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A model for nutrient and water flow and their uptake by plants grown in a soilless culture

M. Silberbush[1], J. Ben-Asher & J.E. Ephrath
*Wyler Department of Dryland Agriculture, J. Blaustein Inst. for Desert Research, Ben-Gurion University of the Negev, Sede-Boker Campus, 84990 Israel. [1]Corresponding author**

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Abstract

The objective of this study was to develop a sensitive means of control to optimize nutrient concentrations in the root zone of a soilless system, considering plant water and nutrient uptake, and solution circulation rates. A model is proposed to simulate ornamental plants' growth in a channel with a non-interacting soilless substrate, irrigated by point sources with constant discharge rates, spaced uniformly along the channel. The model accounts for compensation for transpiration water losses and consequent salinity buildup, and its interactions with plant growth and nutrient uptake. The added water may contain given concentrations of nutrients and/or toxic (saline) compounds, which would cause salinity buildup. Uptake of each solute is specific, according to a Michaelis–Menten kinetics mechanism, but passive uptake by the transpiration stream is also accounted for. Plant growth is affected by time/age and ionic balance in the solution. The model was calibrated with lettuce (*Lactuca sativa* L.) plants grown in volcanic ash. Simulation of potassium concentration change as a result of discharge rate and emitter spacing revealed that the two parameters could compensate one for the other, once a target lower limit is set. Potassium appeared to be most sensitive to sodium accumulation in the growth medium; this accumulation changed ionic concentration balance, which affected pH and bicarbonate concentration. Passive uptake of calcium by the transpiration stream is highly affected by the root fraction involved, but its calculated contribution is below published values is highly affected by the root fraction involved, but its calculated contribution is below published values.

Abbreviations: LAI – leaf area index; NFT – nutrient film technique; RL – root length

Introduction

Modern greenhouse production is associated with a high level of control on inputs and outputs. The high costs of inputs force the grower to act in the highest efficiency possible. Yet, the environmental constraints force a no-spill policy namely, the avoidance of uncontrolled release of pollutants to the environment (Chen et al., 1997). Furthermore, it becomes more and more crucial to enable the grower to meet deadlines of marketing, so he may compete efficiently. Within these constraints, growers cannot rely anymore merely on their senses, but need reliable means to make the right decisions to face fast changes in the market demand and in their own enterprise (Le Bot et al., 1998).

The shift to soilless growth media in horticulture has improved the control on the below-ground conditions. The roots are kept in either hydroponics, aeroponics or in a solid matrix medium (usually with minimal interactions with

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* FAX No: +972-8-6596757. E-mail: silberbu@bgu.ac.il

the solutes), so basically these media may be regarded as some kind of hydroponics. The trend is towards a shallow nutrient film technique (NFT) root system or alike, with a relatively fast circulation rate which allows a high level of control on the nutrient concentrations (Le Bot and Kirkby, 1992; Tadesse et al., 1999). On the other hand, such a system allows also good aeration and gas exchange of the root system with the ambient atmosphere. On the other hand, undesirable compounds, like pathogens and toxic elements, might accumulate in the system (Bar-Yosef et al., 2001).

The presented model is aimed at matching the nutrient supply to the demand by the plants, at real time, while accounting for the accumulation of salinity substances, sodium (Na) and chloride (Cl), and their interactions with nutrient uptake and plant growth. The model may allow the grower to decide when to replace the growth solution or, alternatively, to change the water source and fertilizer formula, while keeping the production under control.

Theory

A schematic description of the model appears in Figure 1; a list of the symbols is provided in Appendix A. A channel is given, with length L and with width w, divided into n imaginary segments ('cells'), filled with a porous material of known hydraulic characteristics. The channel is tilted in an angle α against the horizon. A series of point emitters, one per 'cell', of constant discharge rate q (volume per time unit) is positioned at equal distances d $(=L/n)$ along the channel. At the end of the channel, there is a reservoir tank of volume V_{R} that drains the out-flow, and where evapotranspiration losses would be compensated at each time step, and instantaneously mixed with water that contains concentration C_{ad} of the solute species I. The mixture would then be pumped back to the feeding system.

The term 'water volume' will be used throughout the text, although it also stands for water mass or amount, taking water density as a unity. Assuming that the wetted volume of the matrix is in saturation, the volume of water V in each segment i at time t:

$$V_{(i,t)} = ah_{(i,t)}\theta_{\mathrm{s}}, \tag{1a}$$

where a is lateral area of a cell (equals to $d{\cdot}w$), h is the wetting height, and θ_{s} is volumetric moisture fraction (water volume per soil volume) at saturation. Equation (1a) provides the moisture head in the i segment/cell:

$$h_{i,t} = \frac{V_{i,t}}{a\theta_s} \tag{1b}$$

The temporary change in water amount in the i segment along the channel will be

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = Q_{i-1} + qf_T - a\,T_t\;\mathrm{LAI}_t - Q_i, \tag{2a}$$

where Q_{i-1} and Q_i stand for water flow rate to and from the ith segment, respectively, T is transpiration rate and LAI is leaf area index. The change in water volume of the ith segment with time:

$$\Delta V_i = (Q_{i-1} + qf_T - aT_t\;\mathrm{LAI}_t - Q_i)\;\Delta t, \tag{2b}$$

where Δt is the time step. The coefficient f_T is the fraction of time at which the recycling pump is on, to compensate for actual water losses due to transpiration:

$$f_{T(t)} = f_0 + \frac{aT_t\;\cdot\;\mathrm{LAI}_t}{q}, \tag{3}$$

where f_0 is a constant factor to allow basal water flow during night-time, when transpiration is zero Eq. (12a), to maintain the circulation of the solution at any time.

