Early growth and photosynthesis of tomato (**Lycopersicum esculentum** L.) under nutritional deficiencies*

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COMPENDIO

El efecto de las deficiencias nutritivas de N y Fe se estudió en tomate en los estados tempranos de crecimiento antes de la floración, mediante el análisis del crecimiento, mediciones de la actividad fotosintética, y el análisis del contenido de nutrimentos en las hojas.

Se muestra que el efecto de las deficiencias es especialmente evidente después de cuatro semanas de crecimiento en soluciones deficientes. Hay una correlación significativa entre el contenido de proteína soluble, clorofila y actividad de RuDP-carboxilasa y la edad y estado nutritivo de la hoja, y entre el contenido de proteína soluble y la actividad fotosintética. La deficiencia de N reduce el contenido foliar de todos los nutrientes estudiados en la hoja, mientras que la deficiencia de Fe aumenta notablemente el contenido de P.

Se discuten los resultados en relación con el uso del contenido de proteína soluble y la concentración de P en las hojas, para una detección temprana de las deficiencias en nutrimentos y para determinación del estado fisiológico de plantas de tomate.

Introduction

THE early detection of potential nutritional deficiencies in plants cultures, is relevant for agricultural purposes, in order to prevent yield reductions in growth phases when they can not be avoided through fertilization. Techniques applied to that end have been basically a) leaf analysis of mineral nutrient concentrations (24); b) study of interactions between nutrients (7) and c) study of the effect of nutrient availability on structure and physiology of the photosynthetic apparatus of cultivated or wild plants (3, 4, 18, 22, 29).

Main effort has been laid on leaf area development because its relationship with plant production capacity has been early recognized (31). But in fact there are two interacting absorption surfaces, which to certain extent compete, and regulate the development of the whole plant: the leaf surface for CO_2 absorption and light interception and the root surface for the absorption of mineral nutrients and water. Development and functional capacity of root surface is by far the least known process in crop physiology (9), and the physiological basis of the differences in root performance between species and varieties is still very little understood. Most of the knowledge useful in agriculture of root/shoot interactions is more phenomenological and it has been obtained with growth analysis techniques (10). With this method effects of nutrient deficiencies on organic matter distribution within the plant have been quantitatively described.

In this paper growth and photosynthesis of tomato plants grown in nutrient solutions deficient in Nitrogen and Iron are analysed looking at organic matter production and distribution, photosynthesis and the activity in vitro of RuDP-carboxylase, the enzyme responsible for photosynthetic CO_2 fixation in higher plants (5). Tomato was selected for its easy cultivation under laboratory conditions and because there exists considerable information on different aspects of its nutritional physiology (12, 14, 25, 27, 28).

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Finally, measurements were conducted before flower initiation in order to test early detection of deficiencies and to avoid retranslocation of minerals for seed and fruit formation.

Material and Methods

Plant Material

Seeds of tomato (cv 'Royal Ace', Ferry Morse Seed Co.) were germinated on pure sand moistened with demineralized water. After two weeks when the shoots reach 2-3 cm length and the first leaf is visible, seedlings were transplanted to vermiculite pots irrigated with the different nutrient solutions. These solutions are similar to those used by Hoagland and Arnon (13) differing in the concentration but not in the proportion of salts. Normal solution contained 15 mmoles/l Nitrate and 223 μ moles/l Fe. Nitrogen deficient solution (—N) contained only 0.5 mmoles NO_3/l; while to the Iron deficient solution (—Fe) no Iron was added.

Seedlings were grown thereafter in a growth chamber (photoperiod 12 h; thermoperiod 17° C night, 30°C day) under a light intensity of 550 μ E m^{-2} sec^{-1} produced by 6 25w incandescent bulbs and 14 40w flourescent tubes (Sylvania F72T12/cw/VHO). After 5 to 6 doys from transplanting measurements were done every week until plants were aproximately 50 days old.

