Heat-Induced Damage in Potato (*Solanum tuberosum*) Tubers: Membrane Stability, Tissue Viability, and Accumulation of Glycoalkaloids

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Effects of heat on cell membrane permeability, metabolic activity, and glycoalkaloid content were studied in stored potato tubers. Heat-induced alteration of cell membrane permeability was estimated by ion leakage and tissue viability by the (trichlorophenyl)tetrazolium chloride (TTC) reduction test. Solanidine, α-solanine, and α-chaconine contents were determined colorimetrically. Atlantic (a heat-susceptible cultivar) accumulated 74% more total glycoalkaloids (TGA) after 4 h at 35 °C than after 4 h at 22 °C. LT7 (a heat-resistant cultivar) showed a 50% reduction in TGA content after the same treatment. Ion leakage was similar for both cultivars after 90 min at 35 °C, but for the remainder of the incubation period (4 h), it was 15−20% greater in Atlantic than in LT7. At 35 °C, LT7 showed one-third the TTC reduction activity shown by Atlantic. Calcium treatment reduced ion leakage, while it resulted in higher TTC reduction activity in Atlantic than in LT7. Incubation in a solution of glycoalkaloids caused a 50% decrease in TTC reduction activity in Atlantic but did not affect LT7. Damage was aggravated at elevated temperatures, especially in Atlantic. Possible roles of calcium in protection against glycoalkaloid damage are discussed.

Keywords: *Potato (Solanum); glycoalkaloids; membranes; heat; calcium*

INTRODUCTION

Potato glycoalkaloids, mainly α-solanine and α-chaconine, have been recognized as important natural products with insect deterring and antifungal activity (Sinden et al., 1984; Roddick et al., 1990). Besides genotypic variability (Sanford and Sinden, 1972; Maga, 1980; Olsson, 1986) a number of adverse environmental conditions can result in increased levels of glycoalkaloids in the potato plant, particularly in the tuber. Mechanical bruising, extreme temperatures, and exposure to light have all been reported to cause accumulation of glycoalkaloids in the tuber over the limit recommended by international health regulations (Currier and Kuc, 1975; Sinden et al., 1984; Linnemann et al., 1985; Bergenstrahle et al., 1992; Dale et al., 1993; Percival et al., 1993). Basically, glycoalkaloid accumulation under this variety of circumstances has been interpreted as a nonspecific response against any stress challenge (Friedman and McDonald, 1997).

Recent studies on structure and developmental toxicity of various *Solanum* alkaloids have related the relative toxicity of glycoalkaloids to the presence and composition of the sugar side chain on the steroidal core (Friedman et al., 1992; Rayburn et al., 1994). Although not fully understood, the effects of these alkaloids apparently involve a nonspecific interaction with sterol components in fungal or intestinal cell membranes which results in increased membrane permeability and, ultimately, membrane disruption (Roddick and Rijnenberg, 1986; Roddick et al., 1990, 1992; Blankemeyer et al., 1992; Friedman et al., 1992; Spessard et al., 1994). However, little is known about the effects of these alkaloids on the tuber tissue itself. We are interested in glycoalkaloid accumulation in potato tubers and their possible involvement in heat-induced damage in stored tubers. The very few reports in this regard are conflicting and relate only to total glycoalkaloid content (Currier and Kuc, 1975; Bushway et al., 1981; Linnemann et al., 1985; Percival et al., 1993).

In this paper we report on a series of experiments designed to document the extent of heat-induced glycoalkaloid buildup in two potato cultivars varying in heat resistance and to provide some evidence that glycoalkaloids may be related to heat-induced damage in potato tubers which could potentially lead to altered carbohydrate metabolism in tuber tissue.

