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Root water uptake and profile soil water as affected by vertical root distribution

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Abstract Water uptake by plant roots is a main process controlling water balance in field profiles and vital for agro-ecosystem management. Based on the sap flow measurements for maize plants (*Zea mays L.*) in a field under natural wet- and dry-soil conditions, we studied the effect of vertical root distribution on root water uptake and the resulted changes of profile soil water. The observations indicate that depth of the most densely rooted soil layer was more important than the maximum rooting depth for increasing the ability of plants to cope with the shortage of water. Occurrence of the most densely rooted layer at or below 30-cm soil depth was very conducive to maintaining plant water supply under the dry-soil conditions. In the soil layers colonized most densely by roots, daytime effective soil water saturation (S_e) always dropped dramatically due to the high-efficient local water depletion. Restriction of the rooting depth markedly increased the difference of S_e between the individual soil layers particularly under the dry-soil conditions due likely to the physical non-equilibrium of water flow between the layers. This study highlights the importance of root distribution and pattern in regulating soil water use and thereby improving endurance of plants to seasonal droughts for sustainable agricultural productivity.

Keywords Actual transpiration · Maize · Root length density · Root system architecture · Sap flow · Soil water potential

Introduction

Root water uptake is the gateway for plant water supply, which recycles more than 50% of the annual precipitation on earth (Chahine 1992). It has been considered as a key factor in optimization of modern agricultural practices involving irrigation and fertilization (Clothier and Green 1994; Moroke et al. 2005). Studies indicate that root water uptake is one of the consequences of ecophysiological interactions between belowground and

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aboveground processes (Zhuang et al. 2000), and is largely affected by root system distribution, soil hydraulic properties, and climate conditions (Jackson et al. 2000; Feddes et al. 2001; Zhuang et al. 2001a; Wang and Smith 2004). In most soil profiles, root density usually decreases exponentially with soil depth, but soil compaction and layered soil structure can considerably modify this regular root distribution (Atwell 1993; Tardieu 1994; Passioura 2002; Araki and Iijima 2005). As a result, uptake of soil water by plant roots from different soil depths is affected particularly under water-deficit conditions (Passioura 1983, 1988; Smucker and Aiken 1992; Calmon et al. 1999; Dardanelli et al. 2003).

Effect of root distribution on root water uptake has been addressed by a number of experiments (Fisher et al. 1975; Taylor and Klepper 1978; Clausnitzer and Hopmans 1994; Angadi and Entz 2002; Moroke et al. 2005) and numerous mathematical modeling (Francis and Pidgeon 1982; Boote et al. 1997; Calmon et al. 1999; Bruckler et al. 2004; Hao et al. 2005). All these studies have greatly advanced our understanding on the substantial influence of geometrical distribution of roots on plant water uptake. However, our ability to predicting the complex processes of belowground water uptake is still limited. This is because, on the one hand, many existing models are still not suitable for the scenarios that root distribution deviates from the regular exponential pattern, although different levels of detail and consequently different types of plant root information have been used in the model parameterizations (Smucker and Aiken 1992; Calmon et al. 1999; Wang and Smith 2004). On the other hand, many studies based on the simplified root-soil-water system have not provided a knowledge foundation that is sufficient for our understanding on the complex process of root water uptake. This is why to date a satisfactory description has not yet been made on the practical importance of root distribution that is actually subjected to specific soil water regimes along soil profiles and to the feedback effect of the water uptake on redistribution of soil water under a certain climate condition (Molz 1971; Francis and Pidgeon 1982; Coelho and Or 1999; Guswa 2005). The main obstacle for a thorough understanding and realistic modeling is that few field experimental data have so far been available for examining the effects of root distribution and pattern on both root water uptake and the associated soil water status, particularly when rooting barriers exist in subsoil. Scientific data on these aspects are currently very crucial for addressing the mechanisms responsible for the interaction among root water uptake, root distribution, and dynamics of soil water in field profiles.

The objective of this study was to examine the effect of vertical root distribution on root water uptake of maize plants, and quantify the interaction of root water uptake with profile soil water under distinctive soil water conditions. The root distribution addressed in this study includes unrestrictive distribution and depth-restricted distribution. We hypothesized that depth of the soil colonized most densely by roots was more critical for soil water use by plants than the maximum depth of plant rooting. The hypothesis was tested under both dry- and wet-soil conditions. Significance of vertical root distribution in regulating root water uptake and soil water dynamics is evaluated.

Materials and methods

Site description and soil properties

The observations on root water uptake were carried out on the experimental farm of the Faculty of Horticulture at Chiba University between July 21 and August 20, 1999. The site is situated at Matsudo city, near Tokyo of Japan (35° 46′ N, 139° 54′ E, 7.9 m above sea level), The maize plants (*Zea mays L.*) were sowed on April 25, 1999 in the field with an area about 400 m^2. The within-row spacing was 0.4 m with 0.7 m between the rows. Before the sowing, the field was fertilized with 60 kg N/ha, 44 kg P/ha, and 75 kg K/ha. No irrigation was applied during the plant growth. The soil is a Kanto fine sandy loam developed from volcanic ash. Physical properties of the soil are provided in Table 1. Soil bulk density (ρ_b) was measured using soil core method, and calculated as $\rho_b = M_w/(V+V\theta)$, where M_w is wet soil

Table 1 Physical properties of the field soil

Soil depth (cm)	Sand (%)	Clay (%)	ρ_b (Mg m^{-3})	K_s (10^{-4} cm s^{-1})	θ_s (m^3 m^{-3})	θ_r (m^3 m^{-3})	α	n
0–5	26.79	39.68	0.806	1.56	0.661	0.264	0.12	1.22
5–10	26.21	43.09	0.728	4.05	0.689	0.284	0.11	1.22
10–15	25.63	46.49	0.753	2.95	0.680	0.304	0.10	1.22
15–20	27.60	44.61	0.799	1.68	0.663	0.294	0.12	1.22
20–25	29.57	42.72	0.675	8.31	0.707	0.281	0.12	1.22
25–30	31.25	43.63	0.695	6.33	0.700	0.286	0.12	1.21
30–35	32.92	44.54	0.785	1.99	0.668	0.293	0.14	1.22
35–40	38.48	38.58	0.616	20.01	0.729	0.255	0.13	1.22
40–45	44.20	32.44	0.684	7.39	0.705	0.219	0.15	1.22
45–50	46.98	29.46	0.672	8.74	0.709	0.201	0.16	1.22
50–55	49.75	26.48	0.729	4.01	0.689	0.184	0.14	1.23
55–60	49.75	26.48	0.694	6.45	0.701	0.183	0.13	1.23

K_s: saturated hydraulic conductivity, θ_s: saturated water content, θ_r: residual water content, α and n: parameters of van Genuchten water retention model (van Genuchten 1980)

weight in the core, V is the volume of the cores (5.0 cm inside diameter, 5.1 cm height), and θ is gravimetric soil water content measured at 105°C. At each depth of each of three soil profiles, three undisturbed soil cores were collected for analyses of soil hydraulic properties. Saturated hydraulic conductivity (K_s) was determined using a constant-head method (Klute and Dirksen 1986). Drying curve of the soil water characteristic was measured using pressure plate method (Dane and Hopmans 2002). Saturated and residual water contents refer to the soil water contents at –0.3 kPa and –1500 kPa, respectively.

