

Drought Stress and Plant Nutrition

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ABSTRACT

Drought is a climatic phenomenon that can occur periodically in all climatic zones, but occurs with greater frequency in tropical and sub-tropical regions, causing physiological damage to plants in ecosystems and agroecosystems. Due to climate changes, more frequent and prolonged drought events are expected in different parts of the world, leading to weaker crop yields and, in more severe cases, food shortages. Besides water deficiency itself, which places grave constraints on plant development and production, problems with mineral nutrition can occur as a secondary effect. In higher plants, most of mineral nutrient transport from the soil solution to the roots is dependent on the moisture in the soil. Nutrient transport from the roots to the shoots is also limited by a drought-induced decrease in the transpiration rate as well as an imbalance in active transport and membrane permeability. All these factors acting together have serious consequences for plant development, affecting different physiological processes. A better understanding of the effects of water stress on plant nutrition is useful for developing strategies to minimize the harm caused by drought and consequent nutrient deficiency. The aim of the present literature review is to offer discourse on aspects of water stress regarding nutrient uptake and physiological responses in plants.

Keywords: drought, mineral nutrient, plant physiology, water relations

Abbreviations: Ba, barium; Br, bromine; Cr, chromium; Cs, cesium; HPO_4^{2-} , hydrogen phosphate; H_2PO_4 , dihydrogen phosphate; J/mol, joules per mol; N_2 , molecular nitrogen; Na, sodium; NADH, nicotinamide adenine dinucleotide (reduced form); NADPH, nicotinamide adenine dinucleotide phosphate (reduced form); NO_2 , nitrite; NO_3 , nitrate; Rb, rubidium; Sr, strontium; Ti, titanium; UV, ultra-violet; V, vanadium

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INTRODUCTION

The performance and distribution of plant species depend on their acquisition of water, nutrient uptake and carbon fixation as well as how these aspects are regulated. Among the different abiotic forms of stress, drought is a major limiting factor regarding crop yields and productivity around the world (Valliyodan and Nguyen 2006). Drought is a transient, extreme environmental condition that affects plant growth and development (Coll *et al.* 1995; Larcher 2006). Plants capable of acquiring more water and those with greater water-use efficiency tolerate drought better (Taiz and Zeiger 2006). In semiarid regions of the tropics, the occurrence of drought or water deficit in the soil is common,

whereas crop plants in temperate and other tropical regions undergo seasonal periods of water stress, especially during the summer (Dubey and Pessarakli 2001).

Plant response to water stress depends mainly on the severity and duration of the stress and the growth stage of the plant (Levitt 1980). Different physiological and biochemical processes are altered by drought, such as water relation (Silva *et al.* 2009b), gas exchange, photosynthesis (Pagter *et al.* 2005) and the metabolism of carbohydrates, protein, amino acids and other organic compounds (Šircelj *et al.* 2005). The effects of drought on plant growth, gas exchange, water relation and osmoregulation have been widely studied in recent years (Sadras and Milroy 1996; Hare *et al.* 1998; Sánchez 1998; Tardieu and Simonneau

Table 1 Example of the some drought effects on the mineral nutrient accumulation and other physiological parameters.

Mineral nutrient	Species	Physiological effects	Source
Nitrogen	<i>Trifolium subterraneum</i>	Water stress decreased 50.6% in N accumulation in plants grown with 8 mM NH ₄ NO ₃ and 55.1% in N ₂ -dependent plants.	DeJong and Phillips 1982
	<i>Lactuca sativa</i>	Drought stress (-0,17 MPa) decreased N content in plants, root and shoot dry weight.	Ruiz-Lozano and Azcon 1996
	<i>Vigna unguiculata</i>	Water stress caused decrease in shoot biomass, nitrate reductase activity and increase in nitrate content in the roots.	Silveira <i>et al.</i> 2001
	<i>Coffea canephora</i>	Water stress decreased leaf N concentration in plants grown with low soil nitrogen supply and N did not changed significantly under high soil N supply.	DaMatta <i>et al.</i> 2002
Calcium	<i>Cynodon dactylon</i>	Ca content increased during drought in Mediterranean field conditions.	Utrillas <i>et al.</i> 1995
	<i>Dalbergia sissoo</i>	Seedlings growing under severe irrigation regime increased Ca contents around 270 and 200% in leaves and roots, respectively.	Singh and Singh 2004
	<i>Quercus ilex</i>	Ca concentrations tended to decrease in the aboveground biomass of <i>Q. ilex</i> Mediterranean forest under drought conditions	Sardans <i>et al.</i> 2008
Magnesium	<i>Spartina alterniflora</i>	Reductions of Mg uptake both in roots and shoots accomplished with chlorosis in older leaves.	Brown <i>et al.</i> 2006
Sulphur	<i>Fagus sylvatica</i> L.	None effect on the S concentration in leaves, stems and roots was detected after a 3-week treatment under a simulated summer drought.	Peuke and Rennenberg 2004
	<i>Quercus ilex</i>	Drought increases S concentrations in soil, leaves and roots of <i>Q. ilex</i> in a Mediterranean forest.	Sardans <i>et al.</i> 2008
Chloride	<i>Carica papaya</i>	Drought increases Cl ⁻ as well as K ⁺ and Na ⁺ concentrations in both leaves and roots.	Mahouachi <i>et al.</i> 2006

1998; Thomas *et al.* 2000; Munns 2002; Nogueira and Silva 2002; Serraj and Sinclair 2002; Silva *et al.* 2003; Valliyodan and Nguyen 2006; Ashraf and Foolad 2007; Silva *et al.* 2009a, 2009b). However, studies on the effects on nutrient uptake and the consequences for physiological processes are scarce.

