toxic because of its high oxidizing capacity. Chlorate causes changes in rice chloroplast shape and structure and causes strong lipid peroxidation in rice leaves. It also damages root tissue and withers root surface cells and root hairs (Borges *et al*. 2004). Chlorate-resistance is used to differentiate between indica (more sensitive) and japonica (more resistant) rice varieties. The genetic sources of this resistance involve genes for nitrate reduction, molybdenum cofactor biosynthesis, and nitrate transport (Teng *et al*. 2006).

Vacuole membrane voltage-gated chloride protein channels (CLC) type family mediate passive Cl transport driven by the electrochemical gradient (Nakamura *et al.* 2006). OsCLC1 in rice functions in the osmoregulation of salt-stressed rice and is involved in the maintenance of cellular Na homeostasis. Cellularly, *OsCLC1* expression occurs in mesophyll cells, guard cells, and vascular tissue (Diédhiou and Golldack 2006). While *OsCLC1* is expressed in most tissues, *OsCLC2* is expressed only in the roots, nodes, internodes, and leaf sheaths. *OsCLC1*, but not *OsCLC2*, expression increases with NaCl treatment. The proteins from both genes are located in the vacuole membrane (Nakamura *et al.* 2006).

CHROMIUM

Rice is tolerant of high levels of chromium (Cr), relative to other trace metals (Wallace et al. 1977) but it will reduce plant height, tiller number, root length, and yield in hydroponically grown rice plants (Kasugai and Minami 1936). Most of the Cr stays in the roots and relatively little is translocated above ground. Much less Cr is translocated to the grain of rice compared to other crops. Cr uptake appears to be passive and uptake is not significantly different for two Cr oxidation states (Cr^{+3} and Cr^{+6}) (Mishra *et al.* 1997).

Cr causes distortion of root cells with increased numbers of vacuoles and cell membranes detached from the cell wall (Panda 2007). Of six organic acids, exudation of only oxalic acid from rice roots is clearly increased by Cr treatment (Zeng *et al.* 2008b). Cr triggers an increase in ROS in roots. The ROS appear to be countered more by ascorbic acid and glutathione than by antioxidant enzymes such as glutathione reductase (Panda 2007). A number of genes in rice seedlings have a unique expression pattern under Cr stress compared with other heavy metals (Chakrabarty *et al.* 2009).

GERMANIUM

Rice can accumulate up to ten-fold more germanium (Ge) than other plants (Chino 1981a). There is no metabolic barrier to Ge absorption into rice roots but translocation into the shoots is controlled (Shibabe and Yoda 1984). Ge is chemically similar to Si and is taken up into rice by the same mechanisms used for Si. Rice mutants defective in Si uptake are able to be identified by selecting Ge-resistant rice (Ma *et al.* 2002).

Ge is used in the manufacture of electronic equipment such as integrated circuits and optical fibers and so is becoming more prevalent in some soils. Ge is toxic above certain levels and causes the appearance of necrotic spots on rice leaves as well as a suppression of overall growth. Ge accumulates at the necrotic spots (Matsumoto *et al.* 1975). High levels of Ge decrease rice biomass and have various effects on antioxidant activity: the activity of antioxidative enzymes SOD and catalase decrease but malondialdehyde levels increase. Low levels of Ge have little effect on the above plant growth parameters nor on chlorophyll a or b levels. Low levels, however, increase glutathione peroxidase activity (Lin *et al.* 2005).

IODINE

When exposed to iodine (I), plants develop reddish necrotic spots (Watanabe and Tensho 1970) or small brown spots on older leaf tips which spread so that the leaves become yellow-brown or brown (Ou 1985). Symptoms of I-toxicity include general leaf chlorosis and plant death (Mackowiak and Grossl 1999). Flooding causes iodine in the soil to ionize to I^-, which forms molecular iodine (I_2) when oxidized. The oxidizing rhizosphere of rice roots increases the formation of I_2 in high iodine soils and roots more readily take up the nonpolar I_2 than I^-, which intensifies the occurrence of I-toxicity (Yamada *et al.* 2005). While the oxidizing power of rice roots is beneficial in avoiding Fe-toxicity, the oxidation contributes to I-toxicity, sometimes described as Akagare type III (Ou 1985).

