Absorption and Transport of Water and Ions in Corn and Sunflower Plants Grown Under Saline Conditions

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Abstract

In order to analyze absorption and transport of water and ions in plants affecting the salinization in the root zone through physical and physiological processes, we measured water and ion uptake by roots, transpiration rate, leaf conductance, and ion concentrations in root xylem sap and other plant tissues of corn and sunflower grown under saline conditions using a nutrient film technique system. The rate of root water uptake was lower in corn than in sunflower, where the daytime stomatal closure in response to the excessive water stress induced by the saline solution was occurred in corn but not in sunflower. NO$_3^-$, PO$_4^{3-}$ and K$^+$ were highly concentrated in the xylem sap as a result of the active and selective uptake of nutrients by roots of both corn and sunflower. Na$^+$, which is not an essential element for plant growth, was not highly concentrated in the xylem sap or plant tissues of corn because corn exhibited a poor Na$^+$ absorption and transportation ability. On the other hand, sunflower had a greater ability to absorb water, Na$^+$, Mg$^{2+}$, Ca$^{2+}$, Cl$^-$, and SO$_4^{2-}$, and to transport these ions from the roots to the shoot. These differences in absorption and transport of water and ions indicate that sunflower is more salt tolerant than corn. The effects of these absorption and transport characteristics on plant growth and soil salinity should be taken into account for sustainable and effective plant production in salinized crop fields.

Key words: Corn, Ion absorption, Saline, Sunflower, Water absorption.

1. Introduction

Salinization in irrigated fields is a serious problem in semi-arid and arid regions, and is caused by accumulation of ions (particularly, Na$^+$, Mg$^{2+}$, Ca$^{2+}$, Cl$^-$ and SO$_4^{2-}$) in the root zone to a level that depresses plant production (Rengasamy, 2006). The ion accumulation is affected by the physical and physiological processes that transport water and ions within the plant-environment system (Kitano et al., 2006). Leaf transpiration and the associated uptake of water by roots is the most significant driving force for water transport in the root zone (Yasutake et al., 2007), where ion transport largely depends on active and selective ion uptake by roots.

High concentrations of salts such as Na$^+$ and Cl$^-$ in the root zone induce adaptive functions in plants such as osmoregulation, where leaf water potential and osmotic potential decrease dramatically (i.e. Araki et al., 2001; Wajima et al., 2006). Koyro (2006) studied the effects of salinity on growth, photosynthesis, water relations, and ion content in halophytes, and showed that such stress conditions result in decreased absorption of some essential ions by roots. Therefore, information about uptake of water and ions (not only NO$_3^-$, PO$_4^{3-}$ and K$^+$, but also Na$^+$, Mg$^{2+}$, Ca$^{2+}$, Cl$^-$ and SO$_4^{2-}$) by roots under saline conditions is very important for sustainable and effective plant production in irrigated fields. Until recently, however, very little attention has been paid to the physiological functions of roots in irrigated agriculture. This is because roots are underground, and are therefore more difficult to analyze quantitatively (Kramer and Boyer, 1995). In this study, we analyzed
absorption and transport of water and ions in corn and sunflower plants, which are two major crops cultivated in the irrigated fields in semi–arid and arid regions, under saline conditions using a nutrient film technique (NFT) system developed for evaluating the rate of water and nutrients uptake by roots in a greenhouse.

2. Materials and Methods

2.1 Plant materials

Corn (Zea mays L.) and sunflower (Helianthus annuus L.) seeds were sown in plastic pots filled with vermiculite, and were raised in a growth chamber. Three weeks after sowing, 80 plants each of corn and sunflower were transplanted into two beds within the NFT system in a greenhouse, and were grown for one week in a standard nutrient solution (NO₃⁻, 215.9 mg L⁻¹; PO₄³⁻, 36.7 mg L⁻¹; K⁺, 87.0 mg L⁻¹; Na⁺, 4.3 mg L⁻¹; Mg²⁺, 95.1 mg L⁻¹; Ca²⁺, 80.8 mg L⁻¹; Cl⁻, 217.0 mg L⁻¹; and SO₄²⁻, 25.9 mg L⁻¹; electrical conductivity (EC), 1.0 dS m⁻¹) controlled at a temperature of 25 °C.

