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## Estimation of root water uptake of maize: an ecophysiological perspective

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### Abstract

An understanding of movement and distribution of soil water has been long known essential to the optimization of plant biomass productivity. This study provides an ecophysiological based analytic model for estimating root water uptake rate of maize (*Zea mays* L.). The model can be run with readily available inputs, such as water potentials of leaf, soil and air, solar radiation, potential evapotranspiration, root length, and some soil physical properties, such as bulk density and particle-size distribution. Comparison with measured data showed that the model described root water extraction with acceptable accuracy. Analysis of the response of the model to changes in the input parameters revealed that the model is most sensitive to leaf water potential and root length. Examination of the model response also showed that the model could be improved with more information about the root hydraulic conductance and effective root length responsible for water extraction. © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** Root water uptake; Ecophysiology; Root hydraulic conductance; Modeling

### 1. Introduction

Water uptake by plant roots is a major component of the water balance in field soils. A clear understanding of soil-water uptake by plant roots in situ is fundamental to many applications in agriculture and natural resources. In principle, two approaches can be taken to model the water flow from soil through root to evaporation sites in the leaves. The first is the so-called 'microscopic approach' of water absorption led by the pioneering work of Gardner (1960) through

emphasizing the soil properties in water uptake. Another is the macroscopic approach, in which the flow to individual roots is ignored and the overall root system is assumed to extract moisture from each point of the root zone. This type of model incorporates a root-sink term in the Darcy–Richards equation for water flow in soils. By disregarding the flow towards individual roots, this approach avoids the geometric complication involved in analyzing the distribution of the flux and the potential gradient on a microscale (Molz and Remson, 1970; Hillel et al., 1976; Feddes, 1988). However, as stated by Molz (1981), all of the various sink functions proposed in the literature are more or less empirical and often include implicit assumptions on the location of major resistances to flow.

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### Nomenclature

#### Root water uptake, conductance and resistance

$f_1(\Delta\Psi)$	driving force function of root water uptake
$f_2(L_r)$	root length function of root water uptake
$f_3(K_w)$	hydraulic conductance function of root water uptake
$k$	coefficient of root hydraulic conductance
$L_{r,i}$	root length density in the $i$ th soil layer (cm/cm <sup>3</sup> )
$L_{rv}$	root length in each layer of soil (cm)
$R_{leaf}$	hydraulic resistances in leaf (bar s/cm)
$R_{root}$	hydraulic resistances in root (bar s/cm)
$R_{soil}$	hydraulic resistances in soil (bar s/cm)
$R_{stem}$	hydraulic resistances in stem (bar s/cm)
$\alpha$	regulation factor of the driving force for water uptake by root
$\varepsilon(t)$	time-dependent coefficient related to potential evapotranspiration, EP( $t$ )
$\eta(t)$	root–soil contact degree
$\Phi(t)$	water uptake rate of root (cm <sup>3</sup> /s/plant or g/s/plant)
$\Phi_{est}$	estimated values of water uptake rate of root (cm <sup>3</sup> /s/plant)
$\Phi_{mea}$	measured values of water uptake rate of root (cm <sup>3</sup> /s/plant)
$\bar{\Phi}_{mea}$	mean of the measured water uptake rate of root (cm <sup>3</sup> /s/plant)

#### Environmental variables and physiological parameters

$A_R$	cumulative amount of solar radiation at any time, $t$ , from 7:00 h ( $t_0$ ) to 19:00 h (W/m <sup>2</sup> )
$d_g$	geometric mean particle diameter (mm)
$D_e$	saturation deficit of air at 2 m height above ground surface (hPa)
$e_a$	atmospheric water vapor pressure at 2 m height above ground surface (hPa)
$e_{sd}$	saturation vapor pressures at dry bulb temperature (hPa)
$e_{sw}$	saturation vapor pressures at wet bulb temperature (hPa)
$E_a$	drying power of air (mm/day)
EP	potential evapotranspiration (mm/day)

$M_R$	total cumulative radiation from 7:00 to 20:00 h (W/m <sup>2</sup> )
$R_n$	solar net radiation at 2.2 m height above ground surface (W/m <sup>2</sup> )
$T$	air temperature at 2 m height above ground surface (°C)
$T_d$	dry bulb temperature at 2 m height above ground surface (°C)
$T_w$	wet bulb temperature at 2 m height above ground surface (°C)
$u$	wind velocity at 2.5 m height above ground surface (m/s)
$\gamma$	psychrometric constant (0.66 hPa/°C)
$\delta_g$	geometric standard deviation of the particle diameter
$\Delta$	slope of relation curve of saturated water vapor pressure to air temperature (hPa/°C)
$\theta$	volumetric content of soil water at water potential, $\Psi_{soil}$ (m <sup>3</sup> /m <sup>3</sup> )
$\theta_0$	volumetric content of soil water at the potential of $-100$ cm H <sub>2</sub> O (m <sup>3</sup> /m <sup>3</sup> )
$\lambda$	relative growth rate of the cumulative curve of solar radiation during daytime
$\rho_b$	soil bulk density (Mg/m <sup>3</sup> )
$\Psi_{air}$	water potential of air at 2 m height above ground surface (bar)
$\Psi_{air-max}$	maximum water potential of air during daytime (bar)
$\Psi_{leaf}$	water potential of leaf (bar)
$\Psi_{leaf-min}$	minimum water potential of leaf during daytime (bar)
$\Psi_{root}$	water potential of the root (bar)
$\Psi_{soil}$	water potential of soil (bar)
$\Psi_{soil-eff}$	effective water potential of soil (cm H <sub>2</sub> O)
$\Psi_{soil-eff}^0$	effective air-entry potential of soil (cm H <sub>2</sub> O)
$\Psi_{soil,i}^0$	air-entry potential of soil in the $i$ th layer (cm H <sub>2</sub> O)
$\Psi_{stem}$	water potential at the base of stem (bar)
$\Psi_{xylem}$	water potential at the top of stem (bar)

#### Statistical terminology

$b$	fitting coefficient
ME	mean residual error of the estimated values (cm <sup>3</sup> /s/plant)

$n$	number of data
$R^2$	coefficient of determination of linear regression
RMSE	root mean square error of the estimated values ( $\text{cm}^3/\text{s}/\text{plant}$ )
RRMSE	relative root mean square error of the estimated values (%)
$t$	Student's $t$ value

