Plant Physiol. (1995) 109: 637–643

Effect of High Temperature on Plant Growth and Carbohydrate Metabolism in Potato

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This study was undertaken to determine the role of sucrose-metabolizing enzymes in altered carbohydrate partitioning caused by heat stress. Potato (*Solanum tuberosum* L.) genotypes characterized as susceptible and tolerant to heat stress were grown at 19/17°C, and a subset was transferred to 31/29°C. Data were obtained for plant growth and photosynthesis. Enzyme activity was determined for sucrose-6-phosphate synthase (SPS) in mature leaves and for sucrose synthase, ADP-glucose pyrophosphorylase, and UDP-glucose pyrophosphorylase in developing tubers of plants. High temperatures reduced growth of tubers more than of shoots. Photosynthetic rates were unaffected or increased slightly at the higher temperature. Heat stress increased accumulation of foliar sucrose and decreased starch accumulation in mature leaves but did not affect glucose. SPS activity increased significantly in mature leaves of plants subjected to high temperature. Changes in SPS activity were probably not due to altered enzyme kinetics. The activity of sucrose synthase and ADP-glucose pyrophosphorylase was reduced in tubers, albeit less quickly than leaf SPS activity. There was no interaction of temperature and genotype with regard to the enzymes examined; therefore, observed differences do not account for differences between genotypes in heat susceptibility.

Suc is the main form of translocated sugar in most plants. Its synthesis is catalyzed by SPS and Suc-6-P and its degradation is catalyzed by SS or invertase (Preiss, 1982). A major control point for the partitioning of photosynthate between Suc and starch in the leaves is SPS (Huber, 1983; Huber et al., 1984; Kalt-Torres et al., 1987; Huber and Huber, 1992). This postulate was confirmed when overexpression of maize SPS in tomato leaves was shown to increase foliar Suc concentration but reduce starch (Worrell et al., 1991; Galtier et al., 1993). Some species, such as soybean, have been reported to have endogenous rhythms of SPS activity (Kerr et al., 1985), whereas the enzyme appears to respond directly to the light cycle in other species (Kalt-Torres et al., 1987).

Environmental factors such as water stress and temperature influence SPS activity. SPS activity in mature leaves was reduced in plants subjected to water stress (Vassey and Sharkey, 1989; Vassey et al., 1991; Castrillo, 1992). This decrease in SPS activity was attributed to inhibition of photosynthesis as a result of stomatal closure (Vassey et al., 1991). However, pigeonpea and soybean plants exposed to water stress had increased SPS activity (Cheikh and Brenner, 1992; Keller and Ludlow, 1993). Soybean leaves had lower SPS activity under cool conditions (18/14°C) than under warm conditions (26/22°C; Rufty et al., 1985). Spinach plants acclimated to cold temperature (10°C) had higher SPS activity than plants grown at 24°C (Holaday et al., 1992). Khayat and Zieslin (1987) exposed rose plants to 12 and 18°C night temperatures and found higher SPS activity in shoots exposed to the higher night temperature.

SS is considered the main catalytic enzyme for Suc cleavage in many tissues, and its activity can be used as a biochemical marker for sink strength in plants (Sung et al., 1989; Xu et al., 1989). Growing tubers have high activity of SS and AGPase that declines as tubers mature (Pressey, 1969; Sowokinos, 1976).

Heat stress alters carbohydrate partitioning in potato (*Solanum tuberosum* L.) plants from tubers to shoots and reduces overall plant yield (Borah and Milthorpe, 1962; Ewing, 1981; Wolf et al., 1990). The role of enzymes that control Suc metabolism in potato plants under heat stress has not been well characterized. This study was conducted to investigate the relationship between activity of enzymes involved in Suc metabolism to source-sink relationships of heat-stressed potato plants. Genotypes reported as heat tolerant and heat susceptible (Wolf et al., 1990) were included in this study to ascertain whether observed changes in enzyme activity were associated with susceptibility to heat stress. In a subsequent paper we will discuss the effects of heat stress on other enzymes of carbohydrate metabolism in developing shoots.

