The response of leaves to heat stress in tomato plants with source-sink modulated by growth regulators

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Abstract

The response to heat stress was investigated in heat-sensitive, Roma V. F. and heat-tolerant, Robin, cultivars whose fruit growth was stimulated by NOA + GA₃ or NOA + GA₃ + zeatin. The treated plants were compared with untreated control plant. In each of these series half of the plants were subjected to one or three cycles of heat stress. A single cycle of 38°/25°C day and night did not significantly affect either the respiration rate or chlorophyll content. In PGR-untreated intact cv. Roma, heat stress inhibited starch formation during the day and strongly depressed night export from the blades. High temperature depressed the night transport less in plants having a higher sink demand of fruits in plant treated with PGR. In this case the amount of substances available for export was much higher and both sugars and starch were more intensively remobilized at night. In intact Robin plants, PGR and heat stress much less affected sugar and starch content. High temperature diminished nocturnal starch remobilization only in the NOA + GA₃ series. Leaf disc growth was evaluated as a measure of response to heat stress after elimination of the direct effect of fruit demands. One cycle of high temperature did not negatively affect the growth of leaf discs; it even caused thermal low growth activation in both cultivars. Three cycles of heat stress depressed leaf disc growth after short-term stimulation, especially in Roma plants. Immediately after 3-day heat stress, there was no response of discs to GA₃ or zeatin added to the solution on which the discs were floated. Leaf disc growth of Robin control and NOA + GA₃ series was very similar in plants from optimal temperature conditions. High temperature inhibited only disc growth of the NOA + GA₃ series owing to depression of starch break-down, diminishing the pool of sugars. In contrast, leaf discs of Roma cv. excised from NOA + GA₃ treated plants from the optimal temperature series, grew more intensively as compared with control plants, owing to a higher content of sugar available for growth.

Key words: growth regulators, heat stress, night starch degradation, sugars, tomato

INTRODUCTION

The effect of fruit demand on the metabolism of blades is important in the problem of source-sink relations. Reports that stress conditions affect photosynthesis and export of photosynthates depends on sink demand are of particular interest.

In tomato plants, supraoptimal temperature depresses photosynthesis (Markus et al. 1981, Bar-Tsur et al. 1985) as well as the export of current photosynthates from the tomato blades and photosynthate allocation in the whole plant (Dinar et al. 1983, Dinar and Rudich 1985). The long term effect of plant growth regulators (PGR) which stimulate fruit growth minimizes the effect of high temperature, preventing the decrease of assimilate export out of the blades (Starck and Cieřła 1989). In the experiments by Dinar and Rudich (1985) the higher sink strength of tomato flower buds treated with GA_3 + kinetin, within the 2-day heat stress period, was due to an increase of sink size and, in consequence, sink demand.

The sink demand influences the rate of photosynthesis giving variable results depending on the species (Plaut et al. 1987), developmental stage and environmental conditions (Geiger 1976, Ho 1979a, b, Ho et al. 1983, Roper et al. 1988). In tomato plants, successive removal of all the flowers significantly affected the rate of photosynthesis as late as after 6 weeks but gradual thickening of the blades was observed (Starck et al. 1979). The effect of fruits on the rate of photosynthesis depends on the source-sink balance in the whole organism (Ho 1979a, b). Below a certain level of carbon fixation remobilization of stored organic substances, mainly starch, determined the export rate out of the leaves (Ho et al. 1983). The stabilization of fruit supply with photosynthates is achieved each night and, under conditions drastically reducing photosynthesis, deplets the leaf reserves, as reported by Grange (1985b) for pepper and Ho (1979a) for tomato plants.

Continuous supply of sinks with C-compounds during the dark period causes a nocturnal decrease of leaf carbohydrate content observed in many plant species (Halmer and Bewley 1982). It is very intensive in tomato plants, but depends on leaf age, their position on the plant (Ammerlaan et al. 1986) and external conditions (Madsen 1968, Ehret and Ho 1986) on the one hand and sink strength on the other, as presented by Hammond and Burton (1983) in pepper, Carlson and Brun (1984) in soybean.