Even if, generally, water transfer in soil is well represented by the microscopic or macroscopic approaches, the main problems involved include the following. Firstly, except for root length density, a detailed description of the root system is lacking (Molz, 1981). Based on the observation that mature apple trees are able to alter their extraction strategy from near-surface roots to deeper ones as surface water availability declines, Clothier et al. (1990) pointed out that models of root water extraction in direct proportion to root length density do not always work well. Secondly, a homogeneous root resistance to water flow, unaffected by growth conditions, is often an underlying assumption for many models of root water uptake. For this, large errors will probably occur when hydraulic conductance of plants growing under one root environment is used to model water uptake rate in another (Brar et al., 1990). Moreover, some scientists (Herklerath et al., 1977; Sanderson, 1983; Varney and Canny, 1993) maintain that the interfacial resistance to water transport between the soil and the roots may evolve in space and time with variation in the physiological properties along the root. These, together with many other problems identified in the literatures, clearly reveal the serious limitations of existing mathematical models for water uptake by roots.

While acknowledging the situation is unacceptable, and coming across "...illuminating comprehensive (model) failures that will stimulate us to change the way we think about the workings of the crop and its interactions with its environment" (Passioura, 1996), as well as "A model which could correctly simulate these extraction capacities, and predict the behavior of the stored water in the soil from existing or short-term forecast meteorological data would be an effective decision-aid tool" (Cabelguenne and Debaeke, 1998), we explore, using the soil-plant-atmosphere-conti-

num (SPAC) context, an ecophysiological approach for the solution of water uptake by roots. The ultimate goal for this type of model is its integration into a soil water transfer simulator to study the interactions between soil and plant. This modeling exercise cannot be conducted in the absence of a sound consideration of the biological and environmental aspects of the processes.

The main objectives of this research, therefore, are to develop an analytic model of root water uptake from an ecophysiological perspective by coupling the effects of environmental variables to the simulation of water uptake of a root system growing in a heterogeneous soil profile under varying meteorological conditions, and thereby to clarify some problems involved in simulating water absorption process in SPAC.

## 2. Materials and methods

### 2.1. Experimental site

The experiment was carried out on the experimental farm of the Faculty of Horticulture, Chiba University, located at Matsudo city, near Tokyo, Japan (latitude  $35^{\circ}46'N$ , longitude  $139^{\circ}54'E$ , altitude 7.9 m) over a 4-week period between 19 July and 20 August 1998. The crop *Zea mays* L. was planted on 25 May 1998 in a field with a area about  $400 \text{ m}^2$ . The within-row spacing was 0.4 m with 0.7 m between the rows. The soil is a Kanto fine sandy loam derived from volcanic ash. Some basic properties of the soil are presented in Fig. 1.

### 2.2. Observation of environmental elements

A meteorological station installed nearby within the same field recorded solar radiation (at 2.5 m height by Solarimeter MR-21, EKO), net radiation (at 2.2 and 0.5 m heights by Radiometer CN-21, EKO), wind velocity (at 2.5 m height by 3-cup anemometer AF-750, MAKINO), dry and wet bulb temperatures (at 2.5, 2.0 and 0.5 m heights) and relative humidity (at 2.5, 2.0 and 0.5 m height by ventilated psychrometer) at 1 min interval on a Thermodac EF (Model 20520A) data logger. All the instruments were mounted on a mast in the middle of the field. Ceramic-tipped tensiometer probes (DIK-3100, Daiki Rika) were installed vertically at three locations (W, E1, and E2) within the

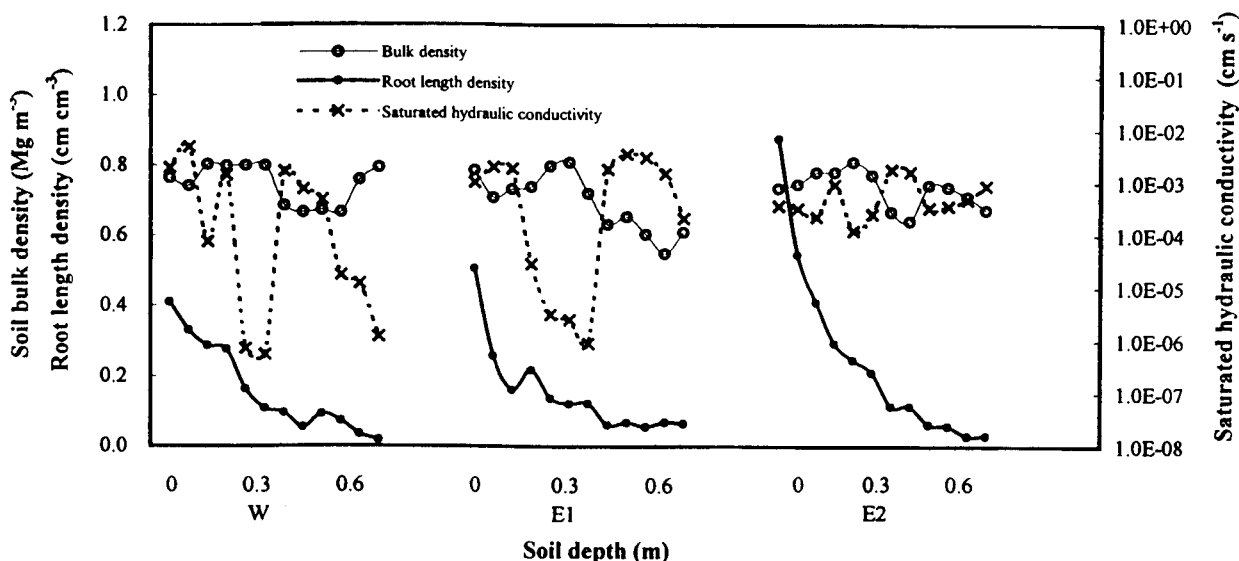


Fig. 1. Some soil properties of the field profiles at the three locations (W, E1, and E2) after the field experiments.

root zone at depths of 0.10, 0.20, 0.30, 0.40, 0.50 and 0.60 m, to record soil water potentials. On the investigation days, a pressure chamber (SOILMOISTURE, 3005) was used hourly from 7:00 to 18:00 h to measure the water potential of leaves in upper, medium and lower positions and 8–10 roots taken at depth 0.10–0.20 m of three plants located around those used for sap flow measurements.

