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Modification of the Health-Promoting Value of Potato Tubers Field Grown under Drought Stress: Emphasis on Dietary Antioxidant and Glycoalkaloid Contents in Five Native Andean Cultivars (*Solanum tuberosum* L.)

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The effects of drought stress on dietary antioxidant and glycoalkaloid contents in potato tubers were investigated using a selection of five native Andean cultivars. Both freshly harvested and 4 month-stored tubers were analyzed. Responses to drought stress were highly cultivar-specific. The antioxidant contents of the yellow tuber-bearing cultivars (Sipancachi and SS-2613) were weakly affected by the drought treatment, whereas the pigmented cultivars demonstrated highly cultivar-dependent variations. A drastic reduction of anthocyanins and other polyphenols was revealed in the red- (Sullu) and purple-fleshed (Guincho Negra) cultivars, whereas an increase was shown in the purple-skinned and yellow-fleshed cultivar (Huata Colorada). The hydrophilic antioxidant capacity (evaluated by Folin−Ciocalteu and H-oxygen radical absorbance capacity assays) was highly correlated with the polyphenol content and followed, therefore, the same behavior upon drought. Carotenoid contents, including β-carotene, as well as vitamin E, tended to increase or remain stable following drought exposure, except for the cultivar Sullu, in which the level of these lipophilic antioxidants was decreased. Vitamin C contents were not affected by drought with the exception of Guincho Negra, in which the level was increased. These variations of health-promoting compounds were associated with increased or stable levels of the toxic glycoalkaloids, α-solanine and α-chaconine. Storage at 10 °C for 4 months tended to decrease the concentrations of all dietary antioxidants, except those of vitamin E. This storage also reduced the drought-induced variations observed in freshly harvested tubers. These results were discussed in terms of their implications for human diet and health as well as in plant stress defense mechanisms.

KEYWORDS: Potato; Andean tuber; *Solanum tuberosum*; antioxidant; polyphenols; chlorogenic acid; vitamin C; α-tocopherol; carotenoids; β-carotene; ORAC; glycoalkaloids; solanine; chaconine; drought; genotype; storage

INTRODUCTION

Plants are adversely affected by environmental abiotic stresses, such as drought, high salinity, and low temperature, and biotic stresses, such as pathogen infections. These stress factors prevent plants from reaching their full genetic potential and limit their growth and productivity. Water availability is one of the major limitations to plant productivity (*1*). The different plant responses to drought stress are generally involved in, at least, one of the three following processes: (i) maintenance of osmotic homeostasis, (ii) growth inhibition, and (iii) detoxification (*2*, *3*). The latter mechanism comprises the protection of the plant against oxidative stress. Indeed, plants produce reactive oxygen species (ROS) during normal metabolism, and under periods of stress, such as drought, the production of ROS can be increased. Therefore, plants have evolved very efficient scavenging systems for ROS to protect themselves from destructive oxidative reactions. The antioxidant defense system

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of plants encompasses a wide range of enzymes like superoxide dismutase, catalase, or ascorbate peroxidase and also some nonenzymatic antioxidants like ascorbate, glutathione, carotenoids, polyphenols, or tocopherols (*4*, *5*). The antioxidant responses under drought stress are highly variable and depend on numerous factors such as the species, the cultivar, the developmental stage, the metabolic state of the plant, as well as the duration and intensity of the stress (*3*). Interestingly, the protective functions of the nonenzymatic antioxidants produced in plants are also of great importance for human health. In recent years, evidence has emerged that elevated dietary intake of antioxidants lowers the incidence of oxidative stress disorders such as cancers or cardiovascular diseases (*6*, *7*).

Potato is currently one of the most important food crops worldwide. This staple crop has a remarkable nutritional value with regard to its high carbohydrate content combined with high-quality proteins and notably vitamin C, vitamin B6, vitamin B3, potassium, phosphorus, and magnesium levels (*9*). Potato is also now recognized as a valuable source of health-promoting antioxidants in the human diet (*10*). Besides, the very diverse native Andean potato landraces are of particular interest from a nutritional point of view. Indeed, previous studies performed by our group have highlighted their high genotypic diversity in terms of dietary antioxidants (*11*, *12*) as well as the particularly high levels of zeaxanthin, β-carotene, α-tocopherol, chlorogenic acid, and petanin in certain cultivars (*13*).

As compared with other crops, potato is very sensitive to drought stress (*14*). Numerous authors have reported that limited soil−water availability may affect the potato plant at all developmental stages, resulting in earlier crop maturity and decreased plant growth, tuber yield, number of tubers per plant, as well as tuber size and quality (*15*, *16*). Recent studies have mainly been devoted to identifying drought tolerant cultivars, that is, with limited tuber yields that declined upon drought, as well as unraveling drought tolerant traits either physiologically (*17*) or by molecular approaches (*18*, *19*). However, little attention has been paid to the consequences of drought on the nutritional or health-promoting value of potato tubers. Yet, many plant secondary metabolites are determinants of both plant stress tolerance and nutritional value (*20*). On top of that, investigating the impact of drought on potato tubers is of major importance with regard to the high consumption level of potatoes worldwide and the current context of global warming in which increases of temperature and changes in rainfall distribution will be inevitably linked to increases of drought in certain areas of the globe.

