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Glycoalkaloid Development during Greening of Fresh Market Potatoes (*Solanum tuberosum* L.)

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Chlorophyll and glycoalkaloid synthesis in potato (*Solanum tuberosum L.*) tubers occur in direct response to light. The two processes are concurrent, but independent. Color photographic indices to subjectively grade fresh market potatoes for the extent of greening were developed under lighting conditions consistent with those of retail markets. Total glycoalkaloid (TGA) and chlorophyll accumulation for four cultivars were determined over the respective greening scales, thus calibrating the scales for TGA content. On average, TGA concentrations in complete longitudinal sections of tubers (flesh samples) were highest in Dark Red Norland followed by Russet Norkotah, Yukon Gold, and White Rose. TGA concentrations of flesh samples of White Rose and Yukon Gold tubers were somewhat variable and did not increase in direct proportion to greening level and chlorophyll content, particularly at higher levels of greening. TGA concentrations in Dark Red Norland and Russet Norkotah tubers were highly correlated ($P \leq 0.001$) with greening level and chlorophyll concentrations. When averaged over greening levels, skin samples contained 3.4- to 6.8-fold higher concentrations of TGAs than flesh samples, depending on the cultivar. The TGA concentration in periderm samples ranged from 37 to 160 mg/100 g of dry wt. Regardless of greening level, concentrations of TGAs in the flesh samples (including attached periderm) remained within limits presumed safe for human consumption. Discrimination of greened tubers on the basis of perceived glycoalkaloid toxicity is likely unfounded for the cultivars and greening levels studied.

KEYWORDS: ***Solanum tuberosum*; greening; chlorophyll development; light; potato tubers**

INTRODUCTION

When potato (*Solanum tuberosum* L.) tubers are exposed to light, a greening reaction occurs (*1*), along with a concomitant increase in the amount of glycoalkaloids (*2*). Glycoalkaloids are a naturally occurring and toxic group of secondary plant compounds common in members of the Solanaceae. Glycoalkaloids are found in all parts of the potato plant, with concentrations highest in the flowers and lowest in the tubers (*3*). Once formed, glycoalkaloids do not degrade and are not destroyed by heat or cooking (*1*, *4*).

Compared to other common poisons, glycoalkaloids are relatively toxic. Estimates of lethal dose are variable and range from 1.75 mg/kg body weight (*5*) to 3−6 mg/kg body weight (*6*). In comparison, strychnine and arsenic are acutely toxic at 5 and 8 mg/kg body weight, respectively. The Joint Expert Committee on Food Additives (JECFA) of the FAO/WHO (*7*) could not determine a safe level of intake of the naturally occurring potato glycoalkaloids, solanine and chaconine, but concluded that 20−100 mg/kg fresh weight were of no concern based on historical consumption trends. The mechanism of glycoalkaloid toxicity is twofold: disruption of the phospholipids in membranes (*8*) and inhibition of acetylcholinesterase (*9*), the latter of which results in depression of the central nervous system and the neurological effects observed during poisoning (hallucinations, convulsions, depression, etc.).

Although no metabolic connection between chlorophyll and glycoalkaloid accumulation has been established, green tubers are perceived as less fit for human consumption and are rejected by the industry and consumers. It is estimated that between 14 and 17% of the U.S. potato crop is lost annually due to greening of tubers (*5*). While green potatoes are routinely culled from retail displays, the process is subjective and variable, due to the absence of specific grading criteria. Greening scales, based on objective measurements of chlorophyll and color, were recently developed as an aid to maintain a standard level of quality in wholesale and retail outlets (*10*). These greening scales were shown to be effective for assessing the levels of greening encountered in a range of cultivars in retail markets (*11*). The objectives of the present study were to (1) calibrate the greening scales for glycoalkaloid concentrations, (2) characterize chlorophyll/glycoalkaloid relationships for each cultivar, and (3) assess the variability among red-, russet-, and white-skinned cultivars for glycoalkaloid development.

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MATERIALS AND METHODS

Plant Materials and General Procedures. Potato tubers (cvs. White Rose, Yukon Gold, Russet Norkotah, Dark Red Norland) were purchased in 23 kg boxes from a local grocery store directly off the supply truck. These potatoes are therefore representative of those normally subjected to greening in stores. All tubers were stored at 4 °C and 95% relative humidity in darkness prior to use. Light intensities and temperatures for the various greening studies (see below) were chosen to match those typically found in grocery stores, as determined in prior surveys of major retailers in the local area (*10*). Light intensity was measured with a quantum sensor (model LI-185B, Li-Cor, Inc., Lincoln, NB) as photosynthetic photon flux density (PPFD, μmol quanta m^{-2} s^{-1}) in the 400−700 nm range. A Nikon Cool-Pix 950 digital camera (Nikon Corp, New York) was used to document the extent of greening.

Glycoalkaloids were measured for both flesh and periderm samples. For flesh samples, greened tubers were cut in half longitudinally to separate green and nongreened portions. A thin slice (approximately 1.5 mm thick, periderm attached) was removed from the cut surface of one tuber half. Samples of periderm for chlorophyll analysis were taken from the greened half with a cork-borer as described below. The remaining periderm from the light-exposed side of the tuber was then excised and used for glycoalkaloid analysis (see below).

Replication of Greening Scales. To produce the greening levels for each cultivar (**Figures 1**−**4**), tubers were placed daily on a light table (24-h photoperiod, 6.8 μmol quanta m^{-2} s^{-1} of PPFD at tuber level, 23 °C) and greened for up to 10 days. The Sylvania RapidStart SuperSaver 34 W Cool White fluorescent lights had spectral peaks at 360, 410, 435, 545, and 575 nm, simulating standard retail conditions (*11*). The tubers were set out in reverse chronological order (the potatoes that would be greening for the longest were placed out first) so that all durations of greening could be sampled simultaneously at the end of the study. The tubers were repositioned randomly on the light table daily to minimize the effects of variation in light intensity. With use of the previously developed greening scales (*10*), tubers were selected visually after 10 days to match each level of the greening scale for each cultivar (three replicates of three tubers for each level of the scales shown in **Figures 1**−**4**). Objective color measurements (CIELAB units $L^*a^*b^*$) were taken with a colorimeter (Minolta Chroma Meter, model CR-200, Minolta Corp., Ramsey, NJ) and hue angle was calculated (*12*) to verify that the greening levels were consistent with the previously established scales (*10*). Chlorophyll and total glycoalkaloids were extracted and quantified from tubers representing each level of the greening scales.

