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Wounding Stress Increases the Phenolic Content and Antioxidant Capacity of Purple-Flesh Potatoes (*Solanum tuberosum* L.)

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Several abiotic stresses, including ethylene, methyl jasmonate, temperature, light, and wounding, were tested for their ability to induce accumulation of phenolic compounds and antioxidant capacity in purple-flesh potatoes (cv. All Blue). Results indicated that temperature, ethylene, methyl jasmonate, and light treatments did not significantly affect the accumulation of phenolic compounds compared to control samples. Only tubers with low initial anthocyanin levels treated with methyl jasmonate showed ~60% anthocyanin accumulation. Wounding induced the accumulation of phenolics compounds and an increase of PAL-activity in sliced tissue compared to the control. Total phenolics increased ~60% with a parallel 85% increase in antioxidant capacity. These results show that selection of appropriate abiotic stresses can enhance the nutritional and functional value of potatoes.

KEYWORDS: Abiotic stresses; *Solanum tuberosum* L.; purple-flesh potatoes; phenolic compounds; wounding; antioxidant capacity

INTRODUCTION

There has been increasing interest in the consumption of natural colorants and antioxidants due to evidence of their positive influence on human health (*1*). Major antioxidants present in plant tissues are phenolic compounds, vitamins C and E, and carotenoids. It is known that antioxidants interfere with oxidation processes through chain-breaking reaction processes (primary antioxidants) or through scavenging of free radicals (secondary antioxidants) (*2*). Phenolic compounds can act as both types of antioxidants (*3*). Several other properties such as antibacterial, antiviral, anti-inflammatory, antiallergic, antimutagenic, and anticarcinogenic activities are as well associated with phenolic compounds (*4*, *5*). All of these health-related properties stimulate the search for new rich phenolic plant sources or the need for development of strategies to increase the content of phenolic compounds in plant tissue (*6*, *7*). For example, purple- and red-flesh potatoes offer a valuable novel source of natural colorants and antioxidants, both associated with their phenolic compounds (*8*, *9*).

Phenolic compounds are the major secondary metabolite products of plant metabolism, and their biosynthesis involves the induction of phenylalanine ammonia-lyase (PAL; EC 4.3.1.5), the first and rate-limiting enzyme in the phenylpropanoid metabolism. These compounds have a wide range of structural classes and biological functions; however, within a single tissue, not all of their pathways may be expressed (*10*). Phenolic compounds accumulate in potatoes and other plant tissues, as protection against mechanical bruising and injury by predators (*4*). Increased phenolic content contributes to stress resistance by forming oxidation compounds (polymeric products) that are more toxic to pathogens, thus helping in the healing process (*11*).

The accumulation of phenolic compounds in plant tissues may be induced by different abiotic stresses (*10*, *12*, *13*). Phytohormones such as ethylene (*14*) and methyl jasmonate (*15*) are known to be involved in the activation of PAL. It is also known that methyl jasmonate can enhance ethylene production (*16*). However, their actions can be considerably different, such that ethylene may prevent anthocyanin accumulation whereas methyl jasmonate may induce it (*17*, *18*). Low-temperature stresses have also been reported to influence the biosynthesis of phenylpropanoid compounds (*19*), and anthocyanin concentration in colored potatoes increased at lower temperatures (4 °C) compared to higher temperatures (*20*). Light is another stress involved in the biosynthesis of phenolics by stimulating the production of PAL (*21*). Moreover, light plays a key role in the anthocyanin biosynthetic pathway (*13*, *22*) and may increase the biosynthesis of chlorogenic acid in potato tubers (*23*, *24*). Wounding has been reported to induce the accumulation of phenolics by triggering PAL activity (*10*) and to induce a parallel increase in antioxidant capacity (*7*).

If phenolic compounds can be induced by abiotic stresses, then there is a potential to use such stresses as tools to increase the health-related and color potential properties of fresh produce. The objective of this study was to assess the effect of selected postharvest abiotic stresses such as temperature, ethylene, methyl jasmonate, light, and wounding on the accumulation of phenolic compounds and the antioxidant capacity of purple-flesh potatoes to enhance their use as a source of natural colorants and antioxidants.