I-toxicity varies with the form of iodine. Iodine in two chemical forms was provided to rice plants growing in a nutrient solution. I^- at low levels has no effect on dry matter accumulation by leaves, stems, panicles, or roots while at high I^- levels, growth was reduced. Iodate (IO^{3-}) reduced growth slightly in the stem and panicle at high levels. While I^- appears to be more toxic to rice than IO^{3-}, the smaller I^- may simply be more easily taken up by the plant. Neither form of iodine accumulated in the seed (Mackowiak and Grossl 1999).

When a rice plant is exposed to gaseous I_2 during flowering and seed development, the hull contains about 90% of the I_2 in the entire seed. Uptake rates of gaseous I_2 do not appear to be different for different growth stages. Levels of iodine decrease in the seed and leaf while transiently increasing in the stem during I_2 exposure (Nakamura *et al.* 1986). Iodine is not mobile in the phloem. At non-toxic levels of KI or KIO_3 in a nutrient solution, little iodine is found in the seed; most is present in the root and stem (Mackowiak and Grossl 1999). Similarly, a study using gaseous CH_3I showed little translocation from leaves and stems to the rice grain. Atmospheric deposition of CH_3I onto the grain resulted in approximately 25% of the iodine in a rice kernel being in the brown rice (Muramatsu *et al.* 1996). Uchida *et al.* (2009) review the transfer factors for ^{125}I for rice.

LANTHANUM

Lanthanum (La) is the most abundant rare earth element in soil. Xie *et al.* (2002) using solution culture showed that low concentrations of La could promote rice growth, while high concentrations depressed growth. Similarly, in a rice plasma membrane system, low La concentrations stimulated redox systems and H^+-ATPase, but high concentrations inhibited them. However, in pot and field tests, La has no effect on rice growth (Zheng *et al.* 2000) although Huang *et al.* (2009c) showed some reduction in root elongation in young rice seedlings. Low levels of rare earth elements are known to enhance germination and root growth. Low levels of La stimulate the basal metabolism of mitochondria from rice seedlings (Dai *et al.* 2008).

La cannot pass through the plasma membrane so its activity occurs at the outer membrane surface. There, La has some physiological activities: functions as a free radical scavenger, inhibits electron transfer from NADH to oxygen, reduces the formation of lipid peroxides, and stimulates proton extrusion by both the standard redox system and H^+-ATPase (Zheng *et al.* 2000). These changes in activities elicited by La increase germination, vigor, and respiration while reducing the membrane permeability of aged rice seeds (Hong *et al.* 2000). La can alter transporter activity, gene expression, and enzyme activity and it is used as a tool in plant systems, for example where trivalent ions are known to activate expression of the abscisic acid-inducible *Em* promoter (Hagenbeek *et al.* 2000; Gampala *et al.* 2001) and as an inhibitor of the Ca channel (He *et al.* 2008).

LEAD

Rice exposed to lead (Pb) does not exhibit any specific foliar symptoms but growth, as measured by leaf size and number, tiller number, etc., is depressed (Chatterjee *et al.* 2004). As observed for other plants, Pb at low concentrations can have a stimulating effect on rice growth and inhibit growth at higher concentrations, depending on the cultivar (Liu *et al.* 2003). While Pb has different levels of toxicity with different rice cultivars, there is no apparent relationship between the amount of Pb taken up and the Pb tolerance of a cultivar. In rice, Pb largely accumulates in the roots. Pb concentrations decrease sharply from roots to grain in rice plants, indicating that Pb is poorly translocated beyond the root (Liu *et al.* 2003). The levels of Pb in different parts of the seed are under genetic control, as indicated by differences among rice cultivars (Chen *et al.* 2008).

