

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 of 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 cells resulting in shrinkage of cell membranes and results in decreased integrity of the cell membrane and the living cell may be destroyed. Drought 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 (Pinstrup-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 (Borlaug and Dowsell, 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 (Smirnov 1993; Asada 2006). Drought inhibits or slows down photosynthetic carbon fixation mainly through limiting the entry of CO₂ into the leaf or directly inhibiting metabolism (Smirnov 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 H₂O₂ is reduced to H₂O by catalase (CAT) and peroxidase (POD) (Mittler 2002; Apel and Hirt 2004). Despite the internal resistance of the plants to drought stress, the 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 also deal with the problem of 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. Increasing 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. (Herandez et al.,

1997). It is an important component of many structural, genetic and metabolic compounds in plants (Hassan et al., 2005; Tisdale and Nelson, 1975) and out of total nutrients absorbed by plant roots, 80% contribution is of N. (Marschner, 1995). It is taken up by plants both in organic (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_4^+ 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 (Rufty et al., 1988). Nitrogen application, where light is not limiting, increases antioxidative defense mechanisms (Marschner, 1995), resulting in reduced photooxidation 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 the 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. Trapni 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., 1991; 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 improves 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 morpho-physiological 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 (Sabour et al., 1997) and cell membrane stability (Ali et al., 2009b) are the characters of interest and had been widely exploited as reliable morpho-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 P_2O_5 in phosphate fertilizers per year are used worldwide, and of

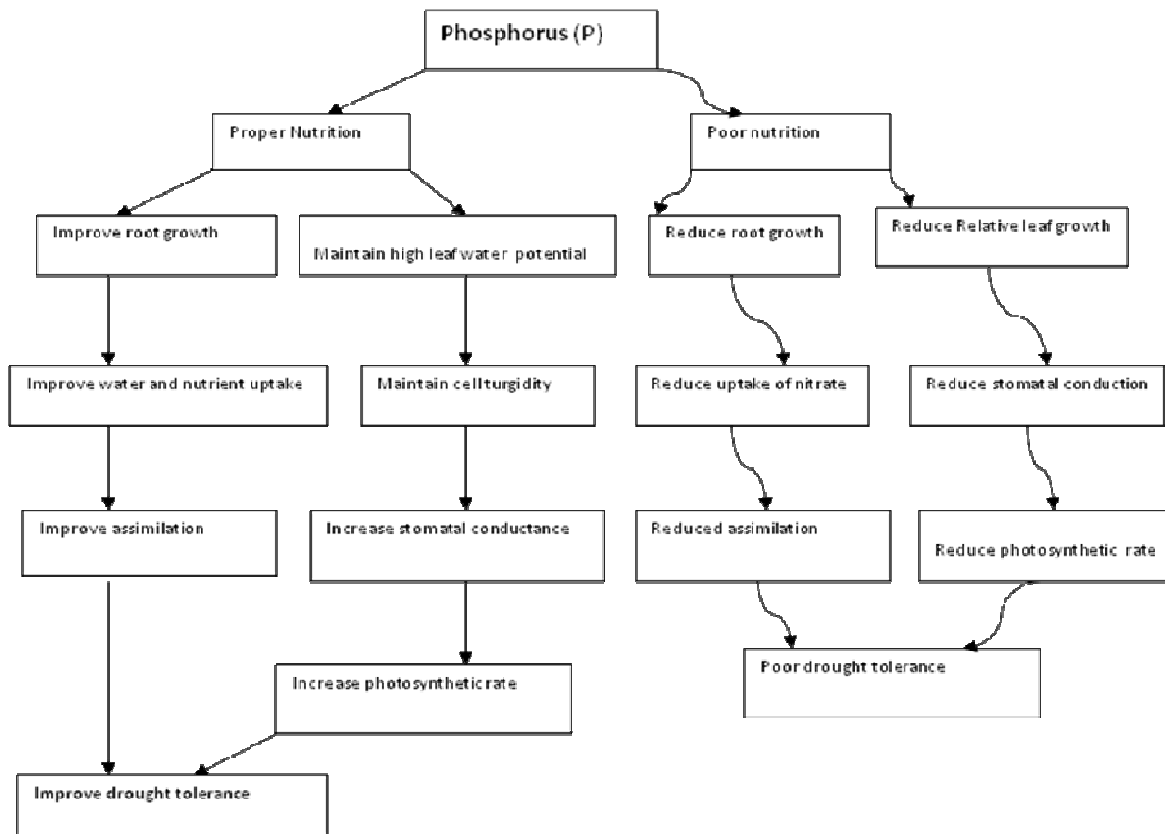


Fig.1. Possible mechanisms through which P nutrition can minimize the detrimental effects of drought in plants.