Numerous reports describe source-sink interaction with special attention to hormone-directed transport and its effect both on allocation of current photosynthates and remobilization from vegetative organs. Leaves and stem function in many cases as a buffering source (Halmer and Bewley 1982, Wardlaw 1984, Franceschi 1986, Herzog 1986). Therefore a mechanism must exist which regulates remobilization of stored materials in case the sink

demand changes. Stimulation of tomato fruit growth, as an effect of treating flowers with PGR drastically depresses growth of blades as well as other vegetative organs (Starck 1983, Starck et al. 1987). Maintaining the integrity of the whole organism, concerning allocation of nutrients, especially under unfavourable external conditions, seems to be under hormonal control. The aim of the reported investigations is to study hormonal modulation of the effect of sink (tomato fruits) on the source of photosynthates, in plants treated with heat stress conditions. Tomato plants with increased sink demand induced by treatment of the flowers with PGR, (NOA, GA_3 and zeatin) were used as models. The response of blades to high temperature treatment was analysed in terms of their capacity to store starch and sugars during daytime and then ability to remobilize them at night. The growth of leaf discs and their response to PGR was used as a measure of the potential leaf growth rate affected by heat stress, but without direct effect of fruit demand.

MATERIAL AND METHODS

Tomato plants of two cultivars: Roma VF — sensitive to high temperature and Robin CUF SF_1 — tolerant were grown in early spring in a greenhouse in two experiments (No. I, II) in hydropeatic culture with complex fertilizer added (Starck 1983). Two clusters were allowed to develop. At that time they were transferred to a growth chamber (KTKL 20.000 Netzschkon, Nema GDR) with the following controlled conditions: air temperature 20°/16°C day/night with a 14-h photoperiod provided by halogenic NARVA Nachroma NC 1000-62 bulbs and incandescent 100 W bulbs with 450 $\mu Em^{-2} s^{-1}$ PAR irradiance intensity at the top of plants, measured at the end of the experiments. The plants were divided into 3 series: control (untreated with PGR); the other two series were sprayed twice a week with PGR solution containing 0.1 percent Tween 20, 50 mg dm^{-3} NOA and GA_3 (as Gribrescol), 30 mg dm^{-3} , series denoted as NG, or treated at the very beginning of flower bud development with zeatin, applied directly on the flower buds with cotton moistened with a 10 mg dm^{-3} zeatin solution. After 2 weeks these flowers were sprayed two times weekly with solutions containing NOA and GA_3 in concentrations as above (series denoted ZNG).

The temperature treatment was as follows. One group of plants in each of the two experiments was grown only in optimal temperature 20°/16°C day and night; the other group was subjected to heat stress. In exp. I (3 weeks after the onset of flowering of the first cluster — cvs. Roma and Robin) the plants were treated for 3 successive days and nights with 36°/25°C. In the second experiment (3 weeks after the onset of flowering — cv. Roma and 4 weeks cv. Robin), the plants were treated only with one cycle of heat stress: 38°/25°C day

and night. These groups in each experiment were denoted as optimal and heated plants.

In expt. II, sugars were extracted with 80 percent ethanol and determined by the Dubois phenol method (Peach and Tracey 1955); starch content was measured in the same samples.

The carbohydrate content was determined in samples collected in the evening and in the morning from the optimal and heated series; discs from the blades were cut out at the end of the 14-h light period of optimal (20°C) or high (38°C) temperature and at the end of the night (16° or 25°C).

The starch content was assayed in the same disc samples used for sugar extraction, cut from upper, mature leaves. After chlorophyll extraction with ethanol, the discs were homogenized and the suspension was converted into glue.

The starch content was determined iodometrically at 680 nm with the use of a spectrophotometer Specol. The method was adapted by Stahl (data not published).

The respiration rate was determined using the Warburg method on 7 mm discs (15 in each replication). The discs were cut early in the morning from leaves below first cluster — in cv. Roma and above it — in cv. Robin; the discs were treated with buffer solution, HEPES 10 mM, MES 5 mM, CaCl_2 — 0.2 M preventing the effect of trauma.

Chlorophyll “a” and “b” contents were determined by the Bruinsma method (1963).

