Role of mineral nutrition in alleviation of drought stress in plants

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Abstract

Water, the most important component of life, is rapidly becoming a critically short commodity for humans and crop production. Limited water supply is one of the major abiotic factors that adversely affect agricultural crop production worldwide. Drought stress influences the normal physiology and growth of plants in many ways. It results in an increase in solute concentration outside the roots compared to the internal environment of the root and causes reverse osmosis. As a result, the cell membrane shrinks from the cell wall and may eventually lead to death of the cell. Water stress tends to shrink away from the interface with water-absorbing roots, creating a gap in the soil-plant-air continuum. As the plant continues to lose water via transpiration, water is drawn from root cell wall and may eventually lead to death of the cell. Water stress inhibits photosynthesis in plants by closing stomata and damaging the chlorophyll contents and photosynthetic apparatus. It disturbs the balance between the production of reactive oxygen species (ROS) and the antioxidant defence, causing accumulation of ROS which induces oxidative stress to proteins, membrane lipids and other cellular component. Mineral elements have numerous functions in plants including maintaining charge balance, electron carriers, structural components, enzyme activation, and providing osmoticum for turgor and growth. In this paper, an overview of some macronutrients (nitrogen, phosphorus, potassium, calcium and magnesium), micronutrients (Zinc, Boron, Copper) and silicon has been discussed in detail as how these nutrients play their role in decreasing the adverse effects of drought in crop plant.

Keywords: Macronutrients; micronutrients; mechanisms; drought; alleviation.

Abbreviations: ROS (Reactive oxygen species); CO2 (Carbon dioxide); SOD (Superoxide dismutase); H2O2 (Hydrogen peroxide); H2O (Water); CAT (Catalase); POD ( Peroxidase); C (carbon); H (hydrogen); O (oxygen); N (nitrogen); P (phosphorus); K (potassium); Ca (calcium); Mg (magnesium); S (sulphur); Zn (zinc); Cu (copper); Fe (iron); Mn (manganese); B (boron); Mo (molybdenum); Cl (chlorine); Ni (nickel); Si (silicon); NH4+ (ammonium); NO3− (nitrate); ATP (Adenosine triphosphate); RuBP (ribulose 1,5 bisphosphate); Chl-a,b (chlorophyll a&b); CHO (carbohydrates); Pn (Photosynthetic rate); gs (stomatal conductance).

Introduction

Water stress is one of the major limitations to the agricultural productivity worldwide, particularly in warm, arid and semi arid parts of the world (Boyer, 1982). The world population is expanding rapidly and is expected to be around 8 billion by the year 2025 (Pinarup-Andersen et al., 1999). This represents an addition of over 100 million people to the present population (6 billion) every year. It is a prediction that the increases in world population will occur almost exclusively in developing countries, which are suffering from serious nutritional problems at present, and population pressure on the agricultural soils is already very high. To feed the increasing world population and sustain wellbeing of humankind, food production must be increased by up to 100% over the next 25 years (Borlang and Dowswell, 1993). The proposed increases in food production must be achieved on the already cultivated land, because the potential for expanding the area of agricultural soils is very limited. However, recent trends indicate that productivity and fertility of soils are globally declining due to degradation and intensive use of soils without consideration of proper soil management practices (Gruhn et al., 2000; Cakmak, 2002).