MATERIALS AND METHODS

Plant Material and Sampling

Source plants of two potato (*Solanum tuberosum* L.) cultivars, Norchip and Up-to-Date, were micropropagated from nodal cuttings and transferred to a peat-vermiculite soil mixture in 15-cm pots. Plants were kept at 19/17°C, day/night, and a 14-h photoperiod in controlled environment chambers that provided 475 μmol photons m^{-2} s^{-1} PPFD. There were four replications of two plants per cultivar in each experiment; plants were randomized in a complete block design. The microcomputer package MSTAT (Michigan State University, East Lansing) was utilized for statistical analysis.

Temperature treatments in experiment 1 were imposed when plants had approximately eight leaves and a total

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Abbreviations: AGPase, ADP-Glc pyrophosphorylase; SPS, Suc-6-P synthase; SS, Suc synthase; UGPase, UDP-Glc pyrophosphorylase.

mass of approximately 30 g fresh weight plant^{-1}. At this time, half of the plants (eight plants of each cultivar) were subjected to high temperaure (31/29°C day/night) in an identical growth chamber. The second experiment was conducted in the same chambers and utilized the same type of experimental design, but temperature treatments were imposed after tubers were initiated and had grown to approximately 30 g plant^{-1}. The high temperature in experiment 2 was 29/27°C (day/night). RH in the warm chamber was adjusted to maintain a similar vapor pressure deficit in both treatments. It was not possible to maintain this humidity during gas-exchange measurements in the reach-in chambers. Gas-exchange measurements were determined for the most recently matured leaves with a Li-Cor (Lincoln, NE) 6200 instrument. Recently matured leaves were defined as the most recently fully expanded leaves, typically the sixth and seventh leaf (>25 mm) from the apex. At the indicated harvest date, plants were divided into leaves, stems, and stolons and tubers for determination of fresh and dry weights.

Activity of SPS in recently matured leaves was determined after 3 d of heat treatment. Activity of SS, AGPase, and UGPase was determined in growing tubers after 3 and 14 d. Samples consisted of 12 to 14 leaf discs of 9.0 mm diameter for mature leaves and 0.6 g of tissue for tubers. Each replicate sample was a composite sample of tissue from at least two leaves or tubers from each of two plants. Samples for carbohydrate analysis were taken at the end of the light period (PM) and at the end of the dark period (AM) after 3 and 8 d of heat treatment. Samples for determination of enzyme activity were taken 4 h after the beginning of the photoperiod. Samples for carbohydrates and enzyme assay were frozen immediately in liquid nitrogen and kept at −80°C until assayed.

Enzyme Extraction and Assay

Crude enzyme extracts were prepared by homogenizing frozen plant tissue in 3.0 mL of extraction buffer containing 50 mM Mops-NaOH buffer (pH 7.5), 10 mM $MgSO_4$, 0.1 M Cys, and 2% polyvinylpolypyrrolidone. The homogenate was strained through Miracloth (Calbiochem) before centrifugation at 20,000*g* for 15 min. The supernatant was desalted through a minicolumn packed with Sephadex G-50. Extraction steps were conducted over ice in a cold room (2°C).

SPS (EC 2.4.1.14) activity was assayed as described by Huber et al. (1989) with some modifications. The reaction mixture for the saturated substrate assay (V_{max}) contained 50 mM Mops-NaOH buffer (pH 7.5), 15 mM $MgSO_4$, 10 mM UDP-Glc, 40 mM Glc-6-P, 10 mM Fru-6-P, and 50 μL of enzyme extract in a total volume of 75 μL. Conditions for the SPS assay with limiting substrate were the same as for the V_{max} assay, except Glc-6-P and Fru-6-P were 12 and 3 mM, respectively, and 10 mM of Pi was added for this assay (Huber et al., 1989). The reaction mixture was incubated at 25°C for 15 min and terminated by adding 75 μL of 30% KOH. Samples were boiled for 10 min to destroy residual hexoses. Suc formed by the reaction was determined by the anthrone method (Van Handel, 1968).