Chlorophyll Extraction and Measurement. After greening, four cores were cut at random from each potato tuber (perpendicular to the apical and basal axis) using a 15-mm-diameter cork borer. A thin slice (approximately 2 mm thick) including the periderm was cut from the end of each core, representing the surface of the tuber exposed to light (total surface area = 7.065 cm^2/tuber). The 12 disks from each sample (three tubers per replicate) were collectively diced into smaller pieces, frozen at −85 °C, and lyophilized. The lyophilized tissue was ground to a fine powder with mortar and pestle and chlorophyll was extracted with 9 mL of *N*,*N*-dimethylformamide (*13*). The extracts were vortexed, covered with foil to exclude light, and refrigerated at 4 °C for 24−72 h. The extracts were then centrifuged twice for 15 min at 2500*g* and A_{647} and $A_{664.5}$ were measured using a Cary 100 Bio UV−visible double-beam spectrophotometer (Varian Instruments, Walnut Creek, CA). Total chlorophyll concentration was calculated as described by Inskeep and Bloom (*13*).

Determination of Glycoalkaloid Concentration. Ground lyophilized potato tissue (500 mg of periderm or flesh samples) was extracted according to Bergers (*14*) and the glycoalkaloids obtained were dissolved in 0.5 mL of 7% (v/v) phosphoric acid and stored at −20 °C. To quantify total glycoalkaloid (TGA) content, 200 μL of extract was added to 1 mL of 0.03% (w/v) paraformaldehyde in concentrated phosphoric acid. After developing for 20 min, A_{600} was measured and TGA concentration was determined based on an α-solanine (Sigma-Aldrich, St. Louis, MO) standard curve. Results are expressed on a dry weight basis.

Data Analysis. Data were subjected to analysis of variance with greening levels and TGA concentrations as independent and dependent variables, respectively. Sums of squares were partitioned into linear, quadratic, or cubic trends. Polynomial models and coefficients of determination are reported. Data are plotted with 95% confidence intervals.

RESULTS

Cv. White Rose. Chlorophyll concentration increased relatively slowly from green-0 to green-2, followed by a more rapid increase through green-9 (**Figure 1**). This resulted in chlorophyll concentrations that were higher than those previously characterized (*10*) at similar levels of greening for this cultivar. The increase in chlorophyll concentration was 17-fold over the 10-level greening scale in this study (from 0.25 to 4.27 μg/cm^2) versus 11-fold (from 0.25 to 2.75 μg/cm^2) in a previous study (*10*). Despite the differences in chlorophyll content of tubers between the two studies, *L*-values and hue angles were comparable with those characterized previously at each level of the greening scale (data not shown), confirming the consistency with which tubers can be subjectively sorted based on color.

The changes in total glycoalkaloid (TGA) content of flesh (longitudinal slices including periderm) and peel (periderm plus approximately 1.5 mm internal tissue) with greening level and chlorophyll concentration were best described by cubic polynomials ($P \leq 0.01$) (**Figure 1**), which accounted for 73−90% of total variation. Flesh TGAs increased approximately 2.3-fold from green-0 to green-3, remained relatively constant at an average of 16 mg/100 g of dry wt from green-3 to green-7, and then increased another 41% through green-9. A similar trend was apparent for the periderm (skin) TGA concentrations which were substantially higher than those of the flesh samples.

The increase in flesh TGAs from green-0 to green-9 was 3.1-fold (from 6.9 to 23.5 mg/100 g of dry wt) (**Figure 1**). Hence, the TGA content of a green-9 tuber was only about one-fifth of that commonly accepted as the upper limit (200 μg/g of fresh wt or approximately 1 mg/g of dry wt) for food safety within the potato industry (*15*−*17*). Concerns regarding buildup of toxic glycoalkaloids in the flesh of green cv. White Rose potatoes under retail lighting conditions are thus unfounded according to industry standards and JECFA guidelines (*7*). It is also improbable that the level of glycoalkaloids in green-9 tubers would adversely affect flavor. TGA-induced bitterness is generally not a problem until concentrations reach 13−15 mg/100 g of fresh wt (approximately 65−75 mg/100 g of dry wt, depending on taste thresholds) (*2*).

As expected, glycoalkaloid concentrations were much more concentrated in the periderm than in the flesh samples (**Figure 1**). Periderm concentrations increased from 77 to 137 mg/100 g of dry wt as greening level increased from 0 to 9, resulting in levels that were 11- and 6.4-fold higher, respectively, than the flesh concentrations in green-0 and green-9 tubers. The periderm TGA concentrations thus exceeded those commonly accepted by industry, reaching levels that would adversely affect flavor (*2*). The concentrations (mg/100 g of dry wt) of TGA in both the periderm and flesh samples of cv. White Rose tubers can be estimated for the given levels of greening and chlorophyll content from the polynomial equations in **Figure 1**.