In the first cell (i.e., $i=1$), where $Q_{i-1}=0$, the updated water volume by Equation (2b) is

$$V_{1(t+\Delta t)} = V_{1,t} + \left(q\,f_{T(t)} - aT_t\;\mathrm{LAI}_t - Q_{1,t}\right)\Delta t, \tag{4a}$$

where Q_1 is calculated according to Darcy's equation as

$$Q_{1,t} = wh_{1,t}\;(\theta_{\mathrm{s}} - \theta_{\mathrm{r}})K_s\left\lfloor\frac{h_{1,t} - h_{2,t}}{d} + \sin\alpha\right\rfloor, \tag{4b}$$

where h serves as the hydraulic head at the ith segment, θ_{s} and θ_{r} are saturated and residual (i.e., immobile) volumetric water fractions, respectively, and K_s is the hydraulic conductivity of the medium in saturation. Segments number *2* to $n{-}1$ have a joint component, as the flow out of one is the flow into the next; thus, by lumping them into one component (named 'no. 2' hereafter), water flow out, Q_2, may be expressed as

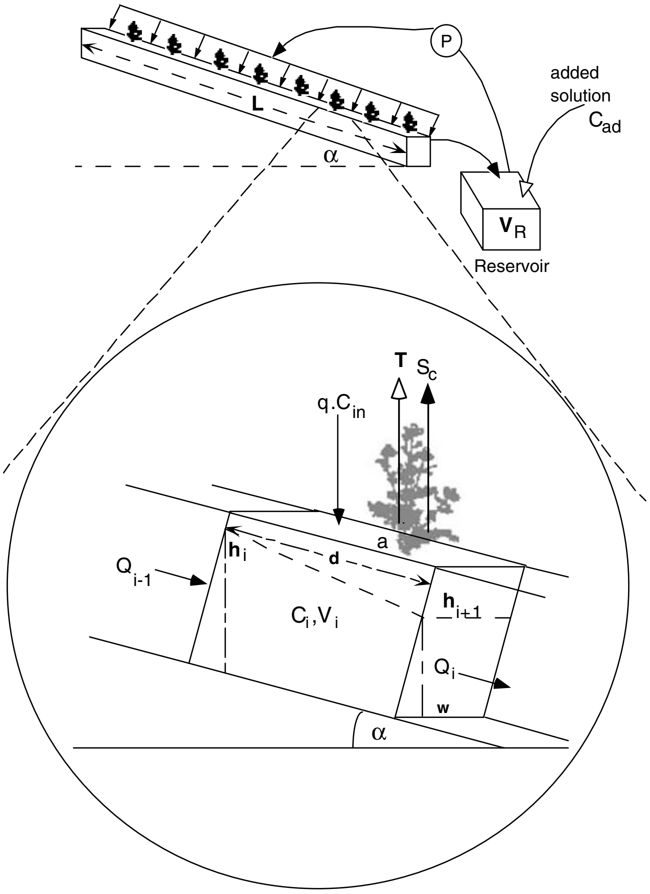

Figure 1. Schematic description of a soilless system (upper part) with length L, tilted at α angle slope, where the nutrient solution drains to the reservoir with capacity V_R and transpiration losses T are compensated with an added solution with concentration C_{ad}, which would be recycled to the channel by the pump (P) and re-applied via a dripping system. To solve the model, the channel was divided into n imaginary 'cells': $n = L/d$, where d is the distance between neighboring emitters. An i 'cell' along the channel (lower, circled part), with width w and length d: Q_{i-1} – flow in from the previous cell; Q_i flow out to the next cell, driven by hydraulic head gradient due to change in the wetted level h_i and h_{i+1} and the slope; q – nominal discharge rate of the emitter, with input solution of concentration C_{in}. The sink term S stands for uptake by the plants as a function of the nutrient concentration C.

$$Q_{2,t} = wh_{2,t}(\theta_s - \theta_r)\ K_s\ \left\lfloor \frac{h_{2,t} - h_{3,t}}{(n-2)d} + \sin\alpha \right\rfloor, \quad (5a)$$

$$\text{where } h_{2,t} = \frac{V_{2,t}}{(n-2)\ a\theta_s} \quad (5b)$$

The updated volume of the liquid in this compartment:

$$V_{2,(t+\Delta t)} = V_{2,t} + \left[Q_{1,t} + (n-2) \times (qf_{T,t} - a\ T_t\ \mathrm{LAI}_t) - Q_{2,t}\right]\Delta t \quad (5c)$$

Flow rate out of the terminal ('no. 3') segment, Q_{out}:

$$Q_{out(t)} = wh_{3,t}(\theta_s - \theta_r)\ K_s\ \left\lfloor \frac{h_{3,t} - H}{d} + \sin\alpha \right\rfloor, \quad (6a)$$

where H is the height of the drainage outlet, which flows to the reservoir. The hydraulic head h_3 is calculated from the volume, according to Equation (1b). The volume of the liquid in this compartment:

$$V_{3,(t+\Delta t)} = V_{3,t} + \left[Q_{2,t} + q\,f_{T(t)} - a\ T_t\ \mathrm{LAI}_t - Q_{out(t)}\right]\ \Delta t \quad (6b)$$

