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Water integration by plants root under non-uniform soil salinity

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Abstract Soil salinity over root zone usually demonstrates temporal and spatial variations. By changing irrigation management practices it is possible to change both the frequency of salinity fluctuations and its distribution over the root zone. The objective of this study was to experimentally investigate how plants integrate soil salinity over its rooting depth when irrigated with saline water. Consequently, detailed experiments with alfalfa were conducted in some lysimeters containing packed loamy sand soil. The target soil salinities were created by changing quantity and quality of applied saline water. Results indicated that the uptake rate preliminary reacts to soil salinity. But at given water content and salinity, the "evaporative demand" and "root activity" become more important to control the uptake pattern. The obtained results also indicate that root activity is inconstant during the stress period. By increasing salinity, the activity of that part of the root system is also increased. Thus, most water is taken from the less saline part and the uptake at other parts with higher salinities never stops. Consequently, the reduced uptake in one compartment resulting from high salinity is not only compensated from other parts with less salinities, but also from the same increment by increasing root activity.

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Introduction

Soil salinity in field scale is seldom uniform with depth and usually varies with time at any given depth. The question of how plants integrate such space and time varying variable is important for agriculturalists as well as modelers. Increases in soil salinity as result of evaporation occur at the soil surface, while the site of separation of salts from the soil water due to root water uptake takes place at the soil–root interface. The actual distribution of salts over the root zone reflects the water extraction pattern, which depends not only on root distribution, but also upon root activity. Root distribution over the root zone largely depends on whether the root system preliminary developed into a saline or nonsaline profile. In heterogeneously distributed soil salinity, roots do not penetrate readily into high saline depths, but once established in nonsaline soil, imposing salinity does not drastically change the root distribution. In numerical simulation models that deal with water movement and solute transport in the root zone, the water budget largely depends on the uptake pattern.

Theoretical concepts of how plants integrate soil salinity have not yet been fully developed or verified. To avoid difficulties arising from plant integration complexities, many studies have been conducted in uniform soil solution salinities. Comprehensive reviews of such studies are well documented by Maas and Hoffman (1977) and Maas and Grattan (1999). While studies under such uniform conditions can improve understanding of root water uptake in saline soils, the question on how plants integrate soil salinity remains unanswered. When salinity is heterogeneously distributed over the root zone, it is frequently assumed that the plant responds to the "average" soil salinity. Some collected experimental data have support this idea (Shalhevet and Bernstein 1968; Bower et al.

1969). Concerning such heterogeneity, there are three contradictory ideas in the literature. The first suggests that the water uptake can better be related to the salinity of the upper part of the root zone. Since the majority of alfalfa roots are within the first 50 cm of the root zone (Smith 1994), Bernstein and Francois (1973) concluded that alfalfa responded to mean soil salinity. Because it is controlled primarily by the salinity of irrigation water (upper root zone salinity), and hence is less affected by deep root zone salinity. The second states that the relative uptake is strongly affected by the more saline part in the root zone which is mainly located at the deeper part of the soil profile. Later research suggested that alfalfa can tolerate high salinity in lower part of the root zone (at 180 cm) by increasing water uptake from higher regions with lower salinities (Shalhevet and Bernstein 1968; Hanks et al. 1977). Consequently, the overall water uptake as well as the transpired water remains unchanged. Francois (1981) reported that significant yield reduction will not occur until salinity increases in the lower part of the root zone (50–60 cm). Ingvalson et al. (1976) suggested that irrigation management, especially the frequency of irrigation, could partially explain these opposing conclusions. They reasoned that immediately after irrigation, plants take up water primarily from the less saline upper part, and the lower part salinities will affect the plant later during the soil drying cycle. The third, proposed that plant response can be described better by some weighted mean salinity (Raats 1974; Hoffman and Van Genuchten 1983; Dirksen 1985; Dirksen et al. 1994). One such an uptake averaging is proposed by Dirksen (1985):

$$\tilde{h}_o = \frac{\int_0^\infty S(z)h_o(z)dz}{\int_0^\infty S(z)dz} \qquad (1)$$

in which S is the volumetric sink term depending on depth (z) and h_o is soil osmotic potential, expressed as osmotic head.

The analyses made by Dirksen (1985) and Dirksen et al. (1994) on the experimentally collected data with this equation provided satisfactory results.

One more approach that can be regarded as an averaging concept is the algorithm used in numerical simulation models. Several models during the past decades were developed in order to quantify water extraction under saline conditions. Those models that aim to predict relative yield are mainly based on the average soil salinity over the root zone (e.g., Maas and Hoffman 1977; Van Genuchten 1987; Dirksen et al. 1993). When incorporated in numerical simulation models as macroscopic reduction functions (Homaee et al. 2002a; Van Genuchten et al. 1999), they calculate the relative uptake for each node. Some extensive discussions on modeling and simulation of root water uptake are given by Homaee et al. (2002a, b, c, d). Usually these models (e.g., Simunek et al. 1998; Van Dam et al. 1997; Simunek et al. 1997; Jarvis 1994; Dirksen et al. 1993) distribute the potential transpiration over the root zone according to the specified root activity distribution. The actual transpiration is then considered to be equal to the potential transpiration until the threshold salinity is reached. The actual transpiration is then calculated for every node according to the specified reduction function. The integration of the calculated transpiration over all nodes gives the actual transpiration for the entire root zone. When the soil salinity differs with depth, the model assumes that water can be taken up independently at every depth according to the specified reduction function and the (relative) root activity. For instance, if the soil solution salinity near the bottom is lower than that of the top, the model calculates the higher water uptake at the bottom for the given root activity. The water contents and salinities are then calculated according to the depleted water at each node.

Investigations on the mentioned controversy are rare and it is not yet clear which idea resembles the reality most. The main reason for this scarcity is that the required data cannot be obtained easily and the subject should be investigated in fully controlled conditions, which is either time consuming and/or expensive. One way to check these contradictory is to create different salt distributions over the root zone in different columns with the same mean salinities. Such conditions were observed in some experimental columns designed by Homaee et al. (2002b) that received no extra water to apply leaching after soil salinization.

Theory

Water flow in unsaturated soil including root water uptake as a sink term S is described with Richards' equation (Richards 1931):

$$\frac{\partial \theta}{\partial t} = C(h)\frac{\partial h}{\partial t} = \frac{\partial}{\partial z}\left(K(h)\frac{\partial h}{\partial z} + K(h)\right) - S(h) \qquad (2)$$

where θ is volumetric water content (L^3L^{-3}), t is time (T), C is the differential soil water capacity (L^{-1}), h is soil water pressure head (L), and z is gravitational head, as well as the vertical coordinate (L) taken positive upward, K is soil hydraulic conductivity (LT^{-1}), and S is soil water extraction rate by plant roots ($L^3L^{-3}T^{-1}$) depending on h.

The soil hydraulic conductivity function can be described by (Mualem 1976; Van Genuchten 1980):

$$K = K_s S_e^l [1 - (1 - S_e^{1/m})^m]^2 \qquad (3)$$

where K_s (LT^{-1}) is the saturated hydraulic conductivity, S_e is effective saturation (–), and l, n (–), and m (–) are dimensionless shape factors.

