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Simulation of the maximum nitrate inflow (Imax) of lettuce (*Lactuca sativa* L.) grown under fluctuating climatic conditions in the greenhouse

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Abstract

Lettuce was grown in nutrient solution under fluctuating climatic conditions in the greenhouse. The maximum nitrate inflow (Imax) was measured twice a week to validate a model for calculating Imax, that was developed for constant conditions in a growth chamber.

Growth and Imax were very similar between greenhouse and growth chamber plants, so that the model was able to predict Imax very precisely. The daily maximum nitrate inflow was calculated and its dependency on fluctuating temperature could be shown.

Introduction

The uptake rate of nitrate per unit root length (inflow) depends on the nitrate concentration at the root surface. This can be described by Michaelis-Menten kinetics if three physiological parameters are known, the minimum concentration, Cmin; the Michaelis-Menten constant, Km; and the maximum inflow, Imax. Often the maximum nitrate inflow of herbaceous plants is already obtained at concentrations as low as 100 μM and lower (Heins and Schenk, 1986), so that Imax is the most important parameter for predicting the nitrate uptake by using Michaelis-Menten kinetics. This was also shown by Barber and Cushman (1981) by means of a sensitivity analysis of their uptake model.

The problem in using Michaelis-Menten kinetics for uptake calculation is, that Imax is not a constant. It changes with varieties (Rodger and Barneix, 1988), plant age (Wild and Breeze, 1981), growing conditions (Hallmark and Huffaker, 1978), and nutrient status (Heins and Schenk, 1986). Therefore a model was developed to calculate Imax from the relative growth rate (RGR) and the root:shoot-ratio (RSR) (Steingrobe, 1992; Steingrobe and Schenk, 1994). This model was developed and validated for lettuce grown under constant conditions in a growth chamber in nutrient solution. The objective of this paper is to validate this model under fluctuating climatic conditions in a greenhouse.

Materials and methods

Lettuce (*Lactuca sativa* L. var. *captitata*) cv. 'Rosalba' was grown in nutrient solution in the greenhouse. The solution and the handling of the plants was similar to the experiments for developing the model in the growth chamber as described by Steingrobe and Schenk (1994). The daily average temperature in the greenhouse is given in the upper part of Fig. 3. The average temperature for the whole growth period was about 19°C, with a colder period at the beginning and a warmer period at the end of the culture. The radiation was between 600 and 2500 (Ø 1220) $Whm^{-2}d^{-1}$ PAR and followed the temperature closely, therefore it is not specifically shown.

Twice a week the maximum inflow was determined in depletion experiments as described by Claassen and Barber (1974). The plants were transferred to a well-stirred, complete, nutrient solution (without Fe), which contained 150 μM NO_3. Every 5 to 20 minutes a sample was taken and the nitrate concentration photometrically measured. Imax was calculated from the decrease of concentration, solution volume, time, and the root length determined after the depletion experiment by a line intersection method.

One day before and immediately after the depletion the plants were weighed to calculate the relative growth rates.

Results and discussion

The maximum inflow follows the nitrogen demand of a plant determined by growth for lettuce, which can be described by the relative growth rate (RGR). This demand has to be satisfied by the root system. Therefore the size of the root system, expressed as 'root:shoot-ratio (RSR)', has also an influence on Imax. Thus, a model could be developed which calculates Imax from its linear relationship to RGR and an exponential relation to RSR as follows (Steingrobe and Schenk, 1994):

$$\text{Imax} = (0.27 + 10.63\ \text{RGR})\ \exp(-0.0017\ \text{RSR})$$

Figure 1a shows the RGR measured in the greenhouse in comparison to data used for developing the model, which were obtained in the growth chamber at a similar average temperature but lower radiation (Steingrobe and Schenk, 1994). For both experiments, the youngest plants had the highest growth rates. These decreased rapidly with increasing shoot weight. There was no difference in RGR between both experiments until the plants had reached a shoot fresh weight of about 100g. Beyond this, the greenhouse plants had higher RGR. This was probably due to the increased daily temperatures at the end of this experiment (see Fig. 3), whereas at the beginning temperatures were in a comparable range as for growth chamber plants. The greater daily amplitudes of temperature could have also led to higher growth rates