Where indicated, statistical analysis of variance was done by the Snedecor method (Tables 5, 7) or only the significance of differences was evaluated by Student’s “t” test.

RESULTS

INTERACTION BETWEEN BLADE RESPONSE TO PLANT GROWTH REGULATORS AND HEAT STRESS

In exp. I three weeks after the onset of first cluster flowering, the average fresh matter of fruit differed markedly in control (untreated with PGR) and treated plants. In Roma cv. it was below 1 g in control to above 20 g — for the PGR-treated series. In cv. Robin, in the control series the fresh matter equalled a few grams as compared to above 60 g in the PGR-treated plants (data not presented).

In exp. II, in both cultivars the fresh matter of the aerial part was lowest in the control series with a similar mass of blades. This suggests that the rate of net photosynthesis was higher in the PGR-treated plants than in control ones at least at some period of plant growth. The stimulating effect of PGR on fruit growth was very strong but smaller in Robin plants (Table 1).

In Roma plants the rate of respiration was not distinctly affected either by

Table 1
Physiological characteristics of plants and their response to heat stress (Exp. II)

Physiological parameters	cv. Roma						cv. Robin					
	optimal temperature			heat stress			optimal temperature			heat stress		
	control	NG	ZNG	control	NG	ZNG	control	NG	ZNG	control	NG	ZNG
Fresh matter (g) — fruits	4	89	149	2	112	122	134	287	361	73	407	428
— blades	407	419	421	405	423	372	363	425	379	432	376	331
— other vegetative parts	242	257	270	267	297	260	367	420	384	430	380	366
— total aerial part	653	765	840	674	832	754	864	1132	1124	935	1163	1125
Respiration of blades (ml O ₂ g ⁻¹ d.m.h. ⁻¹)	2.10	1.92	1.92	1.98	1.81	2.11	1.92	2.25	1.94	1.65	1.79	1.34
Chlorophyll content (mg dm ⁻²)												
— chl. a	2.73	2.89	3.50	2.78	3.15	3.57	1.96	2.38	2.23	2.28	2.41	2.07
— chl. b	1.46	1.40	1.77	1.59	1.83	2.35	1.01	1.27	1.18	1.44	1.28	1.15
ratio $\frac{\text{chl. a}}{\text{chl. b}}$	1.87	2.06	1.98	1.75	1.72	1.52	1.94	1.87	1.89	1.58	1.88	1.80

control — plants not treated with growth regulators, NG — flowers sprayed with NOA and GA₃, ZNG — flowers sprayed with NOA+GA₃+zeatin.

heat stress or by PGR. The highest decrease was observed in Robin heated blades (data statistically insignificant). Most of the changes in the total chlorophyll content, as well as a/b ratio were insignificant, owing to the great variability of the data, but distinct trends in the direction of its increase after heat stress in Roma cv. and only in the PGR-untreated series of Robin plants were observed.

THE POST-EFFECT OF HEAT STRESS ON GROWTH OF DISCS EXCISED FROM TOMATO LEAVES

The dynamics of leaf disc growth was examined according to the Menhenett and Wareing (1975) method. The discs were cut from tomato plants from optimal temperature conditions and immediately after the plants had been treated with 3-day or 1-day high temperature exposure in exps. I or II, respectively.

Leaf discs 7 mm in diameter (10 in each replication) excised from mature leaves were floated in Petri dishes, abaxial side down on distilled water or on solutions containing PGR at the following concentrations (in mg dm^{-3}): exp. I: NOA — 50, GA_3 — 30 and zeatin — 5. In exp. II the concentration of PGR was higher, chosen after more detailed experiments (data not published): GA_3 — 100, zeatin — 10. The Petri dishes were placed in growth chamber at $22-24^\circ\text{C}$ under continuous white fluorescent light ($13 \mu\text{E m}^{-2} \text{s}^{-1}$ PAR). Their fresh matter increment was measured at two-day (exp. I) or one-day intervals (exp. II). There were 3 replications in exp. I and 4 replications — in exp. II.

Experiment I

Discs were cut only from plants untreated with PGR, either from optimal series or immediately after 3-day exposure to high temperature ($36^\circ/25^\circ$ day and night).