Osmotic potential, expressed as osmotic head h_o, assumed to be a linear function of solute concentration c and soil solution salinity EC_{ss} according to (U. S. Salinity Laboratory Staff 1954):

$$h_o = -36c = -360EC_{ss} \quad (4)$$

The linear salinity crop response function of Maas and Hoffman (1977), written in terms of osmotic head reads:

$$\alpha(h_o) = 1 - \frac{a}{360}(h_o^* - h_o) \quad (5)$$

where h_o and h_o* are the osmotic head and osmotic threshold value, respectively; α is the crop reduction in response of a unit osmotic head and 360 is a factor to convert the salinity-based slope (a) to cm osmotic head (Homaee et al. 2002d). Some other non-linear salinity response functions are also introduced in the literature (Van Genuchten and Hoffman 1984; Van Genuchten 1987; Dirksen et al. 1993; Homaee et al. 2002a) that are mainly used in numerical simulation models to predict the water content or salinity of the root zone. Having the salinity dependent reduction function α (h_o) and incorporating the relative root activity parameter δ (L^{-1}), the sink term in Eq. 2 reads:

$$S = \alpha(h_o)T_P\delta \quad (6)$$

Materials and methods

Alfalfa (*Medicago sativa* L.) was seeded in packed cylindrical soil columns with 65 cm height and 21 cm diameter. The soil used in this study was Wichmond sandy loam (Typic Haplaquent, 14% clay, 31% silt, and 55% sand). The soil was first sieved with a 1-cm sieve and then compressed by some impacts from a 65-cm height (3,100 g weight) at 5-cm increments. At a water content of 0.125 g g^{-1}, 15 impacts yielded nearly uniform bulk densities of 1.42 g cm^{-3}. Subsequently, all columns were packed at this water content by the same procedure. To minimize the variations during packing, the bulk density of every 5 cm of packed soil was measured before adding the next soil increment. After packing, all the sensors were installed and the columns were saturated with tap water and drained twice with a suction pump to reduce remaining differences in the soil packing.

Alfalfa was grown from seed in a greenhouse under controlled environmental conditions. To fix nitrogen of air in the roots, the seeds were inoculated with *Rhizobium* bacteria. First the suspension of *Rhizobia* was mixed by Carboxyl Methyl Cellulose CMC and later four parts of seeds were mixed by one part of this mixture. CMC was used to fix the *Rhizobial* cells to the seed coat. The wet seeds were dusted with dry $CaCO_3$ (1 g $CaCO_3$ for 2 g seeds). After this inoculation, alfalfa was immediately seeded at a density of four seeds per location and 20 locations per column. A week later, all locations were thinned to one plant, giving 20 plants per columns.

The measurements started after healthy plants had developed. Since no water stress was allowed, the irrigation intervals were relatively short (48 h). Assuming no significant water uptake during the dark period, all irrigation waters were applied to the columns by flood irrigation immediately before turning off the lights. This was done in order to allow the applied water to distribute over the root zone in the time that plants did not transpire water.

The soil was salinized by twice saturating and draining all columns, applying appropriate amounts of water and salinity. To attain the target leaching fractions all columns were saturated. The target leaching fraction was 0.5. Thus, a large amount of saline water in excess of potential transpiration was applied to the columns, and the same amount of excess water was given to the reference treatment. This provided relatively similar water distribution over the root zone for all columns. The amount of applied water was derived from the reference treatment R. All irrigations of R were with tap water of EC $<$ 0.2 dS/m. Thus, it can be assumed that during the measurements hysteresis in soil water did not occur and the main drying curve of the retention curve can be used. One week later, after allowing relatively uniform salinity distribution over the root zone, the bottoms of columns were closed by some plastic stoppers to prevent any leaching. All measurements started after switching on the lights. The light period normally was 15 h per day until 9.00 pm.

To avoid toxicity effects and precipitation–dissolution reactions of salts with soil solid phase, salinities were created by adding equal molar (charge base) quantities of $CaCl_2$ and NaCl to the irrigation water. The applied water salinities were varied around the salinity threshold value of alfalfa, that is, at 1.5, 2.0, 3.0, 4.0, and 5.0 dS/m, denoted as S_1, S_2, S_3, S_4, and S_5 treatments (three replicates), respectively. A reference treatment (R) without any salt or water stress (four replicates) was also established to compare the stressed treatments data and to obtain the evaporative demands under which the data were collected. To prevent evaporation from the soil surface, the top of each column was covered by inert granules.

The in-situ soil solution salinities EC_{ss} were measured with salinity sensors and a salinity bridge apparatus (Model 5100, Soilmoisture Equipment Company, Santa Barbara, CA, USA). All sensors were installed just after soil packing horizontally into the soil columns in one row at depth intervals of 5 cm in the top 30 cm and at 10-cm intervals below that. The same order of depth intervals was followed for the TDR sensors. Soil water osmotic heads were obtained by converting the corresponding soil solution salinities according to the empirical relation given in Handbook 60 of USDA (U. S. Salinity Laboratory Staff 1954). Since the plants react to the soil solution salinity EC_{ss}, the data were analysed based on EC_{ss} rather than soil bulk electrical conductivity EC_b. Soil water content θ and EC_b were measured with fully automated TDR equipment, using a *Tektronix 1502B* cable tester, a multiplexer and control system, developed by Heimovaara and Bouten (1990). The soil solution salinities and water contents were then recorded and monitored for the entire growth period while salinity was building up heterogeneously over the root zone. Until the end of experiment a large data set was obtained. The collected data were then carefully inspected to find out how salinity builds up after stopping the leaching as well as to select a set of data with similar average characteristics. Consequently, the data reported here belong to different days of the experiment within the same growth period. Soil water pressure heads h were obtained by converting θ to h based on the soil water retention characteristics obtained with the Wind's evaporation method (Wind 1966). The hydraulic parameter values were derived, using the RETC program (Van Genuchten et al. 1991). More details on the experimental set up as well as the soil water retention curve and the hydraulic function of the soil used in this study are given by Homaee et al. (2002a, b). Salinity of irrigation waters was measured by a conductivity cell (Digimeter L21; Eijkelkamp, Agrisearch Equipment, The Netherlands). Actual T_a and potential T_p transpiration measurements were made by weighing the columns, using a digital balance. Leaf water potentials LWP were measured twice a day at 10.00 a.m. and 2.00 p.m. with a pressure chamber. All the LWP data reported here are the mean of at least five leaves, which have been taken from the top of each plant.

