Role of Mineral Nutrients in Tolerance of Crop Plants to Environmental Stress Factors

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Abstract

Around 60% of cultivated soils worldwide have plant-growth-limiting problems caused by mineral nutrient deficiencies and toxicities. Therefore, improving the mineral nutritional status of plants under marginal environmental conditions is of great importance for maintenance of crop productivity. In most cases plants growing under marginal environmental conditions (e.g. salinity, low and high temperatures, and drought) receive much more sunlight than they can utilize in photosynthetic electron transport and CO_2 fixation. This causes excessive accumulation of absorbed light energy and of photoreductants in the chloroplasts, which leads to activation of molecular O_2 to reactive oxygen species (ROS). When ROS are not adequately scavenged, photooxidative damage occurs in the chloroplasts, and leads to chlorophyll damage, lipid peroxidation and, consequently, cell death. By limiting the utilization of absorbed light energy in photosynthesis, environmental stress factors increase the potential for photooxidative damage in chloroplasts. Because an adequate supply of mineral nutrients is indispensable for maintenance of photosynthetic electron transport and carbon metabolism, impairment of the mineral nutritional status of plants under marginal environmental conditions can exacerbate photooxidative damage and limit plant performance. In the present study, several examples are given, which show that plants exposed to environmental stresses require additional supplies of mineral nutrients, particularly nitrogen (N), potassium (K), magnesium (Mg), calcium (Ca) and zinc (Zn) to minimize the adverse affects of stresses. Enhanced production of ROS in plants under marginal conditions is not caused only by impairment of photosynthetic electron transport. It appears likely that an NADPH-dependent oxidase is another important source of ROS, which is stimulated by drought, chilling, and/or salinity. Of the mineral nutrients, K and Zn seem to interfere with the NADPH-oxidizing enzyme and thus to provide additional protection against damaging attack of ROS under salinity, drought and chilling stress. It is concluded that improving the mineral nutritional status of crop plants is of great importance for

minimizing detrimental effects of environmental stress factors on their growth and yield.

Introduction

Crop plants are often exposed to various environmental stress factors, such as drought, soil acidity, salinity and extreme temperatures, which severely affect soil productivity and crop production, worldwide. Bray *et al*. (2000) estimated that the contribution of environmental stress factors to global losses in crop production is becoming increasingly important. Fig. 1 shows that the relative decreases from the record yield capacity (maximum yield under ideal growth conditions) caused by abiotic stress factors vary between 60 and 82% for corn, wheat and soybean. In the case of wheat and soybean, record yields are 14.5 and 7.4 mt/ha, respectively, but the current worldwide average yields are 1.9 and 1.6 mt/ha, respectively (Fig. 1).

In comparison with the yield capacity losses of wheat and soybean caused by biotic stress factors, those caused by abiotic stress factors are much greater. Most of the yield losses caused by abiotic stresses are attributed to drought, salinity, extreme temperatures, acidity, and impairments of the mineral nutritional status of plants, i.e., deficiencies and toxicities. Recently, Cakmak (2002) reported that at least 60% of cultivated soils worldwide have growth-limiting problems arising from mineral nutrient deficiencies and toxicities. Combinations of such soil nutritional problems with other environmental stress factors such as drought, salinity, chilling, etc. are responsible for severe losses in crop production worldwide.

Survival and productivity of crop plants exposed to environmental stresses are dependent on their ability to develop adaptive mechanisms to avoid or tolerate stress. Accumulating evidence suggests that the mineral nutritional status of plants greatly affects their ability to adapt to adverse environmental conditions. In the present paper the role of the mineral nutritional status of plants in their adaptation to environmental stress conditions will be discussed, with emphasis on abiotic stress factors. Of the mineral nutrients affecting plant adaptation to stress conditions, nitrogen (N), potassium (K), magnesium (Mg), calcium (Ca), zinc (Zn) and boron (B) are the most extensively studied, therefore, special attention will be paid to them.
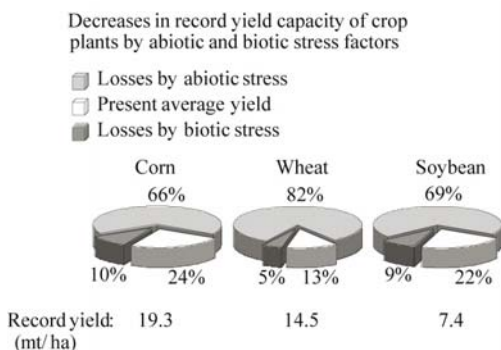
Fig. 1. Record yields (yields under ideal conditions) and decreases from the record yield capacities of corn, wheat and soybean plants, caused by abiotic and biotic stress factors (Bray *et al*., 2000).