The change of a solute I in the i segment will be

$$V_{(i,t)}\frac{\mathrm{d}C_i^I}{\mathrm{d}t} = Q_{i-1}\cdot C_{i-1}^I + q\ f_T\ C_{in(t)}^I - S_c^I - Q_{i,t}\cdot C_{i,t}^I, \quad (7a)$$

where C is concentration and S is the specific sink of I as a function of its concentration. The solute balance in the reservoir:

$$V_{\mathrm{R}}\frac{\mathrm{d}C^{I}}{\mathrm{d}t}=Q_{\mathrm{out}(t)}\cdot C^{I}_{\mathrm{out}(t)}+C^{I}_{\mathrm{ad}}\,wL\,T_t\,\mathrm{LAI}_t-nq\,f_{T(t)}C^{I}_{in(t)} \tag{7b}$$

where V_{R} is the volume of the reservoir, C_{ad} is the concentration of the I solute in the solution added to compensate for transpiration losses, and C_{in} is the concentration of the solute in the mixture that would be pumped back into the irrigation system, assuming an immediate and complete mixing of all components in the reservoir:

$$C^{I}_{\mathrm{in}(t+\Delta t)} = C^{I}_{\mathrm{in}(t)}+\frac{Q_{\mathrm{out}(t)}\cdot C^{I}_{3,t}+C^{I}_{\mathrm{ad}}\,wLT_t\,LAI_t-nq\,f_{T(t)}C^{I}_{\mathrm{in}(t)}}{V_{\mathrm{R}}}\Delta t \tag{8}$$

The change in the solute concentration in each cell, at a time-step:

$$C^{I}_{1,(t+\Delta t)} = C^{I}_{i,t}+\frac{q\ f_{T(t)}C^{I}_{\mathrm{in}(t)}-S^{I}_{c1(t)}-Q_{1,t}\cdot C^{I}_{1,t}}{V_{(1,t)}}\Delta t \tag{9a}$$

$$C^{I}_{2,(t+\Delta t)} = C^{I}_{2,t}+\frac{Q_{1,t}\,C_{i,t}+(n-2)\,q\,f_{T(t)}C^{I}_{\mathrm{in}(t)}-S^{I}_{c2(t)}-Q_{2,t}\cdot C^{I}_{2,t}}{V_{(2,t)}}\Delta t \tag{9b}$$

$$C^{I}_{3,(t+\Delta t)} = C^{I}_{3,t}+\frac{Q_{2,t}\,C_{2,t}+q\,f_{T(t)}C^{I}_{\mathrm{in}(t)}-S^{I}_{c3(t)}-Q_{\mathrm{out}(t)}\cdot C^{I}_{3,t}}{V_{(3,t)}}\Delta t \tag{9c}$$

Plant growth by time and salinity

Root length (RL) growth is assumed to obey a logistic function of time (Barber, 1995):

$$\mathrm{RL}_{(t)}=\frac{\mathrm{RL}_{\mathrm{max}}}{1+K_1\ \mathrm{e}^{-k_1 t}}, \tag{10a}$$

where RL_{max} is maximal length, and K_1 and k_1 are coefficients. To account for growth inhibition by salinity, root length is assumed to correlate to the sensitivity of the plant to Na (Kafkafi and Bernstein, 1996; Kinraide, 1999), and to the molar ratio of Ca to the sum-of-cations up to 0.2, where full recovery occurs (Howard and Adams, 1965):

$$RL_{\mathrm{Na}}=RL_0\left(1-\frac{0.5}{C^{\mathrm{Na}}_{0.5}}C^{\mathrm{Na}}\right)\cdot\left(\frac{5\,C^{\mathrm{Ca}}}{\text{Sum of Cations}}\right), \tag{10b}$$

where $\mathrm{RL}_{\mathrm{Na}}$ and RL_0 are root length in C^{Na} and in 0-Na solution, respectively, and $C^{\mathrm{Na}}_{0.5}$ is Na concentration that would cause the reduction of root elongation by 50%. When a growing root system and Na accumulation with time are both considered, however, Na concentration may determine the actual/marginal root growth, obtained from the first derivative of Eq. (10a), $\delta\mathrm{RL}/\delta\mathrm{t}$. Equations (10a,b) may be therefore combined as follows:

$$\mathrm{RL}_{\mathrm{Na},(t+\Delta t)}=\mathrm{RL}_{\mathrm{Na},t}+\frac{\partial RL}{\partial t}\left(1-\frac{0.5}{C^{\mathrm{Na}}_{0.5}}C^{\mathrm{Na}}_{t}\right)\cdot\left\lfloor\frac{5\,C^{\mathrm{Ca}}_{t}}{(\text{Sum of Cations})_t}\right\rfloor\cdot\Delta t \tag{10c}$$

Root surface area RA_t, may now be calculated, assuming the roots to be smooth cylinders, with constant mean radius r_0:

$$\mathrm{RA}_t=2\pi\ r_0\ \mathrm{RL}_t \tag{10d}$$

Leaf area index also grows following a logistic function of time and would change in a similar manner as root length (Janzen and Chang, 1987). The equivalent of Eq. (10c) for LAI growth will then be

$$\mathrm{LAI}_{\mathrm{Na},(t+\Delta t)}=\mathrm{LAI}_{\mathrm{Na},t}+\frac{\partial\mathrm{LAI}}{\partial t}\left(1-\frac{0.5}{C^{\mathrm{Na}}_{0.5}}C^{\mathrm{Na}}_{t}\right)\cdot\left\lfloor\frac{5\,C^{\mathrm{Ca}}_{t}}{(\text{Sum of Cations})_t}\right\rfloor\cdot\Delta t \tag{11}$$