Results and discussions

Tables 1, 2 and 3 represent the data obtained from the columns with heterogeneously distributed salinity, having some similar averaged characteristics. The data were collected under different evaporative demand conditions, specified by potential transpiration T_p. The calculated uptake rates S in these tables are given for 10 h time intervals. The average soil solution salinity EC_{ss} of the columns in Tables 1, 2 and 3 was about 2.6, 4.4 and 9.5 dS/m. These values are about two times higher than the salinity of the saturation extract EC_e. The water content distributions over the root zone were not exactly the same for all the columns at each table but they were very close to each other, and were high enough to prevent any water deficit. The water content threshold value for the conditions under which the experiment was carried out was about 0.15 cm^3/cm^3 (Homaee et al. 2002b). Since the volumetric water contents depicted in these tables are much higher than this value, no water deficit can be expected. An interesting observation is that the relative uptake (T_a/T_p) as well as the relative leaf water head (LWH_R/LWH_{Si}) for all columns were almost the same. However, such a 1:1 relation did not hold for the entire growth period. Under heterogeneously distributed soil water osmotic head conditions, water uptake depends on several factors such as soil solution electrical conductivity, water content, depth, and root density. Since the plants in each container were treated uniformly before creating any salt stress, we assume that the root density within all columns was the same. Therefore in order to find a conclusion for such heterogeneity, Tables 1, 2 and 3 will be discussed in the following steps.

Low soil solution salinity

Equal water content and same depth, different salinity

In Table 1 column A, the water content from 5 to 15 cm was relatively constant. By increasing EC_{ss} from 2.5 to 3.3 dS/m, the uptake rate S decreased sharply from 2.34 to 0.68×10^{-3} cm^3/cm^3 h. Again, by decreasing salinity from 3.3 to 2.8 dS/m at 15 cm depth S increased drastically from 0.68 to 1.46×10^{-3} cm^3/cm^3 h. At the bottom of this column a decrease of salinity from 2.8 to 1.8 dS/m (having the same water content) increased S by the magnitude of 0.62×10^{-3} cm^3/cm^3 h per 1 dS/m. This increase is comparable but not equal to that at 5–15 cm depth. In column B, θ is the same at 15 and 20 cm. While salinity decreased from 3.3 to 3.0 dS/m, S increased from 0.91 to 1.95×10^{-3} cm^3/cm^3 h. Again, by a salinity increase from 3.0 to 3.4 dS/m, S changed from 1.95 to 1.45×10^{-3} cm^3/cm^3 h, and by a salinity decrease from 3.4 to 3.1 dS/m, S increased from 1.45 to 1.68×10^{-3} cm^3/cm^3 h. In column C, by increasing salinity from 2.4 to 3.3 dS/m at depths 45 and 55 cm, the relative uptake decreased sharply from 1.92 to 0.72×10^{-3} cm^3/cm^3 h. Also in column C, both EC_{ss} and θ are the same at 25 and 35 cm, while S decreased from 0.81 to 0.53×10^{-3} cm^3/cm^3 h. In column D, by salinity increase from 2.0 dS/m at depth 45 cm to 5.6 dS/m at depth 55 cm, S decreased slightly. Even though the magnitude of the S changes per unit salinity is not equal for the reported data, the trend of S variations support the assumption of Dirksen et al. (1994).

Equal salinity, different water content

In column D, the soil solution salinity is about the same over the root zone except for the last increment and the

Table 1 Some experimentally obtained parameters with similar averaged characteristics under low soil solution salinity

Soil column	Depth (cm)	EC_{ss} (dS/m)	θ (cm^3/cm^3)	S (10^{-3} cm^3/cm^3 h)	T_a (mm/day)	T_p (mm/day)	T_a/T_p (–)	LWP_R/LWP_{Si} (–)
A	5	2.5	0.29	2.34	1.79	2.1	0.85	0.86
	10	3.3	0.30	0.68				
	15	2.8	0.30	1.46				
	20	2.2	0.32	1.68				
	25	2.2	0.32	1.47				
	35	2.7	0.33	1.87				
	45	2.8	0.34	1.68				
	55	1.8	0.35	2.30				
	Average	2.5	0.32	1.76				
B	5	4.1	0.27	0.72	1.56	1.86	0.84	0.84
	10	3.6	0.29	0.88				
	15	3.3	0.28	0.91				
	20	3.0	0.28	1.95				
	25	3.4	0.27	1.45				
	35	3.1	0.28	1.68				
	45	2.7	0.37	1.15				
	55	0.3	0.34	2.61				
	Average	2.7	0.30	1.49				
C	5	2.0	0.21	1.65	1.42	1.65	0.86	0.89
	10	2.2	0.27	2.65				
	15	2.7	0.25	1.08				
	20	2.8	0.28	2.09				
	25	2.6	0.24	0.53				
	35	2.6	0.24	0.81				
	45	2.4	0.30	1.92				
	55	3.3	0.31	0.72				
	Average	2.6	0.27	1.36				
D	5	2.0	0.20	1.05	1.39	1.66	0.84	0.78
	10	2.1	0.27	1.89				
	15	1.9	0.25	1.76				
	20	2.0	0.28	2.18				
	25	1.9	0.24	0.66				
	35	1.9	0.24	0.64				
	45	2.0	0.29	0.94				
	55	5.6	0.30	0.89				
	Average	2.6	0.26	1.15				

main difference is in water content. At increment 5–10 cm the water content is quite different, the soil solution salinity is the same, and the uptake rate increased from 1.05 to 1.89×10^{-3} cm^3/cm^3 h. At the next depth (15 cm), by decreasing θ from 0.267 to 0.245 cm^3/cm^3, the S was also decreased from 1.89 to 1.76×10^{-3} cm^3/cm^3 h. At depths of 20 and 25 cm by decreasing θ from 0.281 to 0.239 cm^3/cm^3, the uptake rate was decreased to 0.66×10^{-3} cm^3/m^3 h. However, having the same EC_{ss} and θ at depths 25 and 35 cm, almost the same S values were obtained. These observations suggest that at constant EC_{ss}, higher θ provides higher uptake rate. Note that this conclusion is drawn for low mean soil solution salinities (2.5–2.7 dS/m).

Equal salinity and water content, different depth

In column D, at depth 15 and 35 cm with EC_{ss} = 1.9 dS/m and θ = 0.24 cm^3/cm^3, S decreased sharply from 1.76 to 0.64×10^{-3} cm^3/cm^3 h. Further, in column A at depths 20 and 25 cm both θ and EC_{ss} were equal and S was almost the same. However, S at depth 15 cm was less than that at 5 cm. This can be related to the influence of depth on water

Table 2 Some experimentally obtained parameters with similar averaged characteristics under moderate soil solution salinity

Soil column	Depth (cm)	EC_{ss} (dS/m)	θ (cm^3/cm^3)	S (10^{-3} cm^3/cm^3 h)	T_a (mm/day)	T_p (mm/day)	T_a/T_p (–)	LWP_R/LWP_{Si}(–)
E	5	5.0	0.32	0.60	1.35	1.95	0.69	0.64
	10	5.6	0.33	0.38				
	15	4.7	0.31	0.94				
	20	5.2	0.33	0.53				
	25	4.8	0.31	0.80				
	35	4.7	0.34	1.17				
	45	4.2	0.34	1.75				
	55	3.2	0.34	2.51				
	Average	4.5	0.33	1.22				
F	5	2.7	0.26	3.00	1.42	2.17	0.66	0.63
	10	3.4	0.27	1.74				
	15	3.7	0.28	1.57				
	20	3.4	0.30	1.74				
	25	3.6	0.30	1.66				
	35	3.9	0.31	1.02				
	45	5.0	0.32	0.22				
	55	4.9	0.33	0.94				
	Average	4.0	0.30	1.28				
G	5	2.4	0.21	2.81	3.25	4.06	0.71	0.69
	10	3.3	0.24	2.78				
	15	3.4	0.25	1.46				
	20	3.4	0.26	2.11				
	25	3.4	0.28	2.64				
	35	4.1	0.28	1.26				
	45	5.4	0.30	1.23				
	55	5.7	0.31	0.37				
	Average	4.2	0.27	1.59				
H	5	4.2	0.29	1.19	1.46	2.17	0.68	0.65
	10	5.5	0.30	0.57				
	15	5.0	0.28	0.92				
	20	5.7	0.30	0.49				
	25	5.5	0.29	0.91				
	35	5.0	0.31	0.94				
	45	5.0	0.33	1.06				
	55	3.7	0.33	1.47				
	Average	4.9	0.31	1.00				

uptake rate, in as much as the plants prefer to provide their demand from the upper parts.

