Effect of Heat Stress on Enzymes that Affect Sucrose Levels in Potato Shoots

James H. Lorenzen1 and Abbas M. Lafta
Department of Plant Sciences, North Dakota State University, Fargo, ND 58105

Abstract. Potato (Solanum tuberosum L.) responds to heat stress with a shift in partitioning from tubers to shoots. Enzymes responsible for sucrolysis previously have been used as indicators of sink strength and are likely involved in controlling flow of carbon into developing organs. Changes in activity of enzymes involved in sucrose metabolism were investigated in shoots of two potato cultivars that previously were characterized as susceptible and tolerant to heat stress. Enzyme activity of sucrose synthase (SS) and invertases was determined for mature leaves, young leaves, and stems of plants adapted to 21/19 °C, or after transferring plants to 29/27 °C for 3 days. High temperatures resulted in a nonsignificant increase in activities of SS, acid, and neutral invertase in young growing leaves but not in stems or mature leaves. The combined activity of the two invertases was =40 times higher than SS activity in young leaves. There was no temperature × genotype interaction with regard to these enzymes in the tissues investigated. A previously reported increase in activity of sucro-phosphate synthase in mature leaves of plants subjected to high temperature was reversed after these plants were returned to a normal growing temperature.

Previousy, we reported that elevated temperature increased SPS activity of source leaves and decreased the activity of SS and ADPglc pyrophosphorylase in tubers (Lafta and Lorenzen, 1995). This study was conducted to investigate the effect of heat stress on enzyme activity related to sucrose metabolism of potato shoots and its role in source-sink relationships. Genotypes reported as heat tolerant and heat susceptible (Wolf et al., 1990a) were included in this study to ascertain whether changes observed in enzyme activity were associated with altered partitioning and susceptibility to heat stress.

Materials and Methods

Plant materials. Plants were micropropagated from single-node cuttings. Three-week-old cuttings were transferred to 2.3-L pots filled with peat-vermiculite soil mix (Sunshine Mix no. 1, Fisons Horticulture, Bellevue, Wash.). Plants were watered daily or as needed with a solution containing 15N–7P–14K at 1 g L–1. Plants were kept at a 14-h photoperiod and 21 °C light/19 °C dark in two controlled environment chambers (model PT80; Percival Manufacturing, Boone, Iowa) that provided 475 µmol m–2 s–1 of photons of photosynthetically active radiation at canopy level.

Two potato cultivars (‘Norchip’ and ‘Up-to-Date’) were included in Expt. 1. Plants were maintained at 21/19 °C until there were 10 to 12 leaves ≥3 cm long (about 5 weeks). These plants had initiated tubers, the largest of which were 1.5 cm in diameter. At this time, the temperature of one of the chambers was raised to 29/27 °C for 3 d. Relative humidity was kept at 50% in the 21/19 °C chamber and at 70% in the 29/27 °C chamber to give similar vapor pressure deficits for plants in both chambers. Plants were watered twice daily in the 29/27 °C chamber. Sampling for determination of invertases and SS in Expt. 1 was conducted on day 3 after initiation of treatment as follows. About 3 h after initiating the light period, samples for enzyme assays were collected and immediately frozen in N2(l) and stored at −70 °C until extraction. Tissue samples consisted of 12 to 14 leaf disks (9.0 mm in diameter) for mature leaves (≈0.3 g) and an equivalent weight of fresh tissue for young leaves and stems. There were two repetitions of this experiment, and each repetition had two block replications of two plants of each cultivar for each chamber. Temperature was randomly controlled.