Field experimental design and measurement on sap flow of maize plants

To examine the effect of vertical root distribution on extraction of soil water by maize plants, plant-growing experiments were performed in bulk field and three large containers made of metal sheets (140-cm long, 120-cm wide, and 60-cm deep) with opening top and bottom. The containers were vertically inserted into the field soil before the sowing of maize, with the upper edges at the ground level. By excavating and refilling the soil in 5-cm increment, nylon sheets (140×120 cm^2) for restricting root growth were horizontally placed at 20-cm, 30-cm, and 40-cm depths in three containers, respectively. The nylon sheets had a pore size of 150-μm and were impenetrable to roots but permeable for soil water. The measured bulk densities of soils at each 5-cm depth after the field experiments showed that there was no systematic variation between the bulk field soil and the container soils, suggesting that the repacking did not significantly disturb the soil in the containers. Forty-six days after set-up of the containers in the field, maize plants were sowed in the field, with total six plants in each of the containers in two rows. To guarantee the uniformity in size of the maize plants grown in the containers, we initially sowed four seeds in each of the six sowing pits and subsequently removed the seedlings that were significantly smaller or larger than the averaged size of the bulk field plants when the seedlings were about 15-cm in height. Root distribution of the bulk field plants is referred to as unrestrictive distribution, and root distributions of the container plants with restrictive rooting barriers located at 20-cm, 30-cm, and 40-cm depths are designated here as Depth 20-cm, Depth 30-cm, and Depth 40-cm, respectively, to indicate the maximum rooting depth in the individual containers.

Root water uptake of the maize plants was represented by xylem sap flow, which was measured using heat balance method (Campbell 1991; Ishida et al. 1991; Jara et al. 1998), with the gauges (Dyanmax, SGB25) installed on the base of the plant stems. A Thermodac EF data logger (Model 20520A) was used to record signals every minute for subsequent calculation of sap flow rate. To reduce the variability of the measurement (Jara et al. 1998; Hupet and Vanclooster 2005), two plants were measured for xylem sap flow in the bulk field and in each of the three containers. The averaged values of the two plants for each of 15-min intervals were used to examine the effect of root distribution. All the eight observed plants were similar in height and stem diameter when the gauges were attached on.

Environmental and biometrical measurements

A series of field environmental conditions and plant biometrical characteristics were measured during the plant growth. Ceramic-tipped tensiometer probes (DIK-3100, Daiki Rika) were installed vertically at each 10-cm depth in the middle of two plants within the row to record soil water potentials. Tensiometers at the depths below the restrictive sheets were installed prior to placing of the nylon sheets in the containers. Various meteorological instruments were mounted on a mast in the middle of the field to record solar radiation (at 2.5 m height from the ground with Solarimeter MR-21, EKO), net radiation (at 0.5 and 2.2 m heights with Radiometer CN-21, EKO), wind velocity (at 2.5 m height with 3-cup anemometer AF-750, MAKINO), dry and wet bulb temperatures (at 0.5, 2.0 and 2.5 m heights), relative humidity (at 0.5, 2.0 and 2.5 m heights with ventilated psychrometer), and rainfall (at bare ground surface with rain gauge 657, ISCO) at 1-minute interval on a Thermodac EF data logger (Model 20520A). Potential evapotranspiration ($\mathrm{ET_0}$, mm day^{-1}) was calculated using Penman method, by employing the following formulas

$$E_\mathrm{p} = \frac{\Delta R_\mathrm{n} + \gamma E_\mathrm{a}}{\Delta + \gamma} \tag{1}$$

$$E_\mathrm{a} = 0.26(1 + 0.54u)(e_\mathrm{sd} - e_\mathrm{a}) \tag{2}$$

$$\Delta = \frac{6.1078(2500 - 2.4T)}{0.461(273.15 + T)^2} \times 10^{7.5T/(237.3+T)} \tag{3}$$

$$e_\mathrm{sd} = 6.1078 \exp\left(\frac{17.269T_\mathrm{d}}{237.3 + T_\mathrm{d}}\right) \tag{4}$$

$$e_\mathrm{sw} = 6.1078 \exp\left(\frac{17.269T_\mathrm{w}}{237.3 + T_\mathrm{w}}\right) \tag{5}$$

$$e_\mathrm{a} = e_\mathrm{sw} - 0.5 \times 1013 \times (T_\mathrm{d} - T_\mathrm{w})/755 \tag{6}$$

where R_n is net radiation (W m^{-2}) at 2.2 m height above the ground surface, E_a drying ability of air (mm day^{-1}), γ a psychrometric constant (0.66 hPa °C^{-1}), Δ a slope of relation curve of saturated water vapor pressure (hPa °C^{-1}) to air temperature, u wind velocity (m s^{-1}) at 2.5 m height above the ground surface, e_sd and e_sw saturation vapor pressures (hPa) at dry and wet bulb temperatures (°C), respectively, at 2.0 m height above the ground surface, e_a actual atmospheric water vapor pressure (hPa) at 2.0 m height above the ground surface, T air temperature (°C) at 2.0 m height above the ground surface, and T_d and T_w dry and wet bulb temperatures (°C), respectively, at 2.0 m height above the ground surface. Saturation deficit was calculated as the difference between e_sd and e_a.