These observations indicate that even with this detailed experiment, drawing a clear picture on how plants integrate under heterogeneous low soil solution salinity is rather complicated. Remains the interesting observation; all the experimental columns depicted in Table 1 with about the same mean salinity exhibit almost the same relative transpiration rates as well as relative leaf water potentials.

Moderate soil solution salinity

Equal water content and same depth, different salinity

In Table 2 column E, the water content from 5 to 20 cm was relatively constant. By increasing EC_{ss} from 5 to 5.6 dS/m, the uptake rate reduced to about 64%. But, by decreasing EC_{ss} from 5.6 to 4.7 dS/m, the S increased more than two times. The uptake rate at this depth besides having lower salinity than that of 5 cm, remained much higher.

Table 3 Some experimentally obtained parameters with similar averaged characteristics under high soil solution salinity

Soil column	Depth (cm)	EC_{ss} (dS/m)	θ (cm^3/cm^3)	S (10^{-3} cm^3/cm^3 h)	T_a (mm/day)	T_p (mm/day)	T_a/T_p (–)	LWP_R/LWP_{Si} (–)
I	5	6.3	0.27	1.44	0.87	1.73	0.50	0.60
	10	8.3	0.20	0.70				
	15	13.7	0.26	0.47				
	20	20.0	0.25	0.15				
	25	17.5	0.20	0.35				
	35	10.7	0.33	0.64				
	45	4.8	0.36	1.45				
	55	1.8	0.37	4.47				
	Average	9.1	0.30	1.47				
J	5	5.9	0.24	1.85	1.41	2.71	0.52	0.63
	10	7.5	0.20	1.74				
	15	11.2	0.24	1.10				
	20	16.2	0.24	0.76				
	25	16.5	0.19	0.17				
	35	12.5	0.31	1.02				
	45	7.0	0.35	1.96				
	55	2.1	0.37	4.91				
	Average	9.1	0.29	1.95				
K	5	6.7	0.24	1.09	1.95	4.06	0.48	0.56
	10	9.0	0.19	0.71				
	15	11.5	0.25	0.63				
	20	16.2	0.35	0.13				
	25	16.2	0.36	0.36				
	35	12.5	0.26	0.45				
	45	7.0	0.37	1.04				
	55	2.1	0.38	2.36				
	Average	9.3	0.31	0.96				
L	5	9.0	0.31	1.71	2.38	4.87	0.49	0.57
	10	11.7	0.19	1.43				
	15	13.5	0.23	0.87				
	20	16.0	0.23	0.16				
	25	16.5	0.35	0.13				
	35	13.0	0.23	1.13				
	45	7.3	0.38	1.77				
	55	2.2	0.39	4.91				
	Average	10.1	0.30	1.79				

Also, the water content at 45 and 55 cm of this column was constant. When EC_{ss} changed from 4.2 to 3.15 dS/m, the uptake rate increased considerably (from 1.75 to 2.51 × 10^{-3} cm^3/cm^3 h). This trend can be seen even better in column F when *S* sharply decreased from 3 to 1.74 × 10^{-3} cm^3/cm^3 h by salinity increase of just 0.65 dS/m. Under almost the same water contents at 10 and 15 cm, the uptake rate compares to that of 10 cm slightly decreased by small decrease of EC_{ss}. Columns F and G have exactly the same mean soil solution salinities but different salinity distributions. The salinity of both columns at 10 cm depth is about the same (3.35 and 3.30 dS/m), while the uptake rate value is 1.74 and 2.78 × 10^{-3} cm^3/cm^3 h, respectively. The only difference was the evaporative demand under which the data were collected. One may relate the differences of uptake rate to θ, but as can be seen in Table 2, the water content of the higher uptake rate compartment is even less than that of the lower uptake increment. This again indicates the importance of the evaporative demand on root water uptake pattern. Common to all columns in Table 2 is the observation that the highest uptake rate occurred at the lower soil salinity compartments.

Equal salinity, different water content

In column E, the salinity of the soil solution is about the same at 25 and 35 cm of the root zone; the main difference is in θ, which changes from 0.31 to 0.34 cm^3/cm^3. The corresponding uptake rates are 0.8 and 1.17 $\times$ 10^{-3} cm^3/cm^3 h, respectively. At depth 45 and 55 cm of column F with almost the same EC_{ss}, the sink term increased from 0.22 to 0.94 $\times$ 10^{-3} cm^3/cm^3 h for water contents of 0.32 and 0.33 cm^3/cm^3, respectively. Again, by increasing the water content from 0.31 to 0.33 cm^3/cm^3 in column H at depths 35 and 45 cm the uptake rate was increased from 0.94 to 1.06 $\times$ 10^{-3} cm^3/cm^3 h for the salinity of 5 dS/m. Such a trend can better be seen in column G when the same salinity of 3.4 dS/m at depths 15–25 cm provided widely different uptake rates of 1.46, 2.11 and 2.64 $\times$ 10^{-3} cm^3/cm^3 h for water contents of 0.253, 0.262 and 0.277 cm^3/cm^3, respectively. Similar to what has been concluded for low salinity columns (Table 1), one may draw a conclusion that at given soil salinity, the sink term increases by any increase in water content. While such observations may hold for our experimental data, the magnitude of such an influence seems rather difficult to be quantified.

At depths 5, 45 and 15 cm of columns E, F, and H the EC_{ss} is 5 dS/m, while the corresponding uptake rates are 0.6, 0.22 and 1.06 $\times$ 10^{-3} cm^3/cm^3 h, respectively. The corresponding evaporative demands T_p obtained from the reference treatment R were 1.95, 2.17 and 2.17, respectively. Such considerable change in uptake rate for the same soil solution salinities raises the point that when enough water is available and EC_{ss} is relatively low, the evaporative demand plays more significant role than soil salinity to control the uptake rate. Also, the root activity of each compartment at the time of stress has to be taken into consideration. Besides having uniformly distributed roots in the columns, it seems that the root activity has a dynamic change during the stress period. Figure 1 shows such a dynamic for a column at 2 h time intervals. The salinity dependent reduction functions and the relative root activities in this figure are calculated based on Eqs. 5 and 6, respectively. The data reported in Table 2 were collected under different climatic conditions in the greenhouse (see T_p values for different columns). In column H, EC_{ss} at 15, 35 and 45 cm was also equal to 5 d/Sm, with corresponding S values of 0.92, 0.94 and 1.06 $\times$ 10^{-3} cm^3/cm^3 h. Interestingly, the uptake rate remains relatively constant in these compartments, while for EC_{ss} = 3.4 dS/m in column G the S value changes considerably for the depths 15–25 cm.