Potato is a highly productive crop plant with a high nutritional value. It is a cool-season crop, with optimum productivity at =18 to 20 °C, declining with increasing temperatures. High temperature stress (HTS) reduces total dry-matter accumulation in potatoes and diverts photosynthate from tubers to shoots, especially stems (Borah and Milthorpe, 1962; Ewing, 1981). Neither response has been caused by a reduction in photosynthetic rates (Dwelle et al., 1981, Wolf et al., 1990b). Potato cultivars differ in heat tolerance with respect to yield (Ben-Khedher and Ewing, 1985; Levy, 1978). Although high temperatures in the tuber zone may restrict tuber development (Krauss and Marschner, 1984; Reynolds and Ewing, 1989), air temperature had a greater effect than either root or stolon temperature in increasing number of leaves and dry-matter yield of leaves and stems (Struik et al., 1989a) and reducing partitioning to tubers (Struik et al., 1989b).

Buds of plants exposed to high temperatures had elevated levels of gibberellin-like activity, which was postulated to reduce translocation of photosynthate to the tuber sink (Menzel, 1983). Therefore, shoots are important in determining the effects of HTS.

Sucrose is the principal form of translocated sugar in most plant species, including potato. Its synthesis is catalyzed by sucro-phosphate synthase (SPS), and its degradation is catalyzed by sucrose synthase (SS) or invertase (Preiss, 1982). The partitioning of photosynthate between sucrose and starch in leaves is controlled largely by SPS (Huber and Israel, 1982). Several enzymes have been correlated with sink strength. Invertase and SS are the enzymes that cleave sucrose to make its entry into growth and storage processes possible. SS has been associated with actively growing tissue in leaves and fruit of Solanum melongena L. (Claussen, 1983), the expansion zones of leaves of widely diverse species (Claussen et al., 1985), and generally in growing tissue of plants (Sung et al., 1989). Sucrose synthase is closely associated with sink strength of potato tubers (Sung et al., 1989; Zrenner et al., 1995).

Received for publication 2 Jan. 1996. Accepted for publication 17 June 1996. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

1To whom requests for reprints should be addressed.
assigned to chamber each repetition; plants within a chamber were randomly assigned position within the respective blocks. Data analysis was via PROC GLM (SAS Institute, Cary, N.C.); the term repetition × temperature was used as the error term to determine the significance of temperature.

Experiment 2 was conducted with ‘Up-to-Date’ to determine whether the previously reported HTS-induced increase in SPS activity was reversible. When plants had 10 to 12 leaves, the temperature of one chamber was raised to 29 °C light/27 °C dark, while the other chamber was maintained at 21/19 °C. After 6 d, half the plants in each chamber were switched to the opposite chamber. Leaf disk samples for determination of SPS activity were collected from two recently matured leaves per sample as previously described on days 3, 6, and 9 from the initial imposition of HTS. There were four replications of four plants per initial treatment in this experiment; plants were randomized in a complete-block design. For statistical analysis, we used the microcomputer package MSTAT (Michigan State Univ., East Lansing).

**Enzyme extraction and assay.** Crude enzyme extracts were prepared by homogenizing frozen samples in 3.0 mL of extraction buffer containing 50 mM Mops-NaOH buffer (pH 7.5), 10 mM MgSO₄, 100 mM cysteine, and 2% polyvinylpolypyrrolidone. The homogenate was strained before centrifugation at 20,000 × g for 15 min. The supernatant was desalted through a Sephadex G-50 minicolumn. Samples were kept on ice in a cold room (2 °C) during the extraction process. SPS activity was assayed as previously described (Lafta and Lorenzen, 1995).

SS activity was assayed in the direction of sucrose synthesis (Miron and Schaffer, 1991), as optimized for potato leaves in our laboratory (unpublished data). The reaction mixture contained 50 mM Mops-NaOH (pH 7.5), 15 mM MgSO₄, 25 mM UDP-gluc, 25 mM fructose, and 50 µL 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. Released sucrose was determined by the anthrone method (Van Handel, 1968).

Acid and neutral invertase were assayed in reaction mixtures containing 40 mM phosphate-citrate buffer, 200 mM sucrose, and 50 µL enzyme extract in a total volume of 250 µL (modified from Schaffer, 1986). The reactions were terminated after 30 min at 37 °C by adding 250 µL of 0.5 M Na₂HPO₄. Acid and neutral invertase were assayed at pH 5.0 and 7.0, respectively. Released reducing sugars were determined by the Nelson method (Nelson, 1944). To facilitate the comparison, data are reported as milligram sucrose per hour on a fresh-mass basis for invertases and sucrose synthase.