MATERIALS AND METHODS

Plant Material and Sample Preparation. Cultivars Atlantic and CIP (International Potato Center) clone LT7 were grown with standard commercial management under rainfed conditions during the summer of 1997 in a deep sandy loam in Ocuilan, Mexico, 19° 30′ N, at 2840 m above sea level. Mean daily temperature during the crop cycle was 16 °C. Atlantic is a *S. tuberosum* cultivar extensively used in the chipping industry, while LT7 is a hybrid of *S. andigena* and *S. tuberosum* selected for its adaptability to short day conditions in subtropical and tropical highlands and is currently being used for hybrid true potato seed (TPS) production as a male parent. LT7 is considered to have some resistance to heat and to be high in glycoalkaloids (>25 mg/100 g fwt) under nonstress temperature regimes (Upadhya, 1998). After harvest, tubers from both cultivars were stored in bulk at 11.5 ± 1.0 °C, 88 ± 2% relative humidity, in darkness. One week after tubers were stored, replicated samples, at least three on each occasion, were taken at random from the storeroom. Each sample consisted of three tubers about 60 g each which were washed and disinfected by immersion in 1.5% NaClO for 2 min, then rinsed under running water until the hypochlorite smell had disappeared completely, and blot-dried on a paper towel.

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Experiments with Heat Stress. Unpeeled tubers from each sample were cut into small pieces (about 5 mm in length) and thoroughly mixed. Replicate 0.5-g samples (at least 15 for each experiment) were taken for determination of membrane damage after heat exposure by quantifying electrolyte leakage using conductimetry and estimating tissue viability using the colorimetric TTC [(2,3,5-trichlorophenyl)tetrazolium chloride] reduction test. Determination of electrolyte leakage was done using the procedure by Uemura and Yoshida (1984). Briefly, at least three 0.5-g samples of tuber tissue were incubated in 30 mL of deionized water at either 22, 30, 35, 40, or 50 °C for 4 h. After this period samples were immediately frozen in the same incubation medium and stored at −20 °C overnight. Finally, samples were thawed at room temperature. Electric conductivity of the incubation medium was measured with a conductimeter (CONSORT C731, CONSORTnv, Belgium) every 30 min over the 4 h. Membrane damage was expressed as relative membrane permeability by the following equation: % membrane permeability = $(EC_1 - EC_0)/(EC_2 - EC_0) \times 100$, where EC_0 is the maximum electric conductivity of the incubation medium after the tissue was added (EC_0 reflecting the damage caused by sample preparation), EC_1 is the electric conductivity of the solution at the end of each measuring interval, and EC_2 is the electric conductivity of the solution after the samples were frozen and thawed. Determination of TTC reduction activity was done with the method of Hwei-Hwang et al. (1982). Briefly, for each experiment, at least three samples (0.5 g) were incubated in 3 mL of deionized water at 22, 30, 35, or 40 °C. After 4 h of incubation, the tissues were washed twice with distilled water, vacuum-infiltrated for 1 min with 3 mL of the TTC solution (0.08% TTC prepared in 0.5 M phosphate buffer, pH 7.4), and incubated for 18 h in the dark in 3 mL of the same solution. The tissues were then washed twice with distilled water and incubated in 3 mL of 95% ethanol at 100 °C until complete evaporation of the ethanol. Finally, 10 mL of 95% ethanol was added to each sample followed by vigorous shaking in a vortex mixer for 30 s prior to reading absorbance (Spectronic Genesys 5, Milton Roy, Rochester, NY) of reduced TTC at 485 nm.