High-light stress and photooxidation

Photooxidative damage, i.e., light-dependent generation of reactive oxygen species (ROS) in chloroplasts, is the key process involved in cell damage and cell death in plants exposed to environmental stress factors (Foyer *et al*., 1997; Asada, 2000; Foyer and Noctor, 2005). As shown in Fig. 2, chloroplasts are the main sites of ROS formation, and photosynthesis electron transport provides the main means of formation of ROS such as superoxide radical ($O_2^{.-}$), hydroxyl radical ($OH^{.}$), and singlet oxygen ($^1O_2$). ROS are highly toxic to vital cell constituents and are responsible for destruction of chlorophyll, DNA, membrane lipids and proteins. Formation of ROS is particularly prolific when absorption of light energy exceeds the capacity of photosynthetic electrons to transport it. Environmental stress factors diminish photosynthetic electron transport and CO_2 fixation at various stages of the photosynthesis process (Fig. 2). Therefore, a combination of an environmental stress with high light intensity may induce severe photo-oxidative damage to chloroplasts, and consequently cause decreases in the yield capacity of plants. The mineral nutritional status of plants greatly influences photosynthesis electron transport and CO_2 fixation in various ways (Marschner, 1995; Cakmak and Engels, 1999; Mengel and Kirkby, 2001). Impairment of the mineral nutrition of plants can, therefore, be accompanied by an enhanced potential for photo-oxidative damage, and this threat can be especially serious when plants are simultaneously exposed to an environmental stress.
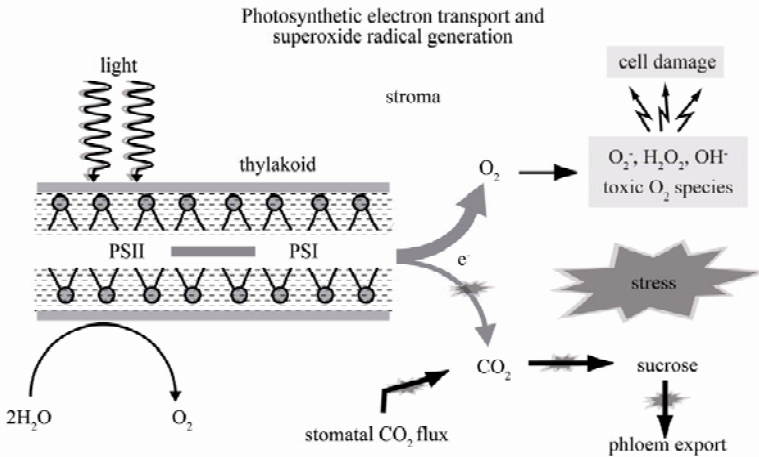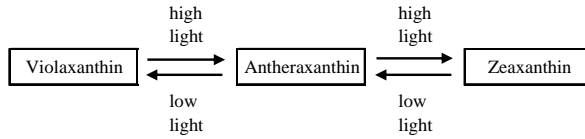
Fig. 2. Schematic representation of ROS formation in chloroplasts under environmental stress conditions. ✱: indicates inhibition of the corresponding reaction by stress. (Cakmak, 2003, 2005).

Nitrogen

Of the mineral nutrients, nitrogen plays a major role in utilization of absorbed light energy and photosynthetic carbon metabolism (Kato *et al*., 2003; Huang *et al*., 2004). An excess of non-utilized light energy can be expected to occur in N-deficient leaves, where it leads to a high risk of photo-oxidative damage. In rice plants under high light intensity, N deficiency is associated with enhanced lipid peroxidation (Huang *et al*., 2004), and Kato *et al*. (2003) recently showed that plants grown under high-intensity light with a high N supply had greater tolerance to photo-oxidative damage and higher photosynthesis capacity than those grown under similar high light with a low N supply. Utilization of the absorbed light energy in electron transport was also much higher in N-adequate than in N-deficient plants. These results indicate that N-adequate plants are able to tolerate excess light by maintaining photosynthesis at high rates and developing protective mechanisms. To avoid the occurrence of photo-oxidative damage in response to excess light energy, the thylakoid membranes have a protective mechanism by which excess energy is dissipated as heat. Dissipation of excess light energy is associated with enhanced formation of the xanthophyll pigment zeaxanthin, which is synthesized from violaxanthin in the light-dependent xanthophyll cycle (Demmig-Adams and Adams, 1992, 1996):