**Results**

Activities of enzymes related to sucrose metabolism were evaluated in mature leaves, young leaves, and stems of potato plants grown at a cool temperature (21/19 °C) and then subjected to high temperature (29/27 °C) for 3 d. There was a 49% increase in SS activity at high temperature in young growing leaves (Table 1). The increase in SS activity at high temperature was greater for ‘Norchip’ than for ‘Up-to-Date’ (data not shown). Relatively small changes in SS activity were observed at high temperature in stems and mature leaves (Table 1).

There were no significant changes in acid and neutral invertase activity at high temperature in mature leaves and stems (Table 1). In young growing leaves, there was a large increase in the activity of acid and neutral invertase of 40% and 71%, respectively, at the higher temperature (Table 1). The activity of acid and neutral invertase was 25 times and 15 times higher, respectively, than SS activity in young leaves. The activity of acid invertase in young leaves was two to three times higher than that of stems and 10 times that of mature leaves at both temperatures. The activity of neutral invertase was similarly 10 times higher in young leaves than in stems and mature leaves.

Young leaves of ‘Norchip’ had nearly twice the level of invertase activity as young leaves of ‘Up-to-Date’ (Table 2). ‘Norchip’ stems also had more invertase activity than stems of ‘Up-to-Date’. Sucrose synthase activity was at least an order of magnitude less than acid invertase activity in young leaves of both cultivars, somewhat less than acid invertase activity of stems, and about one-fourth the activity of acid invertase in mature leaves of both cultivars (Table 2). However, stems of ‘Up-to-Date’ had 50% more SS activity than stems of ‘Norchip’, a statistically significant difference (Table 2). Analysis of variance did not detect significant temperature × genotype interactions for any of the previously mentioned effects.

In Expt. 2, activity of SPS increased in mature leaves exposed to 3 d of elevated temperature (Figs. 1 and 2). The elevated activity remained constant in plants kept at 29/27 °C on days 6 and 9.

### Table 1. Main effect of temperature on enzyme activity expressed as sucrose converted on a fresh mass basis (in mg·g⁻¹·h⁻¹) in young leaves, stems, and mature leaves of potato in Expt. 1. Data represent the combined means of four replications of ‘Norchip’ and ‘Up-to-Date’ (n = 8).

| Enzyme         | Temp (°C) | Young leaf | Stem | Mature leaf |
|----------------|-----------|------------|------|-------------|
| Sucrose synthase | 21/19     | 1.0 ± 0.3⁷  | 4.9 ± 1.2 | 0.6 ± 0.2  |
|                | 29/27     | 1.5 ± 0.3  | 5.4 ± 0.5 | 0.9 ± 0.2  |
| Acid invertase | 21/19     | 25.8 ± 4.9 | 10.8 ± 1.5 | 2.9 ± 0.4  |
|                | 29/27     | 36.1 ± 5.9 | 10.6 ± 1.5 | 3.7 ± 0.3  |
| Neutral invertase | 21/19   | 15.1 ± 3.5 | 2.2 ± 0.4  | 2.5 ± 0.3  |
|                | 29/27     | 25.9 ± 3.0 | 2.7 ± 0.5  | 2.0 ± 0.3  |

⁷Represents the mean ± se.