Transpiration

Relative transpiration T_{rel} is accounted for as a sinusoidal function of daytime: starting at 06:00 with a value of 0.0, increases to 1.0 at 12:00, and declines to 0.0 at 18:00, namely: for daytime; night-time transpiration is taken as zero. The function to account for this effect is

$$T_{\mathrm{rel}}=\begin{cases}\sin\langle 2\pi\,[t-(\tau-1)]\rangle & \text{when} > 0\\ 0 & \text{otherwise}\end{cases}, \tag{12a}$$

where t is time in days, and τ is an integer number of the current day. Temporal water losses due to transpiration may be now obtained from:

$$T_{t,\mathrm{Na}} = T_{\mathrm{rel}}\, T_{\max}\, \mathrm{LAI}_{\mathrm{Na},t}, \tag{12b}$$

where $T_{\max}$ is the maximal temporal transpiration rate, which occurs at midday.

Uptake: the nutrient sink term (S)

This section is based on a former model of plant growth in hydroponics (Silberbush and Ben-Asher, 2001). The ion/nutrient species of interest are NO_3-N, NH_4-N, K^+, PO_4-P, Ca^{2+}, Mg^{2+}, SO_4-S, Na^+ and Cl^-, and the effects of HCO_3^- and solution pH. It is assumed so that each nutrient I is being absorbed by the roots as a function of its concentration C^I, according to its typical mechanism:

High-affinity, active uptake according to *Michaelis–Menten* type kinetics

$$J_c^I = \frac{J_{\max}^I\left(C^I - C_{\min}^I\right)}{K_m^I + \left(C^I - C_{\min}^I\right)},$$
$$I \equiv \mathrm{K},\ \mathrm{NO}_3^-,\ \mathrm{NH}_4^+,\ \mathrm{PO_4\text{-}P},\ \mathrm{SO}_4^{2-},\ \mathrm{Mg}^{2+}, \tag{13a}$$

where J is net influx of I to the root surface; $J_{\max}$, K_{m} and $C_{\min}$ are maximal influx, Michaelis–Menten coefficient (concentration at which influx equals half $J_{\max}$) and minimal concentration (at which $J = 0$), respectively.

Uptake of Ca is active, but also driven passively by the transpiration stream (Adams and Ho, 1993; Mengel and Kirkby, 2001):

$$J_c^{\mathrm{Ca}} = \frac{J_{\max}^{\mathrm{Ca}}\left(C^{\mathrm{Ca}} - C_{\min}^{\mathrm{Ca}}\right)}{K_m^{\mathrm{Ca}} + \left(C^{\mathrm{Ca}} - C_{\min}^{\mathrm{Ca}}\right)} + \beta \cdot \frac{T_t\, a\, \mathrm{LAI}_t}{\mathrm{RA}_t}\, C^{\mathrm{Ca}}, \tag{13b}$$

where β (dimensionless) stands for fraction of water influx active in Ca uptake (assumed constant).

Sodium and chloride

Salinity is assumed to suppress nutrients' *Jmax* and to increase their *Km* as a function of Na and Cl concentrations (Table 1). Sodium would be absorbed passively by the roots (namely, Na influx is linearly correlated to its concentration, with correlation coefficient P_{m}), above a critical concentration threshold C_{cr} (Sonneveld et al., 1999):

Table 1. Coefficients used to simulate ions' uptake and their references.

Ion/nutrient	$J_{\max}$ mol m^{-2} s^{-1}	K_{m} mol m^{-3}	$C_{\min}$ mol m^{-3}	Reference
NO_3^-	1.15×10^{-7} $(1 + 0.21C^{NO^3})$ $(1–0.0184\ C^{Cl})$	$0.015 + 5.3 \times 10^{-4}\ C^{Cl}$	0.002	Barber (1995), Botella et al. (1994), Silberbush and Ben-Asher (1989)
NH_4^+	1.52×10^{-7} $(1–0.02\ C^{Na})$	$0.0539 + 6.45 \times 10^{-4}\ C^{Na}$	0.002	Botella et al. (1994)
K	$5.12 \times 10^{-8}\ e^{-0.023\ Na}$	$0.0127 + 2.34 \times 10^{-4}\ C^{Na}$	0.002	Wild et al. (1979), Silberbush and Ben-Asher (1989)
PO_4-P	$1.06 \times 10^{-8}\ e^{-0.0022\ Na}$	$0.005 + 1.79 \times 10^{-5}\ C^{Cl}$	0.0002	Barber (1995), Martinez and Läuchli (1994), Silberbush and Ben-Asher (1989)
SO_4^{2-}	1.56×10^{-8}	0.028	0.002	Shock and Williams (1984)
Ca	8.90×10^{-9} $(1–2.56 \times 10^{-7}\ C^{Na})$	0.039	0.002	Davenport et al. (1997), Rossi et al. (1988), White et al. (1992)
Mg	7.00×10^{-9}	0.015	0.002	Barber (1995), Rossi et al. (1988)
Na	$2.5 \times 10^{-11}\ C^{Na}\ (C^{Ca})^{-0.24}$, 0.1 m*M* (Equation (13c))	above critical threshold of		Cramer et al. (1987), Davenport et al., (1997), Sonneveld et al. (1999)
Cl	Solution concentration equals to Na			
HCO_3^-	Balance between anions and cations concentrations			