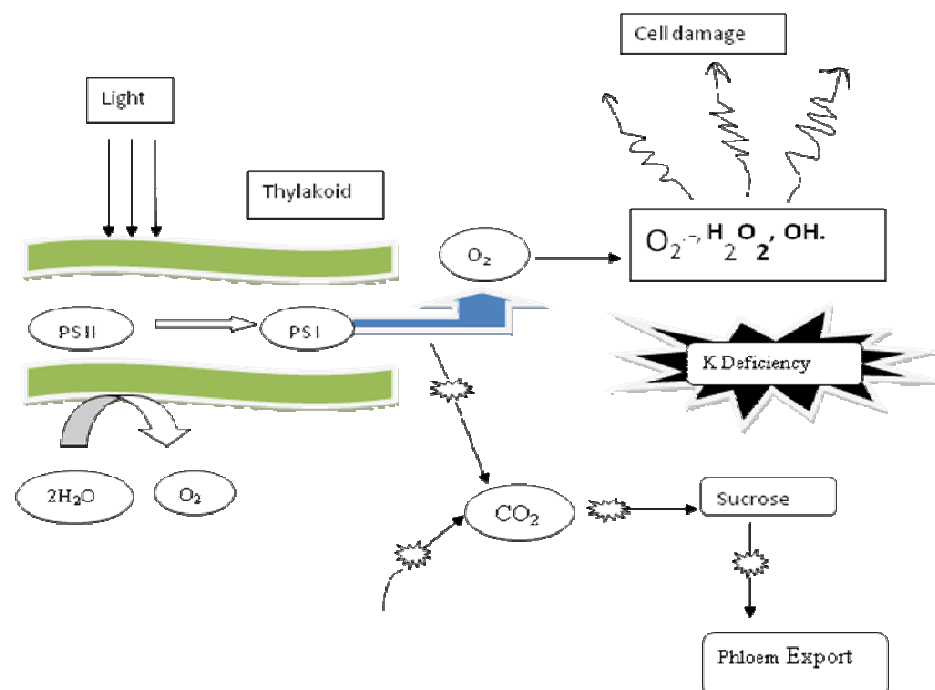


Fig.2: Schematic representation of Reactive Oxygen Species (ROS) generation in chloroplasts of K-deficient leaves as described by Cakmak, 2005.

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. Phosphorus deficiency induced decline in leaf growth and photosynthetic rate may be ascribed to reduction in stomatal conductance and ribulose 1,5 biphosphate (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, phosphorus 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 be

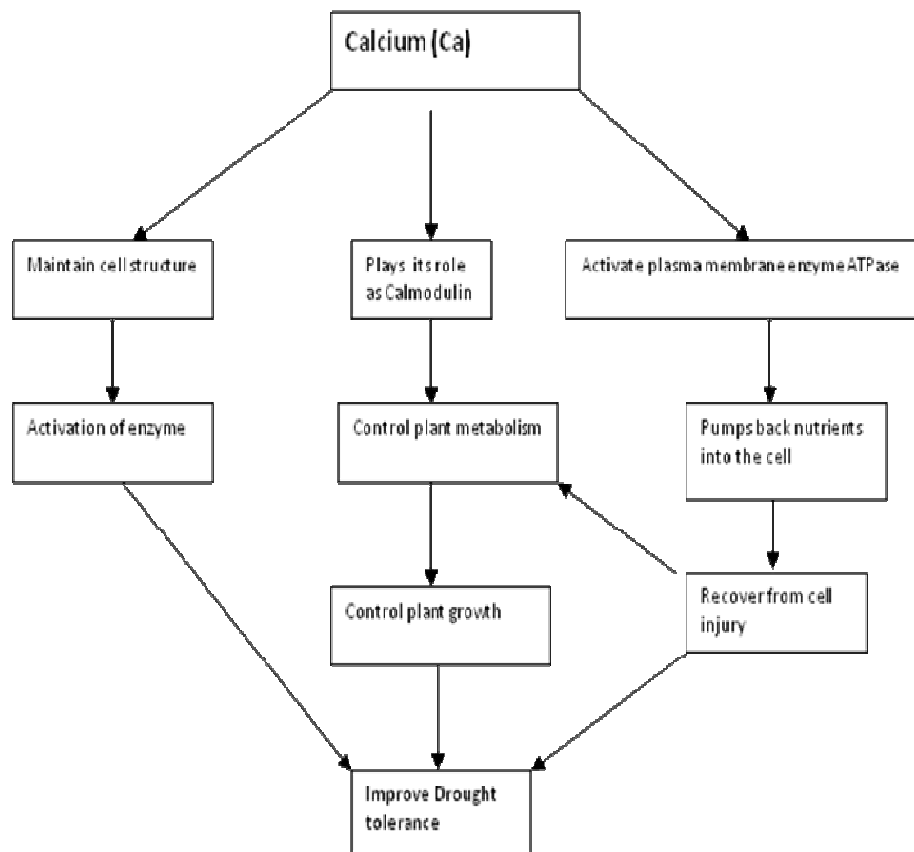


Fig.3. Possible mechanisms through which Ca nutrition can help plant to minimize the detrimental effects of drought in plants.

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 (Lindhauer, 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



Fig.4. Possible mechanisms through which Mg nutrition can help plant to minimize the detrimental effects of drought in plants.

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^+ , NH_4^{++} 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 CO_2 fixation. Impairment of the photosynthetic electron transport to CO_2 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 CO_2 fixation is channelled to molecular O_2 , leading to the generation of highly reactive O_2 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

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 Waraiach 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 et al, 2011). Increase in auxin levels due to Zn application enhances the root growth which in turn 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.

