Fresh Look at Plant Salt Tolerance as Affected by Dynamics at the Soil/Root-Interface Using Leek and Rape as Model Crops

Uwe Schleiff[1*] • Adele Muscolo[2]

[1] Independent Expert for Irrigation and Salinity – Fertilizers and Crops – Soils and Environment; D-38289 Wolfenbuettel; P. O. Box 1934; Germany
[2] Department of Agriculture and Forestry Management, Faculty of Agriculture, University 'Mediterranea' of Reggio Calabria, Reggio Calabria 89060, Italy

Corresponding author: * schleiff@salinity.de (www.salinity.de)

ABSTRACT

In the past decades crop salt tolerance research focussed mainly on two important aspects: (a) study of the effects of vertical salt distribution in the rooted soil layer on crop salt tolerance, which is applied to manage crop growth on saline soils, (b) and to understand biochemical and physiological effects of salinity on plants at cell, tissue, organ and whole plant level as basic information to develop more salt tolerant plants. Unfortunately most biochemical and physiological findings were little relevant to improve plant growth under saline soils conditions. The objective of this paper is to point out an aspect that was rarely considered in the past decades, it is the effect of the transpiration driven lateral salt distribution around roots on crop salt tolerance. It is supposed that root morphology is a most important feature, which affects the process of salt accumulation around roots and thus water uptake from saline soils. Shoot transpiration causes a much steeper increase of soil solution salinity around roots forming small rhizocylinder volumes (e.g. onions, leek) as compared to roots forming larger rhizocylinder volumes (e.g. rape). Consequently root morphology affects conditions for root water uptake from saline soils and crop salt tolerance. At the beginning of the experimental phase, when soil water salinity was relatively low (total soil water potential Ψt about -0.1 to -0.2 MPa in the low saline treatment and -0.3 to -0.4 MPa in the moderately saline treatment), water uptake rate by roots of rape was 300 to 400% higher as compared to leek roots. Leek roots nearly ceased water uptake, when Ψt has dropped to -0.9 to -1.0 MPa, but water uptake by rape roots was still significant. A concept for future research is presented.

INTRODUCTION

The effective use of salt-affected land and brackish water resources for environment-friendly crop production and landscape greening need the design and development of more salt-tolerant plants and adaptation of irrigation technique to saline soils conditions.

In the past decades research to understand and to improve crop salt tolerance basically focussed on two aspects as summarized in **Table 1**. The classical soil-based concept aimed to evaluate quantitatively the effects of root zone salinity on plant growth and yields for a wide range of crops. Controlled leaching of salts below the rooted soil layer was the key to maintain an average root zone salinity that would provide economic crop yields (Maas and Hoffmann 1977; van Hoorn and Alphen 1994; Oster 1999). Much attention was given to the effects and measurement of the soil matric and osmotic water potentials on plant growth and yields (Wadleigh 1946). Predominantly research on crop salt tolerance was practical orientated field work and most pot experiments were carried out with soils.

The emphasis of the subsequent research phase on salt tolerance was more orientated on fundamental reactions of plants and their organs on saline conditions (Munns and Tester 2008; Schubert *et al*. 2009). Most research, however, was aimed at an improved understanding of physiological responses and biochemical mechanisms as a base to develop crops of higher salt tolerance (ion exclusion and compartmentation, organic solutes and osmotic effects, mineral nutrition and specific toxicities, hormones and enzymes, etc.). As pointed out by several authors (Flowers 2004; Yamaguchi and Blumwald 2005; Munns 2007), results from these approaches to improve plant growth for saline soils

conditions are disappointing in spite of considerable efforts. One conclusion from the numerous and very detailed results of those who looked for a specific key factor alleviating salt stress to crops, is the recommendation of Munns (2007) to follow a more holistic approach than concentrating on highly organ-specific research.

Based on earlier results reported from Riley and Barber (1970) and Schleiff (1981, 2010) we suppose that a more holistic concept should not just comprise the plant as a whole, but should be extended to roots and their contact zone to the soil. It seems to be a severe shortcoming of many experimental designs that plant roots are exposed to solutions, which although facilitating handling of experiments, is certainly a severe simplification as compared to the soil-grown conditions. When screening for salt resistant cultivars of wheat and barley is water solution based, selected cultivars often fail under soil grown conditions (Naseem *et al*. 2000).