### Table 2. Main effect of genotype on enzyme activity expressed as sucrose converted on a fresh mass basis (in mg·g⁻¹·h⁻¹) of young leaves, stems and mature leaves of potato in Expt. 1. Data represent the combined means of both temperature regimes (21/19 °C and 29/27 °C) for each cultivar (n = 8).

| Enzyme         | Cultivar | Young leaf | Stem | Mature leaf |
|----------------|----------|------------|------|-------------|
| Sucrose synthase | Norchip  | 1.0 ± 0.2 a⁷  | 4.0 ± 0.3 a | 0.9 ± 0.2 a |
|                | Up-to-Date | 1.6 ± 0.3 a | 6.3 ± 1.1 b | 0.7 ± 0.2 a |
| Acid invertase | Norchip  | 43.7 ± 3.8 a | 13.1 ± 1.3 a | 3.7 ± 0.4 a |
|                | Up-to-Date | 18.3 ± 2.3 b | 8.4 ± 1.1 b | 2.9 ± 0.4 a |
| Neutral invertase | Norchip | 24.6 ± 4.0 a | 2.8 ± 0.5 a | 2.4 ± 0.4 a |
|                | Up-to-Date | 16.4 ± 3.0 b | 2.0 ± 0.4 a | 2.2 ± 0.3 a |

⁷Represents the mean ± se; within a pair of temperatures for one tissue–temperature combination, data followed by a different letter indicate that the data were significantly different at P ≤ 0.05 by Duncan’s means test.
but returned to the same level as control plants after restoring the plants to the control temperature for 3 d (Figs. 1 and 2). Similarly, SPS activity of plants kept at the cooler temperature for an additional 6 d and then transferred to the HTS treatment was similar to plants that had 9 d of HTS (Figs. 1 and 2). Changes in SPS activity were similar whether determined as maximal SPS activity (Fig. 1) or determined under limiting conditions with limited substrate and Pi, an allosteric inhibitor (Fig. 2).

**Discussion**

Potato is sensitive to heat stress, which reduces partitioning of photosynthate to tubers and increases shoot growth (Borah and Milthorpe, 1962; Ewing, 1981; Struik et al., 1989a, 1989b). These experiments investigated changes in enzymes implicated in regulating this shift in partitioning. There was a nonsignificant increase in SS activity of ≈50% in young leaves in plants switched to 29/27 °C and similar nonsignificant increases in acid and neutral invertase activity of young leaves of both cultivars (Table 1). Khayat and Zieslin (1987) reported that SS activity increased but acid invertase activity was reduced with high night temperature (18 °C) relative to cool night temperature (12 °C) in young rose shoots. Invertase activity of bell pepper buds, but not of leaves at any growth stage, was reduced by heat stress (Aloni et al., 1991). The increased activity of sucrolytic enzymes in young leaves of heat-stressed potato plants in this study occurred simultaneously with a decline in SS activity of tubers (Lafta and Lorenzen, 1995) and is consistent with the expected shift in partitioning from tubers to shoot growth under heat stress (Ewing, 1981; Struik et al., 1989a, 1989b; Wolf et al., 1990 a).

There were no significant temperature × genotype interactions for the enzymes tested in leaves or stems in this study. However, combined invertase activity of young leaves of ‘Norchip’ was double that of young leaves of ‘Up-to-Date’ (Table 2), and invertase activity also was significantly higher in ‘Norchip’ stems than in ‘Up-to-Date’ stems. There was no genotypic difference in final weight of leaves or stems at 21/19 °C (Lafta and Lorenzen, 1995), although ‘Norchip’ had more dry matter in leaves and stems than ‘Up-to-Date’ after 4 weeks of growth at 29/27 °C. Therefore, genotypic differences in sucrolytic activity do not appear to be closely related to differences in growth patterns.

