Nitrate and potassium uptake by greenhouse roses (Rosa hybrida) along successive flower-cut cycles: a model and its calibration

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Abstract

Rose (Rosa hybrida L.) plants grown for cut-flower production in greenhouses produce flowers in flushes year-round. Crop models for this system must handle the cyclical nature of productivity, which is determined by the horticultural production methods. Nutrition was not accounted for in previous rose growth models, since little is known about uptake of the essential nutrients by rose roots. The aim of the current study was to measure uptake rates of nitrogen and potassium by roses, to be included in a production model. Rose plants var. ‘Kardinal’ were grown in the greenhouse in aero-hydroponics nutrient solution with 3 mM nitrate (NO₃)⁻N and 1 mM potassium (K). After several flower growth/harvest cycles, the plants were transferred to a growth chamber in groups of three, every 10 days. The growth chamber provided 25°C and 16 h day length. The nutrient solutions were sampled periodically while maintaining the volume constant at 5 l, and analyzed for NO₃ and K concentrations reduction. The roots were harvested at the end of each depletion series, and their lengths measured. Influx of NO₃ and K into roots was obtained by fitting a Michaelis–Menten function to the concentration depletion data. There was a cyclic rhythm of both the nutrients’ influx rates over time, with a decline in uptake after shoot harvest, and an increase during flower development, with maximal values towards flower opening. The results were incorporated in a simulation model for nutrient uptake by roses along successive flower-cutting cycles. This simulation assumes a constant number of identical flowering branches, which would be cut sequentially at flower maturity, and result in new shoot growth, assumed to follow a logistic function of time. Uptake rates of NO₃ and K were assumed to follow the changes in leaf area and shoot nutrient percentage, to compensate for N and K demand by the shoot; the root system dimensions and its effective aging are assumed...
constant. Simulated N and K uptake agreed with published data of their accumulation and percentage in growing rose branches along a flower-cut cycle.

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1. **Introduction**

Intensive crop production typically involves application of many nutrients in precaution excess. The degree to which excessive amounts can be applied is generally limited by the effect of salinity and toxicity on crop growth. The resulting pattern of irrigation and fertilization results in much of the applied fertilizer leaving the system, possibly contaminating water bodies in the environment (or drinking water systems). Thus, while application of luxuriant amounts of fertilizer has been commonplace in many horticultural systems, methods must be found to reduce this excess, so as to protect the environment and human health.

Such methods must be developed from a system’s point-of-view to assure that the reduction in fertilization rates does not threaten the growers’ ability to compete. This type of analysis requires the assembly of mathematical models for the various aspects of the system, so as to ultimately allow optimization. In the case of hydroponics flower production, a considerable amount of systems control is possible. Growers have long searched for ideal production methods. Greenhouse production of cut-flower roses offers an ideal model system because the intensive use of technology allows for testing and implementation of new model-based production technologies.

Considerable model development has occurred for cut flower roses, focusing mostly on dry matter accumulation as a result of photosynthetic carbon assimilation. Little has been done for other essential nutrients. Most the existing models of nutrient uptake deal with annual plants, whose root systems could be taken as young and uniformly active (Tinker and Nye, 2000), even the average uptake rate per unit of root decreases during plant growth (Scaife, 1994; Barber, 1995). Recent models, which do account for this decrease, use simplified assumptions regarding root age and uptake, such as linear decrease in time, or morphology (i.e., root position or hierarchy) of the root system (Somma et al., 1998). Such simplifications might not be valid in modeling nutrient uptake by perennials (Le Bot et al., 1998). These plants are characterized by a wide diversity of roots, of different age, thickness, and suberization. Also, the shoot–root interactions are complex and their effect on nutrient uptake by the roots is poorly understood. The complex lifespan of perennials over time (years), and the relatively large storage capacity for nutrients in their tissues, induce internal transports, which make mechanistic quantification difficult (Le Bot et al., 1998; Eissenstat and Yanai, 2002).

