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Mechanism of Potassium Alleviation of Manganese Phytotoxicity in Barley

Shah Alam,¹ Fumihito Akiha,² Shigeru Kamei,¹ S. M. Imamul Huq,³
and Shigenao Kawai¹

¹Faculty of Agriculture, Iwate University, Morioka, Japan

²Radio Isotope Laboratory, Iwate University, Morioka, Japan

³Department of Soil, Water and Environment, Dhaka University, Dhaka, Bangladesh

ABSTRACT

Manganese (Mn) toxicity and potassium (K) deficiency are the major factors that limit plant growth and development in acid soils. The objective of this study was to assess the role of high K on the alleviation of Mn toxicity in barley (*Hordeum vulgare* L. cv. 'Minorimugi') grown in a phytotron for 14 d. Modified half-strength Hoagland-Aron solution (pH 5.5) was used as the medium. The treatments were (1) 0.25 μ M Mn + 3 mM K (control); (2) 25 μ M Mn + 3 mM K (Mn-toxic); and (3) 25 μ M Mn + 30 mM K (K-alleviated). The Mn-toxic plants showed the symptoms of Mn toxicity and mild iron (Fe) deficiency, whereas in the K-alleviated plants such symptoms were absent. The K-alleviated plants had dry weight, chlorophyll content, and Fe concentration similar to that in the control plants, indicating that high K (30 mM) in the growth medium could alleviate Mn toxicity and Mn-induced Fe deficiency. Roots of plants fed separately with ⁵⁴Mn and ⁵⁹Fe in the presence of 3.0 and 30 mM K for 4 h were also studied. Results showed that high K could help in avoiding the accumulation of ⁵⁴Mn, indicating that K plays an antagonistic role on Mn absorption by roots of barley and its subsequent translocation to the shoots. However, the absorption of ⁵⁹Fe was not influenced by the high K concentration in a short-term experiment (4 h), indicating that high K does not affect short-term Fe absorption by the roots of barley plants. These results suggested that the alleviating effect of high K could be attributed to the antagonistic effect of K on Mn absorption by roots and translocation into shoots.

Keywords: iron-59, K alleviation, manganese-54, Mn phytotoxicity, short-term absorption

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Address correspondence to Shigenao Kawai, Faculty of Agriculture, Iwate University, 3-18-8 Ueda, Morioka 020-8550, Japan. E-mail: akawai@iwate-u.ac.jp

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INTRODUCTION

Potassium (K) is the principal inorganic constituent of the cytosol and plays a critical role in lowering cellular osmotic water potentials, thereby reducing the loss of water from leaf stomata and increasing the ability of roots to absorb water from the soil (Marschner, 1995). Potassium is the dominant counterion in neutralizing the negative charges on proteins and nucleic acids (Marschner, 1995; Wyn-Jones and Pollar, 1983). Potassium can comprise up to 10% of the total dry weight of plants grown in K-replete conditions (Leigh and Wyn-Jones, 1984). It causes no off-site environmental problems when it leaves the soil and also does not cause eutrophication in aquatic systems (Brady and Weil, 2002).

Potassium differs from other cations in that loss of exchangeable K in many soils will be slowly replenished by release of non-exchangeable K (Russell, 1973). Plants are able to survive over a 10^4 -fold range of K in growth media (Maathuis and Sanders, 1996). The concentration of K in the soil solution usually considered adequate for good crop growth is 0.50 mM; but 5.0 mM or above is needed by some crops (Russell, 1973; Asher and Ozanne, 1967), and K does not become toxic to most species until the concentration exceeds 50 to 100 mM (Sheahan et al., 1993).