High soil solution salinity

Table 3 demonstrates relatively high soil solution salinities for alfalfa. While the mean EC_{ss} in the columns is five times larger than alfalfa's threshold value (EC^* = 2 dS/m), soil salinities at some points were even more than ten times of this value. Under such conditions, the important question is whether the root water uptake will cease at extremely high soil salinity compartments. The previously

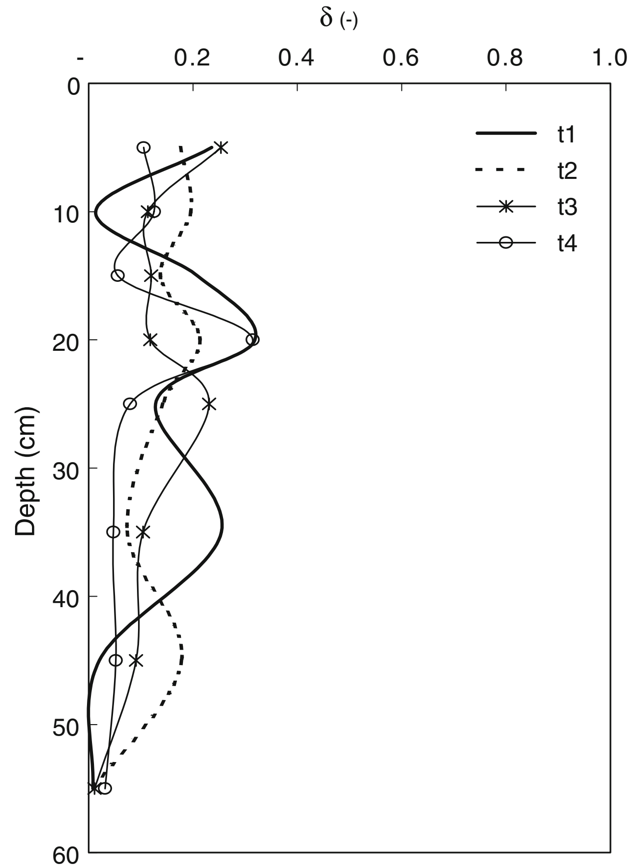

Fig. 1 Dynamic variations of relative root activity δ calculated with Eq. 6 under low soil solution salinity at 2-h time intervals

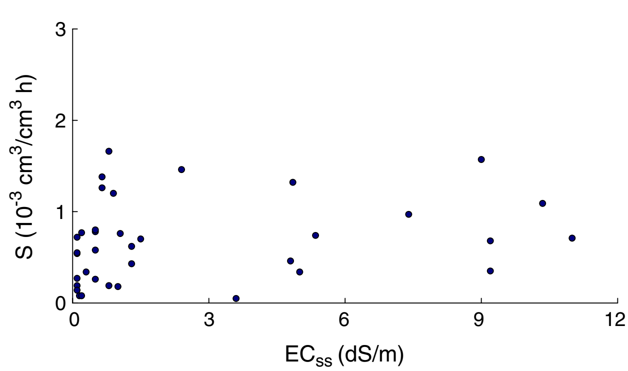

Fig. 2 The relation between root water extraction rates (calculated with Eq. 2 with the reduction term of Eq. 6) and soil solution salinities under corresponding constant water contents

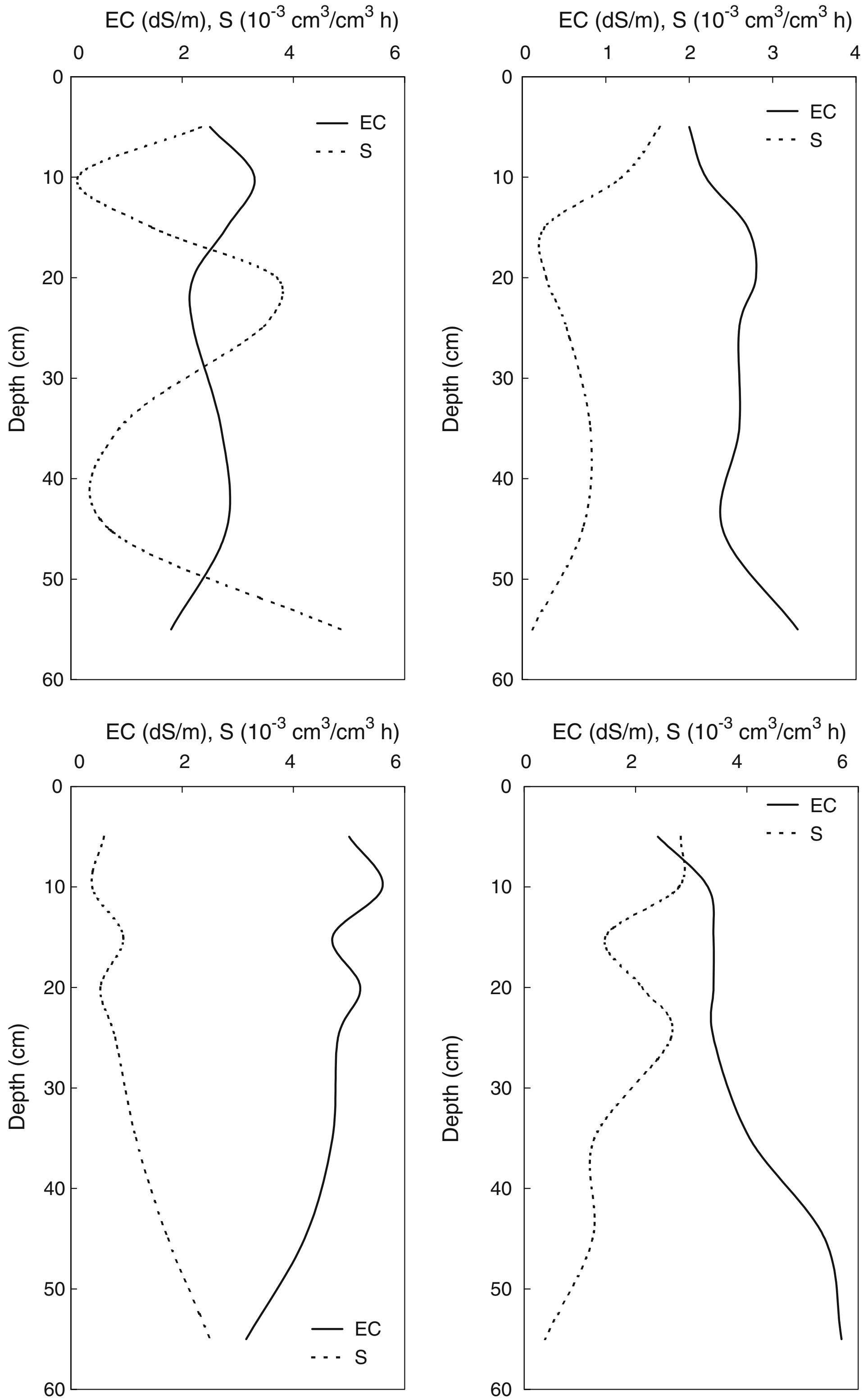

Fig. 3 The distribution of soil solution salinity and corresponding uptake rates (calculated with Eq. 2 and reduction term of Eq. 6) for some of the data given in Tables 1, 2 and 3

reported data (Tables 1, 2) indicated that under heterogeneously distributed low and moderate salinities, the water uptake will take place everywhere in the root zone and no sign of uptake ceasing was observed. Also, the interesting is to find out which concept of water integration can hold under this circumstance. We first follow the same

