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# Impacts of N-deprivation on the yield and nitrogen budget of rockwool grown tomatoes

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**Abstract** – An experiment is related in which well-fed tomato plants, grown within a rockwool tomato culture, were suddenly nourished with a nitrogen-free nutrient solution. For 6 weeks, control (+N) and treated (-N) plants were regularly harvested and analysed in order to determine the impact of the treatment on growth, yield and N composition of several organs. After 6 weeks of the treatment, -N plants had accumulated ca. 20% less dry biomass, mainly because of a reduced vegetative growth. Commercial fruit yield was slightly less affected by N-withdrawal, being decreased by 17%. -N plants invested less N than C in the growth of young fruits, leading to %N decrease in their dry biomass. N movements, mainly feeding fruits, have been characterised. In control plants, the efficiency of N-fertiliser use was low (46%) indicating important nitrate wastage in the drainage ( $> 1000 \text{ kg N} \cdot \text{ha}^{-1}$ ), harmful to the environment.

*Lycopersicon esculentum* / critical N / environment / model / deficiency

**Résumé** – Impacts d'une privation d'azote sur le rendement et le bilan azoté d'une culture de tomate sur laine de roche. Une privation d'azote a été pratiquée sur un lot de plantes au cours d'une culture de tomates sous serre. Pendant 6 semaines, des plants témoins et privés d'azote ont été prélevés et analysés pour déterminer l'impact du traitement sur la croissance, le rendement et la composition des organes. Chez les plantes -N, on a observé 20% d'accumulation de MS en moins après 6 semaine de traitement, majoritairement dus à une faible croissance végétative. Le rendement en fruits récoltés a lui aussi été affecté (-17%). Pendant la privation, la plante a investi moins d'azote que de carbone dans la construction des jeunes fruits, impliquant une teneur moindre en azote. Des mouvements d'azote ont été caractérisés dans la plante, essentiellement vers les fruits. Chez les plantes +N, on a déterminé au cours du cycle cultural, un faible coefficient d'interception de l'engrais azoté (0,46), signifiant un fort rejet d'azote dans les drainages ( $>1000 \text{ kg} \cdot \text{N ha}^{-1}$ ), préjudiciable à l'environnement.

*Lycopersicon esculentum* / carence / environnement / modèle / N critique

## 1. INTRODUCTION

In commercial hydroponic systems, plants are fed both water and nutrients according to their water demand, estimated from climate-based models [4, 13]. Because plant nutritionists have not proposed alternative

models, the tomato growers have been forced to develop this practice, to satisfaction considering the strict viewpoint of productivity. Hence, a typical tomato crop grown in a sophisticated greenhouse produces around 40 tons of total dry matter (DM)·ha<sup>-1</sup> (ca. 3 times more than one ha of the best wheat fields), yielding about

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450 tons of fresh tomatoes [30]. This *efficiency* is fallacious, however, from a nutritionist's viewpoint: while field-grown wheat requires around 230 kg N·ha<sup>-1</sup> to reach a goal of 14 t·ha<sup>-1</sup> DM, the hydroponic tomato crop will receive a minimum of 2000 kg N·ha<sup>-1</sup> (i.e. 10000 m<sup>3</sup> at a minimum concentration of 14 mM of N) of which more than 50% will be leached, the rest being either taken up by the plants or stored in the substrates (rockwool for example) and thus ultimately thrown in the environment. At the greenhouse scale, several studies on soilless cultures report annual nitrogen losses approaching or exceeding 1 t·ha<sup>-1</sup> [14, 43]. The balance sheet is even more impressive at the regional scale. A case study proposed in the professional literature [32] considers the impact of 140 ha of greenhouses on the closed-drainage area of Brest's harbour (Brittany, France). The study calculates that 500 000 m<sup>3</sup>·y<sup>-1</sup> of nutrient solutions are leached to the sea with at least 560 tons of fertilisers.

Because there is no physiological evidence that N is more efficient in building up the DM of wheat than of tomato (N efficiency is only noticeable between C<sub>3</sub> and C<sub>4</sub> species, [21, 38]) such a fertilisation practice can certainly be optimised, in particular to meet environmental standards emerging within the EU. A recent study conducted by Siddiqi et al. [40] concluded that nitrate concentration in nutrient solutions (11 mol·m<sup>-3</sup>) could be halved without noticeable effects on the growth or yield of tomatoes. Moreover, because an ample-fertilisation practice argues against the physiological belief, often evolved from experiments with plantlets rather than crops, that maximum growth rates can be achieved at low nutrient supplies [15, 23, 31] there is also a need to investigate further the precise nitrogen requirements of adult plants.

We report in this paper on an experiment led for 6 weeks with an adult tomato crop using the technique of nutrient (nitrate) interruption. The main purpose of the work was to examine the ability of the crop to maintain growth in the absence of nitrogen in the feeding nutrient solution. We established the nitrogen budget of the crop to assess possible internal N movements (source-sink relationships) and quantify the exploitation of residual N in the substrate (rockwool) by the plants.

