

Modeling the Influence of Cyclical Plant Growth and Nutrient Storage on N, P, and K Absorption by Hydroponically Grown Cut Flower Roses

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Abstract

Previous research found that a model using growth of new rose flower stems as the driving force for nutrient absorption did not adequately predict nutrient absorption of a whole plant. The objective of the current project was to develop a nutrient absorption model to take into account the dynamic nature (change in growth, nutrient demand, storage, and reallocation) of perennial plant parts on nitrogen (N), phosphorous (P), and potassium (K) absorption by roses. In this model we separate the plant into four organs: shoots, base leaves, base stems, and roots. Each organ exerts a relative influence on plant demand for a specific nutrient based on its degree of depletion for that nutrient which influences root nutrient absorption activity. Overall plant demand for the nutrient is expressed using the summation of each organ's relative contribution to plant demand. Nutrient absorption at the root level is expressed using Michaelis-Menten kinetics. Allocation of absorbed and stored nutrients takes place based on relative organ nutrient demand. A sequential harvest experiment was conducted using one-year old *Rosa hybrida* 'Kardinal' plants growing in solution culture to calibrate the model and a simulation was developed to compare predicted nutrient uptake and allocation with measured values from the calibration data set. The simulation demonstrates the importance of accounting for storage and mobilization of phloem mobile nutrients in predicting nutrient uptake dynamics in roses.

INTRODUCTION

Nutrient Use

Current management practices of field, greenhouse, and nursery crops generally use luxuriant amounts of fertilizers. In intensely managed systems, such as greenhouse crops, excessive fertilization can lead to greater than 2,000 kg of nitrogen (N) leached per hectare per year (Cabrera et al., 1993). In order to reduce fertilizer inputs, greenhouse and nursery growers will need to optimize irrigation/fertilization timing and application rates, or develop closed irrigation systems. This requires a greater understanding of the nutrient supply necessary for crop production.

Cut flower rose production is typically done with hydroponics using media that is kept moist through irrigation with a nutrient solution (constant liquid feed). Roses are valuable for studying dynamics of nutrient uptake, storage, and remobilization in woody crops as they exhibit many flushes of vegetative growth every year coinciding with flushes of flower shoot growth (Cabrera et al., 1995a).

Most of the work with nutrient uptake in roses has focused on NO_3^- ; less information is available on uptake of the other macronutrients. Cabrera et al. (1995a) reported NO_3^- absorption of *Rosa hybrida* 'Royalty' over 7 flower shoot growth cycles (393 days) and PO_4^{3-} , K^+ , Ca^{2+} and Mg^{2+} over 2 crop cycles.

Modeling Nutrient Absorption

Bougoul et al. (2000) modeled *Rosa hybrida* 'Sweet Promise' transpiration and NO_3^- over 4 days given light and temperature, but not across a growth cycle. Silberbush

and Lieth (2004) developed mathematical models to predict NO_3^- and K^+ uptake of *Rosa hybrida* 'Kardinal' plants growing in solution culture across a growth cycle, where the 'driving force' for uptake is the growth of new flower shoots. In the model, a logistic equation describes the growth of flower shoots (increase in dry weight and leaf surface area over time), while the other plant parts (roots, leaves and stems on the base of the plant) are assumed to have a constant dry weight (equilibrium between new growth and senescence). Absorption of NO_3^- and K^+ is expressed as Michaelis-Menten function:

$$J = \frac{J_{\max}(C - C_{\min})}{K_m + (C - C_{\min})} \text{RSA} \Delta t \quad (1)$$

where J is nutrient influx; J_{\max} , K_m , C , and C_{\min} are Michaelis-Menten parameters, where C is the concentration of the nutrient solution; RSA is the plant's root surface area; and Δt is the time-step of the simulation. The plant's relative demand for nitrogen and potassium is expressed by varying J_{\max} (maximum rate of nutrient absorption, $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{cm}^{-2}$ RSA) according to the plant's current nutrient concentration (μ); and the current stage into a growth cycle, which is expressed as the plant's current leaf area, $\text{LA}(t)$, divided by the plant's leaf area at the end of the growth cycle, LA_{\max} . This, gives the following equation:

$$J_{\max}(\mu, t) = J_{\max,0} e^{-a\mu(t)} \frac{\text{LA}(t)}{\text{LA}_{\max}} \quad (2)$$

where $J_{\max,0}$ is the theoretical maximum J_{\max} at $\mu=0$; and a is a coefficient.