Discs cut from Roma leaves from the optimal series increased their fresh matter faster at the beginning and more slowly thereafter (Fig. 1A). GA_3 significantly increased disc growth, especially in the initial period. Addition of NOA or zeatin to the floating solution did not have any significant positive effect.

Pretreatment of the plants with heat stress affected the disc growth pattern (Table 5). The curves became much more flatt, due to short term enhancement and after that drastic growth depression was observed (Fig. 1). Therefore the total increase in 4-day intervals was almost the same in the optimal and heated series (Table 2). Nevertheless, the average total increment in 6 days, calculated for data blocked together from all treatments in each set of temperature conditions, was lower for heated plants (Table 3).

Discs excised from the leaves from the optimal series of cv. Robin increased their fresh matter almost linearly. They responded by growth stimulation only

Fig. 1. Dynamics of disc growth: A, B — Roma and C, D — Robin cultivar. A, C — series from optimal temperature; B, D — series treated with heat stress. Bars represent LSD at $\alpha = 0.05$ for each point (Exp. I)

Table 2

Comparison of the growth rate of leaf discs floated on water (H₂O) or water containing plant growth regulators, expressed as an average of total increase of fresh matter (in mg) during 4 or 3 days in exp. I and II, respectively

Cultivar	Temperature treatment	Experiment I				Experiment II					
		control series				control series			NG-series		
		H ₂ O	NOA	zeat.	GA ₃	H ₂ O	zeat.	GA ₃	H ₂ O	zeat.	GA ₃
Roma	optimal	48	41	54	61	16	19	37	28	31	45
		heat stress	46	41	51	51	28	29	45	31	47
Robin	optimal	28	27	45	29	14	14	24	16	13	24
		heat stress	51	44	66	60	21	23	33	17	30

Table 3

Increase of fresh matter of the leaf discs in successive intervals. Averages of blocked data of series: H₂O, +GA₃, + zeatin (exp. I)

Temperature treatment	Increase of fresh matter	cv. Roma				cv. Robin			
		intervals (days)				intervals (days)			
		0-2	2-4	4-6	total	0-2	2-4	4-6	total
Optimal	mg	33.3	11.0	8.5	52.8	24.0	9.8	11.6	45.4
	%	63	20	17	100	52	23	25	100
Stress	mg	36.1	0.7	7.2	44.0	50.9	4.0	7.7	62.6
	%	82.0	1.5	16.5	100	80	8	12	100

to zeatin (Fig. 1C, Table 2). High temperature pretreatment caused strong stimulation of disc growth in the first 2-day interval but depressed further increments in the H₂O and NOA series. Zeatin caused significant (Fig. 1D), stimulation of disc growth also after heat stress (Fig. 1D). The total increment in 6 days for data blocked from individual experimental series was much higher in discs of heated series, in sharp contrast to the results for Roma (Table 3).

The lower response of discs to the growth regulators added to the floating solution in the heated series may suggest that it is the result of changes in the hormone level (or balance) in plants; probably an increase in inhibitor content or reduced responsiveness to PGR immediately after stress.

Experiment II

The leaf discs were excised not only from plants untreated with PGR, but also from the NG-series. To have more detailed information concerning the dynamics of disc growth shortly after being cut, the fresh matter increment was measured at one-day intervals.

Roma leaf discs of the optimal series floated on water or zeatin solution increased their fresh matter with highest rate during the first day; further increases were the highest on GA_3 solution. Zeatin stimulated disc growth much less (Fig. 2A, Tables 2, 5).

In discs from plants untreated with PGR but stressed with one day of high temperature, stimulation of growth was observed in the first 2 days, as in exp. I, in the case of discs floated on water or zeatin solution, with even stronger stimulation on GA_3 solution (Fig. 2C). Higher growth activity was observed in the NG-series as compared with the PGR untreated optimal temperature series (Fig. 2A, B, Table 4). Stimulation of disc growth was observed in the solution with GA_3 (Table 2); it prolonged disc growth, both in optimal and heated plants (Fig. 2B and D). One of the reasons for the greater disc fresh matter increment under both of the conditions of the NG-series seems to be their higher content of sugars available for growth (see Fig. 4).