Roses (*Rosa hybrida* L.) grown under intensive management are subjected to numerous environmental and horticultural variables. This crop follows cyclic nutrient uptake patterns induced by flower harvests (Cabrera et al., 1995a; Takeda and Takahashi, 1998). That pattern makes any attempt to model nutrient uptake by roses unique, as their life span is different
from annual plants and other perennials (Eissenstat and Yanai, 2002). Also, the root system consists of roots of a wide range of hierarchy, age and probably uptake characteristics. Yet, as new roots emerge coincident with new shoot growth after a flower harvest (M. Raviv, personal communication), the root system of mature rose plants would achieve an apparent balance between root emergence and the decay of old ones. As a result, uptake may be accounted for as being induced by the demand of the shoot, not due to changes in the root system dimensions (Brun and Chazelle, 1996; Bougoul et al., 2000; Lorenzo et al., 2000).

The studies of Cabrera et al. (1995a,b), like the others, indicate the lack of information on root regeneration and activity during a cutting span and throughout the year (Takeda and Takahashi, 1998).

In the present study we measured the changes in uptake rates of nitrate (NO$_3$) nitrogen (N) and potassium (K) along a flower-cut cycle of roses, and the relationships between these changes and plant morphology. These data were used to calibrate a conceptual model of nutrient uptake by cut-roses. Our objective was to develop as simple a model as possible so that the resulting model might later be included in other crop models.

2. Materials and methods

2.1. Model theory

Various aspects of the conceptual dynamic system of nutrient uptake were simplified using numerous assumptions so as to focus on the uptake of NO$_3$ and K. The main assumption in this modeling work is the decoupling of plant growth from nutrient uptake. Plant growth is assumed to follow patterns that have been observed in greenhouse production. In future work dry matter accumulation will be modeled to be a function of available nutrients in the plant; the model here must clearly be treated as a first step towards that goal.

Rose plants in greenhouse cut flower production consist of three main components: (1) a ‘static base’ (main stem and residual stem and leaf material), (2) an aboveground ‘growing component’ (flowering shoots), and (3) the root system. In this model, the plant is assumed to be “fully grown” and in a pattern of shoot growth and flower harvesting. The static base consists of some stem material and some old leaves, whose dimensions and contents are assumed to be constant during any simulation run of the model.

It is assumed that the growing component consists of $n$ branches; each consisting of a growing stem and leaf biomass. A flower is assumed to grow on each stem but its impact on nutrient uptake is not considered in this model; only the leaf area and stem biomass are assumed to be involved. All stems are assumed to be identical with the pattern of leaf area growth following the logistic function of time, $t$, described by Cabrera et al. (1995b):

$$A(t) = \frac{A_{\text{max}}}{1 + a_1 e^{-a_2 t}},$$

(1)

where $A_{\text{max}}$ is the maximal area of one stem and $a_1$ and $a_2$ are coefficients. The various flowering stems on the plant are assumed to initially appear at a fixed time-interval $\delta$ followed by the same interval in harvesting and subsequent re-growth. Due to this assumed pattern
of stem growth, the total leaf area, $A_{\text{total}}$, of a plant, at any given time, can be calculated as the sum of the basal area, $A_{\text{base}}$, and the leaf area of each stem:

$$A_{\text{total}}(t) = A_{\text{base}} + \sum_{i=1}^{n} \frac{A_{\text{max}}}{1 + \alpha_1 e^{-\alpha_2[t - \delta(t - 1)]}}$$

where $\delta$ is the time-delay between two successive cuts in a flower wave.

The stem biomass is modeled as stem dry matter. The dry matter of each stem is assumed to grow in a logistic growth pattern with a total growing stem dry matter, $D_{\text{total}}$, at any time is the sum of the dry matter of all $n$ shoots:

$$D_{\text{total}}(t) = \sum_{i=1}^{n} \frac{D_{\text{max}}}{1 + b_1 e^{-b_2[t - \delta(t - 1)]}}$$

$D_{\text{max}}$ is the maximal dry matter of a flowering stem, and $b_1$ and $b_2$ are coefficients. The ‘life span’ of each stem is assumed to be a fixed number of days, from emergence or initiation as a bud after the previous flower harvest until the stem is harvested. At harvest of the $i$th stem, leaf area and dry matter would switch to their initial value. Photosynthesis and respiration are both assumed non-limiting, and not influenced by nutrients. The root system dimensions (length, mean radius, surface area) are assumed constant with the rate of root death equaling new root generation.