Growth analysis

Weekly harvests were done and plant were separated in root, stem and leaves. Leaf area was measured with Ozalid paper printings and dry weight of the whole material was recorded. With this figures, growth parameters were calculated following formulas given by Kvét et al. (16) and Evans (10): Shoot/root radio (Leaf weight + stem weight/root weight); leaf area ratio (Leaf area/total weight); leaf weight ratio (Leaf weight/total weight); specific leaf area (leaf area/leaf weight); root weight ratio (root weight/total weight); relative growth rate ($\ln P_2/\Delta t$) and unit leaf rate (= net assimilation rate) $\left(\frac{1}{\overline{P_1}}\right)\left(\frac{\Delta P}{\Delta A} \times \frac{\ln A_1 / A_2}{\Delta t}\right)$ (P = dry weight; A = leaf area; t = time).

Leaves sampled for this purpose were weighed and its area measured. Extraction procedure has been described by Björkman and Gauhl (6) and it consisted in macerating leaf material (20 mg fresh weight/ml buffer) at low temperature ($\sim$ 2°C) using Tris-HCl buffer 0.1 M, pH 7.9 at 30°C, EDTA-4 Na 0.25 mM, $MgCl_2$ 0.01 M, dithiothreitol (DTT) 0.76 mg/ml and isoascorbic acid 1 mg/ml. Macerated material completely recovered from mortar was centrifuged at 0°C and 20,000 rpm during 1/2 hour. In the supernatant soluble protein (17) and activity of RuDP-carboxylase (6) were measured. The pellet was thereafter extracted with aceton 80% for chlorophyll determination (8).

Nutrient content analysis

Nutrient content of leaves was determined for the last two harvests. Fe concentration could not be measured because plant material was not enough. N was measured with the microKjeldahl procedure while P was analysed colorimetrically with the vanado-molibdo-phosphoric method (15). K, Ca and Mg were measured through atomic absorption in acid digests of dry samples (30).

CO_2 exchange

Photosynthesis was measured in attached leaves with an open system using an infrared gas analyser as detector. The selected leaf was included in a ventilated leaf chamber whose temperature could be regulated circulating water at appropriate temperatures.

The assays were run twice during one year. The significance of the differences between treatments was assayed using the non parametric statistical test of Mann-Whitney (23).

Results

Growth analysis

Fig. 1 shows the typical growth patterns obtained in the experiments. It can be seen that during the 5 weeks measured the growth curves do not stabilize, neither total dry weight nor leaf area (1A and 1B. Nevertheless there is a clear effect of nutrient deficiency, which is obvious during the 5th week of growth. The patterns of unit leaf rate and relative growth rate under our experimental conditions show a clear maximum between the 3rd and 4th week for the complete and the —N nutrient solutions, the reduction in —N between the 4th and 5th week being the most drastic. Growth in the —Fe solutions shows that unit leaf rate changes little during the 5 weeks of observation, while relative growth rate diminishes steadily during the same period. This results are explained on the basis of photosynthate partition, shifted toward the roots in nutrient deficient plants. The low mobility of iron within the plants is probably related to the continuous reduction of relative growth rate.

Regressions between leaf area and leaf weight or weight of different organs against total dry weight were calculated in order to show the differential photosynthate distribution. All regressions were linear. Table 1 presents the values of regression coefficients, which

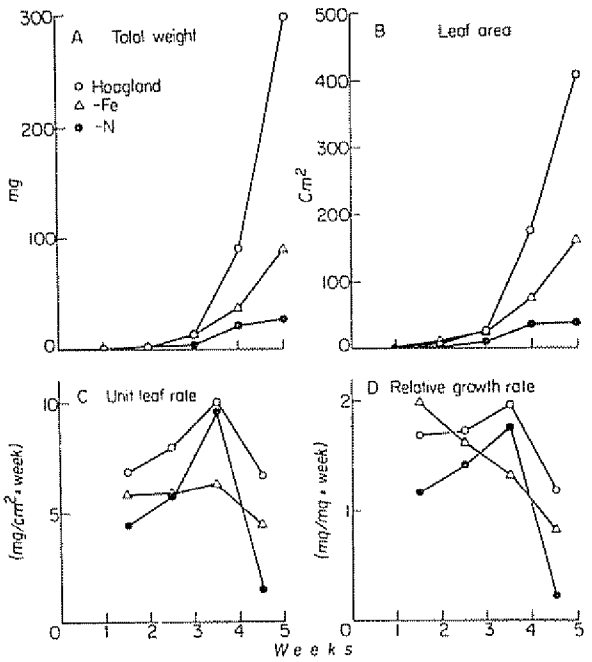

Fig 1 —*Growth characteristics of tomato plants grown in complete (o) Fe deficient (+) and N deficient (•) nutrient solutions Light intensity 550 μE m⁻² sec⁻¹ photoperiod 12h and thermoperiod 17°C night, 30°C day*

in each case correspond to one of the growth parameters described in the section of Methods.