The present study aims at evaluating the effects of drought under field conditions on the health-promoting value of potato tubers. To this end, a panel of five native Andean cultivars has been selected on the basis of their contrasted antioxidant attributes in regular conditions. Specific emphasis has been given to quantifying dietary antioxidants, that is, ascorbate, α-tocopherol, individual carotenoids, and individual polyphenols, as well as hydrophilic antioxidant capacity. Modifications of the level of these molecules are likely to occur since drought is known to modulate the antioxidant response in planta to various extents. Furthermore, during drought stress, potato tubers may also produce some toxic secondary metabolites, mainly as glycoalkaloids (*21*), that may impair their health-promoting properties. In this respect, the contents of the two main glycoalkaloid compounds occurring in potato tuber, α-solanine and α-chaconine, have also been determined in this work. Moreover, as potato tubers can be consumed after a certain period of storage, the impact of drought has been evaluated on both freshly harvested and 4 month-stored tubers.

MATERIALS AND METHODS

Chemicals. Solvents [of analytical or high-performance liquid chromatography (HPLC) grade as required] were obtained from VWR International (Leuven, Belgium). Carotenoid standards (lutein, neoxanthin, violaxanthin, zeaxanthin, antheraxanthin, β-cryptoxanthin, β-carotene, and lutein-5,6-epoxyde) were purchased from Carotenature (Lupsingen, Switzerland). Polyphenols (chlorogenic acid, caffeic acid, gallic acid, tyrosine, tryptophan, and rutin), α-tocopherol, glycoalkaloids (α-solanine and α-chaconine), 2 N Folin−Ciocalteu reagent, fluorescein sodium salt, Trolox (6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid), and 2,2-azinobis (2-amidinopropan) dihydrochlorid (AAPH) were purchased from Sigma-Aldrich (St. Louis, MO). Kaempferol-3-rutinoside was obtained from ExtraSynthese (Genay, France). Petanin (petunidin-3-p-coumaroyl-rutinoside-5-glucoside) was purchased from Polyphenols Laboratories AS (Sandnes, Norway).

Experimental Design and Plant Material. Five potato cultivars from the Andigenum group were included in the study: On the basis of previous results (*13*), 704429-Guincho Negra, 700347-SS-2613, 702535-Sipancachi, and 703905-Huata Colorada were selected for their contrasting dietary antioxidant contents under normal growth conditions; 701997-Sullu was included in the panel for its recently described drought tolerance (*19*, *22*), as well as for its particular flesh feature containing a broad red vascular ring, suggesting an antioxidant pattern different from the other cultivars. Seed tubers from five native Andean potato landraces were transferred on October 8, 2006, in rain-out facilities at the International Potato Center (CIP) experimental station in Huancayo (3280 m above sea level), in a randomized complete block design with four replications (of five plants per genotype). Four rain-out facilities (5 m × 25 m) were used for this experiment, which consisted of screenhouses equipped with roofs protecting the plots from rain and plastic barriers inhibiting uncontrolled water inflow from the sides as well as from below. The plots were filled with humic highland soil at pH 4 to a soil depth of 50 cm. Drip irrigation was installed for controlled watering of the plants. Plants were either fully irrigated (control plants) or submitted to a drought treatment (drought-exposed plants). The drought stress was applied in two screenhouses by withholding irrigation during tuberization on day 86 after planting (January 2, 2007), and plants were exposed to drought for 58 days, until March 1, 2007. In the drought plots, the soil−water content decreased to 30% on average, 37 days after drought onset, and remained at this percentage during the drought treatment, whereas it was maintained at around 45% in the irrigated control plot. The leaf relative water content (RWC) was used to evaluate the plant water status. RWC on drought-exposed potato leaves decreased with time in response to drought treatment in a cultivar-dependent manner and reached the lowest RWC 51 days after drought onset (−12% in Sipancachi to −22% in Guincho Negra as compared to control leaves).

Mature tubers from irrigated and drought plots were harvested on March 27, 2007, and transferred to the laboratory in Lima. Control and drought-exposed tubers were washed, dried, and allowed to stabilize at 10 °C for 2 weeks prior to sampling. Tubers were subsequently divided into two groups. The first group, containing control and drought-exposed tubers from the five genotypes, represented the harvest tubers and were ground and freeze-dried without delay. The second batch of tubers was placed for storage in dark conditions in incubators at 10 °C for 4 months prior to lyophilization. Powdered freeze-dried material was stored at −20 °C under nitrogen prior to extraction and analysis. For each cultivar in each irrigation and storage condition, three samples or biological repetitions (each made up of three whole unpeeled tubers from one plant) were used. Each sample was extracted and analyzed in duplicate.

Polyphenol Analysis. Analysis of polyphenol compounds as well as of the antioxidant aromatic amino acids, tyrosine and tryptophan, was performed as detailed in Andre et al. (*13*). Briefly, extraction was carried out using a solution of methanol/water/acetic acid (80:19.5:0.5; v/v/v). After extract evaporation, compounds were resuspended in water and subjected to HPLC-diode array detector (DAD) analysis

for quantification. The isomers of chlorogenic acid (5-caffeoyl quinic acid, 5-CQA), that is, neochlorogenic (3-CQA) and cryptochlorogenic (4-CQA) acids, were all quantified as 5-CQA equivalents. Polyphenol, tyrosine, and tryptophan contents were expressed in μg g^{-1} DW.