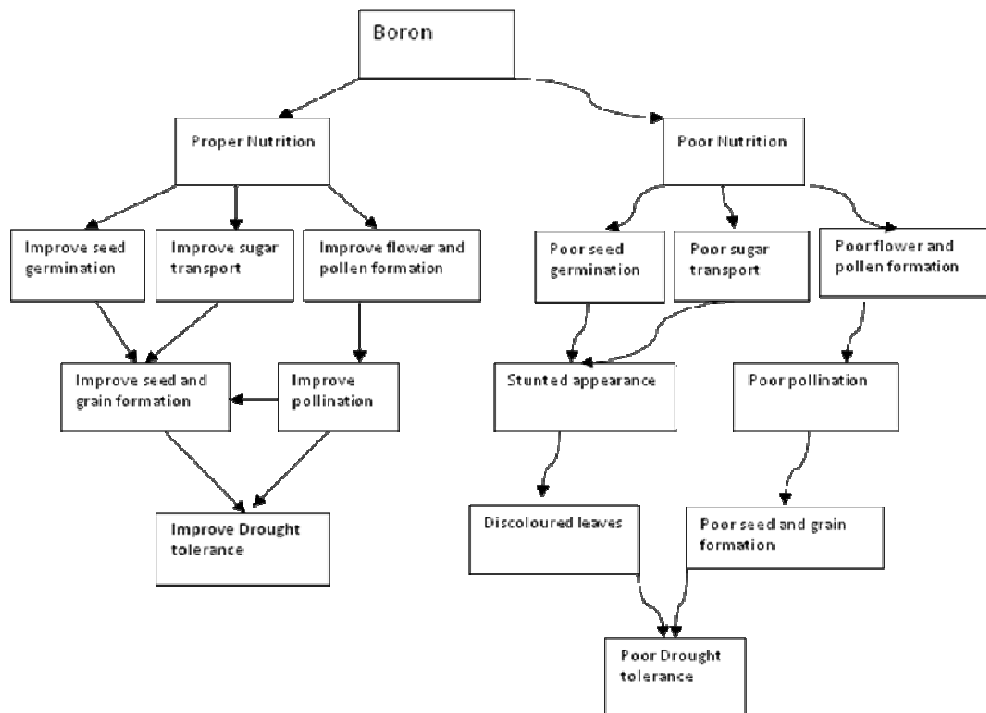


Fig.5. Possible mechanisms through which B nutrition can help plant to minimize the detrimental effects of drought in plants.

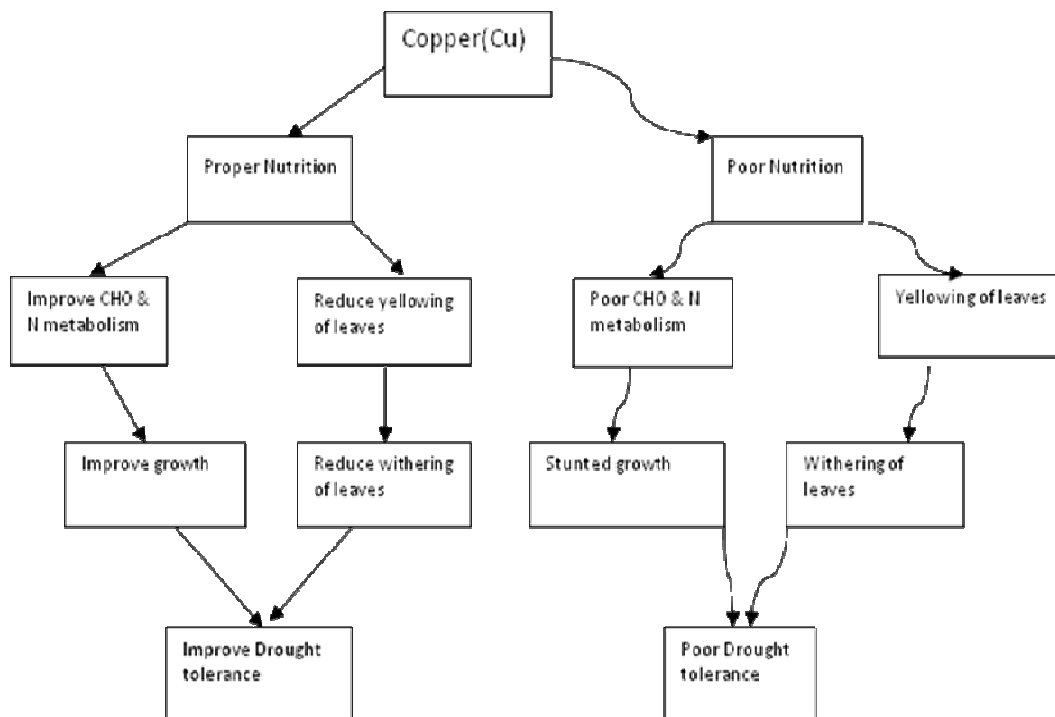


Fig.6. Possible mechanisms through which Cu nutrition can help plant to minimize the detrimental effects of drought in plants.

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 peroxidase (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

Abd El-Hadi AH, Ismail KM , El-Akahawy MA (1997) Effect of potassium on the drought resistance of crops in Egyptian conditions, In Johnston, AE.: Food Security in the WANA Region, the Essential Need for Balanced Fertilization. Int Potash Inst Basel: 328–336.
 Abd-El Baki GK, Siefritz F, Man HM, Weiner H, Kaldenhoff R, Kaiser WM (2000) Nitrate reductase in *Zea mays* L. under salinity. Plant Cell Environ 23: 515-521.