In general specific leaf area decreases with leaf age; in our experiments changes within treatments were sufficiently small so that a linear relationship between leaf area and leaf weight was maintained during the whole experiment. Specific leaf area indices show that deficient leaves, specially —N are significantly thicker than normal leaves.

Table 1 —Dry matter and leaf area ratios in tomato plants grown in complete or N and Fe deficient nutrient solutions

Treatment	Specific leaf area (cm^2/g)	Leaf area ratio (cm^2/g)	Leaf weight ratio (g/g)	Root weight ratio	Stem weight ratio	Shoot/root ratio
Complete nutrient solution	340	179	0.524	0.106	0.370	7.50
—Fe	281*	149*	0.504	0.163*	0.332	5.35*
—N	227*	118*	0.518	0.185*	0.293	3.83**

N = 10

* Differences significant at P = 0.05

** Differences significant at P = 0.01

Table 1 shows that main impact of nutrient deficiency is the relative reduction in the amount of leaf area developed; this reduction reaches 17% in —Fe solutions and 37% in —N solutions.

Correspondingly relatively more roots are built in deficient nutrient solutions (53% in —Fe and 74% in —N), resulting in shoot/root ratios significantly lower in deficient solutions.

Chlorophyll, soluble protein and RuDP-carboxylase activity

As expected, chlorophyll content per unit leaf area and soluble protein content per gram fresh weight diminish markedly with age, and this reduction is more pronounced in plants growing in complete nutrient solution (Fig. 2).

It can be observed that cholorophyll may be used as an indicator of nutrient deficiency if it is severe. In our experiments restrictions of iron supply through the roots diminish chlorophyll content in a lesser extent than in the N deficient treatment.

Soluble protein of leaves is correlated with the measurable activity of RuDP-carboxylase in vitro within species (18, 19). In Fig. 2 it can be seen that RuDP-carboxylase activity follows the same pattern as for soluble protein in leaves of increasing age. Notice that the differences between treatments are more pronounced in young leaves, while in old leaves of all treatments measured activity is similar.

Old leaves of normal plants are also nitrogen deficient because this element is actively transported to growing leaves.

Fig. 3 shows the correlation obtained with all measured values. As leaf soluble protein is affected by age and nutrient deficiencies, RuDP-carboxylase activity is proportionately reduced. Protein content of old and deficient leaves therefore overlap. In order to separate these factors, young, almost fully expanded leaves, should be taken for comparison.

RuDP-carboxylase activity in vitro per unit soluble protein also changes with age and nutrient deficiency. Old and deficient leaves have lower specific carboxylase activities (2, 4, 18, 19).

Young healthy leaves, have always specific activities above 0.4 μ moles CO_2/mg protein × min. and we estimate that this activity is obtained in the average with leaf soluble protein concentrations above 16 mg/g fresh weight.

Photosynthetic activity of attached leaves

Fig. 4 presents the results of typical experiments obtained with 50 days old plants using young, almost fully expanded leaves. Data have been plotted both per unit leaf area and fresh weight in order to emphasize differences in photosynthetic activity determined by