SS (EC 2.4.1.13) activity was assayed in the direction of Suc synthesis (Miron and Schaffer, 1991), as optimized for potato in our laboratory. The reaction mixture contained 50 mM Mops-NaOH (pH 7.5), 15 mM $MgSO_4$, 25 mM UDP-Glc, 25 mM Fru, and 50 μL of enzyme extract in a total volume of 75 μL. The reaction mixture was incubated at 37°C for 30 min and terminated by adding 75 μL of 30% KOH. Samples were boiled for 10 min to destroy residual hexoses, and released Suc was determined as described above. The reaction mixture for AGPase (EC 2.7.7.27) contained 80 mM glycylglycine (pH 7.5), 5 mM $MgCl_2$, 0.6 mM NADP, 2 mM 3-phosphoglycerate, 20 mM Cys, 0.75 unit phosphoglucomutase, 1 mM ADP-Glc, 0.02 mM Glc-1,6-bisP, 0.75 unit Glc-6-P dehydrogenase, 2.5 mM PPi, 0.15 mg BSA, and diluted enzyme extract in a total volume of 750 μL (Sowokinos, 1976). The production of NADPH was monitored continuously at 340 nm at 25°C with a Beckman DU-640 spectrophotometer. The reaction mixture for UGPase (EC 2.7.7.9) was similar to the AGPase assay, except the pH was 8.5, UDP-Glc was substituted for ADP-Glc, and 3-phosphoglycerate and BSA were omitted.

Carbohydrate Extraction and Assay

Sugars and starch were extracted and analyzed by a method modified from that of Ou-Lee and Setter (1985). Lyophilized leaf samples were extracted with 80% ethanol for 48 h at 25°C. Glc was determined colorimetrically in a Glc oxidase-coupled reaction. The reagent contained 1 mM aminoantipyrine, 44 mM *p*-hydroxybenzoic acid, 7 units/mL Glc oxidase, and 0.5 unit/mL peroxidase in 100 mM phosphate buffer (pH 7.0). The A_{490} was measured in a total volume of 180 μL in a microplate reader. Suc was determined as Glc released following hydrolysis with invertase (10 units/mL in 100 mM acetate buffer, pH 4.5) for 1 h at 40°C. Starch was determined from the insoluble residue after ethanol extraction. The residue was dried and rehydrated in 1.0 mL of water and heated at 90°C for 1 h to gelatinize starch. Starch samples were incubated with 1 mL of amyloglucosidase solution (10 units/mL, 20 mM NaF, 100 mM acetate buffer, pH 4.5) for 48 h at 40°C. The Glc released from starch was determined as described above.

RESULTS

Plant growth was reduced at the high temperature. Tuber growth was more affected than shoot growth. This was particularly evident in experiment 1 (Table I), in which tuber initiation had just started at the time plants were separated into different temperature regimes. Total dry mass was reduced 44% in cv Norchip and 72% in cv Up-to-Date. Plants in the warmer regime were significantly taller (Table I). In experiment 2, total dry weights after 2 weeks of heat treatment were reduced by 24% for cv Norchip and by 29% for cv Up-to-Date subjected to high temperatures (Table II).

The transfer of plants from 19/17 to 31/29°C had no immediate effect on photosynthesis, although recorded transpiration rates were increased at the higher temperature (Table III). However, after 8 d, plants in the warmer

Table I. *Growth parameters of potato plants after 4 weeks of heat treatment in experiment 1*

Different temperature treatments were imposed at the time of tuber initiation. Values are means ± SE.

Tissue	Cultivar	Temp	Wt					Plant Height
			Leaf	Stem	Shoot	Tuber	Total	
		°C			g/plant			cm
Fresh	Norchip	19/17	169 ± 3	75 ± 3	244 ± 6	134 ± 3	378 ± 4	35 ± 1
		31/29	135 ± 3	118 ± 3	253 ± 4	5 ± 3	258 ± 4	45 ± 2
	Up-to-Date	19/17	157 ± 11	41 ± 7	197 ± 17	131 ± 14	328 ± 13	42 ± 1
		31/29	49 ± 3	47 ± 1	96 ± 2	0.6 ± 0.6	96 ± 3	57 ± 0.5
Dry	Norchip	19/17	13.7 ± 0.3	4.5 ± 0.3	18.2 ± 0.5	19.4 ± 0.8	37.7 ± 0.9	
		31/29	13.4 ± 0.2	7.6 ± 0.3	21.0 ± 0.5	0.3 ± 0.1	21.3 ± 0.5	
	Up-to-Date	19/17	14.2 ± 0.9	3.4 ± 0.4	17.6 ± 1.3	19.7 ± 2.6	37.3 ± 2.0	
		31/29	6.3 ± 0.3	4.2 ± 0.1	10.5 ± 0.3	0.03 ± 0.03	10.5 ± 0.3	

