

Drought and salinity: A comparison of their effects on mineral nutrition of plants

Yuncai Hu^{1*} and Urs Schmidhalter¹

¹ Chair of Plant Nutrition, Technical University of Munich, D-85350 Freising-Weihenstephan, Germany

Accepted June 11, 2005

PNSS P05/16P

Summary—Zusammenfassung

The increasing frequency of dry periods in many regions of the world and the problems associated with salinity in irrigated areas frequently result in the consecutive occurrence of drought and salinity on cultivated land. Currently, 50% of all irrigation schemes are affected by salinity. Nutrient disturbances under both drought and salinity reduce plant growth by affecting the availability, transport, and partitioning of nutrients. However, drought and salinity can differentially affect the mineral nutrition of plants. Salinity may cause nutrient deficiencies or imbalances, due to the competition of Na⁺ and Cl⁻ with nutrients such as K⁺, Ca²⁺, and NO₃⁻. Drought, on the other hand, can affect nutrient uptake and impair acropetal translocation of some nutrients. Despite contradictory reports on the effects of nutrient supply on plant growth under saline or drought conditions, it is generally accepted that an increased nutrient supply will not improve plant growth when the nutrient is already present in sufficient amounts in the soil and when the drought or salt stress is severe. A better understanding of the role of mineral nutrients in plant resistance to drought and salinity will contribute to an improved fertilizer management in arid and semi-arid areas and in regions suffering from temporary drought. This paper reviews the current state of knowledge on plant nutrition under drought and salinity conditions. Specific topics include: (1) the effects of drought and salt stress on nutrient availability, uptake, transport, and accumulation in plants, (2) the interactions between nutrient supply and drought- or salt-stress response, and (3) means to increase nutrient availability under drought and salinity by breeding and molecular approaches.

Key words: chloride / fertilizer application / mineral nutrients / nutrient availability / sodium

1 Introduction

The increasing frequency of dry periods in many regions of the world and the problems associated with salinity in irrigated areas frequently result in the consecutive occurrence of drought and salinity on cultivated land. Currently, about 50% of irrigated land in the world, which has at least twice the productivity of rainfed land and may produce one-third of the

Trockenstress und Salzstress – Vergleich der Auswirkungen auf die mineralische Ernährung von Pflanzen

Eine Zunahme von Trockenperioden in vielen Ländern der Welt und assoziierte Probleme der Versalzung in bewässerten Gebieten führen häufig zu gleichzeitigem Auftreten von Trockenheit und Salinität. Gegenwärtig sind weltweit ungefähr 50 % aller Bewässerungsflächen durch Salinität beeinträchtigt. Nährstoffstörungen bei Trocken- und Salzstress beeinträchtigen die Verfügbarkeit, den Transport und die Verteilung von Nährelementen in der Pflanze und reduzieren somit das Pflanzenwachstum. Trocken- und Salzstress können sich jedoch unterschiedlich auf die Nährstoffversorgung der Pflanzen auswirken. Salinität kann aufgrund der Konkurrenz zwischen Na⁺ bzw. Cl⁻ und Nährelementen wie K⁺, Ca²⁺ und NO₃⁻ Nährstoffmängel oder -ungleichgewichte in den Pflanzen verursachen. Trockenstress kann sowohl die Nährstoffaufnahme als auch den akropetalen Transport einiger Elemente beeinträchtigen. Trotz kontroverser Schlussfolgerungen in der Literatur hinsichtlich der Wechselbeziehungen von Nährstoffangebot und Trocken- bzw. Salzstress auf das Pflanzenwachstum ist allgemein akzeptiert, dass Nährstoffzufuhr das Pflanzenwachstum nicht verbessert, wenn ausreichend Nährstoffe im Boden verfügbar sind oder bei stark ausgeprägter Trockenheit oder Salinität. Ein besseres Verständnis der Rolle von Mineralstoffen in der Toleranz von Pflanzen gegenüber Trocken- oder Salzstress dürfte gerade in ariden und semi-ariden Gebieten sowie in Regionen, die unter periodischer Trockenheit leiden, zu verbesserten Düngestrategien beitragen. In der vorliegenden Arbeit wird der gegenwärtige Kenntnisstand der mineralischen Ernährung bei Trockenheit und Salinität diskutiert. Schwerpunkte der Betrachtungen sind (1) die Auswirkungen von Trockenheit und Salzstress auf die Verfügbarkeit, die Aufnahme, den Transport und die Anreicherung von Nährelementen in der Pflanze, (2) Wechselbeziehungen zwischen dem Nährstoffangebot und Trockenheit oder Salinität sowie (3) Maßnahmen zur Verbesserung der Nährstoffverfügbarkeit bei Trockenheit und Salzstress mittels züchterischer und molekularbiologischer Ansätze.

world's food, is affected by salinization (*Ghassemi et al., 1995; Hillel, 2000*). Both drought and salinity threaten crop productivity worldwide. Water deficit or osmotic effects are probably the major physiological mechanisms for growth reduction as both stresses lower the soil water potential. However, drought and salinity may differentially affect the mineral-nutrient relations in plants. Generally, drought reduces both nutrient uptake by the roots and transport from the roots to the shoots, because of restricted transpiration rates and impaired active transport and membrane permeability (*Viets, 1972; Alam, 1999*). The decline in soil moisture also results in a decrease in the diffusion rate of nutrients in

* Correspondence: Y. Hu; e-mail: hu@wzw.tum.de

the soil to the absorbing root surface (Pinkerton and Simpson, 1986; Alam, 1999). In contrast, soils contain extreme ratios of $\text{Na}^+ : \text{Ca}^{2+}$, $\text{Na}^+ : \text{K}^+$, $\text{Ca}^{2+} : \text{Mg}^{2+}$, and $\text{Cl}^- : \text{NO}_3^-$ under saline conditions, which cause reduced plant growth due to specific ion toxicities (e.g., Na^+ and Cl^-) and ionic imbalances acting on biophysical and/or metabolic components of plant growth (Grattan and Grieve, 1999).

Fertilizer management can strongly affect crop productivity under conditions of drought or salinity. Thus, the addition of nutrients can either enhance or decrease plants' resistance to drought or salinity or have no effect at all, depending on the level of water availability and salt stress. However, fertilizer management can be more complicated under drought than that under salinity. For instance, under drought conditions, the fertilizer-induced increase in plant growth results in higher water use during the early vegetative period and may have adverse effects through increasing drought stress at critical growth stages. In contrast, the promotion of root growth by mineral application under drought conditions may facilitate the extraction of water and nutrients from deeper soil layers (Viets, 1972). Salinity- or drought-to-fertility relationships have been reviewed during the last decades (e.g., Oertli, 1991; Alam, 1999; Grattan and Grieve, 1999). However, since most dry areas also suffer from salinity, a comparison of mineral-nutrient management for salinity and drought stresses will help to develop strategies that improve plant resistance to either and/or both of these stresses. The objective of this paper is to review the current state of knowledge on plant nutrition under drought and salinity. Specific topics that we will examine include (1) the effects of drought and salt stress on nutrient availability, uptake, transport, and accumulation in plants, (2) interactions between nutrient supply and drought- or salt-stress response, and (3) means to increase nutrient availability under drought and salinity by breeding and molecular approaches.