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            high                      high
            light                     light
┌──────────────┐       ┌──────────────┐       ┌──────────────┐
│ Violaxanthin │ ───▶  │ Antheraxanthin│ ───▶  │  Zeaxanthin  │
│              │ ◀───  │              │ ◀───  │              │
└──────────────┘       └──────────────┘       └──────────────┘
            low                       low
            light                     light
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In plants suffering from N deficiency, the conversion of xanthophyll cycle pigments and formation of zeaxanthin were enhanced, and were accompanied by chlorophyll bleaching, particularly under high light intensity (Verhoeven *et al*., 1997; Kato *et al*., 2003). In spinach, N-deficient plants dissipate a greater fraction of the absorbed light energy than N-adequate ones: up to 64% and only 36%, respectively. This difference was associated with corresponding changes in xanthophyll cycle pigments: about 65% of the total xanthophyll pigments were present as zeaxanthin and antheraxanthin in N-deficient plants compared with 18% in the N-adequate plants (Verhoeven *et al*., 1997). These results indicate impaired use of the absorbed light energy in photosynthetic fixation of CO_2, with consequently enhanced demand for protection against excess light energy, in N-deficient plants. Certainly, the reduction in the utilization of light energy and the consequently elevated need for protection against photo-oxidative damage in N-deficient plants can be more marked when the N deficiency stress is combined with an environmental stress.

The form in which N is supplied affects plant tolerance to photodamage. The light-induced conversion of violaxanthin to zeaxanthin, as a means to dissipate excess light energy was found to be stronger in bean leaves supplied with nitrate than in those supplied with ammonium (Bendixen *et al*., 2001). In good agreement with these findings, Zhu *et al*. (2000) demonstrated that nitrate-grown bean plants had higher tolerance to photodamage than ammonium-grown ones. Under very high light intensity ammonium-grown plants had, therefore, higher levels of lipid peroxidation and higher contents of antioxidative enzymes.

Potassium, magnesium and zinc

Similarly to N deficiency, deficiencies of K, Mg and Zn also enhance the sensitivity of plants to photo-oxidative damage. When supplies of these nutrients are low, leaf symptoms of chlorosis and necrosis, and disturbances of plant growth become more severe when plants exposed to high light intensity (Marschner and Cakmak, 1989; Cakmak and Marschner, 1992; Cakmak *et al*., 1995; Polle, 1996).

Deficiencies of K and/or Mg cause marked decreases in photosynthetic C metabolism and utilization of fixed carbon (Marschner, 1995; Cakmak and Engels, 1999; Mengel and Kirkby, 2001). Consequently, their deficiencies cause massive accumulation of carbohydrates in source leaves, with consequent inhibition of photosynthetic C reduction (Fig. 3). Consistent with these changes in photosynthetic C metabolism, an excess of non-utilized light energy and photoelectrons is expected in K- and Mg-deficient plants, which leads to photoactivation of molecular O_2 and the occurrence of photo-oxidative damage (Fig. 2). This is the main reason why Mg- and K-deficient leaves are highly light sensitive. Partial shading of K- or Mg-deficient leaves delayed or eliminated the occurrence of leaf chlorosis and necrosis (Marschner and Cakmak, 1989; Cakmak, 1994). These observations strongly suggest that photo-oxidative damage to chloroplasts is a key process in the occurrence of leaf symptoms under conditions of Mg or K deficiency. In contrast to Mg and K deficiency, P deficiency had no effect on sucrose transport from source leaves, and there was no accumulation of photosynthates in leaves (Fig. 3). Leaf chlorosis, such as is found in K- and Mg-deficient plants, is not typical of P-deficient plants (Cakmak, 1994). Because of the distinct effects of Mg and K on photosynthetic carbon metabolism and on ROS formation in chloroplasts, photo-oxidative damage in plants grown under marginal conditions, such as drought, chilling and salinity can be exacerbated when the soil supply of Mg or K is low.
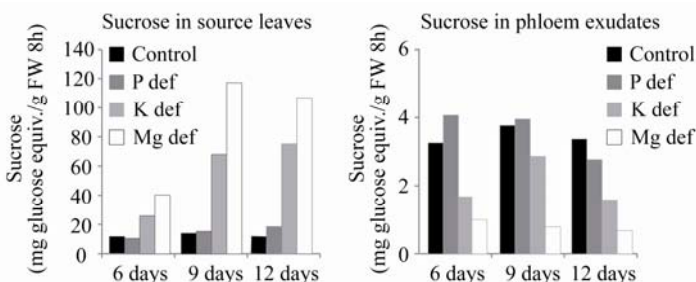