2.2 System for evaluating root uptake

The NFT system was developed for dynamic and simultaneous evaluation of water and ion uptake rate by roots in a greenhouse (Yasutake et al., 2004). A diagram of the system is shown in Fig. 1. The system consists of a circulation unit (NFT bed, reservoir tank, circulation path, etc.) and a supply unit (water supply tank, solenoid valve, flow meter, supply path, etc.) to control the delivery of the nutrient solution. A water level sensor in the reservoir tank detects any decreases in the volume of the nutrient solution because of water uptake by plants. The circulation unit is automatically replenished with fresh nutrient solution from the supply unit. This is achieved by the on-off action of the solenoid valve, which responds to a feedback signal from the water level sensor. Therefore, the rate of water uptake by roots in the bed for a given period (Q_w; L/bed/d) is calculated from the volume and the frequency of the on-off action, or from the flow meter on the supply path. We can evaluate the rate of uptake of any ion, M, (Q_M; g/bed/d) by the roots in the bed based on the quantity of ion M supplied in the replenished fresh nutrient solution and the change in concentration of ion M in the circulation unit. From Q_w, Q_M, and the number (n) of plants grown in the bed, we can calculate the uptake rates of water (Q_w=n/ ; L/plant/d) and ion M (Q_M=n/ ; g/plant/d) by the roots of a single plant. Furthermore, the simultaneous evaluation of Q_w and Q_M enables determination of the ion M concentration in the root xylem sap ([M]_xy=Q_M/Q_w ; g L⁻¹).

2.3 Experimental conditions

On 30 July 2007, saline nutrient solution (EC, 5.3 dS m⁻¹) containing NO₃⁻, 182.4 mg L⁻¹; PO₄³⁻, 17.8 mg L⁻¹; K⁺, 49.5 mg L⁻¹; Na⁺, 787.7 mg L⁻¹; Mg²⁺, 288.4 mg L⁻¹; Ca²⁺, 227.4 mg L⁻¹; Cl⁻, 1603.6 mg L⁻¹; and SO₄²⁻, 1656.0 mg L⁻¹ was applied to the beds and the supply tank in the NFT system. The concentrations of these ions in the solution were almost equal to those

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Fig. 1. Schematic diagram of the nutrient film technique (NFT) system developed for dynamic and simultaneous evaluation of water and ion uptake by the roots of a plant population. The system consists of a circulation unit (NFT bed, reservoir tank, water pump, circulation path, etc.) and a supply unit (supply tank, solenoid valve, integrated flow meter, water pump, supply path, etc.). See Yasutake et al. (2004) for detailed information.
of the extract solution of soil saturated with water in a salinized crop field in the Yellow River basin (Yasutake et al., 2008). The solution temperature in the NFT bed was controlled at around 25°C using a heater, a cooler, and a temperature controller. The nutrient solution in the bed was renewed once every 10 days (i.e. on 9 and 19 August). The sunlight in the greenhouse was reduced by approximately 25% with a shade cloth, except on 20 August. Meteorological elements of solar radiation, air temperature, and vapor pressure deficit in the greenhouse were measured and recorded at 1-minute intervals.

2.4 Analysis of water transport

The integrated flow meter on the supply path in the NFT system was checked at 1900 h (Japan Standard Time) every evening, and the daily change in the rate of water uptake by the roots of corn and sunflower plants was evaluated from 31 July to 30 August.

The liquid phase water absorbed by the roots moves to leaves through the plant body, and most of the water diffuses from the stomata of leaves into the ambient air via transpiration (Kramer and Boyer, 1995). Therefore, the leaf transpiration rate (Tr, mol m⁻² s⁻¹) can be evaluated based on Qw and the total leaf area of a single plant. Tr can also be expressed by the following formula (Jones, 1992):

\[ Tr = G_l (e_{leaf} - e_a) / P \]  

(1)

where \( G_l (\text{mol} \text{m}^-2 \text{s}^-1) \) is the leaf conductance, which is the reciprocal of the sum of stomatal resistance and leaf boundary layer resistance, \( e_{leaf} (\text{kPa}) \) is the saturated vapor pressure at leaf temperature, \( e_a (\text{kPa}) \) is the actual vapor pressure in the ambient air and \( P (\text{kPa}) \) is the atmospheric pressure. On 20 August the shade cloth in the greenhouse was removed, and the diurnal change in the Tr of corn and sunflower plants was evaluated based on Qw (L/plant/h) on an hourly basis. Further, \( G_l \) was evaluated from Eq. (1), where \( e_{leaf} \) was obtained by measuring the leaf temperature (\( T_l \)), and \( e_a \) was obtained from the measurements of air temperature and humidity using a thermo recorder (RS-12, ESPEC MIC Co., Ltd.). \( T_l \) was measured by inserting the thermocouple (0.1 mm in diameter) into the mesophyll of healthy and mature leaves of three individual plants. A constant value of 101.3 kPa was used as the value for \( P \) in Eq. (1).