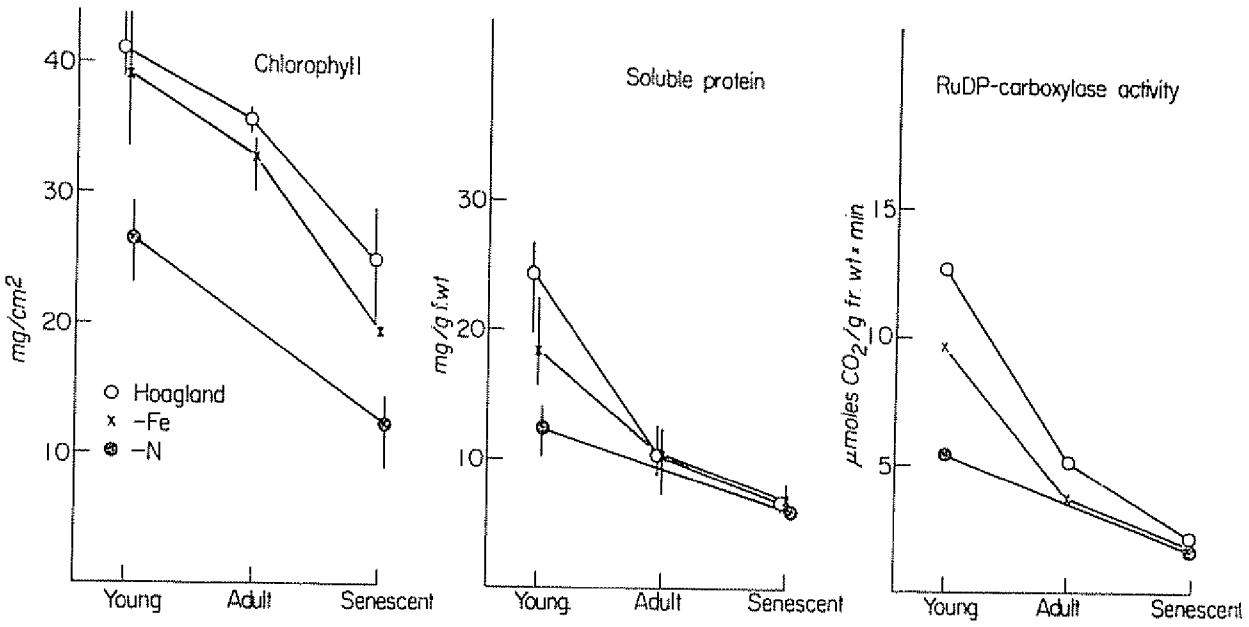

Fig. 2.—*Chlorophyll and soluble protein content and RuDP-carboxylase activity of young (Y), adult (A) and old (S) tomato leaves of seedlings grown in complete, Fe deficient and N deficient solutions during 5 weeks. Conditions and symbols as in Fig. 1.*

structural changes in the leaves. It appears in Fig. 4 that reduction in Fe and N supply reduces significantly net CO_2 exchange, and the effect is more pronounced by the N deficiency. Differences between normal and deficient plants are more striking when data are expressed on a fresh weight basis. The reason is that deficient leaves are considerably thicker (see Table 2).

From curves in Fig. 4 it can be established that nutrient deficiencies affect both light absorption efficiency per unit leaf area and CO_2 fixation at near saturating light intensity. Light absorption efficiency is indicated by the slope of net gas exchange curves and it is increasingly reduced in Fe and N deficient leaves (see Table 2). Reduction in light dependent CO_2 exchange rates is correlated with the lower chlorophyll content per unit area (Fig. 2).

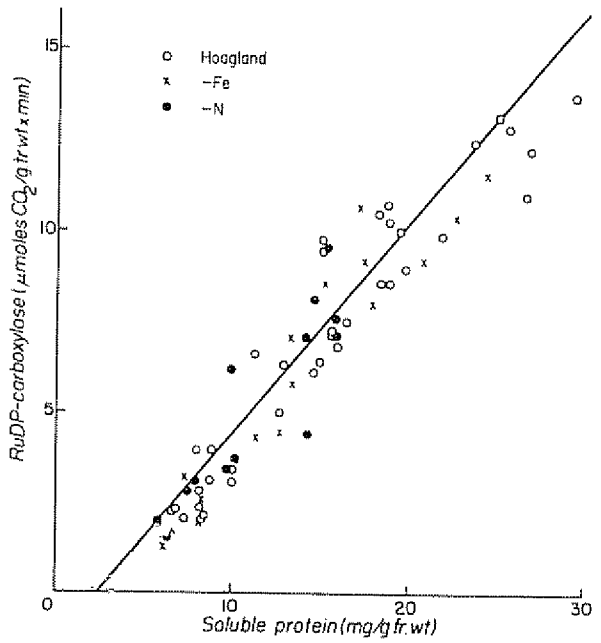

Fig. 3.—*Relationship between RuDP-carboxylase activity per unit fresh weight in vitro and soluble protein content of tomato leaves of different age and grown in complete and N or Fe deficient nutrient solutions.*

Table 2.—Photosynthetic characteristics of tomato plant leaves grown in complete or Fe or N deficient nutrient solutions.