Biometrical measurements were conducted weekly on the field plants four weeks after their emergence. Canopy height was measured from soil surface to the tip of the highest leaf on the stems of three randomly selected plants before the fifth leaf stage, and to the highest point on the undisturbed plant after a distinct bend of the top leaf occurred. After emergence of tassel, plant height was measured to the tip of the tassel. Leaf area index (LAI) was calculated as actual leaf area (LA) of a plant divided by the ground area that the plant sample occupied. The LA was manually measured based on five whole plant samples by following a method described here. After the plants were cut from the ground surface, they were transported immediately to a nearby laboratory, where the plants were divided into leaves, stems, and cobs. It followed that length (L) and width (W) of all the excised leaves were measured. Next, 10 representative leaves covering the smallest to largest leaves were selected from all the leaves and cut into several pieces with dimensions smaller than the A4 sized copy paper. The pieces of each leaf were copied on A4 papers using a photocopy machine, and then the LA of each of the 10 representative leaves was calculated as LA = aM_p, where M_p is the mass of the carbon-darkened area of the A4 papers for all the pieces of a leaf, and a is specific surface area (cm^2 g^{-1}) of the A4 papers. The value of a was determined based on a A4 paper that was carbon-darkened by photocopying a red color A4 sized paper. From the results of the 10 leaves, a regressional relationship was obtained by correlating the product of leaf length and width ($L \times W$) to the LA. At last, total LA of each plant was estimated by summing the individual leaf area, which was calculated using the fitted equation from the length and width of each leaf. The regression equation was also used to nondestructively estimate the total LA of each of the container plants. After the LAI measurement, all the leaves, stems, and cobs were dried to a constant weight in a forced-air oven at 60 °C for aboveground biomass determination. Specific leaf mass was calculated by dividing the total leaf dry mass of a plant by its total LA. Weekly investigation on roots was conducted on three randomly selected bulk field plants using a modified trench-profile method (Bohm 1976). The method has been reported to be the best among the five frequently used methods including soil auger method (Bohm 1977). The roots of the bulk field and container plants on which xylem sap flow was measured were collected along the soil profiles immediately after completion of the final observations on root water uptake. Three soil samples (each $70 \times 40 \times 5$ cm^3) were made at each 5-cm depth from ground surface to 60-cm depth. The soil samples were thoroughly washed with fine spray of water on a 0.25-mm sieve. Roots retained on the sieve were picked by tweezers and their total root length was determined using a line-intercept sampling method (Tennant 1975). The root volume was measured using water-filled graduated cylinders. The root mass was obtained by following the drying procedure as used for determination of the aboveground biomass. Hourly variations of the water potentials of leaves at different positions on the stem and roots colonizing at 10-cm depth were measured with a pressure chamber (Model 3000, Soil Moisture Equipment Corp., Santa Barbara, CA) on the days for sap flow observation.

Results

Field environmental conditions and biometrical characteristics of plants

Due to the insignificant rainfall during the period of water uptake measurements (Fig. 1a), the soil became progressively dry from the initial wet condition (Fig. 1b). In terms of the measured soil water potentials, the 7 days for observation of root water uptake can be roughly divided into two sub-periods: wet-soil days (–100–200 cm of soil potential for days 73, 76 and 77) and dry-soil days (–750–850 cm of soil potential for days 84, 85, 87 and 88). This distinctive soil water regime provided an excellent natural condition for examining the interaction among root water uptake, root distribution, and profile soil water. Converse to the reduction of soil water content, the air temperature progressively increased by ~ 3°C from day 73 to day 88 (Fig. 1c). The canopy saturation deficit became greater with the advance of the wet-soil days (Fig. 1d), but without consistent trend in the dry-soil days. Potential evapotranspiration (ET_0) (Fig. 1f), as a comprehensive index of the climate conditions, changed in a trend similar to the solar radiation (Fig. 1e). The values of ET_0 increased during the wet-soil days (days 73–77) while the soil water potential deceased (Fig. 1b), suggesting a dominated control of climatic conditions to the water loss from the relatively wet soils. During the dry-soil days (days 84–88), ET_0 kept decreasing without clear relation to the change of soil water potentials. This is partly because the soil was already very dry and partly because the short and light rainfalls on days 87 and 88 (Fig. 1a) interfered the relationship between the soil water potentials and the climate.

Water potentials of leaves and roots were measured hourly during the days for observation of the xylem sap flow. The averaged leaf water potentials at 9:00 am were –611, –843, –956, –789, –1019, –602, and –657 kPa on days 73, 76, 77, 84, 85, 87, and 88, respectively. The averaged root water potential at 10-cm soil depth at 9:00 am was –70±15 kPa in those days. The daily growth of field plants is summarized in Fig. 2. Canopy height reached its highest on day 68 after the emergence of plant from the soil. LAI approached its maximum on day 58, and did not show statistically significant difference between the plants grown in the bulk field and the field-containers. The maximum rooting depth of the bulk field plants was attained on day 69. If assuming a similar vertical rooting rate between the container plants and the bulk field plants, the