[a] Plus passive uptake by the transpiration stream (Eq. (13b), Appendix).

$$J_c^{\mathrm{Na}} = \begin{cases} P_m^{\mathrm{Na}} \cdot C^{\mathrm{Na}}, & C^{\mathrm{Na}} > C_{\mathrm{cr}}^{\mathrm{Na}} \\ 0, & \text{otherwise} \end{cases} \tag{13c}$$

Chloride is also assumed to be absorbed passively. As it is abundant in saline environments, its concentration is assumed to equal to C^{Na} and Cl influx equals to that of Na (Lorenzen et al., 2004).

pH and bicarbonate

In an open system, where all components are in soluble forms, the following relation between gaseous carbon dioxide [$\mathrm{CO}_{2(g)}$], Ca (in *M*) and pH may be calculated from the law of mass action:

$$\mathrm{pH} = -0.5\left\{\log\left[\frac{K_{1(\mathrm{CA})}\ K_{2(\mathrm{CA})}\ K_{\mathrm{SP(CO_2)}}}{K_{\mathrm{SP(calcite)}}}\right] + \log(\mathrm{CO_2})_g + \log\left(C^{\mathrm{Ca}}\right)\right\}, \tag{14a}$$

where $K_{1(\mathrm{CA})}$ $(=10^{-6.35})$ and $K_{2(\mathrm{CA})}$ $(=10^{-10.33})$ are the first and second dissociation coefficients of the carbonic acid (CA) and $K_{\mathrm{SP(CO_2)}}$ $(=10^{-1.45})$ and $K_{\mathrm{SP(calcite)}}$ $(=10^{-8.47})$ are the solubility products of $\mathrm{CO}_{2(g)}$ and calcite in water at 25 °C (coefficients were taken from Lide, 1996). With the current ambient atmospheric $\mathrm{CO_2}$ concentration of 370 ppm, its activity is equivalent to 3.7×10^{-4} *M*. On the other hand, the ratio between the two relevant P forms is also pH-dependent, since:

$$\mathrm{H_2PO_4^-} \Leftrightarrow \mathrm{H^+} + \mathrm{HPO_4^{2-}},\quad K = 10^{-7.21}(\text{Lide}, 1996) \tag{14b}$$

To maintain electro-neutrality, the sum of positive and negative ionic charges should equal zero. Therefore, bicarbonate anion ($\mathrm{HCO_3}^-$) concentration is assumed to balance between the sum of cations and anions concentration, when both species are in mole-equivalents:

$$C^{\mathrm{HCO_3}} = C^{\mathrm{K}} + 2C^{\mathrm{Ca}} + 2C^{\mathrm{Mg}} + C^{\mathrm{Na}} - C^{\mathrm{NO_3}} - 2C^{\mathrm{SO_4}} - (P-\text{ratio})\ C^{\mathrm{P}} - C^{\mathrm{Cl}}, \tag{14c}$$

where C^I values are in *M* and *P*-ratio is the ratio between the di- and mono-*o*-phosphate forms, obtained from Equation (14b).

Materials and methods

The model simulation was checked against lettuce (*Lactuca sativa* L. var. 'Nogah 936') grown in containers filled with tuff in the greenhouse for 60 days, 8.5 plants per m^2 (Ben-Asher and Ephrath, unpublished). The nutrient solution ('Shefer-737' liquid fertilizer, Fertilizers & Chemicals Ltd., Haifa, Israel) contained, in addition to microelements and iron (provided as EDTA chelates), 4 m*M* $\mathrm{NO_3}$-N, 2 m*M* $\mathrm{NH_4}$-N, 1.76 m*M* K, and 0.51 m*M* $\mathrm{PO_4}$-P. In this study, the substrate was flushed with the nutrient solution five times a day, and the drainage was collected and analyzed. Uptake of N and K, and transpiration were assessed from the mass balance.

To study the model prediction capacity, it was also checked with parameters of rock-wool as a substrate. The characteristics that were taken as constants or initial values, unless otherwise specified, appear in Appendix A (Fonteno, 1989; da Silva et al., 1995; Orozco et al., 1995). The synthetic simulations used the following initial concentrations (in m*M*): $\mathrm{NO_3}$-N: 3.0; $\mathrm{NH_4}$-N: 1.5; K: 1.5; $\mathrm{PO_4}$-P: 0.5; $\mathrm{SO_4}$-S: 1.0; Ca: 5.0; Mg: 2.0; NaCl: 0.

Results

Figure 2 presents the simulated N and K uptake, and measured values taken up by lettuce plants grown in volcanic ash, at different time from planting. The simulations fitted measured K and

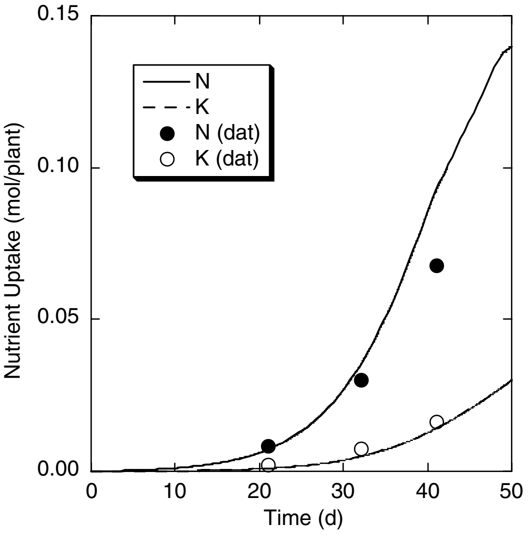

Figure 2. Simulations (curves) and measured (symbols) for nitrogen and potassium uptake by lettuce plants grown in tuff substrate.

