

A model relating the maximum nitrate inflow of lettuce (*Lactuca sativa* L.) to the growth of roots and shoots

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Received 9 July 1993. Accepted in revised form 14 February 1994

Key words: lettuce, maximum inflow (I_{max}), model, nitrate, relative growth rate, root:shoot-ratio

Abstract

The net inflow of nitrate can be calculated from the nitrate concentration at the root surface by means of the Michaelis-Menten equation. Because of maximum inflow (I_{max}) is not constant but varies with plant age and growing conditions, a model for calculating I_{max} during plant growth was derived. Lettuce was grown in nutrient solution. Variations in temperature, radiation and plant age were used to vary growth rates and N-demand of plants. There was a linear relationship between relative growth rates (RGR) and maximum nitrate inflow (I_{max}), that could be described by the following regression function: $I_{max} = 0.24 + 6.57 \text{ RGR}$. A residual analysis showed a further influence on I_{max} from the root:shoot-ratio (RSR), the effects of which could be accounted for by including an e-function in the relationship: $I_{max} = (0.27 + 10.63 \text{ RGR}) e^{(-0.0017 \text{ RSR})}$. This model for calculating I_{max} was validated in two further experiments.

Introduction

The nutrient uptake rate per unit of root (inflow) is related to the concentration of nutrients at the root surface, which can be described mathematically by the Michaelis-Menten function (Barber, 1984; Epstein and Hagen, 1952). For this, three physiological parameters are necessary: (I) I_{max} , the maximum inflow at infinite concentration, (II) K_m , the concentration at the root surface at $1/2 I_{max}$, and (III) C_{min} , the minimum concentration for net uptake to occur (Claassen and Barber, 1974).

Many herbaceous plants take up nitrate at almost the maximum rate at external concentrations of about $100 \mu\text{M NO}_3$ (Burns, 1980; Heins and Schenk, 1986; Steingrobe and Schenk, 1991). This low 'critical' concentration ensures that maximum inflow occurs under most growing conditions. Thus, I_{max} is an important parameter for calculating nitrate uptake, as was shown by Barber and Cushman (1981) by the means of a sensitivity analysis of their model for predicting uptake of nitrate and its transport in the soil.

The maximum inflow is not constant, but varies with plant species and varieties (Rodgers and Barneix, 1988), age (Jungk and Barber, 1975; Warncke and Barber, 1974; Wild and Breeze, 1981), growing conditions (Hallmark and Huffaker, 1978; Jackson et al., 1973), and nutrient status of the plant (Jackson et al., 1972; Lee, 1982). ' I_{max} ' is therefore not the absolute maximum uptake capacity of a unit of root, but the maximum net inflow under the given growing conditions and plant age.

Little is known about magnitude of I_{max} of nitrate and its changes with growing conditions. Therefore it is difficult to calculate nitrate uptake and transport in the soil by means of models which use the Michaelis-Menten equation. For this reason the objective of this study was to build a model for predicting maximum nitrate inflow (I_{max}) during growth. The long-term objective was the prediction of I_{max} for plants growing in the field, but because of the impossibility to measure I_{max} in the soil the experiments were done in nutrient solution under constant climatic conditions.

Clement et al. (1978), Nye and Tinker (1977) and Van De Dijk et al. (1982) indicated that the actual I_{max}

is related to nutrient demand. The demand of a well supplied plant results from changes in the nutrient content of the whole plant and the amount of nutrients in the new growth (Novoa and Loomis, 1981; Wild and Breeze, 1981). Variations in the total nitrogen content in herbaceous plants without storage organs are generally not large, so the influence this has on demand is negligible. Therefore, nitrate demand is largely determined by the amount of nitrogen in the new growth. Assuming that the nitrogen content of the new growth is constant for well fed plants there should be a relation between I_{max} and growth rates.

Further influence on I_{max} could be derived from nitrogen content of the whole plant and the size of the root system. Plants with a higher root:shoot-ratio can meet the nitrogen demand by a lower maximum inflow. In this paper the influence of growth rates, root:shoot-ratio, and N-content on I_{max} of lettuce will be analyzed.

Materials and methods

Butterhead lettuce (*Lactuca sativa* var. *capitata* L.) cv. 'Rosalba' was grown in a growth chamber in nutrient solution. In order to vary growth rates, treatments differed in daily radiation (150, 330, 500 Wh m⁻² d⁻¹ PAR) at 15°C or in temperature from 5°C to 20°C at the highest radiation. The nutrient solution contained 2 mM N as Ca(NO₃)₂, 1.5 mM P and 1.5 mM K as KH₂PO₄, 3.5 mM Ca as Ca(NO₃)₂ and CaCl₂, 1 mM S and 1 mM Mg as MgSO₄, 110 μM Fe as Fe-EDTA and trace elements. It was steadily aerated and changed two or three times a week.

