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Journal of Plant Nutrition
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713597277

Derivation of a Dynamic Model of the Kinetics of Nitrogen Uptake Throughout the Growth of Lettuce: Calibration and Validation

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Online Publication Date: 01 August 2008

To cite this Article Zhang, Kefeng, Burns, Ian G. and Turner, Mary K.(2008)'Derivation of a Dynamic Model of the Kinetics of Nitrogen Uptake Throughout the Growth of Lettuce: Calibration and Validation',Journal of Plant Nutrition,31:8,1440 — 1460
To link to this Article: DOI: 10.1080/01904160802208345
URL: http://dx.doi.org/10.1080/01904160802208345

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Journal of Plant Nutrition, 31: 1440–1460, 2008
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ISSN: 0190-4167 print / 1532-4087 online
DOI: 10.1080/01904160802208345

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ABSTRACT

A kinetic model of nitrogen (N) uptake throughout growth was developed for lettuce cultivated in nutrient solution under varying natural light conditions. The model couples nitrogen uptake with dry matter accumulation using a two-compartment mechanistic approach, incorporating structural and non-structural pools. Maximum nitrogen uptake rates are assumed to decline with shoot dry weight, to allow for the effects of plant age. The model was parameterized using data from the literature, and calibrated for differences in light intensity using an optimization algorithm utilizing data from three experiments in different growing seasons. The calibrated model was validated against the data from two independent experiments conducted under different light conditions. Results showed that the model made good predictions of nitrogen uptake by plants from seedlings to maturity under fluctuating light levels in a glasshouse. Plants grown at a higher light intensity showed larger maximum nitrogen uptake rates, but the effect of light intensity declined towards plant maturity.

Keywords: nitrogen uptake, nitrogen kinetic model, lettuce, hydroponics

INTRODUCTION

Optimizing the nutrient supply is essential to maintain high yield and quality of produce. Any imbalance in matching the nutrient supply to the demand of the plant can reduce growth and increase the incidence of nutrient disorders or the accumulation of potentially harmful elements in edible tissues. Furthermore, it can increase unnecessary build-up of nutrients in the soil. However, the optimum

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nutrient supply can only be achieved when the plant nutrient uptake is accurately predicted.

Nitrogen (N) uptake and plant growth are dynamic and interdependent processes. The uptake rate of nitrogen is controlled by plant growth rate, development stage and environmental factors, such as light and temperature (Edwards and Barber, 1976a; 1976b; Hallmark and Huffaker, 1978; Barber and Cushman, 1981; Cumbus and Nye, 1982; Lim et al., 1990; Raman et al., 1995; Swiader and Freiji, 1996). To date, a number of nitrogen models have been derived in an attempt to quantify the effects of some of these factors on nitrogen uptake (Claassen and Barber, 1976; Edwards and Barber; 1976a; 1976b; Bhat et al., 1979; Bloom and Sukrapanna, 1990; Chapin, 1991). However, most of these models are empirical, designed primarily to fit observations without assigning physiological significance to the parameters. In contrast, Wheeler et al. (1998) developed a quantitative kinetic relationship between maximum uptake rate and shoot growth rate from studies of the effects of light intensity and nitrogen levels on nitrogen uptake. Their model is based on measurements conducted in a controlled environment growth chamber under constant light intensities during a relatively short period (between 23 and 27 days after sowing). It is unclear, therefore, whether their simple kinetic relationship will hold for lettuce grown over longer periods and under naturally varying light conditions. Of particular concern is whether such equations are able to account for changes in plant and canopy development (head formation and canopy closure), which can affect nitrogen uptake in the later stages of growth through their effects on light interception.

As the uptake rate of nitrogen is closely related to plant growth, the quantification of nitrogen uptake rate is strongly dependent on plant dry matter accumulation. Most plant nitrogen uptake models use either the limited dry weight data measured at intervals during the experiments, or employ an empirical approach (Steingrobe and Schenk, 1994; Schenk, 1996; Wheeler et al., 1998; Silberbush and Lieth, 2004) to calculate plant growth rate. Although this makes the calculation of plant growth rate relatively straightforward, the relationship does not explicitly account for any changes in the physiological mechanisms involved.

The aim of the current work is to develop and validate a new dynamic mechanistic model for predicting nitrogen uptake and dry matter accumulation by lettuce from seedling to maturity. The model consists primarily of three interrelated components: a photosynthesis sub-model which fixes atmospheric carbon using instantaneous light intensity to drive growth; a two-compartment dry matter accumulation sub-model which partitions new plant material between structural and non-structural pools; and a N uptake sub-model based on a saturation kinetics equation in which the maximum nitrogen uptake rate decreases with increasing shoot dry weight. An optimization algorithm is used to calibrate values of the parameters in the kinetic equation for nitrogen uptake in order to evaluate their dependence on the light environment. In order to simplify

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the calibration, N uptake rates are assumed to depend on the average light intensity during plant growth, rather than on instantaneous light levels. The use of the model to predict the changing N demand of lettuce during growth is assessed.

MATERIALS AND METHODS

Five experiments were carried out with lettuce grown hydroponically in a glasshouse at different times of the year to measure the effects of light intensity on nitrogen uptake. The methods used were similar to those of Broadley et al. (2000) and Zhang et al. (2005). However, brief descriptions of the experiments are given below.