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Table 1. Average Initial Phytochemical Content of Cv. All Blue Tubers Harvested in Three Planting Locations[a]

	harvest location		
	Center, CO	Springlake, TX	Rio Grande City, TX
harvest time, days after planting	110–120	156	111
anthocyanin content, mg of cyanidin 3-glucoside/100 g of fresh wt	60 ± 21	25 ± 2	11 ± 2
phenolic content, mg of chlorogenic acid/100 g of fresh wt	127 ± 21	108 ± 3	76 ± 2

[a] Data shown represent the mean ± SD ($n = 3$).

MATERIALS AND METHODS

Plant Material. Purple-flesh potatoes (*Solanum tuberosum* L. cv. All Blue) were used in this study. Tubers were harvested in Center, CO, and Springlake and Rio Grande City, TX, at 110−120, 111, or 156 days after planting, respectively, with average weights of ∼217, 138, and 74 g, respectively. The selected harvest sites allowed potatoes with different total anthocyanin and total phenolic contents to be obtained (**Table 1**).

Postharvest Abiotic Stresses. After harvest, potatoes were stored at 2 °C prior to use. Potatoes were taken out of storage, hand washed in cold water, and completely dried at room temperature with paper towels. Samples of three tubers were placed in 4-L clear glass jars and exposed to the stress treatments. Jars with air were used as control. Jars receiving ethylene treatment were injected with 4 mL of ethylene (ET) to a final concentration of 1000 ppm, and to jars receiving methyl jasmonate treatment was added 1 mL of methyl jasmonate (MJ) in a small plastic Petri dish to obtain a saturating headspace concentration. For temperature treatments, jars were stored in rooms at 2, 10, or 20 °C. For temperature fluctuation treatments, jars were transferred back and forth from 2 to 20 °C on a daily basis.

Whole potatoes from Center, Springlake, and Rio Grande City were treated with stresses for 2 weeks. Samples were stored in the dark (inside a cabinet). For those exposed to light, jars were placed sideways under a bed of fluorescent cool white light (eight Phillips FCW40 lamps). Tubers were at a distance of ∼25−30 cm (average light intensity of 146 μmol of photons/m^2•s). For the wounding stress, whole tubers were disinfected with chlorinated water (250 ppm) and cut in half (between the tuber ends), and about six slices (thickness ∼ 0.5 cm) were obtained using a vegetable slicer. Slices were stored in jars for 2 days, and the jars were opened every 4−8 h to avoid high CO_2 accumulation (>0.15%). The CO_2 levels were measured with a PIR-2000 infrared CO_2 analyzer (IRGA, Horiba Instruments, Irvine, CA). At the end of the stress treatments, tubers were cut in slices between the potato ends, weighed, and sampled according to their respective analysis. To analyze peel and flesh samples, potato slices were peeled using a hand peeler before analysis. Sampling was done in triplicates using each tuber as a replicate. Weighed samples were stored at −20 °C until needed for analysis.

Quantification of Total Anthocyanins. Anthocyanins were quantified using the procedure of Fuleki and Francis (*25*). Fifteen-gram samples were homogenized with 15 g of anthocyanin solvent (85:15 95% ethanol/1.5 N HCl) to a uniform consistency using an Ultra-Turrax T25 homogenizer (IKA Labortechnik). Samples were covered and stored overnight at 3−4 °C, and extracts were centrifuged at 31000*g* at 2 °C for 15 min; 2 g of the supernatant was transferred to a graduated cylinder, and anthocyanin solvent was added to obtain a final 1% solution. An aliquot of the sample was placed in a 1-cm quartz cuvette, and absorbance readings were taken at 535 and 700 nm in a Hewlett-Packard 8452A photodiode array spectrophotometer, previously blanked with the anthocyanin solvent. Anthocyanins were quantified as milligrams of cyanidin 3-glucoside using a molar extinction coefficient of 25965 and a molecular weight of 494 (*26*).