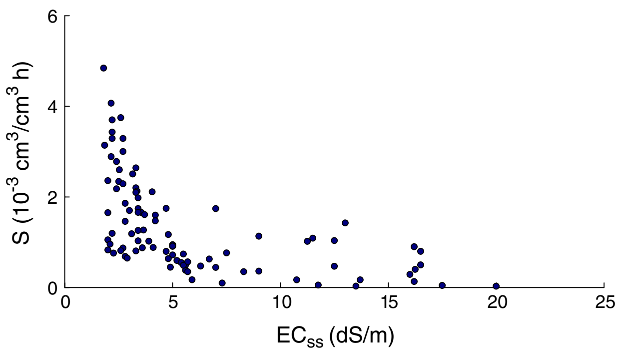

Fig. 4 The relation between the in-point measured soil solution salinities and uptake rates (calculated with Eq. 2 and reduction term of Eq. 6) for all experimental data

discussions for Table 3 as for Tables 1 and 2 and then the above questions will be discussed in more details.

Equal water content and same depth, different salinity

In column J, the water content from 15 to 20 cm was constant. By increasing EC_{ss} from 11.2 to 16.2 dS/m, S was reduced from 1.1 to 0.76 $\times$ 10^{-3} cm^3/cm^3 h. This means under that condition S was decreased about 0.07 $\times$ 10^{-3} cm^3/cm^3 h per dS/m. Also, θ was almost the same at 5 and 15 cm and the decrease in S per unit EC_{ss} for these depths is 0.15 $\times$ 10^{-3} cm^3/cm^3 h. Such a change for 10 and 25 cm depths in column I is 0.11 $\times$ 10^{-3} cm^3/cm^3 h per dS/m. Again in column K, by decreasing EC_{ss} from 7 to 2.15 dS/m at 45 to 55 cm, S increased from 1.04 to 2.36 $\times$ 10^{-3} cm^3/cm^3 h. Such a change for the same depths in column L is about 0.62 $\times$ 10^{-3} cm^3/cm^3 h per dS/m. Also, at almost constant water contents for depths 25 and 45 cm of column K the S increased by 0.07 $\times$ 10^{-3} cm^3/cm^3 h per dS/m. Looking at Table 3, we may find some more observations similar to that indicated above. While the water uptake rate as function of soil solution salinity shows a diminishing trend, it is obvious that S does not decrease uniquely by 1 dS/m increase in soil salinity. This was also shown in Tables 1 and 2. Such a trendless behavior is given in Fig. 2 for our experimental data at constant water contents.

Equal salinity, different water content

In column J, EC_{ss} was almost constant at 10 and 45 cm, while the volumetric water content increased from 0.197 to 0.351. This caused 0.22 $\times$ 10^{-3} cm^3/cm^3 h increase in uptake rate. Also, EC_{ss} was constant at 5 and 45 cm in column K, while by increasing 0.13 cm^3/cm^3 water content the uptake rate showed even a slight reduction. A small change in θ at 20–25 cm of column K, increased the uptake rate by almost three times. An interesting observation as can be seen in columns J and K at 15 cm is that at constant EC_{ss} and θ, the uptake rate demonstrates a significant change. Such considerable variation in S also can be seen in columns J and L at 20 cm depth. This can be related to the different evaporative demand of the columns under which the data were collected (see T_p values for different columns). Thus, if the soil water content remains high enough, the evaporative demand is one of the prime factors to control the uptake rate. Based on all observations reported in Tables 1, 2 and 3 as well as some other non reported data here, it is obvious that at given water content most water is taken from the less saline increments of the root zone, but the water uptake from other compartments with higher salinities was never stopped. These observations are much close to the algorithm used in numerical simulation models than the three other integration approaches. Figure 3, shows the uptake rate distributions as function of depth for some of the data depicted in Tables 1, 2 and 3. The soil solution salinity is also given in these figures. As can be seen, in most cases the S variation resembles the EC_{ss} changes in opposite directions, but does not apply to some others. Also, the magnitude of uptake rate changes per unit salinity is not unique for the reported data. These are shown in Fig. 4, in which the uptake rate is given as function of each soil salinity compartment. Irrespective of the general shape of the figure, the large scatter indicates that beside soil salinity some other factors are influencing the uptake rate; mainly evaporative demand and root activity. To separate the effect of evaporative demand from other factors, the S values for each independent column as function of in-point EC_{ss} are given in Fig. 5. As can be seen, the scatter in these figures is much less than that of Fig. 4. Note that the data presented in Fig. 4 belong to all 12 columns of Tables 1, 2, and 3 that are collected under different climatic conditions. However, Fig. 5 demonstrates the condition under which the evaporative demand was nearly constant for each independent soil column. Looking at this figure, still some scatter can be observed. We assume that this may point the dynamic change of root activity during the stress period. From our reported data (Fig. 1), one may conclude that the root activity is inconstant during the stress period. Probably, one major reason for such variation is the change in root hydraulic conductivity during the stress period. While, this was reported by Meiri (1984) and Homaee et al. (2002d), there seems to be no direct evidence to describe the mechanism in the literature (Steudle 2001, 2000; Hose et al. 2001). Further detailed investigations are then needed to investigate such a dynamic behavior. The osmotic adjustment can be also regarded as a reason for the dynamic change of root activity during the stress period. This may also explain the reason for non-unique response of water extraction rate under similar matric and osmotic