Every 3 to 7 days measurements of relative growth rate (RGR) and maximum inflow (I_{max}) were made on each plant of a set of five. The plants were weighed one day before the inflow measurements and immediately afterwards. RGR was calculated from both weights as follows (Hunt, 1982):

$$RGR = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \quad [1]$$

RGR	relative growth rate (g g ⁻¹ d ⁻¹)
W	Weight (g)
t	time
index	date of weighing

The maximum inflow (I_{max}) was determined in depletion experiments as described by Claassen and Barber (1974). At the beginning of the measurements the plants were transferred into the depletion solution, which contained half the nutrient concentrations of the above growing solution but without Fe, so as to facilitate the measurement of nitrate. The NO₃-concentration at the start of depletion was about 150 μM. Every 5 to 20 minutes solution samples were taken and the nitrate concentration was determined at 210 nm in a UV spectrophotometer (Navone, 1964). At the beginning of the experimental series second measurements were done after nitrate reduction. This showed a rather low concentration of other UV-absorbing compounds in the solution. Apparently, there was no large excretion of disturbing organic compounds from the roots in the short time (6–10 h) the depletion experiments lasted.

An example of a depletion curve is given in Figure 1a. From the decrease of nitrate concentration between two samples and the actual solution volume the amount of nitrate taken up in this time could be calculated. The solution volume was not kept constant during depletion to avoid dilution or other disturbances. The actual solution volume at each sample was interpolated between volume at the beginning and the end of the experiment. Thus, losses by samples and transpiration were taken into account. From the amount of nitrogen taken up and the root length measured after depletion, the net inflow could be calculated. The net inflow (I_n) was related to the nitrate concentration in solution (C) (Fig. 1b) and a curve following the Michaelis-Menten equation [2] was fitted to the measured data by estimating the parameters, especially I_{max} , by the least squares method.

$$I_n = \frac{I_{max} (C - C_{min})}{K_m + (C - C_{min})} \quad [2]$$

I_n	net inflow (pmol cm ⁻¹ s ⁻¹)
I_{max}	maximum inflow (pmol cm ⁻¹ s ⁻¹)
C	concentration at the root surface (μM)
C_{min}	minimum concentration (μM)
K_m	Michaelis-Menten-constant (μM)

The estimation of I_{max} and of factors affecting I_{max} were done with the linear and nonlinear regression analysis of the statistical program BMDP'83 (Bollinger et al., 1983) at the RRZN ('Regionales Rechenzentrum Niedersachsen').