A major symptom of Pb-toxicity is inhibited root growth. Pb^{2+} kills rice root cells. Part of the process includes activation of protein kinases, which mediate responses to a diverse range of biotic and abiotic stresses. Pb^{2+} stimulates a rapid activation of mitogen-activated protein (MAP) kinases. Environmental and heavy metal stresses are known to accelerate the formation of ROS. Pb^{2+} induces ROS production through the activation of a membrane-associated NADPH. Levels of Ca, a second messenger for stress regulation, and a calcium-dependent protein kinase also increase during Pb treatment (Huang and Huang 2008). Hydrogen peroxide levels often rise in response to stress and they rise in Pb-exposed rice seedlings. The effect of Pb on the levels of hydrogen peroxide metabolizing enzymes varies. Chen *et al.* (2007) observed a variable increase in ascorbate peroxidase, no change in SOD, and a decrease in catalase activities with Pb, while Mishra and Choudhuri (1999a) observed an increase in catalase and peroxidase activities and a decrease in SOD. Pb also reduces multiple biochemical components (carotenoids, sugars, etc.), but not chlorophyll a (Chatterjee *et al.* 2004). Pb inhibits nitrate reductase activity in rice seedlings (Hemalatha and Francis 2000).

Rice uses metallothioneins to chelate and thus detoxify Pb. Metallothioneins are cysteine rich low molecular weight proteins that bind metals via the thiol groups of their cysteine residues. A number of metallothioneins appear to be active in conferring Pb tolerance in rice roots (Xu *et al.* 2007). Exogenous ABA ameliorates the effects of Pb on leaf chlorophyll content and on plant growth, apparently through alterations in the activities of ROS scavenging enzymes (Zhao *et al.* 2009b).

A number of genes in rice seedlings have a unique expression pattern under Cd stress compared with other heavy metals (Chakrabarty *et al.* 2009). The expression of certain HMAs is induced by Pb. The expression of *OsHMA 5*, *6*, and *7* increases in shoots and the expression of *OsHMA 8* increases in roots. These HMAs function in heavy metal detoxification by pumping heavy metals out of cells through the plasma membrane. Eliminating *OsHMA9* results in an increase of Pb in shoots and roots (Lee *et al.* 2007).

MERCURY

Mercury (Hg) is highly toxic to rice plants, in accordance with its high electronegativity, indicating that the formation of organo-metal complexes is involved (Chino 1981a) and which have been recently identified (Krupp *et al.* 2009). Hg inhibits seed germination and seedling shoot and root elongation (Mishra and Choudhuri 1998; Mishra and Choudhuri 1999b; Du *et al.* 2005). Growth and grain yield are reduced by Hg, primarily by a reduction in the number of panicles (Zhu *et al.* 2008). Hg inhibits nitrate reductase activity in rice seedlings (Hemalatha *et al.* 1997).

Levels of antioxidant enzymes change significantly with Hg levels, but the specifics can vary. Ascorbate peroxidase and SOD increases in the root and leaf, while guiacol peroxidase increases in the leaf only. Catalase activities increase in both the root and leaf, and glutathione reductase increases in the leaf, but at lower, less toxic Hg concentrations (Ali *et al.* 2002). Activities of catalase, peroxidase, indoleacetic acid (IAA) oxidase, IAA synthase, and ascorbic acid oxidase increase in germinating rice treated with Hg (Mukherji and Nag 1976). In 15-day-old rice seedlings, Hg decreases catalase and SOD activities but increases peroxidase activity. Hg causes loss of membrane integrity through lipid peroxidation and also increases levels of hydrogen peroxide, a reactive oxygen species, in rice roots and shoots (Mishra and Choudhuri 1999a). A Hg-tolerant rice mutant, upon Hg stress, increases its levels of ascorbic acid (Zeng *et al.* 2008a) and proline (Wang *et al.* 2008) to scavenge and lower ROS levels.

