Possible role of growth regulators in adaptation to heat stress affecting partitioning of photosynthates in tomato plants

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Abstract

Tomato plants of two cultivars: Roma — sensitive and Robin — tolerant to heat stress were grown in greenhouse up to the flowering stage and then under controlled environmental conditions. The partitioning of recently fixed $^{14}\text{CO}_2$ by mature tomato leaves was examined as a posteffect of 24-h heat stress (38/25°C day/night) with the interaction of growth regulators (GR) sprayed on the flowers with solution of β -naphthoxyacetic (NOA) and gibberellic (GA_3) acid (denoted as NG), or Zeatin + NOA + GA_3 (denoted as ZNG). In both cultivars GR strongly stimulated fruit growth and transport of ^{14}C -photosynthates to the clusters at the expense of vegetative organs. Heat stress decreased export of ^{14}C -photosynthates from the blades in plants not treated with GR, but even more in cv. Roma. In Roma plants not treated with GR (with very small fruitlets and fruits) the heat stress retarded ^{14}C -transport just in the petioles, diminishing the ^{14}C -supply to the fruits. Reduction of the current photosynthate supplied to the fruits seems to be causally connected with inhibition of the specific activity of acid invertase in that organ. Growth regulators reduced the negative effect of high temperature — they alleviated depression of ^{14}C -export from the blades and increased invertase activity. ^{14}C -photosynthate transport to the fruits, presumably owing to their higher sink strength, was less affected by heat stress. In Robin plants (which had bigger fruits during the experiment) high temperature depressed ^{14}C -fruit supply only in the NG-series, in contrast to enhancement of ^{14}C -movement to that sink in the control and ZNG-series. In spite of these facts, after heat stress, the specific activity of acid invertase decreased in all the experimental series, but much less in the GR-treated series. Therefore, in the Robin cv. there was no relation between invertase activity and ^{14}C -mobilization by fruits, as was observed in Roma plants.

The possible explanation of the different response of the two cultivars with contrasting sensitivity to heat stress, with special reference to the role of GR, diminishing injury of the plants by high temperature is discussed.

Key words: fruits, growth regulators, heat stress, invertase, photosynthate distribution, tomato

INTRODUCTION

In the last few years the attention was devoted to the effect of environmental conditions on the level and balance of growth regulators.

In tomato plants, a temporary increase of temperature above 30°C, drastically diminishes photosynthesis and fruit set (Bar-Tsu et al. 1985). Heat stress diminishes export of photosynthates from the tomato leaf blades (Dinar et al. 1983) and affects the pattern of dry matter allocation (Dinar and Rudich 1985a). Reduced supplying of developing flowers with photosynthates was observed, especially in heat-sensitive cultivar.

A lower mobilizing power of *Vitis* fruit, of plants subjected to high temperature was also reported by Sepulveda et al. (1986).

The main reason for the heat stress injury seems to be unbalanced hormonal activity (Levitt 1980). Even very brief heat shock (a few minutes) drastically decreases the cytokinin content, but promotes ABA synthesis (Itai et al. 1973); cytokinin reverses the stress effect (Itai and Benzioni 1973) or even prevents plant damage (Skoggvist 1974). Analogically, GA₃ + kinetin, applied to the tomato flower buds, treated with high temperature, prevented transport inhibition (Dinar and Rudich 1985a). In tomato plants high temperature negatively affected ¹⁴C-transport to the generative organ especially in heat-sensitive cultivar, because sucrose hydrolysis in its flower buds decreased more than in tolerant plants (Dinar and Rudich 1985b). This seems to be caused by lower invertase activity which is under hormonal control.

Cell growth and acid invertase activity in vegetative organs exhibit response closely coupled to environmental changes and growth regulator treatment (Morris and Arthur 1984, 1985). Auxin seems to be involved in direct action on invertase turnover (Morris and Arthur 1986). Other growth regulators also influence acid invertase activity and/or its synthesis, as Kaufman et al. (1973) presented for GA in their paper concerning *Avena* stem segments and Khayat and Zieslin (1987) for BA in rose buds. In the developing strawberry receptacle, NAA application enhanced both sink strength and invertase activity (Poovaiah and Veluthambi 1985). Growth regulators: IAA, GA₃ and BA promoted acid invertase activity in growing lemon juice vesicle explants (Altman et al. 1982). In tomato plants, low

irradiance enhancing abortion of flower buds, also seem to be causally related to the decline in invertase production (Russel and Morris 1982).