Environmental factors such as drought may cause nutrient deficiencies, even in fertilized fields, as the physiochemical properties of the soil can lead to a reduced mobility and absorbance of individual nutrients (Amtmann and Blatt 2009). Mineral nutrients are essential chemical elements for plant growth and reproduction, acquired primarily in the form of inorganic ions from the soil (Taiz and Zeiger 2006; Barker and Pilbeam 2007). Apart from K and Ca, all macronutrients are integrated into important organic compounds, such as amino acids and proteins (N and S), nucleic acids (N and P), phospholipids (P) and chlorophyll (Mg) (Amtmann and Blatt 2009).

Higher plants predominantly absorb mineral nutrients through the roots and uptake is determined by both supply and demand at the root surface (Bederedse *et al.* 2007). Mineral uptake by plants is a very effective process due to the large surface area of the roots and their ability to absorb inorganic ions at low concentrations in the soil solution. However, most mineral nutrients are dependent on soil moisture to move through the soil matrix and be taken up by plants (Taiz and Zeiger 2006). Under conditions of water stress, roots are unable to take up many nutrients from the soil due to a lack of root activity as well as slow ion diffusion and water movement rates (Dubey and Pessaraki 2001). Moreover, the mineralization process depends on micro-organisms and enzyme activity, which may be affected by drought (Fig. 1).

Water molecules are adsorbed on the surfaces of particles, forming hydration shells that influence the physiochemical reactions. Water in liquid form allows the diffusion and mass flow of solutes and is therefore essential to the translocation and distribution of nutrients and metabolites throughout the entire plant (Mengel and Kirkby 2001). Water and minerals are taken up from the root medium and predominantly translocated to the upper parts of the plant through the xylem (Mengel and Kirkby 2001). Transpiration plays an important role in this process and the water flow rate throughout the root (short-distance transport) and xylem vessels (long-distance transport) is determined by the root pressure and transpiration rate. An increase in the transpiration rate enhances both the uptake and translocation of mineral elements in the xylem (Mengel and

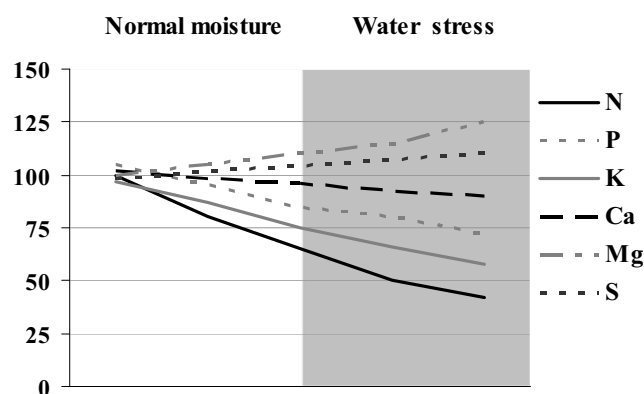


Fig. 1 Alterations in the relative nutrient content in leaves of plants under normal and stressed conditions. Data adapted from Prasertsak and Fukai (1997) (from rice leaves - N), Jin *et al.* (2006) (from soybean leaves - P), Restrepo-Diaz *et al.* (2008) (from Olive leaves - K) and Sardans *et al.* (2008) (from *Quercus ilex* leaves - Ca, Mg and S).

Kirkby 2001).

Under drought stress, there is a reduction in nutrient uptake by the roots partially due to the reduction in soil moisture, which causes a decreased rate of nutrient diffusion from the soil matrix to the absorbing root surface (Hu *et al.* 2007) and translocation to the leaves (Fig. 1). A number of studies have shown decrease in some mineral accumulation and other physiological effects under water stress (Table 1). Drought also causes stomatal closure, which reduces transpiration (Silva *et al.* 2004, 2009a). Thus, nutrient transport from the roots to the shoot is also limited by the decrease in transpiration rate, imbalance in active transport and membrane permeability, resulting in a reduced absorption power in the roots (Hu and Schmidhalter 2005; Hu *et al.* 2007; Farooq *et al.* 2009). Therefore, drought causes low nutrient availability in the soil and lower nutrient transport in plants (Hu *et al.* 2007).

All these factors acting together have serious consequences for plant development, affecting different physiological processes. The aim of the present paper is to offer an overview of the effects of drought on plant physiology and mineral nutrition as well as the interaction of these factors regarding plant development.

Nitrogen

Nitrogen (N) is present in the atmosphere (the main reservoir), lithosphere and hydrosphere (Mengel and Kirkby 2001). It is required in large amounts and constitutes many biologically important organic molecules in plant cell components, including proteins, nucleic acids, purines, pyrimidines, coenzymes (vitamins) and many other compounds (Dubey and Pessaraki 2001; Hu and Schmidhalter 2005; Barker and Pilbeam 2007). N is very mobile and is available to plants in the form of NO_3^- (nitrate) or NH_4^+ (ammonium) ions (Marschner 1995; Mengel and Kirkby 2001). Organic nitrogen needs moist soil for the mineralization process (Bowden and Chmielewski 2001). Nitrate and ammonium are the major sources of nitrogen for plants. Most ammonium has to be incorporated into organic compounds in the roots, whereas nitrate is readily mobile in the xylem and can be stored in the vacuoles of roots, shoots and storage organs (Marschner 1995; Barker and Pilbeam 2007). The conversion from nitrate to ammonium is mediated by enzymatic processes in which NO_3^- is reduced to NO_2^- catalyzed by enzyme nitrate reductase in the nonorganelle portions of the cytoplasm using the energy and reductant (NADH, NADPH) of photosynthesis and respiration in green tissues and respiration alone in roots and non-green tissues (Ferreira *et al.* 2002; Barker and Pilbeam 2007). Nitrite reductase, which is located in the chloroplasts, reduces nitrite to ammonium using the energy and reductant of photosynthesis (reduced ferredoxin) (Barker and Pilbeam 2007). Drought reduces nitrate reductase activity, which comprises N uptake in several species, such as lettuce (Ruiz-Lozano and Azcon 1996), maize (Foyer *et al.* 1998) and the cowpea (Silveira *et al.* 2001).