The lettuce (*Lactuca sativa* L., cv. 'Vegas') plants were grown using a recirculating nutrient film technique (NFT) to provide adequate water and minerals throughout. The macronutrients (mM) used in the nutrient solutions were: 2.0 calcium nitrate [Ca $(NO_3)_2$], 1.0 potassium sulphate (K_2SO_4), 0.5 potassium phosphate (KH_2PO_4), and 0.4 magnesium sulphate ($MgSO_4 \cdot 7H_2O$). The corresponding concentrations of micronutrients (μM) were: 100.0 iron sodium ethylenediaminetetraacetic acid (FeNaEDTA), 30.0 boric acid (H_3BO_3), 10.0 manganese sulphate ($MnSO_4 \cdot 4H_2O$), 1.0 zinc sulphate ($ZnSO_4 \cdot 7H_2O$), 3.0 copper sulphate ($CuSO_4 \cdot 5H_2O$), 0.5 sodium molybdate ($Na_2MoO_4 \cdot 2H_2O$). The solutions were replaced weekly during early growth, and twice a week towards maturity; the nutrient solutions were all adjusted regularly to pH 6.0. Glasshouse temperatures were maintained at about 18°C ± 3°C. Incident solar radiation was recorded at five minute intervals by two solarimeters positioned above the crop canopy at opposite ends of the troughs. Details of the experiments and the associated light intensities are shown in Figure 1 and Table 1.

The lettuce seeds were sown directly in 37 × 37 × 40 mm tapered rockwool blocks and wetted with deionized water. The resulting seedlings were transferred at the 2 true leaf stage to the NFT troughs at a spacing of 22 cm × 22 cm. The first harvest was carried out when individual plants weighed about 0.2g dry matter. Thereafter the harvest interval was twice a week, with four plants taken at each harvest. To minimize any positional effects, plants were harvested using a systematic approach, from one end to the center of two of the troughs and in the opposite direction for other two troughs. Plant spacing was maintained by moving the guard plants.

Shoot fresh and dry weights were measured at each harvest. After drying in an oven for 48 hours at 100°C, nitrogen concentrations were determined on milled samples using the C/protein/N elemental analyzer (CN2000, LECO Corporation, Michigan, USA). There was insufficient material for a full chemical analysis of individual shoots at the early harvests, so material from the 4 replicates was pooled and homogenized at each harvest date before chemical analysis. Changes in the projected area occupied by each plant were determined

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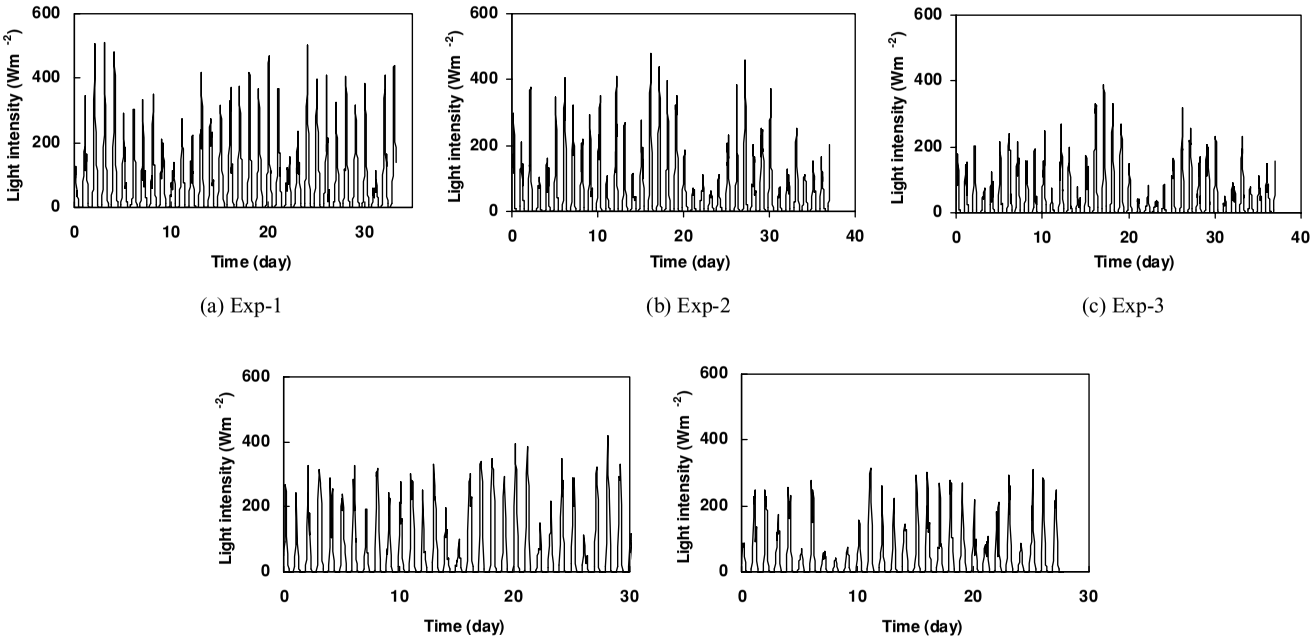

Figure 1. Measured light intensities for Exp-1 (a), Exp-2 (b), Exp-3 (c), Exp-4 (d) and Exp-5 (e) after the 1st harvest. See Table 1 for dates.

Table 1
Experiment periods and average light intensities

Experiment No.	Date of sowing	1st harvest	Final harvest	Average light intensity (MJ m^{-2} day^{-1})
Exp-1	22/04/2003	27/05/2003	23/06/2003	7.1
Exp-2	04/03/2004	07/04/2004	11/05/2004	5.0
Exp-3	04/03/2004	07/04/2004	11/05/2004	3.7
Exp-4	28/07/2003	27/08/2003	25/09/2003	5.7
Exp-5	24/01/2005	22/03/2005	19/04/2005	4.2

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at each harvest. In addition, a leaf area meter (Delta area meter MK2; Delta-T Devices Limited, Cambridge, UK) was also used to measure the total leaf area of individual sample plants at the same time.

MODEL AND CALIBRATION

To model the dynamics of nitrogen uptake, certain assumptions have to be made. One of the most commonly made assumptions in previous models is the decoupling of plant growth from nitrogen uptake. In these models, plant dry matter accumulation is treated simply as a function of time, and is fitted using a limited number of weight measurements, rather than being calculated from the nitrogen concentration in the plants and the properties of the environment in which they grew (Wheeler et al., 1998; Silberbush and Lieth, 2004). In the mechanistic model described below, nitrogen uptake is coupled with dry matter accumulation in order to allow the interactive effects of light environment to influence both processes directly.