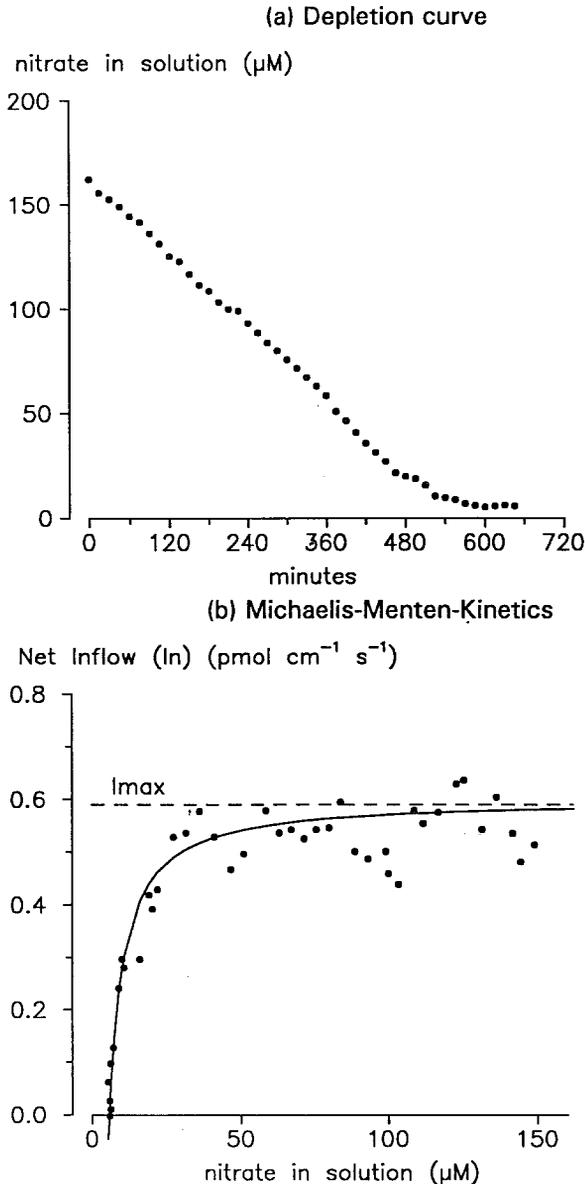


Fig. 1. (a) Depletion of nitrate in the nutrient solution of lettuce and (b) the derived net uptake rates as influenced by NO_3 concentration in solution with a curve fitted by Michaelis-Menten function. (Example)

The plants were harvested after the depletion experiments, fresh and dry weights were measured and the total-N content determined by a modified Kjeldahl method to include nitrate. The total root length was estimated by a line intersection method on subsamples as described by Tennant (1975). Root hairs were not observed. The mean root radius was not affected by treatments or plant age. Therefore the root length

could be chosen as reference quantity for I_{max} without systematic differences to root surface.

Results

Low temperature and radiation retarded plant growth. The comparison of plants at a similar stage of development was therefore done on basis of shoot fresh weight instead of plant age. Small plants had the highest I_{max} under all conditions (Fig. 2a, b). Maximum inflow decreased rapidly from nearly 2 to $0.5 \text{ pmol cm}^{-1} \text{ s}^{-1}$ with increasing shoot fresh weight. This decrease slowed down as plants developed. Lower temperature or radiation reduced I_{max} , but the basic relationship to shoot weight was maintained.

The relative growth rate (RGR) of the whole plant was similarly related to increasing shoot weight (Fig. 3a, b). Small plants had a high RGR, which decreased exponentially with plant size. Unfavorable growing conditions lowered the RGR in a similar way to I_{max} .

The comparable decrease of I_{max} and RGR with increasing plant weight resulted in a close correlation between both parameters as shown in Figure 4. Independent of the reasons for variations in RGR (plant age, temperature or radiation), I_{max} varied in the same way.

The relationship between RGR and I_{max} (Fig. 4) was described by the linear function [3]:

$$I_{\text{max}} = 0.24 + 6.57 \text{ RGR} \quad [3]$$

I_{max} maximum inflow ($\text{pmol cm}^{-1} \text{ s}^{-1}$)
 RGR relative growth rate ($\text{g g}^{-1} \text{ d}^{-1}$)

Coefficient of determination was $R^2 = 0.94$ and highly significant. However, some treatments deviated from the regression line. In particular the 5°C -treatment (filled squares) was overestimated by the linear function [3], indicating that I_{max} depended on other factors beside RGR.

This was investigated by an analysis of residuals, which is shown in Figure 5 exemplary for (a) the total-N content in shoot dry matter (N_t), and (b) the root:shoot-ratio. These factors were chosen as example because of their possible influence on nitrate demand or nitrate inflow, respectively.

The total-N content varied between 3% and 5.5% in dry matter partly influenced by the climatic treatments. But it is evident that there was no influence of the total