The concept proposed here takes into consideration that under controlled brackish/saline irrigation there is not only a vertical soil salinity gradient in the rooted soil layer as reported by Maas and Hoffmann (1977) and usually applied for crop salt tolerance rating. We suggest include also the build-up of a transpiration-driven lateral soil solution salinity gradient that occurs under soil grown conditions between the root contacting soil fraction and bulk soil as already discussed more detailed (Schleiff 2010). It is the objective of this paper to point to dynamic processes happening at the soil/root interface and their relevance for a deepened understanding of crop salt tolerance under field conditions.

Original Research Paper

Table 1 Main features of past, recent and proposed crop salt tolerance research.

Strategies/Approaches for Crop Salt Tolerance Research		
Classical Soil-Based Concept	**Water Solution-Based Concept**	**Proposed Soil Based Concept on Lateral Water and Salt Movement**
● average soil water salinity: relative crop growth is related to ECe or ECsw ● vertical gradients of soil solution salinities resulting from salt leaching (LF) ● soil matric and soil osmotic stress on crop growth	● physiological and biochemical traits of shoots, cells and organs are referred to results preferable investigated in pot water or flow culture experiments ● relevance to soil grown plants questionable	● crop salt tolerance is related to processes happening at the soil/root interface, where plant roots meet soil ● lateral soil water salinity gradients between bulk soil and soil fraction close to roots occur, coming from salt exclusion by roots and significantly affected by root morphology
Few selected, relevant sources: authors/publications		
Wadleigh (1946); Maas and Hoffmann (1977); Ayers and Westcot (1985); van Hoorn and Alphen (1994); Rhoades *et al*. (1992); Oster (1999)	Greenway (1962); Koyro and Huchzermeyer (1999); Bernstein and Kafkafi (2002); Flowers (2004); Munns and Tester (2008); Schubert *et al*. (2009)	Riley and Barber (1970); Schleiff (1981-2010); Jungk (2002); Vetterlein *et al*. (1993, 2004); Homaee and Schmidhalter (2008)

MODEL CALCULATIONS

Root morphology data

Under saline soils conditions uptake of soil water exceeds ion uptake by roots. Ions excluded from root uptake preferably accumulate in the soil fraction close to the root surface at the soil root interface, the rhizospheric soil. Riley and Barber (1970) were the first, who found in pot experiments with soybeans a rhizospheric soil salinity that exceeded the bulk soil salinity for over ten-fold. Similar results were also found in field experiments with onions under brackish irrigation in Saudi Arabia (Schleiff 1981).

However, the increase of rhizospheric soil solution salinity is supposed to differ among plants, their salt tolerance and cultivation conditions. From pot experiments on nutrient uptake (potassium, phosphate, nitrate) we have learned that plant roots differ significantly in their ability to deplete nutrients from their surrounding soil volume. Efficiency of nutrient uptake is often closely related to morphologic features of roots. Roots equipped with fine, strongly haired roots forming a large rhizospheric soil volume are more efficient in nutrient supply of shoots as compared to thicker weakly haired roots forming a smaller rhizospheric soil volume only (Jungk *et al*. 1982). Examples for two crops that differ extremely in the morphology of their roots are given in **Table 2**. It is shown that the rhizospheric soil volume formed by the roots including the root hairs of young rape plants is about 100-fold larger as compared to roots of onions. Simultaneously uptake rate of rape roots for K was 50-fold more efficient than for onion. The result indicates the fundamental importance of root morphology for the efficiency of nutrient depletion from soils and consequently K-supply of shoots. Jungk and Claassen (1986) and Kovar and Claassen (2005) also proved a close relationship for P-uptake by roots and root hair length of different crops. Efficiency of P-uptake by roots of wheat and spinach (root hair length between 0.5 and 0.6 mm) was 100 to 200% higher as compared to P-uptake by roots of bean and tomato (root hair length about 0.25 mm).

It is the objective of the following model calculation to transfer these basic observations on the conditions of root water uptake from saline soils, as shoot water supply is agreed to be the most limiting growth factor under saline soils conditions.