Model Description

Nitrogen Uptake Sub-model

For the purpose of this sub-model, nitrogen uptake rate is defined as the derivative of the amount of nitrogen in the shoot with respect to time (ignoring any N in the roots). It depends on the nitrogen concentration and the dry weight of the shoot, and the availability of nitrogen to the plant. In solution culture, it can be modeled by a saturation kinetics equation (Wheeler et al., 1998; Silberbush and Lieth, 2004), e.g.:

$$\frac{dN_{up}}{dt} = J_{max}\frac{c_N w}{c_N + K}. \quad (1)$$

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Where N_{up} (mmol) is the cumulative nitrogen in the shoot, J_{max} (mmol h^{-1} g^{-1}DM) is the maximum nitrogen uptake rate per unit of shoot dry matter, w is the shoot dry weight, c_N (mM) is the nitrogen concentration in nutrient solution, and K (mM) is the semi-saturation constant for nitrogen uptake.

There is evidence that the maximum nitrogen uptake rate declines with increasing plant age (Edwards and Barber, 1976b; Schenk, 1996). As this is unlikely to be caused by the aging of roots (Kuhlmann and Barraclough, 1987), it is reasonable to assume that the reduced demand for nitrogen is a result of changes in the shoot size. This leads to the assumption that J_{max} declines with shoot dry weight, as suggested by Siddiqi and Glass (1986), Silberbush and Lieth (2004):

$$J_{max} = J_{max,0} e^{-\alpha w}. \tag{2}$$

Where $J_{max,0}$ (mmol h^{-1} g^{-1}DM) is the value of J_{max} when $w = 0$, and α (g^{-1}DM) is a coefficient.

Dry Matter Accumulation Sub-model

A number of models have been developed to simulate the production of lettuce dry matter (Sweeney et al., 1981; Critten, 1991; Van Henten, 1994; Pearson et al., 1997; Seginer et al., 1998). A two-compartment mechanistic model originally proposed by Sweeney et al. (1981) has been validated and extended by others (Van Henten, 1994; Van Henten and Van Straten, 1994; Pearson et al., 1997), who found that it could make reasonable predictions for lettuce dry matter accumulation. Following Sweeney et al. (1981) and Van Henten and Van Straten (1994), our dry matter accumulation sub-model assumes that lettuce has two separate carbon pools: a structural biomass pool and a non-structural biomass pool. Canopy photosynthesis provides carbon assimilate to both structural and non-structural pools. The governing equations for dry matter accumulation in the structural pool and non-structural pool are (Zhang et al., 2004):

$$\frac{dw_G}{dt} = \mu_{max} \frac{w_s}{w_s + w_G} c_{q10,\mu}^{(T-20)/10} w_G \tag{3}$$

$$\frac{dw_s}{dt} = \theta P_g - \frac{1}{Y_G} \frac{dw_G}{dt}, \tag{4}$$

where t is time, w_G (g) is the dry weight of the structural pool, w_S (g) is the dry weight of the non-structural pool, μ (h^{-1}) is the saturation growth rate at 20°C, $c_{q10\mu}$ is the Q_{10} factor for growth, T (°C) is temperature, θ is a factor to convert CO_2 to dry matter, P_G [g(CO2) h^{-1})] is the gross canopy photosynthesis rate, and Y_G is the conversion efficiency. The sum of w_G and w_S represents the total shoot dry weight w (g). The inclusion of P_g and $\frac{1}{Y_G}\frac{dw_G}{dt}$ in Equation (4) provides

the flexibility to predict the reductions in overall growth rate which occur as plants approach maturity.

Photosynthesis Sub-Model

Carbon inputs to the dry matter accumulation sub-model are calculated using a photosynthesis sub-model. As plant photosynthesis rate is closely affected by nitrogen concentration in the leaf tissues, the gross canopy photosynthesis rate, P_g, is calculated using a modification of the Sweeney et al. (1981) approach as follows:

$$P_g = A(1 - e^{-kL_{AI}})f(N_{up})\frac{\xi I(\sigma C_{CO2} - \beta)}{\xi I + \sigma C_{CO2}}, \quad (5)$$

where A (m^2) is the ground cover area per plant, k is the extinction coefficient, L_{AI} is the leaf area index, $f(N_{up})$ is a coefficient between 0 to 1 controlled by nitrogen concentration in the shoot, ξ [$g(CO_2)\ J^{-1}$] is the leaf light use efficiency, β [$g(CO_2)\ m^{-2}h^{-1}$] is the CO_2 compensation point to account for photorespiration, I (J m^{-2} h^{-1}) is the incident photosynthetically active radiation, C_{CO2} [$g(CO_2)\ m^{-3}$)] is the CO_2 concentration in the air, and σ (m h^{-1}) is the leaf conductance to CO_2 diffusion.

Model Calibration

Dry Matter Accumulation

A number of the parameters in the dry matter accumulation sub-model have been estimated in previous studies (Sweeney et al., 1981; Critten, 1991; Van Henten, 1994; Pearson et al., 1997). They appear to be more or less independent of lettuce variety, and are readily available from elsewhere in the literature (see Table 2). In the absence of more specific information, initial values of w_G and w_S were assumed to equal one third and two thirds of the total shoot dry weight (w), respectively, at the first harvest. Subsequent tests showed that the simulated results were not particularly sensitive to the initial values of w_G and w_S.