Potential evapotranspiration was calculated by the Penman method, using the following formulae:

$$EP = \frac{\Delta R_n + \gamma E_a}{\Delta + \gamma} \quad (1)$$

$$E_a = 0.26(1 + 0.54u)(e_{ds} - e_a) \quad (2)$$

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

$$e_{ds} = 6.1078 \exp\left(\frac{17.269T_d}{237.3 + T_d}\right) \quad (4)$$

$$e_{ws} = 6.1078 \exp\left(\frac{17.269T_w}{237.3 + T_w}\right) \quad (5)$$

$$e_a = e_{ws} - \frac{1}{755} \times 0.5 \times 1013(T_d - T_w) \quad (6)$$

where EP denotes potential evapotranspiration (mm/day).  $R_n$  is net radiation ( $W/m^2$ ) at 2.2 m height above ground surface;  $E_a$  drying power of air (mm/day);  $\gamma$  a psychrometric constant (0.66 hPa/C);  $\Delta$  a slope of

relation curve of saturated water vapor pressure (hPa/C) to air temperature.  $u$  is wind velocity (m/s) at 2.5 m height above ground surface.  $e_{sd}$  and  $e_{sw}$  are saturation vapor pressures (hPa) at dry and wet bulb temperatures ( $^{\circ}C$ ), respectively, at 2.0 m height above ground surface.  $e_a$  is actual atmospheric water vapor pressure (hPa) at 2.0 m height above ground surface;  $T$  air temperature ( $^{\circ}C$ ) at 2.0 m height above ground surface;  $T_d$  and  $T_w$  are dry and wet bulb temperatures ( $^{\circ}C$ ), respectively, at 2.0 m height above ground surface. Water potential of air,  $\Psi_{air}$ , was calculated by means of the data of  $e_a$ ,  $e_{sd}$  and  $e_{sw}$ . Saturation deficit,  $D_e$ , was the difference of  $e_{sd}$  and  $e_a$ . The averaged environmental conditions during the investigation period are presented in Table 1.

### 2.3. Measurements of sap flow and root length

In the experiment, root water uptake (RWU) was represented by the xylem sap flow, and measured by the heat balance method (Campbell, 1991) with the gauges (Dyanmax, SGB25) installed on the base of the plant stem. A Thermodac EF (Model 20520A) data logger was used to record signals for subsequent calculation of sap flow rate.

Immediately after completion of the field experiments on 21 August 1998, roots in 12 soil layers (each layer  $70 \times 40 \times 5 \text{ cm}^3$ ) for each of the three locations

Table 1  
Some averaged environmental conditions during the 8-day investigation<sup>a</sup>

Data	Day	$\Psi_{\text{leaf}}$ (bar)	$\Psi_{\text{root}}$ (bar)	$\Psi_{\text{soil}}$ (bar)	$\Psi_{\text{soil-eff}}$ (bar)	$\Psi_{\text{air}}$ (bar)	$\Psi_{\text{air-max}}$ (bar)	$R_a$ (W/m <sup>2</sup> )	$D_c$ (hPa)	EP (mm/day)	$T_{\text{leaf}}$ (°C)
980719	46	5.72	1.30	0.13	0.24	20.13	33.56	373.5	7.70	14.13	28.1
980726	53	5.30	1.14	0.05	0.08	19.22	22.25	388.4	8.82	10.37	29.5
980727	54	8.43	2.52	0.06	0.09	22.56	35.36	568.6	12.41	14.41	31.1
980803	61	6.33	1.85	0.27	0.48	24.66	28.42	393.6	7.56	9.75	31.6
980804	62	4.98	1.39	0.33	0.58	17.74	22.61	265.8	4.83	7.08	29.3
980806	64	7.50	1.14	0.43	0.73	14.65	25.84	283.7	3.89	8.26	28.8
980812	70	5.40	0.97	0.39	0.62	19.79	23.52	234.2	5.56	6.30	29.9
980815	73	6.61	1.14	0.10	0.10	18.66	25.12	259.0	4.69	7.90	27.9

<sup>a</sup>  $\Psi_{\text{leaf}}$ : water potential of leaf (mean of the upper, medium and lower leaves);  $\Psi_{\text{root}}$ : water potential of root;  $\Psi_{\text{soil}}$ : water potential of soil;  $\Psi_{\text{soil-eff}}$ : effective water potential of soil;  $\Psi_{\text{air}}$ : water potential of air;  $\Psi_{\text{air-max}}$ : the maximum water potential of air during daytime;  $R_a$ : solar radiation amount;  $D_c$ : saturation deficit; EP: potential evapotranspiration;  $T_{\text{leaf}}$ : temperature of leaf.

were collected down the soil profile to 0.60 m depth using a knife. A line-intercept sampling method (Tenant, 1975) was used to obtain total root length in each soil layer.

#### 2.4. Index for model evaluation

Four statistical properties, coefficient of determination,  $R^2$ , root mean square error, RMSE, relative root mean square error, RRMSE, and Student's  $t$ , were calculated to evaluate the differences between the measured and estimated RWU rates. RMSE and RRMSE were obtained, respectively, by

$$\text{RMSE} = \left[ \frac{1}{n-1} \sum (\Phi_{\text{est}} - \Phi_{\text{mea}})^2 \right]^{1/2} \quad (7)$$

$$\text{RRMSE} = 100 \frac{\text{RMSE}}{\bar{\Phi}_{\text{mea}}} \quad (8)$$

where  $n$  is the number of data,  $\Phi_{\text{est}}$  the estimated values,  $\Phi_{\text{mea}}$  and  $\bar{\Phi}_{\text{mea}}$  the measured values and their means, respectively. Assuming normal distribution and independence of differences between the measured and estimated RWU rates,  $t$  was calculated as

$$t = \text{ME} \left( \frac{\text{RMSE}^2 - \text{ME}^2}{n-1} \right)^{-0.5} \quad (9)$$

where ME represents mean residual error and is defined as

$$\text{ME} = \frac{1}{n} \sum_{i=1}^n (\Phi_{\text{est}} - \Phi_{\text{mea}}) \quad (10)$$

When calculated  $|t| > t_{0.05}$ , the value of the Student's  $t$  distribution for  $P = 0.05$  and  $n - 1$  degrees of freedom, the differences between the measured and estimated RWU rates are statistically significant. If  $t < 0$ , it is indicated that the RWU rates are underestimated, and vice versa. Thus,  $t$  is a measure for the bias in the simulation results. Values of  $t$  close to 0 indicate that the measured and estimated RWU rates do not differ systematically from each other or, equivalently, that there is no consistent bias. Values of  $t$  that differ greatly from zero indicate the presence of systematic deviation or bias. RMSE is a measure for the scatter of the data points around the 1:1 line. Low RMSE indicates little scatter, while high RMSE indicates large scatter. Low RMSE also implies low ME and  $t$  values. Low  $t$  and high RMSE are combined when negative and positive deviations are distributed evenly on both sides of the measured line.