## 2. MATERIALS AND METHODS

The tomato crop (*Lycopersicon esculentum* Mill. var *Thalis*) was planted on rockwool slabs on December 23rd 1996 in a commercial greenhouse (Station expérimentale INRA du Mas Blanc, Alénia, France). The double row culture was set at a mean plant density of

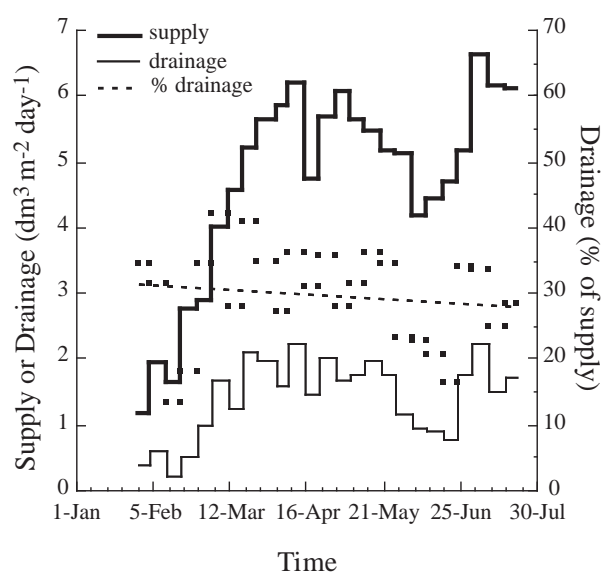
2.2 m<sup>-2</sup>, each plant being fed with one drip. The cultural practice mirrored that used in commercial greenhouses. Partial defoliation was carried out on several occasions (February 20th, March 20th and April 15th). Fruit harvests started on April 1st, and continued at the rhythm of one or two per week. The cultivation lasted until July 20th, the commercial yield attaining 25 kg·m<sup>-2</sup>.

Plants were fed individually through a computer controlled drip irrigation system. The nutrient solution was adjusted to plant phenology, in particular for nitrogen whose concentration decreased regularly from 28 to 16 mol·m<sup>-3</sup> from the beginning to the end of the growth cycle (Tab. I). The drips were dimensioned for a flow of 36 dm<sup>3</sup>·h<sup>-1</sup>, nutrient supply being split into elementary doses of 165 to 230 cm<sup>3</sup> per plant. Irrigation was triggered either by a timer or by calculation, each time the cumulated evapotranspiration exceeded 4 mm. This practice resulted in daily supplies comprised of between 1.2 and 6.6 dm<sup>3</sup>·m<sup>-2</sup>, with a final budget of 810 dm<sup>3</sup>·m<sup>-2</sup> (i.e. 8100 m<sup>3</sup>·ha<sup>-1</sup>) at the end of the crop cycle. Drainage was measured on a weekly basis by collecting the leachates. This regime ensured a mean rate of drainage close to 30% of the supply (Fig. 1).

During the experimental work, two sets of 15 plants each were identified in the greenhouse and fed by independent drip irrigation systems. From March 28th until May 14th (6 weeks) these two groups of plants received either the standard nutrient solution containing nitrogen (called +N thereafter) or a nitrogen-free nutrient solution (called -N thereafter). After that date, -N plants were fed again with the standard nutrient solution until a supplementary harvest, carried out on May 30th to evaluate their ability to recover from the period of N-starvation. The compositions and main characteristics of the two nutrient solutions are given in Table II. Micronutrients were supplied as a commercial mixture. The nutrient solutions were made with water taken from a well and commercial grade fertilisers, which explain the traces of N detected in the -N solution (ca. 0.1 mol·m<sup>-3</sup>).

**Table I.** Nitrogen concentrations of the successive nutrient solutions used during the growth cycle. Prior to plantation, the rockwool slabs were water-saturated for one day, using a nutrient solution with 28.6 mol NO<sub>3</sub>·m<sup>-3</sup>.

Dates	Growth stages	Total N in solution (mol·m <sup>-3</sup> )
23/12 to 23/01	nursery	24.4
24/01 to 05/02	plantation to 2nd leaf	27.6
06/02 to 05/03	2nd leaf to 6th leaf	23.4
06/03 to 16/03	6th leaf to harvest of 2nd truss	16.3
17/03 to 21/07	until final harvest	16.6



**Figure 1.** Regime of irrigation (supply) and drainage during the crop cycle. Data are daily averages. On the Y2 axis, circles and dashed line are the calculated weekly % drainage and the regression throughout the entire growth, respectively.

The slabs holding the -N plants were flushed on March 28th by the -N solution until nitrate concentration in the drainage was less than 1 ppm. This flush lasted 4 days. Afterwards the fertigation rhythm of -N plants mirrored that of +N plants.

At treatment initiation, a ring was placed on the stem of each plant to mark the truss undergoing fruit-set. Arbitrarily we used that ring to split the leaves in two, i.e. the leaves below the ring were considered as old (OL), compared to young leaves (YL) above the ring. Over the experiment, 14 plants +N and 14 plants -N were sampled, on average at the rhythm of one plant per treatment every 3 days. The plants were separated into classes of organs: old and young leaves (OL, YL) and stems and petioles (SP). The fruits were split into large (LFr), medium fruits still in their growth phase (MFr)

and small fruits (SFr). The mature fruits (Fr) were harvested and collected plant per plant. Defoliated leaves and petioles ( $OL_{def}$ ,  $SP_{def}$ ) were analysed separately but the results were pooled with the OL and SP fractions, respectively. For each plant fraction, the fresh weight was measured and the dry weight was determined after drying at 70–80 °C. After grinding, the samples were analysed for total N and nitrate. Total N was determined by the method of Dumas, using an elemental analyser (Carlo Erba, model 1500, Milan, Italy), while  $NO_3$  was determined colorimetrically on water extracts using an automated analyser (Aquatec 5400 analyser, Tecator, Höganäs, Sweden). No analysis was performed on the root system.