The leaf area index was calibrated from the measured total leaf areas and the plant cover data during growth in Exp-1. Figure 2 shows the changes in total leaf area and the ground cover area with time. The equations of best fit for the total leaf area L_A (m^2) and the plant cover area are:

$$\text{Total leaf area}: \quad L_A = -0.0025\ w^2 + 0.072\ w \quad (6)$$

$$\text{Plant cover area}: \quad A = \begin{cases} 0.02\,w & \text{when } w \le 2.4 \\ 0.0484 & \text{otherwise} \end{cases}. \quad (7)$$

Therefore the leaf area index L_{AI} is:

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Table 2
Values of parameters used in simulating dry matter accumulation

Parameter	Unit	Value	References
θ		0.68	Sweeney et al., 1981; Van Henten, 1994
$c_{q10,\mu}$		1.6	Sweeney et al., 1981; Van Henten, 1994
k		0.9	Sweeney et al., 1981; Van Henten, 1994
ξ	g (CO_2) J^{-1}	14×10^{-6}	Sweeney et al., 1981
β	g (CO_2) m^{-2} h^{-1}	0.36	Sweeney et al., 1981
σ	m h^{-1}	7.2	Sweeney et al., 1981
Y_G		0.8	Sweeney et al., 1981
μ_{max}	h^{-1}	0.01	
C_{CO2}	g (CO_2) m^{-3}	0.8	

$$L_{AI} = \begin{cases} -0.125\,w + 3.6 & \text{when } w \le 2.4 \\ -0.0516\,w^2 + 1.49\,w & \text{otherwise} \end{cases}. \tag{8}$$

The effect of shoot nitrogen concentration on photosynthesis rate was calibrated by using data published by Broadley et al. (2001) who carried out experiments on the same lettuce variety used in this study. They investigated the relationship between the maximum photosynthesis rate and organic-N concentration in lettuce leaves. They found that a minimum organic-N concentration of 3.6% dry matter was required to achieve the maximum photosynthesis, and that photosynthesis stopped at a nitrogen concentration of about 2% dry matter. Furthermore, in the range between 2% and 3.6% organic-N concentration, the maximum photosynthesis rate declined with organic-N concentration approximately linearly. They also found that measured nitrate concentrations in the leaves were variable, but seldom exceeded 1.5% nitrate (NO_3)-N in the dry matter. It is, therefore, assumed that the effect of shoot nitrogen concentration on photosynthesis rate is as follows:

$$f(N_{up}) = \begin{cases} 0 & \text{when } (N_{up}/w) < 0.02 \\ \frac{1}{3}\left(\frac{N_{up}}{w} - 0.02\right) \times 100 & \text{when } 0.02 \le (N_{up}/w) \le 0.05 \\ 1 & \text{when } (N_{up}/w) > 0.05, \end{cases} \tag{9}$$

where 0.05 is the sum of the nitrate and organic-N concentrations.

Nitrogen Uptake Kinetics

Three parameters ($J_{max,0}$, α and K) in the nitrogen uptake sub-model were calibrated for the effects of light intensity using measured data. Mathematically

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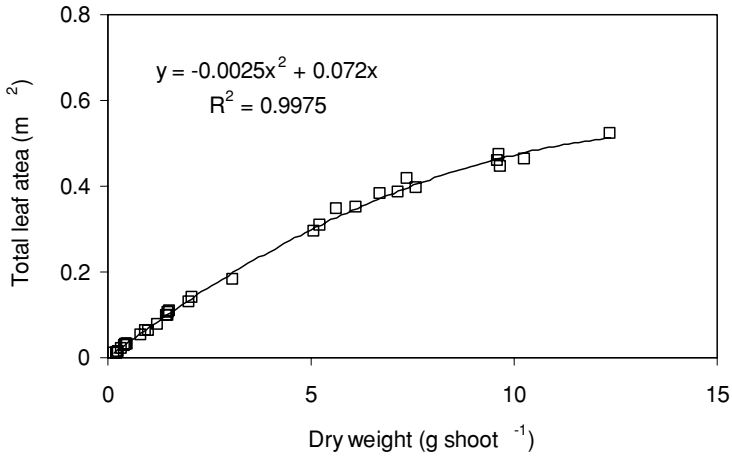
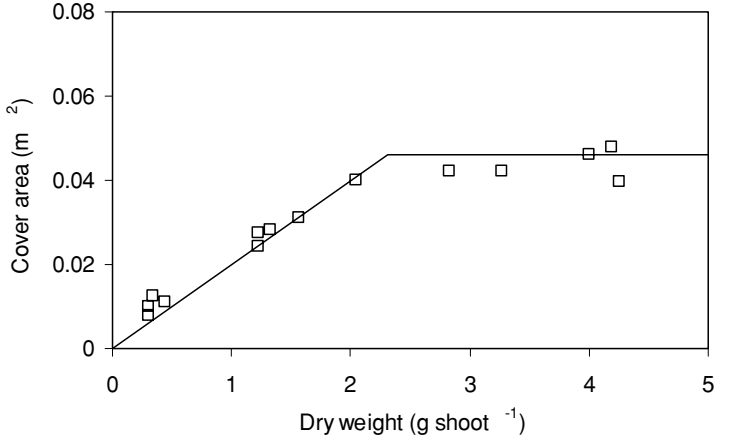


(a) total leaf area



(b) cover area

Figure 2. Measured total leaf area (a) and cover area (b) with shoot dry weight from Exp-1.

this can be expressed as:

$$\begin{aligned} &\text{To find :} \quad J_{max,0},\ \alpha \text{ and } K \\ &\text{To minimise :} \quad \sum_{i=1}^{m} g(N_{upi}, N'_{upi}) \end{aligned} \tag{10}$$

where g is an error function defined as the sum of square differences between measured (N'_{upi}) and calculated (N_{upi}) cumulative nitrogen in a shoot at measurement i, and m is the number of total measurements.

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This is a nonlinear optimization problem with three variables. An optimization algorithm described by Rao (1984) as the 'complex method' was employed to find the optimum values of $J_{max,0}$, α and K, using measurements from Exp-1 to Exp-3.