Cv. Yukon Gold. As with cv. White Rose, chlorophyll concentration increased relatively slowly as Yukon Gold tubers greened from 0 to 3, followed by a more rapid increase through green-7 (**Figure 2**). The chlorophyll concentration of periderm was also higher than that previously characterized (*10*) for

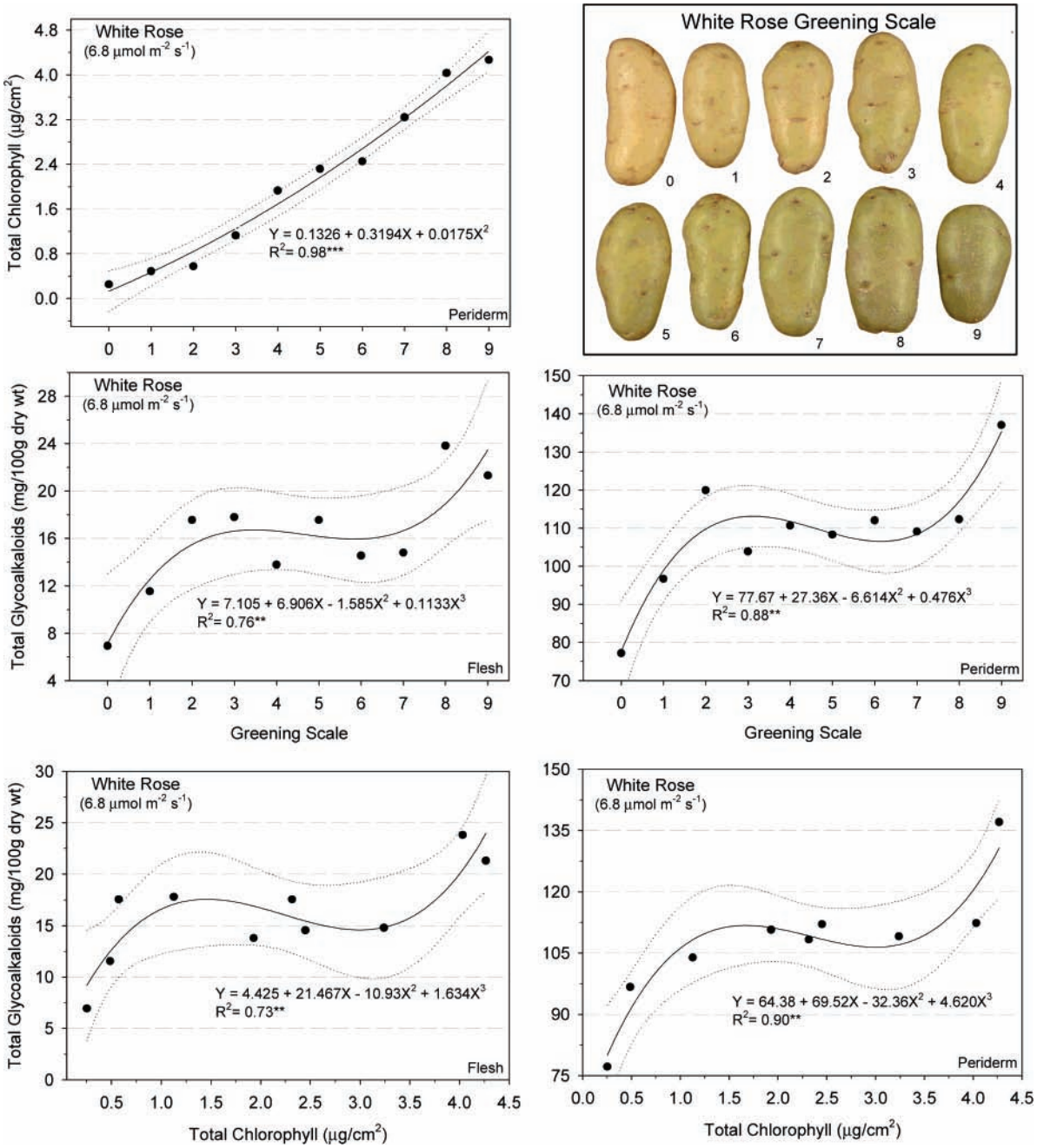

Figure 1. Changes in total chlorophyll and glycoalkaloids in cv. White Rose tubers over the 10-level greening scale. Tubers were incubated under cool white fluorescent light (6.8 μmol quanta m^{-2} s^{-1}, PPFD) for 24 h/day. Chlorophyll was extracted from 1 mm thick × 1.5 cm diameter disks of periderm from the light-exposed side of the tuber. Glycoalkaloids were extracted from a complete longitudinal section representing the entire tuber (flesh samples, left panel) or from periderm (right panel). Dotted lines indicate 95% confidence intervals. ** and *** *F*-values for the regressions were significant at $P \leq 0.01$ and 0.001 levels, respectively.

similar levels of greening. Chlorophyll concentration increased 20-fold (from 0.20 to 4.17 μg/ cm^2) from green-0 to green-7 (**Figure 2**). This compares with a 3.4-fold increase characterized in the former study (*10*). However, similar to cv. White Rose, the disparity in tuber chlorophyll content between studies did not affect the ability to subjectively select cv. Yukon Gold tubers representing each level on the scale. Changes in color (*L*-values and hue angles) of tubers with increasing level of greening were comparable with those characterized in Grunenfelder et al. (*10*) (data not shown). Hence, at a particular level of greening, chlorophyll content may vary somewhat and is not the sole determinant of the subjectively assessed color for the cvs. Yukon Gold and White Rose.

TGA content of flesh samples was somewhat variable, increasing predictably over the first five greening levels only (**Figure 2**). We speculate that TGA concentration remains relatively constant from green-4 to green 7 (as indicated by the dashed line in **Figure 2**); however, further studies will be needed to fully characterize the relationship at the higher greening levels. The TGA concentration of tuber flesh increased 41% as tubers greened from zero to level four on the scale. In contrast to flesh samples, TGA concentration of the periderm was highly correlated with greening over the entire scale, increasing 139% as tubers greened from level 0 to 7. The relationship was best described by a quadratic polynomial ($R^2 = 0.90$, $P \leq 0.01$) with TGA concentration increasing only 34% over the first four