Environmental problems (e.g., water deficiency and salinity) are increasing as a result of burgeoning population of world and intensive use of natural resources. These environmental stresses contribute significantly in reduction of crop yields well below the potential maximum yields. Bray et al. (2000), reported that the relative decreases in potential maximum crop yields (i.e., yields under ideal conditions) associated with abiotic stress factors including drought, vary between 54% and 82%. Therefore, for sustaining food security, a high priority should be given to minimizing the detrimental effects.
of drought. Drought results in the increased generation of reactive oxygen species (ROS) due to energy accumulation in stressed plants which consume less light energy through photosynthetic carbon fixation (Smirnoff 1993; Asada 2006). Drought inhibits or slows down photosynthetic carbon fixation mainly through limiting the entry of CO$_2$ into the leaf or directly inhibiting metabolism (Smirnoff 1993; Loggini et al. 1999; Apel and Hirt 2004). Plants have developed a wide range of adaptive/resistance mechanisms to maintain productivity and ensure survival under drought stress condition. To reduce the toxicity of ROS, plant cells have developed an antioxidative system, consisting of low-molecular-weight antioxidants like ascorbate, α-tocopherol, glutathione, and carotenoids, as well as protective enzymes. Superoxide radicals are scavenged by superoxide dismutase (SOD), while the resulting H$_2$O$_2$ is reduced to H$_2$O by catalase (CAT) and peroxidase (POD) (Mittler 2002; Apel and Hirt 2004). Despite the internal resistance of the plants to drought, stress-related detrimental effects of drought can be minimised by adequate and balanced supply of mineral nutrients. Increasing evidence suggests that mineral-nutrient status of plants plays a critical role in increasing plant resistance to drought stress (Marschner, 1995). Optimal nutrition and most favourable soil tillage greatly affect water circulation within plants, which is a highly effective method of combating drought. Under low nutrient concentrations in soil, plants have to absorb more water to be able to take up the same amount of mineral nutrients for their metabolism than they would from soil with satisfactory fertility. On the other hand, in conditions of lacking soil moisture, plants are unable to get optimal amounts of nutrients, which has negative effects on the overall condition of plants, especially their growth and fruit quality.

Strategies for solving the problem of drought

Drought is a highly complex issue to tackle and its research bears corresponding complexity and requires multidisciplinary approach. Research and development activities relating to this issue are broad and proceed in several directions. Efforts toward solving the problem of drought in plant production are based primarily on the selection of tolerant genotypes. The conventional selection method by crossing exotic germ plasm and adapted elite material has predominated until quite recent times. Over the past several years, however, molecular markers have been used for identification of tolerance carrying genes in addition to adequate selection technology (Miletić et al., 2010). Comparative gene mapping has allowed simultaneous insights into corresponding genes of several crops and their incorporation into domestic selected material for the purpose of increasing their tolerance to drought. At a practical level, the former method includes recombination of genes of different parents, one of which at least is required to have mechanisms and properties of tolerance to drought. The latter method includes an identification of genes playing part in the expression of tolerance to drought, their isolation and transfer into different genotypes by genetic transformation (Miletić et al., 2010). Irrigation is the only method that provides a complete solution to the problem of drought. However, irrigation should not be treated as a method of combating drought as it is essentially a means of intensive and modern agricultural production. It is crucial to determine a rational regime of irrigation and plants’ water requirements. By additionally determining the time, method and rate of irrigation, high and stable yields can be acquired regardless of the duration or intensity of drought spells (Miletić et al., 2010). Intensively cultivated, staple and otherwise most represented agricultural products will be at the focus of efforts toward solving the problem of irrigation and they will primarily be directed toward eastern Serbia and neighbouring regions where high and stable yields can only be secured by providing greater amounts of water than they are already available (Miletić et al., 2010). Apart from developing tolerant genotypes and providing irrigation, rational agricultural practices have been recognized worldwide as yet another basis for planning plant production in arid regions (Miletić et al., 2010). By developing cropping systems, an emphasis is being placed on soil cultivation for the purpose of better absorption, conservation and rational distribution of available water (crop rotation, pre-crop, crop structure, soil cultivation method, conservation tillage, mulching, wind-breaks, choice of crops and cultivars, time of sowing, density, etc.). Depending on available soil moisture, fertility and plant requirements, research should be carried out in search of new plant nutrition. Nutrition of agricultural crops depends also on available moisture (Miletić et al., 2010). Apart from studies of agricultural characteristics, investigation of physiological aspects of adaptation of particular genotypes to drought and stress is crucial in breeding tolerant genotypes with stable yields in drought conditions. It is therefore required that physiological and ecological optimums for plant growth be fully studied. This is all the more important as the physiological optimum is generally achieved in conditions of missing competition. On the other hand, the ecological optimum is closely related with competitive relations among plants. It is therefore necessary that all parameters of plant water status be thoroughly studied (Miletić et al., 2010).