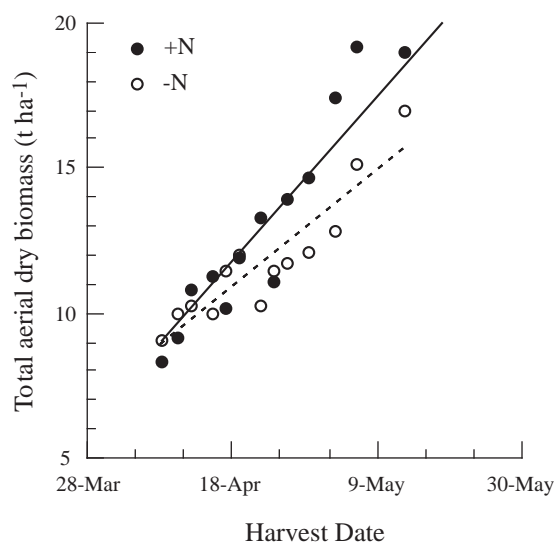
### 3. RESULTS

#### 3.1. Growth and yield

For +N plants, total dry aerial biomass accumulation has been plotted against time (T, days from treatment initiation) in Figure 2. Growth appeared linear with time ( $DM = 0.32 \times T + 4.77$ ,  $R^2=0.91$ ) and from external global radiation data, we calculated a mean daily radiation use efficiency (RUE) of 0.8 g·MJ<sup>-1</sup> Rg. The growth analysis made at the level of individual plant fractions revealed that only two compartments grew actively during the period studied, the fruits (Fr + LFr + MFr + SFr, Fig. 3) and to a lesser extent, the young leaves (YL, see also Fig. 6). Fruit yield of the control plants was linear with time ( $Y_{kg/m^2} = 0.55 \times T + 0.74$ ,  $R^2=0.89$ ). The SP fraction exhibited a very slow but significant growth rate while the OL fraction stopped growing. For -N plants, growth was significantly reduced ( $DM = 0.19 \times T + 6.91$ ,  $R^2=0.84$ ). Dry biomass accumulation was consistently lower 2–3 weeks after starting the treatment, and by the end of the 6 weeks of N-deprivation, growth had been reduced by 20% compared to +N plants. The effect of treatment on fruit yield (i.e. fresh weight of the four fruit fractions) lagged 2 weeks behind the lowering of growth rate, leading after 6 weeks of treatment to a significant loss of about 23% in total yield ( $Y_{kg/m^2} = 0.30 \times$

**Table II.** Results of chemical analyses performed on the nutrient solutions sampled at the drip of the +N and -N fertigation systems. The concentrations are expressed in mol·m<sup>-3</sup> and the electric conductivity (EC) is given in mS·cm<sup>-1</sup>. Micronutrients were not measured.

	$NO_3$	$SO_4$	$H_2PO_4$	Cl	K	Ca	Mg	$NH_4$	pH	EC
+N	16	1.8	1.5	1	7.9	4.75	1.75	0.7	5.6	2.1
-N	traces	5.1	1.5	9.5	7.8	4.75	1.8	–	5.6	2.05



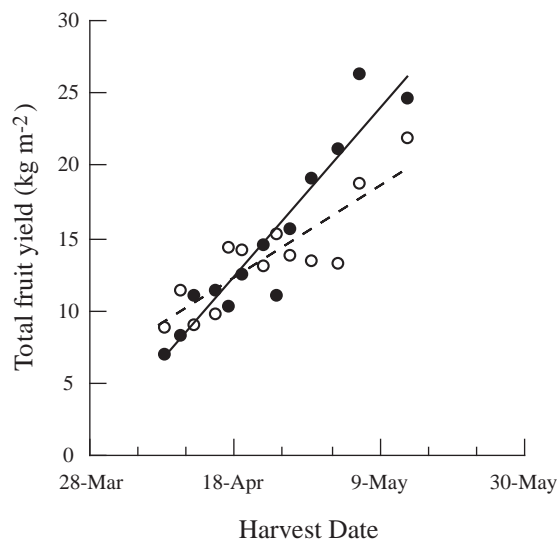
**Figure 2.** Accumulation of total dry aerial biomass ( $\text{t ha}^{-1}$ ) from the date of plantation. The origin of the graph (X-axis) is the time of (-N) treatment initiation. Closed symbols represent +N plants while open symbols are -N plants. Plain and dashed lines are linear regressions fitted through +N and -N points, respectively. The slopes of the two regressions are significantly different.

$T + 5.92$ ,  $R^2=0.75$ ). The commercial yield (Fr fraction, about 30–35% of total fruits) was less affected, being decreased by 17% at the end of the treatment. In the control plants, the cumulated commercial yield attained  $9.3 \text{ kg m}^{-2}$  over the six weeks of the treatment, and over the entire cultivation period the crop yielded  $25 \text{ kg m}^{-2}$ .