Fig. 3. Effect of insufficient supplies of P, K and Mg on sucrose concentration in source leaves, and on the export of sucrose from source leaves of bean plants via the phloem during 12 days of growth (Cakmak *et al.*, 1994).

Salinity

Evidence is accumulating that reactive O_2 species are major mediators of salt-induced cell damage in crop plants. In several plant species, application of NaCl, even at low concentration, stimulated the activities of antioxidative

enzymes, which suggests a role of salt stress in ROS formation (Comba *et al.*, 1998; Tsugane *et al.*, 1999; Wang *et al.*, 2005). On the basis of inhibitor studies and measurement of production of $O_2^{\cdot-}$ it has been shown that a plasma membrane-bound NADPH oxidase is involved in the generation of $O_2^{\cdot-}$ following salt treatments (Kawano *et al.*, 2002; Aktas *et al.*, 2005). Accordingly, salt stress-induced cell damage could be prevented by overexpression of superoxide dismutase (SOD) in chloroplasts of rice plants (Tanaka *et al.*, 1999).

Zinc ions are known to be strong inhibitors of NADPH oxidase. In bean and cotton root cells Zn deficiency caused a significant increase in activity of NADPH-dependent $O_2^{\cdot-}$ production, and a resumed supply of Zn to Zn-deficient plants for 12 or 24 h caused a distinct reduction in the activity of $O_2^{\cdot-}$-generating enzymes (Cakmak and Marschner, 1988a; Pinton *et al.*, 1994). Similarly, in tobacco cell cultures salt-induced $O_2^{\cdot-}$ generation by NADPH oxidase was strongly inhibited by Zn (Kawano *et al.*, 2002). Previously, it has been often hypothesized that improving the Zn nutritional status of plants growing in saline conditions was critical for protection of plants against salt toxicity. This protective role of Zn was ascribed to its role in maintenance of the structural integrity of the plasma membrane and thus controlling the uptake of Na and other toxic ions (Welch *et al.*, 1982; Cakmak and Marschner, 1988b). In light of the protective roles of Zn against ROS it can be suggested that Zn ions protect salt-stressed plants not only from uptake of toxic ions across plasma membranes but also from damaging attack of ROS.

Like Zn, K, too, is a critical mineral nutrient that protects plant cells from salt-induced cell damage. Impairment of the K nutritional status of plants by increased Na uptake is a well-known phenomenon (Liu and Zhu, 1997). The K/Na ratio is plant tissue is, therefore, considered to be a reliable indicator of the severity of salt stress, or for screening plant genotypes for high Na tolerance. In studies with *Arabidopsis* mutant lines Zhu *et al.* (1998) showed that mutant lines showing very high sensitivity to NaCl were also highly sensitive to low K supply, and exhibited a poor capacity for taking up K from a growth medium. As discussed above, salt stress represents an oxidative stress, and causes activation of $O_2^{\cdot-}$-generating NADPH oxidase. Recently, we found that K deficiency resulted in a remarkable increase in NADPH oxidase activity in bean, with concomitant production of $O_2^{\cdot-}$ (Cakmak, 2003, 2005). Shin and Schachtman (2004) also reported that ROS production was an early root response to K deficiency, which was catalysed by $O_2^{\cdot-}$-generating NADPH oxidase. These results suggest that salt stress-induced $O_2^{\cdot-}$ generation by NADPH oxidase could be aggravated by a lack of K. As Na toxicity causes K deficiency at cellular levels, the increase in NADPH-dependent $O_2^{\cdot-}$ generation under salt stress (Kawano *et al.*, 2002) might be the result of an impaired K

nutritional status of the plants. This point seems to be important, and should be elucidated in future studies.

