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Combined Effects of Storage and Processing on the Bioactive Compounds and Pro-Apoptotic Properties of Color-Fleshed Potatoes in Human Colon Cancer Cells

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ABSTRACT: Potatoes can be stored for up to 1 year before being processed and consumed. The objective of this study was to determine the extent to which fresh and stored color-fleshed potatoes retain their anticancer properties after baking and chipping compared with unprocessed potatoes. We utilized white-, yellow-, and purple-fleshed potato clones and tested their phenolic and anthocyanin content, antioxidant activity, metabolite profile, and antiproliferative and pro-apoptotic properties. When compared with unprocessed samples, baking or chipping led to significant losses in the phenolic and anthocyanin content and antioxidant activity of the potatoes. However, with storage, total phenolic and anthocyanin content and antioxidant activity increased in baked samples while in the chipped samples they remained constant. Ethanolic extracts of baked and chipped samples suppressed proliferation and elevated apoptosis ($p < 0.05$) in HCT-116 (p53 wild-type; ras mutated) and HT-29 (p53 mutated; ras wild-type) human colon cancer cell lines. Antiproliferative and pro-apoptotic properties of baked potatoes were similar to that of fresh potatoes, while chipping caused a significant suppression. Phenolic content and antioxidant activity of purple-fleshed potatoes, after baking, were comparable with those of anthocyanin-rich berries. Hence, purple-fleshed potatoes can be a healthier choice for consumers as they possess greater levels of bioactive compounds and anticancer properties even after processing as compared with their white- and yellow-fleshed counterparts.

KEYWORDS: *potato, processing, storage, polyphenols or phenolic content, antioxidant activity, anthocyanins, colon cancer*

INTRODUCTION

The potato (*Solanum tuberosum* L.) is one of the most commonly consumed vegetable crops worldwide. Due to its high consumption it is considered as the third largest source of phenolic compounds in the human diet after oranges and apples.[1] The U.S. Potato Board, through the National Eating Trends Report,[2] revealed that over the past 10 years, though the consumption of traditional white-fleshed potatoes declined, specialty/colored potato consumption increased by 17%, possibly due to their putative health benefits. Anthocyanin-rich color-fleshed (purple and red) potatoes have up to eight times higher antioxidant capacity compared with their white or yellow counterparts.[3,4]

The role of potato polyphenols as antioxidants, anticarcinogenic, and antimutagenic agents has been reported in numerous studies. Potato polyphenols are effective against human liver, colon, and prostate cancer cells.[5,6] Color-fleshed potato anthocyanins are toxic to human stomach cancer cells and suppress growth of benzopyrene-induced stomach cancer in mice.[7] We previously reported that anthocyanin fractions from potatoes induce apoptosis in prostate cancer cell lines through caspase-dependent and -independent pathways.[8] Recently, we also reported that purple-fleshed potatoes were more efficient than white- or yellow-fleshed potatoes in suppressing proliferation and elevating apoptosis in early- and advanced-stage human colon cancer cell lines.[4] Researchers recently found lower levels of inflammatory markers such as plasma C-reactive protein, 8-hydrodeoxyguanosine, and interleukin-6 in healthy men consuming purple-fleshed potatoes as compared with those consuming white ones.[9] Anthocyanins are poorly bioavailable, and their concentration is greater in the colon compared to systemic flow. However, the systemic anti-inflammatory effects might be due to gut metabolites.[10,11]

Previous studies used either unprocessed or baked potatoes with little emphasis on the effect of storage and processing on biological activity. It is known that storage [4] and processing changes the physical and chemical composition of foods,[12,13] thus affecting their antioxidant activity.[14,15] Unprocessed potato phenolic content has been extensively studied,[3,16−18] but potatoes are almost always consumed after processing (baked, chipped, fried, boiled, or microwaved), making it critical to understand the effect of such processing techniques on the activity and composition of bioactive compounds in potatoes. Domestic cooking such as microwaving, boiling, or frying can result in partial losses in the phenolic content.[19] Specifically, chlorogenic acid has been shown to undergo thermal degradation after domestic processing.[20] However, baking has

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also been reported to cause an increase in the phenolic content and antioxidant activity of potatoes.[21] Furthermore, potatoes are stored for months, sometimes up to 1 year before they are processed.[22] Hence, it is necessary to determine the combined effects of storage and processing on the anticancer activity of potatoes. The objective of this study was to analyze the extent to which potatoes, especially colored-fleshed ones, retained their anticancer activity after poststorage processing as compared with unprocessed potatoes.

Potatoes are affordable sources of anthocyanins compared to the other popular sources of anthocyanins such as berries, which have many health benefits.[23−25] Hence, to compare berries with color-fleshed potatoes, we quantified the phenolic and anthocyanin content of anthocyanin-rich berries, such as blueberries, strawberries, raspberries, and grapes.

MATERIALS AND METHODS

Chemicals. Ethanol for phenolic extractions was purchased from the Chem-stock (Fort Collins, CO, USA). Phenolic acid standards, reagents, and chemicals for spectrophotometric quantitative assays were purchased from Sigma (St. Louis, MO, USA). Gallic acid was acquired from Fisher Scientific (Pittsburgh, PA, USA).

McCoy's 5A modified medium, Dulbecco's modified Eagle's medium F-12, bovine serum albumin, and sodium bicarbonate were obtained from Sigma. Fetal bovine serum, streptomycin/penicillin mix, and charcoal powder were procured from Fisher Scientific.

Potatoes and Anthocyanin-Rich Fruits. Seven potato clones—commercial varieties (Atlantic, white-fleshed; Yukon Gold, yellow-fleshed; Purple Majesty, purple-fleshed) and advanced selections (CO97232-2R/Y, AC97521-1R/Y, CO97215-2P/P, and CO97227-2P/PW)—were grown at the San Luis Valley Research Center, Colorado State University, Center, CO, USA. For the advanced selections, the two letters separated by a '/' at the end of the name indicate skin color and flesh color, respectively (R, red; Y, yellow; P, purple; PW, purple with white spots). After harvesting the potatoes were reconditioned at 16 ± 1 °C for 3 weeks to allow sugar−starch conversion and then stored in a dark room at 3 ± 1 °C. Each potato clone was placed in numbered bags weighing 4.5 kg (10 lbs) each for different processing methods (unprocessed, baked, chipped) and storage intervals (0 days of storage, initial; 60 days of storage, 60 DOS; 90 days of storage, 90 DOS) of study, and their weight was recorded at monthly intervals before sampling for analysis.