Manganese (Mn) toxicity is a limiting factor for crop production on acid soils and can also be a problem in neutral or alkaline soils having poor aeration caused by waterlogging or compaction (Foy et al., 1988; Weil et al., 1997). Potassium has been reported to alleviate Mn toxicity by decreasing Mn absorption by roots (Hennan and Campbell, 1981; Alam et al., 2002) and increasing Mn tolerance (Alam et al., 2003a). High levels of Mn may induce iron (Fe) deficiency in plants (Alam et al., 2000; Epstein, 1972; Hewitt, 1948), and K can alleviate Fe deficiency (Alam et al., 2002, 2003a; Barak and Chen, 1984; Bolle-Jones, 1955). Robson and Pitman (1983) suggested that Fe and Mn might compete for a common absorption site so that the interaction of Mn and K may be crossed-linked with an Fe-Mn antagonism. In a previous study, high K decreased the absorption and translocation of ^{54}Mn , but without showing any apparent effect on the absorption of ^{59}Fe (Alam et al., 2003b). The feeding experiments of isotopes in that study were conducted with low-Mn ($0.25 \mu\text{M}$) conditions, leading to the idea that K alleviation of Mn toxicity could not be related directly to Fe-Mn antagonism. In the present paper, the short- and long-term effects of high K in alleviating Mn toxicity and Mn-induced Fe deficiency in barley plants are reported.

MATERIALS AND METHODS

Plant Culture

Germinated seeds of barley (*Hordeum vulgare* L. cv. 'Minorimugi') were transferred to 10 L plastic buckets containing 10 L of various experimental nutrient

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solutions (Alam et al., 2000). The control growth medium was a modified half-strength Hoagland-Amon nutrient solution that contained 0.25 μM Mn and 3 mM K. Plants grown in this solution were compared with those treated with either 25 μM Mn plus 3 mM K (Mn-toxic) or 25 μM Mn plus 30 mM K (K-alleviated). Additional Mn was applied as MnSO_4 , and additional K was supplied as K_2SO_4 . The pH of the nutrient solution was adjusted initially to 5.5 and re-adjusted daily to 5.5 with 1 M HCl or 1 M NaOH. The solutions were aerated throughout the experiment, and the solution level was maintained by the addition of deionized water. The nutrient solutions were renewed weekly, and plants were grown under controlled conditions in a phytotron (day/night, 14/10 h; temperatures, 17°C/10°C; light intensity, 280 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for 14 d.

Feeding of ^{54}Mn and ^{59}Fe in Different Plants

Plants grown in the control, Mn-toxic, and K-alleviated treatments were transferred to beakers containing 100 mL of the basal nutrient solution with two levels of K (3 or 30 mM) to examine the short-term effect of K on ^{54}Mn and ^{59}Fe absorption. Control, Mn-toxic, and K-alleviated plants were supplied with two levels of K (3 or 30 mM) at 0.25, 25, or 25 μM Mn containing 37, 185, or 185 kBq of ^{54}Mn respectively for 4 h. In another experiment, plants were similarly supplied with two levels of K at 10 μM Fe in the solution containing 37 kBq of ^{59}Fe . The ^{54}Mn - or ^{59}Fe -radionuclides were purchased from NEN Life Science Products (Boston, MA). Iron adsorbed in the root apoplast was removed (Bienfait et al., 1985), and plants were rinsed with tap water, separated into shoots and roots, oven dried at 60°C for 1 d, and weighed.

Measurement of ^{54}Mn and ^{59}Fe

Plant samples were digested with concentrated HNO_3 (Zarcinas et al., 1987). Radioactivity of ^{59}Fe in the root apoplast or digested plant tissues and ^{54}Mn in digested plant tissues was determined using a gamma scintillation counter (Auto Well Gamma System ARC-300, Aloka, Tokyo, Japan) (Malcolme-Lawes, 1979). Adsorbed ^{59}Fe in the root apoplast was not included to calculate root Fe. The amount of absorbed ^{54}Mn and ^{59}Fe was calculated based on the molar radioactivity of the elements supplied after correction for their half-life decay.

Chemical Analysis of Plants

Plants were washed with deionized water, separated into shoots and roots, and dried in an oven at 60°C for 1 d to determine dry weights. Dried samples were digested with a nitric-perchloric acid mixture and analyzed for K, calcium (Ca), magnesium (Mg), copper (Cu), Fe, Mn, and zinc (Zn) by atomic absorption

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spectroscopy (170-30, Hitachi, Tokyo, Japan) (Piper, 1950) and for phosphorus (P) by a colorimetric vanadate method (Jackson, 1965). Chemical analyses were based on dry weight.