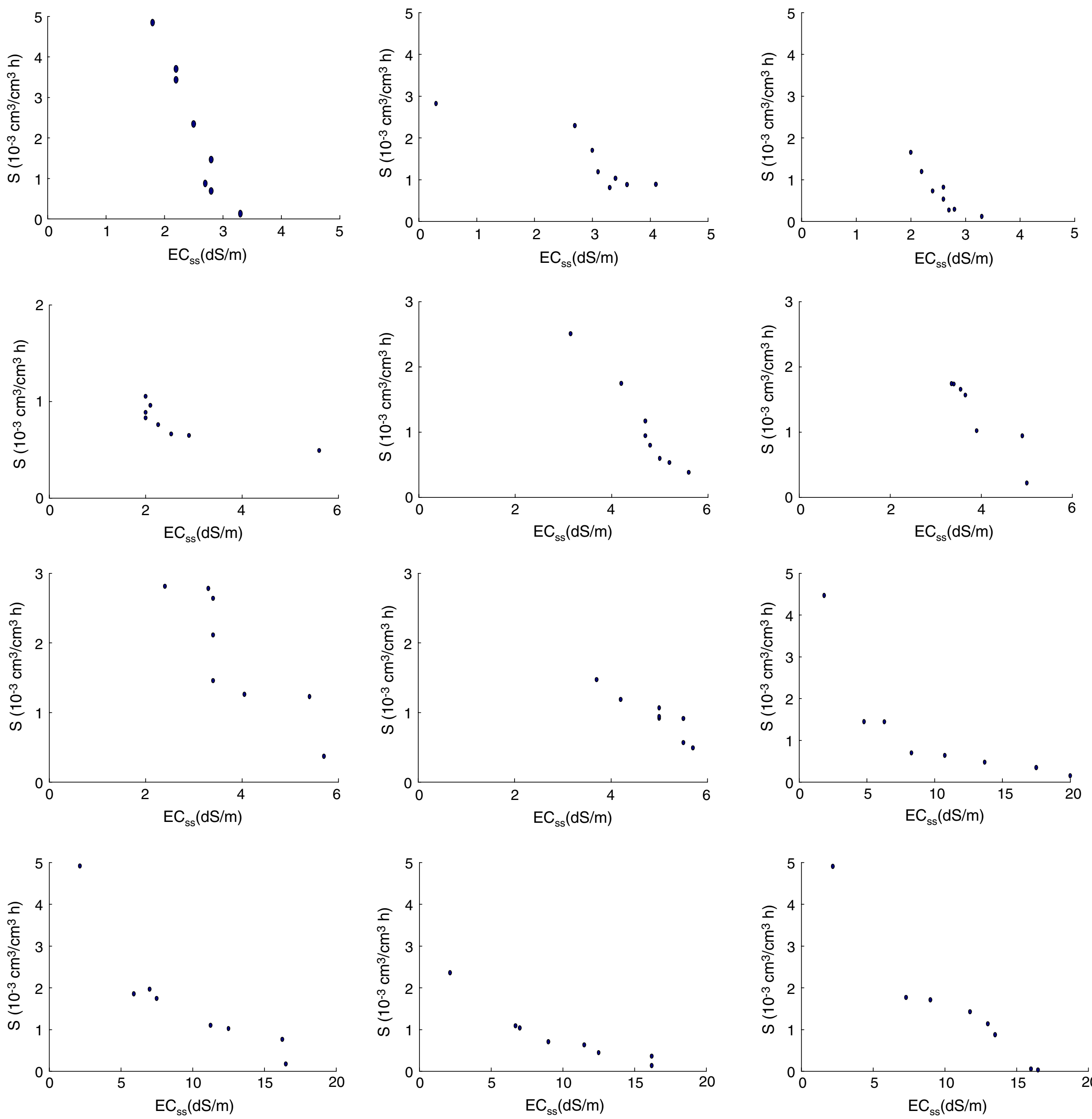

Fig. 5 The uptake rates as function of in-point soil solution salinities under relatively constant evaporative demands

potentials. While roots may adjust to salinity, there seems to be no such short term apparent adjustment for water stress. Also, this may explain the reason for some discrepancies in the numerical simulation models that deal with root water uptake under salinity stress. Because, in those models the root activity is usually assumed to be constant during the stress period. Although these observations can explain some mechanisms involved in adjusting plant water extraction under saline environment, the magnitude of each remains to be verified in more details.

Conclusion

From the results obtained in this study, it may be concluded that under real conditions plants tend to minimize the energy needed to overcome the soil water osmotic head. This means that plants tend to take up water from the depth with minimum salinity and minimize the uptake from other parts as long as the zone with minimum salinity contains enough water to satisfy the evaporative demand. When this zone can no longer satisfy the evaporative demand, the

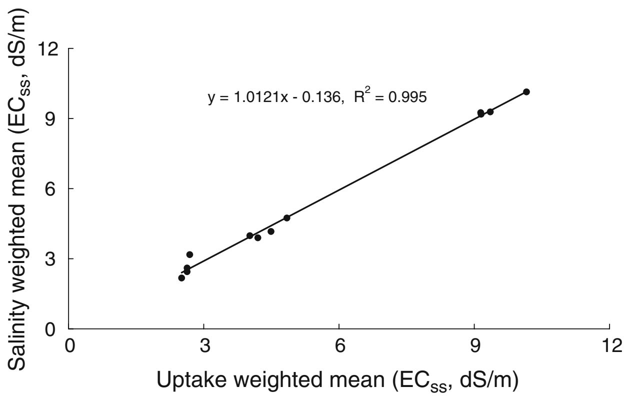

Fig. 6 The relation between the uptake-weighted mean (calculated with Eq. 1) and salinity-weighted mean

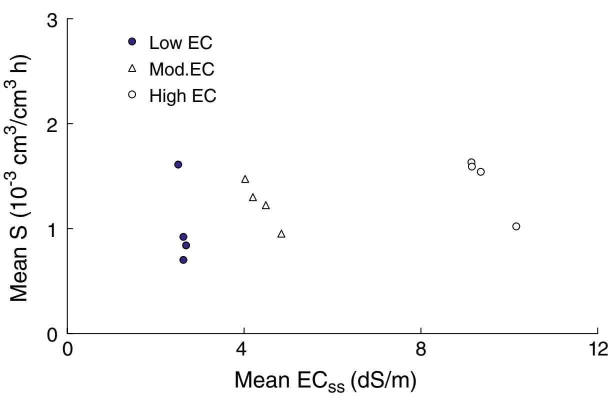

Fig. 7 The calculated mean uptake rates as function of salinity-weighted averages under low, moderate and high-soil solution salinities

major amount of water will be taken up from the next less saline depth. This process continues until the free energy of the soil water due to high salinity decreases to such an extent that the biological energy of the plants has become insufficient and water uptake stops altogether. When plants take up water from one depth (due to lower salinity), the water moves from another depth with higher water content resulting from soil hydraulic head gradient. The soil solution salinity may or may not change due to the transported water at that depth, compared with that before root water uptake. But, the salinity at the depth from which the water was taken up will certainly increase if the water is not replenished from another depth. Thus, at a certain time and depth EC_{ss} may change or remain unchanged due to root water uptake. Therefore, the dynamic change of water uptake patterns under stress period as shown in this paper indeed resembles many mechanisms that act simultaneously in the root zone. As long as the influence of each independent responsible mechanism is not fully understood, the quantitative description of plants water integration remains complicated enough to be verified. More detailed experimental studies are still needed to gain such quantitative description. An overall influence of all these mechanisms does finally appear in crop yield. This means that the water integration is indeed included when crop yield is expressed as function of averaged soil salinity over the root zone. For this purpose, usually the salinity weighted average is used rather the uptake weighted mean (Eq. 1). Fig. 6, compares the two averaging method. Since the relation is almost unique, if an averaging is needed (e.g., to use Eq. 6), one may better use the simple salinity weighted average. In Fig. 7 when the mean uptake rate was plotted against the salinity-weighted average, the nonlinearities of Fig. 5 reduced to almost linear shape. This resembles the hypothesis of Maas and Hoffman (1977). Thus, for practical purposes the available averaged empirical expressions such as that of Maas and Hoffman (1977) seems to be reasonably well to consider the internal water integration and to predict the crop yield under salinity stress.