### 3. Mathematical formulation

#### 3.1. General formula of root water uptake

The model of water uptake by plant roots comprises three components: driving force function,  $f_1(\Delta\Psi)$ , root length function,  $f_2(L_r)$ , and hydraulic conductance function,  $f_3(K_w)$ , of the pathway. Root water extraction rate,  $\Phi(t)$ , can then be formulated as

$$\Phi(t) = f_1(\Delta\Psi)f_2(L_r)f_3(K_w) \quad (11)$$

### 3.2. Driving force function

An uncontroversial view is that difference of water potentials in the transport system causes the flow of water from soil to leaves. The actual calculation of the potential difference, however, differs among researchers. Some prefer to calculate the driving force as the difference of water potential between bulk soil and root surface. For researchers who emphasize the importance of SPAC in water transport, however, the difference of water potential between leaf and roots or soil is usually assumed as the main driving force of water flow in plant (van den Honert, 1948). Unfortunately, to date, no method for measuring water potential of intact roots, especially in heterogeneous field profiles, has been developed. In addition, when taking the difference of water potential between soil and root as driving force, many workers regard the axial resistance in root and stem as insignificant compared to the soil and soil–root resistances, and propose a synchronic change between root potential and stomatal conductance. Therefore, it may be concluded that employment of root potential in the simulation of water uptake by roots is neither feasible nor practical.

As well-known, alternative, using the simple catenary series model of van den Honert (1948), describes the relationships between steady-state flow and water potential within the soil–plant system as

$$\begin{aligned} \Phi(t) &= \frac{\Psi_{\text{soil}} - \Psi_{\text{leaf}}}{R_{\text{soil}} + R_{\text{root}} + R_{\text{stem}} + R_{\text{leaf}}} \\ &= \frac{\Psi_{\text{soil}} - \Psi_{\text{root}}}{R_{\text{soil}}} = \frac{\Psi_{\text{root}} - \Psi_{\text{stem}}}{R_{\text{root}}} \\ &= \frac{\Psi_{\text{stem}} - \Psi_{\text{xylem}}}{R_{\text{stem}}} = \frac{\Psi_{\text{xylem}} - \Psi_{\text{leaf}}}{R_{\text{leaf}}} \end{aligned} \quad (12)$$

where  $\Psi_{\text{soil}}$ ,  $\Psi_{\text{root}}$ ,  $\Psi_{\text{stem}}$ ,  $\Psi_{\text{xylem}}$  and  $\Psi_{\text{leaf}}$  refer, respectively, to the water potentials in the bulk soil, at the surface of the roots, at the base of the stem, at the top of the stem and at surfaces of leaves.  $R_{\text{soil}}$ ,  $R_{\text{root}}$ ,  $R_{\text{stem}}$ , and  $R_{\text{leaf}}$  refer, respectively, to the hydraulic resistances in soil, root, stem, and leaf. To avoid complex physiological characteristics of root systems and to consider their responses to environmental variations as well as interaction between individual plant parts, in this study water potential difference between leaf and soil ( $\Psi_{\text{leaf}} - \Psi_{\text{soil}}$ ) was theoretically

adopted as the driving force. It is assumed to involve a regulation factor  $\alpha$  in establishing the driving function,  $f_1(\Delta\Psi)$ , for root water transport as

$$f_1(\Delta\Psi) = \alpha(\Psi_{\text{leaf}} - \Psi_{\text{soil}}) \quad (13)$$

where  $\alpha$  is defined as

$$\alpha = \begin{cases} 1 - \frac{\Psi_{\text{soil-eff}}^0}{\Psi_{\text{soil-eff}}}, & \Psi_{\text{soil-eff}} < \Psi_{\text{soil-eff}}^0 \\ \frac{\Psi_{\text{leaf}}}{\Psi_{\text{leaf}} - \Psi_{\text{soil}}}, & \Psi_{\text{soil-eff}} \geq \Psi_{\text{soil-eff}}^0 \end{cases} \quad (14)$$

In the expression,  $\Psi_{\text{soil-eff}}$  is effective water potential of soil in cm H<sub>2</sub>O, and  $\Psi_{\text{soil-eff}}^0$  refers to effective air-entry potential of soil in cm H<sub>2</sub>O.  $\Psi_{\text{soil-eff}}$  is calculated with the formula of Campbell (1985)

$$\Psi_{\text{soil-eff}} = \frac{\sum_i L_{r,i} \Psi_{\text{soil},i}}{\sum_i L_{r,i}} \quad (15)$$

where  $L_{r,i}$  is root length density (cm/cm<sup>3</sup>) in the  $i$ th soil layer. When calculating  $\Psi_{\text{soil-eff}}^0$ , we only need to replace  $\Psi_{\text{soil},i}$  in Eq. (15) by air-entry potential (cm H<sub>2</sub>O) of soil in the  $i$ th layer,  $\Psi_{\text{soil},i}^0$ . The air-entry potential for each layer of soil was obtained by using the expression of Campbell (1985)

$$\Psi_{\text{soil}}^0 = 5d_g^{-0.5} \left( \frac{1}{1.3} \rho_b \right)^{0.67(d_g^{-0.5} + 0.2\delta_g)} \quad (16)$$

where  $\rho_b$  is soil bulk density (Mg/m<sup>3</sup>),  $d_g$  the geometric mean particle diameter (mm),  $\delta_g$  the geometric standard deviation of the particle diameter.