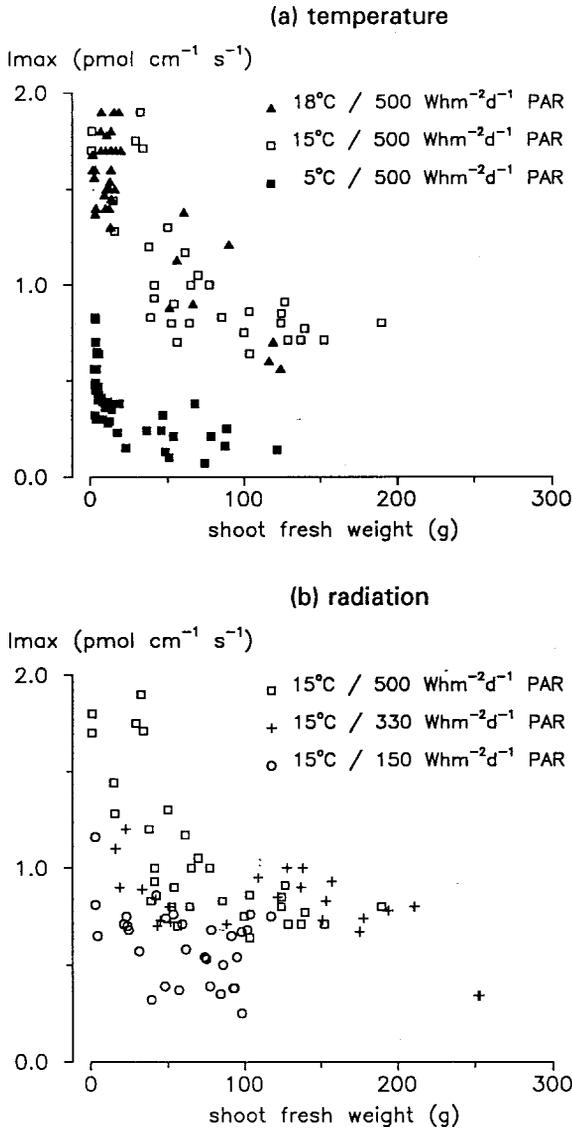


Fig. 2. Relationship between shoot fresh weight and maximum nitrate inflow (I_{max}) of lettuce at various temperatures (a) and radiation levels (b).

nitrogen content of the plants on the residuals between measured and calculated values of I_{max} , because the residuals are randomly distributed around the zero line at each N-content.

Such an influence was observed between the root:shoot ratios (RSR) and the residuals. Most of the plants had root:shoot ratios of about 100–300 cm g^{-1} fresh matter. These plants had mainly positive residuals, which means a slightly underestimation of I_{max} . The plants grown at 5°C (filled squares) had much higher root:shoot-ratios. These plants had larger

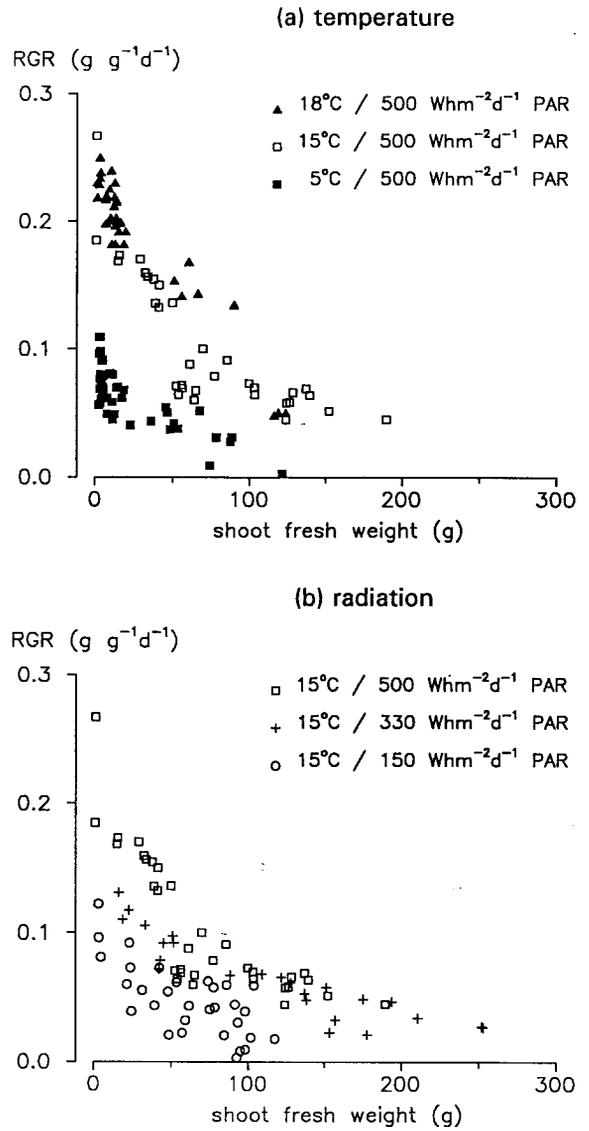


Fig. 3. Relationship between shoot fresh weight and relative growth rate (RGR) of the whole plant at various temperatures (a) and radiation levels (b).

root systems than plants of the other treatments and I_{max} could therefore be smaller to meet the nitrogen demand. This resulted in an overestimation of I_{max} by function [3] and negative residuals in the case of high RSR.