2.5 Analysis of ion transport

We evaluated the daily change in the rate of ion uptake by roots of corn and sunflower plants from 31 July to 30 August. At 1900 h every evening, 50 ml nutrient solution was sampled from the circulation unit, and concentrations of \( \text{NO}_3^- \), \( \text{PO}_4^{3-} \), \( \text{K}^+ \), \( \text{Na}^+ \), \( \text{Mg}^{2+} \), \( \text{Ca}^{2+} \), \( \text{Cl}^- \), and \( \text{SO}_4^{2-} \) in the samples were analyzed with an ion chromatograph system (ICS-90, DIONEX, Osaka).

During the night, roots can generate positive hydrostatic pressure (root pressure) by actively absorbing ions from the dilute soil solution and transporting them into the xylem (Taiz and Zeiger, 2002). If the stem of a plant is cut just above the soil, the stump often exudes sap from the cut xylem for many hours. Therefore, the ion composition of these stem stump exudates reflects active and selective ion absorption by roots without significant dilution effects because of the transpiration stream. In this experiment, a plastic tube was connected to the stump and covered with a film to prevent evaporation of exudates. The xylem sap exuded from the stem stumps of three corn plants and three sunflower plants was collected from the tube during the night on 9, 19, and 30 August. We obtained approximately 3-5 ml of exudates, and analyzed their ion concentrations.

Concentrations of ions within the plant body reflect the active and selective ion uptake by the roots (Kramer and Boyer, 1995). On 30 August, leaves, stems, and roots of the three corn and three sunflower plants were sampled. Their dry weights and concentrations of \( \text{K}^+ \), \( \text{N}^+ \), \( \text{Mg}^{2+} \), \( \text{Ca}^{2+} \), \( \text{Cl}^- \) and \( \text{SO}_4^{2-} \) were measured using standard procedures (Kitano et al., 2006). After combustion, the ash from each sample was dissolved in dilute nitric (HNO₃) acid to completely decompose organic matter, and the ion concentrations were then measured in the dissolved ash solution with the ion chromatograph. Concentrations of \( \text{NO}_3^- \) and \( \text{PO}_4^{3-} \) can not be measured by this procedure.

3. Results and Discussion

3.1 Meteorological conditions and plant growth

Meteorological conditions within the greenhouse during the measurement period (31 July to 30 August) are shown in Fig. 2. Daily cumulative solar radiation (\( R_s \)) varied because of weather conditions, and ranged between 2.2 and 13.6 MJ m⁻² d⁻¹. The maximum value of \( R_s \) was recorded on 20 August when the shade cloth was removed. Daytime mean air temperature (\( T_a \)) ranged from 28 to 37°C. Daytime mean vapor pressure deficit (VPD) showed a similar pattern of variation to \( T_s \), and ranged between 0.7 and 3.0 kPa.
Plant height increased linearly in both corn and sunflower. Corn was approximately 0.2 m taller than corn (Fig. 3). Corn leaf area increased with increasing plant height until 14 August and reached a maximum of 0.3 m²/plant, then leveled off or decreased slowly as the older leaves withered. Sunflower leaf area increased linearly with plant height, but was lower than the corn leaf area during the first 20 days.

### 3.2 Water and ions transport

We evaluated daily water uptake by roots of a single plant ($Q_w$) using the NFT system (Fig. 4). Sunflower data from 14–16 August were not available because of a problem in the NFT system. $Q_w$ changed depending on the $R_s$ and leaf area, increasing gradually until approximately 20 August and then leveling off. Root water uptake per leaf area was much higher in sunflower than in corn. The value of $Q_w$ in corn was 50–80% of the sunflower $Q_w$ value, although the leaf area of corn was larger than that of sunflower until approximately 20 August. To examine this difference in $Q_w$ between corn and sunflower, diurnal changes in leaf gas exchange variables were calculated from $Q_w$ on an hourly basis on 20 August when plants were not covered with the shade cloth (Fig. 5). There was clear weather on 20 August; $R_s$ began to increase at 0600 h and reached approximately 2 MJ m⁻² h⁻¹ at approximately midday. Variations in sunflower’s $T_r$, $T_a$, and $G_L$ were approximately synchronized with the change in $R_s$. In corn, however, $T_r$ reached a maximum value at 1000 h and thereafter was almost constant until 1600 h. The $G_L$ value of corn was extremely low but constant during the daytime. This suggested that in corn, closure of stomata during daytime resulted from the excessive water stress induced by the saline solution and the evaporative demand to plants (Yasutake et al., 2006). This did not occur in sunflower. Therefore, it appears that the daily $Q_w$ was higher in sunflower than in corn (Fig. 4). FAO (2002) has also reported that sunflower is more salt-tolerant than corn.