Water stress and insufficient N supply in the soil limit plant productivity in most natural and agricultural ecosystems (Prasertsak and Fukai 1997; Taiz and Zeiger 2006). It is well known that water stress decreases symbiotic N_2 fixation and growth in nodulated legumes (DeJong and Phillips 1982; Zahran 1999; Hungria and Vargas 2000). The nitrogen status of a plant has a significant influence over its water relation, as nitrogen and water often interact. When the soil faces a prolonged period of drought, nitrogen mobility is severely restricted by the dehydrated soil. Thus, when a plant faces water deficit, nitrogen deficiency occurs (DaMatta *et al.* 2002), which rapidly inhibits plant growth and leads to chlorosis (yellowing of the leaves), as observed by Mahieu *et al.* (2009) in pea where water stress strongly affected dry weight and N accumulation. Chlorosis is of considerable importance in older leaves near the base of the plants, which can fall off the plant if the nitrogen deficiency becomes severe (Taiz and Zeiger 2006).

Water-use efficiency in plants is greatly influenced by the nitrogen supply. Nitrogen deficiency reduces the ability of a crop to convert available water into yield. According to the Potash and Phosphate Institute, the early uptake of nitrogen under conditions of low moisture enhances both shoot and root development, which is critical to the final yield (Jonhston 2002).

According to Bänziger *et al.* (2000), about 50% of all N

in the leaf is directly involved in photosynthesis as either enzymes or chlorophyll. Thus, if the N supply is insufficient, photosynthesis is decreased by reducing the leaf area and photosynthesis rate as well as accelerating leaf senescence. Wu *et al.* (2008) found a decrease in photosynthesis in *Sophora davidii* seedlings under severe water stress, but the N supply improved the photosynthesis capacity by increasing leaf area and photosynthetic pigment content and enhancing photosynthetic efficiency under water deficit. Thus, an appropriated N supply should alleviate photo-damage under conditions of water stress.

The interaction between water availability and mineral nutrition goes beyond the effects of drought. An excess of salts in the soil reduces its water potential, decreasing water uptake even in well-watered soils. In saline soils, this is called physiological drought (Prisco 1980). Quebedeaux Jr. and Ozbun (1973) demonstrated that ammonium (NH_4^+) inhibits water uptake and decreases leaf water potential in tomato plants growing in nutrient solution. This inhibition was readily reversible by NO_3^- through short-term exposure to NH_4^+ . This suggests that either stomatal closure was impaired or that osmotic potential was decreased with NH_4^+ nutrition, but it was not possible to determine which factor contributed to the differential response.

An excess of N fertilizer induces a reduction in the soil water potential and the plant needs to reduce its water potential in order to take up water from the soil. Low water potential in the soil and plant inhibits plant growth, reduces the development of cells and tissues, decreases the uptake of essential nutrients and causes a variety of morphological and biochemical modifications (Dubey and Pessaraki 2001).

Prasertsak and Fukai (1997) conducted an experiment in order to investigate the interaction of N application and water stress on growth and grain yield of two rice cultivars and found that nitrogen application resulted in the rapid development of water stress, decreasing the leaf water potential and causing high leaf death during the stress period. However, some studies have found that N supply can minimize the effects of drought on plants. DaMatta *et al.* (2002) found that *Coffea canephora* plants (clone INCAPER-99) cultivated with high nitrogen nutrition increased their cell wall rigidity under drought conditions, thereby exhibiting some ability for osmotic adjustment. Thus, both mechanisms may improve water uptake from dry soil, maintaining the cell volume and leading to some degree of drought tolerance. Saneoka *et al.* (2004) demonstrated that N nutrition plays an important role in maintaining cell membrane stability and osmotic adjustment in creeping bentgrass (*Agrostis palustris*) cultivated under conditions of water stress. A high level of N nutrition (20 g N m^{-2}) promoted turgor maintenance, which contributed toward reducing cell damage in water-stressed plants and increased K and Ca concentrations in leaf tissue.

Pimratch *et al.* (2008) cite a number of studies in which drought reduced nitrogen fixation in leguminous species. However, the same authors also suggest that the maintenance of high N_2 fixation under drought stress could be a means for a legume genotype to achieve high yield under

Table 2 Nitrogen supply improves the ability of plants to alleviate some drought effect in some plant species.

Species	Physiological effects		Source
	Water stress (WS)	Mineral supply + WS	
<i>Sophora davidii</i>	Decrease P_N^* , Total leaf area (LA) and chlorophyll content in water level of 20% FC	Nitrogen supply (184 mg.kg ⁻¹) increased P_N , LA and chlorophyll content in water level of 20% FC	Wu <i>et al.</i> 2008
<i>Coffea canephora</i>	Do not affect osmotic potential (-2.03 MPa in control plants and -2.12 MPa in stressed plants). Increase cell wall elasticity from 12.0 to 16.3 MPa in stressed plants)	N (20 mol.m ⁻³ in nutrient solution) reduce osmotic potential (from -2,04 MP control plants to -2,42 MPa in stressed plants). Increase wall cell elasticity (13.4 MPa in control and 22.4 in stressed plants)	DaMatta <i>et al.</i> 2002
<i>Agrostis palustris</i>	Decrease cell membrane stability (about 50% in watered plants and 20% in stressed plants cultivated in 30% FC.	Nitrogen supply (20 g.m ⁻² of soil) Increased cell membrane stability from 50% in control plants for about 65% in stressed plants (30%FC) and N, K and Ca concentration in leaves.	Saneoka <i>et al.</i> 2004

* P_N = net photosynthesis; FC= field capacity; N0= without nitrogen supply

conditions of limited water. Some researches have pointed out that a good N supply can alleviate the effects of water deficit on the plants (Table 2).