Quantification of Potato Tuber Glycoalkaloids. Solanidine, α-solanine, and α-chaconine from tuber tissue were quantified by colorimetry after Mackenzie et al. (1979). Briefly, each 10-g sample of tuber tissue incubated at the different temperatures was homogenized individually in 50 mL of absolute methanol using a Polytron homogenizer (Tissuemizer, Tekmar, OH). After evaporative concentration in a rotary evaporator (Rotavapor-R, Buchi, Switzerland) at 70 °C, the glycoalkaloids were precipitated with 10 mL of 30% NH_4OH at pH 11.5 overnight. Samples were then centrifuged at 12 000 rpm (MR22i JOUAN, France) for 1 h. Pellets were resuspended in 1 mL of absolute methanol and separated by gel-filtration thin-layer chromatography (TLC) (Fisher, 1980) on cellulose plates (Merck F254) in absolute chloroform: absolute methanol:3% ammonium (50:50:3) (Bushway et al., 1983). These solvents were JT Baker, analytical grade. Plates ran for 6 h at 6 °C in a sealed glass chamber. Four samples and a standard mixture (1:1:1) of solanidine, α-solanine, and α-chaconine (Sigma) were applied each in a final volume of 100 μL, 1 cm apart on each plate. Upon completion of the run, the plates were developed with iodine vapors, and each marked spot was then scrapped off the plate and resuspended in 1 mL of absolute methanol for quantification. This was achieved by reacting the samples with 5 mL of 0.016% bromophenol blue until maximum color development (usually no longer than 30 min). Absorbency readings at 600 nm were referred to a standard curve, one for each glycoalkaloid.

Experiments on the Effects of Treatment with Calcium or Glycoalkaloids on the Tissue Response to Heat Stress. Tuber tissue samples prepared as described above were incubated in 30 mL of 5 mM $CaCl_2$ or in 3 mL of a 50 μM mixture (1:1:1) of solanidine, α-solanine, and α-chaconine for 2 h at ambient temperature. After this period, the treatment solutions were discarded and the tissue samples transferred for incubation at high temperature in either 30 or 3 mL of distilled water, for conductimetry or the TTC reduction test, respectively. The calcium and glycoalkaloid mixture concentrations were selected from dose−response curves (data not shown) obtained using Atlantic, which indicated a 40−50% decrease in TTC reduction activity, with respect to the control, by incubation in a 50 μM glycoalkaloid mixture at ambient temperature and an almost complete recovery of heat-stressed tissue for TTC reduction capacity by 5 mM $CaCl_2$ in at least three independent experiments.

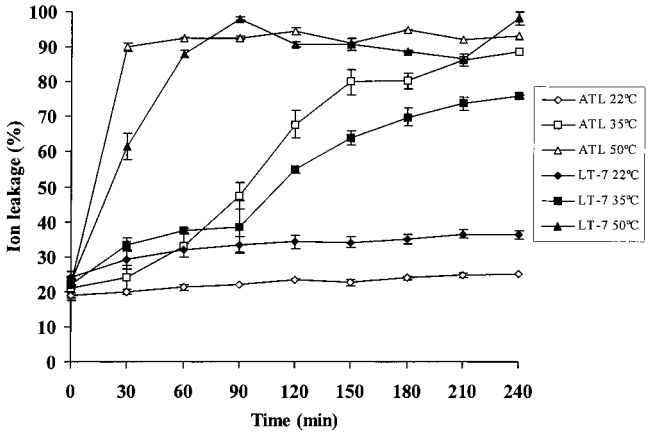

Figure 1. Time course of ion leakage from heat-stressed tuber tissues of potato cultivars Atlantic and LT7. Tissues were incubated for 4 h at the indicated temperatures, and ion leakage was determined at 30-min intervals by conductimetry.

RESULTS AND DISCUSSION

Effect of Heat Stress on Cell Membrane Thermostability in Tuber Tissue. Alteration of membrane permeability properties and ultimate membrane disruption by heat have established cellular membranes as primarily involved in heat-induced cellular damage in a number of plant species (Raison et al., 1980; Hwei-Hwang et al., 1982; Thebud and Santarius, 1982; Wu and Wallner, 1984). In the present study, the effects of heat stress on membrane permeability were evaluated by incubating tuber tissue at high temperatures for 4 h. Ion leakage was monitored during the 4 h at 30-min intervals by conductimetry. The results showed a similar extent of ion leakage at 22 °C in both cultivars tested, but membrane permeability increased significantly with increasing temperature in Atlantic, the heat-susceptible cultivar, and less in LT7, the heat-resistant cultivar (Figure 1). Lytic proportions of ion leakage at 50 °C were observed 60 min before a substantial increase of leakage at 35 °C occurred.