Robin discs had lower growth activity in all examined series (Fig. 3A-D, Tables 2, 4) but with much more uniform fresh matter increments in the particular intervals, especially in discs from plants untreated with PGR from both the optimal temperature and heated series (Table 5).

The stimulation of disc growth on GA_3 solution was observed in contrast to lack of such an effect by zeatin. Heat stress caused stimulation of fresh matter production in discs from PGR-untreated plants (Fig. 3A, C), in contrast to discs from the NG-series (Fig. 3B, D, Table 2). In the heated series, growth of NG-discs floated either on water or solution with zeatin was slightly depressed as compared with the control, heated series (Fig. 3C, D, Table 2), but with a strong stimulating effect of GA_3 .

THE DIURNAL PATTERN OF SUGAR AND STARCH CONTENTS IN TOMATO BLADES AS AFFECTED
BY HEAT STRESS AND GROWTH REGULATORS

Sugar and starch contents were estimated in discs cut from young, not fully expanded leaves, situated near the second cluster. Leaf discs were taken from the plants of three series (exp. II): untreated with PGR and treated with NG or ZNG. In each of these series the stressed discs were taken from the plants immediately after exposure for 14 hours to heat stress (38°C) during the day (evening samples) or after the 14 h of 38°C day and 10 h night at 25° (morning samples). Discs from the plants grown in optimal temperature were taken at the same time. (see: Material and Methods).

Fig. 2. Dynamics of disc growth of Roma cv. A, B — series from optimal temperature; C, D — series treated with heat stress. A, C — control series, not treated with PGR; B, D — series treated with $NOA + GA_3$ (Exp. II)

Table 4

Increase of fresh matter of the blades discs in successive intervals. Averages of blocked data of series: H_2O , $+GA_3$, $+zeatin$ (exp. II)

Cultivars	Temperature treatment	Increase of fresh matter	Control series intervals (days)				NG-series intervals (days)			
			0-1	1-2	2-3	total	0-1	1-2	2-3	total
Roma	optimal	mg	14.7	7.6	1.2	23.5	22.0	13.9	0	35.9
		%	73	32	5	100	61	39	0	100
	stress	mg	24.7	6.0	2.9	33.6	23.4	8.2	4.7	36.3
		%	73	18	9	100	64	23	13	100
Robin	optimal	mg	5.1	3.7	4.6	13.5	8.8	7.4	1.6	17.8
		%	38	28	34	100	49	42	9	100
	stress	mg	9.9	7.9	7.9	25.7	6.5	9.9	4.4	20.8
		%	38	31	31	100	31	48	21	100

Table 5

Analysis of variations (exp. I and II) (leaf disc growth)

Exp.	Cultivar	temp. (t)	time (T)	PGR	txT	txGR	TxGR	txTxPGR
I	Roma	2.4	97.2**	1.5	4.2*	<1	1.8	1.4
	Robin	13.6	156.9**	4.5*	46.6**	<1	3.2*	2.6*
II	Roma — not treated with NG	3.6	38.6**	5.4**	3.8*	<1	<1	1.6
	treated with NG	<1	46.3**	3.7*	<1	<1	3.5*	<1
	Robin — not treated with NG	8.5**	<1	5.6**	1.8	<1	1.7	1.1
	treated with NG	<1	5.2	2.9	1.2	<1	<1	<1

n.s. — not significant, * — significant at $\alpha = 0.05$, ** — significant at $\alpha = 0.01$

In cv. Roma, diurnal changes in sugar content were very pronounced in all cases. The nocturnal decreases in the optimal series constituted approximately 75 percent of the evening level as compared with a slightly lower decrease in the heated series (Fig. 4A, C).

The sugar content strongly increased in discs from PGR-treated plants, especially in the evening samples. This suggests the possibility of a higher rate of net photosynthesis and/or lower photorespiration. Heat stress diminished the above-described effect of growth regulators, but did not alter the sugar level in the control series.