Phosphorus

Phosphorus (P) is an essential mineral nutrient required in a relatively large amount in order to maintain growth. It also plays an important role in conserving and transferring energy in the cell metabolism (Jin *et al.* 2006; Amtmann and Blatt 2009). This mineral nutrient exists in organic form such as non-decomposed plant and animal residuals, microbes and organic matter in the soil as well as in inorganic form, usually associated with aluminium (Al), iron (Fe), and calcium (Ca) compounds of variable solubility and availability to plants (Fawcett 2008). Phosphorus occurs in soil almost exclusively in the form of orthophosphate (Mengel and Kirkby 2001) and plants typically absorb either H_2PO_4^- or HPO_4^{2-} , depending on the pH of the growing medium. However, under certain conditions, plants may absorb soluble organic phosphates, including nucleic acids. A portion of absorbed inorganic phosphorus is quickly combined into organic molecules upon entering the roots or after it is transported to the shoot (Sanchez 2007).

About 75% of the phosphorus is combined into organic ions. Phosphorus acquisition efficiency (the ability to acquire a greater amount of P per unit of root length) and P use efficiency (the ability of the plant to produce yield per unit of P acquired from soil) are the major components of P acquisition, which may be improved if P is added to the soil. The association with arbuscular mycorrhiza (AM) significantly affects each of these attributes (Hendrix 2001).

As with nitrogen, insufficient phosphorus is a frequent limiting factor to plant development (Sardans and Peñuela 2004). Plants cultivated under P deficiency exhibit retarded growth and often a reddish coloration occurs due to enhanced anthocyanin formation (Marschner 1995). Phosphorus-deficient plants (stems or leaves) often have also a darker green colour than normal plants, developing red and purple colours (Sanches 2007). P deficiency leads to a general reduction in most metabolic processes, including cell division and expansion as well as respiration and photosynthesis (Marschner 1995).

A good supply of water is required for phosphate availability and absorption by plants. Phosphate ions move through soils primarily through diffusion and if the water content in the soil decreases, the radii of water-filled pores decrease, tortuosity increases and P mobility decreases (Faye *et al.* 2006). Drought causes a reduction in P absorption and transport in plants. A decrease in available P forms and increase in occluded P in the soil reduces P uptake and consequently induces lower foliar P content (Sardans and Peñuela 2004).

Fisher (1980) studied the Townsville stylo (*Stylosanthes humilis*) and found that phosphorus concentration was greatly reduced by water stress; P concentration in stems was more sensitive to stress than in leaves; and the P level returned to the same level as the control after the relief of stress. The authors concluded that the chemical analysis of plants performed to study the phosphorus status in the soil is unreliable unless the plants have grown without water

stress for at least six weeks. Brown *et al.* (2006) found that phosphorus content decreased in *Spartina alterniflora* (roots and shoot) in response to dry soil. Sardans and Peñuelas (2004) found that a 22% reduction in soil moisture produced a 40% decrease in the accumulated aboveground P content in plants, primarily because there was a smaller increase in aerial biomass. Foliar P content was found to increase in the control plots, whereas it decreased in the drought plots. Thus, after just three years of slight drought, a clear trend towards an accumulation of P in the soil and a decrease in P in the standing biomass was observed. The P accumulation in the soil of the drought plots was mainly in forms that were not directly available to plants.

A number of studies have shown that the addition of P alleviates the negative effect of drought stress on yield (Table 3). Gutiérrez-Boem and Thomas (1998) found that applied P increased the leaf appearance rate, final number of leaves and leaf area per plant in wheat under conditions of water deficit. The ability of plants to cope with mild water stress was enhanced by adequate P nutrition. Jin *et al.* (2006) found that drought stress decreased plant growth and yield, total P uptake and P translocation to seeds, but phosphorus fertilization mitigated the negative effects of drought stress on plant growth in two soybean cultivars. Thus, the application of P fertilizer could offset the impact of drought stress during the reproductive period, resulting in less yield penalty in soybeans. Faye *et al.* (2006) found that water stress affected the leaf water potential of two pearl millet cultivars, but P supply was able to improve the drought response of the more sensitive cultivar.

Potassium

Potassium (K) is a mineral element taken up in large amounts by plants and plays an important role in the regulation of water status (Mengel and Kirkby 2001). K is characterized by high mobility in plants at all levels (within individual cells and tissues as well as in long-distance transport via the xylem and phloem). Potassium is the most abundant cation in the cytoplasm. Its salts make a major contribution to the osmotic potential of cells and tissues in glycophyte species (Marschner 1995). It is accumulated passively by both the cytosol and vacuole, except when extracellular K^+ concentrations are very low, in which case it is taken up actively (Taiz and Zeiger 2006).

The potassium ion is involved in many physiological processes, such as enzyme activation, protein synthesis, photosynthesis, osmoregulation, cell extension, stomatal movement and other processes (Mengel and Kirkby 2001; Marschner 1995; Mengel 2007; Farooq *et al.* 2009). It is well known that potassium activates various enzymes that may also be activated by other univalent cationic species of similar size and water mantle, such as NH_4^+ , Rb^+ and Cs^+ . These other cationic species, however, play no major role under natural conditions, as their concentration in the tissues is low and does not achieve the required activation concentration. A likely function of potassium is in polypeptide synthesis in the ribosome, since this process requires a high K^+ concentration. It is not yet clear, however, what particular enzyme or ribosomal site is activated by K^+ .

Table 3 Phosphorus supply improves the ability of plants to alleviate some drought effects in plants.

