

Uptake of nutrients by lettuce on NFT with controlled composition of the nutrient solution

M. HEINEN, A. DE JAGER* & H. NIERS

Institute for Soil Fertility Research (IB-DLO), P.O. Box 30003, NL 9750 RA Haren, Netherlands

Received 9 January 1991; accepted 30 May 1991

Abstract

An automatically controlled NFT system was developed consisting of a growth unit and a measuring and control unit. A preliminary experiment with lettuce (*Lactuca sativa*, cv. Sitionia) was carried out. Unfortunately, the measuring and control system failed, so that manual control and dosage was necessary. The percentage dry matter of the heads decreased from 6.86 (week 1, 20/6/88) to 3.89 (week 6, 25/7/88). The shoot/root ratio increased from 0.50 (week 1) to 6.47 (week 6). The time courses of dry weight and cumulative uptake of macronutrients were well described by exponential equations. The cumulative uptake determined from the loss of nutrients from the nutrient solution exceeded the cumulative uptake determined from plant analysis. Cumulative uptake against cumulative daily radiation was well described by a logistic equation. Some constant plant uptake ratios between micro- and macronutrients were observed: Cl was related to N, K, P or Mg, and B to K. Dry weight as a function of transpiration was also well described by a logistic model, with an average dry mass production of 3.1 g per liter transpiration. Transpiration as a function of radiation was well described by a logistic model, with an average transpiration of 5.8 l per unit (kJ cm^{-2} increase in radiation).

Keywords: nutrient film technique, NFT, lettuce, *Lactuca sativa*, nutrient uptake, growth and uptake models

Introduction

With soilless culture systems, such as nutrient film technique (NFT) or growing methods based on rockwool, a better control of crop production (quantity and quality) may be possible than with soil-based systems. In free drainage systems, nutrient losses of 40 to 70 % have been observed (de Willigen & van Noordwijk, 1987). In recirculating systems, water and fertilizer use are more efficient, and environmental pollution is reduced. With inert artificial substrates, which have a small buffer ca-

* Present address: Research Station for Fruit Growing, Brugstraat 51, 4475 AN Wilhelminadorp, Netherlands.

capacity, the composition of the nutrient solution can be easily monitored and adjusted. For this purpose a reliable measuring and control system is required. With such a system uptake patterns of a crop can be determined. The composition of the nutrient solution may be kept constant, or changed according to the demand of the crop. The (long-term) uptake of some nutrients (e.g. N, K) is almost independent of the nutrient concentration at the root-solution interface, provided that it is not too low and that other growth conditions (e.g. radiation) are not limiting (Pitman, 1976; Clarkson, 1985; de Jager, 1985; de Willigen & van Noordwijk, 1987). However, since other nutrients do not show steady state uptake, and since the internal regulation system, which accounts for the uptake, may not adapt rapidly to external fluctuations, it is advantageous to keep the concentration of the nutrient solution constant. Ingestad & Lund (1986) proposed a system in which the addition rate of nutrients into the nutrient solution equals the growth and uptake rate of the crop. For a constant relative growth rate, i.e. exponential growth, the nutrient content in the crop will then remain constant. NFT systems (as described by e.g. Cooper, 1979; Graves, 1983; Hall & Wilson, 1986; Wild et al., 1988; Winsor et al., 1979) are suitable to study uptake patterns under commercial conditions, since they have the smallest buffering, i.e. changes can be observed rapidly, and mixing is almost complete.

Water cultures have long been used to determine uptake patterns. A first publication stems from 1660 (Steiner, 1985). Nowadays, controlled NFT systems are used, with a measuring device consisting of ion-selective electrodes (ISE) (e.g. Albery et al., 1986a,b; Bailey et al., 1988; Blom-Zandstra & Jupijn, 1987; Clement et al., 1974, 1978a,b; Glass et al., 1987). ISE measurements are fast, nondestructive, direct and cheap. However, there are also some disadvantages, such as dependence upon temperature, background concentration, and interfering ions (Cammann, 1973, 1980). Bailey et al. (1988) investigated ISE performance installed in an NFT system. They found a decrease in sensitivity and zero-potential with time. To deal with this problem they suggested regular calibrations. The life of a pH glass electrode exceeded 2 years. PVC electrodes for nitrate, potassium and calcium had life spans of 4 and 2 months and of less than 1 month, respectively, making them unattractive for applications on a broad scale.

The purpose of this study was to develop a recirculating NFT system equipped with a reliable measuring and control system, and to use it to study uptake patterns of different crops. In this way a general control model for practical use may be obtained. The system was kept simple so as to be of interest to commercial growers.

A description of the NFT system is presented together with some basic growth and uptake models. Results of a preliminary experiment with lettuce are given.

Materials and methods

Experimental performance

During the period of 13/06/88 until 25/07/88, 144 lettuce (*Lactuca sativa*, cv. Sitonia) plants in peat blocks (4 × 4 × 4 cm) were grown on recirculating NFT system.

Table 1. Set points for the macro- (mmol l^{-1}) and micronutrients ($\mu\text{mol l}^{-1}$) and pH of the nutrient solution, and the salt concentrations of the stock solutions (mol l^{-1}); N was supplied as NO_3 only.