Incubation of the tissue in a 5 mM calcium solution significantly reduced ion leakage in both cultivars at 30 and 35 °C, but not at 40 °C (Figure 2). This beneficial effect of calcium was consistently greater in Atlantic than in LT7 and may suggest important differences in cell membrane composition between these cultivars. In the absence of calcium, TTC reduction activity declined rather linearly with increasing temperature in both cultivars over the temperature range tested, but to a greater extent in LT7 than in Atlantic. The largest difference between cultivars was observed at 35 °C, while no difference between them was observed at 40 °C (Figure 3). When the tissue was incubated in calcium, Atlantic was able to sustain higher TTC reduction activity than LT7 over the temperature range tested, although, in fact, calcium treatment seemed to cause damage in both cultivars at 22 °C, as in this case they showed at least 30% lower TTC reduction activity than the controls.

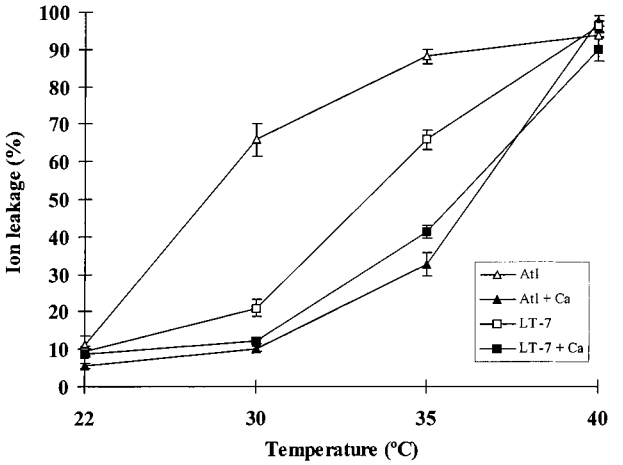

Figure 2. Effect of temperature on ion leakage from tuber tissues of potato cultivars Atlantic and LT7. Tissues were incubated for 4 h at the indicated temperatures with or without previous incubation in 5 mM Ca^{2+} for 2 h. Ion leakage from the tissues was then determined by conductimetry.

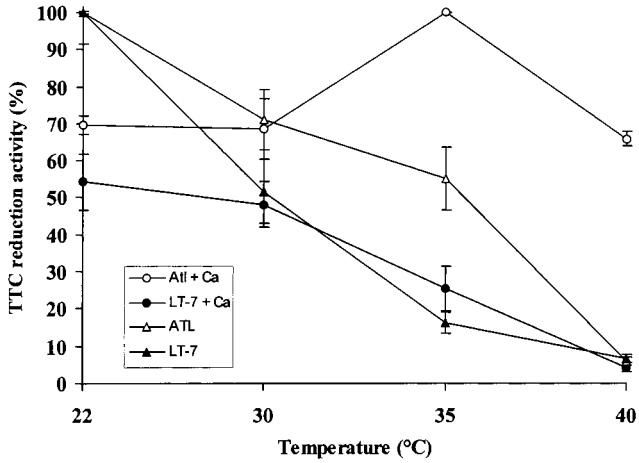

Figure 3. Effect of calcium on TTC reduction activity in tuber tissues of cultivars Atlantic and LT7 subjected to heat stress. Tissues were incubated in 5 mM Ca^{2+} for 4 h at the indicated temperature before measurement of TTC reduction activity by colorimetry.