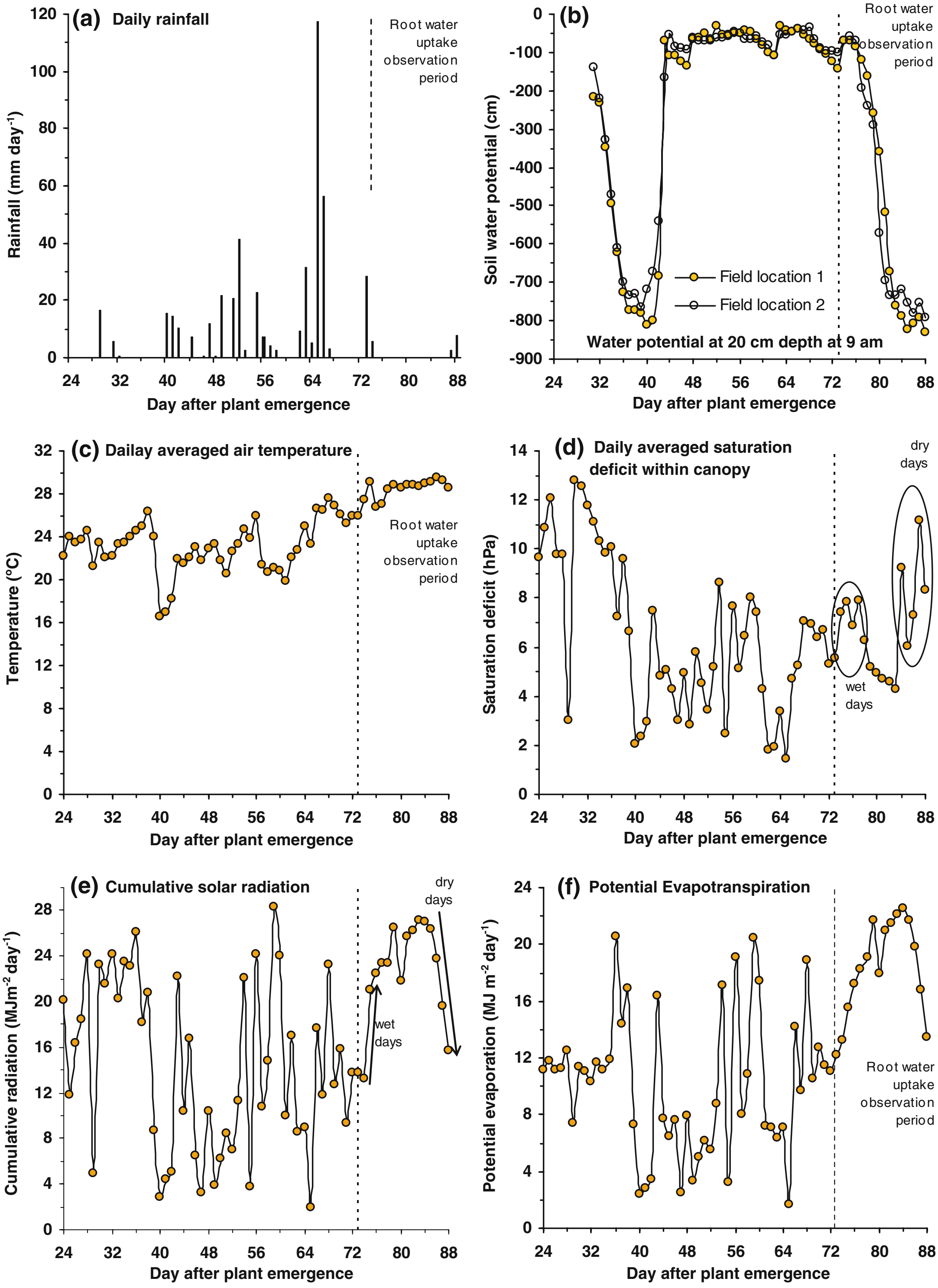

Fig. 1 Environmental conditions during the period of plant growth

roots of the container plants under the treatments of Depth 20-cm, Depth 30-cm, and Depth 40-cm should reach the rooting barriers on days 38, 47, and 57, respectively (Fig. 2a).

Root distribution profile

Vertical distribution of root length density of the investigated plants is summarized in Table 2. The plants grown in the field-containers greatly differed from the bulk field plants in the root profile, particularly in the depth of the most densely rooted soil layer. Since rooting of the bulk field plants was not spatially restricted, its root distribution was basically genetically determined, with the root length density exponentially decreasing with soil depth (Zhuang et al. 2001b). Almost 50% of the total root length occurred in the top 10-cm, another 30% within the next 20-cm, and the remaining 20% below 30-cm. In comparison, the roots of the plants grown in the field-containers exhibited dual peaks of root length density, with about 35–50% of total root length occurring in the top 10-cm soil layer and 30–40% in the 5-cm soil layer above the rooting barriers. The abrupt increase of root length density on the barriers was attributed to impedance of the nylon sheets to downward extension of roots. This barrier-induced deviation of root profiles from the regular unrestrictive distributions as exhibited by the bulk field plants is expected to impact the dynamics of profile soil water and exert a feedback effect on root water uptake.

Root water uptake in relation to root distribution

Figure 3 shows the measured root water uptake of maize plants grown in the bulk field and in the three field-containers under varying soil water conditions. The rates are the averages of the two measured plants in each of the treatments, with coefficients of variation ranging between 5.3% and 29.6%. The results show that both configuration of root system and rooting depth significantly affected the root water uptake, but the extent varied with soil water regimes. Root system configuration examined in the study included the unrestrictive distribution (i.e., exponential decrease of root length density with soil depth) and the restrictive distribution (i.e., an abrupt increase of root length density on the rooting barrier). Comparison of the root water uptake between these two root distributions can reveal the role in water extraction of the fraction of roots colonizing deep soil in the unrestrictive treatment (e.g., deeper than the rooting barriers in the restrictive treatments). Table 2 shows that among the container plants the plant with roots restricted at 20-cm was most similar to the bulk field plant in terms of the root distribution above the depth of rooting barriers. Both plants had 46% of the total root length occurring in the top 10-cm soil layer, except that 38% of the total root length of the bulk field plant accessed to the soil below 20-cm (Table 2). Figure 3 demonstrates that the bulk field plant had a higher uptake rate than the container plant with rooting barrier located at 20-cm (Depth 20-cm) under the wet-soil conditions (days 73, 76 and 77). This indicates that penetration of such a fraction of roots to deep soil effectively increased the amount of soil water directly available to the plant when the water extraction was dominated by climate and root length under the water-sufficient conditions. However, the uptake rates of the two plants differed little when the entire soil profile became water-deficient (days 84, 85, 87 and 88). Deep rooting of a fraction of roots (38% of total root length) seemed insignificant in enhancing the root water uptake of the bulk field plant for compensation of its transpiration. This suggests that role of the deep roots in increasing soil water extraction largely depended on the water availability in the deep soil.

Rooting depth is usually referred to as the maximum rooting depth, which determines the effective soil volume for water uptake by plants. The results for the container plants in Fig. 3 indicates that the plant with rooting depth of 20-cm (Depth 20-cm) had a much lower rate of water uptake than the plants with rooting depths of 30-cm and 40-cm (Depth 30-cm and Depth 40-cm, respectively). Under the wet-soil conditions, the container plant with its roots restricted at 40-cm exhibited a higher uptake rate than the bulk field