Plant Mineral Nutrition

Proper nutrition is the basic need of every living organism. There are now 17 elements which are considered essential for plants to complete their life cycle (Waraich et al., 2011). These essential plant nutrients are divided into two categories; macronutrients and micronutrients. Macronutrients include carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulfur (S). Micronutrients are zinc (Zn), copper (Cu), iron (Fe), manganese (Mn), boron (B), molybdenum (Mo), chlorine (Cl) and nickel (Ni) (Waraich et al., 2011). Although silicon (Si) is not essential, it is considered as a beneficial plant nutrient. These plant nutrients are not only required for better plant growth and development, but also helpful to alleviate different kinds of abiotic stresses like drought stress. Plants have developed a wide range of adaptive/resistance mechanisms to maintain productivity and ensure survival under a variety of environmental stress conditions. The evidence suggests that mineral-nutrient status of plants plays a critical role in increasing plant resistance to environmental stress factors (Marschner, 1995). This review is an effort to highlight the role of essential mineral nutrients in alleviation of drought stress.

A. Macronutrients

Nitrogen

Nitrogen (N) is an essential macronutrient deficient in most soils, especially arid and semi-arid regions. (Hernandez et al., 2010).
Absorbed by plant roots, 80% contribution is of N. (urea as foliar spray) and inorganic (ammonium (NH$_4^+$) and nitrate (NO$_3^-$) as soil application) forms, and in plants, NO$_3^-$ is reduced to NH$_3$ for assimilation into plant organic N (Jalloh et al., 2009). For better crop growth, a combination of ammonium (NH$_4^+$) and nitrate (NO$_3^-$) sources is preferred (Frechilla et al., 1999). Nitrogen absorption and utilization by plants under water stress is very critical for plant growth and productivity. Nitrogen affects carbon partitioning and it improves accumulation of soluble sugars and especially starch which in turn improve leaf growth (Rufy et al., 1988). Nitrogen application, where light is not limiting, increases antioxidative defense mechanisms (Marschner, 1995), resulting in reduced photoproduction of chloroplast pigments, and reduced leaf senescence. Nitrogen applied as fertilizers or in other forms is closely related to the ability of plant roots to absorb water from soil. When water inside the plant declines below a threshold level, stomata close which causes a decrease in transpiration resulting in a reduction in water transport through the plant. This in turn, affects the roots ability to absorb water and nutrients as effectively as supposed to be under normal transpiration (Waraich et al., 2011). Drought-induced Nitrogen deficiency largely contributes to growth inhibition under water deficit (Heckathorn et al., 1997) mainly affecting the leaf size through decreasing cell number and cell size (MacAdam et al., 1989). Toth et al. (2002); Vos and Biemond (1992) reported reduction in leaf production, individual leaf area and total leaf area under N deficient conditions. Trapani et al. (1999) observed increased cell production and cell expansion leading to an increase in final leaf area in sunflower with high N availability. Increased leaf area index, leaf area duration, crop photosynthetic rate, radiation interception and radiation use efficiency have also been reported by enhanced Nitrogen supply (Muchow, 1988). Goudriaan and van Keulen (1979) and Just et al. (1989) observed changes in leaf photosynthesis in response to variations in plant nitrogen supply. Leaf photosynthesis is influenced by lamina nitrogen content over a wide range of irradiance and varies widely between different crop species (Sinclair and Horie, 1989). Consequently, lower rates of photosynthesis under conditions of nitrogen limitation are often attributed to reduction in chlorophyll contents and rubisco activity (Evans and Terashima, 1987; Fahi et al., 1994; Fredeen et al., 1994; Verhoeven et al., 1997; Toth et al., 2002). In C$_3$ plants, three quarters of nitrogen content in leaf is associated with photosynthesis and in sunflower 50% leaf soluble protein accounts for the single photosynthetic enzyme rubisco (Gimenez et al., 1992). Lawlor (2002) reported that plant metabolic processes, based on proteins, leading to increase in vegetative and reproductive growth and yield are totally dependent upon the adequate supply of Nitrogen. Disturbance in protein metabolism as a result of water stress has also been reported by Ranieri et al. (1989). Reduction in protein contents of wheat genotypes under water stress conditions may be the result of reduced RNA contents due to increased RNase activity induced by dehydration (Martin and Dasilva, 1972). Verga et al. (1992) reported an increase in protein content when Nitrogen was applied before sowing in soil and observed no change when applied during later developmental stages in soybean (Glycine max L.). Kettlewell and Juggins (1992) observed increase in protein content with the application of urea and slight increase in leaf starch in wheat. Many studies have indicated changes in behavior of NO$_3$ assimilatory enzymes in plants under water-stress conditions (Larsson et al. 1989; Kaisar and Brendle-Behnisch, 1991; Kenis et al., 1994; Brewitz et al., 1996). Nitrate reductase (NR), the first enzyme in the pathway of nitrogen assimilation has received the maximum attention and has been shown to decrease in water-stressed leaves of sunflower (Azedo-Silva et al., 2004). Increased nitrogen application to water-stressed plants increases nitrate uptake and increases NR activity (Kathju et al., 1990). Dehydration adversely affected the activity of nitrate reductase in roots of sunflower (Azedo-Silva et al. 2004) and in wheat (Larsson et al., 1989), whereas contrasting results were observed in roots of maize and no effect of dehydration on nitrate reductase activity was recorded (Abd-El Baki et al., 2000). Correia et al. (2005) reported that the activity of nitrate reductase (NR; EC 1.6.6.6) in Helianthus annuus L. and non-nodulated Lupinus albus L. was negatively affected by soil drying and a decreased supply of nutrients and the observed changes in NR activity being linearly correlated with the depletion of nitrate. Possible mechanisms to minimize the detrimental effects of drought by improving water use efficiency with N nutrition were described by Waraich et al (2011). Inorganic fertilization has been reported to mitigate the adverse effects of water stress on crop growth and development (Marschner, 1995; Payne et al., 1995; Raun and Johnson 1999). Water stress at different growth stages causes various morphophysiological changes in the plant to acclimatize under such conditions (Ali et al., 2011). Water stress at seedling stage might lead to higher dry root weights, longer roots, coleoptiles and higher root/shoot ratios which could be exploited as selection criteria for stress tolerance in crop plants at very early stage of growth (Takele, 2000; Dhanda et al., 2004; Kashiwagi et al., 2004). Whereas, at later growth phase like reproductive stage, flag leaf area (Karamanos and Papatheohari, 1999; Ali et al., 2010), specific leaf weight, leaf dry matter (Aggarwal and Sinha, 1984), excised leaf weight loss (Bhutta, 2007), relative dry weight (Jones et al., 1980), relative water content (Colom and Vazzana, 2003), residual transpiration (Savour et al., 1997) and cell membrane stability (Ali et al., 2009b) are the characters of interest and had been widely exploited as reliable morph-physiological markers contributing towards drought tolerance for various crop plants.