These results extend a previous report by Tawfik et al. (1996) on the mitigating effect of calcium in heat-induced membrane damage in potato plants. In that study, leaf tissue from Russet Burbank plants supplemented with calcium and nitrogen during the heat stress (30/20 °C, day/night) showed significantly higher membrane thermostability than controls or treated plants. These findings and a direct correlation shown between glycoalkaloids and inhibition of Ca^{2+} transport across cell membranes in rat intestine and different types of cultured cells (Michalska et al., 1985; Toyoda et al., 1991; cited by Friedman and McDonald, 1997) provide strong support to the idea that calcium may improve membrane thermostability due to its incorporation into cell membranes, stabilizing them and preventing glycoalkaloids from binding membrane sterols. Thus this allows continued function of fundamental ion transport mechanisms which are responsible for keeping ionic concentrations inside and outside the cell membrane, as well as membrane-bound carriers, ionic pumps, and ultimately membrane potential, intact (Friedman and McDonald, 1997). Additionaly, there is evidence that Ca^{2+} may be necessary in the regulation vesicle-mediated secretion in plant cells, probably due to Ca^{2+}-dependent phospholipid binding proteins which couple the Ca^{2+} stimulus to the exocytotic response (Blackbourn et al., 1991). Finally, although it is as yet unreported if potato plants exhibit a heat-shock response, calcium has also been shown to be required for induction and continued production of heat-shock proteins in maize seedlings (Gong et al., 1997).

Effects of Heat Stress on Endogenous Levels of Glycoalkaloids. Table 1 summarizes the data from experiments on the effects of heat stress on the endogenous content of glycoalkaloids in tuber tissue. Basal levels of TGA at 22 °C were similar in both cultivars and did not increase significantly in either of them over an 8-h incubation (data not shown) at the same temperature. However, incubation at 35 °C resulted in a mean increase of 74% in TGA content in tubers of Atlantic, while LT7 tubers showed a 50% reduction in TGA content under the same conditions. In Atlantic tubers, the level of α-solanine consistently increased, while in LT7 tubers it consistently decreased. In contrast, the level of α-chaconine invariably decreased at the higher temperature, particularly in LT7, where it became almost undetectable at 35 °C. Since α-chaconine has been identified as the more effective of the two glycoalkaloids in disrupting biomembranes (Roddick and Rijnenberg, 1986; Blankemeyer et al., 1992), it is tempting to speculate that the higher heat resistance of LT7 compared to Atlantic may involve greater efficiency of the former for breakdown of glycoalkaloids, particularly of α-chaconine. In this regard, Friedman and McDonald (1997) have pointed out that the plant may protect itself from the greater cell-disrupting potential of α-chaconine by converting it to the nonlytic β_2-chaconine form, as has been observed in sprouts. Nevertheless, to our knowledge, this is the first report of a differential response of individual or TGA content in potato tubers to heat stress. Percival et al. (1993) found that tubers of cv. Kerrs Pink stored at 24 °C accumulated higher TGA concentrations than tubers stored at 5 °C, but they did not report on individual glycoalkaloid concentrations, and their high-temperature treatment was only slightly high, compared to the corresponding heat treatment in the present study. In contrast, Linnemann et al. (1985) reported reduced TGA concentration in cv. Bintje after 12 weeks of storage at 7, 16, and 28 °C. Yet, in another study, potato slices from cv. Russet Burbank showed increased concentrations of both α-solanine and α-chaconine over a 7-h incubation at 5 and 25 °C (Maga, 1981). Again, this was not a very high temperature. Clearly, the variety

Table 1. Glycoalkaloid Content in Tubers of Two Potato Cultivars Varying in Heat Resistance[a]

	α-solanine (mg/100 g fwt)		α-chaconine (mg/100 g fwt)		TGA (mg/100 g fwt)		
cultivar	22 °C	35 °C	22 °C	35 °C	22 °C	35 °C	Δ (%)
Atlantic	6.7 ± 1.6	35.5 ± 14.4	23.7 ± 11.1	17.3 ± 4.5	30.4 ± 6.3	53.0 ± 9.2	+74
LT7	22.9 ± 9.1	17.2 ± 7.1	14.3 ± 9.6	1.6 ± 0.9	37.2 ± 9.2	18.7 ± 4.2	−50

[a] Tuber tissue samples were incubated for 4 h at the indicated temperature. Glycoalkaloids were extracted and separated by TLC and quantified colorimetrically. Data are means ± SD. TGA values were calculated by addition of values for the individual glycoalkaloids.