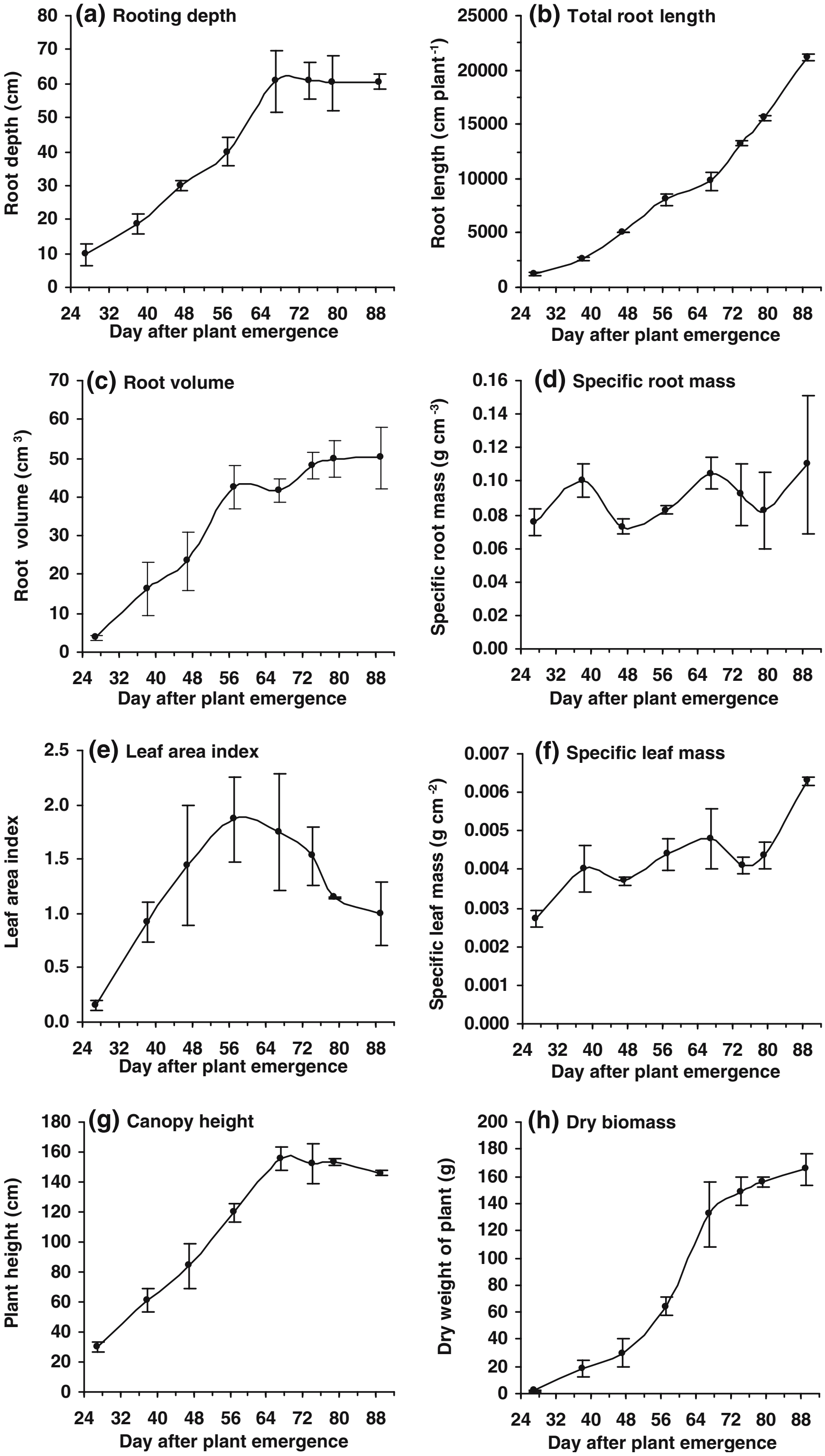

Fig. 2 Evolutions of the biometrical characteristics of the bulk field plants with days

Table 2 Distribution of root length density (cm/cm^3) along soil profile

Soil depth (cm)	Depth 20-cm		Depth 30-cm		Depth 40-cm		Unrestrictive distribution	
	cm/cm^3	%	cm/cm^3	%	cm/cm^3	%	cm/cm^3	%
0–5	0.29±0.11	22	0.33±0.10	21	0.18±0.16	18	0.49±0.14	32
5–10	0.33±0.12	24	0.29±0.15	18	0.13±0.18	13	0.21±0.18	14
10–15	0.20±0.09	14	0.17±0.10	11	0.10±0.04	10	0.15±0.19	10
15–20	0.54±0.14	40	0.16±0.04	10	0.08±0.03	8	0.09±0.07	6
20–25			0.15±0.05	10	0.08±0.02	7	0.09±0.03	6
25–30			0.46±0.13	30	0.04±0.01	4	0.10±0.01	7
30–35					0.07±0.02	7	0.06±0.03	4
35–40					0.33±0.11	33	0.06±0.00	4
40–45							0.08±0.01	6
45–50							0.06±0.01	4
50–55							0.05±0.02	3
55–60							0.07±0.01	4
Total length (cm plant^{-1})	19061		21893		14156		21227	

plant (Fig. 3a, b and c). This is largely attributed to the increased fraction of the roots in the soil below 20-cm in the restrictive treatment (51% of total root length) versus the unrestrictive treatment (38% total root length) (Table 2). The reason for the remarkable shortness in total root length of the plants grown under the treatment of Depth 40-cm relative to other treatments is not clear. However, it may be deducted that occurrence of the highest length-density roots at 40-cm depth might cause even more water extraction than the unrestrictive root distribution if both plants were similar in terms of total root length. Under the dry-soil conditions, the plants with roots restricted at 30-cm or 40-cm depth always took up soil water in higher rates than did the bulk field plants (Fig. 3d, e, f and g). Occurrence of the highest length-density roots at or below 30-cm soil depth proved favorable for the overall root water uptake in the water-deficient soil. This is consistent with the results of the daily amount of water uptake by the plant roots. Figure 3h displays that as soil was dried up (particularly after the 81st day) occurrence of the highest length-density roots at or below 30-cm significantly facilitated the plants to maintain a relatively higher daily uptake rate, as compared to the unrestrictive root distribution of the bulk field plants. It appears that 30-cm was a critical depth at which or deeper occurrence of the most densely rooted layer could promote soil water uptake by maize plants, particularly under water-deficit condition. This implies that depth of the most densely rooted soil layer was more important than the maximum rooting depth for root water uptake under dry-soil conditions.

Figure 4 displays the relationship between the vertical root distribution and the water-stress index of plants (ET/ET$_0$, ratio of actual transpiration (sap flow) to potential evapotranspiration). During the wet-soil days, the plants with deep-rooting (unrestrictive distribution and Depth 40-cm) exhibited larger ratios of ET/ET$_0$ (i.e., less stress of water-deficiency) than the plants with shallow-rooting (Depth 30-cm and Depth 20-cm) (Fig. 4a). However, as the soil was dried up, water stress on the plants with unrestrictive root distribution pronouncedly increased, in contrast to the little change of water stress on the container plants with the rooting restricted at 20-cm. Interestingly, stress of water-deficiency did not increase for the container plants with rooting restricted at 30-cm and 40-cm, in spite of the substantial decrease of soil water contents. This is consistent with the results of daily water uptake as plotted in Fig. 3h. Combination of the results presented in Figs. 3h and 4a produced Fig. 4b, which shows a decrease of the root water uptake with increasing water stress on the plants.