Drought

In plants exposed to high light intensity at very low temperature or under drought stress, development of photo-oxidative damage and generation of ROS is very common (Foyer *et al*., 1997; Jiang and Zhang, 2002a, b; Wang *et al*., 2005). As discussed above, most mineral nutrients are a basic necessity for maintenance of photosynthetic electron transport. Therefore, the occurrence of photo-oxidative damage in plants stressed by drought or low temperature can be more dramatic when the plants also suffer nutrient deficiencies. Of the mineral nutrients, K plays a critical role in the stomatal activity and water relations of plants (Marschner, 1995; Mengel and Kirkby, 2001). Decreases in photosynthesis caused by drought stress in wheat become particularly high in plants growing under K deficiency, but are only minimal when the K supply is adequate. The capacity of plants to maintain high concentrations of K in their tissues seems to be a useful trait to take into account in breeding genotypes for high tolerance to drought stress. In *Hibiscus rosa-sinensis* plants grown under various K treatments, the root survival rate was strongly reduced when the water supply was limited, especially at the lowest K supply (Egilla *et al*., 2001); an adequate supply of K was essential for enhancing the drought resistance of the plants and improving their root longevity. The beneficial effect of an adequate K supply was ascribed to the role of K in retranslocation of photoassimilates in roots, which contributed to better root growth under drought stress (Egilla *et al*., 2001; Fig. 3).

As in salt-stressed plants, also in plants exposed to drought stress, ROS formation by $O_2^{\cdot-}$ -generating NADPH oxidase was enhanced (Zhao *et al*., 2001; Jiang and Zhang, 2002a, b). It appears that, in addition to ROS formation by photosynthetic electron transport, ROS production by NADPH oxidase activity is involved in cell damage and plant growth depression under drought stress. As indicated above, Zn and K strongly influence NADPH oxidation and NADPH-dependent $O_2^{\cdot-}$ generation. Under deficiency of these nutrients, especially of K, the capacity of root cells to oxidize NADPH is markedly increased, with concomitant production of $O_2^{\cdot-}$. In light of these results it may be suggested that the protective roles of Zn and K against drought stress seem also to be related to their inhibitory effects on NADPH-dependent $O_2^{\cdot-}$ generation. Therefore, in case of deficiency of these nutrients, plants become more sensitive to drought stress.

Chilling

Formation of ROS by NADPH oxidase and weakening of the antioxidative defensive systems are also important in chilling-induced cell damage (Shen *et al*., 2000; Aroca *et al*., 2005; Wang *et al*., 2005). Since insufficient supplies of K and Zn lead to significantly increased NADPH oxidase activity, ROS formation in plants grown at low temperatures can be additionally exacerbated under deficiencies of these nutrients. Production of ROS in chilling-stressed plants can also be expected, in parallel with impaired photosynthetic electron transport and CO_2 fixation (Wise and Naylor, 1987; Asada, 2000). There are several examples from field experiments that demonstrate a role of K and Zn in protection of plants under low-temperature conditions: frost damage and related decreases in potato plant yields were alleviated by application of large doses of K (Grewal and Singh, 1980); during winter, citrus trees were found to be more vulnerable to low temperatures and peroxidative damage when grown under Zn-deficient conditions (Cakmak *et al*., 1995). N, too, is involved in protection of plants against chilling stress; in studies with Eucalyptus seedlings it was found that seedlings with impaired N nutritional status were less susceptible to photo-oxidative damage in winter (Close *et al*., 2003). Like low N supply, also excess N results in high sensitivity to environmental stress: stress tolerance of plants can be diminished because of modified root and shoot growth. Marschner (1995) found that a very high supply of N often led to a reduced root-to-shoot ratio that, in turn, impaired the support of shoot biomass with mineral nutrients and water. Also, in plants receiving a high N supply, most parts of the roots may grow near to the soil surface, with consequently higher sensitivity to frost and drought damage (Gordon *et al*., 1999; Saebo *et al*., 2001). Saebo *et al*. (2001) showed that tolerance to frost damage was very low at the highest N supply rate, which led to the suggestion that the tissue N status should not be very high during winter.

Generally, plant genotypes that tolerate low-temperature stress are able to maintain high leaf water potential by closing their stomata and preventing transpirational water loss (Wilkinson *et al*., 2001). Calcium has been shown to be an essential requirement for chilling-induced stomatal closure in chilling-tolerant genotypes. Increasing the Ca supply induces stomatal closure, and this effect is most distinct in plants grown at low temperatures. It is also believed that ABA-induced induced stomatal closure is partially mediated by Ca released from internal guard cell stores or the apoplast (Wilkinson *et al*., 2001), and this function seems to make Ca a major contributing factor to chilling tolerance and protection of leaves from dehydration.