Organic anthocyanin-rich fruits such as blueberries, raspberries, strawberries, and grapes were purchased at Whole Foods Market, Fort Collins, CO, USA.

Potato Baking and Chipping. Uniform-sized potato tubers were baked during 0, 60, and 90 days after storage in a conventional oven preheated to 204 °C for 1 h and 15 min. Before baking, each potato was washed, dried, wrapped in food-grade aluminum foil, and pierced approximately 1.5 cm deep with a knife at approximately 3 cm intervals. Baked potatoes were cooled for 15−20 min, diced with skin into pieces weighing 7 ± 1 g, and stored at −20 °C. For unprocessed samples, potatoes were diced and stored at −20 °C until analysis.

For chipping, potatoes were cleaned and introduced into an industrial chipper (Ditto Dean Food Prep, model TRS 23 with C-2 blade) with 1/16" blade clearance. Raw chips were washed under running warm water for approximately 1 min to remove any water-soluble sugars present on the surface, placed in strainer trays to remove excess water, and fried in Bakers & Chefs Clear Frying Oil at 185 °C till bubbling slowed. Fried chips were placed on paper toweling to absorb any excess oil and then allowed to cool for 10−15 min. Chips were then labeled, bagged, and stored at −20 °C until extracted.

Preparation of Extracts. Unprocessed or baked or chipped potato samples (10 g) or anthocyanin-rich fruits (5 g) were homogenized with 25 mL of acidified ethanol (80%, with 0.1% v/v formic acid). Homogenates were poured into chloroform-resistant tubes and vortexed for 1 min every 15 min for 1 h. Then 15 mL of chloroform was added to the tubes to separate the lipids, and the tubes were vortexed every 10 min for 30 min. The tubes were then centrifuged at 4000 rpm for 10 min and stored overnight at 4 °C to allow layer separation. Ethanol phase was collected and stored at −20 °C until further analyses. Data were corrected for moisture loss due to processing (baking or chipping) and storage. To minimize intraclonal variability, eight randomized samples (biological replicates) were taken and extracted separately for each time point and processing method.

Determination of Total Phenolic Content. Total phenolic content of the potato extracts was determined using a modified Folin-Ciocalteu colorimetric method.[26] In a 96-well microplate, 150 μL of 0.2 M Folin-Ciocalteu reagent was added to 35 μL of potato extract and held for 5 min. Then, 115 μL of sodium carbonate solution (7.5% w/v) was added and the mixture was allowed to react for 30 min at 45 °C and cooled to room temperature for 1 h. Absorbance was read at 765 nm using a microplate reader (Synergy-2, BioTek Instruments Inc., Winooski, VT, USA) and expressed as milligrams of gallic acid equivalents per 100 g of fresh potato sample (mg GAE/100 gfw).

Determination of Total Monomeric Anthocyanin Content. Total monomeric anthocyanin content was determined by the pH differential method.[27] In a 96-well microplate, 290 μL of buffers (pH 1.0 and pH 4.5) were added separately to 10 μL of dilute potato extract. Absorbance (A) was obtained using the equation below.

$$A = (A_{525} - A_{700})_{\mathrm{pH1.0}} - (A_{525} - A_{700})_{\mathrm{pH4.5}}$$

Monomeric anthocyanin concentration (MAC) was calculated in terms of cyanidin-3-glucoside using an extinction coefficient (ε) of 26 900 L/cm/mol, a molecular weight (MW) of 449.2 g/mol, a standard path length of 1 cm, and a dilution factor (DF) of 10 using the formula below.

$$\mathrm{MAC(mg/L)} = \frac{(A \times \mathrm{MW} \times \mathrm{DF} \times 1000)}{(\varepsilon \times 1)}$$

Anthocyanin content was reported as milligrams of cyanidin-3-glucoside per 100 g of fresh potato sample (mg C-3-G equivalents/100 gfw).

Determination of Antioxidant Activity. Antioxidant activity was measured using modified 2,2-diphenyl-1-picryhydrazyl radical (DPPH) assay [28] and modified 2,2′-azino-bis(3-ethylbenzthiazoline-6-sulfonic acid) (ABTS) assay according to published protocols.[29,30] Absorbance was measured with a microplate reader (BioTek Instruments Inc., Winooski, VT, USA) at 517 and 734 nm for DPPH and ABTS assays, respectively, and compared with trolox standards. Antioxidant activity was calculated as milligrams of trolox equivalents per 100 g of fresh potato sample (mg TE/100 gfw).

Ultra Performance Liquid Chromatography and Mass Spectrometry (UPLC-MS) Analysis. Potato extracts (2 μL) were injected in a Waters Acquity UPLC system (Waters Corp., Milford, MA, USA) using a HSS T3 column (1.8 μm, 1.0 × 100 mm) and a gradient from solvent A (100% water, 0.1% formic acid) to solvent B (95% methanol, 5% water, 0.1% formic acid). Injections were made in 100% A, which was held for 2 min, followed by a 13 min linear gradient to 100% B, followed by a 2.0 min hold at 100% B. The column was returned to starting condition over 0.1 min and allowed to equilibrate for 2.9 min. Flow rate was kept constant at 140 μL/min for the duration of the run. The column and auto sampler were held at 50 and 5 °C, respectively.

Column eluent was infused into a Q-Tof Micro mass spectrometer (Waters Corp., Milford, MA, USA) fitted with an electrospray source. Data were collected in positive-ion full-scan mode, scanning from m/z 50 to 1200 at a rate of 2 scans/s with an interscan delay of 0.1 s. Calibration was performed prior to sample analysis via infusion of sodium formate solution with mass accuracy within 3 ppm. Capillary voltage was held at 2200 V, the source temperature at 130 °C, and the desolvation temperature at 300 °C with a nitrogen desolvation gas flow rate of 300 L/h. The quadrupole was held at a collision energy of 7 V. Peak detection was performed using MarkerLynx software (Waters MassLynx, v 4.1, Milford, MA, USA).