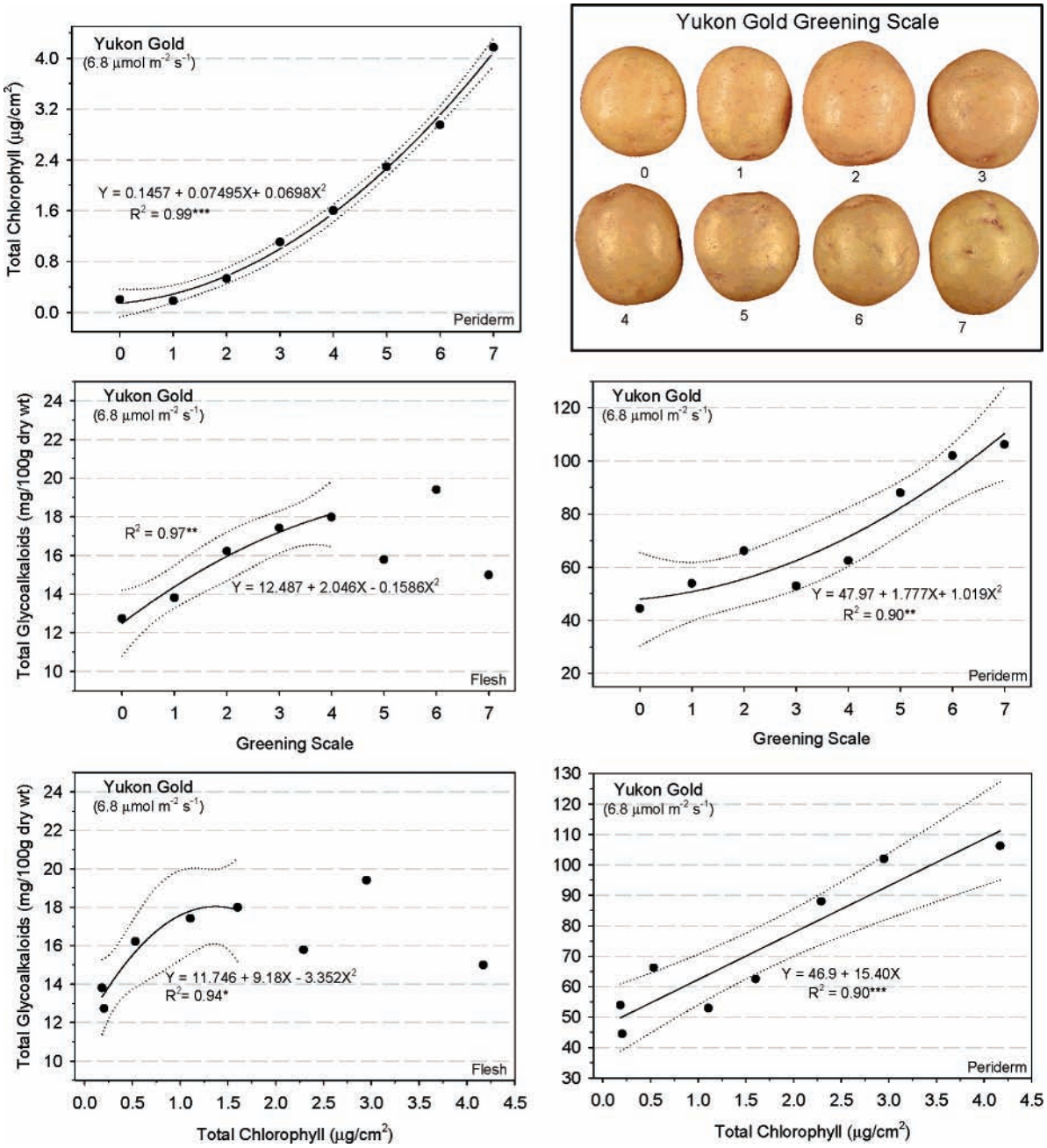

Figure 2. Changes in total chlorophyll and glycoalkaloids (TGA) in cv. Yukon Gold tubers over the 8-level greening scale. Tubers were incubated under cool white fluorescent light (6.8 μmol quanta m^{-2} s^{-1}, PPFD) for 24 h/day. Chlorophyll was extracted from 1 mm thick × 1.5 cm diameter disks of periderm from the light-exposed side of the tuber. TGAs were extracted from a complete longitudinal section representing the entire tuber (flesh samples, left panel) or from periderm (right panel). TGA regressions in flesh samples are valid for the first five greening levels only. Dashed lines indicate speculated trends at higher levels of chlorophyll from green-5 through green-7 (see Results). Dotted lines indicate 95% confidence intervals. *, **, and *** *F*-values for the regressions were significant at $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

greening levels and 75% as greening progressed to level 7. On average, TGAs were 5.2-fold more concentrated in the periderm than in the flesh of Yukon Gold tubers.

While no clear relationship was evident between tuber chlorophyll and TGA content of flesh samples above about 1.5 μg/cm^2 chlorophyll (green-4), TGA concentration of the periderm increased linearly ($R^2 = 0.90$, $P \leq 0.001$) with chlorophyll over the entire greening scale (**Figure 2**). Regardless of greening level, TGA content of the flesh remained well below that considered unsafe for human consumption. Concentrations in the periderm of green-6 and green-7 tubers, however, reached levels considered too high for consumption (*16*, *17*). Except for processed potato skin products, high TGA levels in the periderm are of lesser concern than high levels in the flesh, given that the flesh would dilute the periderm during consumption and that the periderm is often removed prior to consumption.