Dynamics of profile soil water in response to root water uptake

Changes of soil water content partly reflect water uptake processes of roots from soil profiles. Temporal and spatial variations of effective soil

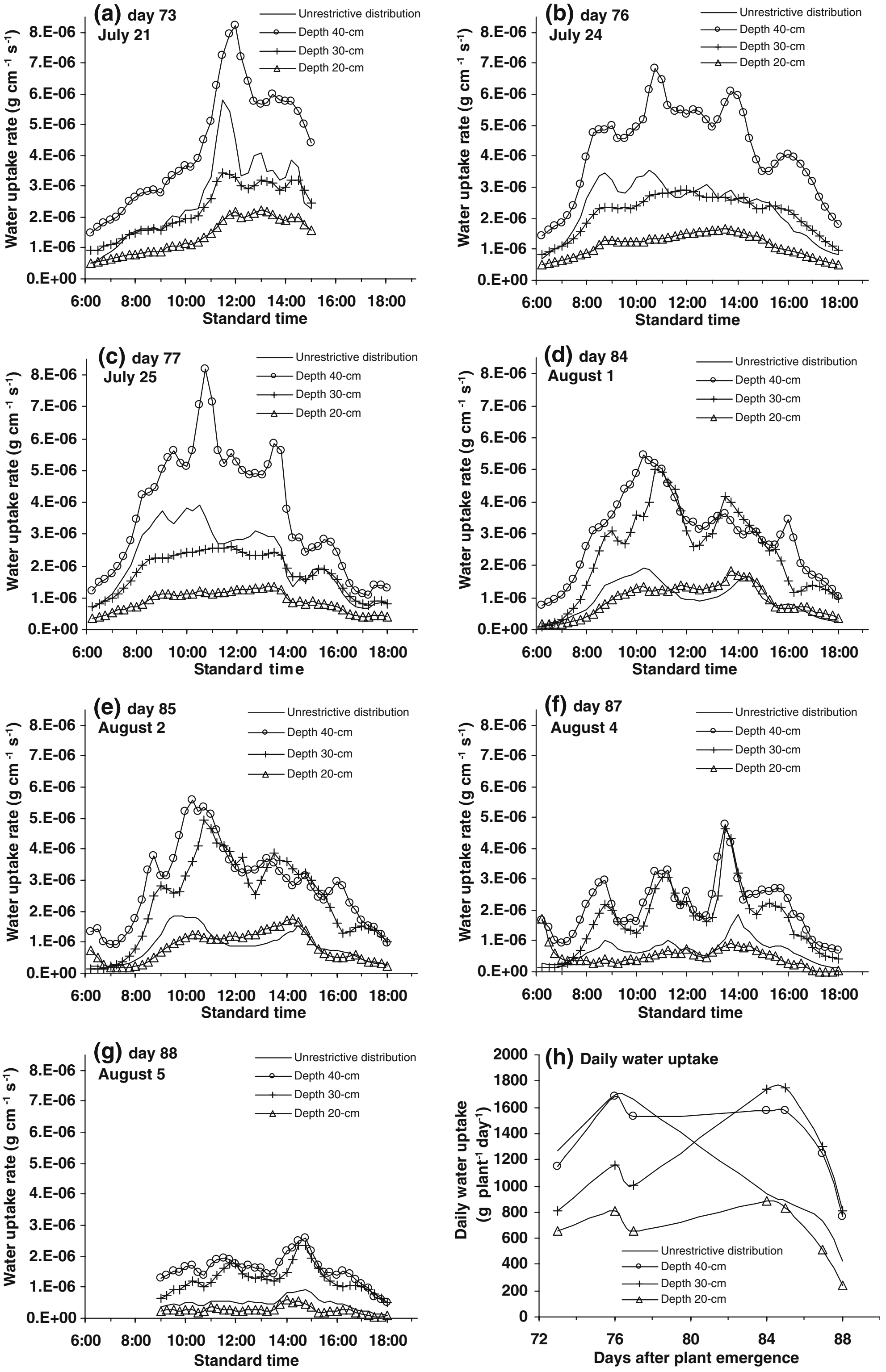

Fig. 3 Dynamics of the root water uptake rates of maize plants

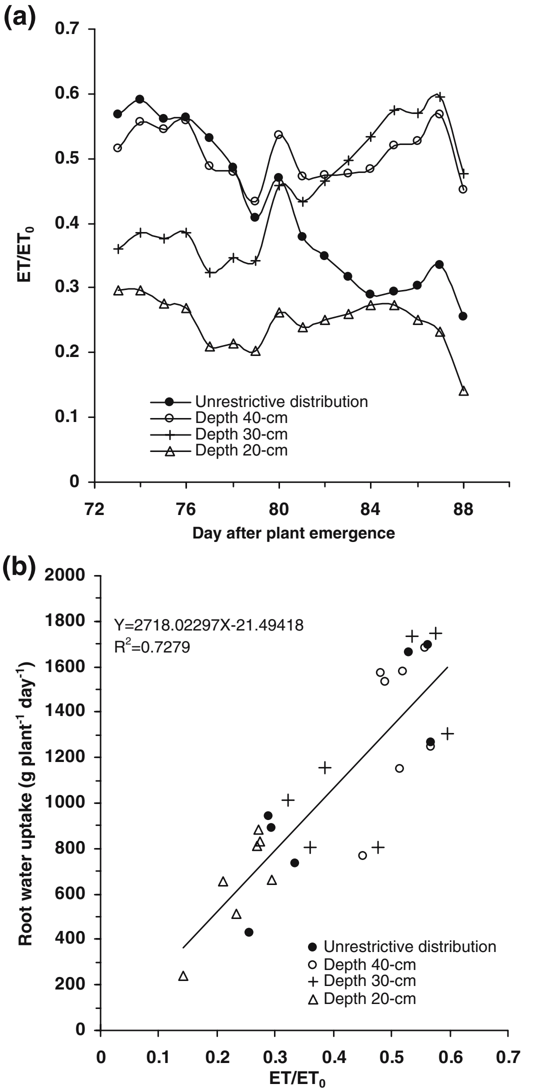

Fig. 4 Relative evapotranspiration (ET/ET_0) of all the experimental plants and its relationship with daily root water uptake

water saturation (S_e) of the four differently rooted soil profiles are plotted for a representative wet-soil day in Fig. 5 and for a representative dry-soil day in Fig. 6. In the wet soil, high-density roots dominated the water uptake, though the other rooting layers also played a significant role. The bulk field plant with unrestrictive root distribution primarily took up water from the top 10-cm soil layer, and the field-container plants extracted most of the water from the depth at which the rooting barriers were set (i.e., the depth with an abrupt increase of root length-density). Dominant water uptake from these most densely rooted soil layers caused the largest drop of values of the local S_e, whereas secondary water uptake from the other depths led to a steady slow decrease of S_e with time in the day. The results suggest that soil water was extracted by roots from the entire soil profile directly or indirectly after water transport. In contrast, S_e decreased most with time in top 10-cm of the dry soil and little changed in deeper layers for both the bulk field plant and the container plant with roots most densely occurring at 40-cm. For the plants with the highest length-density roots occurring at 20- and 30-cm depths, S_e was relatively stable during the daytime at all the depths due to unavailability of soil water to the plants within the limited soil volumes. Figure 6 demonstrates that increase of the rooting depth or space reduced difference of S_e between most of the soil layers under the dry-soil conditions. This suggests that the non-uniform distribution of S_e might be a consequence of non-equilibrium of the earlier water uptake from different soil depths and relatively low rates of water redistribution between the layers.