Quantification of Total Phenolics. Phenolics were quantified following the procedure of Swain and Hillis (*27*). Five-gram samples were homogenized with 25 mL of 95% ethanol to a uniform consistency. Samples were covered, stored overnight, and centrifuged as described above. A 0.5-mL aliquot of the clear supernatant was diluted with 8 mL of Nanopure water. Simultaneously, a blank sample was prepared with 95% ethanol and treated in the same way as the samples. After the addition of 0.5 mL of 0.25 N Folin−Ciocalteu reagent, the diluted extracts were vortexed and allowed to react for 3 min. At 3 min, 1 mL of 1 N sodium carbonate was added and allowed to react for 10 min. Samples were centrifuged again under the conditions already described, and the spectrophotometer was blanked with the prepared ethanol blank. Solutions were placed in 1-cm plastic cuvettes and measurements taken at 725 nm. Phenolics were quantified as milligrams of chlorogenic acid from a standard curve developed for this standard.

Quantification of Antioxidant Capacity. The antioxidant capacity of water-soluble phenolics was quantified using the procedure of Brand-Williams et al. (*28*). Five-gram samples were homogenized with 25 mL of methanol of HPLC grade to a uniform consistency and then centrifuged as described above. To 150 μL of the clear supernatant was added 2850 μL of a 2,2-diphenyl-1-picrylhydrazyl (DPPH) solution with an absorbance ∼1.1 measured at 515 nm, and this mixture was allowed to react for 15 min. Simultaneously, a 150-μL aliquot of methanol was treated in the same way as the samples. The spectrophotometer was blanked with methanol, the solutions were placed in 1-cm plastic cuvettes, and the decrease in absorbance was recorded at 515 nm. Antioxidant capacity was calculated as microgams of Trolox equivalents from a standard curve developed for Trolox, providing a relative activity of the extracts compared to this standard.

Quantification of PAL Activity. The methodology was adapted from that of Zucker (*21*). A 1-g sample was added 0.2 g of polyvinylpolypyrrolidone (PVPP) and homogenized with 19 mL of 50 mM borate buffer (pH 8.5) containing 40 μL of 2-mercaptoethanol/100 mL of buffer at slow speed to a uniform consistency. Samples were kept in ice throughout the assay. The homogenate was filtered through four layers of cheesecloth and centrifuged as previously mentioned. Enzyme extract was transferred to clean test tubes, covered, and assayed for PAL activity. The spectrophotometer was blanked with the borate buffer. Two sets of tubes containing 5 mL of the enzyme were prepared. Samples were warmed at 40 °C for 5 min, and 0.55 mL of Nanopure water was added to the set of tubes used as control. Control samples were placed in 1-cm quartz cuvettes, and their absorbance was measured at 290 nm. To the other set of tubes was added 0.55 mL of 100 mM L-phenylalanine, and their absorbance readings were taken at 290 nm using a 1-cm quartz cuvette. Samples were incubated at 40 °C for at least 1 h, and absorbance was read again. PAL activity was calculated as micromoles of *trans*-cinnamic acid from a standard curve developed for *trans*-cinnamic acid in the borate buffer.

Dry Matter Content. The vacuum oven (Isotemp vacuum oven model 285A from Fisher Scientific, Pittsburgh, PA) was preheated at 70 °C, and 3−5-g samples were weighed into aluminum weigh dishes. Dish and sample weights were recorded. Samples were allowed to dry for 24 h at 70 °C under vacuum at 4−5 in. of Hg. Dry matter content was calculated at 24 h by comparing the sample weight loss.

Graphs and Statistical Analysis. Summary statistics, graphs, and linear regressions were obtained using Microsoft Excel 2000 (Microsoft Corp., 1999). Statistical analyses were performed with the GLM procedure from The SAS System for Windows (version 8.1) (SAS Institute Inc., 1999). Means were compared with Tukey's multiple-range comparison test ($\alpha = 0.05$).