Cv. Dark Red Norland. Total chlorophyll concentration increased at a constant rate of 0.22 μg/cm^2 per greening level as tubers greened over the 8-level scale (**Figure 3**). The rate of chlorophyll increase and the concentration of chlorophyll in tubers at each greening level were comparable with those characterized previously (*10*). Chlorophyll content of tuber periderm increased 5.4-fold from green-0 to green-7. Changes in *L*-value and hue angle with greening level (data not shown) were also consistent with past studies (*10*), demonstrating the

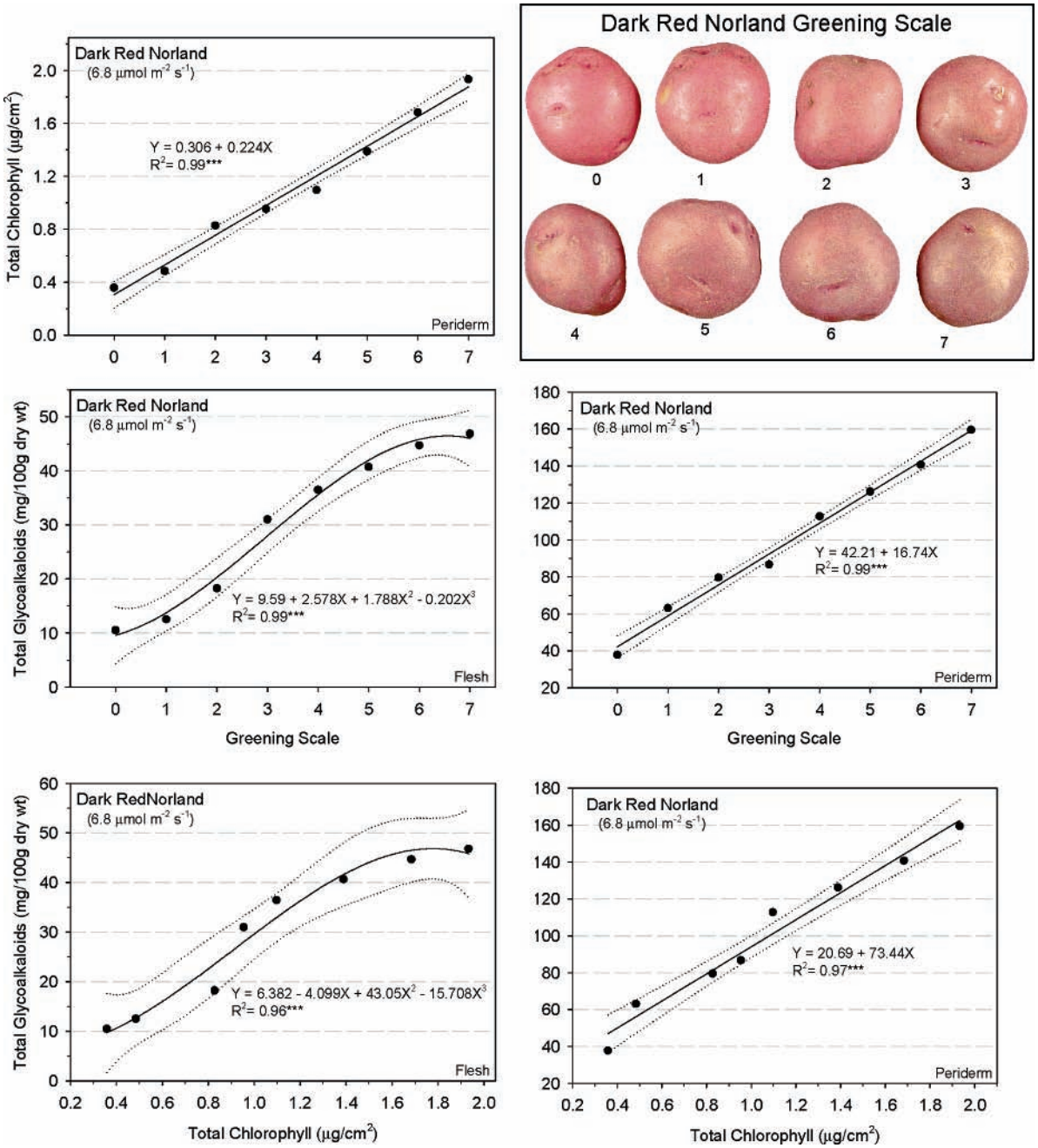

Figure 3. Changes in total chlorophyll and glycoalkaloids in cv. Dark Red Norland tubers over the 8-level greening scale. Tubers were incubated under cool white fluorescent light (6.8 μmol quanta m^{-2} s^{-1}, PPFD) for 24 h/day. Chlorophyll was extracted from 1 mm thick × 1.5 cm diameter disks of periderm from the light-exposed side of the tuber. Glycoalkaloids were extracted from a complete longitudinal section representing the entire tuber (flesh samples, left panel) or from periderm (right panel). Dotted lines indicate 95% confidence intervals. ***F-values for the regressions were significant at $P \leq 0.001$.

close relationships between the objective measures of color (L-value, hue angle) and chlorophyll, and the subjective perception of greening as assessed with the greening scale for this particular cultivar.

The changes in TGA content of flesh samples with greening level and chlorophyll concentration were best described by cubic polynomials (**Figure 3**). Flesh TGA content increased approximately 74% from green-0 to green-2, 123% from green-2 to green-5, and only 15% from green-5 to green-7. The TGA increase was 4.5-fold (from 10.5 to 46.8 mg/100 g of dry wt) over the 8-level greening scale, but the highest level in green-7 tubers was still less than half the maximum safe concentration accepted within the industry (*16*). Unlike cvs. Yukon Gold and White Rose, increases in TGAs paralleled increases in chlorophyll during greening. TGA content of complete longitudinal samples of Dark Red Norland tubers can thus be estimated from greening level and/or periderm chlorophyll concentration with the polynomial equations presented in **Figure 3**.