**Phosphorus**

Phosphorus (P) is found in less quantity in soils as compared to N and K. Total P concentration in surface soils varies from 0.005 to 0.15% (Havlin et al., 2007). After N, it is the 2nd most deficient plant nutrient that is applied to plants as fertilizer. More than 30 million metric tonnes of P2O5 in phosphate fertilizers per year are used worldwide, and of
Fig. 1. Possible mechanisms through which P nutrition can minimize the detrimental effects of drought in plants.

Fig. 2: Schematic representation of Reactive Oxygen Species (ROS) generation in chloroplasts of K-deficient leaves as described by Cakmak, 2006.
which, more than 99% is derived from rock phosphate (IFA, 2005). The use of P fertilizers has increased the crop production many fold, possibly through making N:P ratio narrow. Phosphate is the principal element involved in plant energy processes. Its need is critical because of the role of ATP (Adenosine triphosphate) in recovery (Palta, 2000). Phosphate levels may be low due to dry soil conditions or impaired root uptake and should be reinforced for both types of stresses. The relative leaf-growth rate is one of the most sensitive parameter to phosphorus deficiency (Kirschbaum and Tompkins, 1990), and it affects the photosynthetic rate per unit area. Phosphorous deficiency induced decline in leaf growth and photosynthetic rate may be ascribed to reduction in stomatal conductance and ribulose 1,5 bisphosphate (RuBP) carboxylase regeneration capacity (Brooks, 1986). The reported accumulation of starch indicates that photosynthates cannot be used for plant growth under P limited condition (Fredeen et al., 1989). Phosphorus deficiency is also known to reduce the uptake rate of nitrates and its assimilation by the nitrate reductase (Pilbeam et al., 1993). Radin (1984) reported that P nutrition alters the relation between leaf turgor and stomatal conductance in cotton. Thus, phosphorous deficient plants closed their stomata lower leaf water potential than in late flowering genotypes. Phosphorus is a constituent of nucleic acids, phospholipids, phosphor-proteins, dinucleotides, and adenosine triphosphate. Hence, P is required for processes including the storage and transfer of energy, photosynthesis, the regulation of some enzymes, and the transport of carbohydrates (Hu and Schmidhalter, 2001). Soils in arid areas are often calcareous and have high pHs (e.g., those in Mediterranean regions). In the semi-arid tropics, soils are often rich in aluminum and iron oxides, and the pHs are low. Both of these soil types show a strong tendency for P fixation (Oertli, 1991). It is generally accepted that the uptake of P by crop plants is reduced in dry-soil conditions (Pinkerton and Simpson, 1986). For example, the translocation of P to the shoots is severely restricted even under relatively mild drought stress (Rasnick, 1970). However, Liebersbach et al. (2004) reported that the large amount of molecular exudates (i.e., mainly mucilage) from plants in dry soil counteract the reduced mobility of P under such conditions. Turner (1985) pointed out that P deficiency appears to be one of the earliest effects of mild to moderate drought stress in soil-grown plants. The application of P fertilizer can improve plant growth considerably under drought conditions (Ackerson, 1985; Studer, 1993; Garg et al., 2004). The positive effects of P on plant growth under drought have been attributed to an increase in stomatal conductance (Brück et al., 2000), photosynthesis (Ackerson, 1985), higher cell-membrane stability, water relations (Sawwan et al., 2000) and drought tolerance. An important approach for increasing P uptake involves taking advantage of the symbiosis between the roots and mycorrhiza, the latter of which enhance both the growth or resistance of plants subjected to drought, and also the uptake of P, Zn, Cu, Mn, and Fe (Bagayoko et al., 2000). Ajouri et al. (2004) reported that priming seeds with solutions containing the limiting nutrients under drought conditions (such as P and Zn) can improve barley establishment. Smith (2002) suggested that strategies for increasing nutrient uptake by overexpressing genes encoding for high-affinity P transporters are likely to be an important strategy in the future, especially in light of the increasing problems caused by P-deficient soils of the semi-arid tropics. A schematic diagram of how P deficiency affects plant growth is presented in Fig.1. Phosphorus improves the root growth and maintains high leaf water potential. The improved root growth results in improved water and nutrient uptake and increases the activity of nitrate reductase which improves the assimilation of nitrate under drought condition (Fig.1). Phosphorus also maintains the cell turgidity by maintaining the high leaf water potential which in turn increases the stomatal conductance and increases the photosynthetic rate under drought.