chamber had significantly higher rates of photosynthesis than the control plants. This relationship was still apparent after 21 d, at which time respiration rates were lower at the higher temperature (data not presented). The change in photosynthetic rates was not due to a reduction in specific leaf area, which changed much less than the change in photosynthesis (data not presented). Leaf expansion was affected by temperature; leaves at the higher temperature were smaller than control leaves (data not shown).

Temperature had little effect on Glc levels of mature leaves after 3 or 8 days (Table IV). Leaves from the high-temperature treatment had elevated levels of Suc at the end of the photoperiod compared to leaves from the cool treatment, whereas starch levels were reduced in the leaves from the warm treatment. This was true of both Norchip and Up-to-Date. At the end of the dark period, Suc content was similar for leaves from both temperature treatments, whereas starch levels were greatly reduced at high temperature. Therefore, foliar starch accumulation was reduced at high temperature in mature leaves.

Exposure to 31/29°C for 3 d resulted in increased SPS activity in mature leaves when assayed with saturating levels of substrate (Fig. 1). The temperature × cultivar interaction was not significant at $P \leq 0.05$, but SPS activity at high temperature was 48 and 24% higher than at the normal temperature in Norchip and Up-to-Date, respectively. A similar increase in activity was observed in both cultivars when assayed with limiting substrate and Pi (Fig. 1).

Activity of tuber enzymes was reduced by the elevated temperature (Table V). Activity of SS was reduced 59% in cv Norchip and 72% in cv Up-to-Date after 2 weeks of treatment (Table V). Activity of AGPase was reduced approximately 25% in both cultivars. Activity of UGPase was much higher than that of SS or AGPase and was not affected by temperature. There was no difference in activity of AGPase, SS, or UGPase between the two temperatures after 3 d of treatment (data not presented). Total invertase activity was less than 10% of SS activity and was not significantly affected by temperature (data not presented).

DISCUSSION

The two potato cultivars, Norchip and Up-to-Date, were selected for this study because of their sensitivity to high-temperature stress (Wolf et al., 1990). Norchip was less sensitive to heat stress than was Up-to-Date. Plant growth was severely affected by the warmer temperature in both cultivars, but as has been previously reported (Wolf et al., 1990), accumulation of dry mass was affected more for cv Up-to-Date than for cv Norchip (Tables I and II). Tuber growth was reduced under high temperatures in both cultivars. As has been observed by numerous other authors, leaves were smaller and internodes were longer at the warmer temperature.

Photosynthetic rates of newly matured leaves were not inhibited by the higher temperature during the observed interval but were higher on a per unit leaf area basis than

Table II. *Growth parameters of potato plants after 2 weeks of heat treatment in experiment 2*

Different temperature treatments were imposed approximately 10 d after tuber initiation. Values are means ± SE.

Parameter	Cultivar	Temp	Leaf	Stem	Shoot	Tuber	Total
		°C			g		
Fresh wt	Norchip	19/17	174.8 ± 8.4	47.2 ± 2.5	222.0 ± 7.2	118.5 ± 10.4	340.5 ± 12.2
		29/27	143.9 ± 6.4	55.6 ± 7.8	199.4 ± 12.7	63.3 ± 8.0	262.7 ± 9.3
	Up-to-Date	19/17	146.5 ± 4.4	52.2 ± 3.8	198.7 ± 7.2	62.7 ± 5.4	261.4 ± 7.4
		29/27	95.4 ± 6.7	26.2 ± 2.2	121.5 ± 8.2	38.1 ± 18.2	159.6 ± 11.6
Dry wt	Norchip	19/17	11.8 ± 0.8	2.4 ± 0.2	14.2 ± 0.6	16.3 ± 1.3	30.5 ± 1.1
		29/27	10.9 ± 0.3	3.2 ± 0.3	14.1 ± 0.5	9.0 ± 1.5	23.2 ± 1.4
	Up-to-Date	19/17	11.9 ± 0.5	3.2 ± 0.2	15.1 ± 0.7	8.3 ± 0.7	23.4 ± 0.9
		29/27	9.3 ± 0.4	2.0 ± 0.1	11.3 ± 0.5	5.3 ± 2.7	16.6 ± 2.3