Putative identification of two unknown peaks (phenolic polyamine conjugates) was performed by LC-MS/MS using an Ultimate 3000 HPLC (Dionex, Sunnyvale, CA) coupled with an API 3200 triple quadrupole mass spectrometer (MS) (Applied Biosystems, Foster, CA). Experiments were carried out in positive electrospray ionization (ESI). The MS was operated under the following conditions: curtain gas pressure, 20 psi; capillary voltage, 5500 V; nebulizer and drying gas pressure, 50 psi; and drying gas temperature, 550 °C. MS/MS spectra were recorded between 100 and 300 atomic mass unit (amu), with a collision energy ranging from 10 to 50 V. Filtered polyphenol extracts were injected onto a Nucleodur C18 Pyramid column (250 mm × 4.6 mm internal diameter; 5 μm particle size) (Macherey-Nagel, Düren, Germany). The mobile phases were (A) water with 0.1% formic acid and (B) acetonitrile with 0.1% formic acid. The flow rate was 1.0 mL min^{-1}, and the column temperature was 40 °C. The 95 min gradient was as follows: 0−10 min, 0−9% B; 10−40 min, 9−13% B; 40−80 min, 13−35% B; 80−82 min, 35−100% B; 82−87 min, 100% B; 87−90 min, 100−0% B; and 90−95 min, 0% B.

The total anthocyanins were measured using the pH differential method (*23*). Petanin was used for the standard curve, and total anthocyanins were expressed as petanin equivalents.

Vitamin C Analysis. The vitamin C analysis was performed as described in Andre et al. (*11*). Briefly, vitamin C was extracted using a 5% (w/v) aqueous solution of metaphosphoric acid containing 1% (w/v) dithiothreitol. Isoascorbic acid was added as an internal standard. Ascorbic acid was quantified by HPLC-DAD by measuring its absorbance at 265 nm. The total ascorbate content was expressed in μg g^{-1} DW.

Carotenoid Analysis. Carotenoids were extracted using an acetone solution and were subsequently saponified. Native and saponified carotenoid extracts were then analyzed by HPLC-DAD for quantification as explained in Andre et al. (*13*). Carotenoid contents were expressed in μg g^{-1} DW. The quantity of esters was estimated as the difference in carotenoids between the nonsaponified and the saponified extract. The total carotenoid contents were calculated by summing concentrations of all compounds.

Vitamin E Analysis. α-Tocopherol was extracted and quantified by HPLC using a fluorescence detection according to the method detailed in Andre et al. (*13*). Tocopherol contents were expressed in μg g^{-1} DW.

Hydrophilic Antioxidant Capacity. *Folin−Ciocalteu Assay.* Total phenolics were estimated using the Folin−Ciocalteu assay following the procedure described in Andre et al. (*11*). Total phenolics were expressed as mg of 5-CQA equivalents g^{-1} of dry weight (DW) using a 5-CQA standard concentration curve.

Oxygen Radical Absorbance Capacity (ORAC) Assay. ORAC analyses were performed as explained in Andre et al. (*11*). All samples were analyzed in duplicate at three different dilutions. The final ORAC values were expressed as μmol of Trolox equivalents (TE) g^{-1} DW.

Glycoalkaloid Analysis. The extraction procedure was similar to the one performed for polyphenol extraction. Approximately 150 mg of powdered freeze-dried material was mixed with 1.5 mL of a solution of methanol/water/acetic acid (80:19.5:0.5; v/v/v). This mixture was homogenized using a vortex for 30 s and shaken for 30 min at 4 °C. After centrifugation at 9000*g* for 10 min at 4 °C, the supernatant was collected. Two additional extractions were done on the residue using the same extraction solvent. The supernatants were pooled and evaporated to dryness in a SpeedVac concentrator (Heto, Thermo Electron Corp., Waltham, MA). Glycoalkaloids were resuspended in 500 μL of water, appropriately diluted, and filtered through a 0.45 μm Acrodisc PVDF syringe filter.

A quantification procedure was adapted from Matsuda et al. (*24*). Determination of α-solanine and α-chaconine was performed by LC-MS using a BioLC chromatographic system (Dionex) coupled with a Finnigan MSQ single quadrupole MS detector (ThermoFinnigan, San Jose, CA) equipped with an ESI probe. HPLC analyses were performed on a 100 mm × 1 mm Alltima (C18) reversed phase (RP) column with 3 μm particle size (Grace, Deerfield, IL). Separation at 40 °C was achieved using a binary gradient system consisting of (A) water and (B) acetonitrile, both with 0.1% formic acid. The 18 min gradient was as follows: 0−5 min, 12−30% B; 5−8 min, 30−70% B; 8−9 min, 70−100% B; 9−13 min, 100% B; 13−13.5, 100−12% B; and 13.5−18 min, 12% B, re-equilibration time. The flow rate was 0.1 mL min^{-1}, and the injection volume was 20 μL. The instrument was operated at the following settings: nitrogen gas flow, 12 L min^{-1}; capillary voltage, 3.5 kV; and capillary temperature, 350 °C. Collision energies of 180 and 100 V were used for α-solanine and α-chaconine, respectively. Quantification was performed in positive ion mode by determining the intensities of the protonated molecules of α-solanine (*m*/*z* 868.7) and α-chaconine (*m*/*z* 852.6) using selected ion monitoring (SIM). The total glycoalkaloid content was taken as the sum of the individual values for α-solanine and α-chaconine and expressed in μg g^{-1} DW.