As in the previous two cultivars, glycoalkaloid concentrations were much more concentrated in the periderm than in the flesh samples of Dark Red Norland tubers. Periderm TGA concentrations ranged from 38 to 159 mg/100 g of dry wt, increasing linearly over the greening scale ($R^2 = 0.99$, $P \leq 0.001$) and with chlorophyll concentration ($R^2 = 0.97$, $P \leq 0.001$). Hence, the TGA concentration of skin samples can also be estimated based on greening level and chlorophyll concentration. As tuber greening increased beyond level 3, TGA concentrations in skin samples exceeded the upper limit (20 mg/100 g of fresh wt)

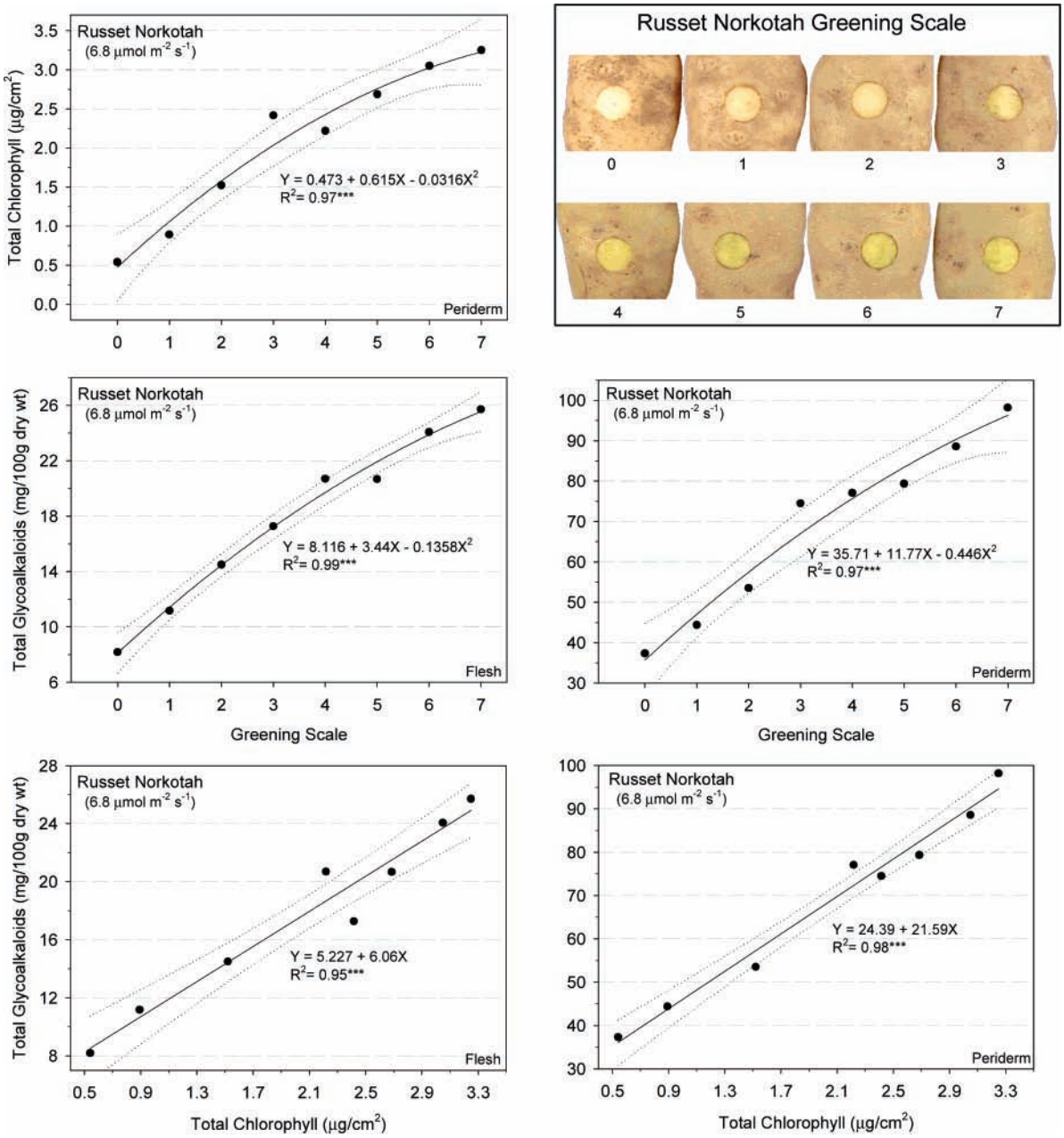

Figure 4. Changes in total chlorophyll and glycoalkaloids in cv. Russet Norkotah tubers over the 8-level greening scale. Tubers were incubated under cool white fluorescent light (6.8 μmol quanta m^{-2} s^{-1}, PPFD) for 24 h/day. Chlorophyll was extracted from 1 mm thick × 1.5 cm diameter disks of periderm from the light-exposed side of the tuber. Glycoalkaloids were extracted from a complete longitudinal section representing the entire tuber (flesh samples, left panel) or from periderm (right panel). Dotted lines indicate 95% confidence intervals. ***F-values for the regressions were significant at $P \leq 0.001$.

recommended for food safety (*4*), a cause for concern for processed potato skin products. However, peeling during preparation or dilution by the flesh during consumption of unpeeled tubers would likely negate any potential danger posed by TGA toxicity in fresh market potatoes. While TGAs increase in parallel with greening of Dark Red Norland tubers, it is unlikely that concentrations would become sufficiently high to induce acute health effects under the lighting conditions common in retail markets, given surveys which document that the extent of greening rarely exceeds level 8 prior to sale (*11*).

Cv. Russet Norkotah. Chlorophyll concentrations were highly correlated with greening levels of Russet Norkotah tubers, increasing 6-fold over the 8-level greening scale (**Figure 4**). Moreover, the change in chlorophyll concentration per greening level, along with the concentration of chlorophyll in the periderm of tubers at each greening level, were consistent with those described previously (*10*). L-values and hue angles fell within the expected ranges (data not shown), characterizing the progressive darkening and changes in color expected for the various greening levels of this cultivar (*10*).

TGA concentration (flesh samples) increased 3.1-fold (from 8.2 to 25.7 mg/100 g of dry wt) as tubers greened from 0 to level-7 and the relationship was best described by a second-order polynomial ($P \leq 0.001$) (**Figure 4**). TGAs increased at a rate of 6.1 mg/100 g of dry wt for every $\mu g/cm^2$ increase in chlorophyll content of the skin. Therefore, the subjective greening scale and chlorophyll content are good predictors of the TGA content in the flesh of tubers of this cultivar. The TGA content of flesh samples from green-7 tubers was about 26 mg/

100 g of dry wt, which is 3.8-fold lower than the upper limit considered safe by industry (*4, 16*).