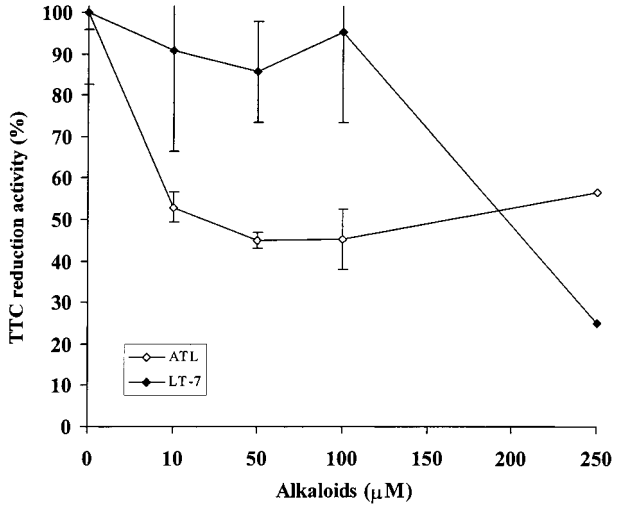

Figure 4. Dose−response curve for the effect of glycoalkaloids on TTC reduction activity in tuber tissues of potato cultivars Atlantic and LT7. Tissues were incubated for 4 h at ambient temperature in a 1:1:1 mixture of solanidine, α-solanine, and α-chaconine at the indicated concentrations. TTC reduction activity was measured by colorimetry.

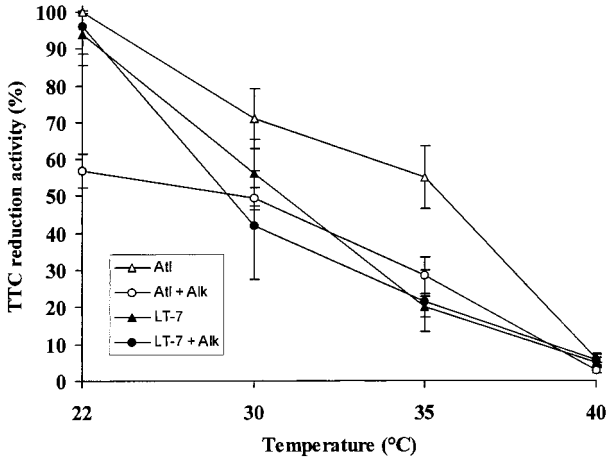

Figure 5. Effect of glycoalkaloids on the temperature dependency of TTC reduction activity by tuber tissues of potato cultivars Atlantic and LT7. Tissues were incubated for 4 h in 3 mL of a 1:1:1 mixture of 50 μM solanidine, α-solanine, and α-chaconine at the indicated temperature. TTC reduction activity was measured by colorimetry.

of experimental conditions makes it hard to draw any firm conclusions, but the evidence suggests that cultivar, time, and temperature of storage can all affect glycoalkaloid concentrations in potato tubers. Also, because wide variation can be expected, monitoring individual glycoalkaloid levels in potato tubers must become a routine practice as it concerns public health.

Effects of Glycoalkaloids on Tuber Tissue Viability. Previous studies have reported the effects of various *Solanum* alkaloids on membrane properties of systems such as liposome membranes (Roddick and Rijnenberg, 1986), frog embryos (Blankemeyer et al., 1992; Friedman et al., 1997), and vacuoles or tonoplast vesicles (Spessard et al., 1994). In these cases, ATPase activity, peroxidase activity, fluorescence parameters, or other such markers have been used as indicators of cell membrane damage caused by treatment with alkaloids. We chose a simpler test which involves detection of dehydrogenase activity to document the effects of incubating tuber tissue in a mixture of glycoalkaloids. This method has been reported in previous studies on the effects of heat stress on plant cell membranes; it is reproducible and fast (Hwei-Hang, 1982; Wu and Wallner, 1984).