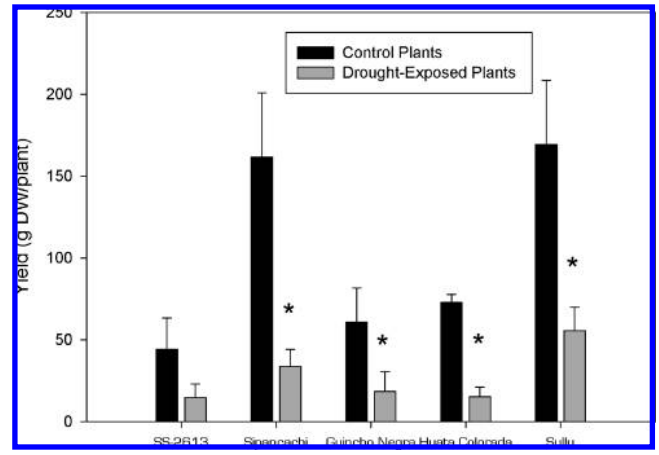

Figure 1. Tuber yield of plants from five native Andean cultivars field grown under control or drought stress conditions, expressed as total tuber fresh weight in g/plant. The asterisk indicates a significant difference at the $p < 0.05$ level.

Statistical Analyses. The data were ranked and subsequently subjected to analyses of variance (three-way ANOVA). The significance of differences between means was evaluated using a pairwise multiple comparison procedure (Tukey's test). The Spearman rank correlation coefficient was determined to evaluate relationships between compounds. SigmaStat software (Systat Software Inc., San Jose, CA) was used for these analyses.

RESULTS AND DISCUSSION

Effect of Drought on Yield and Tuber Characteristics. Important yield losses appeared under drought conditions for all of the genotypes under investigation, ranging from 66.5% in SS-2613 to 79.1% in Huata Colorada on a tuber DW basis (**Figure 1**). Previous investigations on drought tolerance of native landraces showed a certain susceptibility to drought stress of SS-2613, Sipancachi, Guincho Negra, and Huata Colorada. By contrast, Sullu was previously described as a drought-tolerant cultivar (*19*). Interestingly, this tolerant cultivar was also seriously affected by the harsh drought conditions of this experiment. The underlying mechanisms of the difference in drought tolerance have not been fully understood. However, some candidate traits for drought tolerance have been previously described in Sullu (*19, 22*). These traits included (i) at the morphological level, a deeper root system, and (ii) at the biochemical level, the capacity of osmotic adjustment, that is, the potential to rapidly accumulate osmolytes such as soluble sugars (mainly mannitol and galactinol) or proline. Characteristics of the harvest and stored tubers under investigation have been reported in **Table 1**. Differences in tuber color between drought exposed and control plants were observed for Sullu,

Table 1. Characteristics of Freshly Harvested and 4 Month-Stored Tubers from Five Native Andean Cultivars Field Grown under Control or Drought Stress Conditions ($n = 3$)

genotype		weight (g/tuber)		moisture (%)	
treatment	skin and flesh color[a]	harvest	stored	harvest	stored
700347-SS-2613					
control	Y/C	25.5 ± 14.4	17.7 ± 11.9	80.1 ± 1.5	75.8 ± 1.7
drought-exposed	Y/C	8.6 ± 6.5	6.1 ± 5.2	80.1 ± 0.8	74.4 ± 0.3
702535-Sipancachi					
control	Wp/Y	56.6 ± 17.5	56.4 ± 11.1	78.9 ± 1.7	75.8 ± 0.6
drought-exposed	Wp/Y	33.5 ± 9.9	34.9 ± 6.7*	78.5 ± 0.3	76.9 ± 2.8
704429-Guincho Negra					
control	DP/P	16.7 ± 6.2	22.5 ± 1.7	82.4 ± 1.1	78.2 ± 1.4
drought-exposed	DP/Pc	6.0 ± 2.5*	7.3 ± 7.2*	78.8 ± 2.4	72.8 ± 1.1*
703905-Huata Colorada					
control	Py/Y	51.0 ± 13.0	55.1 ± 11.2	81.4 ± 1.3	80.2 ± 0.5
drought-exposed	Py/Y	6.2 ± 3.0*	12.5 ± 10.6*	82.3 ± 0.8	74.3 ± 1.2*
701997-Sullu					
control	Yr/Yr	90.0 ± 17.3	74.9 ± 12.9	75.0 ± 0.4	78.3 ± 0.4
drought-exposed	Yr/Y	56.2 ± 2.4*	41.3 ± 18.2*	74.2 ± 0.3	70.3 ± 1.7*

[a] Primary (in capital) and secondary skin color/primary (in capital) and secondary flesh color. DP, dark purple; P, purple; R, red; Y, yellow; C, cream; and W, white. * indicates that differences between drought-exposed and control plants are significant at the $p < 0.05$ level.