### 3.2. Plant nitrogen status

Total N uptake by the crop was calculated from the results of N analyses done on individual plant fractions (Fig. 4a). Each data point results from the sum of 12 to 18 measurements made on single fractions (i.e. OL + YL + SP + LFr + MFr + SFr + OL<sub>def 1-3</sub> + SP<sub>def 1-3</sub> + Fr<sub>week1...6</sub>). For +N plants, cumulative uptake was linear with time during the period studied but it was less than proportional to the cumulative dry biomass accumulation. Consequently we observed a progressive decline in the nitrogen concentration of the entire plant (%N, Fig. 4b). We modelled satisfactorily this progressive decline of %N in the dry aerial biomass ( $DW_{\text{t ha}^{-1}}$ ) using a power function with two unknown parameters:

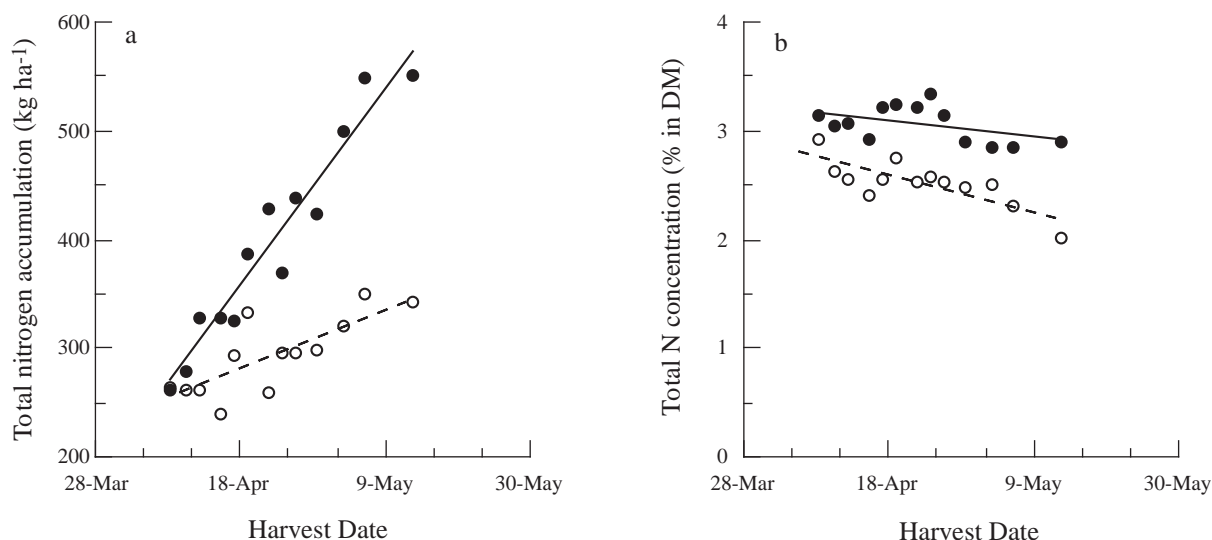
$$\%N = 4.45 \times DW_{\text{t ha}^{-1}}^{-0.15} \quad (1)$$



**Figure 3.** Total fruit yield ( $\text{kg fresh weight m}^{-2}$ ) recovered during the course of the experiment (sum of all fruit fractions). Symbols as in Figure 2. The slopes of the two regressions are significantly different.

During the period from March 28th to May 14th, N supply to the crop amounted to  $560 \text{ kg ha}^{-1}$  for a total recovery (uptake) of  $290 \text{ kg ha}^{-1}$  in the shoots (i.e. 52% of N fertiliser was intercepted by the crop).

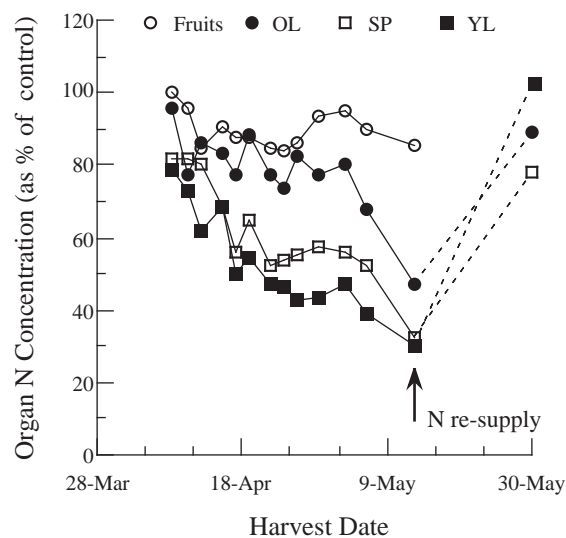
For -N plants, despite the absence of N in the nutrient solution we measured a net nitrogen gain of almost  $130 \text{ kg ha}^{-1}$  after 6 weeks of the treatment. This shows that the flush made with the N-free solution at the beginning of the treatment did not remove all the residual nitrogen from the rockwool slabs. In this treatment, N concentration in the plant decreased by about 1 unit, because of extra-dilution due to biomass accumulation (Fig. 4b). However, the decrease in %N was not uniform in all plant fractions (Fig. 5). In the fruits, N concentration relative to control plants decreased by 15% after 6 weeks of the treatment. In the old leaves (OL), the decrease in %N was moderate over the five first weeks (–20%) but collapsed thereafter (–50%). In the stem and petioles (SP), and even more in the young leaves (YL, smallest fraction), %N decreased rapidly to –66% and –70% of the values found in the control plants. In terms of absolute values, the lowest %N was found in the SP fraction (0.73%) followed by the YL (1.18%), the OL (1.66%) and the fruits (2.15%). In this latter fraction, N was lower in the youngest fruits. Hence, %N in MFr and SFr fell to 1.1% while in Fr and LFr it lay in-between



**Figure 4.** (a) Cumulative total nitrogen uptake by the crop (kg N per hectare) over time. (b) Change of total N concentration in the plant dry biomass (g N per 100 g of DM) during the course of the experiment. Symbols as in Figure 2. In both figures, the slopes of the regressions are significantly different.