Ackerson RC (1985) Osmoregulation in cotton in response to water-stress. 3. Effects of phosphorus fertility. Plant Physiol 77: 309–312.
 Aggarwal PK, Sinha SK (1984) Differences in water relations and physiological characteristics in leaves of wheat associated with leaf position on the plant. Plant Physiol 74: 1041-1045
 Ajouri AH, Asgedom, Becker M (2004) Seed priming enhances germination and seedling growth of barley under conditions of P and Zn deficiency. J Plant Nutr Soil Sci 167: 630–636.
 Ali MA, Hussain M, Khan MI, Ali Z, Zulkiffal M, Anwar J, Sabir W, Zeeshan M (2010) Source-sink relationship between photosynthetic organs and grain yield attributes during grain filling stage in spring wheat (*Triticum aestivum*). Int J Agric Biol 12: 509–515
 Ali MA, Jabran K, Awan SI, Abbas A, Ehsanullah, Zulfikar M. Tuba Acet, Farooq J, Rahman A (2011). Morpho-physiological diversity and its implications for improving drought tolerance in grain sorghum at different growth stages. Australian J Crop Sci 5(3):308-317
 Ali MA, Niaz S, Abbas A, Sabir W, Jabran K (2009b) Genetic diversity and assessment of drought tolerant sorghum landraces based on morph-physiological traits at different growth stages. Plant Omics J 2: 214-227
 Apel K, Hirt H (2004) Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. Ann Rev Plant Bio 55: 373-399.
 Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol 141: 391–396.
 Azedo-Silva JJ, Osorio FF, Correia MJ (2004) Effects of soil drying and subsequent re-watering on the activity of nitrate reductase in root and leaves of *Helianthus annuus*. Funct. Plant Biol 31: 611-621.
 Bagayoko M, George E, Römheld V, Buerkert AB (2000) Effects of mycorrhizae and phosphorus on growth and nutrient uptake of millet, cowpea and sorghum on a West African soil J Agric Sci 135: 399–407.
 Bennett JP, Skoog F (2002) Preliminary Experiments on the Relation of Growth-promoting Substances to the Rest Period in Fruit Trees. Plant Physiol 13:219-225.
 Bhutta WM, (2007) The effect of cultivar on the variation of spring wheat grain quality under drought conditions. Cereal Res Commun 35: 1609-1619
 Borlaug NE, Dowsell CR (1993) Fertilizer to nourish infertile soil that feeds a fertile population that crowds a fragile world. Fert News 387: 11–20.
 Bowler C, Van-Montagu M, Inze D (1992) Superoxide dismutase and stress tolerance. Ann. Rev. Plant Physiol. Plant Mol Biol 43: 83–116.
 Boyer JS (1982) Plant prod. and environ. Sci. 218: 443-448.
 Bray EA, Bailey-Serres J, Weretilnyk E (2000) Responses to abiotic stresses, in Buchanan B, Gruissem W, Jones R: Biochemistry and Molecular Biology of Plants. Amer Soc of Plant Physio pp. 1158–1203.
 Brewitz E, Larson CM, Larson M (1996) Response of nitrate assimilation and N translocation in tomato (*Lycopersicon esculentum* Mill) to reduced ambient air humidity. J Exp Bot 47: 855-861.
 Brooks A (1986) Effects of phosphorous nutrition on ribulose-1, 5-biphosphate carboxylase activation, photosynthetic quantum yield and amount of some Calvin cycle metabolism in spanish leaves. Aus J Plant Physiol 13: 221-237.