Figure 2. Tubers from the cultivar Sullu under control (**A**) and drought conditions (**B**).

Guincho Negra, and Huata Colorada. Surprisingly, the flesh of Sullu exposed to drought was totally yellow, whereas it contained a broad red vascular ring under control conditions (see **Figure 2**). Similarly, Guincho Negra, completely purple-fleshed in normal growth conditions, showed some small yellow spots in the flesh under drought stress. On the other hand, tubers from Huata Colorada had a more intense yellow flesh and purple skin after drought exposure, but this observation was less obvious after 4 months of storage. Drought exposure markedly reduced the tuber weight (size) on a fresh weight basis for all genotypes (not significantly for SS-2613 and Sipancachi), as previously described in the literature (*15*, *16*). At harvest, the moisture content was stable across irrigation conditions for all cultivars. In contrast, following storage, a lower moisture content appeared in drought-exposed tubers as compared to the control ones for tubers from Sullu, Guincho Negra, and Huata Colorada. This suggested that these drought-stressed potato tubers underwent an accelerated process of aging, as it has been reported in tubers of potato plants grown under hot and dry conditions (*25*).

Effect of Drought on Dietary Antioxidants. The contents in polyphenol compounds and hydrophilic antioxidant capacity are shown in **Table 2**, while the levels of vitamin C, vitamin E, and carotenoid compounds are presented in **Table 3** for the five Andean potato genotypes under control, drought, and storage conditions. Three-way ANOVA has been performed to identify the levels of significance for genotype, drought, and storage effects as well as for the interactions between these components (**Table 4**).

Drought Impact on Polyphenol Compounds. The polyphenolic profile of Andean potato tubers was previously characterized (*13*). The comprehensive HPLC-DAD analysis on the five cultivars (**Table 2**) performed here revealed that, with a few exceptions, the polyphenolic profiles were similar in terms of chemical composition in both irrigation conditions. Differences relied mainly on the proportion of individual phenolic components. Variations of contents in antioxidant aromatic amino acids, tryptophan and tyrosine, and polyphenols according to irrigation conditions were strongly cultivar-dependent. The contents in chlorogenic acid (5-CQA), the predominant polyphenol in potato tubers, were not affected by the drought treatment for the yellow tuber-bearing cultivars SS-2613 and Sipancachi. In Guincho Negra and Sullu, however, the levels of 5-CQA decreased drastically in the drought-exposed harvest tubers as compared to the well-watered ones (−54 and −41%, respectively). In contrast, Huata Colorada (purple-skinned cultivar) presented higher values (+62%) under drought conditions as compared to the ones under irrigation. A previous study performed by Delgado et al. (*26*) reported increased or stable levels of chlorogenic acid in potato tubers subjected to drought stress. The extent of variation depended on the genotype, as described in this study, and on the year of cultivation. As expected from the flesh color changes already mentioned, total anthocyanin contents of Guincho Negra tubers were significantly lower (−32%) in drought-exposed plants as compared to their control counterparts. In Sullu, a decrease of anthocyanins was also observed (−65%), leading to complete disappearance of the red flesh part observed under control conditions (see **Figure 2**). In contrast, drought-exposed Huata Colorada tubers (purple-skinned) revealed higher total anthocyanin contents than their control counterparts (+58%). Regarding flavonols, drought did not affect the level of rutin but induced lower kaempferol-3-rutinoside contents in SS-2613 and Sullu (−71 and −77%, respectively) and an increase in Huata Colorada (+192%). A transcriptomic study performed by Watkinson et al. (*18*) on Andean native tubers revealed that the expression of some flavonoid biosynthesis genes was indeed modified upon drought stress, but no biochemical analysis was performed.

Generally, losses of 50% of 5-CQA on average could be noted in tubers from both irrigation conditions following storage.

Table 2. Aromatic Amino Acid Contents, Polyphenolic Compositions, and Hydrophilic Antioxidant Capacities of Harvest and 4 Month-Stored Tubers from Five Native Andean Cultivars Field Grown under Control (C) or Drought Stress (D) Conditions