Calculated soil solution salinity around roots of leek and rape

Principally water uptake by roots is directly affected by solution salinity surrounding them. Under saline conditions, water supply of most crops suffers from increasing salt concentrations and decreasing osmotic water potentials. In saline soils most salts dissolved in the soil solution are excluded from root uptake and thus they affect salt concentration of rhizospheric soil solution. However, as shown for leek and rape as model plants there are significant differences in rhizospheric soil volumes of plants and consequently in their rhizospheric soil water too. We conclude that differences in rhizospheric soil volumes, from where water uptake

Table 2 Some morphologic features of rape and leek/onion roots relevant for soil exploitation (supplemented after Barber 1982; Jungk *et al*. 1982).

Feature	Onion/Leek	Rape
Root length in m/g DM	30	200
Root hair cylinder mm³/cm	4	62
Root hair volume in cm³/g DM root	12	1240
Root radius mm	0.225	-
Root hair length mm	0.04	-
Root hair density, number/cm	1180	-
K-uptake rate, μmol cm^{-1} sec^{-1}	0.01	0.52
K-uptake rate, mmol g [root-DM]$^{-1}$ s^{-1}	0.03	10.4

occurs, affect the build-up of rhizospheric salinity and thus are directly involved in root water uptake and crop salt tolerance (Schleiff 2008).

Based on data for the rhizospheric soil volumes for leek and rape (**Table 2**) it is the objective of the following model calculation to simulate the increase of rhizospheric soil water salinity by root water depletion. At the beginning of a water depletion period succeeding a water application (at field capacity [f.c.] of 30 vol.%) rhizospheric soil water salinity suppositional is 10 dS/m. The salt concentration of the rhizospheric soil water will be doubled (20 dS/m) at a soil water content of 50% f.c. In case of leek an EC of 20 dS/m is already achieved after a water depletion of 1.8 ml/g root dry matter (DM), but in case of rape only after a much higher water depletion of 180 ml/g root DM.

This model calculation indicates two important points: (a) the average soil water salinity may have little to do with the rhizospheric soil water salinity roots are effectively exposed to under real soil conditions, (b) root morphology is assumed to be an important feature affecting root water uptake and consequently crop salt tolerance.

It is the objective of the following pot experiment with leek and rape as model plants to compare their water uptake rates from saline soils. In a first step we selected crops that are known to differ significantly in their root traits and salt tolerance under soil grown conditions.

EXPERIMENTAL SETUP

Pre-cultivation of plants

The experiment was carried out in 300 ml pots with rape (*Brassica napus* cv. 'Lingot') and leek (*Allium porrum*). Pots were filled with 360 g of a dried, silty soil (31% sand, 60% silt and 9% clay). The moisture profile held at soil water potentials of -0.1, -10, -35, -70, -200, -500, -1000 and -1500 kPa were 39, 34, 31, 29, 15, 10, 8 and 6 w/w%, respectively 47, 41, 37, 35, 18, 12, 10 and 7 vol.%. Soil salinity was <0.5 dS/m in the soil saturation extract (ECe), cation exchange capacity (CEC) 6 meq/100 g soil, initial soil-pH 7.2. Before sowing, the soil was wetted with 110 ml nutrient solution (after Hoagland and Arnon, cited at Finck 2007) to achieve a

soil water content of 30.5 w/w% (36.6 vol.%). Evaporation losses from the pot surface were reduced to less than 1 ml d^{-1} per pot by covering all pots with a lid, which was pierced with a small opening for the shoot stem only.

The experiment was divided into two phases, a pre-cultivation period of 5 weeks for rape and 10 weeks for leek and an experimental phase of 2 days. The objective of the pre-cultivation period was to achieve a high rooting density of the soil. During this period rape plants were supplied with 380 ml/pot water in total, leek with 530 ml. The well-controlled water supply contributed to achieve plants that appeared very homogeneous at the end of the pre-cultivation period. In order to adapt plants to slight soil salinity and to avoid sodium (Na) induced calcium (Ca) problems, the water of the last 100 ml–application was salinized with 20 mM NaCl and 20 mval/l CaSO$_4$·2H$_2$O. Consequently rape plants were exposed to a weekly saline soil conditions for about 4 days and leek for about 10 days before experimental phase started.