High root:shoot-ratios above 300 cm g^{-1} occurred at low temperatures of about 5°C, whereas higher temperatures led to lower RSR. Because of this influence of temperature on RSR there was an analogous influence of temperature on the distribution of the residuals, too (data not shown). Based on the data of this study it

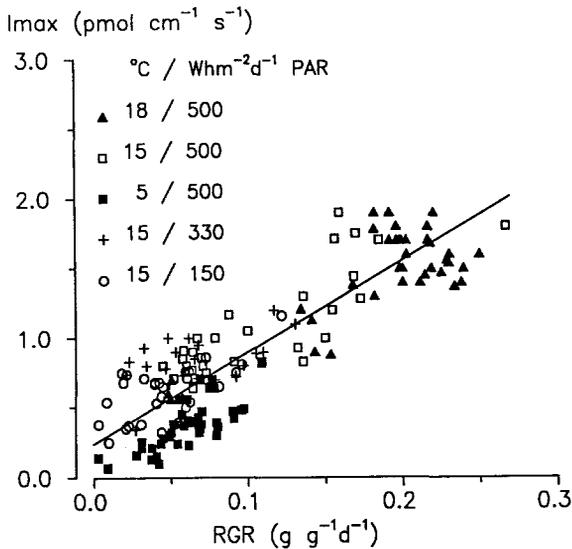


Fig. 4. Relationship between relative growth rate (RGR) of the whole plant and maximum nitrate inflow (I_{max}) of lettuce at various temperatures and radiation levels. The equation of the line is: $I_{max} = 0.24 + 6.57 \text{ RGR}$ (Function [3]) ($R^2 = 0.94$).

is not possible to decide which parameter, temperature or RSR, had the main influence on I_{max} . Engels (1993) could show for wheat and maize that the nutrient demand that has to be satisfied by a unit of root has a much higher influence on P- and K-inflow than the root temperature has. The nutrient demand that has to be satisfied by a unit of root is on the other hand strongly dependent on the size of the root system.

For this reason function [3] was extended by the influence RSR has on I_{max} . The distribution of the residuals in Figure 5b indicated a non-linear influence, therefore an exponential function for RSR was chosen and the parameters were estimated.

$$I_{max} = (0.31 + 9.5 \text{ RGR}) e^{(-0.0014 \text{ RSR})} \quad [4]$$

I_{max}	maximum inflow ($\text{pmol cm}^{-1} \text{ s}^{-1}$)
RGR	relative growth rate ($\text{g g}^{-1} \text{ d}^{-1}$)
RSR	root:shoot-ratio ($\text{cm g}^{-1} \text{ FM}$)

The maximum nitrate inflow calculated by function [4] agreed well with observed I_{max} for the temperature and the radiation treatments (Fig. 6a, b). The coefficient of determination increased from 0.94 to 0.97 and the F-value improved significantly. Further residual analysis revealed that no other factors influenced I_{max}

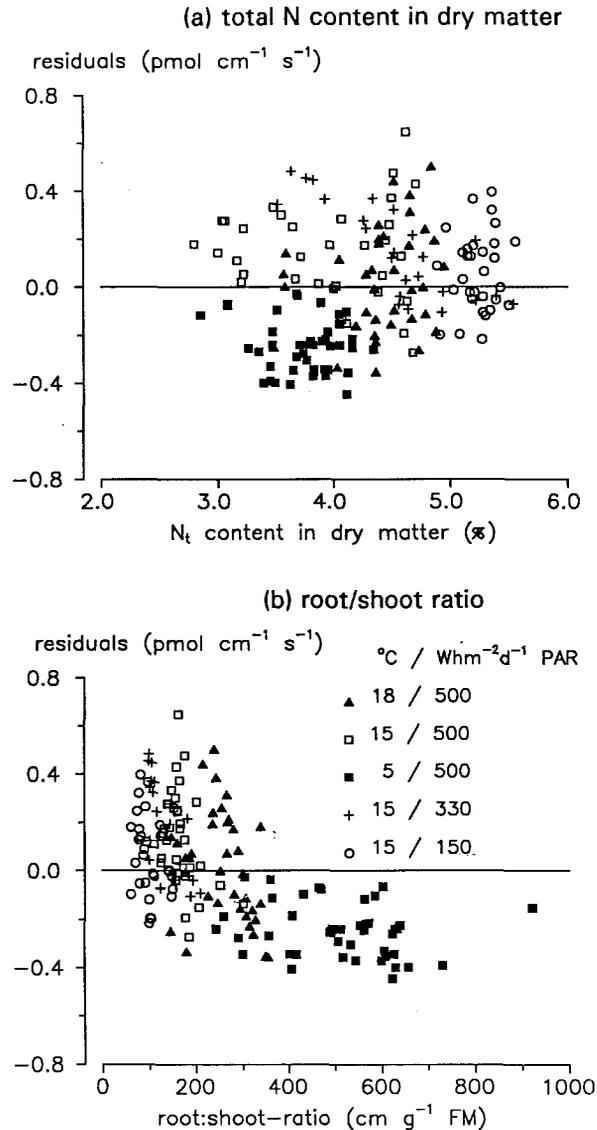


Fig. 5. Effect of the total N_t -content in shoot dry matter (a) and the root:shoot-ratio (b) on the residuals (measured minus calculated) of I_{max} calculated with function [3].

and confirmed the validity of the used functions for RGR and RSR in the model [4].