Human Colon Cancer Cell Lines. HCT116, cells were a generous gift from Dr. Bert Vogelstein, and HT-29 cells were purchased from

Table 1. Total Phenolic Content of Potato Clones after Storage and Processing[a]

	Baked			Chipped			Unprocessed
potato clones	Initial	60 DOS	90 DOS	initial	60 DOS	90 DOS	90 DOS
Atlantic	11.2 ± 0.6^{e,y}	17.9 ± 1.0^{ef,xy}	22.5 ± 0.9^{f,x}	2.51 ± 0.03^{c,x}	2.18 ± 0.02^{c,x}	1.83 ± 0.01^{c,x,*}	25.1 ± 0.4^{e}
Yukon Gold	12.7 ± 0.6^{e,y}	12.8 ± 0.8^{f,y}	25.0 ± 0.8^{ef,x}	3.04 ± 0.03^{c,x}	2.65 ± 0.01^{c,x}	2.27 ± 0.01^{c,x,*}	29.1 ± 0.6^{de}
Purple Majesty	69.6 ± 1.5^{c,z}	125.7 ± 7.2^{c,x}	117.3 ± 3.4^{c,xy}	10.2 ± 0.21^{ab,x}	7.92 ± 0.31^{ab,x}	9.06 ± 0.29^{ab,x,*}	118.1 ± 3.8^{b}
AC97521-1R/Y	20.7 ± 0.6^{de,y}	26.7 ± 1.2^{de,xy}	38.1 ± 1.3^{de,x}	3.54 ± 0.04^{c,x}	2.96 ± 0.03^{c,x}	2.55 ± 0.02^{c,x,*}	38.3 ± 0.6^{cd}
CO97232-2R/Y	31.9 ± 1.1^{d,y}	35.1 ± 2.4^{d,y}	50.2 ± 1.4^{d,x}	3.11 ± 0.04^{c,x}	2.82 ± 0.02^{c,x}	2.33 ± 0.01^{c,x,*}	44.6 ± 0.5^{c}
CO97215-2P/P	143.9 ± 4.5^{b,y}	148.3 ± 2.4^{b,y}	191.7 ± 9.6^{b,x,*}	13.14 ± 0.30^{ab,x}	13.46 ± 0.28^{a,x}	10.86 ± 0.21^{a,x,*}	117.3 ± 5.0^{b}
CO97227-2P/PW	180.1 ± 4.7^{a,z}	213.5 ± 8.5^{a,y}	307.7 ± 8.0^{a,x,*}	18.72 ± 0.50^{a,x}	14.98 ± 0.23^{a,xy}	13.34 ± 0.32^{a,y,*}	205.4 ± 5.5^{a}

[a]The letters P/P, P/PW, and R/Y after some of the advanced selections denote skin/flesh color (P, purple; PW, purple with white patches; R, red; Y, yellow), and DOS denotes days of storage. Results are presented as mean ± SE of eight replicates for each time point and expressed as milligrams of gallic acid equivalents/100 gfw. Different letters denote significant differences among different clones (a, b, c) at a particular storage duration or different storage times (x, y, z) for a single variety. The asterisk (*) indicates significant differences ($p < 0.05$) in the phenolic content compared with the unprocessed potatoes at 90 DOS.

Table 2. Anthocyanin Content of Potato Clones after Storage and Processing[a]

	Baked			Chipped			Unprocessed
potato clones	Initial	60 DOS	90 DOS	initial	60 DOS	90 DOS	90 DOS
Purple Majesty	13.4 ± 0.2^{c,z}	25.7 ± 1.6^{c,x}	18.6 ± 0.9^{c,y,*}	1.24 ± 0.07^{a,x}	0.93 ± 0.05^{a,x}	0.81 ± 0.05^{a,x,*}	29.6 ± 0.9^{b}
CO97215-2P/P	31.3 ± 0.8^{b,z}	36.0 ± 1.9^{b,y}	44.1 ± 1.6^{b,x,*}	1.57 ± 0.09^{a,x}	1.12 ± 0.05^{a,x}	1.07 ± 0.03^{a,x,*}	32.1 ± 2.2^{b}
CO97227-2P/PW	51.2 ± 1.7^{a,z}	61.1 ± 2.7^{a,y}	81.3 ± 2.^{a,x}	3.24 ± 0.14^{a,x}	2.79 ± 0.09^{a,x}	2.61 ± 0.17^{a,x,*}	82.9 ± 2.4^{a}

[a]The letters P/P and P/PW after some of the advanced selections denote skin/flesh color (P, purple; PW, purple with white patches; R, red; Y, yellow), and DOS denotes days of storage. Results are presented as mean ± SE of eight replicates for each time point and expressed as milligrams of cyanidin-3-glucoside equivalents/100 gfw. Different letters denote significant differences among different clones (a, b, c) at a particular storage time or different storage times (x, y, z) for a single variety. The asterisk (*) indicates significant differences ($p < 0.05$) in the anthocyanin content compared with the unprocessed potatoes at 90 DOS.

ATCC (Manassas, VA). Cells were maintained at 37 °C in a humidified 5% CO_2 incubator in McCoy's 5A/DMEM medium supplemented with sodium bicarbonate (2.2 g/L), fetal bovine serum (100 mL/L), and streptomycin/penicillin mix (10 mL/L).

Cell Proliferation and Apoptosis. Cell proliferation was assessed via BrdU assay (Cell Signaling Technology, MA) and cell counting using an automated cell counter (Nexcelom Bioscience, Lawrence, MA). Briefly, HCT-116 or HT-29 cells were grown in 96-well plates at 4000 cells/well in Dulbecco's modified Eagle's medium F-12 (DMEM). After 24 h, cells were treated with potato extracts diluted in DMEM having final phenolic concentrations of 10, 20, and 30 μg GAE/mL. After 24 h incubation, cell viability was assessed by quantifying the amount of 5-bromo-2′-deoxyuridine (BrdU) incorporated into cellular DNA of proliferating cells using an anti-BrdU antibody. For cell counting, cells were plated at 50 000 cells/well in a 12-well plate and treated as above and reported as percent reduction with respect to control. Apoptosis was measured using the Caspase-Glo 3/7 assay (Promega Corp., Madison, WI). Cells undergoing apoptosis have a higher caspase-3 and caspase-7 activity, which result in a stronger luminescence signal. To compare the effects of baking and chipping on the anticancer properties of potatoes, the reduction in cell proliferation and apoptotic index were compared at a single concentration, 30 μg GAE/mL, which was the highest concentration in the study.

Statistical Analysis. The effects of genotype, storage and processing on antioxidant activity, total phenolics and anthocyanins, cell proliferation, and apoptosis were determined by three-way analysis of variance (ANOVA) using the SAS general linear model (GLM) procedure. Pairwise multiple comparisons and mean separations using Fisher LSD were used for comparing group differences with $p < 0.05$ being considered as statistically significant. Pearson correlation coefficients were calculated using SAS Statistical Analysis System, v.9.2 (SAS Institute Inc., Cary, NC). All results have been expressed as mean ± standard error. For principal component analysis, peak areas were exported to SIMCA-P+ (Umetrics AB, v12.0, Sweden). Data were scaled to unit variance and mean centered before principal component analysis.