On average, the TGA concentration was 3.8-fold more concentrated in the periderm than in the flesh samples of Russet Norkotah tubers. Periderm TGA concentrations ranged from 37.3 to 98.2 mg/100 g of dry wt and increased quadratically with greening scale ($R^2 = 0.97$, $P \leq 0.001$) and linearly with chlorophyll concentration ($R^2 = 0.98$, $P \leq 0.001$). Hence, the TGA concentration of skin samples can also be estimated based on greening level and chlorophyll concentration. TGA concentrations in skin samples never exceeded the 20 mg/100 g of fresh wt (approximately 1 mg/g of dry wt) safety limit (*15, 16*). However, TGA levels in the skin of tubers that had greened beyond level 3 on the greening scale were probably high enough (>65 mg/100 g of dry wt) to affect flavor (e.g., increased bitterness) (*2, 18*). TGA levels in the flesh were too low to influence flavor. While TGAs increased in parallel with greening of cv. Russet Norkotah tubers in response to the lighting conditions present in retail markets, the concentrations remained below the level considered a health risk to humans.

DISCUSSION

In contrast to the relatively high light intensities (up to 250 μmol quanta m^{-2} s^{-1}, PPFD) and greening time periods (15−20 days) of past studies (*4, 16, 19, 20)*, the conditions employed in this study more closely simulated those present in retail environments (*10*). The results thus represent the extent of greening and TGA accumulation that could be encountered in stores and are therefore directly applicable to the industry. The lower light intensities and shorter durations of exposure used in this study, however, resulted in smaller changes in TGAs than reported in past studies (*19*), reducing the ability to resolve differences in TGA among the greening levels, particularly for flesh samples.

Variability in light-induced chlorophyll and TGA accumulation among cultivars may be due in part to variations in tuber maturity, tuber size, thickness of skin, and presence of accessory pigments. These pigments may act as "natural" light filters, affecting the quality of light penetrating the outer periderm, thereby influencing the rates of chlorophyll and TGA accumulation. Indeed, Percival (*19*) showed that chlorophyll and TGAs increased to a lesser extent under mercury vapor lighting compared with fluorescent and high-pressure sodium lighting, all of which vary in emission spectra. The fluorescent and high-pressure sodium lights that dominate retail market displays contain ultraviolet and infrared wavelengths that are efficient elicitors of glycoalkaloid and chlorophyll synthesis (*19*).

TGA concentrations decrease in all parts of the potato plant (including tubers) as fresh and dry matter increase with maturity (*3, 6*). It is well-documented that immature and small tubers have higher concentrations of glycoalkaloids, likely due in part to the high surface area-to-volume ratio of the smaller potatoes (*21*). Therefore, early potatoes (such as cv. Dark Red Norland) that tend to be smaller would likely have higher TGAs at harvest than later varieties grown full season that tend to produce larger tubers. Stresses (both pre- and post-harvest) can also enhance tuber TGA concentrations (*3*). However, the two most significant factors affecting TGA concentrations are light (*2, 19*) and cultivar (*2, 22*).

Previous surveys showed wide variation in tuber greening among retail markets and the greening scales (**Figures 1−4**) accounted for the entire range of greening encountered for each cultivar (*11*). While the extent of correlation between greening level and TGA content was cultivar-dependent, in general, higher TGA concentrations were associated with higher greening levels for all cultivars. Therefore, TGA content of fresh market potatoes in stores is expected to be highly variable. Despite this variability, the levels of TGAs that developed in the flesh of tubers in response to the low PPFD lighting conditions characteristic of retail markets were within levels considered safe for human health (*4, 15, 16*), and well under the toxic levels reported by Morris and Lee (*6*). Nevertheless, some authors have questioned the acceptance of 200 μg/g fresh weight as a safe level of total glycoalkaloids in tubers (*23, 24*). They point out that subacute effects of glycoalkaloids such as mild gastrointestinal upset are not identified as such and thus are not connected with the consumption of potatoes. Also, chronic effects have not been adequately defined for humans or animal test subjects. Mensinga et al. (*25*) demonstrated the serum half-life of ingested GAs to be greater than 24 h, thereby posing a potential hazard to individuals who consume low levels of potato TGAs daily.

In summary, tubers sorted subjectively using the greening scales displayed the expected degree of darkening (*L*-value) and color (hue angle) changes previously characterized for the greening levels (*10*). Chlorophyll content was directly correlated with greening level but varied for two of the cultivars (White Rose and Yukon Gold) between studies. These results indicate that chlorophyll is not the sole determinant of tuber surface color. The perceived color is undoubtedly affected by complex interactions among chlorophyll content, accessory pigments, periderm thickness, and flesh color.

Greening scales for cvs. White Rose, Yukon Gold, Dark Red Norland, and Russet Norkotah were calibrated for TGA levels. While both flesh and skin TGA concentrations increased with greening level, the latter was more highly correlated with greening level than the former. Also, in cv. Yukon Gold, the TGA correlation with greening level was stronger in tubers with less greening and was lost at higher greening levels, especially after green-4. In contrast, TGAs increased in tubers of cvs. Dark Red Norland and Russet Norkotah over the entire greening scale. Differences in the degree of light-induced TGA development among the cultivars were also apparent. Before greening, TGAs ranged from 6.9 to 13 mg/100 g of dry wt (flesh samples) in cvs. White Rose and Yukon Gold, respectively. After greening, TGAs in flesh samples of Yukon Gold reached a maximum of 19.4 mg/100 g of dry wt, compared to 23.8 mg/100 g of dry wt in cv. White Rose and 46.8 mg/100 g of dry wt in cv. Dark Red Norland. Regardless of cultivar, TGA concentrations in the flesh of even the greenest tubers were well below the limit considered unsafe for human consumption. While the change in tuber color during greening certainly decreases the appeal of tubers to the industry and consumers, discrimination against greened tubers on the basis of perceived TGA acute toxicity is unfounded for the cultivars and greening levels studied. The effects of chronic low doses of TGAs, particularly in light of prolonged serum half-life, requires further study and may result in revision of food safety guidelines for potatoes.