At the end of the pre-cultivation phase, 2 representative rape and leek plants were harvested in order to obtain some plant parameter at the start of the experimental phase. Rape plants had a shoot dry matter (DM) weight of 0.83 g/plant and root dry matter weight of 0.49 g/plant, which results in a shoot/root-ratio of ~1.7 for. The transpiration coefficient (380 ml/0.83 g shoot-DM) was 460 ml g^{-1} DM. Dry matter based root density 1.63 mg cm^{-3} soil in average.

Leek plants developed somewhat less homogenous as rape plants. Shoot weight of single plants ranged from 1.1 to 1.4 g/plant and root weight from 0.6 to 0.8 g/plant resulting in a shoot/root ratio of 1.8. The average transpiration coefficient (530 ml/1.25 shoot-DM) was about 430 ml g^{-1} DM and DM-based root density 2.3 mg cm^{-3} soil in average. Pre-cultivation phase for both crops ceased when the soil water content has dropped to about 10 vol.%, which corresponded to a soil matric potential (Ψm) of -1.0 MPa.

Experimental phase

The experimental phase began with an irrigation of 2 rape and 2 leek plants with 90 ml water up to a soil water content of 40 vol.% (Ψm -0.01 MPa) close to field capacity (f.c.). In order to expose roots to varying salinity stress, the applied water was salinized with NaCl to achieve concentrations of 25 mM (Ψo ~-0.1 MPa) and 100 mM (Ψo ~-0.4 MPa). Plants were left overnight with no light at 20°C air temperature in a darkened growth room in order to attain a homogeneous water and salt distribution in the soil. During the following days, plants were exposed for 14 h/d to optimal growth conditions in a growth chamber (day/night temperature 23°C/18°C; relative air humidity 50%/80%; illumination 400 µE from 7oo to 23oo; windless at night) and pot water losses were measured bi-hourly until severe plant wilting. Soil water

potentials (matric, osmotic and total) were calculated from the measured pot water losses and related to the root masses. The relative growth rate of shoots (RGR in %/d) was calculated from pot water losses and transpiration coefficients (water consumption of shoots in ml/g DM). Dry root mass was weighted after removing of soil by intensive washing and drying at 70°C. Root water uptake rates were calculated from the dry root mass and pot water losses and related to the effective soil water potentials Ψt. For further details on the applied vegetation technique, the readers are referred to Schleiff (1987a, 1987b).

Statistical analyses

Data analysis for all treatments was carried out by statistical programmes offered by EXCEL 2005. For rape plants, the relationship between root water uptake rates and soil water potentials followed logarithmic regression lines at both salinity levels as given in the diagrams. The regression coefficient R^2 exceeded 0.97 in both treatments. For leek the regression lines were linear for both salinity levels at regression coefficients around 0.95.

RESULTS

Experimental results on water uptake by roots of leek and rape from a low-saline treatment (25 mM NaCl irrigation water) and a high-saline treatment (100 mM NaCl irrigation water) are presented in **Figs. 1-3**.

In the low-saline treatment at the beginning of the experimental phase roots of both plants were exposed to a total soil water potential (Ψt) of -0.15 MPa at about f.c. The experimental phase finished, when shoots strongly wilted in consequence of decreasing soil matric and osmotic water potentials and low root water uptake rates. This happened to leek at Ψt of about -1.0 MPa only, but for rape at Ψt <-2.0 MPa. Water uptake rates for roots of both plants were highest at the starting point, when Ψt was around -0.15 MPa. But uptake rate for rape (~18 ml [gDM]$^{-1}$ h^{-1}) was about 3-fold higher than for leek (~6.5 ml [gDM]$^{-1}$ h^{-1}). At Ψt of about -1.0 MPa leek roots nearly ceased water uptake, but uptake rates of rape roots were still sufficient to cover the water requirement for a relative shoot growth rate (RGR) in the range of about 8-10%/d.