We evaluated the daily ion uptake by roots of a single plant based on the $Q_w$ in Fig. 4 and the ion analysis of the nutrient solution sampled from the NFT
bed every evening. The daily uptake rates of NO$_3^-$, PO$_4^{3-}$, K$^+$, Na$^+$, Mg$^{2+}$, Ca$^{2+}$, Cl$^-$, and SO$_4^{2-}$ by roots of a single plant (Fig. 6) were denoted as $Q_{\text{NO}_3}$, $Q_{\text{PO}_4}$, $Q_K$, $Q_{\text{Na}}$, $Q_{\text{Mg}}$, $Q_{\text{Ca}}$, $Q_{\text{Cl}}$ and $Q_{\text{SO}_4}$, respectively. The sunflower data from 14–16 August was not available because of a problem in the NFT system. $Q_{\text{Ca}}$ data (mean values of 37 and 91 mg/plant/d for corn and sunflower, respectively) and $Q_{\text{SO}_4}$ data (mean values of 159 and 412 mg/plant/d for corn and sunflower, respectively) were omitted for brevity, because similar patterns of variation in $Q_{\text{Ca}}$ and $Q_{\text{SO}_4}$ were found in $Q_{\text{Mg}}$ and $Q_{\text{Cl}}$. In general, the uptake of these ions by roots largely depended on $Q_W$ (Affan et al., 2005), and therefore ion uptake was greater in sunflower than in corn. We estimated the concentrations of NO$_3^-$, PO$_4^{3-}$, K$^+$, Na$^+$, Mg$^{2+}$, Ca$^{2+}$, Cl$^-$ and SO$_4^{2-}$ in the root xylem sap from the simultaneous evaluation of $Q_W$ and $Q_M$ in Figs. 4 and 6. These are denoted as $[\text{NO}_3^-]_x$, $[\text{PO}_4^{3-}]_x$, $[\text{K}^+]_x$, $[\text{Na}^+]_x$, $[\text{Mg}^{2+}]_x$, $[\text{Ca}^{2+}]_x$, $[\text{Cl}^-]_x$ and $[\text{SO}_4^{2-}]_x$, respectively. The data of $[\text{Ca}^{2+}]_x$ (mean values of 119 and 178 mg L$^{-1}$ for corn and sunflower, respectively) and $[\text{SO}_4^{2-}]_x$ (mean values of 545 and 809 mg L$^{-1}$ for corn and sunflower, respectively) were omitted for brevity, because similar variation patterns of $[\text{Ca}^{2+}]_x$ and $[\text{SO}_4^{2-}]_x$ were found in $[\text{Mg}^{2+}]_x$ and $[\text{Cl}^-]_x$. The ion concentrations of the major essential elements for plant growth, NO$_3^-$, PO$_4^{3-}$ and K$^+$, were similar between corn and sunflower and were relatively constant. Koyro

Fig. 5. Diurnal changes in leaf transpiration rate ($T_r$), leaf temperature ($T_L$) and leaf conductance ($G_L$) of corn and sunflower plants on 20 August 2007. Hourly cumulative solar radiation ($R_S$) is also shown. Values of $T_L$ are means ± standard error.

Fig. 6. Time course of daily rates of NO$_3^-$, PO$_4^{3-}$, K$^+$, Na$^+$, Mg$^{2+}$, Cl$^-$ uptake ($Q_{\text{NO}_3}$: a, $Q_{\text{PO}_4}$: b, $Q_K$: c, $Q_{\text{Na}}$: d, $Q_{\text{Mg}}$: e, $Q_{\text{Cl}}$: f) by roots of corn and sunflower from 30 July to 30 August 2007. There are no sunflower data from 14–16 August because of a problem in the NFT system.
reported that the excessive salt stress causes decreased absorption of some essential ions by roots. However, a salt-induced decrease in the absorption of major ions was not observed in this experiment, although concentrations of these essential ions in the NFT bed decreased immediately after the start of the experiment and after renewal of the nutrient solution (data not shown). Furthermore, their concentrations in the xylem sap were remarkably higher than their concentrations in the nutrient solution. These results indicate that active transport processes play important roles in \(\text{NO}_3^-, \text{PO}_4^{3-}, \text{K}^+, \text{Na}^+, \text{Mg}^{2+}, \text{Ca}^{2+}, \text{Cl}^-, \text{SO}_4^{2-}\) uptake by roots (Taiz and Zeiger, 2002). On the other hand, we observed that \([\text{Na}^+]_x, [\text{Mg}^{2+}]_x, [\text{Ca}^{2+}]_x, [\text{Cl}^-]_x, \text{and } [\text{SO}_4^{2-}]_x\) fluctuated below the corresponding ion concentrations in the bed (data not shown). The reason for this fluctuation is unknown, but it may be due to the greenhouse environment or other factors. In the latter half of the experimental period, concentrations of all ions except the major essential elements were higher.