This model tended to underpredict nutrient absorption by the plant following a previous crop cycle and before new shoots appear. One factor that was not accounted for is the capacity of older plant tissues (roots, old stems, old leaves) to store nutrients (phloem mobile nutrients such as N, K, and P) and redistribute these nutrients during growth of flowering shoots. Cabrera et al. (1995b) found that N mobilized from older stems and leaves provided the majority of the N to the growing shoots during rapid flower stem elongation of roses; but as stems reached flower maturity, N uptake from the media provided N to the shoots and to replenish older tissues.

The objective of the current project was to develop a nutrient absorption model to take into account the dynamic nature (change in growth, nutrient demand, storage, and reallocation) of perennial plant parts (roots, old stems, and leaves) on N, P, and K absorption by roses.

MATERIALS AND METHODS

Model Development

In our whole plant model we separate the rose plant into four organs: roots ($i=1$), base stems ($i=2$), base leaves ($i=3$), and new flower shoots ($i=4$). A similar separation was described by Habib et al. (1989) in N absorption by peaches (*Prunus persica*). Each organ exerts a relative influence on plant demand for a specific nutrient based on its tissue concentration of the nutrient similar to the model suggested by Siddiqi and Glass (1986). However, in our model we use degree of depletion of the nutrient in each organ rather than the concentration itself. The organ's relative demand for a nutrient is expressed as its contribution to root nutrient activity (termed J_{\max_i}). In equation 3 this is related to the organ's current tissue nutrient concentration (μ_i) and the maximum tissue nutrient concentration of the organ ($\max \mu_i$):

$$J_{\max_i}(\mu_i) = a_1 e^{a_2([\max \mu_i] - [\mu_i])} \quad (3)$$

where a_1 and a_2 are coefficients.

Overall plant demand for the nutrient is expressed as the plant's root nutrient activity ($J_{\max_{\text{plant}}}$) and is defined as the summation of each organ's contribution to plant demand as in equation 4, scaled for the dry mass of each organ:

$$J_{\max_{\text{plant}}} = \frac{\sum_{i=1}^4 J_{\max_i} DM_i}{\sum_{i=1}^4 DM_i} \quad (4)$$

where DM_i is each organ's dry mass. Nutrient absorption at the root level (J) is expressed using Michaelis-Menten kinetics as in equation 1, but in the modified model J_{\max} represents plant nutrient demand (equation 4) rather than shoot nutrient demand (equation 2). The dynamic nature of shoots and perennial parts is accounted for by allowing DM_i to vary during a growth cycle according to organ specific growth equations.

Once influx of the nutrient has occurred, allocation to each organ takes place based on the organ's relative nutrient demand (J_{\max_i}) scaled for dry mass as in equation 5. In the current model, physical vascular connections and time delays between nutrient influx and allocation are not considered.

$$\text{allocation}_i = J \frac{J_{\max_i} DM_i}{J_{\max_{\text{plant}}} \sum_{i=1}^4 DM_i} \quad (5)$$

Finally, it is assumed that the perennial tissues (roots, base stems and leaves) can act as a source of phloem mobile nutrients for the new shoots. The model accounts for this by allowing a certain proportion of an organ's nutrients (denoted as the parameter a_3) to be diverted from this source organ (denoted as i) to the sink organ (denoted as j). Thus, equation 6 takes into account remobilization of stored nutrients.

$$\text{If } J_{\max_j} > J_{\max_i} \text{ then } \text{reallocation}_{ij} = a_3 (\mu_j DM_j) \quad (6)$$

In addition, equation 6 has the constraints placed upon it that a source organ cannot reallocate more of a nutrient than it has available and the sink organ cannot accept more of a nutrient than would be needed to fully satiate the tissue.