Basically experimental results were similar in the high-saline treatment (**Fig. 3**). At the experimental starting point, when the soil water content was near f.c., Ψt achieved already about -0.3 to -0.4 MPa due to soil osmotic effects. Initial water uptake rate for rape roots was around 15 ml [g root-DM]$^{-1}$ h^{-1} covering the shoot water requirement for an RGR of about 15%/d. The highest water uptake rate by leek

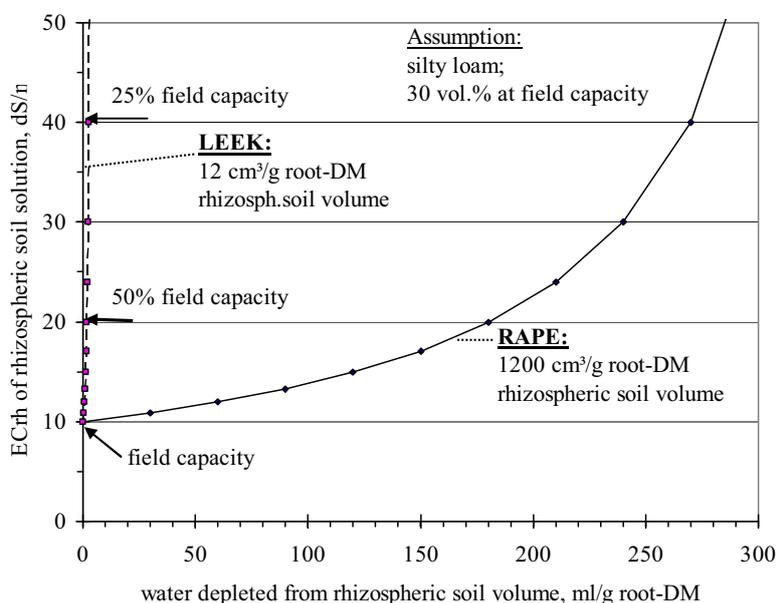**Fig. 1 Results of model calculation for leek and rape on the effect of root water depletion on the development of rhizospheric soil water salinity.**

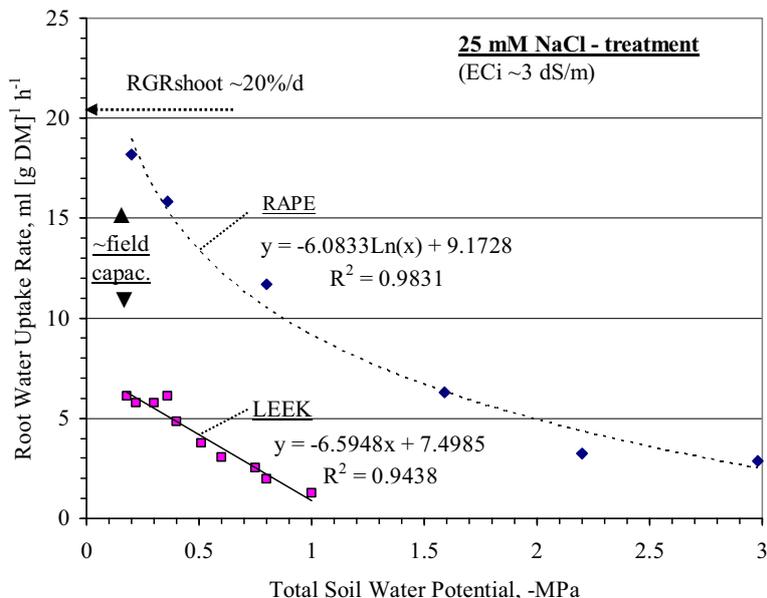**Fig. 2 Root water uptake rates by young leek and rape plants related to the total water potential from a low-saline soil.**
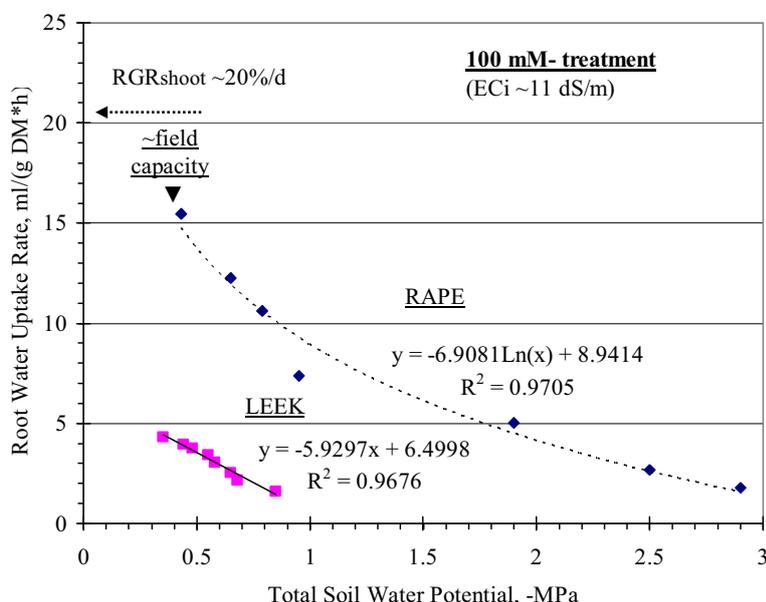