Conclusions

The existing data indicate that it is essential to improve the mineral nutritional status of plants under marginal environmental conditions, in order to sustain their survival and to maintain high yields. Plant requirements for mineral nutrients increase with increasing severity of the environmental stresses imposed by drought, heat, salinity, chilling, or intense light. Impairment of the mineral nutritional status of plants, therefore, exacerbates the adverse effects of environmental stress factors on plant performance. The present paper has focused on one of the major reasons for the aggravation of the adverse effects of stresses by an insufficient supply of mineral nutrients, namely, the enhanced production of highly toxic ROS and the resulting photo-oxidative damage to chloroplast pigments and lipids. The production of ROS during photosynthesis, which is normally an unavoidable process, is intensified because of the limited and diminished utilization of absorbed light energy in photosynthetic electron transport and CO_2 fixation, which results from environmental stresses such as drought, salinity and chilling. Mineral nutrients, such as N, K, Mg, Ca and Zn, supplied at adequate levels are an essential requirement for the maintenance of photosynthesis activities and utilization of light energy in CO_2 fixation. Therefore, the improvement of mineral nutrition of plants becomes a major contributing factor in protecting them from photo-oxidative damage under marginal environmental conditions. Further challenges include the gaining of better understanding of the roles of mineral nutrients in: i) ROS formation during photosynthesis and formation of plasma membrane-bound NADPH oxidase; ii) signaling pathways that affect the adaptive responses of plants to environmental stresses; and iii) expression and regulation of stress-induced genes that contribute to stress tolerance.

References

Aktas, H., L. Karni, D.C. Chang, E. Turhan, A- Bar-Tal, and B. Aloni. 2005. The suppression of salinity-associated oxygen radicals production, in pepper (*Capsicum annuum*) fruit, by manganese, zinc and calcium in relation to its sensitivity to blossom-end rot. Physiologia Plantarum 123:67-74.

Aroca, R., G. Amodeo, S. Fernandez-Illescas, E.M. Herman, F. Chaumont, and M.J. Chrispeels. 2005. The role of aquaporins and membrane damage in chilling and hydrogen peroxide induced changes in the hydraulic conductance of maize roots. Plant Physiology 137:341-353.

Asada, K. 2000. The water-water cycle as alternative photon and electron sinks. Philosophical Transactions of the Royal Society, B. 355:1419-1430.

Bendixen, R., J. Gerendas, K. Schinner, B. Sattelmacher, and U.P. Hansen. 2001. Difference in zeaxanthin formation in nitrate- and ammonium-grown *Phaseolus vulgaris*. Physiologia Plantarum 111:255-261

Bray, E.A., J. Bailey-Serres, and E. Weretilnyk. 2000. Responses to abiotic stresses. *In:* Biochemistry and molecular biology of plants. B. Buchanan, W. Gruissem and R. Jones (eds.). American Society of Plant Physiologists. pp. 1158-1203.

Cakmak, I. 1994. Activity of ascorbate-dependent H_2O_2-scavenging enzymes and leaf chlorosis are enhanced in magnesium and potassium deficient leaves, but not in phosphorus deficient leaves. Journal of Experimental Botany 45:1259-1266.

Cakmak, I. 2000. Possible roles of zinc in protecting plant cells from damage by reactive oxygen species. New Phytology 146:185-205.

Cakmak, I. 2002. Plant nutrition research: Priorities to meet human needs for food in sustainable ways. Plant and Soil 247:3-24.

Cakmak, I. 2003. The role of potassium in alleviating detrimental effects of abiotic stresses in plants. *In:* Feed the soil to feed the people: the role of potash in sustainable agriculture. International Potash Institute, Basel. pp. 325-343.

Cakmak, I. 2005. The role of potassium in alleviating detrimental effects of abiotic stresses in plants. Journal of Plant Nutrition and Soil Science 168:521-530.

Cakmak, I., and C. Engels. 1999. Role of mineral nutrients in photosynthesis and yield formation. *In:* Mineral nutrition of crops: mechanisms and implications. Z. Rengel (ed.). The Haworth Press, New York. pp. 141-168.

Cakmak, I., and H. Marschner. 1988a. Increase in membrane permeability and exudation in roots of zinc deficient plants. Journal of Plant Physiology 132:356-361.