RESULTS AND DISCUSSION

Total Phenolic Content. Total phenolic content was measured for baked and chipped potato samples at three time points (initial and 60 and 90 days of storage; DOS) and for unprocessed tubers at 90 DOS for seven potato clones. Total phenolic content of the baked and chipped potato samples ranged from 11.2 to 307.7 mg GAE/100 gfw and 1.8 to 18.7 mg GAE/100 gfw, respectively, for all seven clones over the entire storage period (Table 1). When compared with unprocessed samples at 90 DOS, baking both decreased and increased the phenolic content depending on the clones. In purple-fleshed clones CO97215-2P/P and CO97227-2P/PW baking resulted in an increase in the phenolic content. Irrespective of the clones chipping retained only 4−7% of the total phenolics compared to unprocessed samples at 90 DOS.

Effects of processing cannot be generalized for all potato clones as they differ depending on potato genotype.[20,21,31,32] Both microwaving and baking significantly reduced the total phenolic content of Dakota Pearl cultivar but not of the Norkotah cultivar.[31] Chipping and frying resulted in greater losses in phenolic content compared to unprocessed samples in many varieties.[19,20] With storage, an increase ($p < 0.05$) was observed in the phenolic content of baked samples of all clones. Baked purple-fleshed potatoes had higher phenolic content ($p < 0.05$) as compared with their white- and yellow-fleshed counterparts throughout the storage duration. Among the chipped samples, CO97227-2P/PW samples had the highest amount of total phenolics, not significantly different from CO97215-2P/P, while the lowest was in Atlantic chipped samples. However, storage did not influence the phenolic content of the chipped samples with the exception of CO97227-2P/PW. Hence, it is important to consider the effects of genotype and farm-to-fork operations, such as storage

Table 3. Antioxidant Activity (ABTS) of Potatoes after Storage and Processing[a]

	Baked			Chipped			Unprocessed
potato clones	Initial	60 DOS	90 DOS	initial	60 DOS	90 DOS	90 DOS
Atlantic	28.3 ± 3.1^{f,z}	102 ± 4.8^{ef,xy}	136 ± 5.1^{e,x}	2.28 ± 0.06^{ab}	3.66 ± 0.36^{ab}	2.75 ± 0.41^{ab,*}	144 ± 4.9^{e}
Yukon Gold	57.5 ± 5.6^{ef,y}	78.8 ± 3.5^{f,y}	147 ± 3.9^{de,x}	3.01 ± 0.10^{ab}	7.11 ± 0.60^{ab}	5.58 ± 0.43^{ab,*}	165 ± 4.1^{de}
Purple Majesty	559 ± 32^{c,y}	649 ± 28^{c,x}	670 ± 27^{c,x,*}	15.77 ± 0.92^{a}	21.11 ± 1.89^{a}	17.41 ± 0.78^{a,*}	908 ± 20.1^{c}
AC97521-1R/Y	93.8 ± 4.6^{e,y}	154 ± 5.04^{de,xy}	185 ± 4.5^{d,x}	4.61 ± 0.07^{ab}	9.02 ± 0.70^{ab}	7.92 ± 0.84^{ab,*}	198 ± 3.4^{de}
CO97232-2R/Y	180 ± 5.0^{d,x}	173 ± 10.3^{d,x}	212 ± 4.1^{d,x}	4.25 ± 0.07^{ab}	6.36 ± 0.28^{ab}	6.61 ± 0.45^{ab,*}	226 ± 4.1^{d}
CO97215-2P/P	585 ± 31^{bc,y}	723 ± 38.6^{b,x}	783 ± 40^{b,x,*}	17.99 ± 1.08^{a}	26.34 ± 3.03^{a}	20.60 ± 1.68^{a,*}	1058 ± 23.4^{b}
CO97227-2P/PW	661 ± 50^{a,z}	866 ± 20.4^{a,y}	1113 ± 22^{a,x,*}	21.49 ± 0.86^{a}	33.85 ± 1.80^{a}	27.18 ± 2.25^{a,*}	1285 ± 25.1^{a}

[a]The letters P/P and P/PW after some of the advanced selections denote skin/flesh color (P, purple; PW, purple with white patches; R, red; Y, yellow), and DOS denotes days of storage. Results are presented as mean ± SE of eight replicates for each time point and expressed as milligrams of trolox equivalents/100 gfw. Different letters denote significant differences among different clones (a, b, c) at a particular storage time or among storage times (x, y, z) for a single variety. The asterisk (*) indicates significant differences ($p < 0.05$) in the antioxidant content compared with the unprocessed potatoes at 90 DOS.

Table 4. Phenolic Acid Profile of Baked and Chipped Potato Samples by UPLC-MS[a]

		Atlantic		Yukon Gold		Purple Majesty		CO97227-2P/PW	
compound	processing	initial	90 DOS	initial	90 DOS	initial	90 DOS	initial	90 DOS
chlorogenic acid	baked	0.05 ± <0.01	1.50 ± 0.19	0.05 ± 0.02	1.40 ± 0.28	16.76 ± 0.20	27.49 ± 0.86	37.97 ± 0.78	52.33 ± 0.68
	chipped	0.21 ± <0.01	0.13 ± <0.01	0.22 ± 0.01	0.20 ± 0.01	1.11 ± 0.02	1.00 ± 0.04	1.10 ± 0.03	1.10 ± 0.04
caffeic acid	baked	0.35 ± 0.06	0.75 ± 0.07	0.34 ± 0.10	0.63 ± 0.07	6.19 ± 0.78	9.97 ± 0.78	11.53 ± 0.50	13.28 ± 0.35
	chipped	0.06 ± <0.01	0.05 ± <0.01	0.05 ± 0.01	0.06 ± <0.01	0.36 ± 0.02	0.31 ± 0.02	0.36 ± 0.01	0.38 ± 0.03
ferulic acid	baked		0.08 ± <0.01		0.07 ± <0.01				
	chipped								
sinapic acid	baked				0.02 ± <0.01				
	chipped								

[a]P/PW and DOS denote purple skin/purple flesh with white patches and days of storage, respectively. Phenolic acid values are expressed as mg/100 gfw potato.

and processing, while selecting clones for breeding potatoes with greater health-benefiting compounds.