2 Mineral nutrition under drought and salinity

2.1 Nitrogen

Nitrogen is the mineral element that plants require in the largest amounts and is a constituent of many plant cell components, including amino and nucleic acids. Therefore, nitrogen deficiency rapidly inhibits plant growth. An early study of the relationships between water availability and the N-fertilizer responses from Smika et al. (1965) demonstrated that fertilizer N will not increase yield without sufficient water being available to the plant, and increasing soil-water availability will not increase production without adequate N supply. A recent study on wheat grown in a sandy soil under different moisture-stress levels (Geesing and Schmidhalter, unpublished) showed similar interactive effects of N supply and drought stress (Fig. 1). Application of additional N enhanced wheat yield only when the drought was not severe. While drought conditions may reduce soil-N mineralization, thus lowering the N availability (Bloem et al., 1992), a reduced crop N uptake may also be attributed to a decreased transpiration rate to transport N from roots to shoots (Tanguilig et al., 1987).

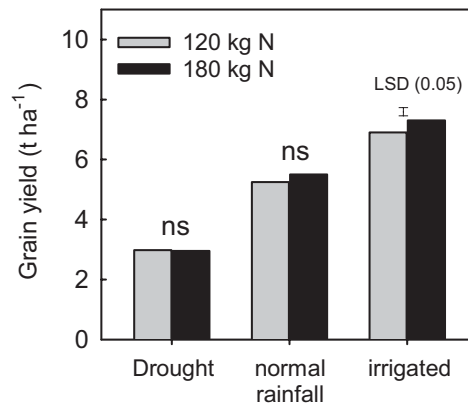


Figure 1: The interactive effect of nitrogen and water supply on the yield of winter wheat grown in sandy soil. Drought was induced by withholding rainfall for one month during the vegetative growth period. The irrigated treatments received an additional 100 mm of water compared to the control treatment, which received only normal rainfall (Geesing and Schmidhalter, unpublished data). Vertical bars and "ns" indicate LSD values at the 0.05 level and not significant, respectively.

Abbildung 1: Interaktiver Einfluss von Stickstoff und Wasser auf den Ertrag von Winterweizen in einem sandigen Boden. Die Behandlungen beinhalteten keine Niederschläge während eines Monats in der Vegetationsperiode, normalen Niederschlag bzw. Zusatzbewässerung von 100 mm (Geesing und Schmidhalter, nicht veröffentlicht). Kleinste gesicherte Unterschiede (Fehlerbalken) bzw. nicht-signifikante Unterschiede (ns) sind angegeben.

For conditions of low N availability, Sinclair and Vadez (2002) suggested to increase crop yields by an increased use of N_2 -fixing legumes. However, a reduced N demand under drought conditions can also reduce the N_2 -fixing activity of legumes (Streeter, 2003). Because the absorption of N shows genetic variation, selection, and breeding of lineages that are more effective in their N uptake may be a more efficient strategy in arid land than in temperate zone (Sattelmacher et al., 1994; Bänziger et al., 2002). Recently, it has been demonstrated that the NH_4^+ transporter AMT1 does function in a high-affinity transport system and that the NO_3^- transporters ANRT1 and ANRT2 function in low- and high-affinity transport systems (reviewed by Dunlop and Phung, 2002). Thus, the beneficial effects of overexpressing an NO_3^- or NH_4^+ transporter would be greatest under conditions where the external NO_3^- or NH_4^+ levels are low, which is true for drought conditions.

Most salinity and N interaction studies were conducted on N-deficient soils (Grattan and Grieve, 1999). Therefore, when the degree of salinity was not severe, the addition of N improved growth and/or yield for cowpea, tomato, clover, and millet (Papadopoulos and Rendig, 1983) and also for wheat (Soliman et al., 1994). A study on the interactive effect of macronutrients (N, P, K^+ , Ca^{2+} , Mg^{2+} , and S) and salinity on the growth of hydroponically-grown wheat by Hu et al. (1997) showed that, for a given salinity level, increases in nutrient supply improved plant growth in the deficient treatment only, and not in those treatments with optimal nutrient supply (Fig. 2).

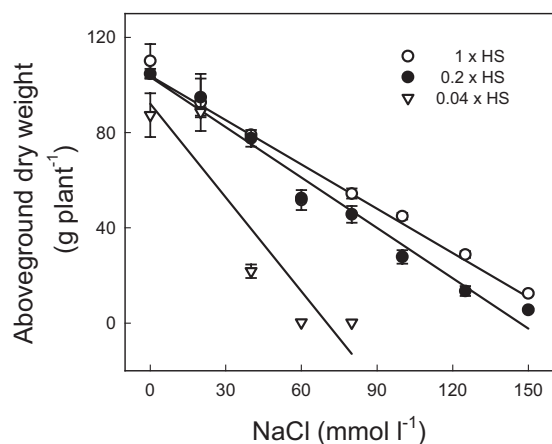


Figure 2: The interactive effects of salinity and macronutrient levels on aboveground dry matter at the final harvest of spring wheat (from Hu et al., 1997). The levels of the macronutrients (N, P, K⁺, Ca²⁺, Mg²⁺, and S) were 1x, 0.2x, and 0.04x that of their strength in the Hoagland nutrient solution. Error bars represent standard deviations.

Abbildung 2: Interaktive Auswirkungen von Salinität und Makronährstoffversorgung auf die oberirdische Trockenmasse von Sommerweizen zum Zeitpunkt der Ernte (nach Hu et al., 1997). Nährstoffkonzentrationen der Makronährstoffe waren das 1-fache, 0,2-fache und 0,04-fache derjenigen einer Hoagland-Nährflösung. Fehlerbalken geben die Standardabweichungen an.