- Bruce WB, Edmeades GO, Barker TC (2002) Molecular and physiological approaches to maize improvement for drought tolerance. *J Exp Bot* 53: 13-25.
- Brück H, Payne WA, Sattelmacher B (2000) Effects of phosphorus and water supply on yield, transpirational water-use efficiency, and carbon isotope discrimination of pearl millet. *Crop Sci* 40: 120-125.
- Cakmak I (2002) Plant nutrition research, Priorities to meet human needs for food in sustainable ways. *Plant Soil* 247: 3-24.
- Cakmak I (2005) The role of potassium in alleviating detrimental effects of abiotic stresses in plants. *J Plant Nutr Soil Sci* 168: 521-530.
- Cakmak I (1997) Role of potassium in protecting higher plants against photo-oxidative damage. In: Johnston, A.E. (Ed.), *Food security in the WANA region, the essential need for balanced fertilization*, International Potash Institute, Basel Switzerland, pp. 345-352.
- Cakmak I, Engels C (1999) Role of mineral nutrients in photosynthesis and yield formation, in Rengel, Zn Mineral Nutrition of Crops: Mechanisms and Implications. The Haworth Press, New York, USA, pp. 141-168.
- Cakmak I, Hengeler C, Marschner H (1994a) Partitioning of shoot and root dry matter and carbohydrates in bean plants and suffering from phosphorus, potassium and magnesium deficiency. *J Exp Bot* 45: 1245-1250.
- Cakmak I, Hengeler C, Marschner H (1994b) Changes in phloem export of sucrose in leaves in response to phosphorus, potassium and magnesium deficiency in bean plants. *J Exp Bot* 45: 1251-1257.
- Castrillo M, Fernandez D, Calcagno AM, Trujillo I, Guenni L (2001) Responses of ribulose-1,5-bisphosphate carboxylase, protein content, and stomatal conductance to water deficit in maize, tomato, and bean. *Photosyn* 39: 221-226.
- Colom MR, Vazzana C (2003) Photosynthesis and PSII functionality of drought-resistant and droughtsensitive weeping lovegrass plants. *Environ Exp Bot* 49: 135-144
- Correia MJ, Filomena F, Azedo-Silva J, Dias C, David MM, Barrote I, Osorio ML, Osorio J (2005) Effects of water deficit on the activity of nitrate reductase and contents of sugars, nitrate and free amino acids in the leaves and roots of sunflower and white lupin plants growing under two nutrient supply regimes. *Physiol Plant* 124: 61-70.
- Dhanda SS, Sethi GS, Behl RK (2004) Indices of drought tolerance in wheat genotypes at early stages of plant growth. *J Agron Crop Sci* 190: 6-12
- Engila JN, Davies FTJ, Drew MC (2001) Effect of potassium on drought resistance of *Hibiscus rosa-sinensis* cv. Leprechaun: plant growth, leaf macro and micronutrient content and root longevity. *Plant Soil* 229: 213-224.
- Elstner, EF, Osswald W (1994) Mechanism of oxygen activation during plant stress. *Proc. Royal Soc. Edinburgh, Section-B* 102: 131-154
- Epstein E (1999) Silicon. *Annu. Rev. Plant Physiol. Plant Mol Biol* 50: 641-664
- Epstein E, Bloom AJ (2004) *Mineral Nutrition of Plants: Principles and Perspectives*, 2nd Edn. Sinauer Associates, Sunderland, MA.
- Evans JR, Terashima I (1987) Effects of nitrogen nutrition on electron transport components and photosynthesis in spinach. *Aust J Plant Physiol* 14: 259-68.
- Fahi JI, Carelli MLC, Vega J, Magalhaes AC (1994) Nitrogen and irradiance levels affecting net photosynthesis and growth of young coffee plants. *J Horti Sci* 69: 161-169.
- Fischer ES, Thimm O, Rengel Z (1997) Zinc nutrition influences the CO₂ gas exchange in wheat. *Photosynthetica* 33: 505-508.
- Foyer CH, Lelandais M, Kunert KJ (1994) Photooxidative stress in plants. *Physiol Plant* 92: 696-717.
- Foyer CH, Valadier MH, Migge A, Becker TW (1998) Drought-induced effects on nitrate reductase activity and mRNA and on the coordination of nitrogen and carbon metabolism in maize leaves. *Plant Physiol* 117: 283-292.
- Frechilla S, Bonzalez EM, Royuela M, Arrese-Igor C, Lamsfus C, Aparicio-Tejo PM (1999) Source of nitrogen nutrition affects pea growth involving changes in stomatal conductance and photorespiration. *J Plant Nutr* 22: 911-926.
- Fredeen AL, Rao IM, Terry N (1989) Influence of phosphorous nutrition on growth and carbon partitioning in Glycine max. *Plant Physiol* 89: 225-230.
- Fredeen AL, Gamon JA, Field CB (1991) Response of photosynthesis and carbohydrate-partitioning to limitations in nitrogen and water availability in field-grown sunflower. *Plant Cell Environ* 14: 963-970.
- Gao X, Zou C, Wang L, Zhang F (2004) Silicon improves water use efficiency in maize plants. *J Plant Nutr* 27(8):1457-1470
- Gao X, Zou C, Wang L, Zhang F (2006) Silicon decreases transpiration rate and conductance from stomata of maize plants. *J Plant Nutr* 29:1637-1647.
- Garg BK, Burman U, Kathju S (2004) The influence of phosphorus nutrition on the physiological response of moth bean genotypes to drought. *J Plant Nutr Soil Sci* 167: 503-508.
- Gimenez C, Mitchell VJ, Lawlor DW (1992) Regulation of photosynthetic rate of two sunflower hybrids under water stress. *Plant Physiol* 98: 516-524.
- Gong H, Zhu X, Chen K, Wang S, Zhang C (2005) Silicon alleviates oxidative damage of wheat plants in pots under drought. *Plant Sci* 169:313-321.
- Goudriaan J, Keulen HV (1979) The direct and indirect effects of nitrogen shortage on photosynthesis and transpiration in maize and sunflower. *Nether J Agric Sci* 27: 227-234.
- Gruhn P, Goletti F, Yudelman M (2000) Integrated nutrient management, soil fertility, and sustainable agriculture: current issues and future challenges. *Food, Agriculture, and the Environment Discussion Paper 32*, International Food Policy Research Institute, Washington, D.C.
- Hacisalihoglu G, Hart JJ, Wang Y, Cakmak I, Kochian LV (2003) Zinc efficiency is correlated with enhanced expression and activity of Cu/Zn superoxide dismutase and carbonic anhydrase in wheat. *Plant Physiol* 131: 595-602.
- Hassan MJ, Wang F, Ali S, Zhang G (2005) Toxic effects of cadmium on rice as affected by nitrogen fertilizer form. *Plant Soil* 277, 359-365.
- Hattori T, Inanaga S, Araki H, An P, Morita S, Luxova M, Lux A (2005) Application of silicon enhanced drought tolerance in Sorghum bicolor. *Physiol Plant* 123:459-466.
- Hattori T, Sonobe K, Inanaga S, An P, Tsuji W, Araki H, Eneji AE, Morita S (2007) Short term stomatal responses to light intensity changes and osmotic stress in sorghum seedlings raised with and without silicon. *Environ Exp Bot* 60:177-182.
- Havlin JL, Tisdale SL, Nelson WL, Beaton JD (2007) *Soil Fertility and Fertilizer, An introduction to nutrient management* 7th Edition Prentice Hall, Upper Saddle River, NJ, U.S.A.