Potassium

Potassium (K) plays an important role in survival of plants under environmental stress conditions. Potassium is essential for many physiological processes, such as photosynthesis, translocation of photosynthates into sink organs, maintenance of turgescence, activation of enzymes, and reducing excess uptake of ions such as Na and Fe in saline and flooded soils (Marschner, 1995; Mengel and Kirkby, 2001). This review deals with the roles of K in minimizing adverse effects of environmental stress conditions on crop production, with particular emphasis on abiotic stress factors. There is increasing evidence that plants suffering from environmental stresses like drought have a larger internal requirement for K (Cakmak and Engels, 1999). Environmental stress factors that enhance the requirement for K also cause oxidative damage to cells by inducing formation of ROS, especially during photosynthesis (Bowler et al., 1992; Elstner and Osswald, 1994; Foyer et al., 1994). The reason for the enhanced need for K by plants suffering from environmental stresses appears to be related to the fact that K is required for maintenance of photosynthetic CO₂ fixation. For example, drought stress is associated with stomatal closure and thereby with decreased CO₂ fixation. Based on the model given in Fig. 2, formation of ROS is intensified because of inhibited CO₂ reduction by drought stress. Obviously, formation of ROS under drought stress would be dramatic in plants exposed to high light intensity, with concomitant severe oxidative damage to chloroplasts. Increases in ROS production in drought-stressed plants are well known and related to impairment in photosynthesis and associated disturbances in carbohydrate metabolism (Seel et al., 1991; Quartacci et al., 1994; Jiang and Zhang, 2002). The figure. 2 represents that when plants are grown under low supply of K, drought-stress induced ROS production can be additionally enhanced, at least due to K-deficiency-induced disturbances in stomatal opening, water relations, and photosynthesis (Marschner, 1995; Mengel and Kirkby, 2001). In addition, most importantly, under drought conditions chloroplasts lose high amounts of K to further depress photosynthesis (Sen Gupta and Berkowitz, 1987) and induce further ROS formation. This discussion strongly support the idea that increases in severity of drought stress result in corresponding increases in K demand to maintain photosynthesis and protect chloroplasts from oxidative damage. Decrease in photosynthesis caused by drought stress is particularly high in plants supplied with low K, and are minimal when K is sufficient (Sen Gupta et al., 1989). Alleviation of detrimental effects of drought stress, especially on photosynthesis, by sufficient K supply has also been shown in legumes (Sangakkara et al., 2000). In field experiments conducted in Egypt, it was found that decreases in grain yield resulting from restricted irrigation could
greatly eliminated by increasing K supply (Abd El-Hadi et al., 1997). In view of these results, it can be concluded that improvement in K nutritional status of plants seems to be of great importance for sustaining high yields under rain-fed conditions. Possible mechanisms helpful in minimizing detrimental effects of drought by improving water use efficiency in crop plants with K nutrition were described by Waraich et al (2011). Under water-deficit conditions, K nutrition increases crop tolerance to water stress by utilizing the soil moisture more efficiently than in K-deficient plants. Potassium maintains the osmotic potential and turgor of the cells (Lindauer, 1995) and regulates the stomatal functioning under water stress conditions (Kant & Kafkafi, 2002). It enhances photosynthetic rate, plant growth and yield under stress conditions (Egila et al., 2001). The protective role of K in plants suffering from drought stress by maintenance of a high pH in stroma and against the photo-oxidative damage to chloroplasts was also reported by Cakmak (1997).