The model was validated in two more experiments, in which plants were grown under similar conditions as before, but temperatures were maintained at 10°C and 20°C. The 10°C temperature was within the range used to build the model, whereas the 20°C temperature was a slight extrapolation.

The agreement between predicted and observed I_{max} for the 20°C-treatment was very good (Fig. 7). I_{max} could be calculated over the whole range from

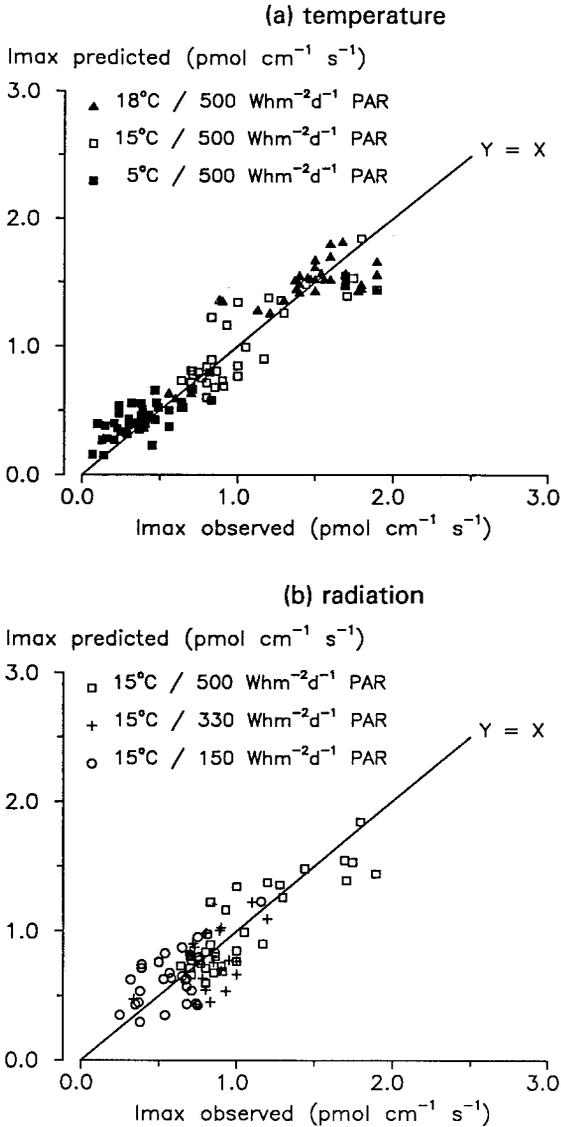


Fig. 6. Comparison of observed and predicted I_{max} (by function [4]) at various temperatures (a) and radiation levels (b). R² = 0.97).

0.3 up to 2.5 (pmol cm⁻¹ s⁻¹) by means of function [4].

The values and range of I_{max} for the 10°C-treatment were much smaller than for the 20°C-treatment because of the slower growth and therefore a lower nitrogen demand at this temperature. Values of I_{max}, predicted by function [4] revealed a slight overestimation for the whole treatment, while the distribution pattern is parallel to the 1:1-line.

A residual analysis (data not given) showed that this overestimation was due to a further influence of the root:shoot-ratio, although the RSR was already

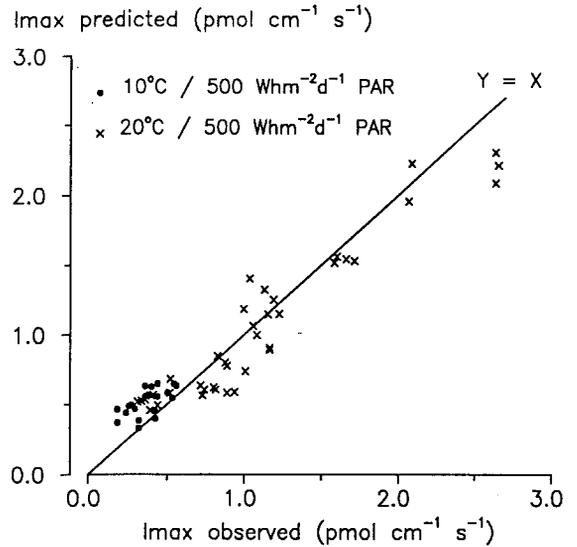


Fig. 7. Validation of function [4]. Comparison of observed and predicted I_{max} at 10°C and 20°C.