Treatment	Specific leaf area (cm^2/g)	Maximum measured photosynthetic rate µ moles CO_2/g fr wt x hour	RuDP-carboxylase activity in vitro µ moles CO_2/g fr. wt. min	Slope of CO_2 exchange curves (on fresh wt. basis)
Hoagland	54	186.8	12.0	1.25
—Fe	41	127.2	10.3	0.74
—N	47	95.5	3.7	0.62

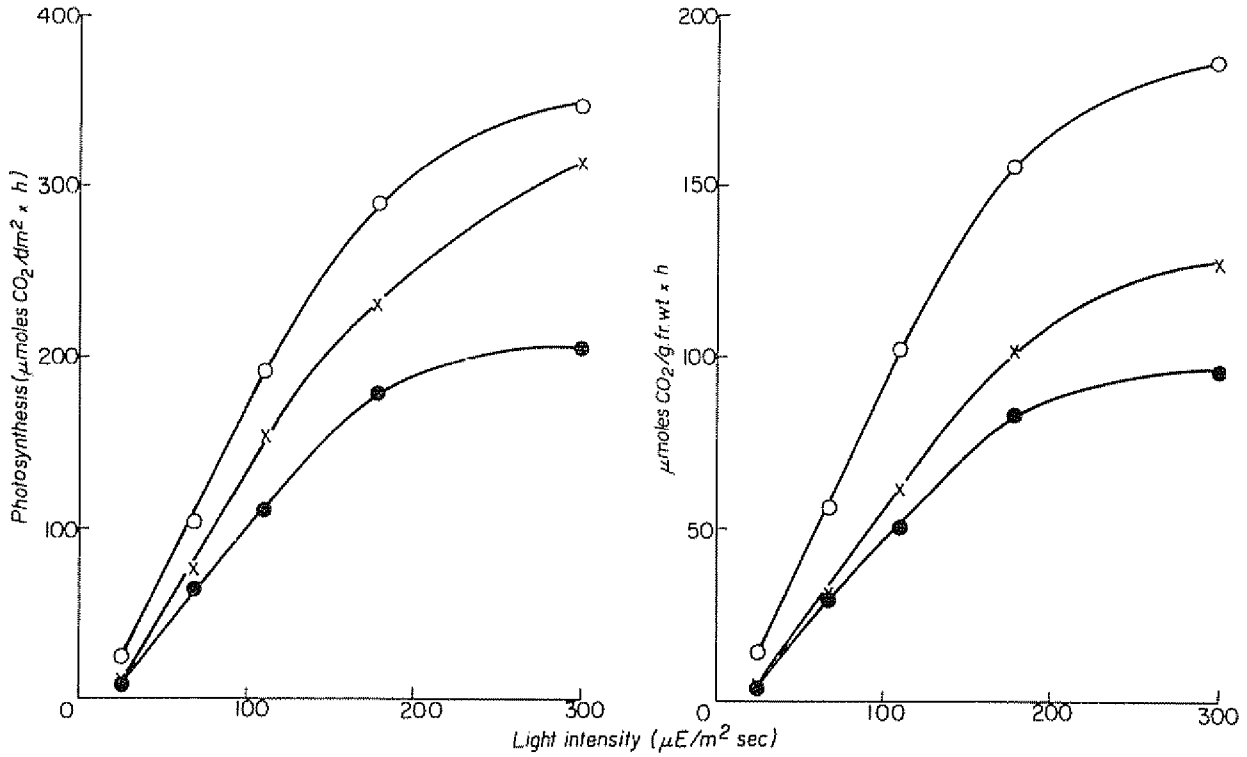

Fig. 1—CO_2 uptake at different light intensity in young leaves of aproximately 50 days old plants grown in complete, Fe deficient or N deficient nutrient solutions. Conditions: Temp. 20-24°C. Relative humidity ~ 65%.

Photosynthetic rates at near saturating light intensity are correlated with activity of RuDP-carboxylase measured in vitro. Table 2 shows maximal measured rates of photosynthesis and the activity of RuDP-carboxylase in similar leaves as those used for CO_2 exchange measurements.