Chlorophyll Content

Chlorophyll content in new leaves of plants was measured non-destructively with a portable chlorophyll meter (SPAD-502, Minolta Camera Co. Ltd., Tokyo, Japan) at the time of harvest (Abadía and Abadía, 1991).

Statistical Analysis

The experiment was arranged in randomized blocks with three replications. Data on shoot and root dry weights, chlorophyll content, and mineral elements were subjected to analysis of variance. Differences between means were evaluated using the Ryan-Einot-Gabriel-Welsch multiple range test ($P \leq 0.05$) (SAS, 1988).

RESULTS AND DISCUSSION

Visual Symptoms

Manganese toxicity symptoms of plants grown with 25 μM Mn and 3 mM K (Mn-toxic) included stunted, brown-colored roots, brown spots on matured leaves, general chlorosis of young leaves, and desiccation of older leaves. These symptoms are similar to those reported by Alam et al. (2000) and Horst (1988). Plants grown with 25 μM Mn and 30 mM K looked green and healthy. Alleviation of Mn toxicity by high K (30 mM) has also been reported for soybean (Hennan et al., 1981), barley (Alam et al., 2002), and rice (Alam et al., 2003a).

Plant Growth

The dry weight of plants grown in the Mn-toxic treatment was significantly lower than that of the control plants (Figure 1). The adverse effect of high Mn on dry weight also has been reported for soybean (Hennan et al., 1981), barley (Alam et al., 2000), and rice (Alam et al., 2003a; van der Vorm and van Diest, 1979). The dry weight of K-alleviated plants was similar to that of the control plants. These results suggest that detrimental effects on growth of plants in acidic soils, or in waterlogged or compacted neutral or alkaline soils, resulting in high levels of available Mn (Foy et al., 1988; Weil et al., 1997), may be alleviated by K amendment.

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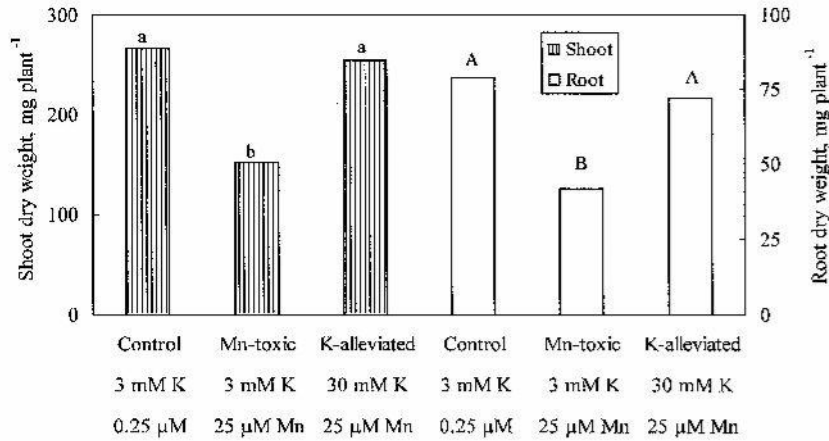


Figure 1. Dry weight of shoots and roots of barley plants with two levels of Mn and K. Bars with the same letter are not significantly different ($p < 0.05$).

Chlorophyll Content

The chlorophyll content of young leaves of plants grown in the Mn-toxic treatment was lower than that of the control plants (Figure 2) and suggests that decreased chlorophyll content in young leaves is an obvious and typical symptom of Mn toxicity-induced Fe deficiency in plants (Marschner, 1995). There was no statistical difference between the chlorophyll content of young leaves of plants grown in the control and in K-alleviated treatments. Although K is neither