Dose−response curves obtained at ambient temperature indicated a 40−50% decline in TTC reduction in Atlantic tubers when incubated for 4 h in 3 mL of a 10−100 μM glycoalkaloid mixture containing solanidine, solanine, and chaconine (1:1:1). In contrast, the same concentrations had only a minor effect on the TTC reduction by LT7 tubers (Figure 4). However, incubation in a 250 μM glycoalkaloid mixture caused a greater decrease in TCC reduction in LT7 than in Atlantic. On the basis of these results, and the levels of total glycoalkaloids commonly found in tuber tissue, a concentration of 50 μM was selected for further studies. When tuber tissue was incubated in the 50 μM glycoalkaloid mixture, TTC reduction activity declined steadily in both cultivars with increasing temperature. This treatment caused a decrease in TTC reduction activity in Atlantic at 22 °C similar to that caused by incubation at 30 °C. Thus, incubation in the alkaloid solution aggravated the damage caused by the temperature treatment alone, indicating a synergistic effect between the two (Figure 5). Whether this effect can be attributed to the membrane disrupting ability of glycoalkaloids cannot be unequivocally asserted at this time, as the effects of heat and glycoalkaloids on ion leakage and TTC reduction activity did not relate in a simple manner.

The data indicate that in Atlantic there was a substantial increase in TGA at high temperature and heat-induced ion leakage was more severe than impairment of TTC reduction capacity; calcium had clearly a remedial effect in both cases, and treatment with exogenous glycoalkaloids aggravated the effects of heat. These observations lend support to the generally accepted idea that glycoalkaloids are bioactive by reason of their ability to bind rather unspecifically to sterol components of biomembranes, causing more or less severe disruption phenomena depending on the specific identity of the sugar side chain on the aglycone and the particular sterol composition of the membrane in question (Roddick et al., 1992; Spessard et al., 1994). In contrast, TGA content in tubers of LT7 decreased at high temperature, and the heat-induced decrease in TTC reduction capacity was more severe than the concomitant increase in ion leakage. Furthermore, calcium was of little help in preventing either effect in this case. The exogenous glycoalkaloids caused little damage by themselves, and only a mild synergistic effect with heat was observed in this cultivar. These results suggest an apparently higher membrane thermostability in LT7 than in Atlantic. We propose that this difference relates to a greater efficiency of LT7 for glycoalkaloid breakdown at higher temperature, particularly of α-chaconine.

In view of the extent of the heat-induced decrease in TTC reduction activity, particularly in LT7 tubers, despite their lower TGA content and their higher membrane thermostability at high temperature, it is clear that metabolic alterations occur beyond the cell membrane level. After 4 h at 30 °C, for example, ion leakage in LT7 did not exceed 12%, yet TTC reduction fell by about 50%, indicating large effects on carbohydrate utilization for energy production. Friedman et al. (1997) recently reported on the protective effects of folic acid, glucose 6-phosphate, and NADP against the action

of α-chaconine on frog embryo cells. Additionally, enzymatic cleavage of the rhamnose, glucose, and galactose residues of α-solanine and α-chaconine by preparations from potato sprouts has been reported (Friedman and McDonald, 1997). This raises the question whether, in addition to the cited effects on membrane thermostability, glycoalkaloids may also affect the size of the pools of hexose, sucrose, starch, and NADP in tuber tissue. Thus, it may be worthwhile to study the effect of heat-induced glycoalkaloid breakdown (as seems to be the case in LT7) or buildup (as seems to be the case in Atlantic) on carbohydrate metabolism in tuber tissue.

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