**Calcium**

Calcium (Ca) was once considered important only for cell-wall structure, but since the recent discovery of Calmodulin, it has become clear that Ca is not just a macronutrient but also a major controller of plant metabolism and development (Poovaiah & Reddy, 2000). Calcium is considered to play a role in mediating stress response during injury, recovery from injury, and acclimation to stress (Palta, 2000). It has been suggested that Ca is necessary for recovery from drought by activating the plasma membrane enzyme ATPase which is required to pump back the nutrients that were lost in cell damage (Palta, 2000). Since dehydration is the common denominator, Ca also has a role to play in freeze injury tolerance. Possible mechanisms to minimize detrimental effects of drought in crop plants by improving Ca nutrition are presented in Fig.3. Calcium has a very prominent role in the maintenance of cell structure. Its activates the plasma membrane enzyme ATPase which pumps back the nutrients lost during cell membrane damage due to Ca deficiency and recover the plant from injury (Fig. 3). Calcium also plays a role as calmodulin which controls the plant metabolic activities and enhances the plant growth under drought condition.

**Magnesium (Mg)**

Magnesium (Mg) is involved in several physiological and biochemical processes in plants affecting growth and development. Epstein and Bloom (2004) reported that Mg is
exceptional in activating more enzymes than any other mineral nutrient. Mg-activated enzymes are ATPases, ribulose-1, 5-bisphosphate (RuBP) carboxylase, RNA polymerase and protein kinases (Marschner, 1995; Shaul, 2002). Mg role as the central atom of the Chlorophyll molecule is perhaps the best-known function of Mg in plants which it is associated with the development of leaf chlorosis, typically interveinal, under Mg deficiency stress. Scott and Robson, (1990) reported that 6 and 35% of the total Mg may be bound in the chloroplasts of the plant. Lateritic soils are also usually poor in Mg. Magnesium deficiency can be induced, however, not only by a direct lack of Mg but also by the presence of competing cations that prevent Mg uptake, such as Ca++, in calcareous soils; H+, NH4+ and Al+++ in acidic soils and Na+ in saline soils (Mengel and Kirkby, 2001; Shaul, 2002). An increasing body of evidence indicates that Mg plays a fundamental role in phloem export of photosynthates from the source to the sink organs, and its deficiency results in dramatic increases in accumulation of carbohydrates in the source leaves (Cakmak et al., 1994a, 1994b; Marschner et al., 1996). Asada (2006) reported that reduced transport and hence accumulation of carbohydrates in Mg-deficient leaves causes alterations in photosynthetic carbon metabolism and restrict CO2 fixation. Impairment of the photosynthetic electron transport to CO2 through photosynthetic membranes may cause an accumulation of non-utilized electrons and absorbed energy. Under such conditions, the electrons and excitation energy not used in photosynthetic CO2 fixation is channelled to molecular O2, leading to the generation of highly reactive O2 species (ROS) and consequently to damage of chloroplast constituents such as Chl and membrane lipids (Mittler, 2002). Possible mechanisms to minimize detrimental effects of drought in crop plants by improving Mg nutrition are presented in Fig.4. Magnesium increases the root growth and root surface area which helps to increase uptake of water and nutrients by root and transport of sucrose from leaves to roots (Fig. 4). Magnesium improves CHO translocation by

Fig.4. Possible mechanisms through which Mg nutrition can help plant to minimize the detrimental effects of drought in plants.
increasing phloem export and reduces ROS generation and photo-oxidative damage to chloroplast under drought conditions.