Activity of SS has been reported as a good indicator for the ability of developing tissues, such as young growing leaves, to import sucrose (Claussen et al., 1985; Sung et al., 1989). However, this was not the case in potato leaves we examined, for which young leaves had only ≈50% higher SS activity than the mature leaves. The activity of acid invertase in young potato leaves was ≈20 times higher than SS activity, while neutral invertase activity was ≈12 times higher (Table 1). This suggests that invertases are the predominant pathway for sucrose catabolism in young sink leaves of potato. In this study, SS activity was a small fraction of SS activity reported for young maize leaves (Nguyen-Quoc et al., 1990), about half that reported for *Vicia* leaves (Hite et al., 1993), and similar to the reported SS activity in mature leaves of eggplant (Claussen et al., 1985). The SS activity of stems was about equal to that reported for potato stolons (Ross et al., 1994). In that study, invertases were the predominant sucrolytic enzymes in developing stolons of potato plants, but tuber initiation coincided with a rapid increase in SS activity (Ross et al., 1994). The SS activity of developing potato berries was >10-fold that of the young leaves in this study (J.H.L. and A.M.L., unpublished data). Therefore, invertase may be the predominant sucrolytic enzyme in “vegetative” sinks in potato, while SS is important for sucrolysis in rapidly growing reproductive and perennating structures.

Previously, we reported that photosynthetic rates of mature leaves were higher at the warmer temperature, but whole-plant use of carbon was lower (Lafta and Lorenzen, 1995). This suggests that photosynthesis was not the limiting factor for partitioning in these experiments. However, the increased activity of sucrolytic enzymes in young leaves and stems may indicate a shift in partitioning from carbohydrates to starch synthesis or storage, which could be a compensatory mechanism to maintain whole-plant growth under heat stress.
of photosynthate, as indicated by accumulation of biomass, was reduced (Lafta and Lorenzen, 1995). Foliar sugars at the end of the period of illumination were higher in source leaves exposed to HTS and were somewhat lower or unaffected in HTS leaves than control leaves at the end of the night period (Lafta and Lorenzen, 1995). The reduced photosynthate use was associated with a decline in activity of SS and ADPglc pyrophosphorylase in tubers, consistent with reduced capacity to use sucrose and to process glucose-1-phosphate into starch. Biomass accumulation in shoots exposed to HTS was unaffected ('Norchip') or decreased significantly ('Up-to-Date'). In this study, we report that activity of SS, invertases, or both of both cultivars increased in shoot tissues exposed to HTS. This increased activity of sucrolytic enzymes might be expected to be associated with an increase in shoot growth if sucrose hydrolysis were a limiting factor, which was not observed in this study. Therefore, changes in shoot growth were not correlated with changes in activity of SS or invertase.

The reduced shoot growth was probably due to factors other than the availability of sucrose in source leaves or the capacity to cleave sucrose in aboveground vegetative sinks. Water stress must be considered in this regard. Plants in the HTS chamber were watered frequently, and the vapor pressure deficit was kept similar in both treatments. Recorded transpiration of the HTS plants was several times that of the plants in the cool chamber (Lafta and Lorenzen, 1995), but these data were affected by the necessity to open the doors of these reach-in chambers to determine leaf gas exchange, which caused a drop in relative humidity. The high stomatal conductance and transpiration when determining gas exchange are an indication that HTS plants were not subjected to significant water stress on days 3 and 8 of that parallel experiment. Since numerous authors similarly have reported growth inhibition of potato under high temperatures (e.g., Struik et al., 1989a), it is unlikely that water relations were involved causally in the growth inhibition. Rather, processes relating to growth were negatively affected. It is likely that plant growth regulators are involved in this process. Further investigations into other physiological processes such as energy metabolism, the cytoskeleton, and events associated with cell wall loosening and deposition may give insight into the process by which heat stress inhibits growth of potato shoots.

The increase in SPS activity in Expt. 2 was similar to that previously reported (Lafta and Lorenzen, 1995), which was associated with a reduction in diurnal starch accumulation in mature leaves exposed to HTS. The rapid return of SPS activity to the normal level in leaves of plants transferred back to the control temperature after 6 d of HTS (Fig. 1) demonstrates that this enzyme is responsive to the environment. HTS had a similar effect on SPS activity under limiting conditions (Fig. 2) as under Vmax conditions (Fig. 1), suggesting that changes in SPS activity were due to changes in the amount of enzyme protein and not due to posttranslational modification. Covalent modification of SPS has occurred in some plant species in response to light (Huber et al., 1989). During ripening of bananas, the kinetic properties of this enzyme were changed (Hubbard et al., 1990). To our knowledge, the rapid and reversible effect of temperature on SPS activity has not been reported previously.