Macro-element	Set point	Micro-element	Set point	Salt	Concentration
N	10.003	Fe	179	$\text{Ca}(\text{NO}_3)_2$	0.595
P	0.667	Mn	6.73	$\text{Mg}(\text{NO}_3)_2$	0.149
K	5.254	B	32.60	KNO_3	0.857
Ca	2.344	Cu	0.58	HNO_3	0.100
Mg	0.784	Zn	2.00	KOH	0.100
S	0.336	Mo	0.41	KH_2PO_4	0.247
		Cl	166	K_2SO_4	0.250
pH	6.0			MgSO_4	0.580
				CaCl_2	0.100

From a supply tank (capacity 400 l), nutrient solution (demineralized water containing 13 nutrients, Table 1) is pumped into 12 gullies, each being 326.5 cm long, 23.5 cm wide and 4.0 cm deep. The gullies have a slope of 1:75 facing south. Just before each plant position incomplete V-shaped thresholds were put in to force the solution to flow to the plants. At the end of the gullies the excess solution is collected in a drainage vessel (capacity 53 l) from where it is pumped back into the supply tank. The glasshouse temperature was set at 15 °C (ventilating at 17 °C) during the day, and at 10 °C during the night. Demineralized water was added daily to the supply tank to replenish the amount of transpiration. One hundred plants were used for harvest at $t = 0$. Each week, a number of randomly chosen plants (48, 24, 24, 24, 12, 12, respectively) were harvested. The random pattern was adjusted such that the remaining plants all had identical growing environments. The positions from which plants were removed were covered to prevent evaporation. The harvested plants were subdivided into heads, roots outside the peat blocks and peat blocks including roots. Fresh weight and dry weight (after oven-drying at 70 °C) were determined, the separate parts were also analysed for macro- and micronutrients. To determine the total root mass the following procedure was used. At $t = 0$ the dry weight of roots washed from several peat blocks was obtained. This gives an estimated initial root weight, since it was not possible to wash out all the roots. At the remaining harvest times the dry weights of the roots inside the peat blocks were obtained from the increase in dry weights of the peat blocks; it was assumed that the dry weight of the peat did not change during the experiment. At the harvest times, nutrient solution samples were taken for macro- and micronutrient analysis. Between harvest times, extra nutrient solution samples were taken to monitor the decrease in concentration in more detail and to determine if intermediate nutrient supplies were correct. Samples were taken one hour after demineralized water was added to the supply tank.

Control of the composition of the nutrient solution

The NFT system was equipped with an automatic measuring and control device.

However, this system failed so that manual control became necessary. The aim was to keep the concentration of the nutrient solution at a constant level. Initially it was assumed that the uptake of nutrients occurs at the same ratios as the average content ratios observed for lettuce by Roorda van Eysinga & Smilde (1971): N:P:S:K:Ca:Mg:Cl is 1.0:0.09:0.025:0.481:0.107:0.069:0.169. Each day the NO_3 concentration of the nutrient solution was determined, so that the daily uptake of N was known from which the daily uptake of the other nutrients could be calculated using the above ratios. Next the amounts of stock solutions (Table 1) to be added were calculated using the metering scheme described below. The above-mentioned ratios were checked and (if necessary) adjusted on the basis of the biweekly analyses of the nutrient solution.

Metering system

Firstly, the amounts to be supplied are corrected (arbitrarily) so that an electrically neutral solution is obtained. If the sum of anions (SA) is larger than the sum of cations (SC), the anion concentrations are multiplied by the ratio SC/SA. For the other case the cation concentrations are multiplied by the factor SA/SC. Then the amounts of salts to be added are calculated (Table 2). The element concentration is the amount of element (mmol) to be added to one liter of nutrient solution. The salt concentration is the concentration of the stock solution (mol l^{-1}). Division of these two gives the amount of stock solution (ml) to be added to one liter of nutrient solution. Finally, to obtain the volume to be added to the whole system, this amount is multiplied by the system volume. The amounts of KH_2PO_4 , CaCl_2 , HNO_3 , KOH

Table 2. Salt dosing scheme. The salt formula represents the amount of salt solution (ml) to be added to 1 l of nutrient solution. Square brackets represent the concentrations of the elements to be added and the salt concentrations of the stock solutions.

CaCl_2	=	$0.5 \cdot [\text{Cl}]/[\text{CaCl}_2]$
HNO_3	=	$[\text{H}]/[\text{HNO}_3]$
KOH	=	$[\text{OH}]/[\text{KOH}]$
KH_2PO_4	=	$[\text{P}]/[\text{KH}_2\text{PO}_4]$
$\text{Ca}(\text{NO}_3)_2$	=	$\{[\text{Ca}] - 0.5 \cdot [\text{Cl}]\}/[\text{Ca}(\text{NO}_3)_2]$

If $[\text{N}] < \{2 \cdot [\text{Ca}] + 2 \cdot [\text{Mg}] + [\text{H}] - [\text{Cl}]\}$ then:

KNO_3	=	0
$\text{Mg}(\text{NO}_3)_2$	=	$\{0.5 \cdot [\text{N}] + 0.5 \cdot [\text{Cl}] - [\text{Ca}] - 0.5 \cdot [\text{H}]\}/[\text{Mg}(\text{NO}_3)_2]$
MgSO_4	=	$\{[\text{Mg}] + [\text{Ca}] + 0.5 \cdot [\text{H}] - 0.5 \cdot [\text{Cl}] - 0.5 \cdot [\text{N}]\}/[\text{MgSO}_4]$
K_2SO_4	=	$\{0.5 \cdot [\text{K}] - 0.5 \cdot [\text{P}] - 0.5 \cdot [\text{OH}]\}/[\text{K}_2\text{SO}_4]$

Otherwise:

MgSO_4	=	0
$\text{Mg}(\text{NO}_3)_2$	=	$[\text{Mg}]/[\text{Mg}(\text{NO}_3)_2]$
K_2SO_4	=	$[\text{S}]/[\text{K}_2\text{SO}_4]$
KNO_3	=	$\{[\text{N}] - 2 \cdot [\text{Ca}] - 2 \cdot [\text{Mg}] - [\text{H}] + [\text{Cl}]\}/[\text{KNO}_3]$

and $\text{Ca}(\text{NO}_3)_2$ are determined by the respective amounts of P, Cl, H, OH and Ca (minus the amount given through CaCl_2) required (Table 2). For the remaining four salts, one of the two following calculation schemes is used.