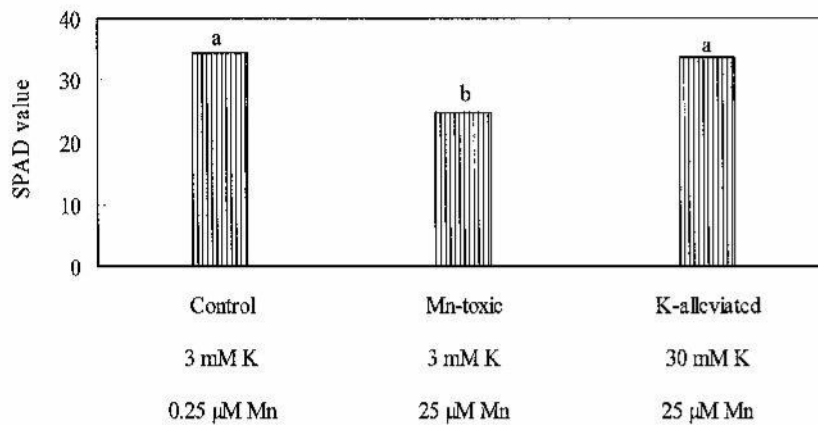


Figure 2. Chlorophyll content in fully opened young leaves of barley plants with two levels of Mn and K. Bars with the same are not significantly different ($p < 0.05$).

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a constituent of chlorophyll nor a regulator of its biosynthesis, high K increased the chlorophyll content of plants grown with toxic levels of Mn, indicating that high K level could alleviate the Mn-induced Fe deficiency. Restoration of normal chlorophyll levels and an alleviation of Fe deficiency may be attributed to the favorable effect of K on Fe absorption in barley (Alam et al., 2002), rice (Alam et al., 2003a), peanut (Barak and Chen, 1984), and potato (Bolle-Jones, 1955).

Mineral Elements in Plants

In comparison with control plants, Mn in shoots and roots increased more than 10- and 148-fold in Mn-toxic plants and four- and 22-fold in K-alleviated plants (Table 1). This large increase in tissue Mn was accompanied by Mn toxicity symptoms on older leaves and restricted plant growth. Vlamis and Williams (1964) reported that Mn toxicity on older leaves suppressed dry weights of barley plants because the active photosynthetic area was limited. The concentration of Mn in shoots and roots of K-alleviated plants was lower than that in Mn-toxic plants. This decrease in tissue Mn might explain the alleviation of Mn-toxicity symptoms. Similar observations were made by Hennan and Campbell (1981) and Alam et al. (2002, 2003b). The present observations are in contradiction to the reports that K fertilization increases tissue Mn in plants (Waddington et al., 1972; Smith, 1975). The reason may be the acidic conditions of the growth media that accompanied Mn toxicity in the present study.

Table 1
Concentration of nutrients in shoots and roots of barley plants grown in nutrient solution with two levels of Mn and K

Treatment		Nutrient							
Mn (μm)	K (mM)	mg g ⁻¹ dry weight				$\mu\text{g g}^{-1}$ dry weight			
		K	P	Ca	Mg	Fe	Mn	Zn	Cu
Concentration in shoots									
0.25	3	87.2c	5.77b	7.16a	1.61a	72.8a	18.5c	15.0b	6.59b
25	3	93.4b	6.70a	5.75b	1.16b	48.1b	190a	21.3a	9.98a
25	30	133a	5.84b	2.23c	0.45c	71.1a	74.6b	21.0a	9.58a
Concentration in roots									
0.25	3	67.0c	6.48b	2.45a	4.23a	278b	24.7c	17.4c	16.9ab
25	3	89.0b	7.02a	2.05b	2.92b	368a	3645a	24.8a	21.3a
25	30	121a	6.58b	0.89c	1.15c	288b	536b	19.6b	13.4b

For plant parts, values with the same letter in each column are not significantly different ($p < 0.05$).