Fig. 3. Dynamics of disc growth of Robin cv. A, B — series from optimal temperature; C, D — series treated with heat stress; A, C — control series, not treated with PGR; B, D — series treated with NOA + GA_3 (Exp. II)

Fig. 4. The changes in the sugar and starch contents in tomato blades (as percentage of d.m.) in the evening and morning: A, B — series from optimal temperature; C, D — series after heat stress; A, C — Roma cv.; B, D — Robin cv. Other explanations — as in Table 1

The starch built up throughout the day caused high accumulation of this compound in the evening samples of control and NG, optimal temperature series. At night, the starch level decreased strongly, except the ZNG series, where accumulation in the daytime was lower.

In the heated samples the relatively low starch level decreased in almost all cases. In the PGR-untreated series, starch was not mobilized during the night, in contrast to the NG-series — its content decreased to one-half and in ZNG — even to 34 percent. This means that in the ZNG series, where the evening level of starch was not affected by high temperature, its nocturnal remobilization even increased as compared with the optimal series (Fig. 4A, C).

The difference between the evening and morning content of sugars and starch may serve as some measure of the photosynthates exported from the blades. This estimate is obviously only approximate with the assumption of a similar respiration rate during the night as in daytime. Night export in the optimal series was strongly stimulated in both PGR-treated plants. Heat stress depressed it most drastically in the control series (Tables 6, 7) where export of carbohydrates was almost completely abolished.

In the Robin cv. optimal series there was only a tendency for a higher sugar content in the discs from the PGR-treated series. The response of the plants to high temperature was much lower with even some increase in the content of sugars in the PGR-untreated series. In all the cases, the sugar level decreased

Table 6

Night decrease of sugars (soluble in 80 per cent ethanol) and starch content expressed as mg per dry matter (exp. II)

Series	Temperature treatment	cv. Roma			cv. Robin		
		sugars	starch	sugars + starch	sugars	starch	sugars + starch
Control	optimal	65	46	111	86	94	180
	heat stress	45	+15	30	125	102	227
NG	optimal	212	35	247	112	117	229
	heat stress	135	24	159	105	39	144
ZNG	optimal	193	12	205	128	79	207
	heat stress	92	52	144	89	114	203

Table 7

Analysis of variations of sugar and starch content (exp. II)

Culti-var	Measurements (per g d.m.)	t	SP	PGR	txSP	txPGR	SPxPGR	SPtx PGR
Roma	sugars	14.3**	180.4**	32.7**	12.5**	3.2	12.4**	n.s.
	starch	35.4**	8.7**	3.7**	<1	9.7**	<1	3.3
Robin	sugars	<1	60**	<1	n.s.	n.s.	n.s.	n.s.
	starch	24**	55**	4.1*	n.s.	n.s.	n.s.	n.s.

t — temperature treatment (optimal and heat stress); SP — sampling period (evening and morning); PGR — plant growth regulators (NG = NOA + GA₃, ZNG = NOA + GA₃ + zeatin); n.s. — not significant; * — significant at $\alpha = 0.05$; ** — significant at $\alpha = 0.01$

during the night in a similar proportion; about 30 percent remained in the morning samples (Fig. 4B, D, Tables 6, 7).

In cv. Robin the starch content was also much more stable after the individual plant treatment, but in all the cases higher after heat stress. Night breakdown was in most cases very strong and dominated in the optimal series but gave a different response after heat stress. In the NG-stressed series, nocturnal decrease of the starch level diminished (Fig. 4D). This resulted in the heat stress depressing sugar + starch night mobilization only in the NG-series (Table 6).

DISCUSSION

Sink demand is one of the most important factors controlling starch and sugar accumulation in the blades (Halmer and Bewley 1982, Hammond and Burton 1983, Ho et al. 1983, Grange 1985a, b, Franceschi 1986,

Hewitt and Marrush 1986). Its amount is the result of starch formation and degradation and prevailing net photosynthesis rate over C-export from the leaves. Starch will tend to accumulate if export is depressed e.g. under stress conditions. Its content declines when export exceeds photosynthesis or when starch synthesis is abolished.

Heat stress decreases export of current photosynthates from the tomato blades and reduces the supply of carbon compounds to fruits (Starck and Cieřła 1989).