Discussion

Interaction between root water uptake and profile soil water

The natural soil water conditions that varied progressively from wetness to dryness during the period of observation (Fig. 1b) were optimum to address the dynamic relationship between root water uptake and soil water availability. The field experiments show that profile soil water influenced both the rate and the pattern of root water uptake. In the wet soil, water was extracted by roots from all the depths (0–70 cm) directly or indirectly after transport. The soil layer colonized most densely by roots exhibited a greater drop in S_e than other soil layers, suggesting a dominant effect of the high length-density roots on water uptake. As the soil was dried out, the rates of root water uptake declined markedly for both the unrestrictive and the restrictive root distributions. Significant water uptake only took place in the most densely rooted soil

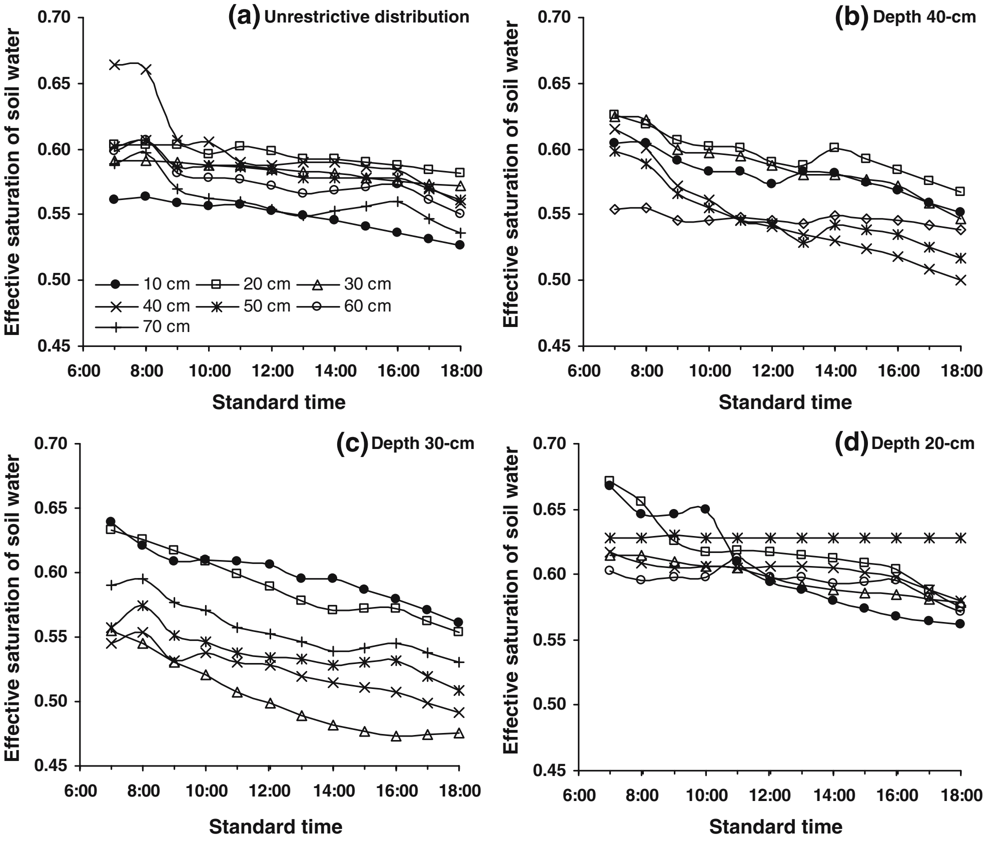

Fig. 5 Temporal change of the effective soil water saturation at different depths under a wet-soil condition (the 76th day after the plant emergence, July 24, 1999). Effective saturation = (actual water content – residual water content)/(saturated water content – residual water content)

layer, although the deeper soil layers were less dried and colonized by lower length-density roots. This implies that water-deficit stress occurring in a particular layer cannot always be compensated through increasing water uptake from other wetter layers in deeper soil. This coincided to the experimental results by Graham and Nobel (1999), who found that rewetting a small fraction of the root system of *A deserti* was insufficient for recharging leaf water storage and recovery of water uptake as well as stomatal opening. Nonetheless, our results differed from some of the previous findings or model simulations. It has been reported that water uptake from deep wet soil takes place only after there has been a substantial depletion in the superficial layers. If the soil surface is rewetted, uptake from the shallow layers is resumed, provided the superficial roots are still alive, and only switches back through the deeper layers as it depletes the water in superficial layers (Arya et al. 1975a, b; Nnyamah and Black 1977). By considering all the observations together, we presume that the reported inconsistence is due mainly to the disparities in root distribution and profile soil water status examined in specific studies, since shift of primary water uptake depth is determined by the combined effect of root distribution, profile soil water, and transient climate conditions.

Another phenomenon worthy noting is that the daily amount of water uptake did not decrease with soil drying from matric potential –100 cm to –750 cm for the container plants with restrictive root distributions, whereas it declined from the 76th day for the root-unrestrictive bulk field plants (Fig. 3h). This is related to the