However, whereas in most cases the total shoot N uptake (mg N per plant) decreases under saline conditions, the N concentration (mg N per kg dry weight) increases or remains unchanged under optimal N conditions (e.g., Munns and Termaat, 1986; Hu and Schmidhalter, 1998). These findings suggest that the slower growth rate of crop plants under salinity might prevent the dilution effect of nutrient elements and that the N concentration in plants might not be associated with salt injury for plant growth. Many studies showed that, in contrast to the total N in the plant, salinity reduces the NO₃⁻ concentration in the leaves without affecting the total N content (e.g., Hu and Schmidhalter, 1998), and that the addition of NO₃⁻ results in a reduction in Cl⁻ uptake and accumulation due to NO₃⁻/Cl⁻ antagonism (Bernstein et al., 1974; Hu and Schmidhalter, 1997). This type of interaction might be particularly important for tree and vine plants that are susceptible to Cl⁻ toxicity (Grattan and Grieve, 1999). Furthermore, the form of N supplied to salinized plants might influence not only the Cl⁻ concentration, but also that of other nutrients such as Ca²⁺ and K⁺. For instance, as the NH₄⁺ : NO₃⁻ ratio was increased in the study of Martinez and Cerda (1989), cucumber plants accumulated more Na⁺ and Cl⁻ and less Ca²⁺ and K⁺ in their leaves. The N form might also influence the sensitivity of the plant to salinity (Speer and Kaiser, 1994). For example, wheat and maize were more sensitive to salinity as the ratio of NH₄⁺ : NO₃⁻ increased (Leidi et al., 1991; Botella et al., 1997).

In summary, because there is an interactive effect between Na⁺ and NH₄⁺ and/or between Cl⁻ and NO₃⁻, NH₄⁺ : NO₃⁻ ratio should be considered when N fertilizer is applied to saline soils. Future research should focus on alternative strategies to increase plants' resistance to salinity or drought, including

using the genetic potential for breeding and/or the gene transporters that function in high-affinity transport system for NH₄⁺ and NO₃⁻ for molecular engineering.

2.2 Phosphorus

Phosphorus is a constituent of nucleic acids, phospholipids, phosphoproteins, 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. The data of the interactive effect between P nutrition and salinity on plant growth in the literature are frequently contradictory. However, the addition of P or the strategies employed to increase P uptake in most cases seem to be more important in drought conditions than in saline ones.

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 (e.g., 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. Therefore, 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 water-use efficiency, stomatal conductance (Brück et al., 2000), and photosynthesis (Ackerson, 1985), to higher cell-membrane stability, and to effects on water relations (Sawwan et al., 2000).

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 (e.g., 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 over-expressing 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.

In contrast to the general reduction in P accumulation that occurs in drought-affected plants, the effect of salinity differs between crop plants and according to the experimental conditions (Champagnol, 1979). Compared to the effect of salinity on NO₃⁻ uptake, it is unlikely that Cl⁻ and H₂PO₄⁻ ions are competitive in terms of plant uptake. However, Zhukovskaya (1973) reported that Cl⁻ and SO₄²⁻ salts reduced P uptake in

barley and sunflower. Salinity-induced reductions in P concentrations in plant tissues were frequently found in studies conducted in soil conditions. The availability of P can be reduced in saline soils, because of ionic-strength effects that reduce the activity of P and because P concentrations in the soil solution are tightly controlled by absorption processes and by the low solubility of Ca-P minerals (Grattan and Grieve, 1999). Thus, some plant species will respond positively to added P. Unlike studies conducted in the field, most studies using sand or solution cultures demonstrated that salinity increased the tissue P level. Thus, a study on the interactive effects of salinity and macronutrients other than P on P accumulation in the leaves of hydroponically grown wheat demonstrated both that grain yield and P content in the leaves are not correlated and that P accumulation in the leaves was higher at low than at high macronutrient supply for a given salinity level (Hu and Schmidhalter, 1997). The results from a study of the effect of NaCl and P nutrition on alfalfa by Rogers et al. (2003) illustrated that high or nonlimiting P levels do not affect the response of alfalfa to NaCl. Because ionic-strength effects and the low solubility of Ca-P minerals decrease P availability under saline conditions, repeated applications of P to saline soils are required.

2.3 Potassium

Potassium is an essential factor in protein synthesis, glycolytic enzymes, and photosynthesis; an osmoticum mediating cell expansion and turgor-driven movements; and a competitor of Na⁺ under saline conditions (Marschner, 1995). Because both drought and salinity affect plant growth similarly through water deficit, K⁺ is equally important for maintaining the turgor pressure in plants under either stress. Additionally, higher K⁺ : Na⁺ ratios will also improve the resistance of the plant to salinity (Asch et al., 2000).

The availability of K⁺ to the plant decreases with decreasing soil water content, due to the decreasing mobility of K⁺ under these conditions. Kuchenbuch et al. (1986) showed that low levels of soil moisture reduced root growth and the rate of potassium inflow in onion plants in terms of both per unit of root growth and per unit of root length. Under drought conditions, wilting in plants suggests possible K⁺ deficiency (Beringer and Trolldenier, 1978). This differs from salt-stressed plants, which are characterized by the absence of wilting at the same water potentials as that for drought stress (Shalhevet and Hsiao, 1986). Numerous studies have shown that the application of K fertilizer mitigates the adverse effects of drought on plant growth (e.g., Andersen et al., 1992; Studer, 1993; Sangakkara et al., 2001). Potassium increases the plant's drought resistance through its functions in stomatal regulation, osmoregulation, energy status, charge balance, protein synthesis, and homeostasis (Beringer and Trolldenier, 1978; Marschner, 1995). It also maintains turgor pressure (Mengel and Arneke, 1982) and reduces transpiration under drought conditions (Andersen et al., 1992). In plants coping with drought stress, the accumulation of K⁺ may be more important than the production of organic solutes during the initial adjustment phase, because osmotic adjustment through ion uptake like K⁺ is more energy efficient (Hsiao, 1973). Working with wheat, Morgan (1992) showed that the

lines displaying high osmotic adjustments had a high accumulation of K⁺ in their tissues. In these lines, K⁺ accounted for about 78% of all osmotica. By contrast, amino acids, which were the only other important contributor, constituted only about 22%. A recent study by Ma et al. (2004) showed that K⁺ accumulation in the expanding leaves in three genotypes of *Brassica napus* oilseeds accounted for about 25% of drought-induced changes in osmotic adjustment.

High Na⁺ concentrations in the external solution cause a decrease in both K⁺ and Ca²⁺ concentrations in the tissues of many plant species (Hu and Schmidhalter, 1997). These decreases could be due to the antagonism of Na⁺ and K⁺ at uptake sites in the roots, the effect of Na⁺ on K⁺ transport into the xylem (Lynch and Läuchli, 1984), or the inhibition of uptake processes (Suhayda et al., 1990). Data from a study by Hu and Schmidhalter (1997; see Fig. 2) illustrate that, although salinity decreases K⁺ accumulation in wheat leaves, the increase in macronutrients that occurs at an optimal K-fertilization level does not alter the K⁺ concentration for a given salinity level. At a deficient level of K⁺, however, K⁺ accumulation under salinity was significantly increased with an increase in the macronutrient content. However, Bernstein et al. (1974) reported that, despite the beneficial effects of K⁺ fertilization on increasing the ratio of K⁺ : Na⁺ within maize plants, it did not reduce the adverse effects of salinity on plant growth.