Differences in photosynthetic activity per unit chlorophyll or soluble protein between the treatments are smaller; therefore reductions observed in net CO_2 exchange are due to the lower light absorption (reduced chlorophyll content per unit area) and lower RuDP-carboxylase activity (less soluble protein per unit area).

Leaf nutrient content

Nutrient content of leaves is strongly influenced by age and nutrient supply to the roots. Fig. 5 shows the results obtained with leaves of different ages during the 5th week after transplanting. During the whole experiment the same pattern is observed, only that differences are less pronounced at the beginning.

Nitrogen deficiency results in a strong reduction in the concentration of all measured nutrients, more pronounced towards the apex leaves. This reflects perturbation in ion absorption and translocation. It seems that inhibition of protein synthesis in the leaves as a result requirements, while proportion between nutrients are maintained similar to normal non nitrogen deficient leaves. This is observed when the relationship (K + Ca + Mg) / (P + N) is plotted for leaves of different ages (Fig. 5).

Fe deficiency does not result in differences in the content of Ca and Mg, but it reduces significantly K content. On the contrary, absolute content of P, and to a less extent N, are drastically increased. It means that there has been a shift in the cation/anion relationship towards an increase in anion absorption. It might be possible that the pronounced increase in P content of Fe deficient plants is the result of higher P availability from the nutrient solution due to the abstence of Fe in it. Nevertheless no significant pH changes of the solution are observed during the experiment, because of the frequent renewal of the nutrient solution, nor insolubilization of P was observed due to precipitation of the Fe salt.

Discussion

The purpose of this paper was to find a useful relationship between growth, photosyntesis and nutrient supply for the early detection of mineral deficiencies in tomato. Therefore measurements were performed under controlled conditions and before flower setting in order to avoid complications in nutrient translocation patterns within the plant. This precaution would

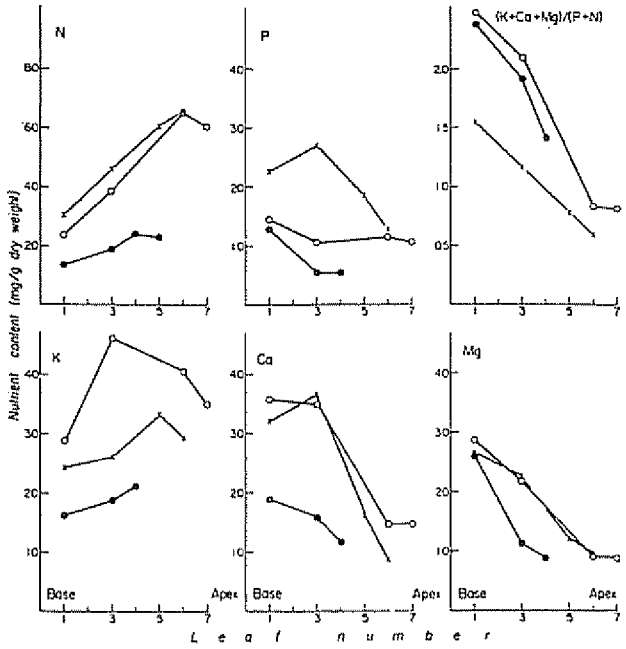

Fig 5 —*Nutrient content per unit dry weight of leaves of different age of tomato plants grown during 5 weeks in complete, Fe deficient or N deficient nutrient solutions*

not be necessary following Tanaka *et al.* (27, 28) paper. These authors showed in tomato that the reproductive and vegetative growth do not compete for mineral nutrients or photosynthates, because fruit growth proceeds with current nutrient flow and photosynthesis from adult leaves.

The experiments reported here indicate that growth disturbances induced by low nutrient supply are clearly observed after 4 weeks of growth in deficient nutrient solutions. Relative growth rate and unit leaf rate are significantly reduced after 5 weeks, being in —Fe aproximately 30 per cent lower than control, while in —N is more than 80% lower than control. —Fe and —N seems to accelerate senescence of adult leaves as has been previously reported (18, 32). Other growth characteristics greatly influenced by Fe and N supply are specific leaf area and shoot/root ratio, both decreasing with deficiency. The apparently most important overall effect on growth is the total reduction of leaf area development.