To compare the phenolic content of baked purple-fleshed clones with traditional anthocyanin-rich fruits, the same extraction procedure and analysis were used. Blueberries, grapes, raspberries, and strawberries had 323.3 ± 4.1, 199.5 ± 5.0, 170.0 ± 3.1, and 113.7 ± 2.8 mg GAE/100 gfw total phenolics, respectively, whereas the phenolic content of baked purple-fleshed clones ranged from 117.0 ± 3.4 to 307.7 ± 8.0 mg GAE/100 gfw (Table 1) after 90 DOS. One pound of conventional blueberries costs approximately $7.98 (U.S. dollars), and even organic purple potatoes cost only $1.99/lb (Whole Foods Market, Fort Collins, 09/23/2012). Thus, the phenolic content of purple-fleshed potatoes was comparable to that of berries, making them an affordable choice for most people.

Anthocyanin Content. For the purple-fleshed baked samples, the anthocyanin content ranged from 13.4 to 81.3 mg C-3-G equivalents/100 gfw while the chipped samples ranged from 0.8 to 3.2 mg C-3-G equivalents/100 gfw (Table 2). Baking either fully retained or slightly increased the anthocyanin content of the purple-fleshed clones studied, with the exception of Purple Majesty, which retained only 63% anthocyanin content. In comparison, chipping resulted in ∼97% losses as compared with unprocessed samples at 90 DOS. Purple Majesty samples had the lowest anthocyanin content throughout the duration of storage, while the CO97227-2P/PW samples consistently had the highest anthocyanin content. The anthocyanin content of most baked potato clones increased ($p < 0.05$) at the end of the storage, while the changes in anthocyanin content of chipped samples with storage were not significant. Purple Majesty baked samples showed a peak at 60 DOS followed by a decrease in the anthocyanin content at 90 DOS. The anthocyanin trend observed was similar to that of the total phenolic content, which suggests the role of anthocyanins in contributing to the total phenolic content.

The anthocyanin content of the baked samples (Table 2) was comparable to that of blueberries (81.8 ± 3.0 mg C-3-G equivalents/100 gfw), raspberries (50.0 ± 0.7 mg C-3-G equivalents/100 gfw), grapes (45.5 ± 0.8 mg C-3-G equivalents/100 gfw), and strawberries (41.9 ± 1.7 mg C-3-G equivalents/100 gfw). Thus, purple-fleshed potatoes can act as a rich and an inexpensive source of anthocyanins in the diet.

Antioxidant Activity. Antioxidant activity of the baked samples ranged from 28.3 to 1113.0 mg TE/100 gfw as measured by the ABTS assay (Table 3). For the chipped samples, the antioxidant activity ranged from 2.3 to 33.8 mg TE/100 gfw (ABTS). When compared with unprocessed 90 DOS samples, baking led up to 26% losses in antioxidant activity for some clones. Similar trends were seen for the DPPH assay (data not shown).

The antioxidant activity of the purple-fleshed samples was significantly higher than the white- and yellow-fleshed samples. Both DPPH and ABTS assays confirmed an increase ($p < 0.05$) in the antioxidant activity of baked samples with storage except for CO97232-2R/Y. Rosenthal also found an increase in antioxidants in stored colored flesh potatoes.[33] DPPH values for baked white-fleshed potatoes have been reported to range from 11.3 to 21.2 mg TE/100 gfw.[31] Chipped samples from most clones showed no change in the antioxidant activity over

the entire period of the storage when measured by the DPPH or ABTS assays.

The antioxidant values of the baked potatoes were comparable to that of anthocyanin-rich fruits. ABTS values for blueberries, strawberries, raspberries, and grapes were 542.9 ± 7.8, 413.3 ± 5.5, 380.8 ± 6.2, and 236.8 ± 6.8 mg TE/100 gfw, respectively. Thus, baked purple-fleshed potatoes can also serve as a rich source of antioxidants.

UPLC-MS Profile of Phenolic Compounds. Three of the four clones selected for metabolite analysis were commercially available clones representative of their color—Atlantic (white fleshed), Yukon Gold (yellow fleshed), and Purple Majesty (purple fleshed)—and the fourth was a purple−white-fleshed advanced selection, CO97227-2P/PW, with high phenolic content, antioxidant activity, and anthocyanin content.

Chlorogenic acid is the most abundant phenolic acid found in potatoes.[34] In the baked white- and yellow-fleshed clones, chlorogenic acid degraded to negligible amounts (Table 4) as compared with unprocessed white- and yellow-fleshed samples, which we previously reported.[4] Degradation may be due to the susceptibility of chlorogenic acid to heat, and similar to our results, the literature suggests a 100% loss after baking in an oven at 212 °C for 45 min.[34] Conversely, some studies show that chlorogenic acid is reduced but not completely destroyed after baking. However, baking was done at 178 °C for 40 min, and the study claims that the peels could act as a barrier against the loss of chlorogenic acid.[31] In our present study, baking was done at 204 °C for 75 min, which could explain the loss of chlorogenic acid in baked Atlantic and Yukon Gold potatoes. Chipped samples showed a decrease in the phenolic acids (Table 4) as compared with our previously reported unprocessed samples.[4] We previously reported that chlorogenic acid is elevated with storage. Indeed, in purple clones, a 13−100% increase in the chlorogenic acid content was observed even after baking after 90 DOS at low temperature. Storage led to an increase in the chlorogenic acid content. Low temperature, strong light, wounding, pathogen attack, and other environmental stresses during storage can lead to the synthesis of phenolic compounds via the phenylpropanoid pathway.[35] Thus, storage at different temperatures might alter the levels of phenolic acids in processed potato products.

Baked purple-fleshed samples contained glycosylated anthocyanins, such as petunidin-3-rutinoside-5-glucoside (Pet-3-rut-5-glc) and malvidin-3-rutinoside-5-glucoside (Mal-3-rut-5-glc). Anthocyanins were also acylated with *p*-coumaric acid, such as peonidin-3-(*p*-coumaroyl)-rutinoside-5-glucoside (peo-3-coum-rut-5-glc), petunidin-3-(*p*-coumaroyl)-rutinoside-5-glucoside (pet-3-coum-rut-5-glc), pelargonidin-3-(*p*-coumaroyl)-rutinoside-5-glucoside (pel-3-coum-rut-5-glc), and malvidin-3-(*p*-coumaroyl)-rutinoside-5-glucoside (mal-3-coum-rut-5-glc) (Table 5). CO97227-2P/PW had approximately a 5-fold higher amount of mal-3-coum-rut-5-glc as compared with Purple Majesty. Pet-3-coum-rut-5-glc was the most abundant anthocyanin, followed by peo-3-coum-rut-5-glc. Storage increased most individual anthocyanins in both purple-fleshed clones. Activation of phenyl ammonia-lyase (PAL), a key enzyme in the phenylpropanoid pathway, [36] could explain the observed increase in the monomeric anthocyanin content from initial to 90 DOS. In chipped samples, pet-3-coum-rut-5-glc was the most abundant anthocyanin followed by peo-3-coum-rut-5-glc and mal-3-coum-rut-5-glc (Table 5).