Species	Physiological effects		Source
	Water stress (WS)	Mineral supply + WS	
Wheat (<i>Triticum aestivum</i> L.)	Shoot biomass dry matter decreased from 317 in well watered plants (80% FC) to 293 mg.plant ⁻¹ (53% FC).	Phosphorus supply (20 mg.kg ⁻¹ soil) increased shoot biomass dry matter in stressed plants (53% FC) from 293 to 521 mg.plant ⁻¹ .	Gutiérrez-Boem and Thomas 1998
Pearl millet Cultivar IBMV 8420	Shoot biomass decreased in stressed plants (withholding water for 7 days) from about 20 g.plant ⁻¹ (control plants) to 10 g.plant ⁻¹ .	Phosphorus supply (34 mg P ₂ O ₅ .kg ⁻¹ soil) increased shoot biomass in stressed plants from 10 to 18 g.plant ⁻¹	Faye <i>et al.</i> 2006
Soybean	Water stress of 35% FC* decrease shoot biomass (from 7.74 to 5.82 g.plant ⁻¹) and grain yield (from 4.42 to 3.58 g.plant ⁻¹) in cv. 'Heisgeng 10'.	Phosphorus supply at 30 mg.kg ⁻¹ soil increased shoot biomass in stressed plants (35% FC) from 5.82 to 6.74 g.plant ⁻¹) and grain yield from 3.58 to 4.03 g.plant ⁻¹ .	Jin <i>et al.</i> 2008

*FC= field capacity

There is indirect evidence that protein synthesis requires K^+ (Mengel 2007).

Water conditions in plants influence the K^+ accumulation in leaves and interact with K^+ nutritional status in some plant species (Restrepo-Diaz *et al.* 2008). The stomatal opening mechanism is governed by the K^+ concentration (Mengel and Kirkby 2001; Larcher 2006; Taiz and Zeiger 2006; Mengel 2007). The opening and closure of K^+ channels are of particular importance to guard cells and this action mechanism is controlled by the reception of red light, which induces stomatal opening (Mengel 2007). Under mild water stress, plants tend to reduce the stomata aperture (Silva *et al.* 2003) and when water stress becomes severe, the stomata generally close (Larcher 2006). Mahouachi (2007) found reduced levels of K^+ in banana plants under drought conditions. Similar results were found by Restrepo-Diaz *et al.* (2008) in the leaves of water-stressed olive plants, regardless of nutritional status.

It has been demonstrated that water is the main factor determining the availability of mineral nutrients such as K^+ in the soil as well as absorption by plants and translocation from the roots to the shoot. However, some studies have shown that higher levels of K fertilization may allow plants such as maize (Premachandra *et al.* 2008) and potato (Khosravifar *et al.* 2008) to tolerate water stress.

Magnesium

Magnesium (Mg) is a small, strongly electropositive divalent cation with a hydrated ionic radius of 0.428 nm and very high hydration energy of 1908 J/mol (Mengel and Kirkby 2001). The major function of magnesium is its role as the central atom of chlorophyll molecules, but magnesium is also involved in energy conservation and conversion (Amtmann and Blatt 2009), protein synthesis, as a cofactor in many enzymatic processes associated with phosphorylation, dephosphorylation, the hydrolysis of various compounds and as a structural stabilizer for various nucleotides (Marschner 1995; Merhaut 2007).

The symptoms of magnesium deficiency between species, but some general characteristics are apparent (Mengel and Kirkby 2001). The principal visual symptom is chlorosis of fully expanded leaves. Moreover, in accordance with the function of Mg^{2+} in protein synthesis, the proportion of protein nitrogen is depressed and that of non-protein nitrogen is increased in magnesium-deficient leaves (Marschner 1995). Since magnesium is an integral component of the chlorophyll molecule and enzymatic processes associated with photosynthesis and respiration, the assimilation of carbon and energy transformation is directly affected by inadequate magnesium (Merhaut 2007).

Magnesium uptake is affected by the conditions of the soil and rhizosphere, such as drought or irregular water availability, which increase the symptoms of magnesium deficiency. As magnesium is not physically or physiologically available under conditions of water deficit, the plant roots are not capable of absorbing adequate magnesium to sustain normal plant growth (Merhaut 2007).

Grabařová and Martinková (2001) found that drought induced a decrease in nitrogen and magnesium content more than phosphorus and potassium in growth periods of the Norway spruce, taking one or more years to restore a sufficient to optimum level of mineral nutrition, depending on the degree stress. Brown *et al.* (2006) found reductions in Mg uptake in both the roots and shoots of *Spartina alterniflora* (coastal smooth cordgrass) under drought conditions. The authors observed symptoms of chlorosis in some older leaves, which they state must be partially due to drought-induced magnesium deficiency, since magnesium is phloem-mobile and young leaves are able to withdraw nutrients from older leaves. However, studies on the interaction between drought and magnesium in plant physiology are scarce.

Calcium

Calcium is the fifth most abundant element by mass in the earth crust. Ca^{2+} is a soft grey alkaline earth metal that plays essential role in living organisms. It is particularly important in the cell physiology, where its movement in and out of the cytoplasm functions as a signal for many cell processes as well as the synthesis of new cell walls in the mitotic spindle during cell division, etc. (Taiz and Zeiger 2006; Shao *et al.* 2008). Ca^{2+} ions bind to a protein called calmodulin (an abbreviation for CALcium MODULated protein) at a minimum of four sites, forming a Ca^{2+} -calmodulin complex. This complex activates numerous target proteins involved in a variety of cell processes, e.g., acting as a second messenger in mediating plant response to abiotic stress (Snedden and Fromm 1998; Taiz and Zeiger 2006).

Calcium is a readily available macroelement for plant uptake in the soil solution. In fact, the release of protons from the roots promotes the exchange reaction of the calcium bond in the organic and mineral soil phases, resulting in calcium desorption (Van Praag *et al.* 2000). According to Jodral-Segado *et al.* (2006) and Utrillas *et al.* (1995), a high calcium concentration in the plant is due to a high concentration of this element in the soil more than uptake efficiency, transpiration velocity or even the addition of liming materials to the soil.