2–3%, being almost unaffected. In the vegetative organs, re-supplying N to the -N plants resulted within two weeks in a rapid increase in %N values, comprised in between 80–100% of those found in +N plants.

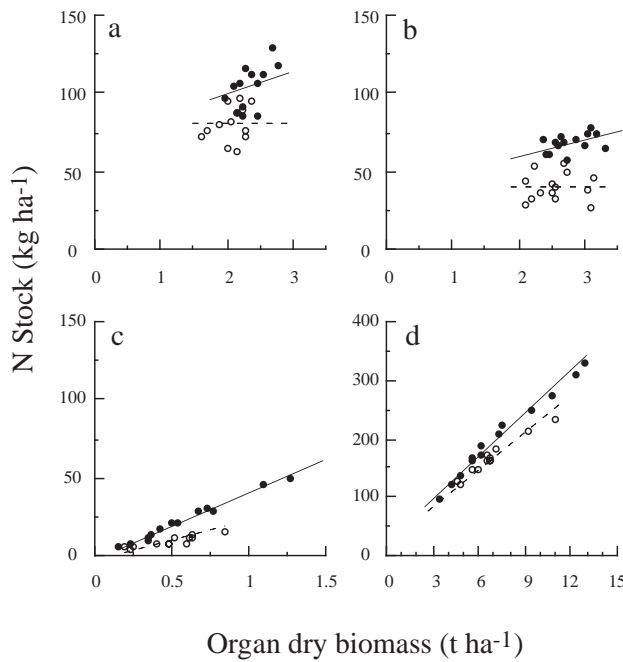
Any decrease in %N of a plant is either due to a dilution effect (i.e. biomass accumulation at constant N stock) and/or nitrogen movements from or toward other organs. The nitrogen budget done at the level of the organs (fractions) gives the changes in N stocks during the period of N deprivation (Fig. 6). The gaps between the N stocks of +N and -N plants and their dynamic evolution during their growth is indicative of source or sink behaviours for nitrogen. The OL were a non-growing plant fraction. Therefore, the differences in dry biomass observed in Figure 6a result from within-plant variability. In this fraction, the -N plants kept their N stock constant. Since this fraction contained little amounts of  $\text{NO}_3^-$ , the reserves were made almost entirely of organic-N. Stems and petioles (SP) grew similarly in both control and treated plants and from the viewpoint of their nitrogen, they hardly changed their stocks (Fig. 6b). However, the N-stock in -N plants was lower than the corresponding +N plants, indicating a loss of N toward other organs (i.e. source behaviour). Thus, we reckon that a small quantity of N (ca.  $28 \text{ kg} \cdot \text{ha}^{-1}$ ) has been remobilised from that compartment. In this fraction, N reserves were made of almost equal quantities of  $\text{N-NO}_3^-$  and organic-N. It is obvious that the major sink for nitrogen in the plants was the fruit compartment. Tight but significantly different



**Figure 5.** Nitrogen concentration in several organs of the (-N) plants expressed as % value of (+N) plants. The organs are: Fruits (total), OL (old leaves), SP (stem and petioles) and YL (young leaves). The arrow indicates the time of N re-supply with the (+N) nutrient solution. At the last harvest the concentration of N in the fruit fraction could not be computed due to missing data.

linear regressions were found between N and DM accumulations in the fruits of both treatments ( $\text{Nfr} = 23.40 \times \text{DM} + 29.23$ ,  $R^2=0.98$  and  $\text{Nfr} = 18.40 \times \text{DM} + 40.96$ ,





**Figure 6.** Changes in the stocks of N in several organs during growth. (a) Old leaves. (b) Stem and petioles. (c) Young leaves. (d) All fruits. Symbols as in Figure 2. Note the changes in scale between plots. In (c) and (d) the slopes of the regressions are significantly different between treatments.

$R^2=0.97$  in +N and -N plants respectively). In -N plants the fruits gained very large amounts of N (ca.  $> 100 \text{ kg} \cdot \text{ha}^{-1}$ , Fig. 6d). The same behaviour was noticed in the YL fraction, although it showed a considerably lower strength (ca.  $< 10 \text{ kg} \cdot \text{ha}^{-1}$ , Fig. 6c).

### 3.3. Speculative nitrogen budget of the crop

In the case of control plants continuously fed with the standard nutrient solutions, it is tempting to sketch a nitrogen budget at the scale of the cultural cycle (i.e. from plantation to final harvest). In this paper, the assay is speculative since data of N exportation concern only the aerial parts. Moreover, some data obtained during a limited period of the cultural cycle must be used for extrapolation, which can be criticised. Nevertheless, this exercise should be seen as an attempt to compare the fertilisation practice of a soilless crop with known soil crops. The overall nitrogen supply to the tomato crop ( $N_{\text{kg} \cdot \text{ha}^{-1}}$ ) is precisely known from the N concentration ( $C_{\text{mol} \cdot \text{m}^{-3}}$ , Tab. I) of the successive nutrient solutions given to the plants and the daily volumes ( $V_{\text{dm}^3 \cdot \text{m}^{-2}}$ ,