N taken up, although measured N uptake at 41 days was somewhat lower than the simulation.

Figure 3 presents certain design considerations of the irrigation system: Figure 3a presents calculated K concentration in the solution after 35 days of plant growth (and uptake), with combinations of emitter discharge rate (*q*) and distance between emitters (*d*). The two parameters should compensate one for the other, which means linear relationships. However, the change of K concentration is curvilinear, which indicates that other mechanisms but simple compensation are involved, indirectly effected by the rate of circulation. Little change of K with *d* as a result of the medium type (i.e., saturated hydraulic conductivity, K_S) was obtained (Figure 3b), except of high emitters' density; it may indicate that solution circulation rate is more effected by the emitter discharge rate and their number, and less by the transferring characteristics of the medium.

Salinity buildup and its results are demonstrated in Figure 4. Sodium accumulation in the

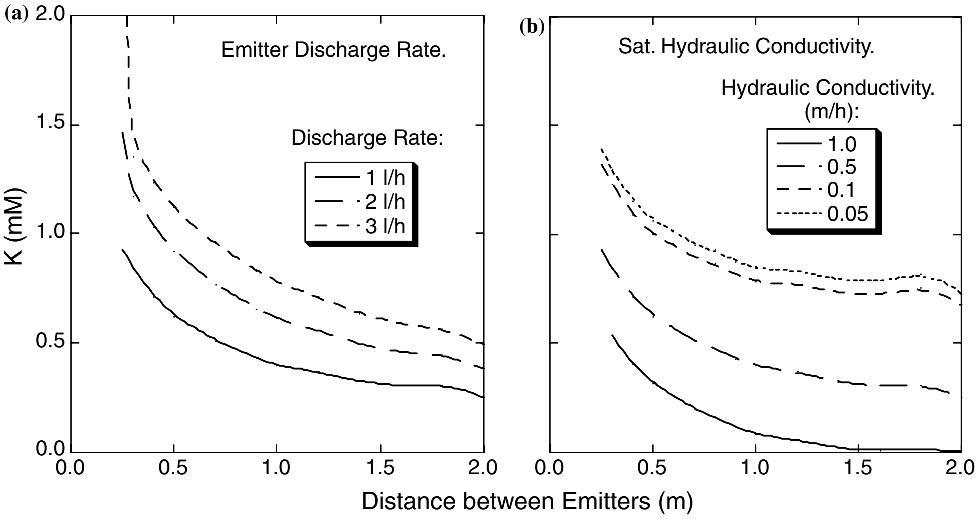

Figure 3. Calculated potassium concentration in the growth medium after 35 days of growth, with initial concentration of 1.5 m*M* K: combinations of distance between emitters and: (a) discharge rate, (b) saturated hydraulic conductivity of the growth medium.

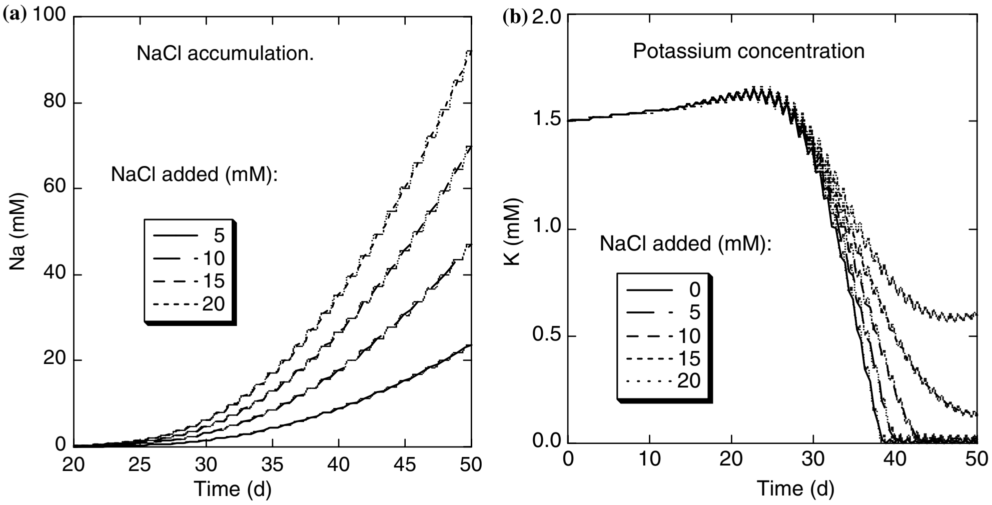

Figure 4. Calculated sodium accumulation (a) and potassium depletion (b) with time due to plant uptake and salinity level of the added water.