RuDP-carboxylase activity is linearly correlated to total soluble protein present in the leaves. Since RuDP-carboxylase activity is strongly correlated to light saturated photosynthetic rate (3, 6, 19) it appears that soluble protein content in tomato can be taken as a useful indicator of the photosynthetic capacity of the leaves. Apparently, young tomato leaves with soluble protein content below 16 mg/g dry weight might be considered as nutrient deficient leaves.

Photosynthetic CO_2 exchange is reduced in Fe and N deficient leaves, both in light dependent and light saturated phases. The decrease in the light saturated rates of CO_2 uptake might be correlated with increase in mesophyll resistance as reported by Ryle and Hesketh (22). In tomato nevertheless, this reduction seems to be related more with the activity of RuDP-carboxylase ("Carboxylation resistance") as was found earlier in *Atriplex patula* (18, 19). Stocking (26) has also shown in maize that Fe deficiency reduces considerably the in vitro measurable activity of RuDP-carboxylase. In our experiments stomatal resistance could not be measured, but the relative water loss per leaf area does not vary significantly between the treatments. This finding is not in agreement with other results obtained with sugar beet, in which stomatal resistance increases in the same manner as mesophyll resistance does (21).

The reduction in the light intensity dependent rate of photosynthesis obtained in Fe and N deficient tomato plants are explained through the decrease in chlorophyll concentration per unit leaf area.

Maximal photosynthetic rates reported here are lower than those reported by Tanaka *et al.* (27, 28). The reason might be that our plants were grown under relatively lower light intensities. Differences in photosynthetic CO_2 uptake are more marked when rates are expressed per unit fresh weight than per unit leaf area, the reason is that deficient leaves are thicker (Table 1).

The impact of N and Fe deficiency on the composition of the leaves is completely different. N deficiency reduces the amount of all mineral nutrients measured, therefore leaves of plants grown in complete and N deficient nutrient solutions have the same proportion of N, P, K, Ca and Mg. Deficiency of Fe results in a significant increase in P content and partially also in N content of the leaves (Fig. 5).

The increase of P does not appear to be related to the interaction between Fe and P in the nutrient solution but to an inhibition of P utilization in the leaves. On the other hand, Fe seems to be involved in the synthesis of a RNA fraction which is needed for cell division in isolated pea roots (1). Under Fe deficiency therefore, less P would be retained in the roots and consequently more is translocated to the shoots.

Abnormal high values of P in young adult leaves might be used as an indicator of impairment in Fe supply through the roots.

The quotient K + Ca + Mg / N + P is inversely correlated with leaf age (Fig. 5) as discussed by Friis-Nielsen (12). It can not be used for comparison between normal and Fe deficient plants due to the change in the proportion of this constituents in the Fe deficient plants.

Summary

By means of growth analysis, measurements of the photosynthetic activity and analysis of nutrient content of the leaves, the effect of nutritional deficiencies of N and Fe is studied in tomato during the early stages of growth before flowering.

It is shown that effect of deficiencies is specially apparent after 4 weeks of growth in deficient solutions.

There is a significant correlation between the soluble protein content, chlorophyll and RuDP-carboxylase activity and the age and nutritional status of the leaf and between soluble protein content and photosynthetic activity.

The N deficiency diminishes the content of all nutrients studied in the leaf, while Fe deficiency increases notably the P content.

The results are discussed in relation to the use of soluble protein content and P concentration in the leaves for the early detection of nutrient deficiencies and for the determination of the physiological status of the tomato plants.

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Reseña de Libros

ALVIM, P. DE T. y KOZLOWSKI, T. T., eds. Ecophysiology of tropical crops. New York, Academic Press, 1977. 502p.

Resulta descorazonante el observar el poco desarrollo tecnológico de los cultivos tropicales. Los estudios hechos muestran una cantidad de observaciones y experimentación aislada sobre fenómenos también aislados, sin una tendencia de grupo o de conjunto, salvo muy honrosas y contadas excepciones.

Es por eso que la tarea a la que se dieron los autores de los distintos capítulos de este libro resulta muy valiosa y útil, aunque en algunos casos se sienta el desaliento que enfrentó el autor al no encontrar suficiente información para armar lo concerniente al cultivo encomendado.