- Heckathorn SA, De-Lucia EH, Zielinki RE (1997) The contribution of drought-related decreases in foliar nitrogen concentration to decreases in photosynthetic capacity during and after drought in prairie grasses. *Physiol Plant* 122: 62-67.
- Herandez LE, Garate A, Caroeba-Ruiz R (1997) Effect of cadmium on the uptake, distribution and assimilation of nitrate in *Pisum sativum*. *Plant Soil* 189: 97-106.
- Hu H, Sparks D (1991) Zinc deficiency inhibits chlorophyll synthesis and gas exchange in 'Stuart' pecan. *Hort Sci* 26:267-268.
- Hu Y, Schmidhalter U (2001) Effects of salinity and macronutrient levels on micronutrients in wheat. *J Plant Nutr* 24: 273-281.
- International Fertilizer Industry Association (IFA), 2005: http://www.fertilizer.org/ifa/statistics/indicators/ind_products.asp Paris, France .
- Jalloh MA, Chen J, Zhen F, Zhang G (2009) Effect of different N fertilizer forms on antioxidant capacity and grain yield of rice growing under Cd stress. *J. Hazard Mater* 162: 1081-1085.
- Jiang MY, Zhang JH (2002) Involvement of plasma-membrane NADPH oxidase in abscisic acid- and water stress-induced antioxidant defense in leaves of maize seedlings. *Planta*, 215: 1022-1030.
- Jones MM, Osmond CB, Turner NC (1980) Accumulation of solutes in leaves of sorghum and sunflower in response to water deficits. *Aust J Plant Physiol* 7: 193-205
- Just D, Saux C, Richaud C, Andre M (1989) Effect of nitrogen stress on sunflower gas exchange. I. Photorespiration and carbon partitioning. *Plant Physiol Biochem* 27: 669-677.
- Kaiser WM, Brendle-Behnisch E (1991) Rapid modulation of spinach leaf nitrate reductase activity by photosynthesis. I. Modulation in vivo by CO₂ availability. *Physiol Plant* 96: 363-367.
- Kant S, Kafkafi U (2002) Potassium and Abiotic Stresses in Plants. Pasricha, N. S., Bansal, S.K. (Eds.), Role of potassium in nutrient management for sustainable crop production in India, Potash Research Institute of India, Gurgaon, Haryana.
- Karamanos AJ, Papatheohari AY (1999) Assessment of drought resistance of crop genotypes by means of the water potential index. *Crop Sci* 39: 1792-1797
- Kashiwagi J, Krishnamurthy L, Upadhyaya HD, Krishna H, Chandra S, Vadez V, Serraj R (2004) Genetic variability of drought avoidance root traits in the mini-core germplasm collection of chickpea (*Cicer arietinum* L.). *Euphytica* 146: 213-222.
- Kathju S, Vyas SP, Garg BK, Lahiri AN (1990) Fertility Induced Improvement in Performance and Metabolism of Wheat under Different Intensities of Water Stress. Proceedings of the Int Cong of Plant Physio 88 , New Delhi, India, pp. 854-858.
- Kenis JD, Rouby MB, Edelman MO, Silvente ST (1994) Inhibition of nitrate reductase by water stress and oxygen in detached oat leaves: a possible mechanism of action. *J Plant Physiol* 144: 735-739.
- Kettlewell PS & Juggins SA (1992) Can foliar application of nitrogen fertilizer to winter wheat reduce nitrate leaching. *Aspects Appl. Biol.* 30: 103-108.
- Khan HR, McDonald GK, Rengel Z (2003) Zn fertilization improves water use efficiency, grain yield and seed Zn content in chickpea. *Plant Soil* 249: 389-400.
- Kirschbaun MUF, Tompkins D (1990) Photosynthetic response to phosphorous nutrition in *Eucalyptus grandis* seedling. *Trop Agric* 64: 91-96.
- Lal A, Edwards GE (1996) Analysis of inhibition of photosynthesis under water stress in the C4 species *Amaranthus cruentus* and *Zea mays*: electron transport, CO₂ fixation and carboxylation capacity. *Aust J Plant Physiol* 23: 403-412.
- Larsson M, Larsson CM, Whitford PN, Clarkson DT (1989) Influence of osmotic stress on nitrate reductase activity in wheat (*Triticum aestivum* L.) and the role of abscisic acid. *J Exp Bot* 40: 1265-1271.
- Lawlor DW (2002) Carbon and nitrogen assimilation in relation to yield mechanisms are the key to understanding production systems. *J Exp Bot* 53: 773-787.
- Liang YC, Sun WC, Zhu YG, Christie P (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants, a review. *Environ Pollut* 147:422-428.
- Lindhauer MG (1995) Influence of K nutrition and drought and water stressed nonflower plants differing in K nutrition. *J Plant Nutr* 10: 1965-1973.
- Liu XB, Yang Q, Chu TD, Wang SH, Li SR, Wu XF (1993) Effect of Zinc application on corn. *Acta pedol sin* 30:153-162. [In Chinese].
- Liu Z (1996) Microelements in Soils of China. - Jiangsu Science and Technology Publishing House, Nanjing 1996. [In Chinese].
- Loggini B, Scartazza A, Brugnoli E, Navari-Izzo F (1999) Antioxidative defence system, pigment composition, photosynthetic efficiency in two wheat cultivars subjected to drought. *Plant Physio* 119: 1091-1099.
- MacAdam JW, JJ Volenec, CJ Nelson (1989) Effects of nitrogen on mesophyll cell division and epidermal cell elongation in tall fescue leaf blades. *Plant Physiol* 89: 549-56.
- Marschner H (1995) Mineral Nutrition of Higher Plants, 2, Academic Press, London, U.K., pp. 889.
- Marschner H, Kirkby EA, Cakmak I (1996) Effect of mineral nutritional status on shoot-root partitioning of photo assimilates and cycling of mineral nutrients. *J Exp Bot* .47:1255-1263.
- Martin B, Dasilva JV (1972) Effect of dehydration on cellular distribution of ribonucleic acid in cotton leaves. *Physiol Plant* 27: 150-155.
- Mengel K, Kirkby EA (2001) Principles of Plant Nutrition. 5th ed., Kluwer Academic Publishers, Dordrecht.
- Miletić RPR, Dodig D, Milutinović S, Mihajlović I, Nikodijević SM (2010). Strategies for solving the problem of drought in Eastern Serbia. <http://www.wg-crop.icidonline.org/40doc.pdf>
- Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. *Tren. Plant Sci.* 7:405-410.
- Muchow RC (1988) Effect of nitrogen supply on the comparative productivity of maize and sorghum in semi arid tropical environment I. Leaf growth and leaf nitrogen. *Field Crops Res* 18: 1-16.
- Neumann D, Niede U (2001) Silicon and heavy metal tolerance of higher plants. *Phytochem* 56: 685-692.
- Oertli JJ (1991) Nutrient management under water and salinity stress, in: Proceeding of the symposium on nutrient management for sustained productivity. Depart. Soils Punjab Agric. Unver. Ludhiana, India, pp. 138-165.
- Ohki K (1976) Effect of zinc nutrition on photosynthesis and carbonic anhydrase activity in cotton. *Physiol Plant* 38: 300-304.
- Palta JP (2000) Stress Interactions at the Cellular and Membrane Levels. *Hort. Sci.* 25(11): 1377