The uptake rate of a nutrient through the root surfaces, $J$, is modeled as a function of the nutrient concentration $C$ in the growth medium, according to Michaelis–Menten kinetics (Barber, 1995):

$$J(C) = \frac{J_{\text{max}} (C - C_{\text{min}})}{K_m + (C - C_{\text{min}})}$$

where $K_m$ and $C_{\text{min}}$ are coefficients. $J_{\text{max}}$, the maximal influx coefficient, is assumed to change over time in relation to total plant leaf area and nutrient status in the growing tissue. Calculation of shoot nutrient deficiency or surplus is done by assuming that $J_{\text{max}}$ is a function of the nutrient concentration in the ‘growing’ shoot dry matter, $\mu$:

$$J_{\text{max}}(\mu) = J_{\text{max},0} e^{-\alpha \mu}$$

as suggested by Siddiqi and Glass (1986). In this equation $\alpha$ is a coefficient and $J_{\text{max},0}$ the (theoretically-maximal) value of $J_{\text{max}}$ when $\mu = 0$. The value of $\mu$ represents the ‘growing’ shoot as a whole (Cabrera et al., 1995b; Gonzalez-Real and Baille, 2000). The combined equations allow calculation of the nutrient uptake of either NO$_3$ or K during simulated time-steps used in the model:

$$J_{\text{max}}(\mu, t) = J_{\text{max},0} e^{-\alpha \mu(t)} \frac{A_{\text{total}}(t)}{A_{\text{base}} + nA_{\text{max}}}$$

and

$$\mu(t + \Delta t) = \frac{\mu(t)D_{\text{total}}(t) + J_{\text{max}}(\mu, t)R \Delta t}{D_{\text{total}}(t + \Delta t)}$$

where $\Delta t$ is the time-step and $R$ the root area, which is assumed to be constant.
2.2. Plant material and horticulture

Twenty rose plants (R. *hybrida* cv. Kardinal grafted on ‘Natal Brier’ rootstock) were selected from a stock of plants previously grown for 8 years in 7.6 or 18.9 l containers with ‘UC Mix’ substrate. The branches were trimmed, the roots were washed and the fine roots removed. The plants were then transplanted in pairs into ten 18 l aero-hydroponics systems (Soffer and Burger, 1988), containing 5 l of nutrient solution and grown in the greenhouse. The nutrient solution, prepared with de-ionized water, contained 1.5 mM Ca(NO$_3$)$_2$, 0.5 mM K$_2$SO$_4$, 0.25 mM Ca(H$_2$PO$_4$)$_2$, 1 mM MgSO$_4$, 4 mg/l Fe-EDDHA [ethylenediaminedi(o-hydroxyphenylacetic) acid] chelate, and microelements according to Hoagland and Arnon (1950). The pH was adjusted to 5.5 with Ca(OH)$_2$. The nutrient solution was replaced at least every week, while its volume was maintained by additions of de-ionized water. While in the greenhouse, an artificial light system maintained 16 h day length.

After 4 months, 18 plants were transplanted into aero-hydroponics systems, one plant per unit. These were moved into a growth chamber in groups of three at 10-day intervals, with fresh nutrient solutions; the order and position in the growth chamber were randomly predetermined. The growth chamber was illuminated at 16/8 h day/night regime by a series of 400 W metal halide lamps (model MH400/U, Philips Lighting Co., Somerset, NJ), which provided 235 μmol m$^{-2}$ s$^{-1}$ PAR at plant level. Air temperature was approximately constant at 25 °C. Temperature of the nutrient solution was monitored by thermocouples positioned in the solution at the bottom of each container. Readings were taken every 10 s, averaged over 10 min by a data-logger (CR23X Micrologger, Campbell Scientific), and stored. The solutions were adjusted periodically to a volume of 51 with de-ionized water to maintain the changes below 5%; two 100 ml additions of a 10 times concentrated No N–No K nutrient solution (see below) were made during the depletion period to avoid the depletion of the other nutrients. The solutions sampling frequency varied between every 8 h during the high-concentration range depletion, to every hour towards the end of the depletion. The 10 ml samples were stored in vials and kept in the refrigerator until further analysis; NO$_3$ and K concentrations were determined in the lab in stirred solutions, using ion-specific electrodes (Nos. 27502-30 and 27502-38, respectively; Cole-Parmer Instrument Co., Vernon Hills, IL), after they reached room temperature. The relative potential was measured with Oakton® pH/mV/°C meter. The electrodes were calibrated against KNO$_3$ standards, before and during the analysis of every batch (no substantial drifts were observed); a nutrient solution, in which the NO$_3$ and K salts were replaced with 1.5 mM CaSO$_4$, served as an ionic strength adjuster. Between measurements, the electrodes were soaked in a 10 mM KNO$_3$ solution.