Reasonable amounts of both K⁺ and Ca²⁺ are required to maintain cell-membrane integrity and function (Wei et al., 2003). In glycophytes, which comprise most crop species, exclusion is the predominant strategy for plant resistance to salt stress. Glycophytes restrict both the uptake of toxic ions like Na⁺ by the roots from the soil and also the movement of the toxic ions to the shoot by controlling their influx into the root xylem from the root cells. A high K⁺ : Na⁺ ratio in the plants is also maintained by the roots, showing a selectivity of K⁺ over Na⁺ and by a preferential loading of K⁺ rather than of Na⁺ into the xylem. Toxic ions like Na⁺ can also be transported away from the cytoplasm into the vacuole of cells (intracellular compartmentalization). In fact, the underlying mechanism for maintaining adequate tissue K⁺ levels under salt stress seems to be dependent upon selective K⁺ uptake and selective cellular K⁺ and Na⁺ compartmentalization and distribution in the shoots (Carden et al., 2003). Plants use both low- and high-affinity transporters to take up K⁺ from the growth medium (Blumwald, 2000). The three classes of low affinity channels—K⁺ inward rectifying channels (KIRCs), K⁺ outward rectifying channels (KORCs), and voltage-independent cation channels (VICs)—play important roles in maintaining cellular K⁺ : Na⁺ ratios (Amtmann and Sanders, 1998). In addition, two families of high-affinity transporters have also been reported to play a role in K⁺ transport (Quintero and Blatt, 1997) and thus in also determining the K⁺ : Na⁺ ratio in plant cells. For example, the KUP-HAK high-affinity K⁺ transporters, which have been found in *Arabidopsis* (Kim et al., 1998) and barley (Santa-Maria et al., 1997), couple K⁺ transport to the H⁺ gradient and are highly selective for K⁺. However, Na⁺ blocks them in even small concentrations (Kim et al., 1998), and the high-affinity K⁺ transporter (HAK1) in barley allows Na⁺ permeation (Santa-Maria et al., 1997).

2.4 Calcium

Calcium plays a vital role in regulating many physiological processes that influence both growth and responses to environmental stresses. Included among these are water and solute movement as influenced through the effects of Ca^{2+} on membrane structure and stomatal function, cell division and cell-wall synthesis, direct or signaling roles in systems involved in plant defense and repair of damage from biotic and abiotic stress, and rates of respiratory metabolism and translocation (McLaughlin and Wimmer, 1999). Despite its obvious importance, the low mobility of Ca^{2+} make the rates of its uptake and distribution limiting processes for many key plant functions. Furthermore, the general lack of recognition of the limiting role of Ca^{2+} is due in part to the fact that some important plant functions are controlled by changes in very small physiologically active pools of Ca^{2+} within the cytoplasm. As such, whole-leaf Ca^{2+} levels might not reflect any potential limitations (McLaughlin and Wimmer, 1999).

Although Ca uptake, as for other elements, is decreased under drought conditions, overall Ca accumulation is depressed only slightly compared with P and K. In mature maize plants grown in dry conditions, for example, component accumulations of P, K, and Ca were 40%, 71%, and 91%, respectively, of those found in mature plants grown in well-watered conditions (Jenne et al., 1958). Oertli (1991) also reported that sufficient Ca^{2+} should be present in arid soils with high pHs. However, the Ca^{2+} status of more acidic tropical soils in semi-arid regions can be more problematic.

By contrast, the ameliorative effects of Ca^{2+} on Na^+ toxicity in plants have received considerable attention. Although these effects have been reported since as far back as 1902 (Kearney and Cameron, 1902), few papers have addressed this topic in the first half of the 20th century (LaHaye and Epstein, 1971). Instead, it was only since the importance of external Ca^{2+} on the selectivity of ion transport was realized by Epstein in 1961 (Epstein, 1961) that the very large number of papers on $\text{Na}^+/\text{Ca}^{2+}$ interactions in plants have been published.

A recent review (Cramer, 2002) summarizes the research on $\text{Na}^+/\text{Ca}^{2+}$ interactions under salinity stress from a physiological perspective. Because Na^+ readily displaces Ca^{2+} from its extracellular binding sites, Ca^{2+} availability could be seriously reduced under salinity, especially at low $\text{Ca}^{2+} : \text{Na}^+$ ratios (Cramer et al., 1988). Furthermore, the decreased uptake of Ca^{2+} under saline conditions might be due to its precipitation and the increase in ionic strength that reduces its activity. Calcium deficiency, in general, can impair the selectivity and the integrity of the cell membrane and permit the passive accumulation of Na^+ in plant tissues. In addition, the low $\text{Ca}^{2+} : \text{Na}^+$ ratio in saline media plays a significant role in inhibiting plant growth as well as causing significant changes in morphology and anatomy (Cramer, 1992).

As for many other elements, the addition of supplemental Ca^{2+} has beneficial effects. For instance, supplemental Ca^{2+} in the growth medium increased the relative growth rate of barley under saline conditions (Cramer et al., 1990). Similarly, Fig. 3 from a study by Hu and Schmidhalter (1997) shows that although salinity significantly reduced the Ca^{2+} accumulation in wheat leaves, an increase in the Ca^{2+} concentration in the nutrient solution enhanced Ca^{2+} accumulation. However, Hu and Schmidhalter (1998) later found no difference in Ca^{2+} accumulation between the control and saline treatments in growing leaves of wheat plants grown in soil. Supplemental Ca^{2+} has also been reported to alleviate the adverse effects of salt stress on the germination and vegetative growth of bean (Awada et al., 1995). By contrast, various $\text{Ca}^{2+} : \text{Na}^+$ ratios had no significant effect on the uptake of Na^+ by rice (Yeo and Flowers, 1985).

The relationship between salt resistance and Ca^{2+} accumulation among different plant species was investigated by Unno et al. (2002) using salt-tolerant maize and squash and salt-sensitive reed canary grass and cucumber. The distribution of Ca^{2+} in the shoots decreased greatly in the salt-sensitive plants under salt stress, suggesting that the ability of plants to retain Ca^{2+} is associated with their salt resistance. Calcium maintenance and Na^+ exclusion, which are both related to salinity resistance in *Lycopersicon esculentum*, were geneti-

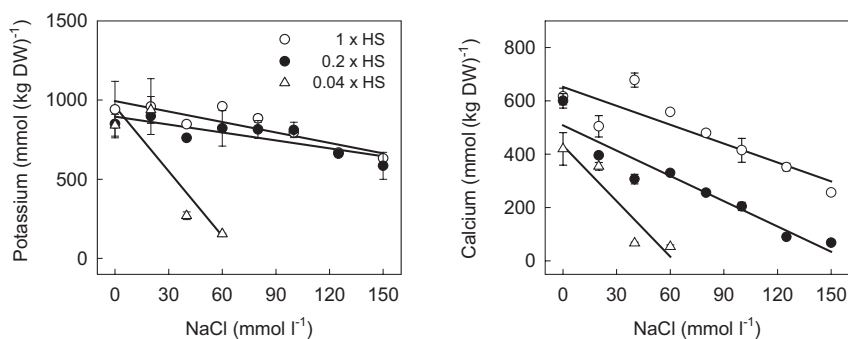


Figure 3: The interactive effects of salinity and macronutrient levels on K and Ca accumulation in wheat leaves at final harvest (from Hu and Schmidhalter, 1997). The levels of the macronutrients (N, P, K⁺, Ca²⁺, Mg²⁺, and S) were 1x, 0.2x, and 0.04x that of their strength in the Hoagland nutrient solution. Error bars represent standard deviations.