Fig. 3 Root water uptake rates by young leek and rape plants related to the total water potential from a moderately saline soil.

roots was only about 25% (~4 ml [g root-DM]$^{-1}$ h^{-1}) of uptake by rape roots and covered the water requirement for an RGR of less than 5%/d only. Both plants wilted when water uptake dropped to uptake rates in the range of 1 to 2 ml [g root-DM]$^{-1}$ h^{-1}. Water uptake by leek roots nearly ceased already at Ψt near to -0.9 MPa, but for rape only at Ψt <-2.0 to -2.5 MPa.

DISCUSSION AND CONCLUSIONS

Soil-grown roots often modify features of their direct soil environment, the rhizospheric soil fraction, as compared to the bulk soil. This basic ability can be watched visually for rice roots (Marschner 2006), which oxidize their immediate soil contact zone (reddish brown discolouration), and for plants growing in low-gypsum soils, which accumulate gypsum crystals near the root surface (Jungk 2002). As reported earlier in this paper it is also well-known for the distribution of several nutrients in the root surrounding soil, that the soil fraction close to the roots is usually lower in plant available nutrients than the bulk soil. The most effective uptake of nutrients occurs from the soil fraction contacting the root surface and penetrated from root hairs, the

rhizocylinder. Consequently a gradient between the soil fractions close to and far from roots develops, where the soil fraction distant from the root surface is principally less depleted.

Riley and Barber (1970) pointed to a contrary case, where the rhizospheric soil is not depleted, but where accumulation occurs as compared to the bulk soil. This happens around roots of plants growing in saline soils. The authors showed a rhizospheric accumulation for easily water soluble ions such as sodium and chloride. Unfortunately the authors did not relate the accumulated salts to the soil moisture of the rhizospheric soil, which is needed to estimate the soil water potential roots were actually exposed to. The measurement of rhizospheric soil water potentials is a pre-condition to evaluate the constraints for root water uptake. Technical approaches using electrodes and mini-cups were applied to measure relevant data, but seem to be less suitable as they do not cover the fully required measuring range (Vetterlein *et al.* 1993). As shown earlier the applied vegetation technique is a practical tool to obtain the required set of soil data on the rhizospheric soil and additionally the quantitative relationship to crop growth (Schleiff 1987). The experimental results indicate that root
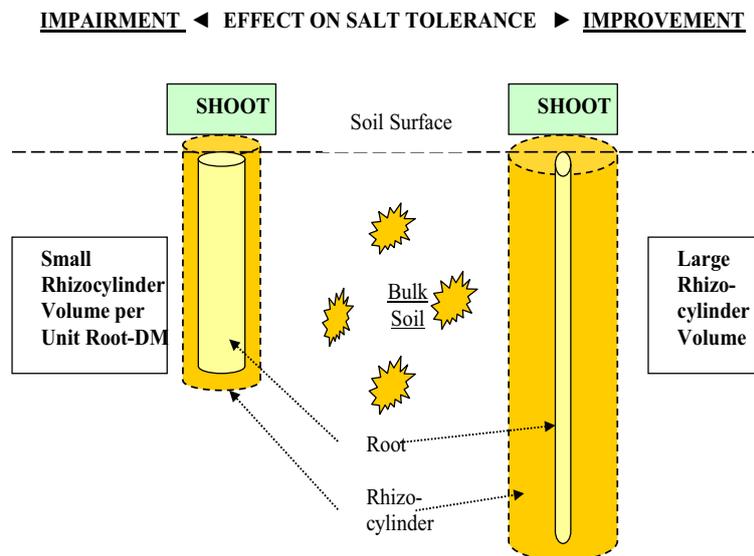
IMPAIRMENT ◄ EFFECT ON SALT TOLERANCE ► **IMPROVEMENT**