Table III. *Effect of temperature on leaf photosynthesis and transpiration of potato plants in experiment 1*
Values are means ± SE.

Cultivar	Temp	Photosynthesis		Transpiration	
		3	8	3	8
	°C	μmol m^{-2} s^{-1}		mmol m^{-2} s^{-1}	
Norchip	19/17	10.8 ± 1.7	9.5 ± 1.0	1.7 ± 0.3	1.5 ± 0.1
	31/29	11.2 ± 0.4	14.4 ± 0.2	8.8 ± 0.4	8.8 ± 0.5
Up-to-Date	19/17	12.3 ± 0.2	10.7 ± 0.7	2.3 ± 0.3	2.0 ± 0.2
	31/29	10.7 ± 1.1	14.6 ± 0.2	9.9 ± 0.9	9.7 ± 1.0

photosynthetic rates of equivalent leaves on control plants. Although leaves of heat-stressed plants were smaller, the increase in photosynthetic rates was not related to a change in specific leaf area. Chl concentration was not determined, nor were the photosynthetic rates of older leaves.

The increase in foliar SPS activity at higher temperature (Fig. 1) is similar to that observed by Rufty et al. (1985), who found higher SPS activity in soybean plants acclimated to 26/22°C than in plants acclimated to 18/14°C. The increase in SPS activity in source leaves of potato plants transferred to high temperature coincided with altered carbohydrate-partitioning patterns at the whole-plant level. As has been reported in other studies (Ewing, 1981; Wolf et al., 1991), partitioning to tubers was reduced relative to shoots. The changes in SPS activity at high temperature in this experiment were coordinated with changes in enzymes of carbohydrate metabolism in young, growing tissues that were associated with increased partitioning to young leaves and stems (J.H. Lorenzen and A.M. Lafta, unpublished data).

The comparison of SPS activity under saturated and limiting conditions would be expected to show changes in the activation level of this enzyme (Stitt et al., 1988; Huber et al., 1989). Such changes were not observed in our study. The increase in SPS activity in mature potato leaves at high temperature is more likely due to an increase in the amount of the enzyme rather than to altered kinetic properties of pre-existing SPS molecules. Covalent modification of SPS has been reported in some plant species in response to light (Huber et al., 1989). During ripening of bananas, the kinetic properties of SPS were changed (Hubbard et al., 1990). Changes in SPS activity of potato leaves at high temperature in the present study were apparently not related to covalent modification of SPS protein, since increases in SPS activity at high temperature were similar in both saturating- and limiting-substrate assays. Western blots also showed a small increase in SPS antigen at the warmer temperature (data not shown). Guy et al. (1992) observed that increased SPS activity in cold-acclimated spinach was associated with an increase in SPS protein.

Water stress can affect foliar SPS activity (Quick et al., 1989; Vassey et al., 1991). In the present experiments, RH was maintained to keep a similar vapor-pressure deficit in both chambers. Plants were watered frequently to minimize water stress. Therefore, it is likely that the observed difference in SPS activity was related to the elevated temperature and were not related to water stress.

Accumulation of starch in recently matured leaves was reduced at the higher temperature (Table IV). Similar reductions in foliar starch have been reported for mature leaves of plants subjected to water stress (Huber et al., 1984; Zrenner and Stitt, 1991; Keller and Ludlow, 1993).

Table IV. *Effect of temperature on carbohydrate levels in recently matured potato leaves in experiment 1*
Values are means ± SE.