Principal component analysis of approximately 1600 peaks obtained through UPLC-MS revealed overall differences in the metabolite profiles of unprocessed, baked, and chipped Atlantic and Purple Majesty potato samples independent of storage (Figure 1). It was observed that unprocessed and baked samples had similar metabolite profiles, while that of the chipped samples varied significantly. The metabolite profile of the purple-fleshed potato was significantly different from the white-fleshed potato. This difference is partly due to the presence of anthocyanins in purple-fleshed potatoes.

Table 5. Anthocyanin Profile of Baked and Chipped Potato Samples by UPLC-MS[a]

		Purple Majesty		CO97227-2P/PW	
compound	processing	initial	90 DOS	initial	90 DOS
pet-3-rut-5-glc	baked	1131	2286	3084	4428
	chipped	312	274	464	476
mal-3-rut-5-glc	baked	151	214	634	753
	chipped	44	41	121	122
peo-3-coum-rut-5-glc isomer	baked			5051	5072
	chipped			494	458
pet-3-coum-rut-5-glc	baked	25099	31280	38112	42186
	chipped	5749	5088	6057	5143
pel-3-coum-rut-5-glc	baked	665		5089	5142
	chipped	12		854	879
peo-3-coum-rut-5-glc	baked	4456	1015	29008	32074
	chipped	358	172	4705	4833
mal-3-coum-rut-5-glc	baked	1617	1845	6531	9146
	chipped	538	336	1589	1655

[a]P/PW and DOS denote purple skin/purple flesh with white patches and days of storage, respectively. Anthocyanins have been reported as area under the curve/gfw.

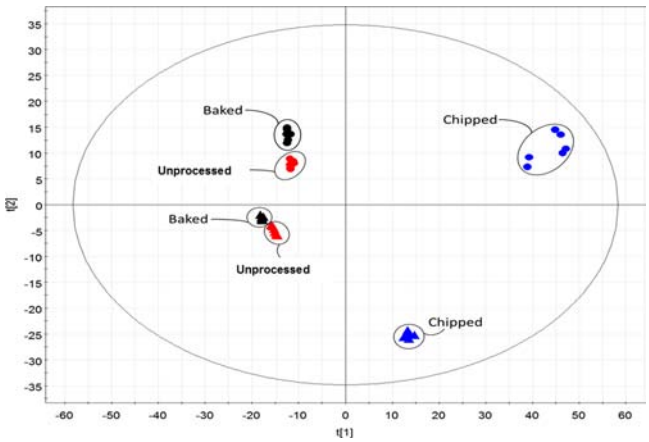

Figure 1. Principal component analysis revealed differences in polyphenol profiles as measured by an UPLC Q-Tof Micro mass spectrometer based on variety and processing. *x* axis represents PC1 scores, and *y* axis represents PC2 scores. Chipped samples had different phenolic profiles compared to baked and unprocessed samples. Bubbles point out the difference in phenolic profiles due to processing methods independent of storage. Plot shows all individual data points. Data are represented for Atlantic (▲) and Purple Majesty (●) varieties for different processing methods.

Human Colon Cancer Cell Proliferation and Apoptosis. The antiproliferative and pro-apoptotic activity of baked and chipped potato samples from four potato clones (Atlantic, Yukon Gold, Purple Majesty, and CO97227-2P/PW), at initial and 90 DOS, were tested against HCT-116 and HT-29 human

Table 6. Effect of Baked and Chipped Potato Extracts on Cell Proliferation and Apoptosis of HT-29 Human Colon Cancer Cells[a]

BrdU (% cell proliferation; control = 100%)									
		Baked				Chipped			
		Atlantic	Yukon Gold	Purple Majesty	CO97227-2P/PW	Atlantic	Yukon Gold	Purple Majesty	CO97227-2P/PW
initial (μg/mL)	10	95 ± 2.4^{a,x,†}	101 ± 5.3^{a,x}	87 ± 2.3^{b,x,†}	95 ± 2.4^{a,x}	101 ± 1.4^{ab,x,†}	104 ± 1.2^{a,x}	97 ± 2.7^{ab,x,†}	95 ± 2.3^{b,x}
	20	93 ± 1.0^{a,xy,†}	94 ± 2.6^{a,xy}	83 ± 1.5^{b,x,†}	80 ± 3.1^{b,y,†}	99 ± 2.1^{a,xy,†}	97 ± 1.4^{a,xy}	99 ± 1.4^{a,x,†}	96 ± 2.4^{ab,x,†}
	30	87 ± 2.6^{a,y,†}	87 ± 2.3^{a,y,†}	66 ± 1.4^{b,y,†,*}	65 ± 5.8^{b,z,†,*}	96 ± 3.5^{ab,y,†}	95 ± 2.3^{ab,y,†}	97 ± 1.6^{a,x,†}	89 ± 3.7^{c,xy,†}
90 DOS (μg/mL)	10	98 ± 2.4^{a,x}	97 ± 3.4^{a,x}	85 ± 1.8^{b,x,†}	96 ± 0.3d^{a,x}	103 ± 0.4^{a,x}	102 ± 2.3^{a,x}	97 ± 1.5^{ab,y,†}	99 ± 1.5^{a,x}
	20	95 ± 1.3^{a,xy}	96 ± 2.5^{a,xy}	87 ± 0.8^{b,x,†}	84 ± 4.1^{b,yz,†}	100 ± 2.7^{a,xy}	100 ± 3.3^{a,x}	102 ± 2.2^{a,x,†}	91 ± 2.5^{b,xy,†}
	30	89 ± 1.8^{a,y,†}	88 ± 2.1^{a,y,†}	73 ± 1.0^{b,y,†,*}	77 ± 0.8^{b,z,†,*}	101 ± 1.2^{a,x,†}	99 ± 1.4^{ab,x,†}	99 ± 0.2^{ab,xy,†}	94 ± 5.3^{b,x,†}
apoptosis (lumens)[b]									
	B	Baked (control 397 ± 10)				Chipped (control 441 ± 18)			
		Atlantic	Yukon Gold	Purple Majesty	CO97227-2P/PW	Atlantic	Yukon Gold	Purple Majesty	CO97227-2P/PW
initial (μg/mL)	10	487 ± 7^{a,z}	469 ± 19^{a,z}	458 ± 33^{a,z}	484 ± 23^{a,z}	426 ± 58^{a,xy,†}	421 ± 29^{a,x,†}	402 ± 37^{a,x,†}	393 ± 43^{a,x,†}
	20	673 ± 15^{b,y,†,*}	574 ± 21^{c,y,†}	686 ± 26^{b,y,†}	824 ± 14^{a,y,†,*}	385 ± 31^{a,y,†}	358 ± 45^{a,x,†,*}	432 ± 34^{a,x,†}	437 ± 32^{a,x,†}
	30	758 ± 35^{d,x,†,*}	865 ± 16^{c,x,†,*}	991 ± 11^{b,x,†,*}	1019 ± 18^{a,x,†,*}	483 ± 24^{a,x,†}	428 ± 25^{a,x,†}	465 ± 48^{a,x,†}	472 ± 60^{a,x,†}
90 DOS (μg/mL)	10	416 ± 30^{b,z,*}	458 ± 16^{ab,z}	420 ± 17^{b,z}	511 ± 11^{a,z}	451 ± 62^{a,x,†}	451 ± 19^{a,x,†}	446 ± 10^{a,x,†}	416 ± 35^{a,x,†}
	20	518 ± 18^{c,y,†,*}	546 ± 46^{c,y}	697 ± 4^{a,b,y,†}	743 ± 58^{a,y,†,*}	387 ± 28^{b,x,†}	463 ± 61^{a,x,†,*}	455 ± 30^{ab,x,†}	489 ± 8^{a,x,†}
	30	640 ± 27^{c,x,†,*}	732 ± 61^{b,x,†,*}	922 ± 27^{a,x,†,*}	946 ± 49^{a,x,†,*}	448 ± 9^{a,x,†}	422 ± 38^{a,x,†}	443 ± 38^{a,x,†}	433 ± 34^{a,x,†}