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Shoot Fe in Mn-toxic plants was within 30 to 50 $\mu\text{g Fe g}^{-1}$ dry weight (Table 1). This level is considered critical for physiological Fe deficiency in plants (Römheld and Marschner, 1991). This result was expressed as Fe chlorosis. On the other hand, shoot Fe concentration in K-alleviated plants was similar to that of the control plants, where no chlorosis was apparent. Similar results have been reported in rice (Hennan et al., 1981), barley (Alam et al., 2002), and potato (Bolle-Jones, 1955). Smith (1975) reported no effect of K fertilization on Fe in shoots of alfalfa, whereas Li et al. (2001) reported that adequate K reduced Fe translocation from roots to shoots of rice plants grown under Fe-toxic conditions. The concentration of Fe in roots of Mn-toxic plants was higher than in control plants (Table 1). This increase in root Fe could be partly explained by the adverse effect of high Mn on root growth. The shoot Fe concentration in the same treatment was much lower than either control or K-alleviated plants, suggesting the repression of upward translocation of Fe.

It appears that toxic levels of Mn influenced synergistically the absorption of Cu and Zn (Table 1). This effect might have a different consequence (Cu and Fe toxicity) if the elements are present in excess in the growth medium.

The concentration of Ca and Mg in shoots and roots of Mn-toxic plants was negatively affected by the presence of high Mn level (Table 1). Application of high K (30 mM) could not alleviate the situation. This finding is consistent with earlier reports (Alam et al., 2003a). Horst (1988) reported that excess Mn induces Ca and Mg deficiency due to action on absorption kinetics. Lower Ca and Mg concentrations in K-alleviated plants than in Mn-toxic plants possibly were due to competition between K and Mg or Ca for absorption, which usually involves the risk of K-induced Ca or Mg deficiency (Marschner, 1995). No Ca- or Mg-deficiency symptoms, however, were observed in any of the treatments in this study.

Manganese toxicity increased P and K in shoots and roots compared with control plants (Table 1) and is consistent with reports for rice (Alam et al., 2003a), barley (Alam et al., 2001), and bean (Horst, 1978). The K-alleviated plants had higher K and lower P in tissues than did Mn-toxic plants, as previously reported (Alam et al., 2002, 2003a).

Effect of Potassium on the Absorption and Translocation of ^{54}Mn and ^{59}Fe

The interacting effects of Mn and K in nutrient solution were reflected in differences in ^{54}Mn concentrations in shoots and roots of different plants (Figure 3). The K concentration in the growth media of the control and the Mn-toxic plants was 3 mM and that of K-alleviated plants was 30 mM K, but the feeding of ^{54}Mn or ^{59}Fe was conducted with solutions containing 3 or 30 mM K. Plants supplied with high K (30 mM) contained less ^{54}Mn than plants supplied with low K (3 mM), indicating that high K inhibited absorption and translocation of ^{54}Mn .

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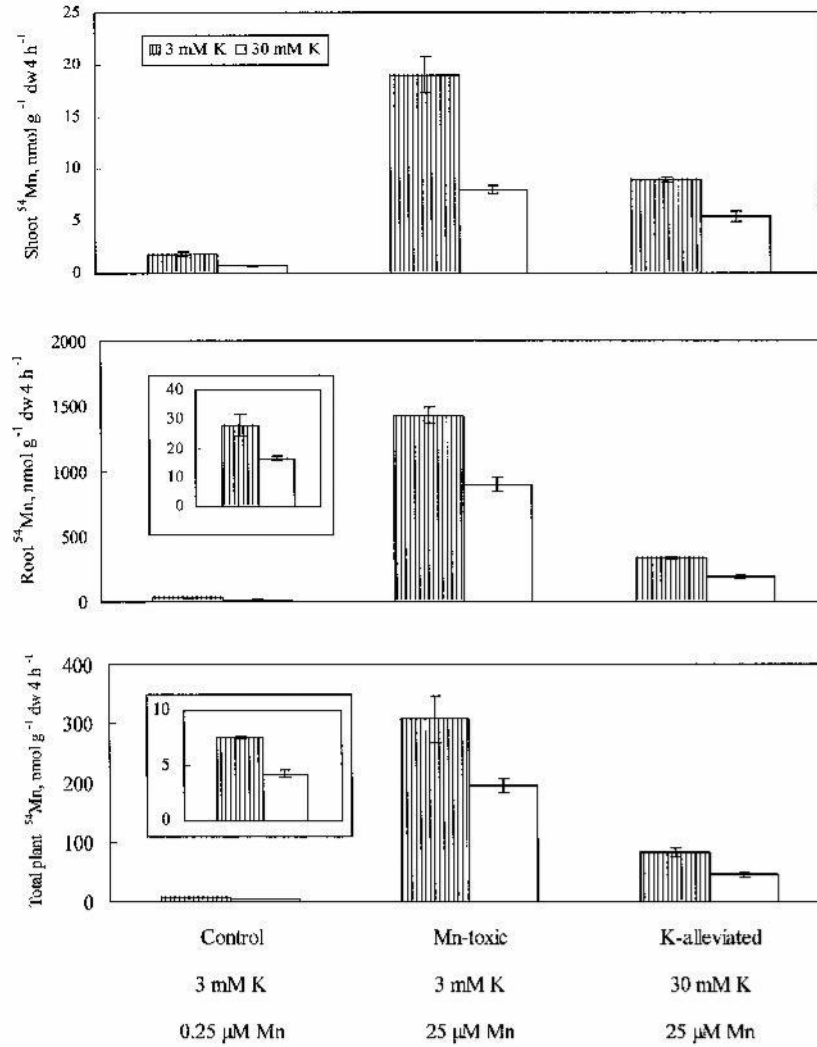