Abbildung 3: Interaktive Auswirkungen von Salinität und Makronährstofflevel auf K- und Ca-Gehalte in Weizenblättern zum Zeitpunkt der Ernte (nach Hu und Schmidhalter, 1997). Die Konzentrationen der Makronährstoffe waren das 1-fache, 0,2-fache und 0,04-fache derjenigen einer Hoagland-Nährlösung. Fehlerbalken geben die Standardabweichungen an.

cally determined with the major genetic components being additive in nature (Foolad, 1997). In particular, the inherent genetic capability to maintain Ca^{2+} in the tissues and to exclude Na^+ from the shoots were highly heritable traits, suggesting that $\text{Ca}^{2+} : \text{Na}^+$ ratios might be promising indicators of salt resistance. Ashraf and Naqvi (1992) reported that supplemental Ca^{2+} in the presence of salinity improved the growth of *Brassica juncea* and *Brassica napus*, but not of *Brassica carinata* and *Brassica rapa*, thereby demonstrating genotypic differences to the addition of Ca^{2+} in plant-growth responses. Calcium was also the only ion for which the change in concentration was highly correlated with the relative salt resistance of six *Brassica* species (He and Cramer, 1992).

In recent years, intracellular Ca^{2+} has been found to regulate the responses of the plant to drought and salinity and has also been implicated in the transduction of drought- and salt-stress signals in plants, which play an essential role in osmoregulation under these conditions (Knight et al., 1997; Bartels and Sunkar, 2005). Key discoveries include drought- and high salt-induced expression of Ca^{2+} -dependent protein kinases (Urao et al., 1994) and hyperosmotic shock-induction of putative Ca^{2+} -binding proteins (Ko and Lee, 1996). Sadiqov et al. (2002) found that Ca^{2+} participates on signaling mechanisms of drought-induced proline accumulation for osmotic adjustment. They supported the findings of Knight et al. (1997), who indicated that this was due to the induction of a transcript for proline biosynthetic enzyme (P5CS) being inhibited in the presence of Ca^{2+} channels in *Arabidopsis* (also shown in wheat and maize; Nayyar, 2003).

2.4 Other elements

Little information is available on the effect of drought on Mg and S nutrition of plants. However, we expect that drought reduces both Mg and S uptake because Mg deficiency is occurring more frequently as the cropping intensity increases and because the decrease in atmospheric S during the past decade has been associated with the appearance of S-deficiency symptoms (Scherer, 2001) and has had severe consequences for S nutrition and crop production. Although many studies have analyzed plant tissues for Mg^{2+} , few salinity-nutrient studies have directed any attention to Mg^{2+} nutrition as affected by salinity (Grattan and Grieve, 1999). A study by Hu and Schmidhalter (1997) revealed that the Mg^{2+} concentration in wheat leaves was reduced, but could be increased for a given salinity level by increasing the Mg^{2+} concentration in the nutrient solution. A correlation between wheat yield and Mg^{2+} accumulation in the plant under saline conditions was also noted, suggesting that Mg^{2+} supplementation could play a role in increasing plant salt resistance when this nutrient is available at low levels.

Because the transport of micronutrients to the plant roots occurs via diffusion, low soil moisture content, as with P uptake, will reduce micronutrient uptake. However, because plants require much smaller quantities of micronutrients, the effects of drought stress are not as great as for P. Temporary B deficiency is common under drought and is related both to low mineralization, because much of the B is in the organic

matter, and also to the lower subsoil B in some areas (relative to the surface soil), because water uptake occurs predominantly from the subsoil under dry conditions. By contrast, excessive rainfall can leach some of the available soil B in sandy soils. Low soil moisture can also induce deficiencies in Mn, Mo, Fe, and Zn. On the other hand, Mn and Fe become increasingly available under moist conditions because of its conversion to reduced and more soluble forms (Havlin et al., 1999). Several recent studies have shown that an increased Si accumulation in plants can improve growth under drought conditions, due to a reduction in transpiration (Epstein, 1999; Ma, 2004).

In contrast to the situation in dry soils, the availability of micronutrients in saline and/or sodic soils depends on the solubility of the micronutrients, the pH and pE of the soil solution, and the nature of the binding sites on the organic- and inorganic-particle surfaces. Thus, salinity can differentially affect the micronutrient concentrations in the plant, depending upon the crop species and the salinity level (Oertli, 1991). For example, salinity increased the Mn and Zn concentrations in the shoots of barley (Hassan et al., 1970a) and rice (Verma and Neue, 1984), but decreased it in corn (Hassan et al., 1970b). Salinity similarly increased the Fe concentration in the shoots of lowland rice (Verma and Neue, 1984), but decreased it in barley and corn (Hassan et al., 1970a, b). Concentrations of B in the shoots at anthesis and in the wheat grain were decreased by increasing salinity (Holloway and Alston, 1992). From recent studies in solution and soil cultures, Hu et al. (2000) and Hu and Schmidhalter (2001) reported that the micronutrients Mn, Zn, Fe, and B in growing and mature leaves of wheat were largely unaffected by salinity. Although B deficiency is more widespread than B toxicity, particularly in humid climates, the latter is a concern in arid areas where salinity problems also exist (Nicholovaichuk et al., 1988). Finally, results in literature show that Si can alleviate the adverse effects of salinity on soybean (Schmidhalter and Oertli, 1993) and cucumber (Zhu et al., 2004).

Micronutrient deficiencies are very common in arid regions. However, they are often localized such that each case must be examined individually. For example, although the contents of micronutrients in the soil might be high, the plants can still suffer from nutrient deficiencies. Thus, the addition of a micronutrient to a soil would have little effect and, instead, foliar application would prove to be more useful (Oertli, 1991).

3 Conclusions

Both drought and salinity disturb the mineral-nutrient relations in plants through their effects on nutrient availability, transport, and partitioning in plants. Additionally, salinity stress also induces ion deficiency or imbalance due to the competition of nutrients such as K^+ , Ca^{2+} , and NO_3^- with the toxic ions Na^+ and Cl^- . Mineral nutrients play a vital role in determining plant resistance to drought or salinity. Because both drought and salinity cause a similar effect on plant growth through a water deficit, K^+ is equally important to maintain the turgor pressure of the plant under either stress. High $\text{K}^+ : \text{Na}^+$ ratios will also improve the resistance of the plant to salinity.