Plant Data Collection for Model Calibration

A sequential harvest experiment was conducted to collect data for model calibration. Shoots and roots of thirty-five one-year-old 'Kardinal' rose plants on 'Natal Briar' rootstock were established in solution culture in 8 L containers and trimmed back to achieve uniformity. The nutrient solution contained: 0.5 mM NH_4^+ , 7.0 mM NO_3^- , 0.5 mM H_2PO_4^- , 3.0 mM K^+ , 2.0 mM Ca^{2+} , 1 mM Mg^{2+} , 1 mM SO_4^{2-} , and micronutrients according to Hoagland and Arnon (1950). The solution was kept aerated by continuously bubbling air into the solution. Plants were grown in solution culture for one-month before the experiment was initiated.

At experiment initiation (day 0) plants were trimmed by cutting back shoots to the second five-leaflet leaf. Plants were randomly divided into seven groups of five plants. Plants were placed in a controlled environment chamber (18 hour photoperiod at 700 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR with average daily temperature of 25°C). Every five days, one group of five plants was selected for harvest. Nutrient solution samples were taken two days prior to harvest and at harvest to determine N, P, and K absorption rates of each plant. Methods of analysis included: NO_3^- and NH_4^+ by the diffusion conductivity method; K^+ through flame emission with an ion absorption spectrophotometer; and PO_4^{3-} by the stannous chloride colorimetric method.

At harvest, plants were separated into the following components: roots, base stems, base leaves, and flower shoots. Plant parts were dried in an oven and weighed. Dry

tissue samples were ground and analyzed for total N, P, and K. Prior to roots being dried, root samples were prepared for image analysis by staining them and spreading samples on a transparent tray with a thin layer of water. An image was collected with a modified desktop scanner and images were analyzed using Delta-T Scan software to determine length, diameter and root surface area.

Simulation Model

Using the above equations, a simulation model was developed to predict N and K absorption and distribution within the plant (i.e. tissue concentrations) of rose plants growing in solution culture. For the purposes of this simulation we used measured rates of dry matter accumulation from the experimental plants. Plant root surface area of the experimental plants did not differ significantly over time during the crop cycle and averaged $14400 \text{ cm}^2 \text{ plant}^{-1}$. The simulation was initialized using tissue analyses for day 0 (Fig. 3), mean dry weight data of the organs (Fig. 1), root surface area, and calculated parameter values (Table 1). The simulation was implemented with a time step of one day.

RESULTS

Model Calibration

We attempted to use data on nutrient solution concentration, root surface area and measured absorption rates for each plant at harvest to determine values for J_{max} , K_m , and C_{min} for N, P, and K using nonlinear regression of equation 1 in SAS (Statistical Analysis System). However, the range of nutrient concentrations was too narrow for the program to determine best fit parameters. As an alternative approach we used reported values for K_m and C_{min} of NO_3^- and K^+ (Silberbush and Lieth, 2004) and solved for J_{max} . The values for J_{max} across a crop cycle are reported in Table 2. There were no existing data on Michaelis-Menten parameters for P in roses so we were unable to calculate J_{max} for P.

Nonlinear regression of equations 3 and 4 was conducted by equating plant organ tissue concentrations with calculated N and K J_{max} values to determine values for a_1 and a_2 (Table 1).

The proportion of a sink organ's nutrient content that could be remobilized to a source organ was estimated using the tissue data to determine the accumulated content of the nutrient in shoots. The difference between the accumulated nutrient in shoots for each time step versus the amount of the nutrient projected to come from root absorption would represent the amount of the nutrient that must come from source organs. For the experimental plants, an estimated 41 mg of N and 38 mg of K per day was required by the flower shoots from the sink organs during days 11 to 25 to make up this difference (data not presented). The parameter a_3 was calculated as the percentage of nutrient content in sink organs that must be remobilized to the shoots at each time step (Table 1).