Scheme 1: if the amount of NO_3 to be added is smaller than the sum of $2 \cdot \text{Ca} + 2 \cdot \text{Mg} + \text{H} - \text{Cl}$, no KNO_3 is added and the amounts of NO_3 , Mg and K to be added are complemented by $\text{Mg}(\text{NO}_3)_2$, MgSO_4 and K_2SO_4 , respectively (Table 2).

Scheme 2: if the condition of Scheme 1 is not met, then no MgSO_4 is added. All Mg and S is added as $\text{Mg}(\text{NO}_3)_2$ and K_2SO_4 , respectively. Then the amount of NO_3 to be added is complemented by KNO_3 (Table 2).

There is no unique dosage possible to supply the nine elements. In Scheme 1 the true amount of SO_4 added is not based upon the need for SO_4 , while in Scheme 2 this is true for K. The metering schemes are valid for certain boundary conditions in order to obtain positive additions. Epstein (1972; Table 4-3) presented the average composition of a plant. Assuming that the uptake ratios of the nutrients are equal to these average ratios of atoms present in a plant, these boundary conditions are met.

Uptake of nutrients by the plant and their decrease in solution

Due to the uptake of nutrients by the crop, the amount of nutrients increases in the plant and decreases in the solution. The total loss from the nutrient solution can be expressed as the uptake by the plants and the accumulation in peat blocks in which the plants were grown:

$$U = N \cdot (A_t - A_{t-1}) \quad (1)$$

U (mmol week^{-1}) is the total uptake by N plants plus peat blocks during the time interval of one week. A_t and A_{t-1} (mmol) are the nutrient contents of a plant plus peat block at the end and at the start of a week, respectively.

The total uptake is compared with the loss of nutrients from the solution. The loss of nutrient from the solution is defined as:

$$L = (C_{t-1} - C_t + D) \cdot V \quad (2)$$

L (mmol week^{-1}) is the loss of nutrient from the solution. C_t and C_{t-1} (mmol l^{-1}) are the nutrient concentrations at the end and at the start of a week, respectively. D is the amount of nutrient added to the nutrient solution during the week (mmol l^{-1}), and V is the volume of system ($= 300 \text{ l}$). Ideally the nutrient concentration of the solution is constant so that $C_{t-1} = C_t$ and thus $L = D \cdot V$.

Modelling growth

France & Thornley (1984) described several exponential growth curves. In this study the dry mass and the cumulative uptake of macronutrients were fitted to the ordi-

nary logistic (Equation 3), the Gompertz (Equation 4), the general logistic or Richards (Equation 5), and a second-order exponential polynome (Equation 6), using Genstat 5 (Genstat 5 Committee, 1987):

$$W_{i1} = \frac{W_{i1} \cdot W_{f1}}{W_{i1} + (W_{f1} - W_{i1}) \cdot \exp(-k_1 \cdot t)} \quad (3)$$

$$W_{i2} = W_{i2} \cdot \exp \left[\frac{k_0 \cdot (1 - \exp(-k_2 \cdot t))}{k_2} \right] = W_{i2} \cdot \exp \left[\frac{-k_0 \cdot \exp(-k_2 \cdot t)}{k_2} \right] \quad (4)$$

$$W_{i3} = \frac{W_{i3} \cdot W_{f3}}{[W_{i3}^n + (W_{f3}^n - W_{i3}^n) \cdot \exp(-k_3 \cdot t)]^{1/n}} \quad (5)$$

$$W_{i4} = \exp(a + b \cdot t + c \cdot t^2) \quad (6)$$

W_i represents the mass or cumulative uptake at time t . Subscripts 1 through 4 are used to distinguish between the four models. The notation $\exp(x)$ represents e^x (approved by the international standards ISO 31/XI, 1978). W_i represents the initial weight at $t = 0$, W_f the final weight for $t \rightarrow \infty$, and k is a proportionality factor and a measure of the relative growth rate at the point of inflection (if present). Parameter n determines the shape of the curve and should be ≥ -1 in order to achieve a finite growth rate in the limit $W \rightarrow 0$. For $n = 0$ and 1 the Richards equation reduces to the Gompertz and logistic equations, respectively. Parameter a equals the weight at $t = 0$, b equals the relative growth rate at $t = 0$, and c is a measure of the difference between the times at which inflection and maximum of the second-order exponential polynome occur and a measure of the relative growth rate at the point of inflection.

The logistic and Richards models assume that the growth rate (dW/dt) is proportional (proportionality factor k) to the plant mass already formed (W) and to the difference ($W_f - W$). The Gompertz model assumes that the growth rate is proportional to W , but the proportionality parameter decreases with time according to first-order kinetics, which can be ascribed to ageing or differentiation. The second-order exponential polynome does not have a physiological background.

Results and discussion

Fresh and dry weights

The fresh and dry weights and the percentage dry matter of the lettuce heads are presented in Table 3, together with the dry weights of the roots out- and inside the peat blocks. After the first week a decrease in percentage dry matter with time was observed. This is in good agreement with results of Hansen (1976) who obtained dry matter percentages between 6.33 and 3.63, and between 6.53 and 3.93 during (early) spring growth, with a maximum dry weight of about 11 g per head. Roorda van Eysinga & Smilde (1971) observed a (final) percentage dry matter of healthy lettuce

Table 3. Fresh and dry weights (g) and percentage dry matter (%DM) of the lettuce heads, and the dry weights (g) of the roots outside and inside the peat blocks at seven weekly harvest times per plant.