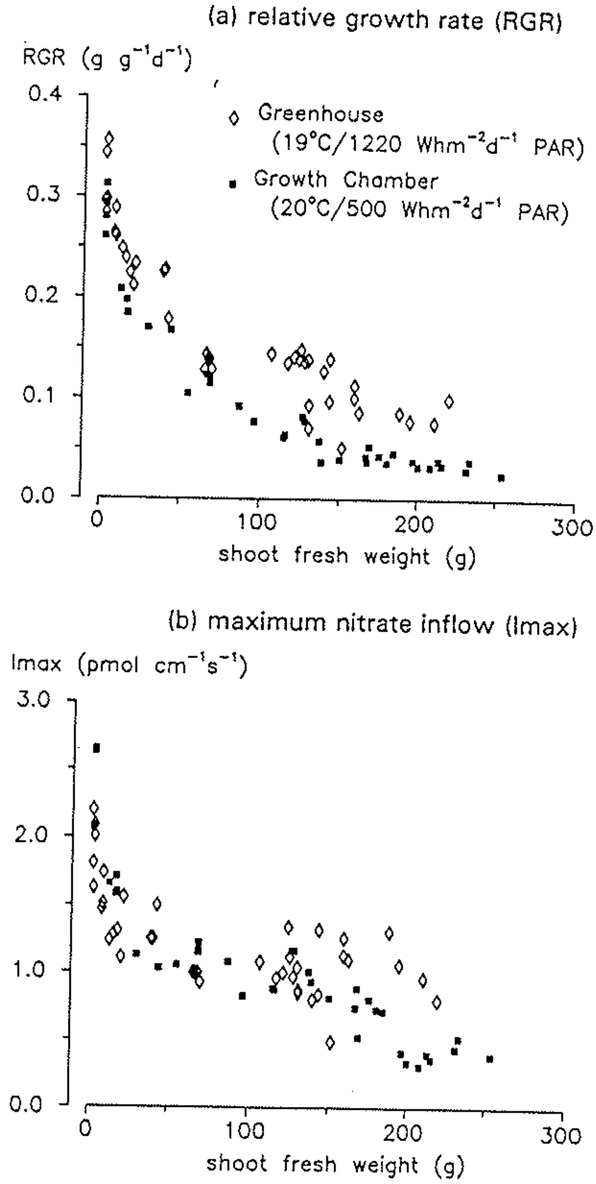

Fig. 1. Influence of the shoot fresh weight on (a) the relative growth rate (RGR) and (b) the maximum nitrate inflow (Imax) of lettuce grown in the greenhouse and in the growth chamber under comparable average temperature conditions.

(Wiebe and Lorenz, 1977).

The higher radiation in the greenhouse compared to the growth chamber apparently had no measurable effect on growth rates. This means, that at radiation beyond 500 $Whm^{-2}d^{-1}$ PAR growth was mainly influenced by temperature. This is in accordance with results of Krug and Liebig (1988) for young plants of lettuce. They reported a very shallow response curve of growth at radiations above 1200 $Whm^{-2}d^{-1}$, which is in a similar magnitude if transferred to PAR.

Since the fluctuating climatic conditions had nearly the same effect on growth as comparable constant conditions, the maximum inflow also followed the plant weight in both experiments in a similar pattern (Fig. 1b). The differences between the growth chamber plants and the greenhouse plants were very small. Only at the end of the culture was Imax in the greenhouse slightly higher than in growth chamber. A similar observation appear to RGR in Figure 1a. The higher radiation in the greenhouse had no effect on Imax as well.