There was a discrepancy in the amount of N and K absorbed by the plants if the values were calculated by integrating the absorption data (Fig. 2) or calculated from tissue analysis and dry weight data. 2750 mg of N was calculated to be absorbed based on integration of absorption data, while only 1600 mg of N was calculated to be absorbed based on tissue analysis. 2300 mg of K was calculated to be absorbed based on integration of absorption data, while 960 mg of K was calculated to be absorbed based on tissue analysis. To account for this discrepancy, the simulation model assumed that 58% of N and 41% of predicted K uptake is absorbed by the plant and allocated to the organs.

Simulation Results

The simulated patterns of N and K uptake follow values observed during the sequential harvest experiment (Fig. 2). The simulation tends to over predict N absorption at days 20 and 25 as well as over predict K absorption at days 5-15. The somewhat scattered observed data illustrate the variability that is present from plant to plant. The simulation accurately predicts the decline in N and K absorption following cut back of the plant and the increase in absorption rates following appearance of the new flower shoots.

Simulated N tissue concentrations follow a cyclical pattern according to the crop cycle. The time sequence of developmental events of representative flower shoots occurred as follows: day 7 – bud break (new shoots 1 cm long), day 12 – unfolding of first leaf on flower shoots, day 16 – flower bud becomes visible, day 20 – unfolding of last leaf on flower shoots, day 30 – flower shoots reached harvestable stage. After cycle initiation, the perennial tissues accumulated N until new shoots are initiated. Following appearance of new flower shoots around day 10 there is a decline in N concentration until day 20-25, which coincides with the stage where nutrients are mobilized from perennial tissues to support new flower shoots. Around day 25, remobilization from perennial tissues is predicted to cease. During the final 5 days of the cycle the N absorbed by the plants goes to new flower shoots as well as to begin to replenish the base tissues. Immediately following appearance of the new shoots they have a relatively high N concentration, as the shoots grow and begin to rapidly accumulate biomass the high concentrations are not sustained and tissue concentrations decline over time. Similar patterns were observed with K, though the magnitude of changes in tissue concentration during a crop cycle were not as great as N (data not presented).

DISCUSSION

In the current model we did not separate influx of N into NO_3^- and NH_4^+ components. This simplification was necessary as data were not available on the Michaelis-Menten parameters for NH_4^+ in roses. Overall more data is needed on influx rates of roses over a wide range of nutrient concentrations to directly determine Michaelis-Menten parameters for NO_3^- , NH_4^+ , K, and P.

It was estimated that remobilization of N and K from perennial tissues was necessary to sustain the flower shoots during days 10-25. To directly determine the contributions of each organ experiments would need to be conducted with labeled nutrients. In experiments with labeled N, Cabrera et al. (1995b) calculated that base leaves, base stems, and roots provided 21, 43, and 20 percent, respectively, of the N accumulated by flower shoots during the stage of rapid stem elongation.

There was a discrepancy between N and K absorption calculated by integrating the absorption data versus the amount accumulated by tissues during the crop cycle. A similar discrepancy is found in Cabrera et al. (1995) where integration of absorption should result in plants gaining 1750 mg of N, but tissue analysis revealed that plants gained only 1120 mg. In our experiment, the nutrient solution was replenished every five days, but nutrient absorption rates were measured only during the first two days following replenishment. It is likely that absorption rates declined during the subsequent three days in response to declining nutrient concentrations in solution or as a response to the relatively rapid influx rates following replenishment. It would be useful to measure uptake rates across the entire interval between replenishments.

Simulated N and K uptake rates closely matched the patterns observed in our rose plants (Fig. 2), but the simulation tended to overpredict rates of uptake during the middle stages of the crop cycle. For future experiments it would be useful to calibrate J_{max} based on influx rates across the entire interval between nutrient solution replenishments. In our simulation, allocating nutrients according to relative depletion of tissues (as in equation 5) results in tissue accumulation patterns similar to that observed in rose plants (Fig. 3). Calibration of organ specific parameters for allocation and remobilization parameters (a_1 , a_2 , and a_3) may further increase model accuracy.