	SS-2613				Sipancachi				Guincho Negra				Huata Colorada				Sullu			
	harvest		stored		harvest		stored		harvest		stored		harvest		stored		harvest		stored	
compound[a]	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D
aromatic amino acids[b]																				
tryptophan	62 a	79 a	137 b	191 c	61 ac	43 c	144 b	97 ab	15 a	8 b	128 c	148 c	22 a	27 a	41 b	92 c	43 a	23 b	119 c	109 c
tyrosine	411 a	458 a	1057 b	1533 c	412 a	334 a	1003 b	1063 b	299 a	308 a	1060 b	827 b	119 a	146 ab	204 b	494 c	148 a	98 b	581 c	670 c
phenolic acids[b]																				
5-caffeoyl-quinic acid	572 a	621 a	156 b	211 b	431 a	292 a	41 b	71 b	10033 a	4614 b	5627 b	2145 c	940 a	1527 b	363 c	516 c	808 a	481 b	329 b	382 b
3-caffeoyl-quinic acid	17 a	47 b	32 b	35 b	7 a	14 b	4 a	6 a	53 a	174 b	193 b	186 b	10 a	20 ab	31 b	65 c	12 a	20 b	37 c	39 c
4-caffeoyl-quinic acid	89 ab	125 b	52 a	50 a	22 a	29 a	6 b	10 b	506 a	398a b	539 a	306 b	110 a	139 a	57 b	94 a	72 a	51 b	67 ab	57 ab
caffeic acid	30 a	82 b	8 c	18 ac	12 a	18 a	1 b	1 b	91 a	134 a	41 b	48 b	42 a	129 b	18 a	100 ab	28 a	17 b	13 bc	8 c
ferulic acid	1 a	3 a	ND[c]	ND	ND	ND	ND	ND	trace	trace	38 a	22 b	4 a	8 b	1 c	3 ac	trace	trace	0.4 a	0.2 b
flavonoids[b]																				
rutin	256 a	215 a	58 b	57 b	86 a	40 a	5 b	4 b	ND	ND	ND	ND	73 a	133 a	3 b	22 c	92 a	78 a	12 b	25 c
kaempferol-3-rutinoside	61 a	17 b	22 b	6 c	3 a	1 a	2 a	1 a	ND	ND	ND	ND	55 a	160 b	4 c	31 a	41 a	9 b	9 b	6 b
total anthocyanins	ND	ND	ND	ND	ND	ND	ND	ND	21419 a	14630 b	16987 b	8110 c	199 a	315 a	38 b	184 ab	421 a	145 b	158 b	54 c
conjugated polyamines[b]																				
caffeoyl-putrescine[d]	26 a	7 b	4 bc	1 c	55 a	21 b	1 c	5 c	253 a	77 b	205 a	76 b	12 a	37 c	2 b	17 abc	27 a	24 c	5 b	3 b
p-CHA[e]	4 a	3 a	2 ab	1 b	20 a	16 ac	5 b	8 bc	103 a	264 b	50 c	125 a	7 a	ND	2 c	6 a	11 a	9 a	8 a	7 a
antioxidant capacity																				
Folin[f]	3.6 a	4.5 a	2.3 b	3.4 ab	3.0 a	2.6 a	1.5 b	1.6 b	29.7 a	16.6 b	28.2 a	16.6 b	3.5 a	7.2 b	2.3 a	4.1 ab	3.9 a	2.6 b	2.4 b	2.3 b
H-ORAC[g]	57 a	64 a	42 a	58 a	41 a	34 a	23 b	23 b	323 a	238 b	385 c	243 b	38 a	68 b	28 a	52 ab	42 a	27 b	33 b	30 b

[a] Mean values have been averaged from three samples ($n = 3$), each one corresponding to a different plant. Each sample has been assayed in duplicate. Different letters within one genotype for each parameter indicate a significant difference ($p < 0.05$, Tukey's test) among the drought or storage treatment. [b] Data are expressed in μg g^{-1} of DW. [c] ND, not detected. [d] Putative structure proposed by LC/MS-MS. Expressed in caffeic acid equivalent. [e] *p*-Coumaroyl-hydroxyagmatine, putative structure proposed by LC/MS-MS. Expressed in *p*-coumaric acid equivalent. [f] Expressed in mg 5-CQA equivalent g^{-1} of DW. [g] Expressed in μmol TE g^{-1} of DW.

Table 3. Vitamin C, Vitamin E, Carotenoid and Glycoalkaloid Contents of Freshly Harvested and 4 Month-Stored Tubers from Five Native Andean Cultivars Field Grown under Control (C) or Drought Stress (D) Conditions[a]