Week	Head			Root dry weight	
	fresh weight	dry weight	% DM	outside	inside
0	0.94	0.06	6.56	0.001	0.005
1	7.23	0.48	6.86	0.006	0.960
2	35.78	1.80	5.07	0.045	1.470
3	91.38	4.95	5.47	0.144	1.670
4	253.57	12.33	4.87	0.362	1.870
5	385.65	15.77	4.11	0.433	2.070
6	478.23	18.53	3.89	0.593	2.270

heads grown under glass ranging from 3.5 to 5.5.

The shoot/root ratios increased from 0.50 in week one to 6.47 at the end of the experiment. They are in good agreement with values for 'butterhead' lettuce cultivars calculated (assuming 5 % dry matter) from data by Reinink & Eenink (1988), Silva & Toop (1986), and Toop et al. (1988): 6.5 - 8.5. The shoot/root ratio at the start of the experiment (10) is unrealistically high. This can be explained by the fact

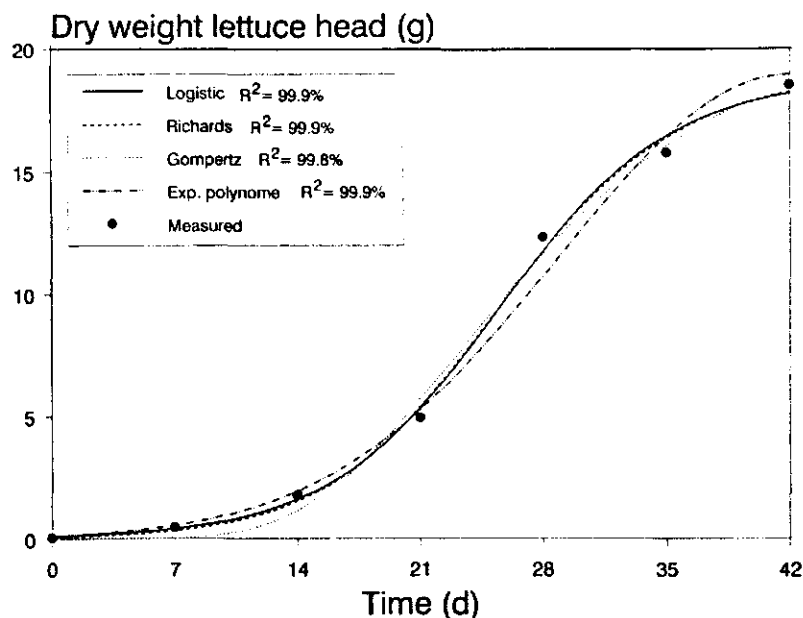


Fig. 1. Dry lettuce head weight versus time. Measured data adapted to four growth models: logistic (Eq. 3), Richards (Eq. 4), Gompertz (Eq. 5), and second-order exponential polynome (Eq. 6).

that at $t = 0$ not all the roots could be washed out of the peat blocks, so that this shoot/root ratio is overestimated.

The head dry weight data (but also the head fresh, and plant fresh and dry weight data; not shown here) were well described by the growth models Equations 3-6 (Figure 1). In the fitting procedure the second-order exponential polynome was forced to achieve its maximum at the last harvest time. The Gompertz curve was less satisfactory in the beginning, and better at the end. The second-order exponential polynome fitted closely in the beginning and less so at the end. On average, the logistic and the Richards curves described growth well. S-shaped dry matter production was also observed with lettuce grown in soils (Slangen et al., 1987).

Cumulative uptake

In Table 4 the cumulative uptake of the macronutrients is presented for the plants (shoot plus roots), and plants plus peat blocks. These values were obtained from Equation 1. The loss from the nutrient solution (using Equation 2) is also presented in Table 4, as well as the cumulative uptake of Cl and Na and the cumulative loss of Cl, Na and H. The cumulative loss from the nutrient solution should be compared with the cumulative uptake by the plant plus peat block. Both uptake balances showed electrically neutral uptake. It was assumed that the net uptake of H equals the net loss from the nutrient solution. The difference between the sum of anions and the sum of cations is less than 10 % after week three. However, in general the cumulative loss from the nutrient solution exceeded the cumulative uptake by plants plus peat blocks for all macronutrients. For example, the ratio loss/uptake for N varied between 1.2 (week 4) and 2.0 (week 1), for K (week 1 excluded) between 1.1 (week 4) and 1.7 (week 2), and for P between 1.0 (week 6) and 1.5 (week 2). Possible sources of error are: two different laboratories were involved: one for analysis of the solution samples, and one for the plant samples; there has been a small leak in the system, so that there was always an extra loss of nutrients (there was, however, no unique leakage discharge which can explain the difference); some poor plant material had been removed before harvesting, so that nutrients present in this material were not measured; immobilization by microorganisms present in peat and solution; precipitation of salts; denitrification. Willumsen (1980, 1984) expected that due to immobilization and/or precipitation the total consumption, i.e. loss from nutrient solution, will not be equal to the uptake. For lettuce he observed no great differences between the two mass balances, but for tomato the difference was between about 10 % for N up to a maximum of 35 % for P, with no difference for K.

The cumulative uptake in time by one lettuce plant was well described by the models Equations 3-6. Figure 2 shows the results for the logistic model. It presents the relative cumulative uptake, i.e. the cumulative uptake divided by the fitted W_f value. For comparison the relative dry weight is also presented. The relative cumulative uptake of N, K, B, Zn and Cl (and to a lesser extent of Ca, Mg and S) has the same shape as the relative growth rate, i.e. the content of these elements in the plant remains constant. The uptake of P was relatively smaller as plants grew older, while

Table 4. Cumulative uptake by plant and plant plus peat block, and loss from nutrient solution per plant for macronutrients N, P, S, K, Ca and Mg, and for Cl, Na and H (mmol per plant) as obtained from Equations 1 and 2.