The current simulation illustrates the importance of accounting for storage and mobilization of phloem mobile nutrients in base tissues of perennial plants. For example, the Silberbush model (Silberbush and Lieth, 2004) uses only flower shoots as the driving force for nutrient uptake and so predicts little to no N and K uptake at the beginning of a new cycle until shoots appear. In our experiments, we have found a somewhat sustained rate of N and K uptake following cycle initiation which coincides with replenishment of base tissues; a decline in base tissue concentration while remobilization to new flower shoots occurs, and the beginning of replenishment of base tissues nears the end of a cycle.

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Tables

Table 1. Parameter values used in the model simulation and their source.

Parameter	Value(s)	Source
N K_m	86.7 μ M	Silberbush and Lieth (2004)
N C_{min}	2.4 μ M	Silberbush and Lieth (2004)
N a_1	3.614	nonlinear regression of equation 3
N a_2	1.003	nonlinear regression of equation 3
N $a_3(\text{time, } t)$	$t \leq \text{day } 10$	0% calculated from difference of N
	$\text{day } 10 < t \leq \text{day } 25$	2.30% accumulated in shoots versus amount of N
	$t > \text{day } 25$	0% projected to come from root absorption
K K_m	71.5 μ M	Silberbush and Lieth (2004)
K C_{min}	0.15 μ M	Silberbush and Lieth (2004)
K a_1	2.438	nonlinear regression of equation 3
K a_2	1.910	nonlinear regression of equation 3
K $a_3(\text{time, } t)$	$t \leq \text{day } 10$	0% calculated from difference of K
	$\text{day } 10 < t \leq \text{day } 25$	2.67% accumulated in shoots versus amount of K
	$t > \text{day } 25$	0% projected to come from root absorption

Table 2. Calculated values for N J_{\max} and K J_{\max} for rose plants in a 30 day growth cycle.

Day of crop cycle	J_{\max} ($\mu\text{mol cm}^{-2} \text{s}^{-1}$)	
	Nitrogen ($\text{NO}_3 + \text{NH}_4$)	Potassium
-2-0	$8.73 \pm 0.26 \text{ a}^1$	$3.33 \pm 0.33 \text{ a}$
3-5	$4.40 \pm 0.28 \text{ bcd}$	$1.43 \pm 0.05 \text{ cd}$
8-10	$3.99 \pm 0.55 \text{ cd}$	$0.67 \pm 0.05 \text{ d}$
13-15	$3.14 \pm 0.53 \text{ d}$	$1.14 \pm 0.11 \text{ cd}$
18-20	$4.54 \pm 0.46 \text{ bcd}$	$1.75 \pm 0.16 \text{ c}$
23-25	$8.01 \pm 1.00 \text{ abc}$	$1.96 \pm 0.15 \text{ bc}$
28-30	$8.34 \pm 2.31 \text{ ab}$	$2.77 \pm 0.45 \text{ ab}$

¹ Letters denote mean separation comparisons of J_{\max} for each nutrient across days in the crop cycle utilizing Tukey's HSD ($P=0.05$).

Figures

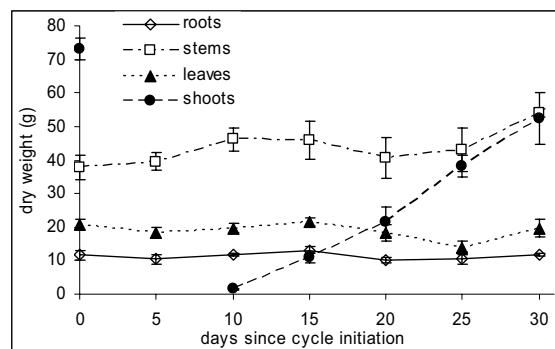


Fig. 1. Dry weight of rose plants over the course of a thirty day crop cycle. Data are means (\pm SE) of five plants harvested every five days.