Although Ca^{2+} is a key signal messenger for regulating plant resistance to both drought and salinity, the interaction between Ca^{2+} and each stress has been studied more intensively for salinity than for drought stress. By contrast, the increase in N and P uptake by plants will be more crucial under drought conditions only. The competition between Cl^- and NO_3^- under saline conditions means that the form of N plays a critical role in determining the growth of salinized plants. Compared to N, P, K^+ , and Ca^{2+} , however, micronutrients might be less important with respect to plant resistance to drought and salinity.

Although increasing the supply of nutrients to the growth medium under drought or saline conditions can alleviate the adverse effects of either stress on plant growth, it is generally accepted that such increases will not improve plant growth when the nutrient is already present in the soil in sufficient amounts and the drought or salt stress is severe. This is especially true for N. Thus, more research should focus on alternative strategies of increasing plant resistance to drought or salinity, including the use of the genetic potential for conventional breeding and/or molecular technologies to introduce appropriate genes and regulatory systems.

References

- Ackerson, R. C. (1985): Osmoregulation in cotton in response to water-stress. 3. Effects of phosphorus fertility. *Plant Physiol.* 77, 309–312.
- Ajourri, A., Asgedom, H., 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.
- Alam, S. M. (1999): Nutrient uptake by plants under stress conditions, in Pessaraki, M.: Handbook of Plant and Crop Stress. Marcel Dekker, New York, pp. 285–314.
- Amtmann, A., Sanders, D. (1998): Mechanisms of Na^+ uptake by plant cells. *Adv. Bot. Res.* 29, 75–112.
- Andersen, M. N., Jensen, C. R., Lösch, R. (1992): The interaction effects of potassium and drought in field-grown barley. 1. Yield, water-use efficiency and growth. *Acta Agric. Scand. Sect. B Soil Plant Sci.* 42, 34–44.
- Asch, F., Dingkuhn, M., Miezani, K., Dörffling, K. (2000): Leaf K/Na ratio predicts salinity induced yield loss in irrigated rice. *Euphytica* 113, 109–118.
- Ashraf, M., Naqvi, M. I. (1992): Growth and ion uptake of 4 Brassica species as affected by $\text{Na}^+/\text{Ca}^{2+}$ ratio in saline sand culture. *Z. Pflanzenernähr. Bodenkd.* 155, 101–108.
- Awada, S., Campbell, W. F., Dudley, L. M., Jurinak, J. J., Khan, M. A. (1995): Interactive effects of sodium-chloride, sodium-sulfate, calcium-sulfate, calcium-chloride on snapbean growth, photosynthesis, ion uptake. *J. Plant Nutr.* 18, 889–900.
- Bagayoko, M., George, E., Römheld, V., Buerkert, A. B. (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.
- Bänziger, M., Edmeades, G. O., Lafitte, H. R. (2002): Physiological mechanisms contributing to the increased N stress tolerance of tropical maize selected for drought tolerance. *Field Crops Res.* 75, 223–233.
- Bartels, D., Sunkar, R. (2005): Drought and salt tolerance in plants. *Crit. Rev. Plant Sci.* 24, 23–58.
- Bennett, J. M., Jones, J. W., Zur, B., Hammond, L. C. (1986): Interactive effects of nitrogen and water stresses on water relations of field-grown corn leaves. *Agron. J.* 78, 273–280.
- Bernstein, L., Francois, L. E., Clark, R. A. (1974): Interactive effects of salinity and fertility on yields of grains and vegetables. *Agron. J.* 66, 412–421.
- Beringer, H., Trolldenier, G. (1978): Influence of K nutrition on the response to environmental stress, in: Potassium Research – Review and Trends. Proceedings of the 11th Congress of the International Potash Institute. Internat. Potash Inst., Bern, pp. 189–222.
- Blom, J., Deruiter, P. C., Koopman, G. J., Lebbink, G., Brussaard, L. (1992): Microbial numbers and activity in dried and rewetted arable soil under integrated and conventional management. *Soil Biol. Biochem.* 24, 655–665.
- Blumwald, E. (2000): Sodium transport and salt tolerance in plants. *Curr. Opin. Cell Biol.* 12, 431–434.
- Botella, M. A., Martinez, V., Pardines, J., Cerda, A. (1997): Salinity induced potassium deficiency in maize plants. *J. Plant Physiol.* 150, 200–205.
- Brück, H., Payne, W. A., 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.
- Carden, D. E., Walker, D. J., Flowers, T. J., Miller, A. J. (2003): Single-cell measurements of the contributions of cytosolic Na^+ and K^+ to salt tolerance. *Plant Physiol.* 131, 676–683.
- Champagnol, F. (1979): Relationships between phosphate nutrition of plants and salt toxicity. *Phosphorus Agric.* 76, 35–43.
- Cramer, G. R. (1992): Kinetics of maize leaf elongation. 2. Responses of a Na^+ -excluding cultivar and a Na^+ -including cultivar to varying $\text{Na}^+/\text{Ca}^{2+}$ salinities. *J. Exp. Bot.* 43, 857–864.
- Cramer, G. R. (2002): Sodium-calcium interactions under salinity stress, in Läuchli, M., Lüttge, U.: Salinity: Environment-Plants-Molecules. Kluwer Academic Publishers, London, pp. 205–228.
- Cramer, G. R., Epstein, E., Läuchli, A. (1988): Kinetics of root elongation of maize in response to short-term exposure to NaCl and elevated calcium-concentration. *J. Exp. Bot.* 39, 1513–1522.
- Cramer, G. R., Epstein, E., Läuchli, A. (1990): Effects of sodium, potassium and calcium on salt-stressed barley. 1. Growth analysis. *Physiol. Plant.* 80, 83–88.
- DaMatta, F. M., Loos, R. A., Silva, E. A., Loureiro, M. E., Ducatti, C. (2002): Effects of soil water deficit and nitrogen nutrition on water relations and photosynthesis of pot-grown coffee *Canephora pierre*. *Trees Struct. Funct.* 16, 555–558.
- Dunlop, J., Phung, T. (2002): Transporter genes to enhance nutrient uptake: Opportunities and challenges. *Plant Soil* 245, 115–122.
- Epstein, E. (1961): The essential role of calcium in selective cation transport by plant cells. *Plant Physiol.* 36, 437–444.
- Epstein, E. (1999): Silicon. *Annu. Rev. Plant Physiol.* 50, 641–664.
- Foolad, M. R. (1997): Genetic basis of physiological traits related to salt tolerance in tomato, *Lycopersicon esculentum* Mill. *Plant Breeding* 116, 53–58.
- Garg, B. K., 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.
- Ghassemi, F., Jakeman, A. J., Nix, H. A. (1995): Salinisation of Land and Water Resources. University of New South Wales Press Ltd., Canberra, Australia.
- Grattan, S. R., Grieve, C. M. (1999): Mineral nutrient acquisition and response by plants grown in saline environments, in Pessaraki,