- Payne WA, Hossner LR, Onken AB, Wedt CW (1995) Nitrogen and phosphorous uptake in pearl millet and its relation to nutrient and transpiration efficiency. *Agron J* 87: 425-431.
- Pilbeam DJ, Cakmak I, Marschner H, Kikby EA (1993) Effect of withdrawal of Phosphorous on nitrate assimilation and PEP carboxylase activity in tomato. *Plant soil* 154: 111-117.
- Pinkerton A, Simpson JR (1986) Interactions of surface drying and subsurface nutrients affecting plant-growth on acidic soil profiles from an old pasture. *Aust J Exp Agric* 26: 681-689.
- Pinstrup-Andersen P, Pandya-Lorch R, Rosegrant MW (1999) World food prospects, Critical issues for the early twenty-first century, 2020 Vision Food Policy Report, International Food Policy Research Institute, Washington, D.C.
- Poovaiah BW, ASN Reddy (2000) Calcium Messenger Systems in Plants. *CRC Crit Rev Plant Sci* 6: 47-102
- Quartacci MF, Sgheri CLM, Pinzino C, Navariizzo F (1994) Superoxide radical production in wheat plants differently sensitive to drought. *Proc. Royal Soc. Edinburgh, Section B*, 102: 287-290.
- Radin JW (1984) Stomatal responses to water stress and to abscisic acid in phosphorous deficient cotton plants. *Plant Physiol* 76: 392-394.
- Ranieri A, Bernardi R, Lanese P, Soldatini CF (1989) Changes in free amino acid content and protein pattern of maize seedlings under water stress. *Environ Exp Bot* 29: 351-357.
- Rasnack M (1970) Effect of mannitol and polyethylene glycol on phosphorus uptake by maize plants. *Ann Bot* 34: 497-502.
- Raun WR, Johnson GV (1999) Improving nitrogen use efficiency for cereal production. *Agron J* 91: 357-363.
- Rengel Z (1995) Carbonic anhydrase activity in leaves of wheat genotypes differing in zinc efficiency. *J Plant Physiol* 147: 251-256.
- Rufty TW, Huber SC, Volk RJ (1988). Alterations in leaf carbohydrate metabolism in response to nitrate stress. *Plant Physiol* 88: 725-730
- Sabour I, Merah O., El Jaafari S, Paul R, Monneveux PH (1997) Leaf osmotic potential, relative water content and leaf excised water loss variations in oasis wheat landraces in response to water deficit. *Arch Int Physiol Biochem Biophys* 105: 14.
- Saccardy K, Cornic G, Brulfert J, Reyss A (1996) Effect of drought stress on net CO₂ uptake in *Zea* leaves. - *Planta* 199: 589-595.
- Sangakkara UR, Frehner M, Nosberger J (2000) Effect of soil moisture and potassium fertilizer on shoot water potential, photosynthesis and partitioning of carbon in mungbean and cowpea. *J Agron Crop Sci* 185: 201-207.
- Sawwan J, Shibli RA, Swaidat I, Tahat M (2000) Phosphorus regulates osmotic potential and growth of African violet under in vitro-induced water deficit. *J Plant Nutr* 23: 759-771.
- Scott BJ, Robson AD (1990) Changes in the content and form of magnesium in the first trifoliate leaf of subterranean clover under altered or constant root supply. *Aust J Agric Res* 41: 511-519.
- Seel W, Hendry G, Atherton N, Lee J (1991) Radical formation and accumulation in vivo, in desiccation tolerant and intolerant mosses. *Free Rad Res Commu* 15: 133-141.
- Sen Gupta A, Berkowitz GA (1987) Osmotic adjustment, symplast volume, and non-stomatally mediated water stress inhibition of photosynthesis in wheat. *Plant Physiol* 85: 1040-1047.