### 3.3. Root length function

For the factor of root length, actual root length  $L_{rv}$  (cm) in each layer of soil was used, together with a root–soil contact degree,  $\eta(t)$ , according to Van Noordwijk et al. (1992). Root length function, thus, is expressed as

$$f_2(L_r) = \eta(t)L_{rv} \quad (17)$$

In this study

$$\eta(t) = \begin{cases} \frac{\theta(t)}{\theta_0}, & \theta < \theta_0 \\ 1, & \theta \geq \theta_0 \end{cases} \quad (18)$$

$\theta$  and  $\theta_0$  are volumetric content (m<sup>3</sup>/m<sup>3</sup>) of soil water at water potential,  $\Psi_{\text{soil}}$ , and at the potential of  $-100$  cm H<sub>2</sub>O, respectively.

### 3.4. Hydraulic conductance of root water uptake

It is difficult to determine the hydraulic conductance involved in the uptake of water by roots. The recorded values of root hydraulic conductance ( $K_w$ ) of maize (*Z. mays* L.) that vary between 0.1 and  $28 \times 10^{-7}$  cm/s (Huang and Nobel, 1994) were measured using different methods in various environmental conditions. Here, we have defined the function  $f_3(K_w)$  of the whole transport process from soil to leaves as

$$f_3(K_w) = k \times 10^{-7} \quad (19)$$

where  $k$ , with a range 0.1–1, selected from the observed values, is defined as

$$k = \left( \frac{\Psi_{\text{air-max}} - \Psi_{\text{leaf}}}{\Psi_{\text{air-max}} - \Psi_{\text{leaf-min}}} \right)^{\lambda \Psi_{\text{soil-eff}}(t)/\varepsilon(t) \Psi_{\text{soil-eff}}^0} \quad (20)$$

$\Psi_{\text{air-max}}$  is the maximum water potential of air (bar) during daytime.  $\Psi_{\text{leaf}}$  is water potential of leaf (bar);  $\Psi_{\text{leaf-min}}$  the minimum water potential of leaf (bar) during daytime (generally from 7:00 to 19:00 h).  $\varepsilon(t)$  is a time-dependent coefficient related to potential evapotranspiration,  $EP(t)$  (mm/day) at particular time, calculated with Penman method, given by

$$\varepsilon(t) = \begin{cases} 1.0, & \frac{\Psi_{\text{soil-eff}}}{5 \Psi_{\text{soil-eff}}^0} \geq 15 \\ \text{MIN} \left[ \frac{EP(t), 15 - \Psi_{\text{soil-eff}}(t)}{5 \Psi_{\text{soil-eff}}^0} \right], & \frac{\Psi_{\text{soil-eff}}}{5 \Psi_{\text{soil-eff}}^0} < 15 \end{cases} \quad (21)$$

In Eq. (20),  $\lambda$  is a relative growth rate of the cumulative curve of solar radiation during daytime. This parameter can be obtained through fitting the cumulative curve using a sigmoid function, such as

$$A_R = \frac{M_R}{1 + b e^{-\lambda(t-t_0)}} \quad (22)$$

$A_R$  is the cumulative amount of solar radiation ( $\text{W/m}^2$ ) at any time,  $t$ , from 7:00 ( $t_0$ ) to 19:00 h.  $M_R$ , the total cumulative radiation from 7:00 to 20:00 h, was assumed to be the maximum value of  $A_R$ , and  $b$  is a fitting coefficient.

### 3.5. The developed model

The general analytic model for RWU rates,  $\Phi(t)$ , in  $\text{cm}^3/\text{s}/\text{plant}$  or  $\text{g}/\text{s}/\text{plant}$ , therefore, can be

rewritten as

$$\Phi(t) = 10^{-7} \sum_i \eta(t) L_{\text{rv},i}(t) \alpha \{ \Psi_{\text{leaf}}(t) - \Psi_{\text{soil},i}(t) \} \times \left\{ \frac{\Psi_{\text{air-max}} - \Psi_{\text{leaf}}(t)}{\Psi_{\text{air-max}} - \Psi_{\text{leaf-min}}} \right\}^{\lambda \Psi_{\text{soil-eff}}(t)/\varepsilon(t) \Psi_{\text{soil-eff}}^0} \quad (23)$$

where  $L_{\text{rv},i}$  denotes root length in the  $i$ th soil layer of the field profile.

## 4. Verification of the model

### 4.1. Verifying the model scheme

The ability of the developed model to estimate RWU rates was examined using 17 sets of RWU data measured during 8 days at three locations. In the calculations, the soil profile at each location was divided into 12 layers, 5–60 cm depth from the ground surface. Root length density, soil particle-size distribution, and soil bulk densities were measured for each of those layers. The data of RWU, solar radiation, relative humidity of atmosphere and EP were averaged for 15 min intervals. Water potentials of soil, leaf and root were interpolated at 15 min intervals from the data recorded hourly.

The comparisons presented in Table 2 and Fig. 2, reveal that the model could predict RWU rates with reasonable accuracy. The  $t$ -test indicated that, as a whole, the model showed no significant systematic deviation, suggesting acceptable model calibration and that RMSE or RRMSE is derived mainly from the measurement errors. The difference between the observed and estimated RWU rates might be due to inaccurate records of fluctuation of the sap flow. Also noteworthy is that distribution of root length density, which was determined at the end of the experiments, may be inappropriate for the estimation of RWU rates on earlier days because of root growth during the investigation period. Another factor that might cause some estimation deviation is relative rate of variation of solar radiation. In the formulation of the model, the relative rate of variation of RWU rates was represented by that of solar radiation,  $\lambda$ , based on the assumption that fluctuations in radiation load were mainly responsible for sudden changes in the hourly pattern of leaf

Table 2  
Examination of the proposed model for RWU<sup>a</sup>

Data set No.	RMSE (g/s/plant)	RRMSE (%)	<i>t</i>	<i>R</i> <sup>2</sup>	<i>n</i>
980719-W	0.0053	26.3	-0.85	0.69	41
980726-W	0.0034	19.5	-0.65	0.69	37
980727-W	0.0054	18.6	-0.81	0.71	37
980803-W	0.0027	15.9	1.26	0.85	45
980803-E1	0.0023	17.1	3.33	0.87	41
980803-E2	0.0019	16.9	1.90	0.83	41
980804-W	0.0022	16.8	1.49	0.81	41
980804-E1	0.0017	13.5	-2.95	0.93	41
980804-E2	0.0024	21.8	0.08	0.83	41
980806-W	0.0021	11.7	-1.38	0.88	38
980806-E1	0.0024	17.1	-1.17	0.79	41
980806-E2	0.0030	29.9	4.30	0.79	41
980812-W	0.0025	16.9	0.01	0.65	41
980812-E1	0.0037	30.2	-0.49	0.55	41
980812-E2	0.0018	18.9	3.39	0.83	41
980815-W	0.0035	19.4	4.03	0.84	33
980815-E1	0.0029	20.3	-0.87	0.66	33
Mean	0.0029	19.5	1.70	0.78	

<sup>a</sup> The critical value of  $t_{0.05}$  is 2.005 for degrees of freedom 45, 2.021 for degrees of freedom 40, and 2.042 for degrees of freedom 30.

potential. In fact, changes in plant water storage generally tend to buffer sudden fluctuations of the sap flow. Nevertheless, the RWU rates were generally well simulated, despite some deviations in RWU rates.