2.3. Data collection and analysis

At the end of each depletion cycle, the fine roots of each plant were removed from the plant, and the root length and mean radius were measured using Tennant’s (1975) line intersect method. Root surface area was calculated assuming the roots to be cylindrical. It was assumed that all changes in the NO$_3$ and K concentrations were caused by the plants (no microbial activity). Also, no substantial changes in concentration depletion rate were observed between light and dark periods. Thus the influx of these nutrients into the root system (cm$^{-2}$ root surface area) was calculated.
During the entire experimental period, every growing stem on each plant was observed daily. The number of flowers harvested was recorded each day. The plants were managed so that flushes of flowering stems occurred which all flowered within a few days of each other. The “day of peak flowering”, $T_0$, was calculated from the flowering data as

$$T_0 = \frac{\sum_{i=start}^{i=end} IF_i}{\sum_{i=start}^{i=end} F_i}$$

(8)

where $i$ is the date of the observation, $i_{start}$ and $i_{end}$ are the start and end dates of the flowering flush. $F_i$ is the number of flowers harvested on each date.

Leaf area on the plants was estimated by measuring leaf lengths that were used to calculate the leaf area of individual leaves using the correlation function:

$$A = 1.0193(-10.35 + 2.294x + 0.234x^2)$$

(9)

where $A$ is the leaf area (cm$^2$) and $x$ the leaf length in cm (Lieth, unpublished data).

2.4. Model calibration

The model for flowering stem leaf area over time was calibrated by fitting Eq. (1) to the observed leaf area estimates over time. The model for dry matter of a rose stem over time was calibrated by using the non-linear regression routine in SAS Institute (1988) to fit Eq. (3) to data published by Cabrera et al. (1995b), resulting estimates for $D_{max}$, $b_1$ and $b_2$ of 54.24 g, 226.84, and 0.177 per day, respectively.

Data of nutrient concentration depletion in each of the 18 aero-hydroponic units with time and root surface area were used to relate the uptake rate with concentration. Eq. (4) was fitted as follows. The net influx can be expressed as the negative ratio of the solution volume to root surface area times the change in concentration (Nielsen and Barber, 1978):

$$J(C) = -\frac{V}{R} \frac{dC}{dt}$$

(10)

which, when equated to Eq. (4) and solved results in the expression

$$t = c_1 - \frac{V}{R J_{max}} K_m \ln(C - C_{min}) - \frac{V}{R J_{max}} \frac{1}{C - C_{min}}$$

(11)

which was fit to the collected data of concentration over time to obtain the values of $J_{max}$, $K_m$ and $C_{min}$. The root surface area was assumed to have been the observed value for the duration of the measurements and the volume of the solution was assumed to be 5 l.

The change in ion uptake rate along a cutting cycle was expressed as its value with time from the previous $T_0$. Eq. (11) was fit separately for NO$_3$ and K for these data using the non-linear regression routine NLIN in SAS Institute (1988). The resulting $J_{max}$ estimates were further related to tissue concentration, $\mu$. However, since no tissue concentration data were available, parameter estimates of Eq. (5) were selected based on Mengel and Kirkby (1987, p. 107). They speculated that nutrient content could be characterized as ‘adequate’ and ‘toxic’ and present values of these tissue concentrations for various plants; it was arbitrarily assumed that $J_{max}$ at ‘toxic’ levels is $10^{-3}$ times the value at ‘adequacy’.
Thus, estimating the values of adequate $J_{\text{max}}$ to be 6.745 and 2.837 pmol cm$^{-2}$ s$^{-1}$ for NO$_3$ and K, respectively, results in estimates of $\alpha = 2.37$ and 6.43 per day, and $J_{\text{max,0}}$ of 174.3 and 23.95 pmol cm$^{-2}$ s$^{-1}$, respectively.

### 2.5. Simulation model

A simulation model was developed to allow rapid calculation of the nutrient status in hydroponic rose production over time using the parameter estimates from the model calibration. This was implemented as an Excel spreadsheet (as an initial analysis) and also as a Delphi (Borland) Pascal program (so as to be able to study the model behavior). The two implementations of the model were compared to verify that no computational errors impacted the simulation results.