RESULTS AND DISCUSSION

Temperature and Phytohormone Stresses. Cv. All Blue potatoes harvested in Center, CO, showed no significant difference ($P > 0.05$) in the accumulation of total anthocyanins or total phenolics after storage at different temperatures (2, 10, and 20 °C) and fluctuating temperature (from 2 to 20 °C) when compared to control samples at room temperature. Similarly, ethylene treatments and air-stored samples showed no significant differences ($P > 0.05$) in either anthocyanin or phenolic content

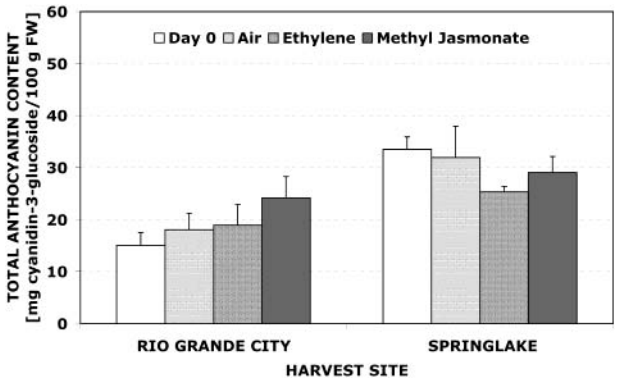

Figure 1. Effect of air, ethylene, methyl jasmonate, and temperature on total anthocyanin content of All Blue tubers from Rio Grande City and Springlake, TX, stored in the dark at 20 °C. Results are expressed on a fresh weight (FW) basis. Vertical lines represent SD ($n = 3$).

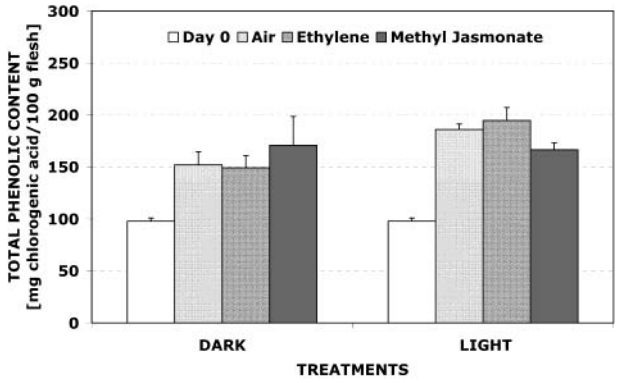

Figure 2. Effect of air, ethylene, methyl jasmonate, and light on total phenolic content in the flesh of wound-sliced All Blue tubers from Springlake, TX, stored at 20 °C. Results are expressed on a fresh weight basis. Vertical lines represent SD ($n = 3$).

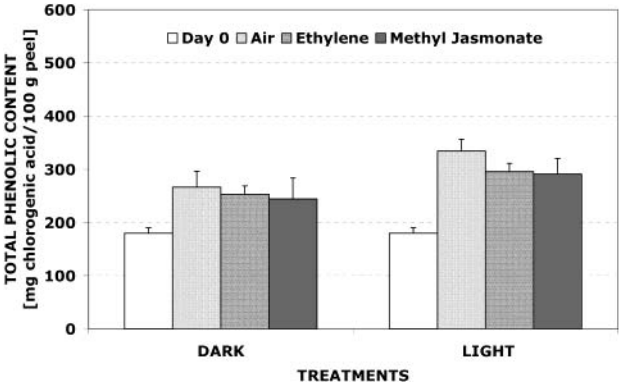

Figure 3. Effect of air, ethylene, methyl jasmonate, and light on total phenolic content in the peel of wound-sliced All Blue tubers from Springlake, TX, stored at 20 °C. Results are expressed on a fresh weight basis. Vertical lines represent SD ($n = 3$).

when compared to samples from day 0. These initial results suggest that neither temperature nor ethylene affected the phenylpropanoid metabolism in purple-flesh potatoes.