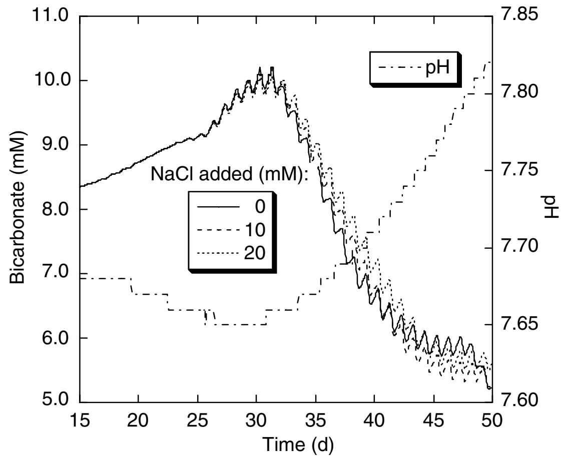

Figure 5. Calculated pH (rises) and bicarbonate concentration (decreases) in the growth medium with time from planting as affected by three NaCl concentrations added with the water and accumulate (see Fig. 4a).

system (Figure 4a) is highly affected by its concentration in the added water, and it reduces the uptake of a sensitive nutrients as K (Figure 4b), whose depletion is negatively affected by Na accumulation; its concentration might even increase as a result of lower depletion and accumulation due to water transpiration, as in the case of NH_4-N depletion (not presented).

Sodium chloride accumulation in the growth medium both suppress nutrient uptake, which is probably the reason for the changes of HCO_3^- with Na accumulation (Figure 5). The different pace of uptake, however, resulted in changes in HCO_3^- concentration with nutrient depletion (with time), but with little or no changes in the solution pH. Note that the two parameters change in opposite directions, due to Ca depletion (Figure 6), but also by the change in mono- and di-phosphate ratio (Equations 14a–c).

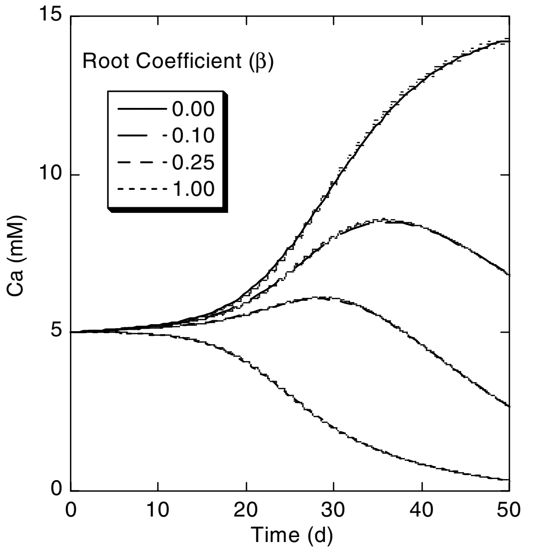

Figure 6. Calculated Ca concentration depletion in the growth medium solution with time from planting due to uptake by active plus the transpiration stream, with different values of root coefficients for transpiration flux (*β*, Eq. (13b)).

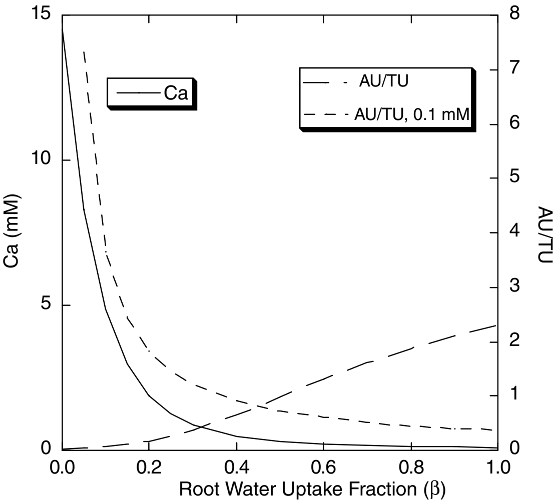

Figure 7. Calculated ratio of Ca active uptake (AU) and passive uptake by the transpiration stream (TU) with different values of root fraction that contributes to TU (*β*, Eq. (13b)). AU/TU ratio was calculated for 40 days (at mid-day) of Ca depletion (Ca) due to uptake by grown plants, or when Ca concentration was kept constant at 0.1 m*M* (AU/TU, 0.1 m*M*).

The contribution of the transpiration stream to Ca influx is addressed in Figures 6 and 7. In Figure 6, Ca concentration change due to uptake by growing plants with time is highly affected by *β*, the coefficient of the root fraction involved (Equation 13b). The relative contribution of active and passive (via the transpiration stream) Ca uptake is illustrated in Figure 7, with plants of constant size: the ratio between active uptake AU by Michaelis–Menten influx function of concentration (Equation 13b), and passive uptake TU by the transpiration stream (AU/TU) increased with root active fraction *β*, because it was associated with a decrease in Ca concentration (Ca), after a constant period of 40 days of uptake. When Ca concentration was kept constant at 0.1 m*M*

(AU/TU, 0.1 m*M*), this ratio decreased with the increase in β. That is, because active uptake was constant, but passive uptake increased.

Discussion

Water flow in saturation

Some simplifications were made in this model regarding the nature of water flow. The assumption of flow under saturation in the wetted portion of the matrix is of question (Otten et al., 1999). Drying-wetting cycles are hysteretic by nature (da Silva et al., 1995; Otten et al., 1999). Also, both moisture retention and hydraulic conductivity decrease with progressive wetting cycles (da Silva et al., 1995). Although the moisture content drops below saturation, the hydraulic conductivity would not change much up to 1 kPa water suction, which corresponds to the 10 cm thickness of an NFT soilless system (Fonteno, 1989). Consequently, changes in the hydraulic conductivity due to hydraulic head in this range are small (da Silva et al., 1995), which makes the above assumption valid. As the substrate is very thin, gas exchange typically does not restrict root respiration, as the solution is continuously recycled, dripped and flows, unlike roots grown in soils. Furthermore, the hysteretic behavior of water retention is believed to be due to a large portion of entrapped air (da Silva et al., 1995), which also enhances gas exchange.