Carbohydrate	Cultivar	Temp	3 d		8 d	
			PM	AM	PM	AM
		°C				
Glc (mg g^{-1} dry wt)	Norchip	19/17	3.3 ± 0.2	2.8 ± 0.1	5.2 ± 0.9	3.8 ± 0.3
		31/29	5.3 ± 1.1	2.5 ± 0.0	6.2 ± 0.9	3.0 ± 0.1
	Up-to-Date	19/17	3.0 ± 0.1	2.9 ± 0.3	3.5 ± 0.0	2.9 ± 0.2
		31/29	4.2 ± 0.2	2.6 ± 0.2	6.2 ± 0.6	3.1 ± 0.7
Suc (mg g^{-1} dry wt)	Norchip	19/17	10.6 ± 0.1	6.4 ± 0.8	10.1 ± 1.0	3.4 ± 0.2
		31/29	13.1 ± 1.4	3.8 ± 1.0	17.6 ± 0.9	4.8 ± 0.6
	Up-to-Date	19/17	9.8 ± 0.3	5.2 ± 0.8	12.5 ± 0.8	4.6 ± 0.3
		31/29	12.9 ± 1.3	3.6 ± 0.3	17.0 ± 1.2	4.5 ± 0.9
Starch (mg Glc g^{-1} dry wt)	Norchip	19/17	294 ± 2	195 ± 9	290 ± 9	180 ± 12
		31/29	202 ± 14	92 ± 9	129 ± 2	72 ± 3
	Up-to-Date	19/17	222 ± 32	117 ± 19	242 ± 14	126 ± 17
		31/29	168 ± 16	64 ± 1	99 ± 12	50 ± 6

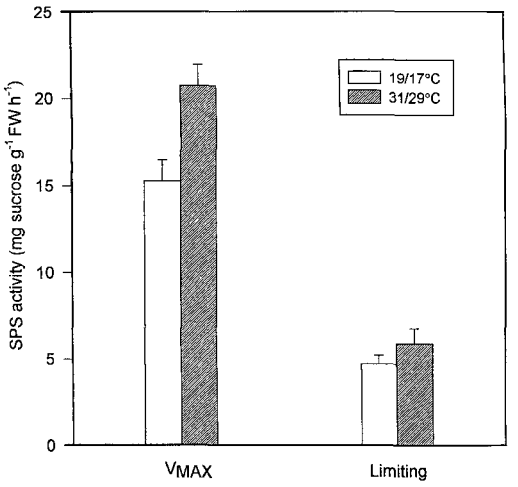

Figure 1. Effect of temperature on SPS activity in mature leaves of cv Norchip and cv Up-to-Date after 3 d of temperature treatment in experiment 1. The temperature in the cool treatment was 19/17°C and the temperature in the warm treatment was 31/29°C. Enzyme activity was assayed with V_{max} and limiting-substrate conditions as described in "Materials and Methods." The temperature difference was statistically significant for both assays. There was no temperature × genotype interaction. Each data point represents the mean of eight composite samples from each of the cultivars. FW, Fresh weight. Error bars indicate SE.

The decrease in starch and the increase in Suc levels at high temperature in the present study coincided with an increase in SPS activity. The results support a significant role of SPS in stimulating the pathway of Suc synthesis at high temperature and diverting current photosynthate from foliar starch to Suc in mature leaves of potato plants.

Maximal SPS levels were similar in the two genotypes, although Norchip had more SPS activity than Up-to-Date in the limiting assay. The trend is similar to that observed by Basu and Minhas (1991), who reported that "heat-tolerant" potato cultivars had more SPS activity than "heat-susceptible" genotypes. However, it is difficult to make a comparison with that study, since their tolerant group was composed of potato genotypes adapted to long days, whereas the susceptible group was composed of genotypes adapted to SD, winter production in the plains of India.