	SS-2613				Sipancachi				Guincho Negra				Huata Colorada				Sullu			
	harvest		stored		harvest		stored		harvest		stored		harvest		stored		harvest		stored	
compound[b]	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D
vitamin C																				
total ascorbate	1058 a	1235 a	1072 a	1094 a	1093 a	1272 a	731 b	866 b	701 a	975 b	795 a	621 a	1779 a	1872 a	1227 b	957 b	1041 a	947 a	1045 a	637 b
vitamin E																				
α-tocopherol	24.77 a	34.79 b	26.96 ab	32.25 ab	7.45 a	8.32 a	7.16 a	8.74 a	13.33 ab	11.76 a	17.55 b	16.27 ab	10.24 a	20.88 b	13.90 c	13.89 c	8.03 a	5.02 b	10.28 c	11.83 c
carotenoids																				
lutein	5.11 a	10.22 b	6.60 ab	5.06 a	5.00 a	5.53 a	4.66 a	5.32 a	7.56 a	11.12 b	5.08 c	8.88 ab	7.96 a	17.11 b	10.09 a	10.77 a	11.43 a	9.21 ab	8.41 b	8.70 ab
violaxanthin	3.43 a	5.11 b	1.41 c	1.22 c	5.54 a	6.18 a	2.29 b	2.66 b	2.81 a	4.24 b	1.61 c	2.16 d	11.66 a	20.19 b	3.53 c	3.13 c	6.07 a	4.32 b	1.96 c	1.65 c
neoxanthin	1.15 a	1.57 b	0.87 a	0.97 a	1.73 a	1.93 a	1.13 b	1.25 b	0.68 a	1.08 bc	1.00 b	1.21 c	1.49 a	2.60 b	2.17 b	2.82 b	1.44 a	1.64 a	1.36 a	1.77 a
zeaxanthin	4.17 a	4.94 a	2.46 b	2.33 b	2.99 ab	3.68 a	2.33 b	2.36 b	2.73 ab	3.09 b	2.30 c	2.69 a	4.31 a	5.52 b	2.99 c	2.91 c	2.65 ab	2.80 a	2.50 b	2.49 b
antheraxanthin	1.23 a	1.23 ab	0.55 b	0.57 b	0.74 a	1.30 a	0.58 a	0.70 a	2.97 a	3.35 b	0.56 c	0.68 c	1.67 a	2.94 b	1.90 ab	1.39 a	2.61 a	3.18 b	1.07 c	0.73 c
β-carotene	2.36 a	4.07 b	1.85 c	1.33 c	0.52 a	0.90 a	0.90 a	1.58 b	1.47 a	5.24 b	1.82 a	2.93 c	2.41 a	4.16 b	1.32 c	2.51 a	0.94 a	0.50 b	0.97 a	1.63 c
esters	2.31 a	2.03 a	0.89 b	0.68 b	4.18 a	4.25 a	1.21 b	1.14 b	1.00 a	1.39 a	0.84 a	0.96 a	5.88 a	4.48 ab	2.40 b	2.77 b	3.24 a	1.94 b	0.89 c	0.51 c
total	19.76 a	29.55 b	14.63 c	12.15 c	20.70 a	23.77 a	13.03 b	15.78 b	19.20 a	29.51 b	13.21 c	19.52 a	35.39 a	57.00 b	22.89 c	24.13 c	28.37 a	23.60 b	17.21 c	17.48 c
glycoalkaloids																				
α-solanine	111 a	369 bc	232 ab	401 c	106 a	96 a	93 a	148 a	300 a	1258 b	536 a	1750 b	80 a	222 b	75 a	165 a	221 a	205 a	153 a	434 b
α-chaconine	171 a	552 b	348 ab	555 b	179 a	184 a	169 a	261 a	371 a	1351 b	585 a	1732 b	140 ac	282 b	119 c	213 ab	333 a	269 a	267 a	613 a
total	282 a	921 b	581 ab	956 b	284 a	280 a	261 a	409 a	671 a	2609 b	1122 a	3482 b	220 a	504 b	194 a	378 b	554 a	475 a	420 a	1047 b
ratio α-c/α-s	1.55:1	1.49:1	1.50:1	1.38:1	1.69:1	1.91:1	1.82:1	1.76:1	1.24:1	1.07:1	1.09:1	0.99:1	1.75:1	1.27:1	1.60:1	1.30:1	1.50:1	1.31:1	1.74:1	1.41:1

[a] All data, except the ratios, are expressed in μg g^{-1} of DW. [b] Mean values have been averaged from three samples ($n = 3$), each one corresponding to a different plant. Each sample has been assayed in duplicate. Different letters within one genotype for each parameter indicate a significant difference ($p < 0.05$, Tukey's test) among the drought or storage treatment.

Table 4. Results of the Three Way ANOVA (*F* Values) Performed on Ranks for Dietary Antioxidant Contents, Hydrophilic Antioxidant Capacities, and Glycoalkaloids on Freshly Harvested and 4 Month-Stored Tubers [i.e., According to Two Storage Conditions (SCs)] from Five Native Andean Potato Genotypes (G) Grown under Two Different Irrigation Conditions (ICs)[a]

	G	IC	SC	G × IC	G × SC	SC × IC	G × IC × SC
			vitamin C				
total ascorbate	42.4***	1.8	59.3***	6.8***	9.2***	14.4***	2.7*
			polyphenols				
tryptophan	32.5***	0.0	462***	7.4***	16.6***	2.0	2.4
tyrosine	79.5***	4.6*	505***	3.9**	4.7**	5.4*	2.1
5-caffeoyl-quinic acid	164***	0.2	201***	3.8**	10.9***	4.2*	1.1
3-caffeoyl-quinic acid	146***	48.9***	55.7***	1.5	22.4***	13.1**	3.7**
4-caffeoyl-quinic acid	206***	0.1	45.7***	7.7***	9.1***	0.1	1.8
caffeic acid	108***	14.7***	176***	9.9***	4.7***	0.1	0.6
ferulic acid	923***	4.5*	166***	14.7***	1286***	2	2.6*
rutin	172***	3.4	228***	4.2**	15.8***	5.3*	1
kaempferol-3-*R*	384***	8**	114***	32.5***	20.7***	7.8**	4.1**
anthocyanins	219***	10.4***	67.5***	36.1***	3.5*	0.5	0.2
caffeoyl-putrescine	101***	33.5***	15.2***	31.6***	0.5	2.5	1.1
p-CHA	123***	24.9***	23.2***	26.6***	15.8***	2.2	3.6*
			antioxidant capacity				
Folin	104***	1.9	72.5***	9.7***	4.8**	3.3	1.4
H-ORAC	88.7***	1.1	22.5***	10.6***	3.9**	1.4	0.9
			vitamin E				
α-tocopherol	165.3***	7.8**	22.1***	4.3**	9.9***	0.9	8.6***
			carotenoids				
neoxanthin	83.6***	51.6**	13.7***	0.9	22.8***	3.4	2.7*
violaxanthin	60.3***	3.2	595***	7.6***	5.6*	1.9	1.3
antheraxanthin	46.4***	5.2*	335***	1.3	21.3***	7.9**	3.3*
lutein	33.8***	14.6***	7.3*	3.7**	1.4	3.8	3.8**
zeaxanthin	28.5***	8**	231***	3.2*	12.1***	2.6	0.7
β-carotene	104***	62.9***	1.1	15.4***	30.4***	0.7	12.2***
esters	62.9***	4.4*	223***	4.8**	18.7***	0.4	1.3
total	39.1***	17.3***	210***	8.6***	1.2	0.8	2.9*
			glycoalkaloids				
α-solanine	102***	99.1***	9.4**	5.1**	5.3**	0.8	8.9***
α-chaconine	64.9***	58.7***	12.3**	2.1	5.7***	1.3	6.3***
total	80.1***	73.0***	10.1**	2.9*	5.5***	0.9	7.1***