B. Micro nutrients

Micronutrients help the macro nutrients in drought alleviation by activation of certain physiological, biochemical and metabolic processes within the plant body. However, the contributions of micro nutrients (boron, iron, copper, manganese, molybdenum and chloride) in drought alleviation are not well-defined. The role of micronutrients in drought alleviation is discussed as under.

Zinc

Zinc (Zn) is an important micronutrient essential for plant growth and development. The soil in dry regions is often poor in plant-available Zn associated with high calcium carbonate content and alkaline pH (Liu, 1996). Drought stress reduces the net photosynthetic rate (Pn) of the plants. This decline may be related to a reduction in light interception due to lower leaf area, to reduction in carbon fixation per unit leaf area or to damage of the photosynthetic apparatus (Lal and Edwards, 1996; Saccardy et al., 1996; Foyer et al., 1998; Castrillo et al., 2001; Bruce et al., 2002). Zn deficiency symptoms such as stunted stems and chlorotic leaves were often observed in maize plants grown in the field (Liu, et al., 1993; Liu, 1996). In cauliflower, a reduction in photosynthesis induced by Zn deficiency was associated with a decrease in stomatal conductance (gs) and intercellular CO₂ concentration (Sharma et al., 1994). A decrease of carbonic anhydrase activity due to Zn deficiency also contributed to the reduced PN (Ohki, 1976; Rengel, 1995; Cakmak and Engels, 1999; Hacisalihoglu et al., 2003; Fischer et al., 1997). In cabbage, Zn deficiency lowered osmotic potential and increased water saturation deficit (Sharma et al., 1984, 1994). The transpiration rate (E) of pecan plants declined under Zn deficiency (Hu and Sparks, 1991). Khan et al., 2003 reported that applying Zn increased chickpea grain yields when the plants were well-watered, but not under water stress, except for the Zn-efficient and drought-resistant genotype. Possible mechanisms to minimize detrimental effects of drought in crop plants by improving Zn nutrition were described by Waraich et al. (2011). They reported that Zn is important for its ability to influence auxin levels and has long been known to be a co-enzyme for production of tryptophane, a precursor to the formation of auxin. (Bennett and Skoog, 2002; Waraich etal, 2011). Increase in auxin levels due to Zn application enhances the root growth which inturn improves the drought tolerance in plants. As indicated above, normal auxin functions are likely to be disrupted in drought condition. Maintaining adequate hormone levels gives a competitive advantage to withstand adverse conditions of all kinds. In another mechanism, Zn application reduces the activity of membrane-bound NADPH oxidase which in turn decreases the generation of ROS (Waraich et al., 2011) and reduces photooxidation damage while the activities of SOD, POD, and CAT are enhanced indicating that Zn lowers the ROS generation and protect cells against ROS attack under water stress (Waraich et al., 2011).

Boron (B)

A primary function of boron (B) is related to cell wall formation in plants. The plants suffering from drought stress may be stunted. Sugar transport in plants, flower retention, pollen formation, seed germination and grain production are reduced with drought stress. By improving the B nutrition, the detrimental effects of drought can be corrected. Possible mechanisms to minimize detrimental effects of drought in crop plants by improving B nutrition are presented in Fig. 5. Boron improves the drought tolerance in plants by improving sugar transport, flower retention, pollen formation and seed germination. Seed and grain production are also increased with proper B supply. Boron nutrition under drought condition results in reduction in stunted appearance (rosetting), barren ears due to poor pollination, hollow stems and fruit (hollow heart) and brittle, discolored leaves and loss of fruiting bodies.