Figure 3. Concentration of ⁵⁴Mn in shoots and roots of barley plants in the presence of two levels of K (3 or 30 mM K). Vertical bars represent \pm SE (n = 3). Insert shows the concentrations in the control.

The ⁵⁹Fe concentration in shoots and roots was lower in Mn-toxic plants than in the control plants (Figure 4), indicating that high Mn inhibited absorption and translocation of Fe. These results are consistent with the general fact that Fe deficiency in plants occurs because of factors that inhibit its absorption and translocation or impair its utilization in metabolic processes (Brown, 1961; Welch et al., 1991). The ⁵⁹Fe in shoots and roots of

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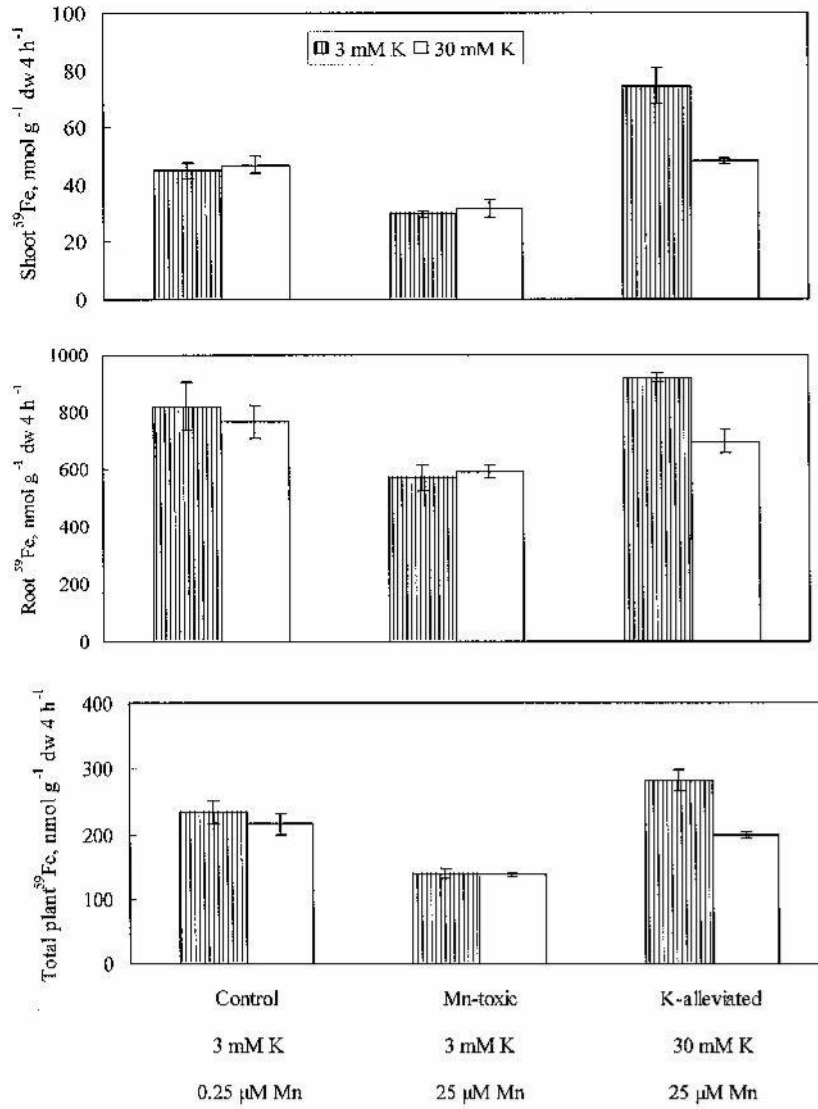