Week	Plant			Plant + peat			Loss		
	N	P ¹	S ²	N	P ¹	S ²	N	P	S
1	5.91	0.44	0.03	2.55	0.30	0.33	4.99	0.35	-0.22
2	12.95	0.86	0.09	7.34	0.71	0.15	12.10	1.03	0.28
3	24.09	1.90	0.24	17.94	1.76	0.25	28.65	2.03	-0.14
4	53.81	3.94	0.98	47.34	3.80	0.67	58.19	5.28	0.49
5	70.48	5.52	1.09	64.65	5.38	0.71	81.94	6.41	1.74
6	77.95	7.28	1.58	71.80	7.14	1.13	129.36	7.16	9.90

Week	K ³	Ca ⁴	Mg ⁴	K ³	Ca ⁴	Mg ⁴	K	Ca	Mg
	1	0.84	0.11	0.05	0.62	0.74	0.09	3.39	1.24
2	4.05	0.68	0.29	3.83	1.21	0.27	6.53	1.06	0.07
3	14.96	1.30	0.56	14.74	2.32	0.55	17.81	3.21	0.90
4	37.11	2.75	1.25	36.90	4.57	1.29	40.19	5.15	1.53
5	48.18	3.50	1.74	47.96	5.44	1.58	57.65	10.23	1.94
6	54.12	4.32	2.04	53.90	6.35	1.91	87.81	15.98	6.61

Week	Cl	Na ³	Cl	Na ³	Cl	Na	H
	1	0.14	0.02	0.08	-0.01	-1.11	-0.42
2	0.32	0.06	0.20	-0.03	1.84	0.63	0.63
3	0.80	0.21	0.70	0.06	0.00	-1.67	2.71
4	2.03	0.43	1.90	0.30	1.88	2.50	7.50
5	2.78	0.38	2.64	0.24	1.25	-2.50	11.25
6	3.16	0.45	3.03	0.30	2.50	7.50	13.75

¹ No P analysis of root at $t = 0$ due to small root mass.

² No S analysis of shoot at $t = 0$, and of root $t = 0, 1, 2, 3, 4$ due to small shoot or root mass.

³ No K and Na analysis of root at $t = 0, 1, 2$ due to small root mass.

⁴ No Ca and Mg analysis at $t = 0, 1$ due to small root mass.

uptake of Fe, Mn and Na was relatively larger. S-shaped uptake of N, P, K, Ca, and to a lesser extent also of Mg and Cl, was observed in lettuce grown in soils (Slangen et al., 1987).

The cumulative uptake of macronutrients as a function of cumulative radiation was well described by a logistic model (cf Equation 3). In Figure 3 the relative cumulative uptake of N, P and K versus cumulative radiation is presented. For tomato, Adams & Massey (1984) found a linear correlation between N as well as K uptake and radiation with coefficients of correlation equal to 0.91 and 0.94, respectively.

During the last four weeks of the experiment, some constant ratios of cumulative uptake, loss and content (Table 5) between macro- and micronutrients were observed. For this purpose an arbitrary difference of 20 % between maximum and minimum ratio was allowed (in relation to their mean). The cumulative uptake by the plants grown until a given week (case nr 1) and the matching loss from the nutrient