RESULTS

Model Calibration

Simulations were run over the period of lettuce growth from the time of the first harvest with an interval of time of 1h. The measured light intensity and air temperature together with the values of the parameters listed in Table 2 were used as input data. Also included in the input data were the fitted relationships of plant cover area and leaf area index against shoot dry weight, Equations (7) and (8). The initial conditions for the 3 state variables w_G, w_S and N_{up} were based on estimates at the first harvest. It was also assumed that 50% of the incoming light (Wheeler et al., 1998; Nobel, 1999) was photosynthetically active.

The optimum values of parameters $J_{max,0}$, α and K were sought by solving Equation (10) with successive measurements of nitrogen concentration in shoots for the three experiments using the optimization algorithm. Table 3 shows the deduced values of parameters $J_{max,0}$, α and K for different light conditions. This shows that both $J_{max,0}$ and α increased with increasing light intensity in an approximately linear manner (Figure 3). The optimum value of K was always below 0.04 mM, much lower than the nitrogen concentration of 4 mM in the nutrient solution.

The calculated shoot dry weights (obtained using the optimized parameters) are plotted against time in Figure 4(a), together with the measurements. The corresponding calculated and measured cumulative amounts of nitrogen in the shoots are compared in Figure 4(b). Generally the calculated values are in good agreement with the experimental data, indicating that the model used for nitrogen uptake and the deduced parameters are appropriate for the cases tested.

Table 3
Deduced kinetic parameter values

Experiment No.	Average light intensity (MJ m^{-2} day^{-1})	$J_{max,0}$ (mmol h^{-1} g^{-1}DM)	α (g^{-1}DM)	K (mM)
Exp - 1	7.1	0.0505	0.161	0.04
Exp - 2	5.0	0.0374	0.151	0.02
Exp - 3	3.7	0.0349	0.148	0.02

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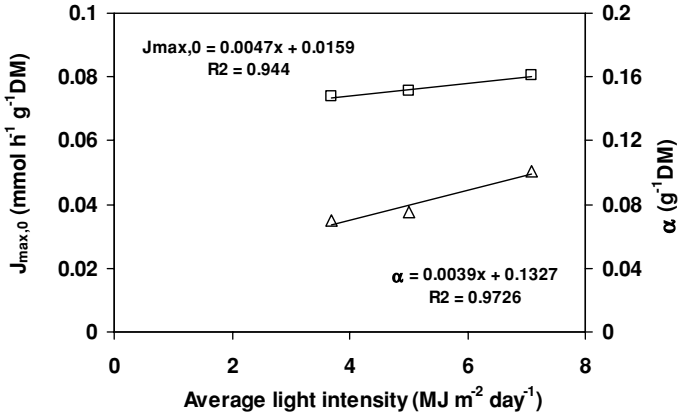

Figure 3. Changes in deduced $J_{max,0}$ and α values with average light intensity during the growth period for Exp-1, Exp-2 and Exp-3.

Model Validation

The model was validated against measured data from Exp-4 and Exp-5. Values of the nitrogen uptake parameters $J_{max,0}$, α and K used for these new experiments were obtained by applying the linear interpolation shown in Figure 3. They were 0.0423 mmol h^{-1} g^{-1}DM, 0.154 g^{-1}DM, and 0.027 mM for Exp-4, and 0.0359 mmol h^{-1} g^{-1}DM, 0.15 g^{-1}DM, and 0.02 mM for Exp-5.

The simulated shoot dry weights are plotted against time in Figure 5, together with the measurements. Figures 6 and 7 show the corresponding calculated relative growth rates and cumulative nitrogen in the shoots over time at the different light intensities. Basically the predicted values are in satisfactory agreement with the observations, although the model tended to overestimate both dry weights and nitrogen contents of the plants as they approached maturity.

Nitrogen uptake rate increased faster early in growth than at the later stages (Figure 8), but as the plants approached maturity the uptake rate declined. The figure also shows that the light intensity had a clear positive effect on the nitrogen uptake rate independent of any associated effects on shoot dry matter production.

The effects of light intensity and shoot dry matter accumulation on the maximum nitrogen uptake rate J_{max} are shown in Figure 9. The maximum nitrogen uptake rate increased with increasing light intensity. The effect of light on J_{max} was greater at the early plant growth stages, and diminished towards plant maturity. For a given light intensity, J_{max} decreased with increasing shoot dry matter, and the decrease rate was much more evident in early growth stages than the later ones.

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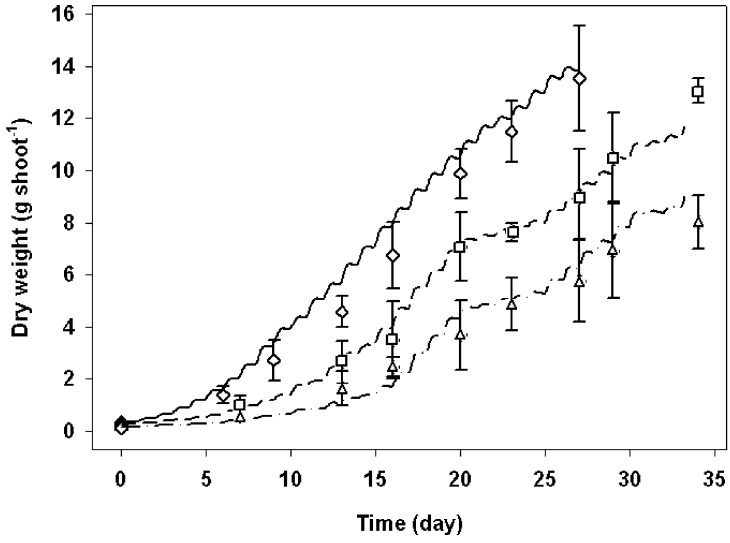
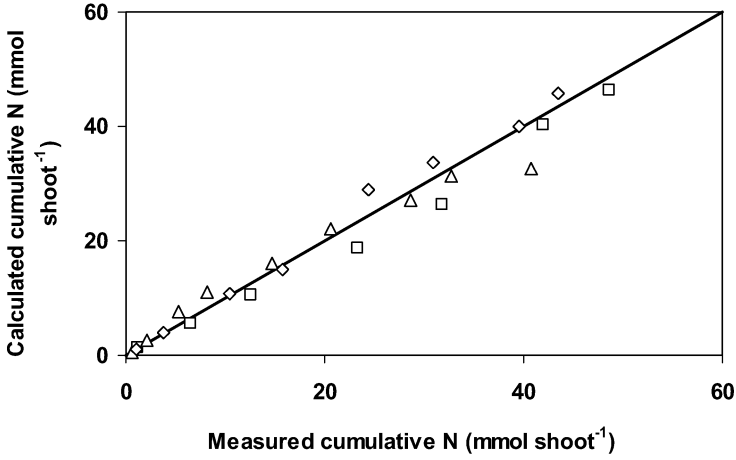