In the presented paper, higher fruit demand for photosynthates in PGR-treated plants affected the response of leaves to heat stress. Measurement of the diurnal pattern of sugars and starch in the blades at the end of the day and in the morning, allowed to calculate their night decrease. It was approximately the sum of export out of the blades, respiration loss and some metabolic incorporation. It was calculated on the basis of the respiration rate during 10 h of darkness, that in cv. Roma respiration loss (per g d.m.) is about 25 mg with rather small differences between experimental series (about 10 percent). Therefore night decrease of sugars + starch determined in Roma blades of heated plants seems to be nearly equal to respiration losses (Table 6).

High temperature decreased the carbohydrate content in the blades of Roma cv. probably owing to inhibition of photosynthesis. The diminished amount of starch content in the blades of heat stressed plants was also observed by Dinar and Rudich (1985) in sensitive cv. Roma and even more — in tolerant Saladetta cv. In contrast, in our experiments, the sugar content in the tolerant cv. Robin was much less affected and the starch level even slightly increased.

The decrease in the starch content of the blades of heated plants in the experiments of Dinar et al. (1983) was caused by strong inhibition of its synthesis, observed in both compared cultivars, but a decrease of its break-down (probably hydrolysis), was observed only in sensitive Roma plants.

In our previous experiments (data not published), ^{14}C -incorporation into the ethanol insoluble fraction (mainly starch) was also strongly depressed in the blades of both Roma and Robin plants after high temperature treatment, suggesting also inhibition of starch synthesis. Indirect information concerning starch degradation may be gained from its break-down at night, which was completely abolished by heat stress in PGR-untreated plants of heated Roma blades. In plants of this cultivar with enhanced sink demand lower transport inhibition was observed, as presented by Starck and Cieřła (1989), on the basis of data which concerned part of the same experiment.

In tolerant to high temperature Robin control plants, starch hydrolysis seems not to be affected by heat stress, supporting Dinar's et al. (1983) observations.

Special attention has to be paid to the Robin heated NG-series with drastically decreased night breakdown of starch, causing diminished export of photosynthates. In that case inhibition of α -amylase activity, may be postulated, as presented by Itai and Benzioni (1973b) who observed this in heated tobacco leaves, suggesting cytokinin limitation. In our previous experiments, heat stress inhibited supplying fruit with current photosynthates in Robin plants, in series with fruit growth stimulated by NOA + GA₃ (Starck and Cieřla 1989). A hypothesis was advanced that this may be a consequence of low cytokinin content (or activity), depressed both by high temperature and affected perhaps by GA₃, as postulated by Bender et al. (1986) in carrot and Nawata et al. (1985) in tomato. The low level of cytokinin in the blades of Robin plants of the NG-treated series is indirectly suggested by strong stimulation of leaf disc growth by zeatin (Fig. 1).

Relatively small changes in the rate of disc growth, respiration and chlorophyll contents, and the ratio of chlorophyll a/b, as response to heat stress of both cultivars suggest rather small injury of leaves. As Yordanov et al. (1986) reported, chlorophyll b is specially sensitive to high temperature.

In our previous experiments, stimulation of fruit growth by PGR was observed at the cost of vegetative organ growth (Starck et al. 1987), suggesting competition between them and generative organs for photosynthates (Starck et al. 1989). Therefore, measurement of leaf disc growth, after elimination of other organ effects, may answer if the potential growth activity of the blades, is similar in control and PGR-treated plants and if it is affected by the temperature stress.

Leaf disc growth of Robin control and NG-series was very similar in plants from optimal temperature conditions. Leaf discs of Roma cv. grew even more intensively as compared with control plants. It suggests, that leaf growth depression in the intact PGR-treated plants is an consequence of direct nutrient competition with fruits.

The 3-day cycle of high temperature (exp. I) caused, cessation of disc growth, after short-term stimulation, especially in Roma cv. The positive responses to GA₃ observed in both cultivars probably were due to stimulation of mitotic activity and cell elongation, as presented by Coleman and Greyson (1977) for tomato cortical parenchyma cells. On the other hand GA₃ may directly stimulated starch hydrolysis by its influence on α -amylase. Immediately after heat stress, the stimulation of disc growth by growth regulators added to the floating solution was completely abolished. It was probably owing to an alteration in their hormonal content and induction of ABA formation, (Itai et al. 1973a), and/or other inhibitors, abolishing the stimulating effect of GA₃ (or zeatin). Coleman and Greyson (1977) observed that ABA exogenously introduced to the floating solution diminished GA₃-induced growth stimulation of tomato leaf discs.