The simulation allows the user to set any of the parameters described above and to select starting conditions and model constants. For our simulations we selected initial conditions and constants similar or equal to those of our experimental plants. The number of growing flowering stems was set to 5. These were assumed to initiate every second day (i.e. $\delta = 2$). The base leaf area ($A_{\text{base}}$) was assumed to be 1600 cm$^2$ (which is the area of approximately 10 mature leaves).

The nutrient solution was assumed to start out with a volume of 5 l and NO$_3$ and K concentrations of 3000 and 1000 µM, respectively; initial tissue concentrations of N and K were assumed to be 1.37 and 0.332 mmol/g dry weight, respectively. Root surface area was assumed constant with time, taken as 7841.4 cm$^2$, which was the mean value of the plants used in the calibration study.

### 3. Results

#### 3.1. Model calibration

Fitting Eq. (1) to leaf area data resulted in estimates for the parameters $A_{\text{max}}$, $a_1$, and $a_2$ of 622.3 cm$^2$, 22.6, and 0.243 per day, respectively. The goodness of fit information was $R^2 = 0.34$, which reflects the heterogeneity of the 18-plant group used in the calibration study.

The parameter estimates of $J_{\text{max}}$, $K_m$, and $C_{\text{min}}$ show quite a bit of variability over time (Table 1) for both NO$_3$ and K. The analysis of variance indicated that the significance of the changes in $J_{\text{max}}$ with time was marginal for both nutrients and also for $K_m$ for NO$_3$. Yet, nutrient influx to the roots, represented by the measured $J_{\text{max}}$ values, exhibited a cyclic pattern with time along the flower-cut cycle as evidenced by significant quadratic and cubic effects (best fit with a third-order polynomial; see Fig. 1a). Mean influx, which was highest towards flower maturity, decreased after flower-cut, but increased again during the next wave of stem growth and the consequent flower production.

The change in uptake rate along a flower-cut cycle (Fig. 1b) showed that the observed frequency of rose flowering (and harvesting) as a function of time from the previous mean flower peak ($T_0$) was 37 days, for all the plants in the study, along three flower-cut cycles.
Table 1
Analysis of variance of the Michaelis–Menten kinetics coefficients for nitrate and potassium influx to roots of ‘Kardinal’ roses along a flower-cut cycle (degrees of freedom for the error: 16)

<table>
<thead>
<tr>
<th></th>
<th>Nitrate</th>
<th>Potassium</th>
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<tbody>
<tr>
<td></td>
<td>$J_{\text{max}}$</td>
<td>$K_{\text{m}}$</td>
</tr>
<tr>
<td>Mean</td>
<td>4.92</td>
<td>86.73</td>
</tr>
<tr>
<td>$F$-value</td>
<td>4.15</td>
<td>4.68</td>
</tr>
<tr>
<td>$P$-value</td>
<td>0.059</td>
<td>0.046</td>
</tr>
</tbody>
</table>

3.2. Simulation results

Comparing the simulated with observed stem leaf areas of ‘Kardinal’ roses over time showed that the simulations followed the observed leaf area (Fig. 2); the scattered observed data illustrate the variability of the plant population with respect to leaf areas of individual stems.

![Graph showing nutrient influx and flowers per plant over days from flowering peak.](Image)

Fig. 1. (a) Nitrate and potassium influxes to rose roots (means and 95% confidence range) along a flower-cut cycle (b); the data were best fitted to third-order polynomials (curves and legends).
The trajectories of N and K tissue concentrations in the growing shoot were parallel and showed sharp changes that coincided with times when stems were harvested (Fig. 3A). The first cycle, from 0 to 37 days, was highly affected by the fact that all branches started from zero growth, with 1.37 mmol N/g dry wt and 0.332 mmol K/g dry wt. From the second cycle on, the cutting cycles each show similar patterns and correspond to observations by Cabrera et al. (1995b) and Tamimi et al. (1999).

The data of N accumulation in a growing rose branch along a cutting cycle (Fig. 3B) were adapted from Cabrera et al. (1995b), where curve (a) is a logistic function fitted to the data. In that study, the time from bud to harvest was 45 days, but the simulated curve for a 45-day cycle (b) under-estimates the actual accumulation of N in the branch. When a 37-day cycle was accounted for in the simulation, the agreement between the data (a) and the simulation (c) is much improved.