Copper (Cu)

Copper (Cu) is an important micronutrient essential for carbohydrate and nitrogen metabolism. Copper is also required for lignin synthesis which is needed for cell wall strength and prevention of wilting. Drought stress adversely affects all these processes in plants. Proper Cu nutrition alleviates the adverse affects of drought by reducing dieback of stems and twigs, yellowing of leaves, stunted growth, pale green leaves that wither easily, and improves CHO and nitrogen metabolism which in turn improves the growth of plants. The possible mechanisms to minimize detrimental effects of drought in crop plants by improving Cu nutrition are presented in Fig. 6.

C. Beneficial element

Silicon

Silicon (Si) is the second most abundant element in soil after oxygen. It occurs in two major forms: silica and oxides of silicon, and both types exist in crystalline and/or amorphous forms such as quartz, flint, sand-stone, opal and diatomaceous earth’s silicates. In soil solution, it occurs as silicic acid at concentration ranging from 0.1-0.6 mM, which is two folds in magnitude higher than macronutrient P. (Epstein, 1999). Plants absorb most of Si in mono-silicic acid form. Despite Si being ubiquitous and prominent of constituent of plants, it is still widely not recognized as an essential nutrient for plants. However, it is proved to be beneficial for better plant growth and development, especially in plants of gramineae family (Shi et al, 2005). Silicon can improve plant growth and tolerance to biotic and abiotic stresses (Epstein, 1999; Liang et al., 2007; Neumann and Niede, 2001). The possible mechanisms to alleviate detrimental effects of drought in crop plants by improving silicon nutrition were described by Waraich et al. (2011). Silicon has a positive effect on plants under drought stress.
Fig. 5. Possible mechanisms through which B nutrition can help plant to minimize the detrimental effects of drought in plants.

Fig. 6. Possible mechanisms through which Cu nutrition can help plant to minimize the detrimental effects of drought in plants.
Gao et al. (2004, 2006) reported that the addition of Si increased water use efficiency by reducing leaf transpiration and the water flow rate in the xylem vessel in maize. Si could facilitate water uptake and transport in *Sorghum bicolor* (L.) in drought conditions (Hattori et al., 2005, 2007). Si alleviated oxidative stress by regulating the activities of antioxidant enzymes under drought in potted wheat. (Gong et al., 2005). However, the effect of Si on the concentrations of antioxidants glutathione (GSH) and ascorbic acid (AsA) has not been investigated. In addition to antioxidant defense, plants can also adapt to water stress by changing solute levels so that turgor and hence physiological activity are maintained at low leaf water potentials (Zhu et al., 2005). It has been suggested that accumulation of solutes in the stressed leaves contributes to dehydration tolerance (Wood et al., 1996; Smienoff, 1998). However, this might be a beneficial result of Si as opposed to a direct effect because it is unlikely that Si affects the activity of antioxidant enzymes. Silicon nutrition increases the antioxidants production and reduces ROS generation which in turn reduces the photo-oxidative damage and maintain the integrity of chloroplast membrane and enhances the drought tolerance in plants (Waraich et al., 2011).

**Conclusions**

Drought stress is one of the major limitations to the agricultural productivity worldwide. The management of plant nutrients is very helpful to develop plant tolerance to drought. Better plant nutrition can effectively alleviate the adverse effects of drought by a number of mechanisms. Drought results in increased generation of the reactive oxygen species (ROS) due to energy accumulation in stressed plants which increases the photo-oxidative effect and damage the chloroplast membrane. Application of macro-nutrients like N, K and Ca reduce the toxicity of ROS by increasing the concentration of antioxidants like superoxide dismutase (SOD); Catalase (CAT) and peroxidise (POD) in the plant cells. These antioxidants scavenge the ROS and reduce the photo-oxidation and maintain the integrity of chloroplast membrane and increase the photosynthetic rate in the crop plants. Similarly, the application of some micro-nutrients like Zn, Si and Mg also increase antioxidants concentration and improves drought tolerance in plants. In other mechanism, nutrients like P, K, Mg and Zn improve the root growth which in turn increases the intake of water which helps in stomatal regulation and enhances the drought tolerance. Application of nutrients like Potassium and Calcium help to maintain high tissue water potential under drought condition and improve drought tolerance by osmotic adjustment. The micronutrients like Cu and B alleviate the adverse effects of drought indirectly by activating the physiological, biochemical and metabolic processes in the plants.

**References**


variable nitrogen supply on sunflower (Helianthus annuus L.) leaf cell number and size. Annals Bot 84: 599-606.