The growth regulators NOA and GA_3 applied together to tomato flowers, stimulate fruit growth even under stress conditions enhancing transport of photosynthates to the fruits and their remobilization from vegetative organs (Starck 1983, Starck et al. 1987a, b and in press). Most of these results were obtained in experiments done in greenhouse under variable temperature, exceeding on some days 30-35°C, causing various response depends of experiments with tomato plants and environmental conditions (Starck et al. 1988). Therefore suggestion was advanced, that GR may temper negative effect of stresses.

The aim of present study was to investigate the effect of heat stress on assimilate partitioning in two tomato cultivars with contrasting responses to high temperature and with source sink modification the growth of their fruit were stimulated by GR. The compositions of GR used was chosen on the basis of our previous experiments (data not printed), to give maximal stimulation.

MATERIAL AND METHODS

PLANT MATERIAL

Plant of Roma V. F. and Robin CUFS F_1 cultivars were grown in early spring in a greenhouse, in hydropeatic culture with complex fertiliser added (Starck 1983). When the first inflorescence started to develop, the plants were placed in a phytotron (kTKL 20.000, Netzschkam, Nema, GDR) at an air temperature 20/16°C day and night and 75/85% relative humidity, with a 14 h photoperiod provided by halogenic bulbs NARVA Nachroma NC 1000-62 and incandescent ones, 100 W, at 450 $\mu E m^{-2} s^{-1}$ measured above the top of plants, at the end of the experiment.

When plants developed two clusters with an uncontrolled number of fruits, plants were decapited and three experimental series was established: control (untreated) and treated with growth regulators (GR): as in previous experiments with a mixture of 50 ppm NOA and 30 ppm GA_3 (Gibrescol) with 0.1% Tween 20 (series denoted as NG), spraying twice a week on the open flowers (each flower was treated 3-4 times). In the other series, zeatin was applied according to the Kinet method (1977), directly on the inflorescences at the very beginning of flower development two times a week (cotton moistened with a solution containing 10 ppm zeatin), this preceeded the treatment with 50 ppm NOA and 30 ppm GA_3 (series ZNG) applied 2 weeks later. Three weeks from the onset of flowering of the first cluster (when the first spraying with NOA + GA_3 was applied) (Roma) or 4 weeks (Robin) half

of the plants of each series were kept for 24 h at a temperature of 38/25°C day and night (heat stress) and the other half — were still grown under optimal conditions of 20/16°C day and night. Each of these series included four plants as replications.

RADIOACTIVE LABELLING WITH $^{14}\text{CO}_2$ AND SUGAR ESTIMATION

The upper part of the plant — the leaf with second cluster below and small part of the stem, was detached and labelled in the morning with $^{14}\text{CO}_2$ in open air, under natural light conditions. The blades were enclosed in plastic bags, containing thick filter paper, saturated with 1.85 MBq $\text{Na}_2^{14}\text{CO}_3 + \text{Na}_2\text{CO}_3$. The bags were sealed around the petioles with plasticin and CO_2 was liberated inside the bag by lactic acid injection. After 40 min of $^{14}\text{CO}_2$ exposure the bags were removed. Transport of ^{14}C -photosynthates was allowed for 10 h in a very humid atmosphere, to prevent wilting and then the plants were divided into organs, placed at -20°C where they were stored to the time of homogenization in 80 per cent ethanol. Radioactivity was measured by a G-M gas flow counter. Data are expressed either as per cent of total ^{14}C -photosynthates exported from the blades or as relative specific activity (RSA) which was calculated (according to Dinar and Rudich 1985b) as follows:

$$\text{RSA} = \frac{\text{cpm} \cdot (\text{g fresh matter in the organ})^{-1}}{\text{cpm} \cdot (\text{g fresh matter in the whole plant without the } ^{14}\text{C-blades})}$$

Sugars were estimated in the ethanol-soluble fraction by the Dubois phenol method (Peach and Tracey 1955).

Fruits of the first clusters (older) were collected for estimation of invertase activity. Unfortunately, in the Roma heat-treated control series there was not enough material to estimate enzyme activity. The tomato fruits were homogenized in 0.1 M citrate-phosphate buffer (pH 5.0). The homogenate was centrifuged at $14\,000 \times g$ for 15 min and ammonium sulphate was added to the supernatant to 50% saturation. After centrifugation ($16\,000 \times g$ for 15 min) the precipitate was dissolved in 0.1 M citrate-phosphate buffer (pH 5.0) and desalted on a Sephadex G-25 column. All procedures were carried out at 4°C . The protein content of the preparation was determined by Bradford's method (1976).