The simulated $J_{\text{max}}$ values over time follow the changes in leaf area and plant nutrient accumulation along successive 37-day flower-cut cycles (Fig. 3C). The presented values are of the second simulated cycle; the data included in this figure are the measured values. The 95% confidence intervals (CI) bars attached to the data reflect variance of the fitted coefficient for each plant. Although scattered, the data follow the path of the simulated curve, for either the nutrients; the scattered pattern reflects the variability of the plant population.

Representative simulations by Delphi of adjacent NO$_3$ and K in the hydroponics solution and the plant along 100 days, together with plant growth, are presented in Fig. 4. Uptake
Fig. 3. Simulated (curves) and measured (symbols) of (A) N and K weighted percentage in a rose plant with growing branches along 37-day flower-cut cycles, considering five branches flower (and cut) at 2-day intervals; data from Cabrera et al. (1995b), closed circles were synchronized to match a 37-day cycle; opened symbols: from Tamimi et al. (1999). (B) Nitrogen accumulation with time in a rose branch: (a) data and a fitted logistic function (adapted from Cabrera et al., 1995b); (b) along a 45-day or (c) 37-day flower-cutting cycle, respectively. (C) Maximal influx rates ($J_{max}$) of nitrate (solid line, open symbols) and potassium (dashed line, closed symbols, with 95% confidence intervals) uptake by roots of Kardinal roses.

In this figure, NO$_3$ concentration would be replenished to 3 mM once it depleted below 0.5 mM; K will be replenished to 1 mM when it would deplete below 0.1 mM. The simulation indicates that the frequency of nutrient replenishments would increase towards flower maturity, but decrease again as a result of flower-cuts. The curvilinear shape of each depletion phase reflects the effect of $K_m$ on nutrient influx close to the lower concentration boundary. The discontinuities of the different phases reflect both nutrients’ replenishments (which would induce an increase in uptake rate) and branch trim at flower-cut, which would
lower the demand for the nutrients (implemented by the reduction in leaf area and shoot biomass).

4. Discussion

The objective of this study was to develop mathematical descriptions for NO$_3$ and K uptake from the root solution by rose plants. Such models can have utility in fertigation control and crop optimization. Although there are previous reports on sequential changes in uptake
by roses, they were not provided in forms that enabled their use in crop modeling. When a perennial plant like rose is grown under controlled conditions, as allowed by the modern greenhouses technology, external signals such as irradiance, temperature, day length, etc. may play a secondary role. In the case of roses, the rhythm is associated with man-induced flowering cycles.

Earlier studies by Cabrera et al. (1995a,b) presented cyclic uptake of NO$_3$-N by intact plants along a flower-cut cycle. Also, the highest N contents occur in the upper, youngest leaves of a rose branch (Tamimi et al., 1999). Cabrera et al. (1995a,b) further showed that the flower contained the highest amount of K of all branch parts, namely: an enhanced requirement for both nutrients at flower set. No changes in root absorbance were reported which may be linked to this enhanced nutrient uptake. One should expect such changes in the root system absorption capacity (Glass, 2002), as new roots emergence are associated with the new burst of growth, following flower-cut (M. Raviv, personal communication). Such differences were reported in other evergreen, perennial plants, but the integration of solitary roots to uptake by the whole tree or bush is still non-realistic (Eissenstat and Yanai, 2002). Furthermore, the poor correlation between root growth and mean uptake rate (not presented), of both the nutrients measured in the present study, indicates that uptake is controlled mainly by shoot demand. The fine roots of the plants used in this study were trimmed 4–5 months prior to the plants’ transfer to the aero-hydroponics system. Consequently, the whole population of fine roots may be considered as active in nutrient absorbance, as their color was bright, unlike the dark color typical to suberized roots (Comas et al., 2000). We may conclude therefore that uptake by the whole plant reflected a weighted activity of all sections of the root system, and its dimensions were already in balance with the shoot. Under these conditions, uptake measured by the entire root system reflects the behavior of a mature rose plant. Furthermore, the cyclic absorption pattern has to be induced by the cyclic changes in shoot growth and the associated demand for the two studied nutrients.