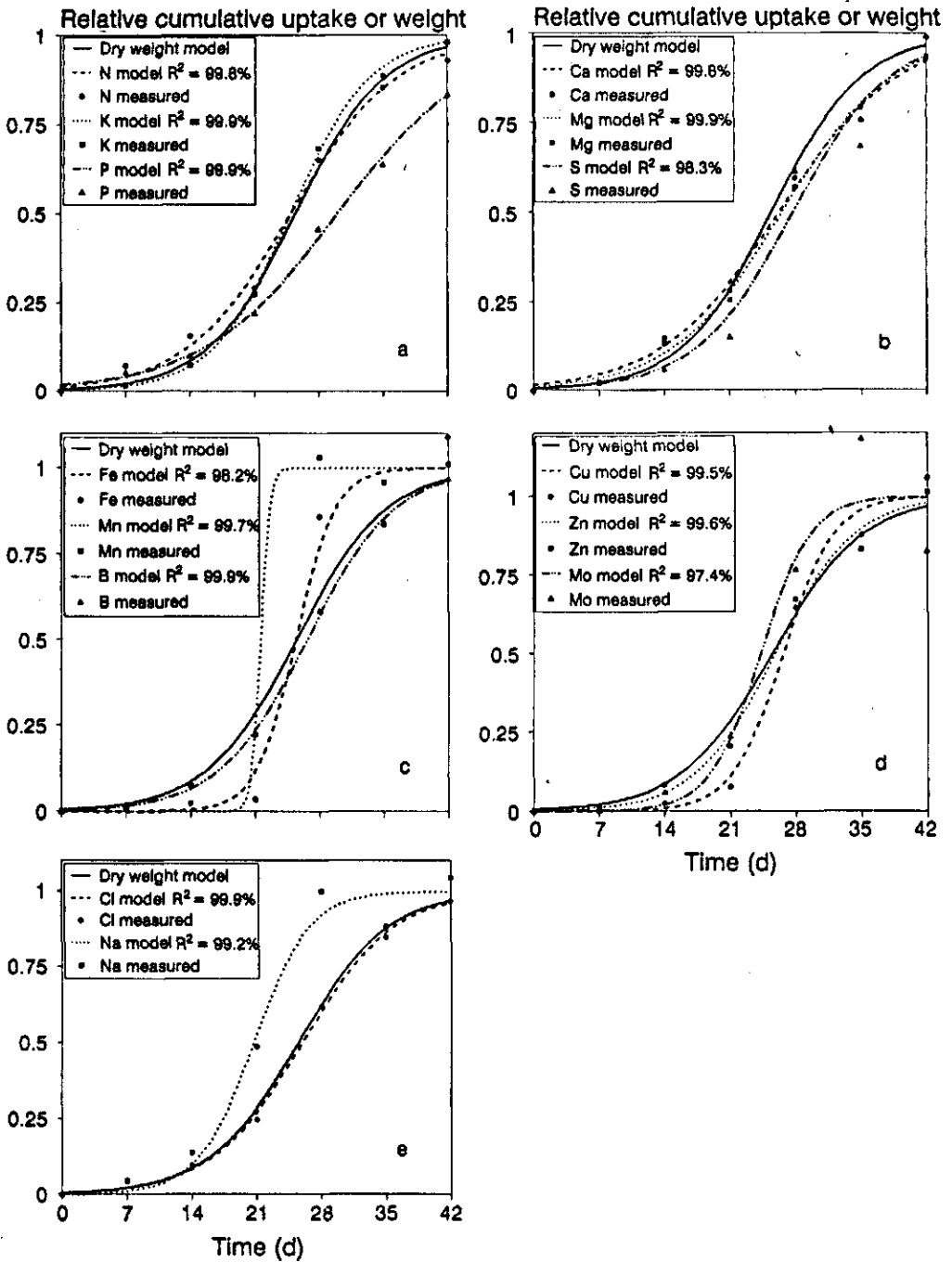


Fig. 2. Relative cumulative uptake of N, P, K, (a), Ca, Mg, S (b), Fe, Mn, B (c), Cu, Zn, Mo (d), and Cl, Na (e) by one lettuce head, and relative dry weight as a function of time. Measured data are described with the logistic model (Eq. 3).

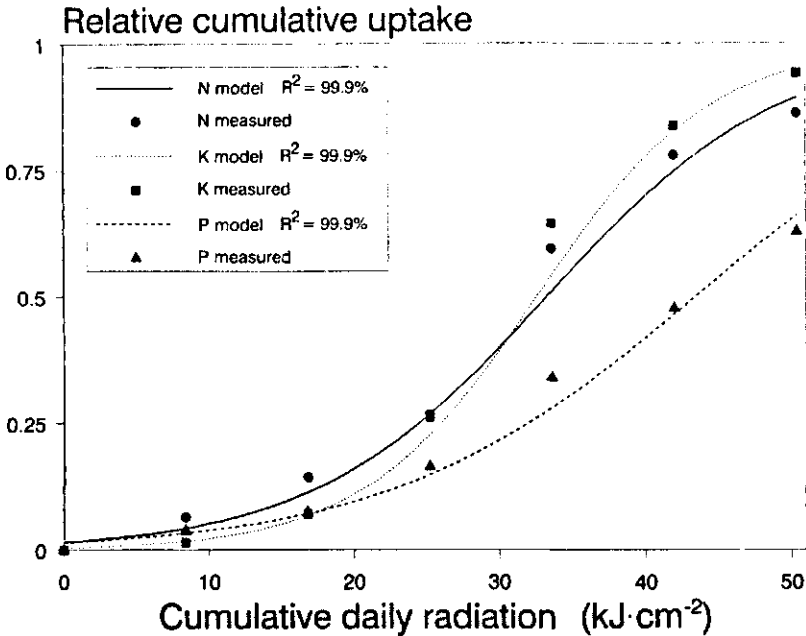


Fig. 3. Relative cumulative uptake of N, P, and K by one lettuce head as a function of cumulative daily radiation. Measured data are described with the logistic model (Eq. 3).

solution (case nr 2) do not have any common ratios, except for the ratios between N, P and K. The head content (case nr 4) and the plant content or cumulative uptake by one plant (case nr 3) have common ratios, which are equal to each other. When considering constant uptake ratios between a micro- and a macronutrient, Table 5 shows that, based upon cumulative uptake by one plant (case nr 3), Cl may be added in relation to N, K, P or Mg, and B in relation to K. Based upon head content (case (case 4), Cl may be added in relation to N, K, Ca or Mg, and B in relation to N, K, P, Ca or Mg, and Zn in relation to N, Ca or Mg, and Cu in relation to P. The cumulative uptake by plant plus peat block gave only four constant ratios (not shown here).

Water use

The transpiration per plant was calculated from the amounts of demineralized water added to the supply tank. The dry weight data as a function of the transpiration (both expressed per plant) were well described by a logistic model (cf Equation 3) (Figure 4). On average, the dry mass production was 3.1 g per liter transpired. The transpiration as a function of daily radiation (both expressed per plant) was well described by a logistic model (cf Equation 3) (Figure 5). On average, the transpiration was 5.8 l per unit increase in radiation.

Table 5. Uptake or content ratios between macro- (mmol) and micro- (μmol) nutrients, with less than 20 % difference between maximum and minimum observed ratios (in relation to their mean) during the last four weeks. If the difference was less than 10 % the ratio is printed bold. Four cases are considered: case nr 1: weekly cumulative uptake by whole system; case nr 2: weekly cumulative loss from solution by whole system; case nr 3: weekly cumulative uptake by one plant week or content of one plant at the end of every week; case nr 4: content of one head at the end of every week.

	K	P	Ca	Mg	S	Fe	Mn	B	Cu	Zn	Mo	Cl	Na
Case nr 1													
N	0.742	0.092		0.030				0.809				0.038	
K	1	0.124		0.040				1.091				0.052	
P		1		0.323	0.222			9.082					
Ca			1	0.241	0.168								
Mg				1	0.695			27.588					
S					1								
Fe						1	0.139						
Mn							1						
B								1				0.048	
Cu									1			0.234	
Zn										1			
Mo											1		
Cl												1	
Case nr 2													
N	0.647	0.079	0.112					0.487					
K	1	0.119						0.743					
P		1											
Ca			1					4.227					
Mg				1				17.678					
S					1								
Fe						1						0.001	
Mn							1						
B								1					
Cu									1	0.991			
Zn										1			
Mo											1		
Cl												1	

UPTAKE OF NUTRIENTS BY LETTUCE ON NFT

Table 5 continued.