(a) shoot dry matter accumulation



(b) cumulative nitrogen uptake in shoot

Figure 4. Graphs of measured (means and 95% confidence range) and calculated shoot dry matter accumulation over time (a); and of a comparison of calculated and measured cumulative nitrogen (b) in lettuce. The solid, dotted and dot dash lines represent the simulations for Exp-1, Exp-2 and Exp-3. Symbols ◇, □ and △ represent the measurements from Exp-1, Exp-2 and Exp-3, respectively.

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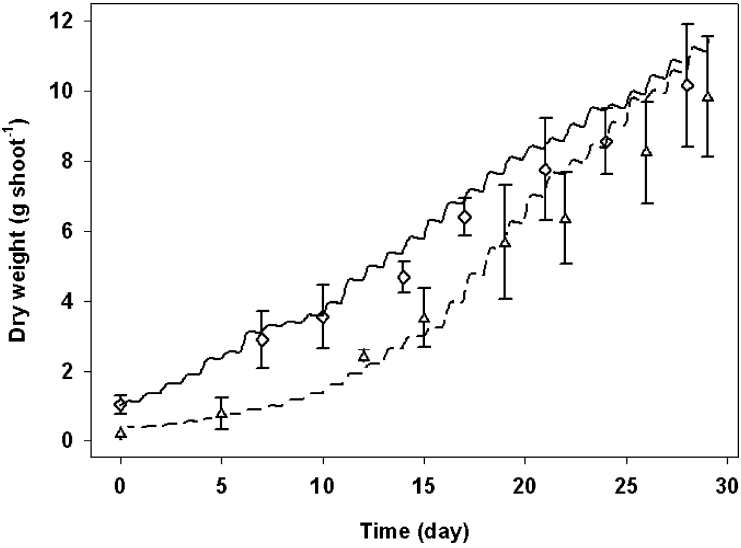

Figure 5. Graphs of measured (means and 95% confidence range) and simulated shoot dry matter accumulation in lettuce over time. The solid and dotted lines represent the simulations for Exp-4 and Exp-5. Symbols ◇ and △ represent the corresponding measurements.

DISCUSSION

Dry Matter Accumulation

The adopted two-compartment approach for modeling lettuce growth proved to make reasonable predictions of shoot dry matter accumulation. It not only reproduced the general patterns of shoot growth, but also caught the distinctive feature of reduced dry matter accumulation between 20 and 23 days after the first harvest in Exp-2 and Exp-3, when the light intensities were significantly lower than average. The overall agreement between the predicted dry weights, and their corresponding measurements in the validation experiments was also generally good, although the calculated dry weights slightly overestimated the experimental data, particularly towards maturity. There are a number of possible reasons for these discrepancies. One likely explanation is from systematic errors in the measured plant cover data. When the sample plants were lifted from the troughs for plant cover measurement, the leaves tended to relax and the resulting changes in leaf angles almost certainly caused an overestimation of the actual plant cover area data. As plant cover is one of the key factors in the calculation of photosynthesis, such a bias would cause an overestimation of both shoot

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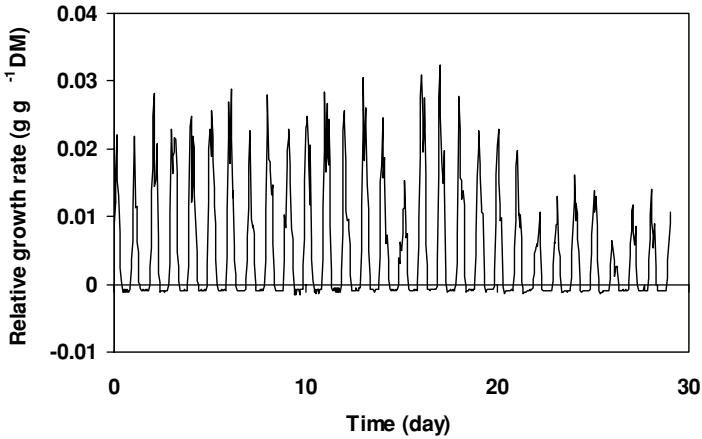
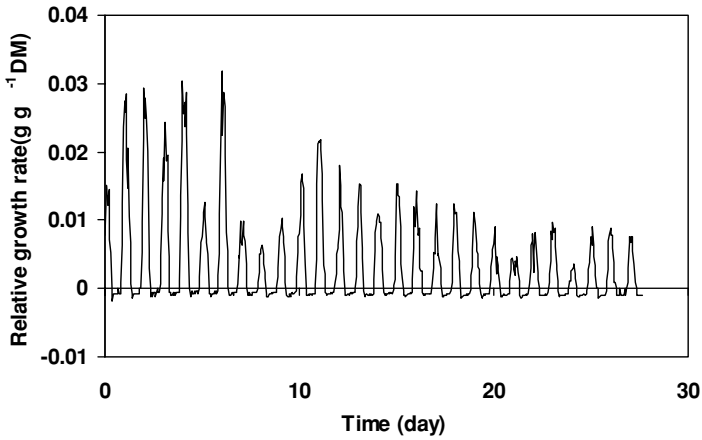


(a) Exp-4



(b) Exp-5

Figure 6. Fluctuations in calculated shoot relative growth rates over time for Exp-4 (a); and Exp-5 (b).

photosynthetic capacity, and its resulting dry weight. An additional explanation is that the parameter values used in the simulations were not sufficiently precise for the particular lettuce variety used in this study.