A fundamental aspect of the model presented here is the concept of “shoot demand” as a driving force in nutrient uptake. In our model this is implemented through the tissue concentration in Eq. (5). That equation can be reviewed as an adjustment factor to Eq. (4), and the selection of this particular approach might be controversial (Le Bot et al., 1998; Glass, 2002). There are several ways to handle this adjustment. It is clear that such an adjustment must be incorporated so as to prevent simulation of accumulation of nutrients at levels that are clearly toxic (Scaife, 1994). Our model assumes that uptake rates are governed by the concentration in the nutrient solution (or rooting medium) while the maximal uptake rate is affected by shoot demand. Our implementation of this approach was suggested by Siddiqi and Glass (1986); it appears to be valid also in roses (Cabrera et al., 1996). It has the drawback of adding more assumptions regarding ‘adequate’, ‘deficient’ and ‘toxic’. However, use of the exponential response function has a fundamental advantage over a simple linear relationship in that the later can result in negative values of $J_{\text{max}}$ for high tissue concentrations, which results in a complete inversion of Eq. (4) (which is unsuitable in all circumstances).

Dry matter production and leaf area were both assumed to grow logistically over time, in different patterns. The previous argument on a linkage between demand and uptake raises the question of the use of leaf area as correlated with uptake (via $J_{\text{max}}$, Eq. (6)), and not with the growth of dry matter. The correlation between nutrient uptake and leaf area is probably
due to photosynthesis (Thornton and Millard, 1996). In the present model, photosynthesis is disregarded, so its effect may be accounted for via the correlation with leaf area. The use of Eq. (6) allows the inclusion of photosynthesis in the model, even indirectly. Also, it may permit in the future to link this model with a photosynthesis module, which may create a more comprehensive crop model.

The simulated N contents (Fig. 3A) closely agree with data adapted from Cabrera et al. (1995b); that is, when the length of the flower-cut cycle in both cases were synchronized: in the cited study, the time from trimming to harvest was 45 days; in the simulation, the cycle was taken as 37 days, based on the calibration study. Even the two studies used different cultivars, the difference is probably due to the growth conditions: Cabrera’s study was carried out in the greenhouse, with natural light and day length; the plants in the calibration study obtained 16 h day length, which apparently shortened the flowering cycle, either directly or indirectly by inducing higher shoot temperature (Menard and Dansereau, 1995; Bredmose, 1997). Even so, the synchronization of the two cycles is valid, as the cycles in both studies were defined according to the morphological development of the branch, i.e., from one flower-cut to the next. The proximity of curves (a) and (c) in Fig. 3B supports this idea.

The measured concentration depletion with time indicated the occurrence of one phase of high-affinity influx mechanism, for both nutrients, up to 3 mM NO$_3$ and 1 mM K. It agrees with Cabrera et al. (1995a), who reported constant uptake rate up to 10 mM NO$_3$, which contradicts the occurrence of concentration-dependent additional phases (Glass, 2002). Also, no linkage was observed between NO$_3$ and K influx, as addition of one did not change the pace of the other’s depletion (not presented); this observation indicates that the two nutrients were practically absorbed by a single high-affinity mechanism which supports the use of the Michaelis–Menten kinetics.

The model, in its present version, does not account for differences in environmental conditions such as shoot and root temperature, light, CO$_2$, root respiration, etc. Also, uptake was measured in the calibration study under controlled conditions of illumination, temperature and root aeration. Those effects may be introduced to the model in the future as variables. The same is regarding photosynthesis and dry matter accumulation, which are treated in the present version as functions of time. This approach is further supported by Blom-Zandstra and Jupijn (1987), where NO$_3$ uptake rate of 56-day-old lettuce plants was unaffected by 12 h light/dark alterations, and by the consequent changes in the transpiration rate.

Fig. 4b may serve as a recommendation for rose growth management: Nutrient concentration should not deplete close to the lower boundary; insufficient uptake rates might cause inadequate nutrient supply in the long run. This effect may be moderated once the concentration is kept well above the $K_m$ value of the particular nutrient’s influx.

5. Conclusions

The presented model was aimed to serve as a module in a comprehensive rose management model. It treats two major nutrients’ uptake by grown up, productive roses grown in hydroponics under controlled growth conditions. Any deviation from the assumptions made in the essence of this model, such as constant temperature, day length, unlimited root oxygen
supply, photosynthetic radiation, might cause differences between the simulated and actual uptake. When these growth factors are provided as variables generated by other modules, this model has the potential to serve as a useful tool in rose production management.

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