	K	P	Ca	Mg	S	Fe	Mn	B	Cu	Zn	Mo	Cl	Na
Case nr 3													
N	0.658		0.053	0.025									0.037
K	1		0.080	0.036				0.985					0.056
P		1	0.646	0.299									0.472
Ca			1	0.464									
Mg				1									1.539
S					1								
Fe						1							
Mn							1						
B								1					0.058
Cu									1				
Zn										1			
Mo											1		
Cl												1	
Case nr 4													
N	0.714		0.052	0.026				0.830		0.200			0.043
K	1		0.074	0.036				1.162					0.061
P		1						10.936	0.543				
Ca			1	0.500				16.144		3.777			0.843
Mg				1				31.367		7.621			1.681
S					1								
Fe						1							
Mn							1						
B								1		0.244			0.053
Cu									1				
Zn										1			0.219
Mo											1		
Cl												1	

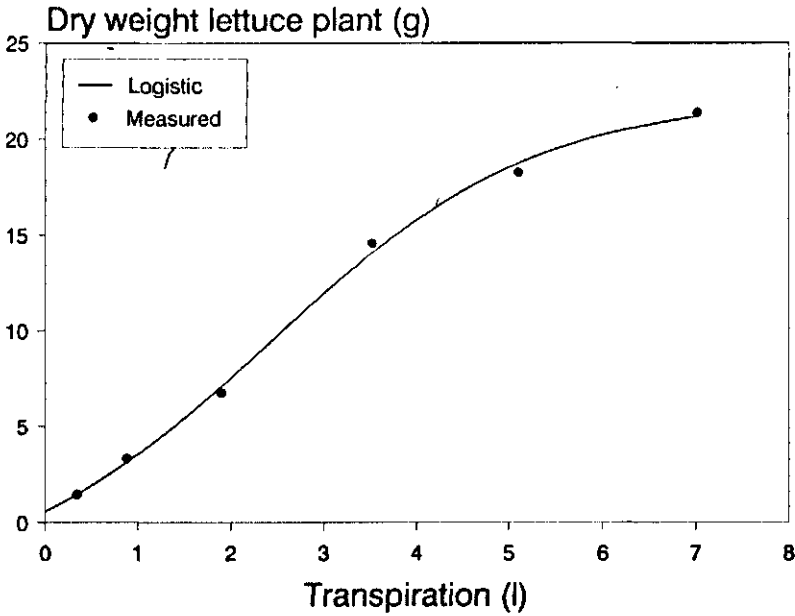


Fig. 4. Dry weight of lettuce as a function of transpiration expressed per plant. Measured data are described with the logistic model (Eq. 3).

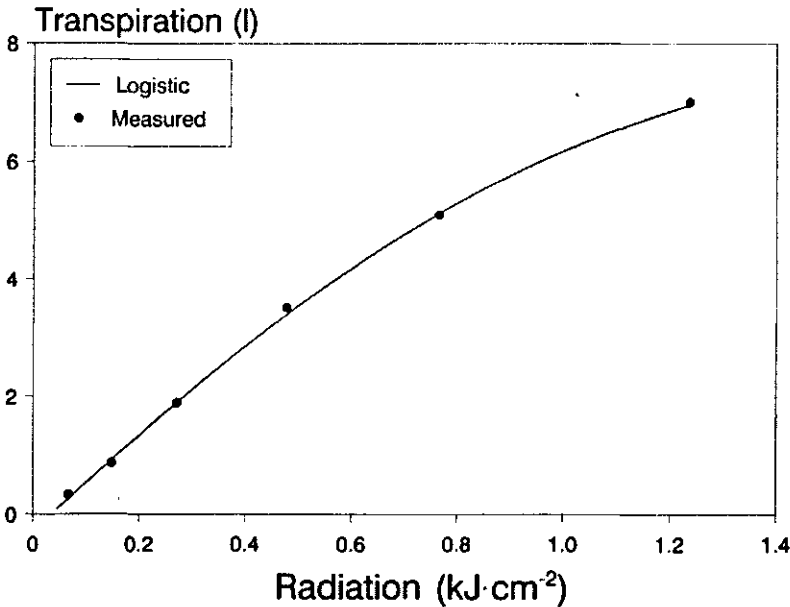


Fig. 5. Transpiration as a function of daily radiation expressed per plant. Measured data are described with the logistic model (Eq. 3).

Acknowledgements

This research was funded by the Dutch Directorate of Arable Farming and Horticulture. We thank P. Zandt for developing the computer program, and G. Heling and K. Boersma for constructing the technical parts of the system.