considered in function [4]. This means that the parameter for the root:shoot ratio (-0.0014) in the function was inadequate. This was not surprising, because the data set for estimating this parameter was relatively small. Only the 5°C-treatment showed a wider range of root:shoot-ratios (Fig. 5b) and affected the estimation more than the other treatments.

A second estimation of the parameters with the whole data set, including the 10°C and 20°C-treatments, produced the following function:

$$I_{max} = (0.27 + 10.63 \text{ RGR}) e^{(-0.0017\text{RSR})} \quad [5]$$

- I_{max} maximum inflow (pmol cm⁻¹ s⁻¹)
- RGR relative growth rate (g g⁻¹ d⁻¹)
- RSR root:shoot-ratio (cm g⁻¹ FM)

The parameters differed slightly from those in [4] and gave greater emphasis to the root:shoot-ratio. The agreement between observed and predicted I_{max} was still good for all treatments and slightly better for 5°C and 10°C (Fig. 8). The coefficient of determination was 0.97. Another residual analysis showed no other influences on I_{max}. The model [5] was able to predict the maximum nitrate inflow in nutrient solution under the given conditions.

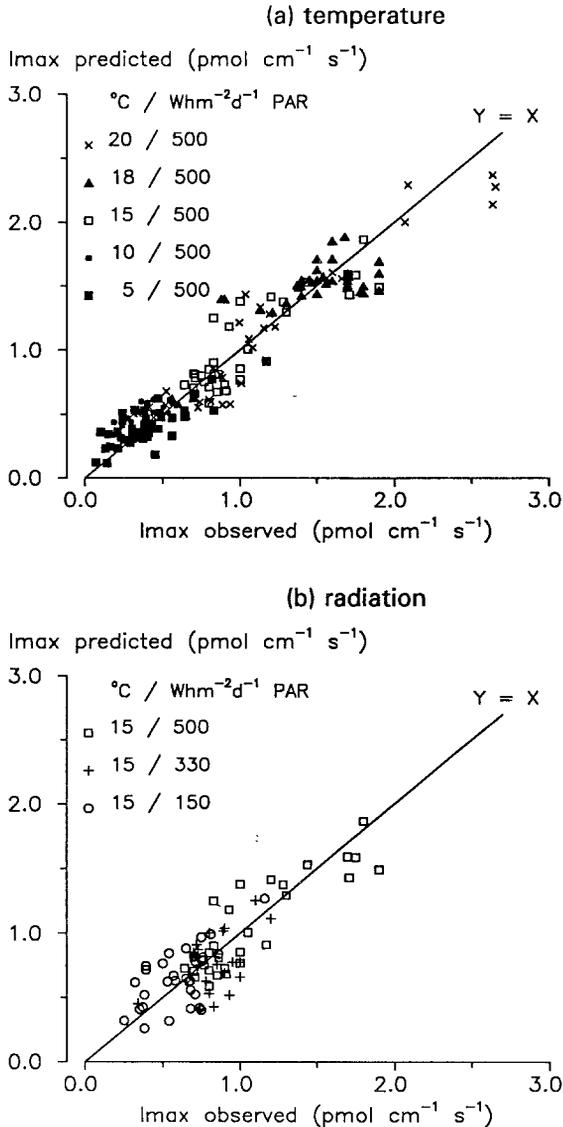


Fig. 8. Comparison of observed and predicted I_{max} (by function [5]) at various temperatures (a) and radiation levels (b). (All data, $R^2 = 0.97$).

Discussion

The measured maximum nitrate inflow was between 0.2 and 2.5 $\text{pmol cm}^{-1} \text{s}^{-1}$ (Fig. 8), depending on the climatic regime and age of the plants. This is in the range of I_{max} for herbaceous plants reported by other authors, for example 1.3 $\text{pmol cm}^{-1} \text{s}^{-1}$ for peas (Robinson, 1986), 4–6 $\text{pmol cm}^{-1} \text{s}^{-1}$ for rape (Bhat et al., 1979; Robinson, 1986), 0.44–1.04 $\text{pmol cm}^{-1} \text{s}^{-1}$ for sugar beet (Strebel and Duynisfeld, 1989), and 0.3 and 0.6 $\text{pmol cm}^{-1} \text{s}^{-1}$ for spinach and kohlrabi,

respectively (Steingrobe and Schenk, 1991). Letey et al. (1982) reported a daily N-uptake by lettuce of 0.5–3 mmol/plant, which agrees with the uptake reported here at comparable plant age.