Invertase activity of the preparation was measured with sucrose as a substrate following 30 min incubation at 37°C (pH 5.0). The reaction was stopped by heating the samples in a bath of boiling water for 10 min. Reducing sugars were estimated by the method of Bernfeld (1955). The activity of the preparation is expressed for convenience data as $\text{nkat} \cdot \text{mg proteins}^{-1}$.

RESULTS

Growth regulators (GR) strongly stimulated fruit growth in both cultivars. The average size of one fruit in Roma was approximately 0.2 g of fresh matter in control plants and about 10 g in both GR-series, without significant differences between NG- and ZNG plants. In the control Roma series fruit set was poor, but improved in GR-series from an average of 5 to 7 in each cluster (data not presented).

In cv. Robin the average fresh matter of one untreated fruit was about 9 g, and in the NG or ZNG-series about 29 g without significant differences in fruit number per plant (data not presented).

Heat stress reduced ^{14}C -export out of the blades in both cultivars (Fig. 1), but in all cases GR-treatment enhanced is especially in Robin plants by about 70%.

In Roma control plants, of both temperature regimes, in spite of high ^{14}C -retention in the blades, the ^{14}C -exported was already retarded in the petioles, accumulating a dominant part of labelled photosynthates at the cost of fruit supply. Growth regulators strongly enhanced ^{14}C -supply to the fruits mainly at the expense of petiole (Fig. 2). The high contribution of petioles to ^{14}C -exported from the blades was perhaps a function of less reduced export rate from the blades than import to the developing fruits, which had a very low mobilizing power in the untreated with GR-series.

Heat stress drastically depressed ^{14}C -transport to the fruits in all series, diminishing their sink strength (Fig. 2). In the GR-series of Roma cv. the share of ^{14}C -substances transported to the peduncle with pedicels increased, presumably owing to a most drastic reduction of ^{14}C -unloading in the fruits. Therefore radioactivity of green part of cluster was negatively related to the

Fig. 1. Export of ^{14}C -photosynthates in percentage of radioactivity of the whole labelled plant part. Control — untreated plants, NG — treated with NOA + GA_3 , ZNG — treated with zeatin + NOA + GA_3 .

sink strength of fruits, as a sink, as has been presented before (Starck et al. 1988).

In Robin plants, GR also promoted the main sink strength, diminishing the proportion of ^{14}C -substances in the petioles and stem. Under optimal temperature conditions, the effect of NG was even more pronounced than of ZNG. In Robin plants, heat stress depressed transport of ^{14}C -photosynthates to the fruits only in the NG-series, whereas stimulation was observed in control and ZNG-series (Fig. 2).

Fig. 2. Effect of heat stress and growth regulator treatment on the ^{14}C -distribution to individual organs, expressed as percentage of ^{14}C -photosynthate export from the ^{14}C -source blades (assumed as 100 percents): 1 — petioles, 2 — stem, 3 — peduncle with pedicels, 4 — fruits. Series denoted — as in Fig. 1

To compare fruit ability to mobilize current photosynthates (sink strength), with the changes in their activity (expressed in relation to their fresh matter), the relative specific radioactivity (RSA) was calculated according to Dinar and Rudich's (1985b) formula, described in Material and methods. The RSA calculated jointly for petioles, stem, pedicels and peduncle was compared to the RSA of the fruits in the individual series (Fig. 3).

Fig. 3. Comparison of relative specific activity RSA for: 1 — all vegetative part (petioles + stem + peduncle + pedicels), 2 — fruits. Series denoted — as in Fig. 1

The RSA of a very small fruitlets and fruits of Roma control plants exceeded that of the much bigger fruit, of the GR-treated series, similarly as in Dinar and Rudich's (1985a) paper. Heat stress in all cases, but much less in GR-treated plants, reduced fruit activity in contrast to increasing of the RSA of vegetative organs.

In Robin cv., unexpected stimulation of fruit mobilizing power caused by high temperature in the control and ZNG-series was also manifested in their activity, expressed as RSA.

In contrast to the post-stress effects on the distribution of current photosynthates, the changes in the content of sugars (soluble in 80% ethanol) are a consequence of changes both in metabolism and distribution of C-compounds.