Nitrogen Uptake Kinetics

Nitrogen uptake rates at the different light intensities used in the present study are in agreement with those in previous work under similar environmental

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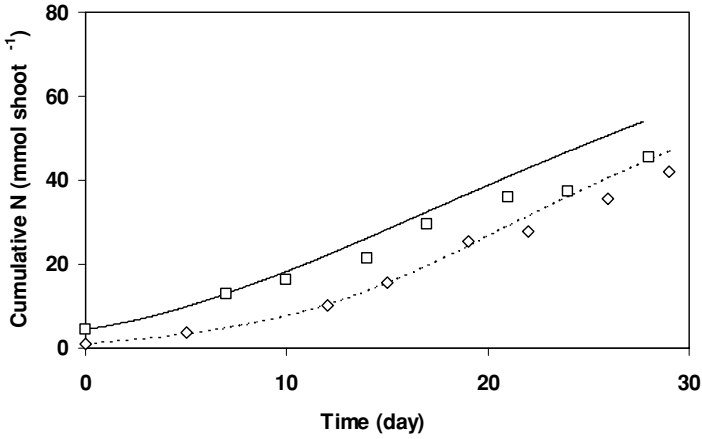

Figure 7. Graphs of measured and calculated cumulative nitrogen in lettuce over time. The solid and dotted lines represent the simulations for Exp-4 and Exp-5. Symbols □ and ◇ represent the corresponding measurements.

conditions (Wheeler et al., 1998). These authors investigated the effects of light and the concentration of nitrogen in their nutrient solutions on nitrogen uptake kinetics on lettuce (*Lactuca sativa*, cv. 'Ostinata'). Their measurements were conducted at light intensities of 350, 250, and 150 μmol m^{-2} s^{-1} (PAR) which,

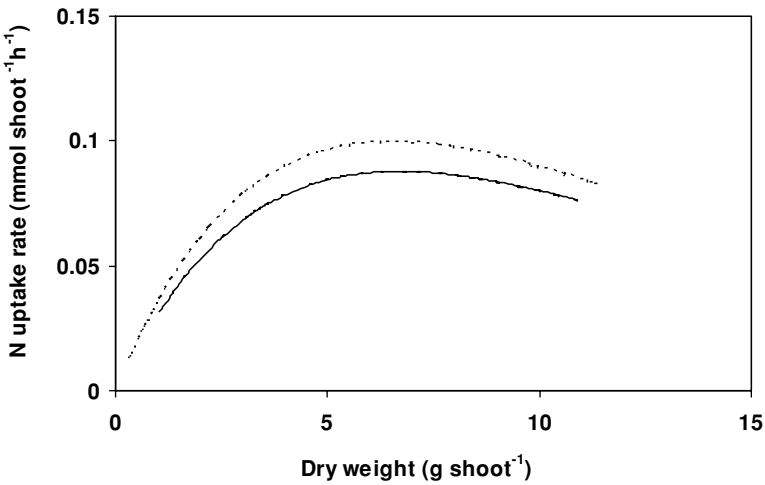

Figure 8. Simulated changes in nitrogen uptake rate with shoot dry weight. The solid and dotted lines represent simulated data from Exp-4 and Exp-5 for high and low light intensities respectively.

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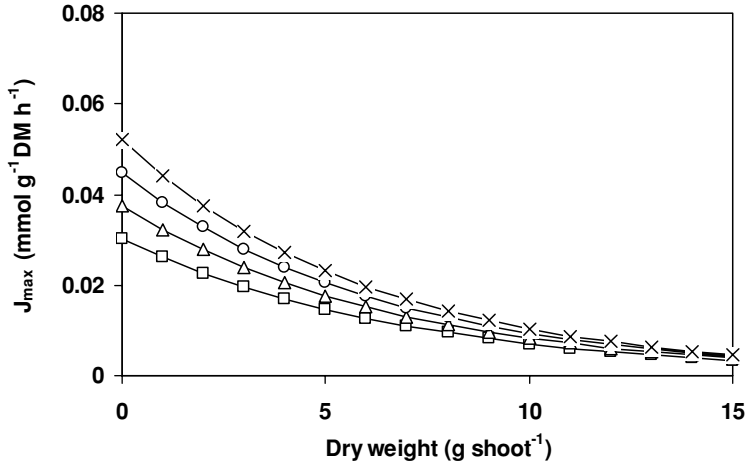

Figure 9. Simulated changes in maximum nitrogen uptake rates J_{max} with shoot dry weights at different light intensities. Symbols □, △, ○ and × represent the light intensities of 3.0, 4.5, 6.0 and 7.5 MJ m^{-2} day^{-1}, respectively.

assuming that the PAR is about 50% of incoming light (Wheeler et al., 1998; Nobel, 1999), are similar to those used in our study. For a nitrogen supply of 4 mM, Wheeler et al. (1998) found maximum nitrogen uptake rates in the range of 0.023 to 0.038 mmol $h^{-1}g^{-1}$DM shoot between 23 and 27 days after sowing. These are close to our findings of 0.029 to 0.045 mmol $h^{-1}g^{-1}$DM shoot derived from our data for the same period. Likewise our values of K_m, which fall within the range of 0.02 to 0.04 mM, are also in good agreement with values of 0.06 to 0.26 mM (Wheeler et al., 1998) and 0.015 mM (Swiader and Freiji, 1996).