- Sen Gupta A, Berkowitz GA, Pier PA (1989) Maintenance of photosynthesis at low leaf water potential in wheat. *Plant Physiol* 89: 1358-1365.
- Sharma CP, Mehrotra SC, Sharma PN, Bisht SS (1984) Water stress induced by zinc deficiency in cabbage. *Curr Sci* 53:44-45.
- Sharma PN, Kumar N, Bisht SS (1994) Effect of zinc deficiency on chlorophyll content, photosynthesis and water relations of cauliflower plants. *Photosynthetica* 30: 353-359.
- Shaul O (2002) Magnesium transport and function in plants: the tip of the iceberg. *Biometals* 15: 309-323.
- Shi XH, Zhang CH, Wang H, Zhang FS (2005) Effect of Si on the distribution of Cd in rice seedlings. *Plant Soil* 272: 53-60.
- Sinclair TR, Horie T (1989) Leaf nitrogen, photosynthesis and crop radiation use efficiency, a review. *Crop Sci* 29: 90-98.
- Smienoff N (1998) Plant resistance to environmental stress. *Curr Opin Biotech* 9:214-219.
- Smirnoff N (1993) The role of active oxygen in the response of plants to water deficit and desiccation. *New Phytol* 125: 27-58.
- Smith FW (2002) The phosphate uptake mechanism. *Plant Soil* 245: 105-114.
- Studer C (1993) Interactive effects of N-P-K-nutrition and water stress on the development of young maize plants. Ph.D. Thesis, ETHZ, Zurich, Switzerland
- Takele A (2000) Seedling emergence and growth of sorghum genotypes under variable soil moisture deficit. *Acta Agron Hung* 48: 95-102
- Tisdale SL, Nelson WL (1975) Elements required in plant nutrition, in Soil fertility and fertilizers, ed. by Tisdale SL and Nelson WL. Macmillan Publishing Co., Inc., New York, NY, U.S.A., pp. 66-104.
- Toth VR, Meszkaros I, Veres S, Nagy J (2002) Effect of the available nitrogen on the photosynthetic activity and xanthophylls cycle pool of maize in field. *J Plant Physiol* 159: 627-634.
- Trapni N, Hall AJ Weber M (1999) Effect of constant and Vos J, Biemond H (1992) Effect of nitrogen on development and growth of potato plant. I. Leaf appearance, expansion growth, life span of leaves and stem branching. *Ann Bot* 70: 27-35.
- Waraich EA, Amad R, Ashraf MY, Saifullah, Ahmad M (2011). Improving agricultural water use efficiency by nutrient management. *Acta Agri Scandi - Soil & Plant Sci* 61(4): 291-304.
- Wood AJ, Saneoka H, Rhodes D, Joly RJ, Gildsbrough PB (1996). Betaine aldehyde dehydrogenase in sorghum. Molecular cloning and expression of two related genes. *Plant Physiol* 110:1301-1308.
- Zhu X, Gong H, Chen G, Wang S, Zhang C (2005) Different solute levels in two spring wheat cultivars induced by progressive field water stress at different developmental stages. *J Arid Environ* 62:1-14.
- variable nitrogen supply on sunflower (*Helianthus annuus* L.) leaf cell number and size. *Annals Bot* 84: 599-606.
- Turner LB (1985) Changes in the phosphorus content of *Capsicum annuum* leaves during water-stress. *J Plant Physiol* 121: 429-439.

Verga B, Corni A, Kalsan M (1992) Effects of mineral fertilizer and soybean sowing methods on protein contents of soybean (*Glycine max* L. Merr.). *Pojoprivredna Znanstvena Smotra.*, 57(1): 91-100.

Verhoeven AS, Demming-Adams WW, Adams III (1997) Enhanced employment of the xanthophylls cycle and thermal energy dissipation in spinach exposed to high light and nitrogen stress. *Plant Physiol* 113: 817-824.