Cakmak, I., and H. Marschner. 1988b. Enhanced superoxide radical production in roots of zinc deficient plants. Journal of Experimental Botany 39:1449-1460.

Cakmak, I., and H. Marschner. 1992. Magnesium deficiency and high light intensity enhance activities of superoxide dismutase, ascorbate peroxidase and glutathione reductase in bean leaves. Plant Physiology 98:1222-1227.

Cakmak, I., and V. Romheld. 1997. Boron deficiency-induced impairments of cellular functions in plants. Plant and Soil 193:71-83.

Cakmak, I., C. Hengeler, and H. Marchner. 1994. Changes in phloem export of sucrose in leaves in response to phosphorus, potassium and magnesium deficiency in bean plants. Journal of Experimenal Botany 45:1251-1257.

Cakmak, I., M. Atli, R. Kaya, H. Evliya, and H. Marschner. 1995. Association of high light and zinc deficiency in cold induced leaf chlorosis in grapefruit and mandarin trees. Journal of Plant Physiology 146:355-360.

Close, D.C., C.L. Beadle, and M.J. Hovenden. 2003. Interactive effects of nitrogen and irradiance on sustained xanthophyll cycle engagement in *Eucalyptus nitens* leaves during winter. Oecologia 134:32-36.

Comba, M.E., M.P. Benavides, and M.L. Tomaro. 1998. Effect of salt stress on antioxidant defence system in soybean root nodules. Australian Journal of Plant Physiology 25:665-671.

Demming-Adams, B., and W.W. Adams III. 1992. Photoprotection and other responses of plants to high light stress. Annual Review of Plant Physiology Plant Molecular Biology 43:599–626.

Demming-Adams, B., and W.W. Adams III. 1996. The role of the xanthophyll cycle carotenoids in protection of photosynthesis. Trends in Plant Science 1:21–26.

Egilla, J.N., F.T. Davies, and M.C. Drew. 2001. Effect of potassium on drought resistance of *Hibiscus rosa-sinensis* cv. Leprechaun: plant growth, leaf macro- and micronutrient content and root longevity. Plant and Soil 229:213-224.

Foyer, C.H., and G. Noctor. 2005. Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell and Environment 28:1056-1071.

Foyer, C.H., H. Lopez-Delgado, J.F. Dat, and I.M. Scot. 1997. Hydrogen peroxide- and glutathione-associated mechanisms of acclimatory stress tolerance and signalling. Plant Physiology 100:241-254.

Gordon, C., S.J. Woodin, I.J. Alexander, and C.E. Mullins. 1999. Effects of increased temperature, drought and nitrogen supply on two upland perennials of contrasting functional type: *Calluna vulgaris* and *Pteridium aquilinum*. New Phytology 142:243-258.

Grewal, J.S., and S.N. Singh. 1980. Effect of potassium nutrition on frost damage and yield of potato plants on alluvial soils of the Punjab (India). Plant and Soil 57:105-110.

Huang, Z.A., D.A. Jiang, Y. Yang, J.W. Sun, and S.H. Jin. 2004. Effects of nitrogen deficiency on gas exchange, chlorophyll fluorescence, and antioxidant enzymes in leaves of rice plants. Photosynthetica 42:357-364.

Jiang, M.Y., and J.H. Zhang. 2002a. Involvement of plasma-membrane NADPH oxidase in abscisic acid- and water stress-induced antioxidant defense in leaves of maize seedlings. Planta 215:1022-1030.

Jiang, M.Y., and J.H. Zhang. 2002b. Water stress-induced abscisic acid accumulation triggers the increased generation of reactive oxygen species and up-regulates the activities of antioxidant enzymes in maize leaves. Journal of Experimental Botany 53:2401-2410.

Kato, M.C., K. Hikosaka, N. Hirotsu, A. Makino, and T. Hirose. 2003. The excess light energy that is neither utilized in photosynthesis nor dissipated by photoprotective mechanisms determines the rate of photoinactivation in photosystem II. Plant Cell Physiology 44:318-325.

Kawano, T., N. Kawano, S. Muto, and F. Lapeyrie. 2002. Retardation and inhibition of the cation-induced superoxide generation in BY-2 tobacco cell suspension culture by Zn^{2+} and Mn^{2+}. Physiologia Plantarum 114:395-404.