Utrillas *et al.* (1995) found that calcium content increased in bermudagrass (*Cynodon dactylon* (L.) Pers.) during drought when grown in Mediterranean field conditions. Evaluating the soil nutrient mobility and uptake of *Dalbergia sissoo* seedlings grown under different irrigation regimens, Singh and Singh (2004) found an increase in calcium content of around 270 and 200% in the leaves and roots, respectively, at the end of seven months in the most severe treatment. Contradictory results have been found by some researchers. According to Hu and Schmidhalter (2005), Ca uptake is slightly decreased under drought conditions in comparison to P and K, for which absorption is strongly depressed. Analysing the long-term effects of drought in a Mediterranean evergreen (*Quercus ilex*) forest, Sardans *et al.* (2008) concluded that drought tended to decrease Ca concentrations in the aboveground biomass and this effect was attributed to the reduction in transpiration flux. Pomper and Grusak (2004) conclude that transpiration and growth-induced water uptake by developing plant organs appear to drive the transport of Ca in the xylem pathway to vegetal tissues of the snap bean plant. Recently, Abdul Jaleel *et al.* (2007) reported that calcium could improve drought tolerance in *Catharanthus roseus* by increasing γ -glutamyl kinase and reducing the proline oxidase activity.

Sulphur

Sulphur (S) is an essential mineral nutrient to growth and physiological functions in plants (Barker and Pilbeam 2007). It is considered an element of low mobility that can be taken up from soil as sulphate (SO_4^{2-}), which is the main source of this nutrient for higher plants. From the atmosphere, S can be taken up as volatile S compounds, such as S dioxide (SO_2), hydrogen sulphide (H_2S), carbonyl sulphide (COS), methyl mercaptan (CH_3SH) and carbon disulphide (CS_2) (Marschner 1995; Ernst 1998).

S is component of some amino acids, which are essential for protein synthesis. It is also necessary for the formation of chlorophyll, vitamins, enzymes and aromatic oils in some plant species (e.g., mustard) (Itanna 2005; Taiz and Zeiger 2006). Adequate sulphate concentration for growth in most plant species is around 3 to 5 ppm in the soil solution, although crops such as rape and alfalfa require higher concentrations (Itanna 2005). Sulphate is passed through the root epidermis and cortex up to the xylem and translocated into the shoot and leaves. In the leaves, sulphate is activated in the cells and then transferred into an as-yet unidentified carrier and finally reduced to the level of sulphide,

which is incorporated into a nitrogen/carbon skeleton to form cystein (Cys) or homocysteine (HCys) (Brunold 1990; Droux 2004). S availability is partially related to soil moisture, as observed in rainfall gradients in tropical areas of Africa (Itanna 2005).

Evaluating the effects of prolonged drought on a manipulated drought experiment in an evergreen *Quercus ilex* forest, Sardans *et al.* (2008) found that drought increased the total S concentration in the soil and increased S concentrations in the leaf and root in the dominant tree *Q. ilex*. These results may be attributed to the inhibition of S export out of the leaves towards apical tissues due to a reduction in growth of the *Q. ilex* tissues. Schulte *et al.* (1998) found that drought apparently inhibited the basipetal transport of reduced S at the level of phloem loading and/or phloem transport in young pedunculate oak trees (*Quercus robur* L.). However, evaluating the consequences of drought on macronutrients in beech (*Fagus sylvatica* L.) seedlings, Peuke and Rennenberg (2004) found drought to have no effect on the sulphate concentration in the leaves, stems and roots after a three-week treatment simulating a summer drought. As drought induces changes in the metabolism of protein and amino acids (Rabe 1990; Šircelj *et al.* 2005; Knipp and Honermeier 2006), it is possible that such phenomenon may occur in drought-induced S-deficient plants.

Other nutrients

It is well known that diffusion drives most of the micro-nutrient transport from the soil to the roots and low water availability reduces the total uptake and absorption of nutrients from the soil (Hu and Schmidhalter 2005). On this subject, Baligar *et al.* (2001) and Marschner (1995) affirm that a reduced absorption of mineral nutrients results from the interference with nutrient uptake, unloading mechanisms and reduced transpiration flow.

Moreover, due to the much lower amounts of micro-nutrients necessary for the maintenance of plant physiology in comparison to macronutrients, the effects of drought on micronutrient uptake are not as expressive as P uptake, for example. This may explain why little attention has been given to the effects of water stress on micronutrient uptake by plants. On the other hand, many studies have concentrated on the effects of the application of these mineral nutrients on the improvement of water-tolerance. Thus, some essential, beneficial micronutrients and the effects of water stress on their accumulation in plant tissues are presented below.

Zinc

Zinc is taken up predominantly as a divalent cation (Zn^{2+}). At high pH, however, it is likely absorbed as a monovalent cation ($ZnOH^+$). In most soils, the Zn content ranges from 10 to 30 ppm (Marschner 1995; Storey 2007). This nutrient acts as a metal component of enzymes (alcohol dehydrogenase, Cu-Zn superoxide dismutase, carbonic anhydrase, RNA polymerase, etc.) and as a functional, structural or regulatory cofactor of a large number of enzymes. Zn also plays an important role in carbohydrate metabolism, protein synthesis, the metabolism of auxins, etc. (Marschner 1995;

Reddy 2006; Broadley *et al.* 2007). Zn nutrition may affect the water relation in plants as well as stomatal conductance (Khan *et al.* 2004). Evaluating the interactive effect of applied Zn and soil moisture on the early vegetative growth of three alfalfa (*Medicago sativa* L.) varieties, Grewal and Williams (2000) suggest that the ability of alfalfa plants to cope with water stress and excessive soil moisture during the early vegetative stage was enhanced by adequate Zn nutrition.

Silicon

Although silicon (Si) has not been traditionally recognized as an essential nutrient due to a lack of evidence regarding its role in plant metabolism, a recent review of the criteria of nutrient essentiality performed by Epstein and Bloom (2005) may permit the reclassification of Si as an essential nutrient (Liang *et al.* 2007; Ma and Yamaji 2008).

This metalloid can be found in the tissues of all higher plants grown in soil and its beneficial effects have been observed in a wide variety of plant species. Normally, the Si concentration in the soil ranges from 3.5 to 40 mg.L⁻¹ in the form of silicic acid (Marschner 1995; Ma 2005), while its concentration in plants has broader values (ranging from 0.1 to 10.0% of Si in dry weight) (Ma and Takahashi 2002). Silicon increases root endodermal silicification and improves the water balance in cells (Farooq *et al.* 2009). Under stress conditions, the application of silicon offers beneficial effects for plant growth and development, promoting enhanced water uptake and alleviating oxidative stress (Gong *et al.* 2005; Pulz *et al.* 2008).