Less severe heat stress (one-day only, exp. II) did not only depress leaf disc growth but in some cases stimulated it, especially in Robin plants. Depression of disc fresh matter increment in the Robin, stressed NG-treated series, seems to be caused by inhibition of starch degradation (Fig. 4D) creating a deficiency of substances available for growth. This supposition may be confirmed by the fact that even in that case, GA₃-increased disc growth, as in other conditions, perhaps owing to its stimulating effect on α -amylase activity (or its synthesis).

The presented data support the previously proposed suggestion that at least sensitive cultivars of tomato plants, treated with plant growth regulators with strong sink demand are more tolerant to unfavourable environmental temperatures, at least concerning transport processes.

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Reakcja liřci pomidorów na przegrzanie w rořlinach przy zmienionym przez regulatory wzrostu stosunku akceptor-donor

Streszczenie

Reakcję pomidorów na krótkotrwały stres termiczny badano na 2 odmianach: wraźliwej Roma VF i odpornej – Robin, których wzrost owoców był stymulowany przez oprysk kwiatów regulatorami wzrostu: NOA + GA₃ (skrót NG), lub NOA + GA₃ + zeatyna (skrót ZNG). U obu odmian jednodobowy stres (38°/25°C dzień i noc) nie wpłynął istotnie ani na intensywność oddychania liřci, ani na zawartość i stosunek chlorofilu a/b. U odmiany Roma (nie traktowanej regulatorami wzrostu), po przegrzaniu, inhibicji syntezy skrobi w ciągu dnia towarzyszył silny spadek eksportu cukrowców z blaszek w nocy. U rořlin z kwiatami traktowanymi regulatorami wzrostu, u których aktywność owoców jako akceptorów wzrastała, po stresie termicznym nocny transport cukrowców był mniej ograniczony. Było to wynikiem intensywniejszej remobilizacji większej ilości produktów dziennej fotosyntezy. U odmiany Robin, odpornej na przegrzanie, wysoka temperatura w mniejszym stopniu wpływała na nocny eksport asymilatów z blaszki liřciowej, w serii nie traktowanej regulatorami wzrostu i w rořlinach traktowanych ZNG, przy zahamowaniu remobilizacji skrobi – w serii NG. Intensywność wzrostu blaszki liřciowej, jako reakcji na przegrzanie, określano mierząc dynamikę przyrostu dysków wycinanych z liřci. Taki pomiar eliminował bezpośredni wpływ owoców (akceptorów) na wzrost donorów asymilatów. U obu odmian jednodobowy stres termiczny wpłynął nawet stymulująco na wzrost dysków wycinanych z rořlin nie traktowanych regulatorami wzrostu, natomiast 3-dobowy spowodował zahamowanie ich wzrostu po krótkotrwałej, nieznacznej stymulacji co silniej wyraziło się u odmiany Roma. Ponadto bezpośrednio po 3-dobowym przegrzaniu stwierdzono obniżoną stymulację wzrostu, indukowaną u rořlin z warunków optymalnej temperatury przez GA₃ i zeatynę.

Dyski liřciowe odmiany Roma wycięte z serii rořlin traktowanych NG wykazywały nieco większą aktywność wzrostową w porównaniu z dyskami z rořlin nie traktowanych regulatorami wzrostu, szczególnie w serii z optymalnych warunków termicznych, co wydaje się być konsekwencją wyższej zawartości w nich cukrów. Giberelina stymulowała ich wzrost. U odmiany Robin wzrost dysków pochodzących z rořlin traktowanych NG przebiegał podobnie, jak w seriach kontrolnych u rořlin z warunków optymalnej temperatury, lecz był hamowany przez stres termiczny, co może wynikać z zahamowanego rozkładu skrobi w nocy, zmniejszającego pulę cukrów. W tych warunkach GA₃ stymulowała wzrost dysków, być może poprzez wpływ na α -amylazę.