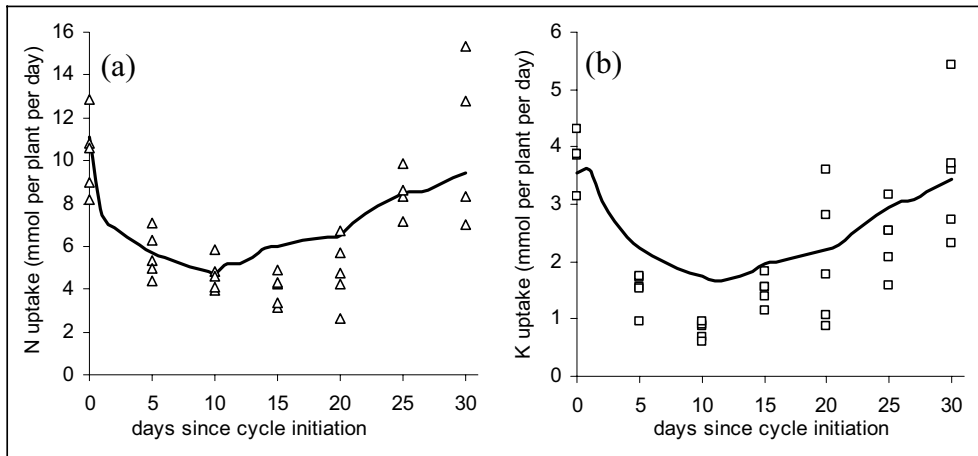


Fig. 2. Measured and simulated nitrogen (a) and potassium (b) absorption. Simulation predictions are noted with the solid line. Measured values (symbols) represent data from five plants at each sampling date.

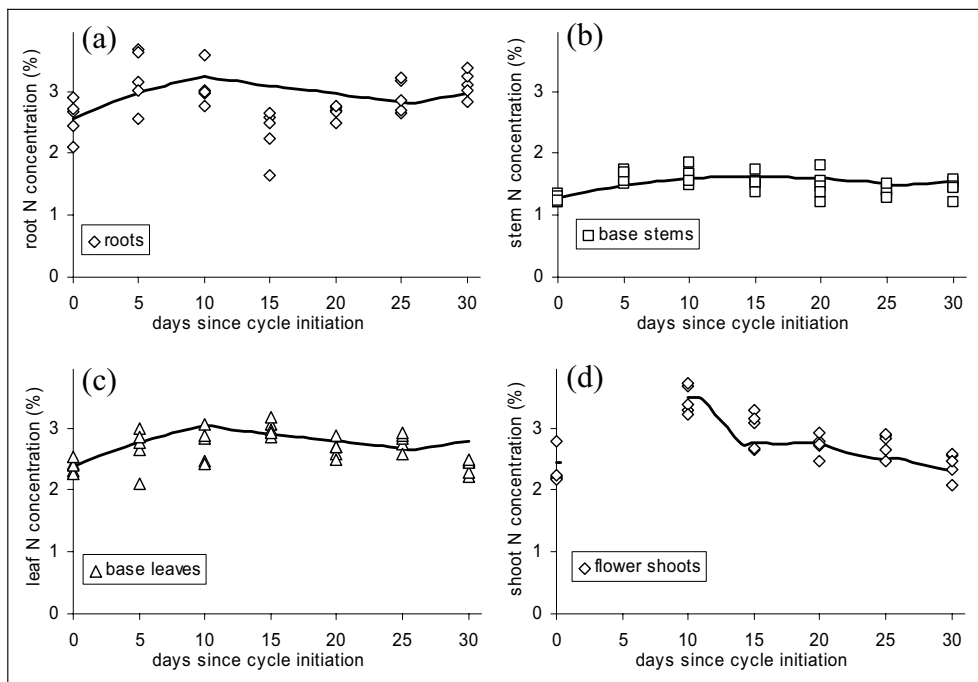


Fig. 3. Measured and simulated nitrogen concentrations of roots (a), base stems (b), base leaves (c), and flower shoots (d) during a crop cycle. Simulation predictions are noted with the solid line. Measured values (symbols) represent data from five plants at each sampling date.