[a]Values with different letters indicate significant differences ($p < 0.05$) in cell proliferation or apoptosis among different clones (a, b, c) at a given concentration and storage time and different concentrations (x, y, z) for a clone at a given storage period. Dagger (†) and asterisk (*) indicate a significant difference ($p < 0.05$) between proceesing methods and storage times, respectively, for a given variety and concentration. [b]Caspase activity, a marker for apoptosis, is measured in lumens. The higher the value the greater the apoptosis. Results are presented as mean ± SE of four replicates for each time point.

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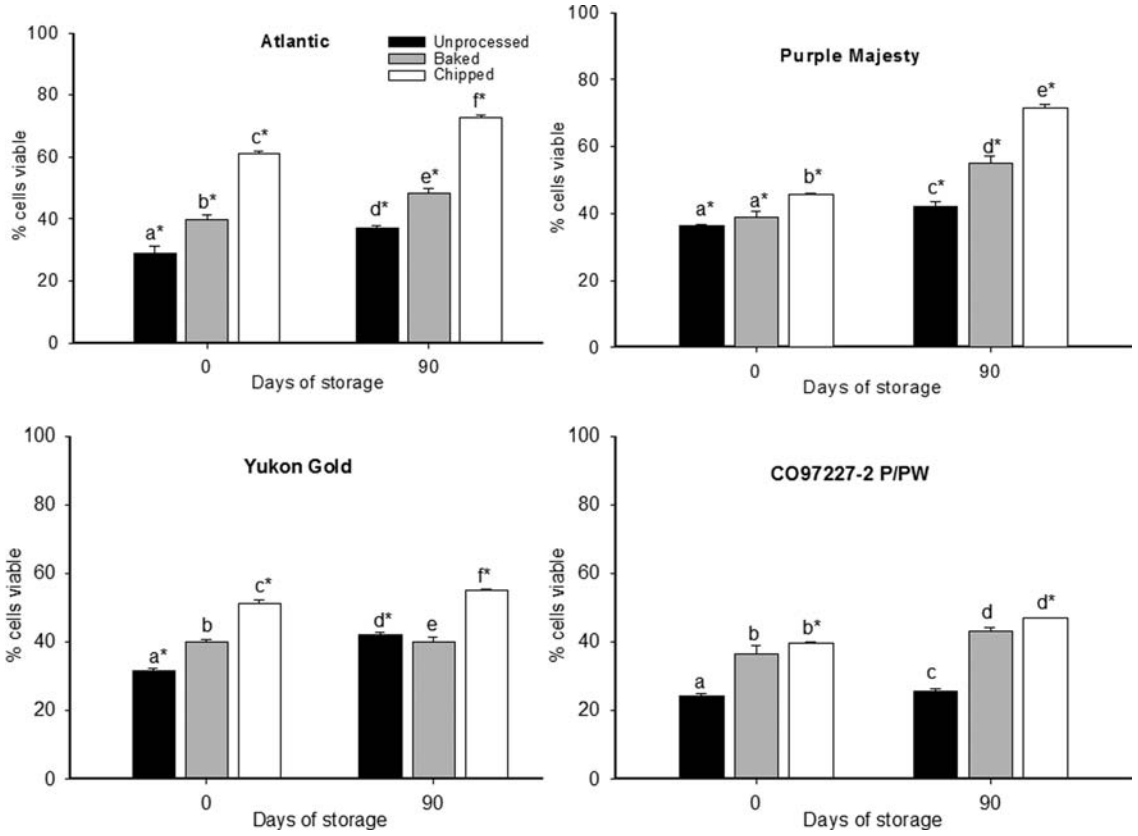

Figure 2. Baking and chipping suppressed antiproliferative activity in most potato clones at 30 μg GAE/mL concentration in HCT-116 human colon cancer cells. Values with different letters in each graph indicate significant difference ($p < 0.05$) between % cells viable for different processing methods at a given time point. Asterisk (*) indicates a significant difference ($p < 0.05$) between percentage reduction between 0 and 90 DOS for a given processing method. Results are presented as mean ± SE of four replicates for each time point.

colon cancer cell lines (Table 6). Compared to unprocessed samples, bioactivity of the baked potato samples against cell proliferation was reduced for most potato clones (Figure 2), while the ability to induce apoptosis was comparable at 30 μg GAE/mL (Figure 3). In spite of dosing at the same phenolic content, chipping significantly suppressed the antiproliferative and pro-apoptotic properties of potatoes against HCT-116 cells, as compared with unprocessed samples. This might be due to a change in the metabolite composition of the potatoes due to chipping. In general, storage suppressed the antiproliferative properties of potatoes, but some clones were superior in retaining their antiproliferative properties (Table 6). Baked and chipped CO97227-2P/PW samples had more antiproliferative and pro-apoptotic activity against HCT-116 cell lines, compared with the other three clones.