On an average, RRMSE was 19.5% for the estimation, giving confidence that the RWU rates were well simulated by the model for the field situation in this experiment.

In addition to 15 min averages, the model was also used to estimate RWU rates at 9:00 h during a period of 19 days. When the observed and simulated values were displayed in a scatter plot (Fig. 3), the data conformed reasonably well to the 1:1 line ( $R^2 = 0.72$ ). This behavior further supports the validity of the model as Eq. (23).

#### 4.2. Sensitivity analysis

The purposes of sensitivity analysis is to identify those input factors that most strongly affect the model's response and to determine the required precision of inputs and constants used in the models. Here, the parameters included in the sensitivity test were effective water potential of soil, effective air-entry potential of soil, leaf water potential, the minimum water potential of leaf during daytime, the maximum water potential of air, root length density, relative rate of variation of solar radiation at particular daytime, and EP. The test was established to monitor the effects on RWU rates of increasing (+) or decreasing (-) values of the parameters by 10, 20, 30, 40, 50, 60, 70%, one

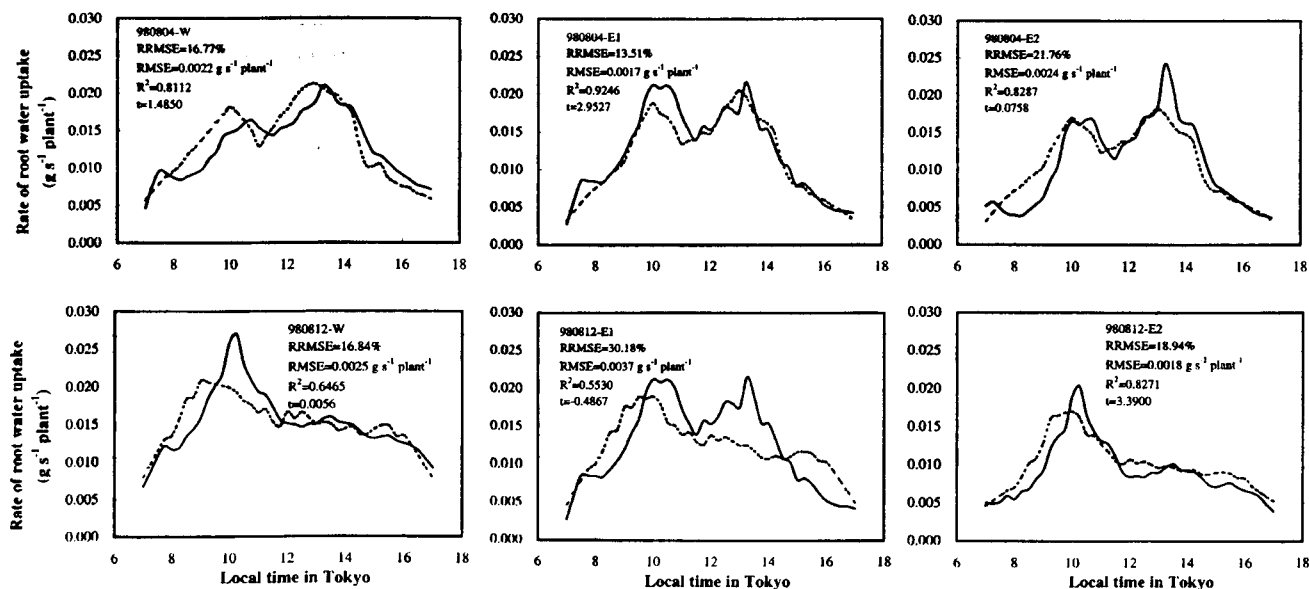


Fig. 2. Times series of RWU rates on 4 and 12 August 1998. Solid and dashed lines denote the values measured and estimated by the model, respectively. W, E1 and E2 indicate observation sites in the field. The critical value of  $t_{0.05}$  is 2.021 for 40 degrees of freedom.



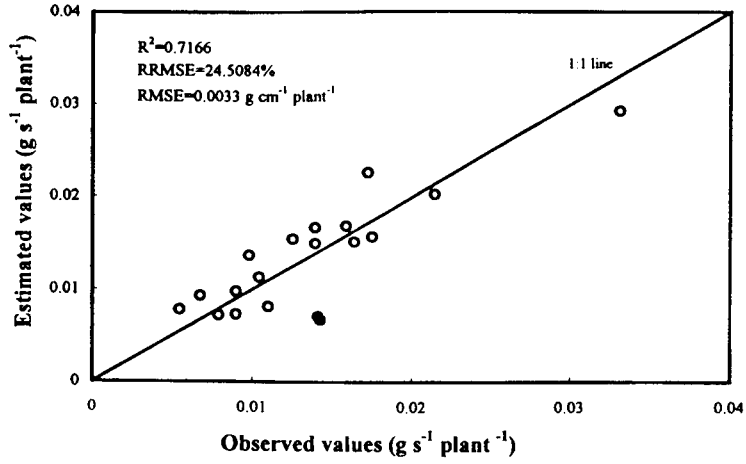


Fig. 3. Comparison of measured and estimated values of RWU rates at 9:00 h during a period of 19 days in August 1998.