Fig. 1) delivered by the computerised fertigation system:

$$N_{\text{kg} \cdot \text{ha}^{-1}} = \sum_{\text{plant}}^{\text{final}} \left( C_{\text{mol} \cdot \text{m}^{-3}} \times V_{\text{dm}^3 \cdot \text{m}^{-2}} \times 0.14 \right). \quad (2)$$

Nitrogen uptake by the crop ( $N_{\text{kg} \cdot \text{ha}^{-1}}$ ) has been measured experimentally during a period of the cultural cycle, and it has been modelled as a power function of total dry aerial biomass accumulation ( $DW_{\text{t} \cdot \text{ha}^{-1}}$ ):

$$N_{\text{kg} \cdot \text{ha}^{-1}} = 44.5 \times DW_{\text{t} \cdot \text{ha}^{-1}}^{0.85}. \quad (3)$$

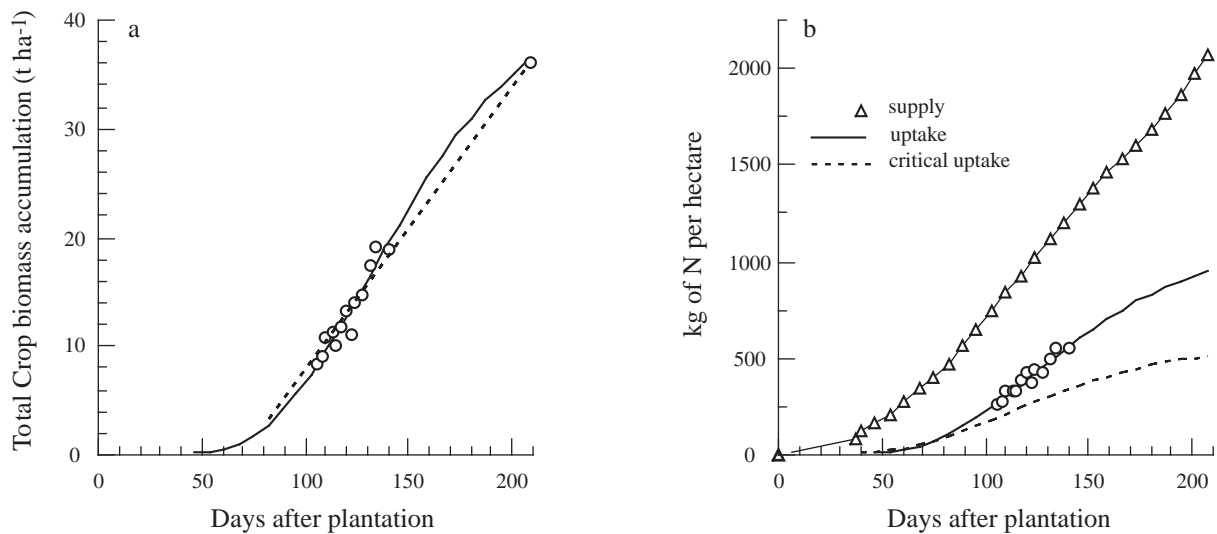
Although the function was calibrated over a limited period of the cultural cycle, its extrapolation to the entire crop cycle seems reasonable considering the general concepts developed in Lemaire [28]. The dynamics of dry aerial biomass accumulation can be estimated from the knowledge of initial conditions (plantation,  $DW \approx 0 \text{ t} \cdot \text{ha}^{-1}$ ), the measurements realised during the period of the treatment ( $8 < DW_{\text{t} \cdot \text{ha}^{-1}} < 19$ ) and the final biomass estimated from the commercial yield of  $25 \text{ kg} \cdot \text{m}^{-2}$  obtained with the crop (i.e. considering a fruit to total DM ratio of 0.7). DM accumulation may be considered linear with time, although in the long term it is more realistic to invoke a Gompertz function [11]. In the case of our experiment, both functions may be used:

$$DW_{\text{t} \cdot \text{ha}^{-1}} = 0.27 \times T - 19$$

$$\text{or } DW_{\text{t} \cdot \text{ha}^{-1}} = 44 \times \exp(-\exp(-0.021 \times (T - 130))) \quad (4)$$

where variable T represents the time (days) after plantation in the greenhouse.

Figure 7a represents the simulated crop growth curves (according to Eq. (4)) fitted to the measured data points, for a final estimated total DW of  $36 \text{ t} \cdot \text{ha}^{-1}$ . Figure 7b represents two components of the nitrogen budget drawn over the entire growth cycle: the cumulative nitrogen supply curve ( $N_s$ ), calculated from the data of fertigation (according to Eq. (2)), and the cumulative nitrogen uptake curve ( $N_u$ ), estimated by the model (Eqs. (3) and (4)) and fitted through the data points. The main outcome of this calculation is the finding that from the period of the experiment until the end of the culture, only 46% of the nitrogen supply has been taken up by the crop, the rest being partly lost by drainage and partly accumulated in the rockwool slabs, but ultimately lost to the environment. On the scale of the cultural cycle, nitrogen loss amounted to  $1100 \text{ kg} \cdot \text{ha}^{-1}$ .



**Figure 7.** (a) Total dry aerial biomass accumulated by the (+N) crop (tons per hectare) over time. Data points are fitted both by a linear (dashed line) and a Gompertz function (plain line, Eq.(4), see text). The last point is estimated from the final commercial yield ( $25 \text{ kg} \cdot \text{m}^{-2}$ , see text for details). (b) Total N supply ( $\text{kg} \cdot \text{ha}^{-1}$ ) and total N uptake by the (+N) crop. The solid line is a power function ( $N_u = 44.5 \text{ DW}^{0.85}$ ) fitting the data point and extrapolated to the entire crop cycle (DW is derived from the previous Gompertz function). The dotted line is the hypothetical critical N uptake of  $C_3$  species ( $48 \text{ DW}^{0.66}$ ) defined by Lemaire and Gastal [29].