A dim photoperiodextension increased SPS activity in mature leaves of potato more than a photoperiod extension with full illumination but had the opposite effect on tuberization (Lorenzen, 1988). Long days and HTS are known to inhibit tuberization of potato. Therefore, environmental changes that reduce or delay tuberization have been associated with increased foliar SPS activity with regard to photoperiod and temperature. Gibberellins may be involved in this response, since gibberellin-like activity in potato shoots increased in response to HTS (Menzel, 1983) and gibberellins caused an increase in SPS activity in leaves of soybean and spinach (Cheikh et al., 1992).
In conclusion, a previously reported increase in SPS activity of mature leaves exposed to HTS was reversible on returning heat-stressed plants to the control temperature. In coordination with the increased SPS activity under HTS, sucrolytic activity of young sink leaves exposed to HTS increased. Invertase activity exceeded that of SS in leaves and stems. However, increased sucrolytic activity of potato shoots did not result in a corresponding increase in shoot growth.

Literature Cited

Aloni, B., T. Pashkar, and L. Karni. 1991. Partitioning of \([^{14}C]\) sucrose and acid invertase activity in reproductive organs of pepper plants in relation to their abscission under heat stress. Ann. Bot. 67:371–377.

Ben-Khedher, M. and E.E. Ewing. 1985. Growth analyses of eleven potato cultivars grown in the greenhouse under long photoperiods with and without heat stress. Amer. Potato J. 62:537–544.

Borah, M.N. and F.L. Milthorpe. 1962. Growth of the potato as influenced by temperature. Indian J. Plant Physiol. 5:53–72.

Cheikh N., M.L. Brenner, J.L. Huber, S.C. Huber. 1992. Regulation of sucrose-phosphate synthase by gibberellins in soybean and spinach plants. Plant Physiol. 100:1238–1242

Claussen, W. 1983. Untersuchungen über den Zusammenhang zwischen der Verteilung der Assimilate und der Saccharose-Synthetase Aktivität in \(Solanum melongena\) L., 2. Assimilatverteilung und Saccharose-Synthetase Aktivität. Z. Pflanzenphysiol. 110:175–182.

Claussen, W., B.R. Loveys, and J.S. Hawker. 1985. Comparative investigations on the distribution of sucrose synthase activity and invertase activity within growing, mature and old leaves of some \(C_3\) and \(C_4\) plant species. Physiol. Plant. 65:275–280.

Dwelle, R.B., G.E. Kleinkopf, and J.J. Pavek. 1981. Stomatal conductance and gross photosynthesis of potato (\(Solanum tuberosum\) L.) as influenced by irradiance, temperature, and growth stage. Potato Res. 24:49–59.

Ewing, E.E. 1981. Heat stress and the tuberization stimulus. Amer. Potato J. 58:31–49.

Hite, D.R.C., W.H. Outlaw, and M.C. Tarczynski. 1993. Elevated levels of both sucrose-phosphate synthase and sucrose synthase in \(Vicia\) guard cells indicate cell-specific carbohydrate interconversions. Plant Physiol. 101:1217–1221.

Hubbard, N.L., D.M. Pharr, and S.C. Huber. 1990. Role of sucrose phosphate synthase in sucrose biosynthesis in ripening bananas and its relationship to the respiratory climaticer. Plant Physiol. 94:201–208.

Huber, S.C. and D.W. Israel. 1982. Biochemical basis for partitioning of photosynthetically fixed carbon between starch and sucrose in soybean (\(Glycine max\) L. [Merr.] leaves). Plant Physiol. 69:691–696.

Huber, S.C., T.H. Nielson, J. Huber, and D.M. Pharr. 1989. Variation among species in light activation of sucrose-phosphate synthase. Plant Cell Physiol. 30:277–285.