Evaluating the effects of Si application on drought tolerance in sorghum (*Sorghum bicolor* (L.) Moench), Hattori *et al.* (2005) found that Si application ameliorated the decrease in dry weight under conditions of drought stress, but had no effect on dry matter production under conditions of moisture. Furthermore, sorghum grown with silicon application under dry conditions had a lower shoot to root ratio, indicating the facilitation of root growth and the maintenance of the photosynthetic rate and stomatal conductance at a higher level when compared to plants grown without silicon application.

According to Marschner (1995), Si uptake and transpiration rate have a close relationship. Some studies have shown that the addition of Si alleviates the negative effects of drought in some plant species (Table 4). Studying the effect of silicon on drought-stressed wheat plants, Gong *et al.* (2005) found that the application of silicon increased the activity of superoxide dismutase (SOD), catalase (CAT) and glutathione reductase (GR), the fatty acid unsaturation of lipids and content of photosynthetic pigments and soluble proteins as well as total thiols. This suggests that silicon can increase antioxidant defence abilities and consequently alleviate the oxidative damage to functional molecules in the cells of stressed plants. Moreover, Gunes *et al.* (2008) found that application of Si under drought stress significantly improved Si, K, S, Mg, Fe, Cu, Mn, Na, Cl, V, Al, Sr, Rb, Ti, Cr, and Ba uptake in sunflower cultivars, whereas Zn, Mo, Ni, and Br uptake was not affected. These data suggest an important role of Si in the improvement of drought-tolerance in plants under water stress.

Table 4 Silicon (Si) supply ameliorates the negative effects of drought in some plant species.

Nutrient	Species	Physiological effects of supply nutrient	Source
Silicon	<i>Sorghum bicolor</i> (L.) Moench)	Si application ameliorated the decrease in dry weight under drought stress conditions, facilitation of root growth and the maintenance of the photosynthetic rate and stomatal conductance.	Hattori <i>et al.</i> 2005
	Wheat (<i>Triticum aestivum</i> L.)	The application of Si on drought-stressed wheat plants increased the activities of enzymes of antioxidative stress (SOD, CAT and GR*), the fatty acid unsaturation of lipids, and the contents of photosynthetic pigments and soluble proteins as well as total thiols.	Gong <i>et al.</i> 2005
	Sunflower (<i>Helianthus annuus</i> L.)	Application of Si on drought stressed sunflower plants improved Si, K, S, Mg, Fe, Cu, Mn, Na, Cl, V, Al, Sr, Rb, Ti, Cr, and Ba uptake.	Gunes <i>et al.</i> 2008

*SOD = superoxide dismutase, CAT= catalase, GR= glutathione reductase

Iron

Iron (Fe) was first described as an important essential micronutrient for plant growth in 1860 by Julius von Sachs. Fe is a key component in heme proteins (e.g., cytochromes, catalase and Fe-S proteins such as ferredoxin) and a range of other enzymes (Ma 2005; Römheld and Nikolic 2007). The free Fe concentration in soil solutions is usually very low (less than 10^{-15} M) due to the low solubility of Fe-bearing minerals. To overcome this situation, plants possess two distinct and mutually exclusive strategies for the solubilisation and absorption of Fe. Strategy I is used by all plants except grasses to reduce and solubilise Fe(III) prior to the transport of Fe(II) across the plasma membrane of the root cells. The initial reduction and solubilisation are carried out by two plasma membrane-bound enzymes: H^+ -ATPase and Fe(III) chelate reductase. Strategy II is used by grasses and consists of the synthesis and secretion of low-molecular-weight Fe(III)-specific ligands called phytosiderophores (mucigenic acids, namely nonproteinous amino acids synthesized from methionine). These ligands have high chelation affinity for Fe(III), but not for other polyvalent cations. Fe transport is regulated by a specific uptake system that transports the phytosiderophore-Fe(III) complex across the plasma membrane (Jacoby and Moran 2001).

Fe is not readily mobile between different plant organs. In order to ensure optimal growth, plants need to maintain a continuous iron supply. The effects caused by Fe deficiency include chlorosis in young leaves, yield losses and decreased nutritional quality in crop plants (Ma 2005).

The moisture of the soil can affect Fe content and availability. In wet soils, the Fe^{2+}/Fe^{3+} ratio is higher, which therefore results in greater Fe availability for plants. Under drought conditions, the greater presence of O_2 in the soil induces a decrease in the Fe^{2+}/Fe^{3+} ratio, leading to a decrease in available Fe for plant absorption, since Fe^{2+} is more soluble than Fe^{3+} (Sardans *et al.* 2008).

Chlorine

Chlorine is mainly found in soils as a monovalent ion such as chloride (Cl^-) and is a nutrient involved in the photolysis of water by photosystem II. It is required for cell division in both leaves and roots, plays an important role in stomatal movement and has important functions in osmoregulation and the water relation. This latter function is due to biochemical inertness, which enables Cl^- to play osmotic and cation neutralization roles that may have biophysical or biochemical consequences (Heckman 2007; Reddy 2006; Taiz and Zeiger 2006).

Plants usually contain more chloride than necessary for optimal growth. While it is possible to find Cl^- in the range of 2 to 20 $mg \cdot g^{-1}$ of dry weight in plant tissues, the required content is around 0.20 to 0.40 $mg \cdot g^{-1}$ of dry weight. Wilting of the leaf tips with subsequent chlorosis and necrosis are common symptoms of Cl^- deficiency in higher plants. However, due to the available sources of Cl^- (soil reserves, rain, irrigation water, fertilizers and air pollution), concern regarding this ion is more related to toxicity than deficiency in plants (Reddy 2006; Taiz and Zeiger 2006).