Hg affects the cellular Ca^{+2} signature which affects protein phosphorylation which in turn affects cellular processes, particularly those involved in stress responses. Hg promotes the active transport of Ca from rice roots to leaves as well as across the plasmalemma of root cells in the short-term (8-12 h). Hg causes Ca channels or pumps in the plasmalemma in roots and leaves to open transiently; concurrently Ca levels and protein phosphorylation increase in rice roots and leaves (Ge *et al.* 2007).

Certain water channels in rice roots are sensitive to Hg and will close in the presence of Hg though water will continue to flow through different water pathways (Lu and Neumann 1999), which provides a means of studying the different channels. The specificity of the Hg inhibition of water flow is used to study uptake of silicon by rice (Mitani *et al.* 2008).

NICKEL

Nickel (Ni) is an essential microelement for rice, but only when nitrogen is provided as urea. When nitrogen is present as NO_3, as occurs in flooded conditions, the Ni-requiring urease that is involved in converting urea to nitrate is not transcribed. Urease is the only Ni-requiring enzyme in plants, so the essentiality of Ni is dependent on growth conditions (Gerendás *et al.* 1998).

Of greater concern, particularly for growth of flooded rice, is the toxicity of Ni. At excess levels, Ni is toxic to rice and plants exhibit chlorosis and necrosis (Samantaray *et al.* 1997/8), though rice is relatively more tolerant of Ni stress than other crop plants (Llamas and Sanz 2008). Ni reduced plant height, tiller number, root length, and yield in hydroponically grown rice plants (Kasugai and Minami 1936). Net photosynthesis (Moya *et al.* 1993); growth rates of individual plant parts (Moya *et al.* 1993; Rubio *et al.* 1994; Moya *et al.* 1995); and fresh weight, water content, CO_2 balance, and root respiration (Llamas and Sanz 2008) are all reduced by Ni.

Ni inhibits the transport of carbohydrates from seed reserves to a developing seedling though the carbohydrate levels in Ni treated shoots are greater than in control shoots (Moya *et al.* 1993); the inhibition of transport was not observed when younger seedlings are used for testing (Lin and Kao 2006). Abscisic acid and gibberellic acid decrease the uptake of Ni (Rubio *et al.* 1994) but most growth parameters remain reduced without any significant lessening of the Ni-induced growth inhibition (Rubio *et al.* 1994; Moya *et al.* 1995). In the short term, Ni does not alter membrane permeability. In the long term, shoot and root cells lose large amounts of K which causes osmotic loss of water from the cells and results in the symptoms of wilting and necrosis (Llamas *et al.* 2008). The long term effects are not due to changes in the membranes (Sanz *et al.* 2009).

Ni induces oxidative stress, increasing the activity of the ROS scavenging enzymes except for catalase (Maheshwari and Dubey 2009). Ni triggers the activation of mitogen-activated protein kinases (MAPK), key molecules in signal transduction of the oxidative stress induced by Ni (Chen *et al.* 2007b); triggers proline accumulation, a stress response (Lin and Kao 2007; Maheshwari and Dubey 2007); and inhibits RNase and protease activities resulting in higher levels of RNA, soluble proteins, and free amino acids (Maheshwari and Dubey 2007).

Nicotianamine will complex with Ni and, in maize, the YS1 transporter will take up the complex. It is not known if the rice YS1 transporter takes up the complex, but there is evidence that rice takes Ni up actively at low concentration, while at excessively high levels the rice plant's absorption is passive.

SELENIUM

Selenium (Se) is an essential microelement for animals but its role in plants is unresolved. Se can increase rice plant height, root length, protein and glutathione levels, and antioxidant activity (Zhang *et al.* 2002). Se has variable effects on rice root and shoot growth, especially at different phosphate concentrations (Liu *et al.* 2004).

Rice mostly takes up SeO_3^{-2} (selenite), the dominant form of available Se in paddy soils. Se absorption is not related to root proton secretion. Se appears to enter the root cells through water channels, especially at lower pH's. However, Se does not enter through Ca^{+2}, K^+, or anion channels (Zhang *et al.* 2006). Se uptake levels are controlled by the activity of cysteine synthase in the roots (Zhang *et al.* 2006). Cysteine synthase forms Se-Cys, which is converted to selenomethionine, the primary form of Se in rice (Beilstein *et al.* 1991).