Work with lettuce has shown that tissue with low initial levels of phenolic compounds had a higher phenolic accumulation in response to heat shock stress (*29*). In our study, tubers from Colorado were 2.4 and 5.3 times higher in total anthocyanin content than tubers from Springlake and Rio Grande City, TX, respectively, and 1.2 and 1.7 times higher in total phenolics, respectively (**Table 1**). Thus, the initial phenolic content of purple-flesh potatoes may be an important factor influencing the stress responses.

To see this possible effect, we compared whole tubers from Springlake and Rio Grande City with distinct initial anthocyanin and phenolic contents (**Table 1**), under phytohormone (ethylene and methyl jasmonate) treatments at 20 °C. Tubers were exposed to stresses for 2 weeks. In the case of Springlake tubers, the experiment was stopped after 10 days due to signs of tuber sprouting. Results indicated that phytohormone stresses on tubers from both locations produced no significant differences ($P > 0.05$) in total phenolic content compared to day 0. However, tubers from Rio Grande City with lower initial anthocyanin content exposed to MJ showed significant ($P < 0.05$) anthocyanin accumulation (~60%), whereas tubers from Springlake did not show an increase when compared to day 0 (**Figure 1**). A similar percentage increase in anthocyanin accumulation due to methyl jasmonate was also observed in Rio Grande City tubers when stored at 2 °C, suggesting again that temperature was not involved on anthocyanin accumulation (data not shown).

Because ethylene did not affect anthocyanin accumulation, results suggest that anthocyanin induced by methyl jasmonate in tubers with only low initial anthocyanin content was not related to ethylene production stimulated by MJ. The stress-induced anthocyanins in tissues can be used to obtain healthier fresh or processed products to prevent chronic diseases or be the source of extractable nutraceutical colorants.

Wounding Stress. The effect of wounding was analyzed by slicing tubers from Springlake. Because the flesh and peel phenolic content represent 80% and 20% of a 100-g tuber sample, respectively, any increase of phenolic content measured in the peel could be overlooked if evaluated as a whole sample. Thus, in this part of the study we analyzed potato slices by separating their flesh and peel sections. The total phenolic contents in potato flesh and peel were 98 mg/100 g of flesh and 180 mg/100 g of peel, respectively.

Our results indicate that wounding stress did not affect the anthocyanin content ($P > 0.05$) of flesh or peel tissue under dark or light conditions or when they were exposed to both phytohormone stresses, when compared with samples at day 0. However, when results were analyzed on a dry matter basis, the anthocyanin content significantly decreased ($P < 0.05$) only in peel tissue under light conditions (a 30−40% decrease from the initial 192 mg/100 g of dry weight). The differences in results were caused by the weight loss of the tissues exposed to light (~6%). The anthocyanin decrease in peels could be due to a photobleaching effect, to oxidation, or to both (*30*).

On the other hand, wounding stress induced ($P < 0.05$) the accumulation of total phenolics in the flesh and peel of potato tubers by ~61 and 41%, respectively (**Figures 2** and **3**). Ethylene or MJ treatments did not result in differences from air-treated samples. The increase in phenolic content was slightly higher for light-treated samples. This effect was related to the weight loss (~6%) of tissues exposed to light compared to tissues exposed to dark (~1%). Thus, when samples were compared on a dry basis, there were no differences in total phenolic content ($P > 0.05$) between dark and light treatments.

The initial PAL activities of flesh and peel samples averaged 0.003 and 0.04 μmol of *trans*-cinnamic acid/g of tissue. Upon wounding, the initial PAL activity levels in flesh and peel tissues showed ~73- and 14-fold increases, respectively ($P < 0.05$). The larger increase in flesh PAL activity led to a higher increase in phenolic content (**Figure 2**). On the other hand, we observed similar PAL activity between dark- and light-treated samples,