The inflow decreased with plant age. Similar observations were made by Edwards and Barber (1976) and Pitman and Cram (1976). In split root experiments, Kuhlmann and Barraclough (1987) showed that this was not due to a lower uptake capacity of older roots, but to a decreasing demand that has to be satisfied per unit root. The nutrient demand during the linear growth phase is nearly constant, but the root system is still growing, thus the demand per unit root is decreasing (Barber, 1984). If the N-supply to plants is not limited, the N-demand reflects the increase of the amount of N in the growing plant. This increase is due to (a) changes in N-content of the whole plant and (b) the amount of N in the new growth (Novoa and Loomis, 1981; Wild and Breeze, 1981). Though the total N-content varied between 3.0% and 5.5% over all treatments (Fig. 5a) and decreased with plant age (data not shown), there was no influence of the N-content on I_{max} (Fig. 5a). Probably the changes of N-content during a depletion experiment were too small. Thus the N-demand of lettuce was mainly due to the N amount in the new growth.

Data about N in the new growth were not available, but it is likely that the N-content is nearly constant for lettuce given an adequate nitrogen supply. This may not be the case for perennial species that have an alternating pattern of generative and vegetative growth or woody species that temporarily store N.

Thus, the daily N-demand of lettuce is determined by daily new growth. This can be described by the absolute growth rate (AGR), but there was no close relationship between AGR and I_{max} in the present work (data not shown), because both small plants and plants under adverse climatic conditions had similar AGR, but different I_{max} . A better relationship has been found between I_{max} and the relative growth rate (RGR), because both parameters are ratios related to the existing amount of plant material, RGR to shoot weight and I_{max} to root length. Thus, for a constant root:shoot-ratio there must be a linear relationship between RGR and I_{max} as can be seen in Figure 4.

A linear relation between nitrogen uptake rates and RGR was also reported by Rodgers and Barneix (1988) for different wheat varieties. Cheeseman and Wickens (1986b) showed a very close relationship between the relative K^+ - and Na^+ -absorption rate and RGR of

Spergularia marinara even through discontinuities in growth conditions and considered a co-regulation of uptake and growth rather than a correlation.

The root:shoot-ratio was not constant (Fig. 5b), so changes in this had to be incorporated into the predictive functions [4] and [5] for I_{max} . Cheeseman and Wickens (1986a) reported also a significant negative correlation between K^+ - and Na^+ -uptake of *S. marinara* and RSR, either in a single linear regression or in a stepwise multiple regression combined with plant size and K^+ content in the roots. For the present data, an exponential function gave the lowest sum of squares and the best fit and was therefore chosen. Wild and Breeze (1981) used a reciprocal function to describe the influence of the root:shoot-ratio on I_{max} . This function can be deduced from the relation between AGR and RGR. The reason that an e-function gave a better fit might be due to the fact that the root:shoot-ratio was affected by temperature, and temperature also affects the inflow (MacDuff and Hopper, 1986). Thus, the root:shoot-ratio reflects two factors. The physiological relevance of the e-function remains to be proven.

Function [5] is a simple model for calculating I_{max} during plant growth. The input parameter 'RGR' can be derived from growth models, which are available for several species. It is more difficult to obtain values of the input parameter 'root:shoot-ratio', as no models are available relating this to growing conditions. In the first instance, empirical values will have to be employed.

This model for calculating I_{max} was derived and validated under constant climatic conditions in nutrient solution. Also a validation under changing climatic conditions in the greenhouse was possible (Steingrobe and Schenk, 1993). But for the prediction of I_{max} of plants growing in the fields further investigations in soil are necessary. Knowledge about the size and distribution of the root system is essential, especially in soil, and further factors like root temperature, NH_4 -supply, nutrient status of the plant, and heterogeneous NO_3 -distribution in the soil could be important.

Acknowledgements

The research project was financially supported by the Deutsche Forschungsgemeinschaft. The authors thank Dr P Barraclough, Rothamsted Exp. Station, for valuable comments and correction of the English.

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Section editor: T W Ruffy