The blades of GR-treated Roma plants had a lower level of sugars both in plants from optimum temperature, and after heat stress probably due to higher export of sugars (Table 1). After heat treatment, the sugar content in the blades strongly decreased in the ZNG-series (Table 1), much less in control

Table 1

The effect of growth regulators (GR) and temperature on the content of sugars soluble in 80 percent ethanol, expressed as percentage of fresh matter of tomato plants

Plant organs	Temperature conditions	Roma			Robin		
		not treated with GR	NG	ZNG	not treated with GR	NG	ZNG
Blades	optimal	1.31	0.79	1.20	2.08	1.95	1.84
	heat stress	0.91	0.71	0.50	2.07	1.98	2.14
Petioles	optimal	0.59	0.49	0.44	2.73	1.72	1.52
	heat stress	0.36	0.22	0.21	1.90	1.71	1.44
Fruits	optimal	1.39	1.87	1.71	1.58	2.00	2.07
	heat stress	1.23	2.14	2.07	2.36	2.02	1.87

Explanations: NG — NOA + GA₃, ZNG — zeatin + NOA + GA₃.

plants and not at all in NG-series. Diminished sugar content in the petioles of all the heated plants suggests their exhaustion during the period of high temperature, when the demand of fruits (especially those of the GR-series) perhaps exceeded supply with current photosynthates; it caused sugar retranslocation from the petiole to the generative organ. This probably preceded retardation of ¹⁴C-photosynthate translocation, observed as a post-effect of stress. In the fruits of GR-treated plants grown under optimal temperature, their sugar content was higher than in control ones due to stimulation of fruit supply with photosynthates. Heat treated fruits of GR-series had even higher sugar content probably owing to smaller reduction of photosynthate movement than their growth depression which probably caused lower use of sugars available for growth.

The sugar content in all plant organs of Robin cv. was higher than in Roma cv. (Table 1). In the control series from optimal temperature conditions with a relatively low fruit mobilizing power, the sugar level in the petiole was high, presumably due to excess of its supply from blades over export to the fruit where the sugar content was rather low. High temperature causing enhanced both fruit activity and its strength in the control series, increased transport not only of current photosynthates, but also of sugars remobilized from the petioles (Table 1). Heat stress affected much less sugar content in GR-treated series (Table 1).

The specific activity of acid invertase, extracted from the fruits of the first cluster in Robin cv. was almost 5-times higher than in Roma, and positively responded to GR-treatment in both cultivars but especially in the ZNG series (Fig. 4). In all the case, high temperature diminished the specific activity of acid invertase. The depression in Robin control plants amounted 38 percents.

Therefore in Roma cv. the response of specific invertase activity was parallel to the depression of ^{14}C -transport to the fruits of individual series, but in Robin plants it did not correlate with the changes in the supply of fruits with photosynthates, except in the NG-series.

Fig. 4. Specific activity of acid invertase in tomato fruits. Series denoted — as in Fig. 1. Bars mean significant differences as evaluated by Student's "t" test at $p = 0.05$

DISCUSSION

The marked stimulating effect of GR on fruit growth and their strength was observed in both cultivars. High temperature reduced ^{14}C -export from the blades, ^{14}C -import to the fruits was depressed by stress and counteracted by GR application in all the cases of sensitive Roma plants and the Robin NG-series.

Interpretation of the presented results should be done with caution, owing to the fact that immediately after GR application hormonal imbalance may arise in plants. This may lead to metabolic disturbances, dependent on the current endogenous hormone concentration, and/or their activity. In the investigations of Bender et al. (1986) GA_3 treatment of carrot plants reduced the cytokinin level. A similar conclusion was drawn from Navata's (1985) experiments done with tomato. On the other hand, as posteffect of heat stress, diminished cytokinin content was observed (Itai et al. 1973a). Strong cytokinin deficit would also take place in tomato plants of our experiments, especially in the NG-series. This was the reason for investigating of the high

temperature effect in tomato plants treated not only with auxin and gibberellin, but also with zeatin. Nevertheless in most cases there were no appreciable differences between the NG and ZNG-series except for the fact that in Robin plants, heat stimulated ^{14}C -supply to the fruits of control and ZNG-series, but depressed it in the NG-series, where the cytokinin level would be a limiting factor. In the GR-treated series of both cultivars, ^{14}C -export and transport of current photosynthates to the fruits were strongly enhanced at the expense of petioles.