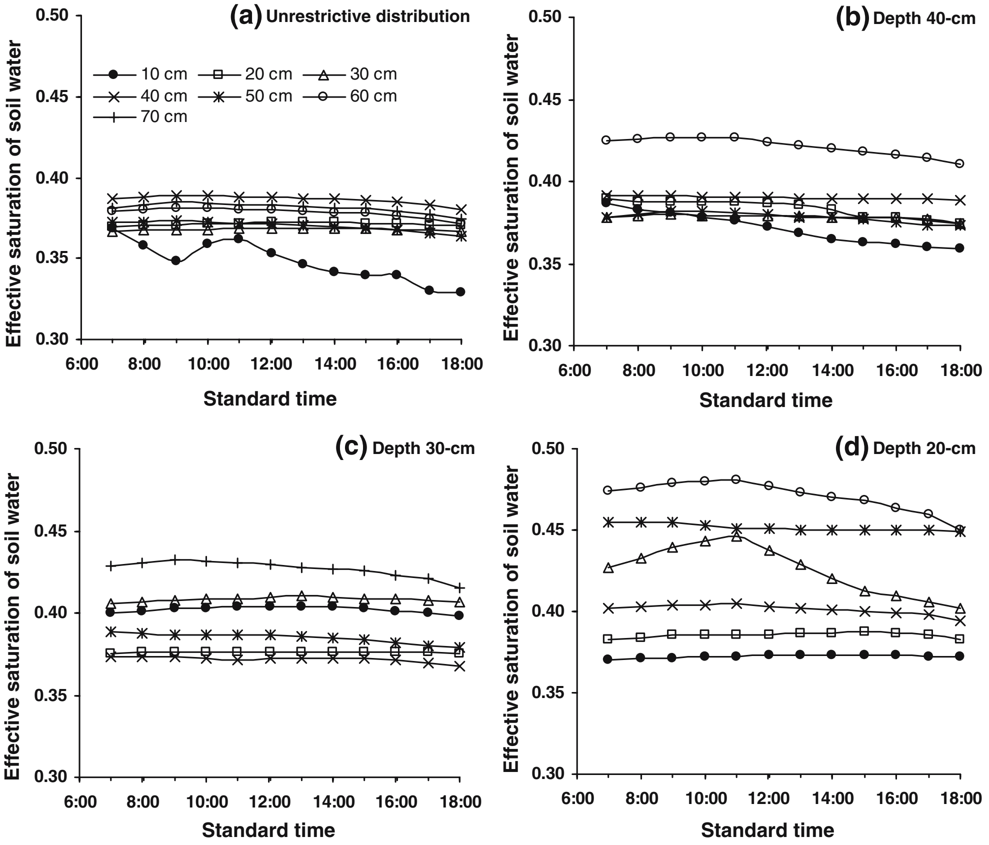

Fig. 6 Temporal change of the effective soil water saturation at different depths under a dry-soil condition (the 85th day after the plant emergence, August 2, 1999)

amount of plant-available water in the soil profiles, particularly the water condition at the depth where water extraction was most efficient. Figure 6 illustrates that the resulted S_e values in the soil profile with unrestrictive root distribution were overall lower than the S_e values in the soil profiles with restrictive root distribution. This might be resulted from the early higher rate of depletion of soil water by the bulk field plants as compared to the container plants. Figure 6 also shows that the values of S_e were greater at the most densely rooted soil depths (i.e., rooting barrier depths) under the restrictive treatments than at the superficial soil (e.g., 10-cm) under the unrestrictive treatment, where the bulk field plant had its highest root length density. This is a result of the larger decrease of S_e values in the primary water-uptake layers where root density was highest in the root-unrestrictive soil profile than in the root-restrictive soil profiles. Comparison of the daily amounts of extracted water between the wet-soil days and the dry-soil days suggests that climate controlled the water uptake when the soil was relatively wet, whereas soil water availability became a limiting factor when the soil was dry. In the dry-soil days, water content in the densely rooted soil layer became particularly critical for the water uptake by plants. It seemed that occurrence of roots with the highest length-density at relatively deep soil (e.g., at or below 30 cm) could induce a relocation of water extraction toward the depth where soil was less dry under dry-soil conditions. Consequently, exploration of the length-densest roots to deep soil became more important than extension of the maximum rooting depth (e.g., 60 cm in this study) for the plants to survive the drought stress.

Preferential uptake of water from the most densely rooted soil layer

Root length density of the field-container plants demonstrated a dramatic increase just above the restrictive nylon sheets (Table 2). The results in Fig. 3 reveal that water uptake and profile soil water were significantly affected by this densely rooted layer and the effects depended upon soil water conditions. In the wet soil, shallow colonization of the highest length-density roots (e.g., Depth 20-cm) reduced root water uptake rate. However, this effect nearly disappeared as the most densely rooted layer approached to depth 30-cm or depth 40-cm. Great changes of S_e in the most densely rooted soil layers indicate that the rooting depth of the highest length-density roots determined the primary water depletion depth (Fig. 5). In the dry soil, occurrence of the highest length-density roots at depths 30-cm and 40-cm, where soil was less dry than the shallow soil, favored maintenance of a moderate water uptake rate to meet the physiological requirements of the plants. Within the most densely rooted layer, soil resistance to water movement toward roots might not be very large because high root length densities could result in a short averaged flowpath length (Newman 1969). Therefore, occurrence of the highest length-density roots at proper soil depths (e.g., at or below 30-cm for maize plants in this study) can be expected to enhance the ability of crops to cope with water shortage because of less soil drying by climate in deeper soils. However, if the most densely rooted layer occurs too shallow (e.g., 20-cm depth), plants might become very vulnerable to the adverse effect of water deficiency.

Root distribution versus drought resistance and irrigation strategies of crops

Although the pattern of root growth is guided by a genetic code, ultimate configuration of the root system virtually reflects ecologically optimized responses of the root genetic code to environmental factors, such as water availability (Smucker and Aiken 1992), nutrient distribution (Drew et al. 1973), soil physical properties (Zhuang et al. 2001b), and chemical conditions (e.g., salinity) (Feddes et al. 2001). This study indicates that root water uptake is a consequence of the combined effect of root distribution and spatial availability of soil water under a definite climate condition. Change of root profile in soil (e.g., deep occurrence of the roots having high length-density) can be an effective measure for maintaining root water uptake and extending the period of tolerance of plants to water shortage (Hurd 1968, 1974; Hoad et al. 2001). Effective agricultural practices for this purpose include deep incorporation of fertilizers, deep drip-irrigation, and breakup of the shallow compacted plow pans. Because the distribution of root length density determines the pattern of root water uptake and further affects the soil water dynamics in soil profile, irrigation strategies that rely on monitoring soil water regime must consider the heterogeneous root distribution. Under the circumstance that the highest length-density roots occur in relatively deep soil, water storage prior to the season would become important for crop production in the entire season, and irrigation management is thus less critical. However, if dominant amount of roots grow only in very shallow soil, crops are more susceptible to the adverse effects arising from dry conditions of soil and climate. Sound irrigation based on the patterns of root water uptake and the soil water dynamics are thus essential for the crop growth. This is particularly important for the management of crops grown in the soil with subhorizon compacted, because the rooting-unfavorable horizons, such as fragipan that extensively exists in the subsurface of cultivated soils, can cause high root density in the shallow soil layers and water in deep soil may become unavailable for plant use (Fig. 6d). When irrigation is applied, presence of the most densely rooted layer provides a potential for increasing irrigation efficiency by only dripping that layer.

In summary, this study shows that root water uptake of maize plants interacted strongly with profile soil water conditions, with the interactive patterns and mechanisms depending upon specific root distribution of plants. Rooting depth of the roots having highest length-density was more vital than the maximum rooting depth for maintaining water uptake rate under dry- than wet-soil conditions. In the wet soil, soil water was absorbed from nearly the entire field profile but with majority from the most densely rooted layer, and occurrence of a fraction of roots in deep soil increased root water uptake. In the dry soil, the water uptake only significantly took place in the most densely rooted layer; and occurrence of the highest length-density roots at soil depth 30-cm or 40-cm where soil was less dry helped maintain a certain rate of water uptake by plants as soil progressively dehydrated; this is physiologically very important at the critical stages of plant growth.

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