#### 4. DISCUSSION

This study characterises the impact of N withdrawal from the nutrient solution on the growth and final yield of an adult tomato crop. The main results (arrest of leaf area expansion, decrease in biomass accumulation, yield reduction) are typical of N-limitation experiments [5, 9, 37] and need, therefore, little comment. However, they occurred after a consequent lag period (from 2 to 4 weeks after starting the treatment) showing the capacity of the plants to use N-reserves. In that respect, both external and internal reserves must be considered. External reserves are those accumulated in the rockwool slabs since the beginning of the fertigation practice. The data of Figure 4 show that approximately  $130 \text{ kg N} \cdot \text{ha}^{-1}$  accumulated in the aerial dry biomass of -N plants during the 6 weeks of the experiment. This amount was recovered despite the attempt made to flush residual nitrogen from the slabs with the -N solution. Little information is available in the literature to quantify residual nitrogen in rockwool slabs during a cultural cycle. However, it is common to observe higher EC values in the slabs than in the drainage, and heterogeneous spatial distribution of nutrients (EC) in the slab, probably due to the particular flow patterns set by the fertigation regime. For instance, De Rijck and Schrevens [12] used a standard solution ( $\text{EC} = 2 \text{ mS} \cdot \text{cm}^{-1}$ ) to measure both vertical

and horizontal EC gradients in slabs. They found a build-up of salinity both in the bottom half of the slab ( $\text{EC} = 10 \text{ mS} \cdot \text{cm}^{-1}$ ) and in the entire profile between the drips. Since nitrate is the main anion contributing to salinity in solution, and because water flow is mainly restricted to the zone underneath the drip (wet bulb), we may conclude from their observations that important amounts of N (we figure around  $120 \text{ kg} \cdot \text{ha}^{-1}$  in wet slabs) can be stored in the slabs, in particular in zones poorly explored by the roots. Thus for our conditions, it is probable that the flush with the -N solution at the beginning of the experiment only deprived the wet bulb of N. During the course of the experiment, we can speculate that diffusion gradients moved N towards the bottom parts of the slabs, where roots develop, thus rendering N available for uptake. Internal reserves must also be considered in the N budget of -N plants. Hence, the root system was not recovered during the experiment although it is a reservoir of N for shoot growth. We reckon that for a crop yielding almost  $10 \text{ t} \cdot \text{ha}^{-1}$  of dry aerial biomass, the roots represent ca.  $2 \text{ t} \cdot \text{ha}^{-1}$  containing around  $90 \text{ kg}$  of N, of which a figure between 30 to 50% (i.e. 27–45 kg) can be considered as alterable N-reserves available for internal transport. These observations suggest that the slabs are capable of buffering abrupt changes in nitrogen (nutrients) supply and thereby of sustaining plant growth, at least on the time scale of one to two weeks.



From this viewpoint any attempt to precisely control nutrition so that daily supply adjusts to growth-related plant demand, is a utopia as long as the current growth systems keep their inertia.

From the environmental viewpoint, the results highlight the importance of residual nitrate in the slabs to sustain plant growth. Therefore, it may be suggested that slab disposal at the end of a growing season represents a real risk of pollution. In order to avoid nitrate leaching after disposal, nitrate uptake by the plants should be promoted before the end of the growing season. One way to achieve this could be (1) to decrease progressively N concentration in nutrient solutions during the crop cycle and (2) to terminate nitrate supply before the final harvest, and leave the plants to feed on the residual nitrate present in the slabs. The first proposal comes from recent findings of Siddiqi et al. [40] that decrease of nitrogen supply at the end of the growing season has no adverse effect on growth and yield of tomatoes. Our study shows that the second proposal would have moderate effects on fruit yield (Fig. 3). In both cases, important savings can be expected, in particular on the grounds of the ecological impacts. The budget given by Figure 7b estimates that from the 2000 kg N applied to the crop, less than 50% are taken up. This indicates that the supply is excessive. In order to reduce N supply, either the volume of the daily dose of solution or its N concentration could be decreased. Because the daily dose is mainly set by plant water demand for transpiration, and because the mean drainage was correctly controlled (Fig. 1) ca. 30% of supply, the latter proposal may be favoured. Table I indicates that N concentration already decreased along the cultural cycle, but further decrease of N concentrations should be envisaged. In their experiments, Siddiqi et al. [40] found that nutrient solutions at 11 and 5.5 mol N·m<sup>-3</sup> given to adult plants, produced the same tomato yield. In our experiment, the lower N concentration in the feeding solution was close to 16 mol·m<sup>-3</sup>. Furthermore, by applying such practice we may expect for crops ending during summer that the older the crop, the larger the potential economy for N. Hence, at least two arguments back such a view.

(i) High radiation, air temperature and water vapour pressure deficit levels (typical of summer weather) favour the uncoupling between water and nutrient uptake rates [2]. Thus, increasing the delivery doses of nutrient solution to balance higher transpiration fluxes leaches larger quantities of mineral nutrients in the run-off. Because drainage recycling is not a wide-spread cultural technique, at least in France, the run-off enriches the groundwater with unwanted pollutants such as nitrate.