A dose dependency was observed for the antiproliferative and pro-apoptotic effects of extracts from baked samples against HT-29 cell lines. However, the effect was less pronounced than the effects observed in the HCT-116 cell line (Table 6). In general, storage did not alter the antiproliferative activity but reduced the pro-apoptotic properties of the baked samples in HT-29 cell line. Baked samples were more effective in elevating apoptosis as compared with chipped samples, suggesting that baking minimally alters bioactivity when compared with chipping. CO97227-2P/PW extracts induced more apoptosis in HCT-116 cell line than Purple Majesty. This could be due to the presence of more petunidin and malvidin anthocyanins, which have been reported to be pro-apoptotic and antiproliferative, respectively.[3]

This study demonstrated the effect of poststorage processing on the bioactive compounds found in white-, yellow-, and purple-fleshed potato clones. Purple-fleshed potatoes can deliver health-benefiting polyphenolic compounds in levels comparable to blueberries and grapes with fewer calories being consumed with respect to traditional clones. We observed that one-half a baked purple-fleshed potato (~100 g) has total phenolic content equivalent to 3.5 yellow-fleshed Yukon Gold/white-fleshed Atlantic potatoes or 45 blueberries or 25 grapes. This study, for the first time, showed that potato compounds retained bioactivity against colon cancer cells even after poststorage processing. Processing caused a shift in the metabolite profile of the potato samples, which could possibly explain the suppression of anticancer properties of chipped potato samples. However, some clones retained their anticancer properties better than others. Hence, these clones could be utilized as parent material for breeding programs to develop genotypes that retain their bioactive properties poststorage and processing. As purple-fleshed potato clones differed in the content and composition of bioactive compounds and their anticancer properties, flesh color alone may not be a good indicator of health-benefiting properties. Even then, purple-fleshed potatoes can be a healthier choice as they possess greater levels of bioactive compounds and anticancer properties even after processing as compared with their white- and yellow-fleshed counterparts. We are currently confirming these in vitro results by evaluating the baked and chipped color-fleshed potatoes for their anti-inflammatory properties using obese pigs, a highly relevant model for human paradigm. Farm-to-fork

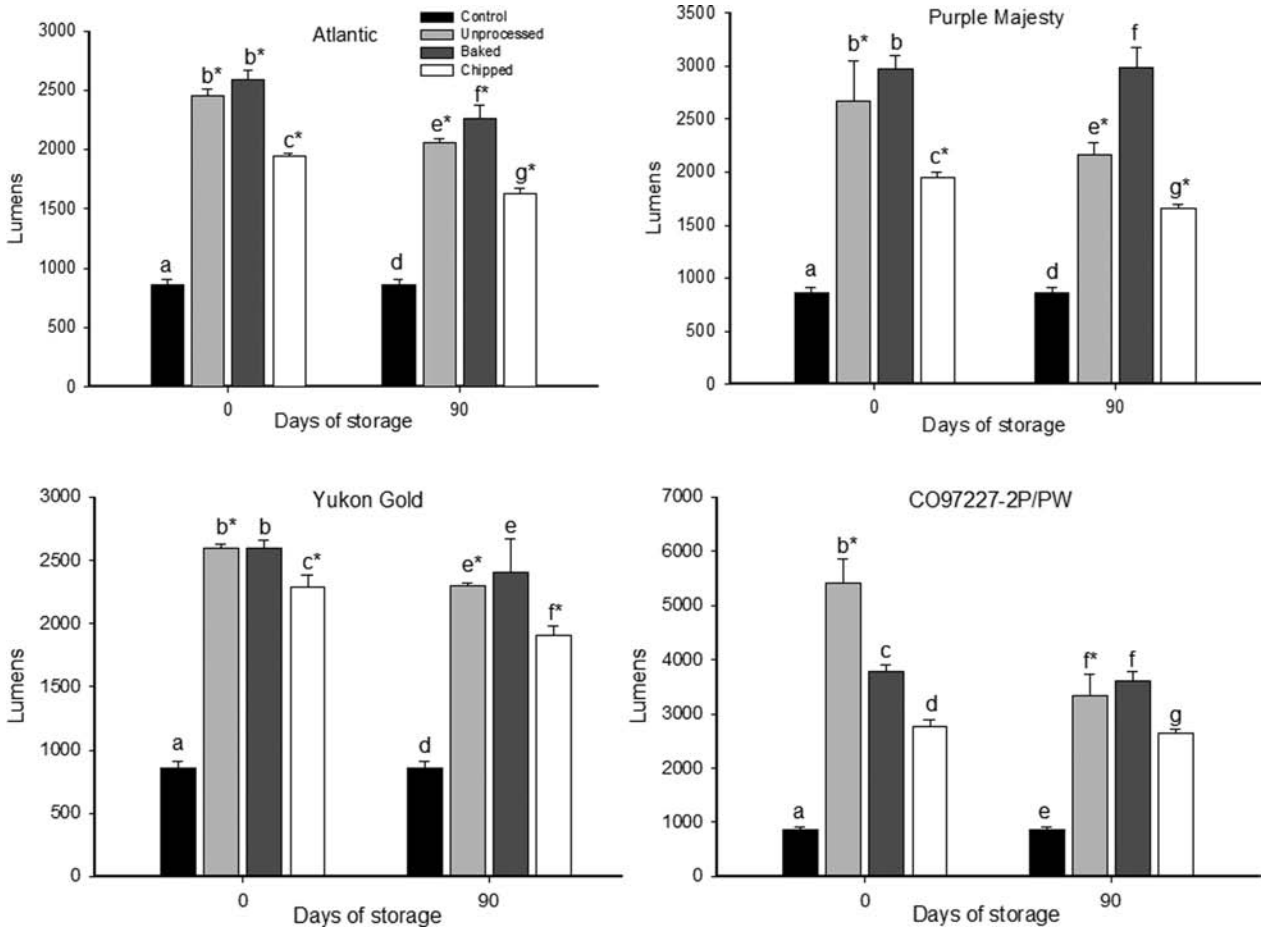

Figure 3. Baking retained while chipping suppressed pro-apoptotic activity in most potato clones at 30 μg GAE/mL concentration in HCT-116 human colon cancer cells. Values with different letters in each graph indicate significant difference ($p < 0.05$) between apoptotic cells for different processing methods at a given time point. Asterisk (*) indicates a significant difference ($p < 0.05$) between apoptotic cells at 0 and 90 DOS for a given processing method. Results are presented as mean ± SE of four replicates for each time point.

operations need to be systematically studied and optimized for maximizing bioactivity in fruits and vegetables and thus serve as effective delivery mechanisms for health-promoting compounds.

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Notes

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