Milled rice from Se-fertilized plants has higher antioxidant activity (Xu and Hu 2004). A Se-binding protein in rice, OsSBP, plays a role in the rice defense response. Its RNA expression is upregulated by inoculation with rice blast fungus as well as by endogenous signaling molecules involved in pathogen resistance (Sawada *et al*. 2004).

STRONTIUM

Radioactive strontium (Sr) is a constituent of fallout from atomic bomb explosions. Rice plants have access to Sr from either the air or the soil/water, with most (about 60%) of the Sr found in milled rice (Ichikawa *et al*. 1962; Bourdeau *et al*. 1965) and in the shoots (Bourdeau *et al*. 1965) originating in the soil/water. Irrigated rice absorbs more Sr than non-irrigated rice (Myttenaere and Bourdeau 1968). The distribution of Sr through the rice plant is highest in the lower leaf blades (Tensho *et al*. 1959). Rice has a relatively low ratio, compared to other cereals, of Sr activity in the grain relative to that remaining on the leaves (Colle *et al.* 2009). Relatively little Sr from airborne sources finds its way into milled rice since the endosperm is protected by husks and bran and Sr is not mobile within the plant (Kodaira *et al*. 1973). Likewise, Sr in irrigation water has a low transport level into the seed (Myttenaere and Bourdeau 1968). The maximum uptake of Sr into the rice plant occurs at the flowering stage and Sr has an affinity for cell membranes (Kodaira *et al*. 1973). Very little of the Sr absorbed by the rice plant at the panicle-forming stage ends up in the panicle; about 10x more Sr absorbed by the rice plant at the booting stage ends up in the panicle (Asada and Kasai 1960). Less than 1.5% of the Sr in the above ground rice plant is found in the hulled rice (Tensho *et al*. 1961). Uchida *et al.* (2009) review the transfer factors for ^{90}Sr for rice.

VANADIUM

Vanadium (V) has varying effects on rice growth. V can reduce the growth of rice seedlings (Tham *et al*. 2001) though, in concentrations up to 150 ppm, V increases the height, root length, and weight of rice seedlings (Chiu 1953). These increases in seedling-treated plant growth apparently do not carry over after being transplanted to the paddy since the growth and yield of the mature plants are not affected (Chiu 1953). V added to pot-grown rice increases the tiller number and the number of seeds per plant (Shibuya and Saeki 1934). However, V does not affect rice seed germination (Tham *et al*. 2001).

At the biosynthetic level, V drastically inhibits chlorophyll biosynthesis and net photosynthesis (Somasundaram *et al*. 1994). V blocks the H^+-pumping activity that generates proton gradients across the plasma membrane (Bucker *et al*. 2006). V has been used to demonstrate inhibition of proton extrusion and K^+ uptake in different rice varieties (Bucker *et al*. 2006) and along the length of the rice root (Tanoi *et al*. 2005).

CONCLUSIONS

Rice is a valuable organism for genetic, biochemical, and physiological studies of plant responses to toxic minerals. Rice has numerous cultivars and mutants that are available to screen for resistant and tolerant lines for use in research such as studies of the uptake of non-nutritive minerals at non-toxic levels are valuable for understanding of the uptake of nutritive minerals.

A common response of rice to toxic minerals is the generation of ROS. The ROS scavenging pathways induced in tolerant rice cultivars vary with the mineral, indicating specificity of the signaling mechanisms. Rice is more tolerant of high levels of toxic minerals than most other crop species. This is at least partially due to sequestration in the iron plaque that forms on the submerged roots. This may be true for many of the minerals that are found in the roots but for which further uptake into the plant and subsequently into the consumable endosperm is often low enough that rice can be grown on soil not suitable for other crops.

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