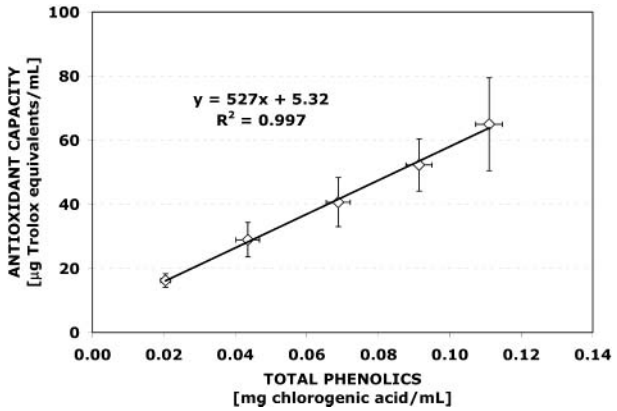

Figure 4. Increase in antioxidant capacity due to an increase in total amount of phenolics in several dilutions of phenolic extracts from whole All Blue tubers harvested in Springlake, TX. Vertical and horizontal bars represent SD ($n = 3$).

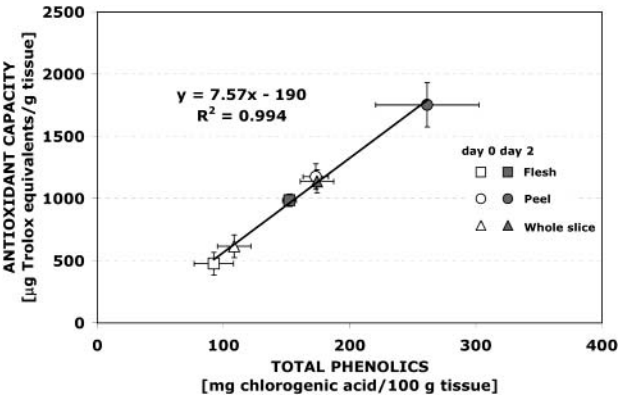

Figure 5. Increase in total phenolic content and antioxidant capacity of wound-sliced All Blue tubers from Springlake, TX, after 2 days in the dark at 20 °C and exposure to air. Results are expressed on a fresh weight basis. Vertical and horizontal bars represent SD ($n = 3$).

which was also reflected in similar accumulated amounts of phenolic compounds (**Figures 2** and **3**). This confirms that light did not trigger the phenylpropanoid pathway in purple-flesh potatoes.

Antioxidant Capacity. We determined the antioxidant capacity and phenolic content of different dilutions of phenolic extracts from whole purple-flesh potatoes from Springlake (**Figure 4**). The obtained curve shows a high correlation, $R^2 = 0.997$, suggesting that phenolics are the main compounds responsible for antioxidant capacity. From the curve's slope, we determine that phenolic compounds have a specific antioxidant capacity of 527 μg of Trolox/mg of phenolics.

In a second experiment, when purple-flesh potatoes were wounded, the phenolic content experienced 65 and 51% increases in the flesh and peel, respectively (average of 60% for whole slices). Wounding also induced a parallel response in antioxidant capacity with 107 and 49% increases in the flesh and peel, respectively (average of 85% for whole slices) (**Figure 5**). The correlation between antioxidant capacity and phenolic content was high with an $R^2 = 0.994$, indicating that wounding induced the synthesis of phenolic compounds similar to those initially present in flesh and peel tissues. Because chlorogenic acid is the main phenolic compound reported in different cultivars of colored-flesh potatoes (*31*) and is the main phenolic compound synthesized during wound healing (*32*), this would suggest that the wound-induced antioxidant capacity observed in our study would be associated with chlorogenic acid.

Results from our study indicate that wounding stress induced the accumulation of phenolic antioxidant compounds. These compounds have been associated with health-promoting activities (*1*, *2*). Because wounding stress is normally used in commercial activities, such as the fresh-cut industry, to obtain different minimally processed fruits and vegetables, or the food-processing industry, to obtain potato chips or French fries, wounding can be used as a tool to obtain healthier products. In general, our results indicate that the selection of appropriate abiotic stresses could enhance the color potential (e.g., by using methyl jasmonate in whole tubers with low initial anthocyanin content) and antioxidant properties of purple-flesh potatoes (upon wounding). These results suggest that controlled postharvest abiotic stresses may be used as tools to induce the accumulation of phytochemicals to enhance the commercial and nutritional value of horticultural food crops by offering a product with added functional properties.

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