- M.: Handbook of Plant and Crop Stress. Marcel Dekker, New York, pp. 203–229.
- Hassan, N. A. K., Jackson, W. A., Drew, J. V., Knudsen, D., Olson, R. A. (1970a): Influence of soil salinity on production of dry matter and uptake and distribution of nutrients in barley and corn. 1. Barley (*Hordeum vulgare* L.). *Agron. J.* 62, 43–45.
- Hassan, N. A. K., Drew, J. V., Knudsen, D., Olson, R. A. (1970b): Influence of soil salinity on production of dry matter and uptake and distribution of nutrients in barley and corn. 2. Corn (*Zea mays* L.). *Agron. J.* 62, 46–51.
- Havlin, J. L., Beaton, J. D., Tisdale, S. L., Nelson, W. L. (1999): Soil Fertility and Fertilizers: An Introduction to Nutrient Management. Prentice-Hall, Inc., London, pp. 406–425.
- He, T., Cramer, G. R. (1992): Growth and mineral-nutrition of six rapid-cycling *Brassica* species in response to seawater salinity. *Plant Soil* 139, 285–294.
- Hillel, D. (2000): Salinity Management for Sustainable Irrigation. The World Bank, Washington, D.C.
- Holloway, R. E., Alston, A. M. (1992): The effects of salt and boron on growth of wheat. *Aust. J. Agric. Res.* 43, 987–1001.
- Hsiao, T. C. (1973): Plant responses to water stress. *Annu. Rev. Plant Physiol.* 24, 519–570.
- Hu, Y., Schmidhalter, U. (1997): Interactive effects of salinity and macronutrient level on wheat. 2. Composition. *J. Plant Nutr.* 20, 1169–1182.
- Hu, Y., Schmidhalter, U. (1998): Spatial distributions and net deposition rates of mineral elements in the elongating wheat (*Triticum aestivum* L.) leaf under saline soil conditions. *Planta* 204, 212–219.
- Hu, Y., Schmidhalter, U. (2001): Effects of salinity and macronutrient levels on micronutrients in wheat. *J. Plant Nutr.* 24, 273–281.
- Hu, Y., Oertli, J. J., Schmidhalter, U. (1997): Interactive effects of salinity and macronutrient level on wheat. 1. Growth. *J. Plant Nutr.* 20, 1155–1167.
- Hu, Y., von Tucher, S., Schmidhalter, U. (2000): Spatial distributions and net deposition rates of Fe, Mn and Zn in the elongating leaves of wheat under saline soil conditions. *Aust. J. Plant Physiol.* 27, 53–59.
- Jenne, E., Rhoades, H., Yien, C., Howe, O. (1958): Change in nutrient element accumulation by corn with depletion of soil moisture. *Agron. J.* 50, 71–80.
- Kearney, T. H., Cameron, F. K. (1902): The effect upon seedling plants of certain components of alkali soils. *USDA Office of the Secretary Report* 71, 1–60.
- Kim, E. J., Kwak, J. M., Uozumi, N., Schroeder, J. I. (1998): AtKUP1: an *Arabidopsis* gene encoding high-affinity potassium transport activity. *Plant Cell* 10, 51–62.
- Knight, H., Trewavas, A. J., Knight, M. R. (1997): Calcium signalling in *Arabidopsis thaliana* responding to drought and salinity. *Plant J.* 12, 1067–1078.
- Ko, J. H., Lee, S. H. (1996): Biochemical studies of purified 23 kD calcium-binding protein in *Dunaliella salina* and its cDNA cloning. *Plant Physiol.* 111, 714–720.
- Kuchenbuch, R., Claassen, N., Jungk, A. (1986): Potassium availability in relation to soil-moisture. 1. Effect of soil-moisture on potassium diffusion, root-growth and potassium uptake of onion plants. *Plant Soil* 95, 221–231.
- LaHaye, P. A., Epstein, E. (1971): Calcium and salt toleration by bean plants. *Physiol. Plant.* 25, 213–218.
- Leidi, E. O., Silberbush, M., Lips, S. H. (1991): Wheat growth as affected by nitrogen type, pH and salinity. 1. Biomass production and mineral-composition. *J. Plant Nutr.* 14, 235–246.
- Liebersbach, H., Steingrobe, B., Claassen, N. (2004): Roots regulate ion transport in the rhizosphere to counteract reduced mobility in dry soil. *Plant Soil* 260, 79–88.
- Lynch, J., Läuchli, A. (1984): Potassium-transport in salt-stressed barley roots. *Planta* 161, 295–301.
- Ma, J. F. (2004): Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. *Soil Sci. Plant Nutr.* 50, 11–18.
- Ma, Q. F., Turner, D. W., Levy, D., Cowling, W. A. (2004): Solute accumulation and osmotic adjustment in leaves of *Brassica* oilseeds in response to soil water deficit. *Aust. J. Agric. Res.* 55, 939–945.
- Marschner, H. (1995): Mineral Nutrition of Higher Plants. Academic Press, London.
- Martinez, V., Cerda, A. (1989): Influence of N-source on rate of Cl, N, Na and K uptake by cucumber seedlings grown in saline condition. *J. Plant Nutr.* 12, 971–983.
- McLaughlin, S. B., Wimmer, R. (1999): Transley Review No. 104 – Calcium physiology terrestrial ecosystem processes. *New Phytol.* 142, 373–417.
- Mengel, K., Arneke, W. W. (1982): Effect of potassium on the water potential, the pressure potential, the osmotic potential and cell elongation in leaves of *Phaseolus vulgaris*. *Physiol. Plant.* 54, 402–408.
- Morgan, J. A. (1986): The effects of N-nutrition on the water relations and gas-exchange characteristics of wheat (*Triticum aestivum* L.). *Plant Physiol.* 80, 52–58.
- Morgan, J. M. (1992): Osmotic components and properties associated with genotypic differences in osmoregulation in wheat. *Aust. J. Plant Physiol.* 19, 67–76.
- Munns, R., Termaat, A. (1986): Whole-plant responses to salinity. *Aust. J. Plant Physiol.* 13, 143–160.
- Nayyar, H. (2003): Accumulation of osmolytes and osmotic adjustment in water-stressed wheat (*Triticum aestivum*) and maize (*Zea mays*) as affected by calcium and its antagonists. *Environ. Exp. Bot.* 50, 253–264.
- Nicholaichuk, W., Leyshon, A. J., Jame, Y. W., Campbell, C. A. (1988): Boron and salinity survey of irrigation projects and the boron adsorption characteristics of some Saskatchewan soils. *Can. J. Soil Sci.* 68, 77–90.
- Oertli, J. J. (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.
- Papadopoulos, I., Rendig, V. V. (1983): Interactive effects of salinity and nitrogen on growth and yield of tomato plants. *Plant Soil* 73, 47–57.
- Pinkerton, A., Simpson, J. R. (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.
- Quintero, F. J., Blatt, M. R. (1997): A new family of K⁺ transporters from *Arabidopsis* that are conserved across phyla. *FEBS Letters* 415, 206–211.
- Rasnack, M. (1970): Effect of mannitol and polyethylene glycol on phosphorus uptake by maize plants. *Ann. Bot.* 34, 497–502.
- Rogers, M. E., Grieve, C. M., Shannon, M. C. (2003): Plant growth and ion relations in lucerne (*Medicago sativa* L.) in response to the combined effects of NaCl and P. *Plant Soil* 253, 187–194.