References

Bernstein L, Francois LE (1973) Leaching requirement studies: sensitivity of alfalfa to salinity of irrigation waters. Soil Sci Soc Am Proc 37:931–943

Bower CA, Ogata G, Tucker JM (1969) Root zone salt profiles and alfalfa growth as influenced by irrigation water salinity and leaching fraction. Agron J 61:783–785

Dirksen C (1985) Relationship between root uptake weighted mean soil water salinity and total leaf water potentials of alfalfa. Irrig Sci 6:39–40

Dirksen C, Kool JB, Koorevaar P, Van Genuchten MTh (1993) HYSWASOR—simulation model of hysteretic water and solute transport in the root zone. In: Russo D, Dagan G (eds) Water flow and solute transport in soils. Springer, Heidelberg, pp 99–122

Dirksen C, Huber MJ, Raats PAC, Rawlins SL, Van Schilfgaarde J, Shalhevet J, Van Genuchten MTh (1994) Interaction of alfalfa with transient water and salt transport in the root zone. Research report No. 135, US Salinity Lab, Riverside, CA, USA, 127 p

Francois LE (1981) Alfalfa management under saline condition with zero leaching. Agronomy J 73:1042–1046

Hanks RJ, Sullivan TE, Hunsaker VE (1977) Corn and alfalfa production as influenced by irrigation and salinity. Soil Sci Soc Am J 41:606–610

Heimovaara TJ, Bouten W (1990) A computer-controlled 36-channel time-domain reflectometry system for monitoring soil water contents. Water Resour Res 26:2311–2316

Hoffman GJ, Van Genuchten MTh (1983) Soil properties and efficient water use: Water management for salinity control. In: Taylor HM, Jordan WR, Sinclair TR (eds) Limitation to efficient water use in crop production. Am. Soc. Agronomy, Madison, WI, pp 73–85

Homaee M, Dirksen C, Feddes RA (2002a) Simulation of root water uptake I. Nonuniform transient salinity stress using different macroscopic reduction functions. Agric Water Manage 57:89–109

Homaee M, Feddes RA, Dirksen C (2002b) Simulation of root water uptake II. Nonuniform transient water stress using different reduction functions. Agric Water Manage 57:111–126

Homaee M, Feddes RA, Dirksen C (2002c) Simulation of root water uptake III. Nonuniform transient combined salinity and water stress. Agric Water Manage 57:127–144

Homaee M, Feddes RA, Dirksen C (2002d) A macroscopic water extraction model for nonuniform transient salinity and water stress. Soil Sci Soc Am J 66:1764–1772

Hose E, Clarkson DT, Steudle E, Schreiber L, Hartung W (2001) The exodermis: a variable apoplastic barrier. J Exp Bot 52:2245–2264

Ingvalson RD, Rhaods JD, Page AL (1976) Correlation of alfalfa yield with various index of salinity. Soil Sci 122:145–153

Maas EV, Grattan SR (1999) Crop yields as affected by salinity. In: Skaggs RW, van Schilfgaarde J (eds) Agricultural drainage, Agronomy Monograph No. 38, Chap. 3. ASA, CSSA, SSSA, Madison, pp 55–108

Maas EV, Hoffman GJ (1977) Crop salt tolerance-current assessment. J Irrig Drainage Div ASCE 103:115–134

Mualem Y (1976) A new model for predicting the hydraulic conductivity of unsaturated porous media. Water Resour Res 12:513–522

Meiri A (1984) Plant response to salinity: experimental methodology and application to the field. In: Shainberg I, Shalhevet J (eds) Soil salinity under irrigation. Springer, Heidelberg, pp 284–297

Jarvis NJ (1994) The MACRO model (Version 3.1). Technical description and sample simulations. Reports and Dissert. 19, Dept. Soil Sci., Swedish Univ. Agric. Sci., Uppsala, 51 pp

Raats PAC (1974) Movement of water and salts under high frequency irrigation. In: Proceedings of 2nd international drip irrigation congress, San Diego, CA, July, 1974, pp 222–227

Richards LA (1931) Capillary conduction of liquids in porous mediums. Physics 1:318–333

Shalhevet J, Bernstein L (1968) Effect of vertically heterogeneous soil salinity on plant growth and water uptake. Soil Sci 106(2):85–93

Simunek J, Huang K, Van Genuchten MTh (1998) The HYDRUS code for simulating the one-dimensional movement of water, heat, and multiple solutes in variably-saturated porous media. Version 6.0. USSL Research Report No. 144

Simunek J, Suarez DL, Sejna M (1997) The UNSATCHEM software package for simulating one-dimensional variably saturated water flow, heat transport, carbon dioxide production and transport, and solute transport with major ion equilibrium and kinetic chemistry. USSL Research Report No. 141, 186 p

Smith SE (1994) Salinity and production of alfalfa. In: Pessarakli M (ed) Handbook of plant and crop stress. Marcel Dekker Inc., New York, pp 431–448

Steudle E (2001) The cohesion tension mechanism and the acquisition of water by plant roots. Annu Rev Plant Physiol Plant Mol Biol 52:847–875

U. S. Salinity Laboratory Staff (1954) Diagnosis and improvement of saline and alkali soils. Handbook 60, U. S. Government printing office, Washington, DC

Van Dam JC, Huygen J, Wesseling JG, Feddes RA, Kabat P, Van Walsum PEV, Groenendijk P, Van Diepen CA (1997) Theory of SWAP, version 2.0. Simulation of water flow, solute transport and plant growth in the soil–water–atmosphere–plant environment. Report No. 71. Dept. of Water Resour., Wageningen Agricultural Univ. 167 pp

Van Genuchten MTh (1987) A numerical model for water and solute movement in and below the root zone. Res. Report, U. S. Salinity Lab, Riverside, CA, USA

Van Genuchten MTh (1980) A closed form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Sci Soc Am J 44:892–898

Van Genuchten MTh, Hoffman GJ (1984) Analysis of crop production. In: Shainberg I, Shalhevet J (eds) Soil salinity under irrigation. Springer, Heidelberg, pp 258–271

Van Genuchten MTh, Leij FJ, Yates SR (1991) The *RETCE* code for quantifying the hydraulic functions of unsaturated soils. US Environmental Protection Agency, pp 85

Van Genuchten MTh, Schaap MG, Mohanty BP, Simùnek J, Leij FJ (1999) Modeling transport processes at the local scale. In: Feyen J, Wiyo K (eds) Modelling of transport process in soils at various scales in time and space. Wageningen Pers, Wageningen, pp 23–45

Wind (1966) Capillary conductivity data estimated by a simple method. Water in the unsaturated zone, symp. In: Proceedings of UNESCO/IASH, Wageningen, pp 181–191