Fig. 4 Crop salt tolerance as affected by root morphology and volume of rhizocylinder.

morphology impacts the water uptake from saline soils and consequently might be a key factor for an extended understanding of crop salt tolerance. Water uptake rates and shoot growth rates were in the range of 3- to 5-fold higher by an efficient root system forming large rhizocylinder volumes as compared to a less efficient root systems forming smaller rhizocylinder volumes.

Fig. 4 visualizes the basics of our concept to improve understanding of plant salt tolerance growing in saline soils. The plant root on the left hand side is relatively short, thick and has few short root hairs, which form a small rhizocylinder volume. These features are assumed to support the salt sensitivity of a plant, as the concentration of easily soluble salts per unit water uptake occurs in a small soil volume and is high. On the left hand side the root is longer, thin and root hairs are plenty and longer forming a large rhizocylinder volume. These features contribute to a slower increase of rhizospheric soil solution salinity per unit water uptake, which tends to promote crop salt tolerance.

We conclude that modification of root morphology has a big potential to develop crop salt tolerance. It is recommended to include this aspect in breeding programmes for higher salt tolerant crops and research for optimization of brackish irrigation.

ACKNOWLEDGEMENTS

REFERENCES

Ayers RS, Westcot DW (1985) Water quality for agriculture. Irrigation and Drainage Paper 29, FAO, Rome, pp 15-51

Barber SA (1982) Soil-plant root relationships determining phosphorus uptake. In: Scaife A (Ed) *Proceedings 9th International Plant Nutrition Colloquium*, Warwick University Coventry, Commonwealth Agricultural Bureaux, pp 39-44

Bernstein L, Kafkafi U (2002) Root growth under salinity stress. In: Waisel Y, Eshel A, Kafkafi U (Eds) *Plant Roots – The Hidden Half* (3rd Edn), Marcel Dekker, N.Y., pp 787-805

Finck A (2007) *Pflanzenernaehrung und Duengung in Stichworten* (6th Edn), Gebrueder Borntraeger, Berlin, pp 231-233

Flowers TJ (2004) Improving crop salt tolerance. *Journal of Experimental Botany* **55**, 307-319

Greenway H (1962) Plant response to saline substrates. I. Growth and ion uptake of several varieties of *Hordeum* during and after sodium chloride treatment. *Australian Journal of Biological Science* **15**, 16-38

Homaee M, Schmidhalter U (2008) Water integration by plants root under non-uniform soil salinity. *Irrigation Science* **27**, 83-95

Jungk A, Claassen N, Kuchenbuch R (1982) Potassium depletion of the soil-root interface in relation to soil parameters and root properties. In: Scaife A (Ed) *Proceedings 9th International Plant Nutrition Colloquium*, Warwick University Coventry, Commonwealth Agricultural Bureaux, pp 250-255

Jungk A, Claassen N (1986) Availability of phosphate and potassium as the result of interactions between root and soil in the rhizosphere. *Zeitschrift für Pflanzenernaehrung und Bodenkunde* **149**, 411-427

Jungk A (2002) Dynamics of nutrient movement at the soil-root interface. In: Waisel Y, Eshel A, Kafkafi U (Eds) *Plant Roots – The Hidden Half* (3rd Edn), Marcel Dekker, N.Y., pp 587-616

Kovar JL, Claassen N (2005) Soil-root interactions and phosphorus nutrition of plants. In: *Phosphorus: Agriculture and the Environment*, American Society of Agronomy, Agronomy Monograph no. **46**, 379-414

Koyro HW, Huchzermeyer B (1999) Plant and crop stress: Salt and drought stress effects on metabolic regulation in maize. In: *Advanced Short Course on 'Saline Irrigation: Halophyte Production and Utilization, Proceedings*, April 6-15, Agadir, Morocco, CIHEAM-IAMB/UNESCO, pp 251-322

Maas EV, Hoffmann GJ (1977) Crop salt tolerance - current assessment. *Journal of the Irrigation and Drainage Division* **103 (IR 2)**, 115-134