References

- Adams, P. & D. M. Massey, 1984. Nutrient uptake by tomatoes from recirculating solution. In: Proceedings 6th International Congress on Soilless Culture, p. 71-79. ISOSC, Wageningen.
- Albery, W. J., P. N. Bartlett, A. E. G. Cass, D. H. Craston & B. G. D. Haggett, 1986a. Electrochemical sensors: Theory and experiment. *Journal of the Chemical Society. Faraday Transactions. 1. Physical Chemistry* 82: 1033-1050.
- Albery, W. J., B. G. D. Haggett & L. R. Svanberg, 1986b. The development of electrochemical sensors. In: Gensler, W. G. (Ed.), *Advanced agricultural instrumentation: design and use. Proceedings of the NATO Advanced Study Institute on 'Advanced Agricultural Instruments'*, p. 349-392. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Bailey, B. J., B. G. D. Haggett, A. Hunter, W. J. Albery & L. R. Svanberg, 1988. Monitoring nutrient film solutions using ion-selective electrodes. *Journal of Agricultural Engineering Research* 40: 129-142.
- Blom-Zandstra, M. & G. L. Jupijn, 1987. A computer-controlled multi-titration system to study transpiration, OH⁻ efflux and nitrate uptake by intact lettuce plants (*Lactuca sativa* L.) under different environmental conditions. *Plant, Cell and Environment* 10: 545-550.
- Cammann, K., 1973. *Das Arbeiten mit ionenselektiven Elektroden*. Springer-Verlag, Berlin, 226 pp.
- Cammann, K., 1980. Fehlerquellen bei Messungen mit ionenselektiven Elektroden. In: Kienitz, H., R. Bock, W. Fresenius, W. Huber & G. Tölg (Eds.), *Analytiker Taschenbuch 1*, p. 245-267. Springer-Verlag, Berlin.
- Clarkson, D. T., 1985. Factors affecting mineral nutrient acquisition by plants. *Annual Review of Plant Physiology* 36: 77-115.
- Clement, C. R., M. J. Hopper, R. J. Canaway & L. H. P. Jones, 1974. A system for measuring the uptake of ions by plants from flowing solutions of controlled composition. *Journal of Experimental Botany* 25: 81-99.
- Clement, C. R., M. J. Hopper & L. H. P. Jones, 1978a. The uptake of nitrate by *Lolium perenne* from flowing nutrient solution. 1. Effect of NO₃-concentration. *Journal of Experimental Botany* 29: 453-464.
- Clement, C. R., M. J. Hopper, L. H. P. Jones & E. L. Leafe, 1978b. The uptake of nitrate by *Lolium perenne* from flowing nutrient solution. 2. Effect of light, defoliation, and relationship to CO₂ flux. *Journal of Experimental Botany* 29: 1173-1183.
- Cooper, A., 1979. *The ABC of NFT*. Grower Books, London, 255 pp.
- De Jager, A., 1985. Response of plants to a localized nutrient supply. Doctoral thesis, University of Utrecht, Netherlands, 137 pp.
- De Willigen, P. & M. Van Noordwijk, 1987. Roots, plant production and nutrient use efficiency. Doctoral thesis, Wageningen Agricultural University, Netherlands, 282 pp.
- Epstein, E., 1972. *Mineral nutrition of plants: principles and perspectives*. John Wiley and Sons, New York, 412 pp.
- France, J. & J. H. M. Thornley, 1984. *Mathematical models in agriculture: a quantitative approach to problems in agriculture and related sciences*. Butterworth, London, 335 pp.
- Genstat 5 Committee, 1987. *GENSTAT 5 reference manual*. Clarendon Press, Oxford, 749 pp.
- Glass, A. D. M., M. Saccomani, G. Crookall & M. Y. Siddiqi, 1987. A microcomputer-controlled system for the automatic measurement and maintenance of ion activities in nutrient solutions during their absorption by intact plants in hydroponic facilities. *Plant, Cell and Environment* 10: 375-381.
- Graves, J., 1983. The nutrient film technique. *Horticultural Reviews* 5: 1-44.

- Hall, D. A. & G. C. S. Wilson, 1986. The development of hydroponic culture in Scotland. *Research and Development in Agriculture* 3: 61-69.
- Hansen, H., 1976. The content of nitrate and protein in lettuce (*Lactuca sativa* var. *capitata* (Butterhead lettuce)) grown under different conditions. (In Danish with summary, figures and tables in English). *Tidsskrift Planteavl* 80: 370-380.
- Ingestad, T. & A. B. Lund, 1986. Theory and techniques for steady state mineral nutrition and growth of plants. *Scandinavian Journal of Forestry Research* 1: 439-453.
- Pitman, M. G., 1976. Ion uptake by plant roots. In: Lüttge, U & M. G. Pitman (Eds), *Encyclopedia of Plant Physiology, Vol 2B, Tissues and Organs*, p. 95-128. Springer-Verlag, Berlin.
- Reinink, K. & A. H. Eenink, 1988. Genotypical differences in nitrate accumulation in shoots and roots of lettuce. *Scientia Horticulturae* 37: 13-24.
- Roorda van Eysinga, J. P. N. L. & K. W. Smilde, 1971. Nutritional disorders in glasshouse lettuce. Pudoc, Wageningen, 56 pp.
- Silva, G. H. & E. W. Toop, 1986. Lettuce growth in a nutrient film with carbon dioxide enrichment within a controlled-environment system. *Soilless Culture* 2: 41-47.
- Slangen, J. H. G., T. Breimer & C. J. Roelands, 1987. Yield and nutrient uptake by lettuce (*Lactuca sativa* L. var. *capitata*). (In Dutch). *Ad Fundum* 4: 36-46.
- Steiner, A. A., 1985. The history of mineral plant nutrition till about 1860 as source of the origin of soilless culture methods. *Soilless Culture* 1: 7-24.
- Toop, E. W., G. H. Silva & G. Botar, 1988. Comparison of 24 lettuce cultivars in a controlled environment with extra CO₂ in NFT and stagnant solution. *Soilless Culture* 4: 51-62.
- Wild, A., L. H. P. Jones & J. H. Macduff, 1988. Uptake of mineral nutrients and crop growth: the use of flowing nutrient solutions. *Advances in Agronomy* 41: 171-219.
- Willumsen, J., 1980. pH of the flowing nutrient solution. *Acta Horticulturae* 98: 191-199.
- Willumsen, J., 1984. Nutritional requirements of lettuce in water culture. In: *Proceedings 6th International Congress on Soilless Culture*, p. 777-791. ISOSC, Wageningen.
- Winsor, G. W., R. G. Hurd & D. Price, 1979. Nutrient film technique. *Growers' Bulletin* 5, Glasshouse Crops Research Institute, Littlehampton, England, 47 pp.