Khayat, E. and N. Zieslin. 1987. Effect of night temperature on the activity of sucrose phosphate synthase, acid invertase, and sucrose synthase in source and sink tissues of \(Rosa hybrida\) cv Golden Times. Plant Physiol. 84:447–449.

Krauss, A. and A. Marschner. 1984. Growth rate and carbohydrate metabolism of potato tubers exposed to high temperatures. Potato Res. 27:297–303.

Lafta, A. and J.H. Lorenzen. 1995. Effect of high temperature on plant growth and carbohydrate metabolism in potato. Plant Physiol. 109:637–642.

Levy, D. 1978. Heat tolerance in potato and its effect on tuber yielding capacity in hot climates. Israel J. Bot. 27:35.

Lorenzen, J.H. 1988. Effects of photoperiod and temperature on growth, leaf carbohydrates, and export in potato (\(Solanum tuberosum\) L.). Ph.D. Diss., Dept. of Vegetable Crops, Cornell Univ., Ithaca, N.Y.

Menzel, C.M. 1983. Tuberization in potato at high temperatures: Gibberellin content and transport from buds. Ann. Bot. 52:697–702.

Miron, D. and A.A. Schaffer. 1991. Sucrose-phosphate synthase, sucrose synthase, and invertase activities in developing fruit of \(Lycopersicon esculentum\) Mill. and the sucrose accumulating \(Lycopersicon hirsutum\) Humb. and Bonpl. Plant Physiol. 95:623–627.

Nelson, N. 1944. A photometric adaptation of the somogyi method for determination of glucose. J. Biol. Chem. 153:375–380.

Ngyuen-Quoc, B., M. Krivitzky, S.C. Huber, and A. Lecharny. 1990. Sucrose synthase in developing maize leaves. Regulation of activity by protein level during the import to export transition. Plant Physiol. 94:516–532.

Preiss, J. 1982. Regulation of the biosynthesis and degradation of starch. Ann. Rev. Plant Physiol. 33:431–454.

Reynolds, M.P. and E.E. Ewing. 1989. Effects of high air and soil temperature stress on growth and tuberization in \(Solanum tuberosum\). Ann. Bot. 64:241–247.

Ross H.A., H.V. Davies, L.R. Burch, R. Viola, and D. McRae. 1994. Developmental changes in carbohydrate content and sucrose degrading enzymes in tuberising stolons of potato (\(Solanum tuberosum\)). Physiol. Plant. 90:748–756.

Schaffer, A.A. 1986. Invertases in young and mature leaves of \(citrus sinensis\). Phytochemistry 25:2275–2277.

Struik, P.C., J. Geertsema, and C.H.M.G. Custers. 1989a. Effects of shoot, root and stolon temperature on the development of the potato (\(Solanum tuberosum\) L.) plant. I. Development of the haulm. Potato Res. 32:133–141.

Struik, P.C., J. Geertsema, and C.H.M.G. Custers. 1989b. Effects of shoot, root and stolon temperature on the development of the potato (\(Solanum tuberosum\) L.) plant. III. Development of tubers. Potato Res. 32:151–158.

Sung, S.S., D.P. Xu, and C.C. Black. 1989. Identification of actively filling sucrose sinks. Plant Physiol. 89:1117–1121.

Van Handel, E. 1968. Direct microdetermination of sucrose. Anal. Biochem. 22:280–283.

Wolf, S., A. Marani, and J. Rudich. 1990a. Effects of high temperature and photoperiod on assimilate partitioning in potato plants. Ann. Bot. 66:513–520.

Wolf, S., A.A. Olesinski, J. Rudich, and A. Marani. 1990b. Effect of high temperature on photosynthesis in potatoes. Ann. Bot. 65:179–185.

Zrenner, R., M. Salanoubat, L. Willmitzer, and U. Sonnewald. 1995. Evidence of the crucial role of sucrose synthase for sink strength using transgenic potato plants (\(Solanum tuberosum\) L.). The Plant J. 7:97–107.