Marschner H (2006) *Mineral Nutrition of Higher Plants* (2nd Edn), Academic Press, Amsterdam, pp 626-641

Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology* **59**, 651-681

Munns R (2007) Utilizing genetic resources to enhance productivity of salt-prone land. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 2, no. 009*, CABI, Wallingford, UK

Naseem A, Qureshi RH, Akhtar J, Masood MA (2000) Screening of wheat (*Triticum aestivum* L.) genotypes against salinity in solution culture. *Pakistan Journal Agricultural Science* **37**, 1-6

Oster JD (1999) Use of marginal quality waters for irrigation. In: *Proceedings Irrigation Management and Saline Conditions*, Regional Symposium, JUST, Irbid, Jordan, pp 1-16

Rhoades JD, Kandiah A, Mashali AM (1992) The use of saline waters for crop production. *FAO Irrigation and Drainage Paper 48*, Rome, pp 23-69

Riley D, Barber SA (1970) Salt accumulation at the soybean (*Glycine max* L. Merr.) root-soil interface. *Soil Science Society of America Proceedings* **34**, 154-155

Schleiff U (1981) Osmotic potentials of roots of onions and their rhizospheric soil solutions when irrigated with saline drainage waters. *Agricultural Water Management* **3**, 317-323

Schleiff U (1982) Maximum salt concentration in the rhizospheric soil solution of young sugar beets. *Plant and Soil* **64 (3)**, 307-314

Schleiff U (1986) Water uptake by barley roots as affected by the osmotic and matric potential in the rhizosphere. *Plant and Soil* **94**, 143-147

Schleiff U (1987a) A vegetation technique to study the water uptake by roots from salinized rhizospheric soils (Eine Vegetationstechnik zur quantitativen Bestimmung der Wasseraufnahme durch Wurzeln aus versalzten Rhizoboeden). *Zeitschrift Pflanzenernaehrung und Bodenkunde* **150**, 139-146. Available online:
http://www.salinity.de/downloads/SCHLEIFF_Vegetationstechnik_zur_quantitativen_Bestimmung.pdf

Schleiff U (1987b) A comparison of transpiration rates of young rape plants grown on salinized soils of different texture. *Zeitschrift Pflanzenernaehrung und Bodenkunde* **150**, 403-405

Schleiff U (2005) Research aspects for crop salt tolerance under irrigation with special reference to root environment. *Special issue 286 FAL – Agricultural Research Station Braunschweig, Germany*, pp 83-94. Available online:

http://www.salinity.de

Schleiff U (2008) Analysis of water supply of plants under saline soil conditions and conclusions for research on crop salt tolerance. *Journal of Agronomy and Crop Science* **194 (1)**, 1-8

Schleiff U (2010) The forgotten link in improving crop salt tolerance research under brackish irrigation - lateral soil salinity gradients around roots. In: Pessarakli M (Ed) *Handbook of Plant and Crop Stress* (3rd Edn), Taylor & Francis Group, pp 1147-1154

Schubert S, Neubert A, Schierholt A, Suemer A, Zoerb C (2009) Development of salt-resistant maize hybrids: The combination of physiological strategies using conventional breeding methods. *Plant Science* **177**, 196-202

van Hoorn JW, van Alphen JG (1994) Salinity control. In: Ritzema HP (Ed) *Drainage Principles and Applications*, ILRI Publication 16, pp 533-600

Vetterlein D, Marschner H, Horn R (1993) Microtensiometer technique for *in situ* measurement of soil matric potential and root water extraction from a sandy soil. *Plant and Soil* **149**, 263-273

Vetterlein D, Kuhn K, Schubert S, Jahn R (2004) Consequences of sodium exclusion for the osmotic potential in the rhizosphere – comparison of two maize cultivars differing in Na+ uptake. *Journal of Plant Nutrition and Soil Science* **167**, 337-344

Wadleigh CH (1946) The integrated soil moisture stress upon a root system in a large container of saline soil. *Soil Science* **61**, 225-238

Yamaguchi T, Blumwald E (2005) Developing salt-tolerant crop plants: Challenges and opportunities. *Trends in Plant Science* **10 (12)**, 615-620