Effect of circulation rate

Figure 3a illustrates the combined effect of two means of solution circulation: the nominal discharge rate of an emitter and number of emitters (dictated by the distance when the total length of the line is constant) should be equivalent. The simulation yields, however, that the change in K concentration with d after 35 days is curvilinear. Furthermore, the difference between the concentrations with different q values is not constant at small d values. Higher circulation rate means a faster mixing rate with the solution in the reservoir. As uptake is a function of concentration, and its non-linearity increasing when the concentration drops closer to K_m, higher circulation rate means also keeping K concentration relatively higher, which in turn affects uptake. The same mechanism is effective in the effect of the hydraulic conductivity of the substrate (Figure 3b).

Sodium accumulation and nutrient uptake

Sodium accumulation in the system (Figure 4a) is highly affected by its concentration in the added water; it directly reduces the uptake of a sensitive nutrient as K^+ (Figure 4b), but also indirectly reduces uptake by the reduction of growth, both of shoot and root (Equations 10 and 11). The result is that the depletion of K^+ concentration in the growth medium due to uptake changes its trend, and the concentration should even increase when Na accumulates in the growth solution due to transpiration. Similar behavior of the model was obtained also with NO_3^-- and NH_4^+-N.

Bicarbonate and pH

Under non-saline conditions, pH of the medium during 50 days of simulated growth and uptake only slightly increased, from 7.6 to 7.8, while HCO_3^- ion decreased from 10 to 5 m*M* (Figure 5). This opposite trend does not agree with Pearce et al. (1999). In the cited reference, however, bicarbonate was added as $NaHCO_3$, so bicarbonate was directly associated with the salinity level. It resulted in a positive correlation between Na, HCO_3^- and pH, unlike the results presented in Figures 4 and 5, where these changes are the result of ionic balance (Equations 14a–c, Table 2).

Calcium uptake by the transpiration stream

The contribution of the transpiration stream to Ca uptake and mobility in plants varies widely. Extent of the contribution of this mechanism to Ca uptake is genetically and physiologically controlled (Mengel and Kirkby, 2001). Calculation based on data of Adams and Ho (1993) for fruiting tomato plants revealed uptake of 1.67 mmol Ca per l transpired water; this value is about an order of magnitude higher than the simulated value for grown plants (Figure 7), and it decreases with the increase of β, the root fraction which contributed to Ca uptake due to the transpiration stream. Adams and Ho (1993) did their measurements on fruiting tomatoes, where transpiration substantially enhanced Ca flow to the leaves and fruits. Also, their results are of short-period measurements, with widely stimulated transpiration. The value used for β in our simulations ($\beta = 0.25$) seems reasonable according to the rate of Ca depletion in the growth solution (Figure 6).

The proposed model, although it simplifies certain mechanisms, focuses on the main components of the soilless system. It may therefore be used for designing purposes, and to compose together conflicting processes that are effective in this system, both technical and physiological mechanisms.

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Appendix A. Parameters used in the model, their symbols and initial/constant values

Symbol	Parameter	Value	Reference
a ($= w \cdot d$)	Cell area	0.2 m^2	
AU, TU	Active, passive Ca uptake		
C, C_{ad}, C_{in}, C_{out}	Concentration, added, into, out soln.	0.1, 100 mM	Kafkafi and Bernstein (1996)
C^{Na}_{Cr} $C^{Na}_{0.5}$	Na concentration: critical, half-growth		
d	Distance between emitters	0.5 m	
f_0, f_T	Basal and time fraction for pump	0.0084	Silberbush (unpublished)
I, i	Ion index, cell no. index		
H, h	Outlet height, hydraulic head	0.1 m	
J, J_{max}, K_m, C_{min}	Ion influx and influx parameters		
K_1, K_2, k	Root and shoot growth parameters	770, 500, 0.25	Silberbush (unpublished)
K_I, K_{sp}	Dissociation coef., solubility product		
K_s	Saturated hydraulic conductivity	0.5 m h^{-1}	Raviv et al. (2001)
L	Channel length	10 m	
LAI, LAI_{max}	Leaf area index, maximal LAI	4 m^2 m^{-2}	Ben-Asher (unpublished)
NFT	Nutrient Film Technique		
P-ratio	$HPO_4^{2-}/H2PO_4^-$ ratio		
P^{Na}_m	Coef. of passive Na influx	2.5×10^{-11} m s^{-1}	Sonneveld et al. (1999)
q	Emitter discharge rate	dm^3 1 h^{-1}	
Q, Q_{out}	Moisture flow rate, flow rate out		
r_0	Mean root radius		
RL, RL_0, RA	Root length, initial RL, Root area		
RL_{max}	Maximal RL	800 m $plant^{-1}$	
S	Sink/uptake		
Δt, t, τ	Time step, running time, day number	1 h	
T_{max}, T_{rel}, T	Maximal, Relative, Transpiration	4 mm day^{-1}	Ben-Asher (unpublished)
V_R, V	Reservoir volume, moisture volume	1 m^3	
w	Channel width	0.4 m	
α	Channel slope angle	$\sin \alpha = 0.01$	
β	Root active fraction (Ca uptake)	0.25	
θ_s, θ_r	Moisture at saturation, residual	0.84, 0.15	da Silva et al. (1995)

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