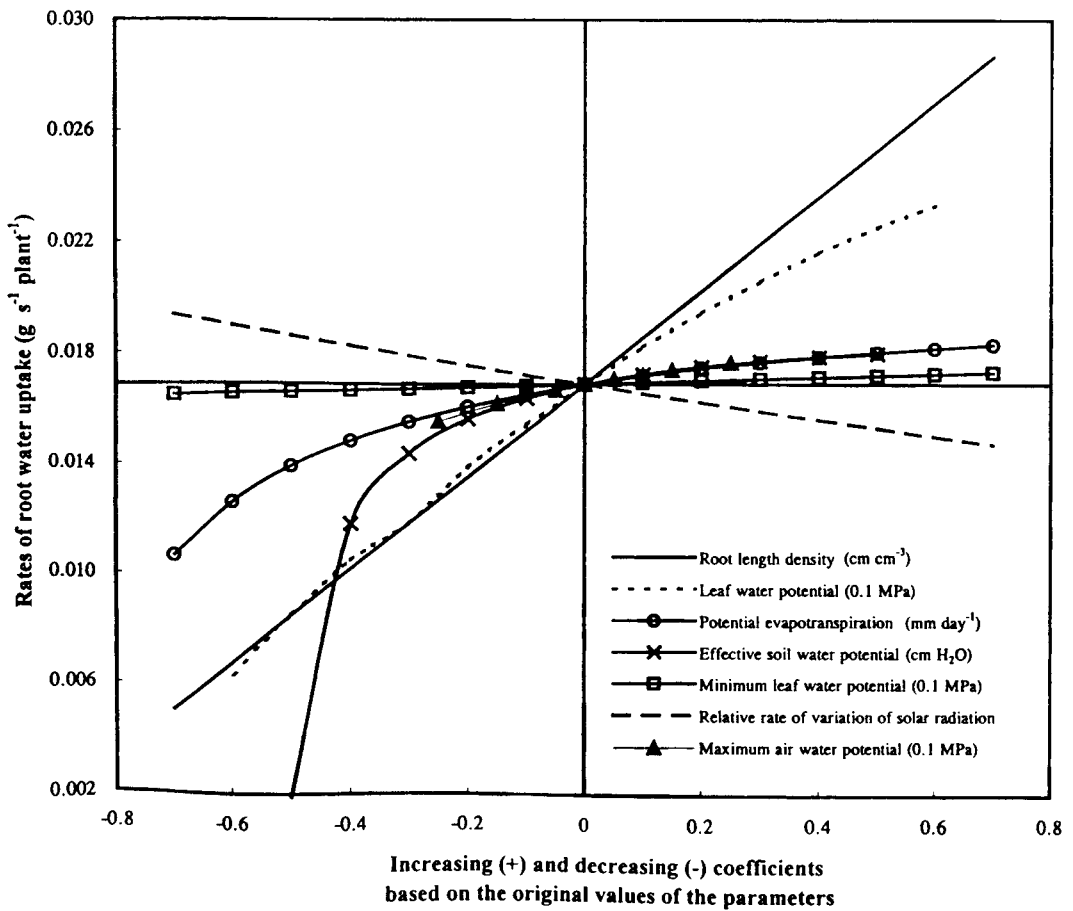


Fig. 4. Plot of sensitivity of estimated RWU rate to the model parameters.

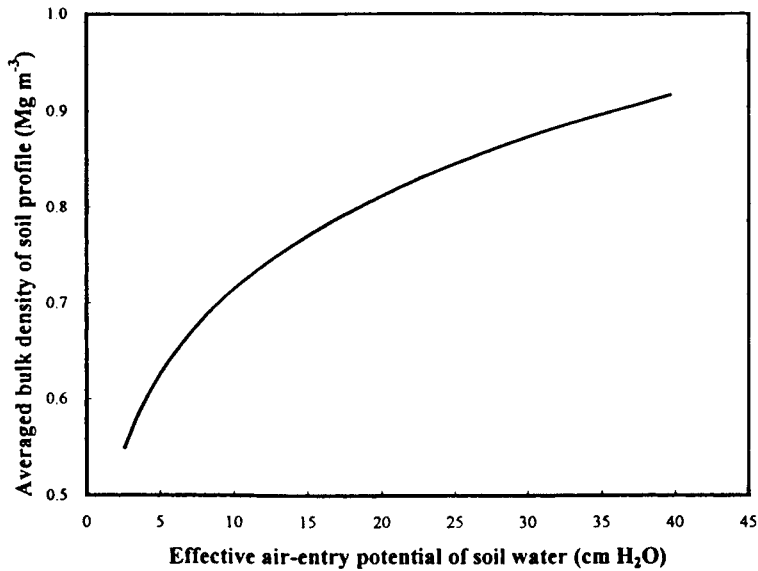


Fig. 5. A schematic illustration of the influence of bulk density on effective air-entry potential of soil water in the soil profile, according to Eqs. (15) and (16).

parameter at a time. This analysis allows the parameters to be 'ranked' in terms of importance. As depicted in Fig. 4, the minimum water potential of leaf during daytime had the least effect on the model performance. This arises because the absolute value of this parameter is small as compared to that of the maximum water potential of air, so that changes of this parameter have little effects on the difference of both of them as shown in Eq. (20). The parameters that displayed some sensitivity include maximum water potential of air, effective water potential of soil, and EP. In general, they had the same influence on model predictions. By comparison, the model was shown having a higher linear sensitivity to the relative rate of variation of solar radiation during daytime. Both leaf water potential and root length density were found to be highly dominant in defining the behavior of the model. The model was, to some degree, non-linearly sensitive to leaf water potential, especially with increasing value. In contrast, root length density expressed a linear influence on performance of the model. Although both of these parameters had approximate sensitivity behavior when values of the parameters decrease, the root length was found to be the most sensitive parameter among all inputs of model for the case when values of the parameters increase. In addition, in the developed model as Eq. (23), soil bulk

density was also shown to be a factor capable of significantly influencing WRU rates, since it is closely related to effective air-entry potential of soil water, as indicated in Fig. 5.