Figure 4. Concentration of ⁵⁹Fe in shoots and roots of barley plants in the presence of two levels of K (3 or 30 mM). Vertical bars represent ± SE (n = 3).

K-alleviated plants and control plants did not differ significantly and indicated that K did not affect Fe absorption. The ⁵⁹Fe in the control and Mn-toxic plants was not affected by levels of K in solution, although K-alleviated plants fed low K had more ⁵⁹Fe. These results suggest that high K did not enhance Fe absorption and that the mechanism of K-alleviation of Mn toxicity does

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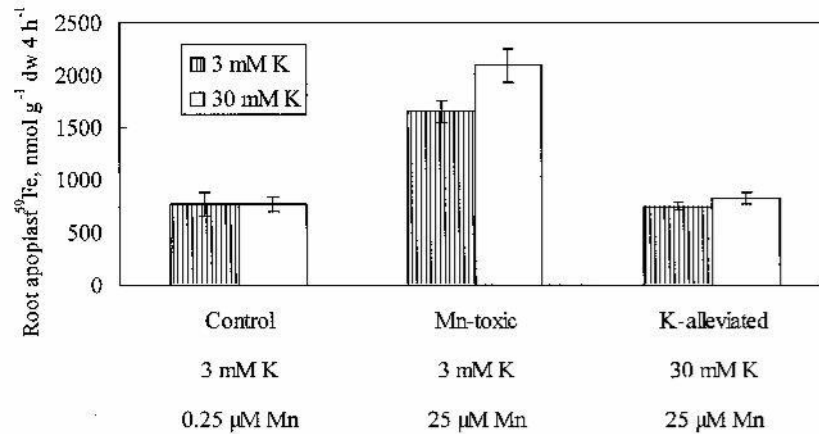


Figure 5. Concentration of ⁵⁹Fe in root apoplast of barley plants in the presence of two levels of K (3 or 30 mM). Vertical bars represent \pm SE ($n = 3$).

not involve the enhancement of Fe absorption. Therefore, the higher amount Fe in K-alleviated plants than in Mn-toxic plants, calculated based on data of Table 1 and Figure 1, may be the result of a secondary effect of high K.

The root apoplast of Mn-toxic plants had more ⁵⁹Fe than did control plants (Figure 5), indicating that high Mn could influence the formation of Fe pool in the root apoplast. More ⁵⁹Fe in the root apoplast was consistent with higher Fe concentration in roots of Mn-toxic plants (Table 1) since root Fe represents absorbed Fe as well as Fe adsorbed to the fixed negative charges in the root apoplast (Branton and Jacobson, 1962). No significant difference was observed in root apoplast ⁵⁹Fe concentration between K-alleviated and control plants, suggesting that K-alleviated plants were physiologically similar in Fe absorption to control plants. High K increased root apoplast ⁵⁹Fe only in Mn-toxic plants. The reasons as to why Mn-toxic plants had more ⁵⁹Fe in their root apoplast and why high K increased ⁵⁹Fe in the root apoplast remains unexplained.

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