Figure 1b also shows, that Imax decreased with increasing shoot weight in a similar way like RGR did. This was consistent with the linear relationship between Imax and RGR used in the model. Thus, the prediction of Imax by the model corresponded very well with the observed maximum inflow in the greenhouse (R^2 = 0.83) (Fig. 2). An analysis of residuals showed no further influences on Imax and supported the

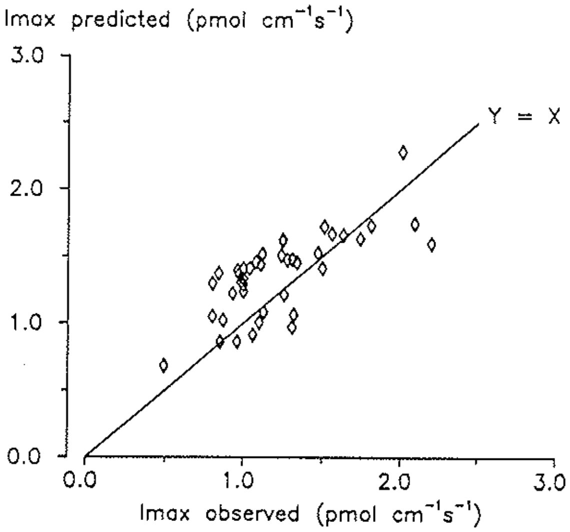

Fig. 2. Relationship between observed and predicted maximum nitrate inflow (Imax) of lettuce grown in the greenhouse under fluctuating climatic conditions.

function types used. Thus, it was possible to simulate Imax under fluctuating climatic conditions, even under the extreme average daily temperatures of about 25-30°C at the end of the culture, when maximum temperatures were about 40°C.

It was now possible to calculate Imax for each day during crop growth by the model. For this it was also necessary to compute RGR for the days between the depletion experiments. This could be done by a modified Feldmann-function using temperature and radiation as described by Steingrobe (1992). The daily root:shoot-ratio was calculated by interpolation of the measurements. Figure 3 shows the course of predicted Imax in comparison to the daily temperature and the observed inflow.

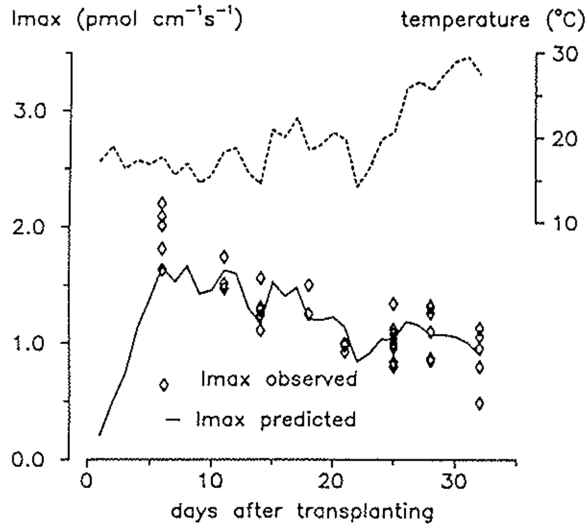

Fig. 3. Course of the predicted maximum nitrate inflow (Imax) of lettuce grown in the greenhouse under fluctuating climatic conditions, observed Imax, and average daily temperature.

The rapid increase of predicted Imax in the first 6 days was due to an increase of predicted RGR for young plants. After this Imax decreased steadily and the influence of the fluctuating temperature was evident. In this model the temperature did not affect Imax directly, but it affected Imax through RGR.

The influence of the temperature on Imax seemed to decrease with plant age. The high temperatures after day 25 did not increase the uptake much, it just slowed down the decrease to a more stable Imax. This could be due to the low RGR, allowing no extensive variations at this growing stage. Also, the increase of temperature in this high range does not have the beneficial effect on growth that it would at lower temperatures.

The correspondence between predicted and observed Imax was very good for the whole course of the experiment. This indicates a close correlation between temperature, growth rate and Imax. But this correlation was not so close, that an influence of temperature variation during a depletion experiment on Imax could be determined. Thus, a daily calculation of Imax should be accurate enough for the simulation of nitrate uptake.

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