## 5. Discussion

### 5.1. Leaf–soil water potential difference acting as driving force

Currently, in theory and measurement methods, there is no clear-cut distinction of transpiration and RWU. If anything, difference lies in that transpiration stresses interaction of leaf and atmosphere, while the RWU more emphasizes adaptation of root function to soil environment and changes of water storage in stem. Regardless, it is transpiration that initially causes the decrease of water potential in the leaf cells and provides the sink for water flow toward the evaporating surfaces. This flow continues as long as the gradients, which are established step by step through the plant–soil system, are adequate to cause the desired rate of water flow to the leaf. The resistance for water transport from soil to leaves is assumed to include soil resistance, soil–root interfacial resistance, root radial resistance, shoot xylem resistance, and

stomatal resistance. Some efforts for qualitative identification of resistance distribution in SPAC have been made (Yu et al., 1997). However, the large number of parameters involved in the model and the lack of consideration for the hydraulic continuity and environmental heterogeneity seriously impede utilization of the estimated resistance in modeling water uptake or leaf transpiration. In practice, a common and simple method in identifying the driving force of water flow in the soil–plant system is to treat the potential difference between the source and sink as the driving force, rather than addressing the complications involved in accounting for variations in the properties of parts, say, distribution of root hydraulic characteristics.

Most of the present models of RWU adopt water potential difference between root and bulk soil as the driving force, because the measurement of root water potential remains a difficulty. Various techniques have been used to measure root water potential, but all have proved inadequate. For example, Kaufmann (1968) allowed roots of pine seedlings to emerge from the bottom of a soil column into an atmosphere of humid air, and then from time to time, measured water potential in a thermocouple psychrometer. It is unlikely that the measurements represent the true water potential of the roots growing in the soil because the hanging roots were constantly maintained in an atmosphere of humid air. DeRoo (1969) measured the water potential of tobacco roots by placing an entire root system together with any adhering soil in a pressure chamber. These measurements gave an effective average value of the water potential of the soil plus roots but not the true root water potential. Fiscus (1972) made a good attempt at measuring root water potential of corn plants. In his experiments, specially constructed thermocouple psychrometers were attached *in situ* to roots of corn seedlings growing in a container of soil. There was uncertainty, however, regarding which part of the root system was being measured.

For the above reasons, water potential difference between soil and leaf was adopted to be the driving force of water uptake in this study. Further, considering interaction of water potentials between root and leaf, and preferential uptake of water from wetter parts of the root zone as well as a rapid return in the activity of previously dry roots once they are reirrigated (Ritchie, 1973; Blackman and Davies, 1985; Gowing

et al., 1990; Green and Clothier, 1995), a coefficient related to soil water potential was proposed to modify the water potential difference of leaf–soil as effective driving force.

## 5.2. Root hydraulic conductance

Hydraulic conductance of root is an important factor in the water relations of plants. To a large extent, the root conductance will determine water status of the shoot because, next to the stomata, the root usually offers the lowest conductance to water within the SPAC (Yu et al., 1997). However, the hydraulic conductance of root is a rather complex parameter that depends on the root structure and anatomy as well as on the pattern by which different parts of the root contribute to the overall water transport at different stages of the root development. Several methods have been developed for measurement of hydraulic conductance of single roots or entire root systems. Most of them use excised roots or intact plants. However, experiments with excised, pressurized root systems may be criticized because the conditions are quite different from those in the intact plant. For the root pressure probe technique, two serious concerns are that excision might change transport properties of roots and that working with a range of positive pressures is not representative of the transpiring plant in which negative tensions are exerted within the xylem. The use of intact plants may also cause problems because of the difficulty of exactly determining the driving forces for root water transport in field condition. In this method, under the assumption of a steady-state water uptake, root hydraulic conductance is calculated from the slope of the plot of amount of water transpired or rates of water uptake versus leaf water potentials (Newman, 1976; Rieger, 1989; Moreshet et al., 1990; Simmonneau and Habib, 1991). The evident limitation for this method arises because in most of cases water uptake by roots in the field is characteristically of non-steady state.

A number of observations suggest that the root hydraulic conductance is dependent on root metabolism, since inhibitors such as CCCP and KCN, and plant hormones such as ABA and kinetin reduce root hydraulic conductance. At present, the question of how these different effects determine the absolute value of root hydraulic conductance cannot be

answered completely. Also, many studies (Fiscus, 1975; Weatherley, 1982; Passioura, 1988; Hainsworth and Aylmore, 1989; Steudle and Brinckmann, 1989) have shown that root hydraulic conductance is flow-rate dependent; i.e. hydraulic conductance becomes large as water flow across roots increases. This implies that the root hydraulic conductance depends on environmental changes and could contribute to balance the various demands of the shoot for water. From physiological and ecological points of view, it is, therefore, important to emphasize variations of the root hydraulic conductance resulting from hydraulic properties of the roots, interaction with solute flow, and hormonal actions.

In view of the complication mentioned above, it seems better to estimate root hydraulic conductance of maize based on its order of magnitude ( $k \times 10^{-7}$ ). In this study, we assumed the coefficient,  $k$ , as an environmental-related value, which varies between 0.1 and 1 due to fluctuations of environmental variables. The coefficient,  $k$ , links simulation of RWU to environmental dynamics closely. It relates not only to relative rate of variation of solar radiation during daytime but also to demand strength for water, which can be specified by a synthetic index of climatic environment, i.e. EP. Additionally,  $k$  is assumed subject to soil water status, leaf water potential, and the maximum water potential of air on particular days. Although the determination of  $k$ , by Eq. (20) might lack a sufficient basis in theory, it could provide an estimate of the root hydraulic conductance of maize plants in the leaf–soil potential gradient context for some practical purposes. Eventually, this may lead to the inclusion of many environmentally related parameters in the model.

## 6. Concluding remarks

The RWU scheme in this study, by attempting to develop an operational model incorporating characteristics of soil, plant and atmosphere, has led to a simple approach for estimating RWU rates with acceptable accuracy, in the absence of water stress. The behavior of the model was validated by comparing measured and estimated RWU rates. Sensitivity analysis highlighted the need for accurate measurements of leaf water potential and root length density, soil physical properties, and weather conditions, espe-

cially of solar radiation. This work has emphasized the importance of a sound consideration of the biological and environmental factors in the modeling of the RWU rates.

Although some of this work remains hypothetical due to the difficulty of accurately measuring root water potential and root hydraulic conductance, it is proposed that the approach can be practically useful. Various assumptions will need refining, especially those concerning the calculation of  $k$  in Eq. (20) and the usefulness of the coefficient,  $k$ , of the root hydraulic conductance. There is also a need to investigate the time lag of RWU rate relative to leaf potential changes that result from water storage within the plant (Simmonneau and Habib, 1994). Despite these limitations and some difficulties in estimating RWU rates, the model is able to offer some insight into the impact of environmental conditions on RWU.

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