![Graph](image_url)
in sunflower than in corn.

To elucidate the difference in the root uptake characteristics between corn and sunflower, we analyzed ion concentration in the xylem sap exuded from the stem stump during the night (Table 1). Although Na\(^+\) is not an essential element for plant growth, a high Na\(^+\) concentration was found in sunflower but not in corn, while there was a reverse relationship was observed in K\(^+\) concentration. Quintero et al. (2007) and Slama et al. (2008) studied this antagonistic relationship between Na\(^+\) and K\(^+\) uptake by roots. Concentrations of other ions (Mg\(^{2+}\), Ca\(^{2+}\), Cl\(^-\), and SO\(_4^{2-}\)) were also higher in sunflower. We measured concentrations of K\(^+\), Na\(^+\), Mg\(^{2+}\), Ca\(^{2+}\), Cl\(^-\), and SO\(_4^{2-}\) in the leaves, stems, and roots of sunflower and corn (Table 2). Concentrations of these ions are considered to reflect the active and selective ion uptake by roots, and ion transport within the plant tissues. Except for Cl\(^-\) and SO\(_4^{2-}\), there was no significant difference in ion concentrations in the roots of corn compared with sunflower. In the leaf and stem, the concentrations of all ions were higher in sunflower than in corn. These facts suggest that sunflower is more able to absorb ions and transport them from the roots to the shoot within the transpiration stream. On the other hand, corn exhibited a poor Na\(^+\) absorption and transportation ability in this study. Yasutake et al. (2008) suggested that this poor ability appears to be one of the factors causing salinization in irrigated fields in semi-arid and arid regions. Therefore, crop rotation or mixed cultivation using plants with a high ability to absorb and transport Na\(^+\), e.g. sunflowers or halophytes, should be carried out in irrigated fields. Reclamation of saline wastelands using halophytes has been reported by Lieth et al. (1999) and Irshad et al. (2005).

Thus, we analyzed transport of water and ions (NO\(_3^-,\) PO\(_4^{3-}\) and K\(^+\), and also Na\(^+\), Mg\(^{2+}\), Ca\(^{2+}\), Cl\(^-\), and SO\(_4^{2-}\)) in corn and sunflower plants grown under saline conditions. Our results suggest that the physiological functions of the roots that affect water and ion transport should be taken into consideration for sustainable and effective plant production in salinized fields in irrigated agriculture.

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References


塩性条件下のトウモロコシおよびヒマワリにおける水とイオンの吸収と輸送

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要 約

物理的・生理的過程を通じて根圏の塩類化に影響を及ぼす植物の水とイオンの輸送を解析するために、NFT水耕栽培システムを用いて、塩性条件下におけるトウモロコシとヒマワリの根による水とイオンの吸収、蒸散速度、リーフコンダクタンス、根の導管液のイオン濃度、植物体内のイオン含量を計測した。根の吸水速度は、ヒマワリよりトウモロコシにおいて小であり、これは塩ストレスに対する気孔閉鎖がトウモロコシにおいて発生したことによる。植物にとって必須元素であるNO₃⁻、PO₄³⁻、K⁺は、根の能動的および選択的吸収によって導管内に高濃度に集積した。植物の生育に必要でないNa⁺は、トウモロコシにおいてはその導管内で器官内に高い集積は見られず、トウモロコシによるNa⁺の吸収機能が低いことが分かった。一方、ヒマワリにおいては、水分吸収に伴なって、Na⁺に加えてMg²⁺、Ca²⁺、Cl⁻、SO₄²⁻の高い吸収・輸送機能が観察された。以上のように、植物の種間差による水とイオンの輸送機能の差異が認められた。乾燥・半乾燥地域の重要課題である塩類化農地の持続的かつ効果的な管理を行ううえでは、このような植物による輸送機能を考慮に入れることが必要と考える。

キーワード： トウモロコシ、ヒマワリ、塩性、水の吸収、イオンの吸収