The effects of water stress on chloride content in plants are not well studied. Mahouachi *et al.* (2006) found an increase in Cl^- as well as K^+ and Na^+ concentrations in both leaves and roots after 34 days of water stress in papaya. Hence, together with organic solutes, these ions contribute to osmotic adjustment in plants in order to tolerate drought.

Copper

In plants, copper (Cu) plays an important role as a structural element in regulatory proteins and as a cofactor of many enzymes (such as, Cu/Zn superoxide dismutase, amino oxidase, laccase, plastocyanin, and polyphenol oxidase). It also participates in electron transport in photosynthesis, mitochondrial respiration and in response to oxidative stress as

well as cell wall metabolism, protein transcription and translocation and hormonal signalling (Clemens 2001; Yruela 2005).

Copper is an element with low mobility in plants and, therefore, under conditions of low supply, symptoms are visible mainly in aerial meristems, young leaves and reproductive organs (Larcher 2006). Cu is available for plant uptake only when it appears as the free divalent ion Cu^{2+} . Its critical free concentration in the media ranges from 10^{-14} M to 10^{-16} M. Below this range, Cu deficiency occurs. Cu availability is affected substantially by soil pH, decreasing by 99% for each unit increase in pH (Barker and Pilbeam 2007). Specific copper transporters have not yet been characterized, but there is evidence that copper is reduced during plant uptake (Yruela 2005). Although micronutrient deficiencies are very common in arid regions (Hu and Schmidhalter 2005), no up-to-date information is available regarding the effects of drought on Cu uptake and distribution in higher plants.

Boron, Nickel, Molybdenum, Manganese and Selenium

Boron (B) is an essential nutrient for plants and acts as a structural element, together with Ca^{2+} , for the formation of cell walls. Other functions of B have recently been discovered (Basil *et al.* 2004; Goldbach and Wimmer 2007). In the soil solution, B is found as boric acid (H_3BO_3), which is easily leached by excessive amounts of rainfall. In areas with low rainfall conditions, the B concentration can become toxic to plant growth (Blevins and Lukaszewski 1998; Camacho-Cristóbal *et al.* 2008). According to Reddy (2006), B deficiency is mainly seen in soils with high pH and under drought conditions. In plants, B is considered a non-mobile element and a constant supply from the soil is necessary in order to avoid its deficiency (Taiz and Zeiger 2006).

Recently discovered as a micronutrient, nickel (Ni) can form chelated compounds and can replace other metals in physiologically important centres of plant metabolism. The importance of nickel in higher plants is due to its role in urea and ureide metabolism, iron absorption, N fixation and seed development (Reddy 2006; Seregin and Kozhevnikova 2006). To date, few studies have described the mechanism and kinetics of Ni^{2+} absorption in plants. Similar to other metals, Ni^{2+} absorption may take place through passive diffusion as well as active transport (Seregin and Kozhevnikova 2006).

Molybdenum (Mo) is a metal that occurs in aqueous solutions as molybdate oxyanion (MoO_4^{2-}) in its highest oxidized form [Mo (VI)]. Despite its essentiality for plant metabolism, Mo is considered the nutrient required in the lowest quantity among all nutrients (0.1 ppm) (Marschner 1995; Taiz and Zeiger 2006). Molybdenum enzymes participate in essential redox reactions in global C, N, and S cycles (Bittner *et al.* 2001; Taiz and Zeiger 2006). Both nitrate assimilation and nitrogen fixation processes require the involvement of Mo. Therefore, Mo deficiency can induce N deficiency if nitrate is the primary source or if the N supply in the plant depends on symbiotic N fixation (Taiz and Zeiger 2006). Low moisture in the soil can induce Mo deficiency (Hu and Schmidhalter 2005).

Manganese (Mn) is an essential trace element for plant systems, involved in photosynthesis, respiration and the activation of several enzymes. Its main role is as an electron transporter and it is involved in the antioxidative metabolism. Low moisture in the soil can also induce Mn deficiency. The conversion of Mn to its reduced and more soluble forms is increased in moist soil conditions (Hu and Schmidhalter 2005).

Selenium (Se) is an important microelement for animals, humans and micro-organisms. In plants, Se can increase tolerance to UV-induced oxidative stress, delay senescence and promote the growth of ageing seedlings. Moreover, Se has been shown to have the ability to regulate water status in plants under conditions of drought (Kuznetsov *et al.*

2003; Germ *et al.* 2007).

Despite the considerable importance of these micronutrients as essential to plant life, studies on drought and its effects on micronutrient uptake and metabolism are scarce and little attention has been given to these nutrients due to their lower required concentration for plant development.

CONCLUSIONS AND FINAL REMARKS

Mineral nutrients participate in the synthesis of essential organic molecules, such as amino acids and proteins, and nutrient imbalance can affect many biological processes. Drought disturbs mineral nutrient relations, inhibiting plant growth and development, which reflects on the final crop yield. Drought normally reduces mass flow-dependent mineral nutrient uptake and the translocation of these nutrients from the roots to the shoot, affecting all metabolic processes of plant physiology. On the other hand, adequate macro and micronutrient supply could ameliorate the effects of drought on plant growth and development.

More attention has been given to the studies addressing the effects of drought on macronutrients than on micronutrient requirements. One of the possible causes for this is the lower amount of micronutrients required to maintain the normal functioning of plant metabolic processes. Nevertheless, the role of fertilization of plants with some micronutrients (such as selenium and silicon) has proven to be a successful practice for mitigating the effects of drought on crops.

Global climate changes are expected to increase the occurrence and duration of drought in arid and semi-arid regions, leading farmers and governments to face an increasing risk of food security. As possible technological alternatives, the use of more drought-tolerant plants associated with high nutrient-use efficiency may help cope with or at least ameliorate this problem. Thus, efforts should be made to find alternatives in order to minimize the effects of water stress on plants.

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