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LITERATURE CITED

(1) Anstis, B. J. P.; Northcote, D. J. Development of chloroplasts from amyloplasts in potato tuber discs. *New Phytol.* **1973**, *72*, 449−463.

(2) Edwards, E. J. Ph.D. Thesis, Nottingham Trent University, Nottingham, UK, 1997.

(3) Friedman, M.; McDonald, G. M. Potato glycoalkaloids: chemistry, analysis, safety, and plant physiology. *Crit. Rev. Plant Sci.* **1997**, *16*, 55−132.
(4) Sotelo, A.; Serrano, B. High-performance liquid chromatographic determination of the glycoalkaloids α-solanine and α-chaconine in 12 commercial varieties of Mexican potato. *J. Agric. Food Chem.* **2000**, *48*, 2472−2475.
(5) van Gelder, W. M. J. Chemistry, toxicology, and occurrence of steroidal glycoalkaloids: potential contaminants of the potato (*Solanum tuberosum* L.). In *Poisonous Plant Contamination of Edible Plants*; Rizk, A., Ed.; CRC Press: Boca Raton, FL, 1991; pp 117−156.
(6) Morris, S. C.; Lee, T. H. The toxicity and teratogenicity of *Solanaceae* glycoalkaloids, particularly those of the potato (*Solanum tuberosum*). *Food Technol.* **1984**, *36*, 118−124.
(7) Joint FAO/WHO Expert Committee on Food Additives. Solanine and chaconine in *Toxicological Evaluation of Certain Food Additives and Naturally Occurring Toxicants*; 39th Meeting of the JECFA, WHO Additives Series 30; World Health Organization, Geneva, 1993.
(8) Roddick, J. G**.** The acetylcholinesterase-inhibitory activity of steroidal glycoalkaloids and their aglycones. *Phytochemistry* **1989**, *28*, 2631−2634.
(9) Orgell, W. H.; Vaidya, K. A.; Dahm, P. A. Inhibition of human plasma cholinesterase in vitro by extracts of solanaceous plants. *Science* **1958**, *128*, 1136−1137.
(10) Grunenfelder, L. A.; Hiller, L. K.; Knowles, N. R. Color indices for the assessment of chlorophyll development and greening of fresh market potatoes. *Postharvest Biol. Technol.* **2006**, *40*, 73−81.
(11) Grunenfelder, L. A. M.S. Thesis, Washington State University, Pullman, WA, 2005; 114 pp.
(12) McGuire, R. G. Reporting of objective color measurements. *HortScience* **1992**, *27*, 1254−1255.
(13) Inskeep, W. P.; Bloom, P. R. Extinction coefficients of chlorophyll *a* and *b* in *N*,*N*-dimethylformamide and 80% acetone. *Plant Physol.* **1985**, *77*, 483−485.
(14) Bergers, W. W. A. A rapid quantitative assay for solanidine glycoalkaloids in potatoes and industrial potato protein. *Potato Res.* **1980**, *23*, 105−110.
(15) Percival, G. C. Light-induced glycoalkaloid accumulation of potato tubers (*Solanum tuberosum* L.). *J Sci. Food Agric.* **1999**, *79*, 1305−1310.
(16) Edwards, E. J.; Cobb, A. H. Effect of temperature on glycoalkaloid and chlorophyll accumulation in potatoes (*Solanum tuberosum* L. cv. King Edward) stored at low photon flux density, including preliminary modeling using an artificial neural network. *J. Sci. Food Agric.* **1997**, *45*, 1032−1038.
(17) Sinden, S. L.; Sanford, L. L.; Webb, R. E. Genetic and environmental control of potato glycoalkaloids. *Am. Potato J.* **1984**, *61*, 141−156.
(18) Sinden, S. L.; Deahl, K. L.; Aulenbach, B. B. Effect of glycoalkaloids and phenolics on potato flavour. *Food Sci.* **1976**, *41*, 520−523.
(19) Percival, G. C. The influence of light upon glycoalkaloid and chlorophyll accumulation in potato tubers (*Solanum* tuberosum L). *Plant Sci.* **1999**, *145*, 99−107.
(20) Reeves, A. Varietal differences in potato tuber greening. *Am. Potato J.* **1988**, *65*, 651−658.
(21) Wolf, M. J.; Duggar, B. N. Estimation and physiological role of solanine in the potato. *J. Agric. Res.* **1946**, *73*, 1−32.
(22) Griffiths, D. W.; Dale, M. F. B.; Bain, H. The effect of cultivar, maturity, and storage on photo-induced changes in the total glycoalkaloid and chlorophyll contents of potatoes (*Solanum tuberosum*). *Plant Sci.* **1994**, *98*, 103−109.
(23) Smith, D. B.; Roddick, J. G.; Jones, J. L. Potato glycoalkaloids: Some unanswered questions. *Trends Food Sci. Technol.* **1996**, *7*, 126−131.
(24) Korpan, Y. I.; Nazarenko, E. A.; Skryshevskaya, I. V.; Martelet, C.; Jaffrezic-Renault, N.; El'skaya, A. V. Potato Glycoalkaloids; True safety or false sense of security? *Trends Biotechnol.* **2004**, *22*, 147−151.
(25) Mensinga, T. T.; Sips, A. J. A. M.; Rompelberg, C. J. M.; van Twillert, K.; Meulenbelt, J.; van den Top, N. J.; van Egmond, N. P. Potato Glycoalkaloids and adverse effects in humans; an ascending dose study. *Regul. Toxicol. Pharmacol.* **2005**, *41*, 66−72.

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