In reference to the hypothesis that acid invertase is involved in the mechanism controlling phloem unloading (Eschrich 1980, Eschrich and Eschrich 1987), it is worth underlining the very strong stimulation of the specific activity of acid invertase in fruits of all series treated with GR under both temperature regimes and in both cultivars. This may be coupled with growth promotion of fruits followed by enhanced demand for photosynthates. In contrast heat stress diminished the specific activity of invertase parallel to the reduction of the fruit mobilizing power of photosynthates only in Roma plants. The results obtained with Robin indicate that, as a post-effect of high temperature, invertase activity was also depressed in contrast to stimulation in control and ZNG-series of ^{14}C -transport to the fruits. This apparently seems to be in contrast with the hypothesis presented above. The ability of Robin to sustain normal or even enhanced fruit supply with photosynthates after heat stress was not determined by the greater thermostability of invertase, but could be associated with the presence of a heat-stable protein synthesis mechanism, which enables quick replacement of enzymes denaturated by stress, as postulated McWilliam and Ferrar (1974). This synthesis could be stimulated more in activity growing fruits of ZNG-treated series, and less depressed in control plants, possibly with a higher cytokinin content, as compared with the NG-series.

The other explanation of the stimulating effect of high temperature on fruit supply with photosynthates, in spite of decreased invertase activity, may reflect the possible existence of an alternative metabolic pathway for transported sucrose, during unloadings, as proposed by Khatay and Zieslin (1987) in experiments with the rose plant.

All the arguments presented prompt the suggestion, that the tomato plant, even of cultivars sensitive to heat stress, treated with growth regulators, possesses a greater "plasticity" to unfavourable environmental conditions. According to the sophisticated model presented by Salisbury and Marinos (1985), it may be postulated that translocation of photosynthates in heat-sensitive Roma plants may operate within a narrower elastic strain limit (only slightly expanded by growth regulators) than in Robin, tolerant to high temperature, possessing perhaps better regulated systems maintaining its homeostatic status, regulated possibly by phytohormones.

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Rola regulatorów wzrostu w adaptacji do stresu przegrzania wpływającego na dystrybucję asymilatów u pomidorów

Streszczenie

Porównywano reakcję pomidorów na stres termiczny u dwóch odmian: Roma – wrażliwej i Robin – odpornej. Do kwitnienia rośliny uprawiano w szklarni, po czym przeniesiono je do warunków kontrolowanych. Dystrybucję produktów $^{14}\text{CO}_2$ asymilacji badano po 24 godzinnym stresie termicznym (38/25°C dzień/noc) w roślinach kontrolnych i traktowanych regulatorami wzrostu (oprysk kwiatów roztworem kwasu β -naftoksyoctowego – NOA i gibreskolem – GA_3 (skrót NG) lub zeatyną+NOA+ GA_3 (skrót ZNG)).

U obu odmian regulatory wzrostu silnie stymulowały wzrost owoców i transport ^{14}C -asymilatów do gron, kosztem organów wegetacyjnych. Przegrzanie hamowało eksport ^{14}C -asymilatów z blaszki liściowej u roślin obu odmian nie traktowanych regulatorami wzrostu.

Odmiana Roma, nie traktowana regulatorami wzrostu, miała bardzo małe owoce (lub tylko zawiązki owoców). W serii kontrolnej przegrzanie hamowało ^{14}C -transport już w ogonkach

liściowych i obniżało zaopatrzenie owoców w bieżące asymilaty. Zahamowanie transportu asymilatów do owoców po stresie termicznym wydaje się być uzależnione od zmniejszonej aktywności kwaśnej inwertazy w tych organach.

Regulatory wzrostu zmniejszały ujemny wpływ podwyższonej temperatury stymulując aktywność inwertazy, ^{14}C -eksport z blaszek i transport znakowanych asymilatów do owoców. Wynikało to z ich wpływu na "siłę akceptora", która w seriach traktowanych regulatorami wzrostu była w mniejszym stopniu zmniejszona przez stres termiczny.

Rośliny odmiany Robin, w czasie pomiaru miały większe owoce przy mniejszych różnicach między serią kontrolną i seriami traktowanymi regulatorami wzrostu. Przegrzanie hamowało zaopatrzenie owoców w ^{14}C -asymilaty tylko w serii NG, przy jego wzroście w seriach kontrolnej i ZNG. Aktywność inwertazy kwaśnej po stresie termicznym była jednak zmniejszona w owocach wszystkich serii, choć znacznie bardziej — u roślin nie traktowanych regulatorami wzrostu. U tej odmiany nie stwierdzono zatem zależności między zmianami w aktywności inwertazy i w zaopatrzeniu owoców w bieżące produkty fotosyntezy.

Przedyskutowano przyczyny rozbieżnej reakcji obu odmian na stres termiczny, ze szczególnym uwzględnieniem roli regulatorów wzrostu, zmniejszających wrażliwość pomidorów na stres termiczny.