- Sadiqov, S. T., Akbulut, M., Ehmedov, V. (2002): Role of Ca²⁺ in drought stress signaling in wheat seedlings. *Biochem. Moscow* 67, 491–497.
- Sadras, V. (2004): Yield and water-use efficiency of water- and nitrogen-stressed wheat crops increase with degree of co-limitation. *Eur. J. Agron.* 21, 455–464.
- Sangakkara, U. R., Frehner, M., Nösberger, J. (2001): Influence of soil moisture and fertilizer potassium on the vegetative growth of mungbean (*Vigna radiata* L. Wilczek) and cowpea (*Vigna unguiculata* L. Walp). *J. Agron. Crop Sci.* 186, 73–81.
- Santa-Maria, G. E., Rubio, F., Dubcovsky, J., Rodriguez-Navarro, A. (1997): The HAK1 gene of barley is a member of a large gene family and encodes a high-affinity potassium transporter. *Plant Cell* 9, 2281–2289.
- Sattelmacher, B., Horst, W. J., Becker, H. C. (1994): Factors that contribute to genetic-variation for nutrient efficiency of crop plants. *Z. Pflanzenernähr. Bodenkd.* 157, 215–224.
- Sawwan, J., Shibli, R. A., 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.
- Scherer, H. W. (2001): Sulphur in crop production – Invited paper. *Eur. J. Agron.* 14, 81–111.
- Schmidhalter, U., Oertli, J. J. (1993): Increasing salt tolerance of soybean plants by adding silicon to nutrient solutions, in: International Symposium on Strategies for Utilizing Salt Affected Lands. Bangkok, Thailand, pp. 542–549.
- Schmidhalter, U., Burucs, Z., von Tucher, S., Hu, Y., Gutser, R. (1999): Foliar fertilization applied to droughted and salinized wheat and maize seedlings, in: Proceedings of the 2nd International Workshop on Foliar Fertilization. Bangkok, Thailand, pp. 345–358.
- Shalhevet, J., Hsiao, T. C. (1986): Salinity and drought – a comparison of their effects on osmotic adjustment, assimilation, transpiration and growth. *Irrig. Sci.* 7, 249–264.
- Sinclair, T. R., Vadez, V. (2002): Physiological traits for crop yield improvement in low N and P environments. *Plant Soil* 245, 1–15.
- Smika, D., Haas, H., Power, W. (1965): Effects of moisture and nitrogen fertilizer on growth and water use by native grass. *Agron. J.* 57, 483–486.
- Smith, F. W. (2002): The phosphate uptake mechanism. *Plant Soil* 245, 105–114.
- Soliman, M. S., Shalabi, H. G., Campbell, W. F. (1994): Interaction of salinity, nitrogen, and phosphorus fertilization on wheat. *J. Plant Nutr.* 17, 1163–1173.
- Speer, M., Kaiser, W. M. (1994): Replacement of nitrate by ammonium as the nitrogen-source increases the salt sensitivity of pea plants. 2. Intercellular and intracellular solute compartmentation in leaflets. *Plant Cell Environ.* 17, 1223–1231.
- Streeter, J. G. (2003): Effects of drought on nitrogen fixation in soybean root nodules. *Plant Cell Environ.* 26, 1199–1204.
- 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.
- Suhayda, C. G., Giannini, J. L., Briskin, D. P., Shannon, M. C. (1990): Electrostatic changes in *Lycopersicon esculentum* root plasma-membrane resulting from salt stress. *Plant Physiol.* 93, 471–478.
- Tanguilig, V. C., Yambao, E. B., O'Toole, J. C., Dedatta, S. K. (1987): Water-stress effects on leaf elongation, leaf water potential, transpiration, and nutrient-uptake of rice, maize, and soybean. *Plant Soil* 103, 155–168.
- Turner, L. B. (1985): Changes in the phosphorus content of *Capsicum annuum* leaves during water-stress. *J. Plant Physiol.* 121, 429–439.
- Unno, H., Maeda, Y., Yamamoto, S., Okamoto, M., Takenaga, H. (2002): Relationship between salt tolerance and Ca²⁺ retention among plant species. *Soil Sci. Plant Nutr.* 73, 715–718.
- Urao, T., Katagiri, T., Mizoguchi, T., Yamaguchishinozaki, K., Haya-shida, N., Shinozaki, K. (1994): Two genes that encode Ca²⁺-dependent protein-kinases are induced by drought and high-salt stresses in *Arabidopsis thaliana*. *Mol. Gen. Gen.* 244, 331–340.
- Viets Jr., F. G. (1972): Water deficits and nutrient availability, in Kozlowski, T. T.: Water Deficits and Plant Growth. Vol. III: Plant Responses and Control of Water balance. Academic Press, New York, pp. 217–240.
- Verma, T. S., Neue, H. U. (1984): Effect of soil-salinity level and zinc application on growth, yield, and nutrient composition of rice. *Plant Soil* 82, 3–14.
- Wei, W. X., Bilsborrow, P. E., Hooley, P., Fincham, D. A., Lombi, E., Forster, B. P. (2003): Salinity induced differences in growth, ion distribution and partitioning in barley between the cultivar Maythorpe and its derived mutant golden promise. *Plant Soil* 250, 183–191.
- Yeo, A. R., Flowers, T. J. (1985): The absence of an effect of the Na⁺/Ca²⁺ ratio on sodium-chloride uptake by rice (*Oryza sativa* L.). *New Phytol.* 99, 81–90.
- Zhu, Z. J., Wei, G. Q., Li, J., Qian, Q. Q., Yu, J. Q. (2004): Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (*Cucumis sativus* L.). *Plant Sci.* 167, 527–533.
- Zhukovskaya, N. (1973): Absorption and accumulation of phosphate by plants under conditions of salinization. *Soviet. Plant Physiol.* 20, 55–61.