El enfoque adoptado fue el de ver a la planta con su potencial genético, desarrollándose en un ambiente dado por una serie de factores, los que concomitantemente actúan sobre la fisiología de la planta, determinando en última instancia el comportamiento de esa planta.

El comportamiento en ese sentido es susceptible de ser manipulado por el hombre y en tal forma puede aumentarse o disminuirse su producción de hojas, flores, frutos, raíces, latex, etc.

Por lo tanto, se dedican dos capítulos introductorios a explicar el clima y los suelos de los trópicos. El clima contempla en este capítulo los componentes más importantes como la luz, la temperatura y el agua, con todas sus posibles variantes. Sin embargo, en capítulos posteriores se mencionan factores como el viento, que resulta sumamente importante en los trópicos, y la altura sobre el nivel del mar por su influencia en los otros factores del ambiente. El fuego, el rocío, el ambiente social, las plagas y las enfermedades y hasta las tempestades o rayos también se mencionan en relación con algunos cultivos.

Los cultivos que se tomaron en cuenta fueron: arroz, caña de azúcar, piña, pastos, raíces alimenticias, camote, café, cacao, hule, té, palma de aceite, coco, cítricos, bananos, marañón, mango. Es notoria la falta de fibras, especias, otras oleaginosas tropicales, plantas medicinales y desde luego, muchos frutales y verduras. Obviamente, hubiera sido imposible incluir todos los cultivos, pero se siente la tendencia a pensar que por ejemplo, el aguacate hubiera sido más importante que el marañón, o que quizás hizo falta un capítulo específico sobre yuca.

El tratamiento dado a cada cultivo varía mucho en razón de la información existente, pero en todos se hace un esfuerzo por puntualizar todas las incógnitas que aún existen y que deben ser investigadas. Los autores trataron de volcar en cada capítulo toda su experiencia y, como es natural, haciendo énfasis en la literatura de sus áreas de trabajo. Por ejemplo, es curioso observar que en el capítulo de suelos, que por cierto está muy bien tratado, casi no se citan trabajos latinoamericanos, con excepción de los brasileños.

Documentos como este resultan sumamente útiles en la medida en la que ayudan a comprender mejor el comportamiento básico de los cultivos tropicales y en consecuencia a hacer un aprovechamiento más eficiente de la abundancia de luz, altas temperaturas y lluvias.

El hecho de que el libro esté escrito en inglés limitará su uso entre los técnicos latinoamericanos y muy especialmente entre los estudiantes.

Con mucha frecuencia se hacen reuniones de expertos y técnicos de reconocida competencia, pero muy pocas veces se publican las conclusiones de manera que sean de utilidad a todos los interesados. Este libro es el resultado del Simposio Internacional sobre Ecofisiología de los Cultivos Tropicales, que se celebró en Manaus, Brasil, en 1975, en el que se revisó el concepto de ecofisiología y el estado del conocimiento de esa disciplina en relación con los cultivos tropicales.

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PEST CONTROL in tropical root crops. London, Centre for Overseas Pest Research, PANS, Manual Nº 4. 1978. 235 p. £ 2.50 net.

Las raíces son alimentos importantes en los trópicos, por lo que es apropiado que el cuarto Manual PANS trate sobre camote, yuca, ñames y taro *(Colocasia esculenta)*.

Este manual contiene capítulos generales sobre control de malezas, de roedores y sobre almacenamiento, seguidos por secciones sobre control de enfermedades, nematodos y plagas en cada cultivo. De los cuatro cultivos estudiados, el camote predomina en Asia (92% de la producción mundial), mientras que en Africa tienen la supremacía los ñames (97% de la producción mundial), el taro (80%) y la yuca (42%). Este último es el que más importancia tiene en América del Sur (30%). La distribución de los cuatro cultivos está equilibrada en el libro, desde 50 páginas para la yuca hasta 30 para los ñames. El volumen está bien ilustrado y con abundantes referencias en la literatura. Al final tiene un glosario, y listas, ordenadas por nombres científicos, de enfermedades, de nematodos, de insectos y ácaros, y de nombres comunes de plaguicidas, con algunos nombres comerciales. Tiene índice de materias.