(ii) Because %N in the dry matter of all C<sub>3</sub> and C<sub>4</sub> plants naturally declines with growth, following a power func-

tion %N = a × DM<sup>-b</sup> [10, 21, 25, 29, 36], the N-cost for building-up an extra-unit of DM also declines regularly along growth (i.e.  $\frac{dN}{dDM} = (1 - b) \times 10 \times a \times DM^{-b}$ ) and

thus, if supply was to match crop requirements, N delivery should decrease along growth. In practice, the opposite happens because nitrate concentration in the feeding solution is kept high (i.e. above 15 mM), while doses of nutrient solution fed to each plant increase to counterbalance plant water losses by transpiration. For the tomato plants, Andriolo [2] observed a progressive decline in %N along growth, as exposed above, and from his findings, we can calculate that when the crop yields 3 tons DM·ha<sup>-1</sup> it costs 27 g of N to construct an additional kg of DM, but when the crop yields 30 tons DM·ha<sup>-1</sup> this cost decreases to only 13 g of N. The reason for this relies on structural properties of the canopy, in particular the non-uniform distribution of N in the foliage [16–18, 24, 42] and quantitative differences in %N of different plant organs, in particular the fruits (for reviews, [26, 29]). All these arguments support the view that any increase in the doses of a N-rich nutrient solution feeding adult plants goes against what is required to economise nitrogen in soilless cultures. Furthermore, if the crop is shortly due to harvest, most of the nitrogen taken up by the adult plants will boost young fruit growth with therefore no, or minute, contribution to economic yield.

The measurement and interpretation of plant N status are imperative to control N fertilisation. The ubiquitous plant tissue and sap chemical analyses are common techniques allowing plant nutrient status determination [19]. Several methods to interpret such analytical data have been proposed, all based on their comparison to norms established empirically from high-yielding crops grown in agronomic assays. Hence, for greenhouse tomato crops, the critical nutrient range (CNR), the diagnosis and recommendation integrated system (DRIS) and its interpretative sum of nutrient indices irrespective of sign (NII) have been proposed [7, 8, 34]. These mathematical methods, devised to account for nutrient interactions in plant tissues, lack basis for physiological interpretation [41]. For the specific nitrogen diagnosis, however, the statistical approach of critical nitrogen concentration (%N<sub>c</sub>) changes in plant tissues, developed by Salette and Lemaire [39], Greenwood et al. [20, 21] and summarised by Lemaire [28] can be interpreted by mechanistic plant growth theories [6, 22]. A single relationship models the ontogenic %N<sub>c</sub> progressive decline in the dry matter of crops grown in closed canopies: %N<sub>c</sub> = a × DM<sup>-b</sup>. Although, it is proposed that on average, a = 4.8 or 3.6 for C<sub>3</sub> or C<sub>4</sub> plant species, respectively, and b = 0.34 [29], comprehensive studies made on various crops

including wheat [25], maize [35, 36], pea [33] and oilseed rape [10] have yielded specific parameters. Concerning vegetable crops, only scarce data is available in the literature. Andriolo [2] and Le Bot et al. [27] have reported on a trial with tomato grown in hydroponics with ample N nutrition (a concentration of  $11.5 \text{ mol NO}_3\text{-m}^{-3}$  was maintained in the root zone). They observed an ontogenic decline in %N (not %N<sub>c</sub>), adequately formalised by a power function ( $\%N = 5.77 \times \text{DM}^{-0.33}$ ). A similar observation was made in NFT-grown tomatoes subjected either to different fruit loads (i.e. 1 or 4 fruits per truss) or different air water vapour pressure deficits [3]. However, due to various experimental difficulties, soil-less-grown crops lack trials whereby growth is impaired by the regime of N fertilisation and so far no data characterises the dynamics of %N<sub>c</sub> decline in tomato. In contrast, such trials are common for soil-grown crops. For instance, recent results obtained with tomato cv. colonial [1] reckon that %N<sub>c</sub> at commercial harvest (DM of total aerial biomass =  $23 \text{ t}\cdot\text{ha}^{-1}$ ) is close to 1.7%. From the general model exposed above ( $\%N_c = 4.8 \times \text{DM}^{-0.34}$ ) this value is expected to approach 1.63%. Similarly in the experiment described in this paper, we may regard %N<sub>c</sub> as the concentration measured in the plant when growth impairment occurred in the -N treatment. This happened when DM was about  $9.9 \text{ t}\cdot\text{ha}^{-1}$  yielding %N<sub>c</sub> close to 2.5% (Figs. 2 and 4). Prediction of the above general model ( $\%N_c = 2.2\%$ ) also compares with our experimental estimate of %N<sub>c</sub>. These coherent findings allow us, therefore, to use the concept of progressive %N<sub>c</sub> decline in the case of tomato and model critical N uptake ( $\text{kg N}\cdot\text{ha}^{-1}$ ), i.e. the minimum uptake maximising dry biomass ( $\text{t}\cdot\text{ha}^{-1}$ ) accumulation, as the power function derived from the above relation:  $N_c = 48 \times \text{DM}^{0.66}$ . This relation has been plotted in Figure 7b together with actual N supply and N uptake during the experiment. The model predicts in particular that critical N requirement is only 25% of the actual supply, and that the gap between critical and actual uptakes increases along time, leading to N storage in plant tissues. This addresses important questions about the impacts of this storage on the quality of production, but so far they have not been tackled yet.

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