SPS activity is often higher under conditions of greater sink strength (Claussen and Lenz, 1983; Rufty and Huber, 1983). However, the conditions in this study that promoted SPS activity would be expected to reduce biomass accumulation in potato (Ewing, 1981; Ben Khedhar and Ewing, 1985). In fact, overall plant biomass accumulation was reduced in the high-temperature treatment (Tables I and II). Therefore, as was the case with photoperiod in other experiments (J.H. Lorenzen and E.E. Ewing, unpublished data), conditions that promoted SPS activity in potato leaves led to reduced overall sink strength in potato, as indicated by a reduction in growth before photosynthesis was affected. The coordinate control of diurnal starch accumulation in potato leaves appears to be related to propensity to tuberize and partition biomass to potato tubers. Tubers have been reported to be a strong sink that stimulates photosynthesis and biomass accumulation (Moorby, 1968; Oparka et al., 1987).

Overexpression of maize SPS in tomato leaves resulted in altered partitioning and an increased shoot:root ratio (Galtier et al., 1993). In that study, SPS activity was also elevated in root tissue, and interpretation of the relative impact of foliar versus root SPS on whole-plant partitioning was somewhat ambiguous. In the present study, SPS activity of tubers was slightly reduced at the higher temperature treatment (data not presented); therefore, elevated SPS activity in that sink was not a factor. Since Suc is implicated in controlling the expression of several tuber-specific genes in potato (Wenzler et al., 1989; Müller-Röber et al., 1990), it is intriguing to speculate that leaf starch metabolism may be involved in controlling whole-plant partitioning and that night export of foliar carbohydrates may be preferentially directed to roots and tubers.

Both SS and AGPase have been shown to be important enzymes that are associated with tuber growth and starch synthesis. The activity of both enzymes declines as tubers mature (Pressey, 1969; Sowokinos, 1976). Detachment of growing tubers reduces activity of SS and AGPase (Oparka et al., 1990; Geigenberger et al., 1994). Transgenic mutants with tuber-specific expression of an AGPase clone insensitive to allosteric regulation accumulate more tuber starch (Stark et al., 1992). The activity of SS was approximately equivalent to AGPase in the present study, but SS activity was more temperature sensitive than was AGPase (Table V). Activity of SS in tubers of cv Up-to-Date was affected more by heat stress (72% reduction) than was SS activity in cv Norchip (59% reduction). The reduction in tuber growth was greater under heat stress in cv Up-to-Date than in cv Norchip (Table II), as would be predicted by earlier studies (Wolf et al., 1990). Therefore, although AGPase activity has been previously shown to be reduced by heat stress (Krauss and Marschner, 1984), reduction in SS may be more important in determining import of Suc under these conditions. Sugar levels in potato tubers were not affected by temperature in these experiments (data not shown), which

Table V. *Enzyme activity of potato tubers after 2 weeks of heat treatment in experiment 2*

Different temperature treatments were imposed approximately 10 d after tuber initiation. Values are means ± SE.

Cultivar	Temp	SS	AGPase	UGPase
	°C	mg g^{-1} h^{-1}	μmol g^{-1} min^{-1}	μmol g^{-1} min^{-1}
Norchip	19/17	33.4 ± 11.9	1.20 ± 0.11	40.2 ± 5.1
	29/27	13.7 ± 3.8	0.93 ± 0.05	39.9 ± 5.2
Up-to-Date	19/17	15.0 ± 4.2	1.17 ± 0.12	27.8 ± 3.1
	29/27	4.2 ± 2.3	0.84 ± 0.08	24.4 ± 3.1

likely indicates coordinate control of sugar metabolism under stress.

The lack of a significant temperature × cultivar interaction for the enzymes investigated suggests that these enzymes do not have a significant involvement in the difference between these cultivars with respect to susceptibility to heat stress.

In summary, we observed an increase in foliar SPS activity in source leaves of potato subjected to heat stress. The changes in SPS activity in source leaves preceded a reduction in activity of SS and AGPase in tubers. Associated with the increase in SPS activity was an increase in foliar Suc and decrease in foliar starch under high temperature in source leaves. This supports a physiological role of SPS in potato leaves with respect to diurnal partitioning of current photosynthate to Suc at high temperature. In light of the sugar-responsive nature of several enzymes related to development, it remains to be determined whether increased foliar partitioning to Suc under heat stress is involved in signal transduction or is merely coordinately regulated with other changes in whole-plant partitioning.

Received April 27, 1995; accepted June 26, 1995.

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