Liu, J., and J. Zhu. 1997. An arabidopsis mutant that requires increased calcium for potassium nutrition and salt tolerance. Proceedings of the National Academy of Sciences of the USA 94:14960-14964.

Marschner, H. 1995. Mineral nutrition of higher plants. 2nd Edition. Academic Press, San Diego. 889 pp.

Marschner, H., and I. Cakmak. 1989. High light intensity enhances chlorosis and necrosis in leaves of zinc-, potassium- and magnesium-deficient bean (*Phaseolus vulgaris*) plants. Journal of Plant Physiology 134:308-315.

Mengel, K., and E.A. Kirkby. 2001. Principles of plant nutrition. 5th edition. Kluwer Academic Publishers, Dordrecht. 848 pp.

Pinton, R., I. Cakmak, and H. Marschner. 1994. Zinc deficiency enhanced NAD(P)H-dependent superoxide radical production in plasma membrane vesicles isolated from roots of bean plants. Journal of Experimental Botany 45:45-50.

Polle, A. 1996. Mehler reaction: friend or foe in photosynthesis? Botanica Acta 109:84-89.

Saebo, A., A. Haland, O. Skre, and L.M. Mortensen. 2001. Influence of nitrogen and winter climate stresses on *Calluna vulgaris* (L.) Hull. Annals of Botany 88:823-828.

Shen, W., K. Nada, and S. Tachibana. 2000. Involvement of polyamines in the chilling tolerance of cucumber cultivars. Plant Physiology 124:431-439.

Shin, R., and D.P. Schachtman. 2004. Hydrogen peroxide mediates plant root cell response to nutrient deprivation. Proceedings of the National Academy of Sciences of the USA 101:8827-8832.

Tanaka, Y., T. Hibino, Y. Hayashi, A. Tanaka, S. Kishitani, T. Takabe, S. Yokota, and T. Takabe. 1999. Salt tolerance of transgenic rice overexpressing yeast mitochondrial Mn-SOD in chloroplasts. Plant Science 148:131-138:

Tsugane, K., K. Kobayashi, Y. Niwa, Y. Ohba, K. Wada, and H. Kobayashi. 1999. A recessive arabidopsis mutant that grows photo autotrophically under salt stress shows enhanced active oxygen detoxification. Plant Cell 11:1195-1206.

Verhoeven, A.S., B. Demmig-Adams, and W.W. Adams III. 1997. Enhanced employment of the xanthophyll cycle and thermal energy dissipation in spinach exposed to high light and N stress. Plant Physiology 113:817–824.

Wang, Y.J., M. Wisniewski, R. Melian, M.G. Cui, R. Webb, and L. Fuchigami. 2005. Overexpression of cytosolic ascorbate peroxidase in tomato confers tolerance to chilling and salt stress. Journal of the American Society for Horticultural Science 130:167-173.

Welch, R.M., M.J. Webb, and J.F. Loneragan. 1982. Zinc in membrane function and its role in phosphorus toxicity. *In:* Proceedings of the Ninth Plant Nutrition Colloquium. Warwick, England. A. Scaife (ed.). Commonwealth Agricultural Bureau, Farnham Royal, Bucks. pp. 710-715.

Wilkinson, S., A.L. Clephan, and W.J. Davies. 2001. Rapid low temperature-induced stomatal closure occurs in cold-tolerant *Commelina communis* leaves but not in cold-sensitive tobacco leaves, via a mechanism that involves apoplastic calcium but not abscisic acid. Plant Physiology 126:1566-1578.

Wise, R.R., and A.W. Naylor. 1987. Chilling-enhanced photooxidation. The peroxidative destruction of lipids during chilling injury to photosynthesis and ultrastructure. Plant Physiology 83:272-277.

Zhao, Z.G., G.C. Chen, and C.L. Zhang. 2001. Interaction between reactive oxygen species and nitric oxide in drought-induced abscisic acid synthesis in root tips of wheat seedlings. Australian Journal of Plant Physiology 28:1055-1061.

Zhu, J., J. Liu, and L. Xiong. 1998. Genetic analysis of salt tolerance in arabidopsis: Evidence for a critical role of potassium nutrition. Plant Cell 10:1181-1191.

Zhu, Z., J. Gerendas, R. Bendixen, K. Schinner, H. Tabrizi, B. Sattelmacher, and U.P. Hansen. 2000. Different tolerance to light stress in NO_3^-- and NH_4^+-grown *Phaseolus vulgaris* L. Plant Biology 2:558-570.