In the early growth stages when the plants had high relative growth rates (Figure 6), the nitrogen uptake rate increases with time (Figure 8). However, the rate of increase slowed during growth and then declined towards maturity. In the early growth stages, these changes may be attributed to canopy development, and its association with photosynthetic capacity. When the plants were young, both the total leaf area and the plant ground cover increased with time, and the resulting increase photosynthetic capacity would have created an increased demand for nitrogen. However, once the plants reached their maximum ground cover, both the photosynthesis rate and the associated nitrogen uptake rate would have become approximately constant, despite the continuing increase in total leaf area. Later, as the plants approached maturity, the expected gradual decline in maximum uptake rate (Schenk, 1996) would be expected to influence the amounts of N taken up, causing an apparent reduction in plant demand for nitrogen, much as simulated in Figure 8.

This decline in the maximum nitrogen uptake rate with plant weight agrees with the simulated data in Figure 9, which also shows that the effect occurs

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independently of light intensity. The larger nitrogen concentrations in the shoots at higher light intensities are mainly a result of the greater nitrogen uptake rates. At the start of the simulations, the calculated maximum nitrogen uptake rate was about 0.052 mmol h^{-1} g^{-1}DM at a light intensity of 7.5 MJ m^{-2} day^{-1}, nearly 75% higher than that at a light intensity of 3.0 MJ m^{-2} day^{-1}. However the difference in the maximum nitrogen uptake rates at different light intensities reduced dramatically towards plant maturity, indicating that light has a greater effect on uptake rates in the early stages of growth.

Shoot Nitrogen Concentrations

The model assumes that P_g (and hence growth rate) are only restricted when the total nitrogen concentration in the shoot dry matter (N_{up}/w) falls below 5% (Equation 9). This concentration comprises a minimum of the 3.6% organic-N required to maximize P_g (Broadley et al., 2001), with the remainder as the associated additional organic-N and/or nitrate in the shoot. All or part of this additional nitrogen could be considered to represent luxury consumption, as technically any extra organic-N will be in excess of requirements. In addition, it has been reported that lettuce can 'store' large amounts of nitrate in their shoots (Greenwood and Hunt, 1986) and, by inference, none of this nitrogen is required for growth. However, the underlying mechanism governing nitrate accumulation in lettuce leaves is still under discussion. Some workers argue that it is caused by the insufficient carbon assimilation to reduce nitrate when irradiances are limited (Laine et al., 1995; Cardenas-Navarro et al., 1999). Others believe that nitrate acts as an important osmoticum, helping to maintain sufficient osmotic potential for leaf expansion (Blom-Zandstra and Lampe, 1985; Behr and Wiebe, 1988; Blom-Zandstra et al., 1988; Drews et al., 1995; McCall and Willumsen, 1999). The latter implies that nitrate could be an important component of growth, unless an alternative osmotica can be found without detriment to plant production. This view is reinforced by the results of Burns (1994a; 1994b), who showed that once nitrate has accumulated within the shoot, it cannot readily be 'recycled' for new dry matter production without some reduction in growth rate. Thus, for the purposes of this model, it was assumed that lettuce plants require a minimum of 5% total N in their dry matter to maximize photosynthesis rates.

The model also assumes that the total concentration of nitrogen in the shoot at any time is governed primarily by the N uptake rate (Equations 1 and 2) and the rate of dry matter accumulation (Equations 3 and 4). The latter depends on the photosynthesis rate (Equation 5), which, in turn, is affected by the total nitrogen concentration in the shoot (Equation 9). Thus, because the nitrogen uptake rate depends only on the shoot weight and the concentration of N in the nutrient solution, there is no explicit feed-back mechanism within the model for controlling the maximum nitrogen concentration in the shoot. So provided the

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N concentration in the nutrient solution remains substantially greater than the semi-saturation constant for nitrogen uptake (i.e., $c_N \gg K$), the total nitrogen concentration in the shoot will remain at, or above, 5% of the dry matter, as was observed in our experiments (data not shown). Only when nutrient solution concentrations are very low (i.e., $c_N \approx K$), will the nitrogen uptake rate decline, with concomitant effects on growth rate and nitrogen concentration within the shoot. However, maintaining the external nitrogen at such low levels without sophisticated equipment to continually adjust its concentration can be difficult (see, for example, Clement et al., 1978). Further work to validate the model under conditions of sub-optimal N supply will, therefore, be made using lettuce plants grown in soil and other growing media, where uptake is more easily controlled by the restricted rate of transfer of nitrogen to the root surfaces (Baldwin et al., 1973; Burns, 1980).

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CONCLUSIONS

A model based on a kinetic theory for nitrogen uptake by lettuce grown in adequate nutrient solution under different light intensities was derived and calibrated. Instead of using measured data for shoot dry matter accumulation, a two-compartment mechanistic sub-model was incorporated with a nitrogen uptake kinetics sub-model, in order to develop a more process-based approach.

Good agreement between the calculated and simulated cumulative nitrogen concentrations suggests that the calibrated model is capable of making reasonable predictions for nitrogen uptake over extended periods. The results show that for lettuce grown at natural light conditions, using a light intensity averaged over the whole growing period can give good predictions of nitrogen uptake, despite diurnal and short-term fluctuations in light intensity. Maximum nitrogen uptake rates declined significantly towards lettuce maturity, with the effects of light having a greater influence at early growth stages than at later ones.

Because the model can account for the effects of plant and canopy development on nitrogen uptake rate, it is applicable for the whole growth period. As such, it has the potential for use as a tool for nitrogen management of both hydroponically- and soil-grown lettuce, provided it can be shown to be robust enough to function accurately under conditions of restricted N supply.

ACKNOWLEDGMENTS

The authors would like to thank the Department for Environment, Food and Rural Affairs UK for financing this work through Project HH1414.

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