[a] *, **, and *** indicate significant effects of the parameter for the considered variable at the $p < 0.05$, $p < 0.01$, and $p < 0.001$ levels, respectively.

Concerning the difference between control and drought-exposed tubers, the same tendency observed at harvest for 5-CQA could also be noted after 4 months of storage for Guincho Negra (−62%). In Huata Colorada and Sullu, on the other side, the significant effect of drought stress on 5-CQA observed in harvest tubers disappeared following storage. The contents in flavonoids decreased after 4 months of storage, and the effects of drought on stored tubers were similar to the ones observed for harvest tubers. Yet, there was a higher rutin content in stored drought-exposed tubers from Huata Colorada and Sullu as compared to the stored control ones, while no difference appeared at harvest. Delgado et al. (*26*) and Lewis et al. (*27*) showed an increase of phenolic acid and anthocyanin concentrations in cold-stored (4 °C) potato tubers, which was associated to increased sugar contents. Higher storage temperatures (10 °C) may, however, inverse this tendency and result in nonaffected or decreased phenolic contents, as was described in the present study. Higher contents of the aromatic amino acids, tyrosine and tryptophan, which have been shown to exhibit antioxidant capacity in vitro (*13*), were found following storage. This could be explained by the effective proteolysis occurring during storage (mainly of the storage protein, patatin) (*28*).

Identification of Two Phenolic Polyamine Conjugates. HPLC-DAD profiling of the hydrophilic potato extracts revealed major peaks that were quantified (**Table 2**) as described in Andre et al. (*13*), as well as several minor components. Notable among these were two compounds, which showed variable concentrations upon drought stress treatment. Their identification was therefore undertaken by means of LC-MS/MS. UV and mass spectra of the molecules were combined and compared with the available data from the literature. A first broad mass scan of the two compounds revealed molecular ions $[M + H]^+$ at *m*/*z* 251 and *m*/*z* 293, respectively. The first compound exhibiting a molecular ion at *m*/*z* 251 was fragmented into three major fragments at *m*/*z* 163, *m*/*z* 135, and *m*/*z* 117, suggesting a hydroxycinnamic acid amide, caffeoyl-putrescine, as previously reported by other authors (*29, 30*). The *m*/*z* 163 ion was likely generated by the loss of putrescine (88 u) and confirmed the presence of a caffeoyl derivative. Loss of CO (28 u) and CO and (28 u + 18 u) from the caffeoyl produced the fragment ions *m*/*z* 135 and *m*/*z* 117, respectively. The second compound showing a $[M + H]^+$ at *m*/*z* 293 had never been reported in potato tubers but presented the UV and mass spectra characteristics of *p*-coumaroyl-hydroxyagmatine (*p*-CHA), another hydroxycinnamic amide previously described in barley (*31*). A λ_{max} at 290 nm and fragment ions at *m*/*z* 275 (loss of 18 u), *m*/*z* 147 (*p*-coumaroyl, loss of hydroxyagmatine), and *m*/*z* 119 [loss of CO (28 u) from *p*-coumaroyl] was indeed representative of this molecule. However, the putative structure of both compounds unraveled herein by LC-MS/MS needed further confirmation by NMR or by comparison of mass spectra with standards.

Concerning the concentrations of the phenolic polyamine conjugates, drought has a cultivar-dependent significant impact on both molecules. These molecules have generally

been described in the literature for their important role in plant defense responses to pathogens (*32*). Caffeoyl-putrescine has been shown to accumulate to important amounts in Solanaceae in response to jasmonate treatment and fungal infection (*33*) as well as more specifically to β-1,3-oligosaccharide elicitor in potato tubers (*29*). *p*-CHA has never been reported in potato but in barley in response to powdery mildew fungus (*31*). Information concerning the involvement of the phenolic polyamine conjugates in abiotic stresses has, however, been scarce and limited to a few studies [reviewed in Edrava (*34*)].

Yet, the significant role played by free polyamines in plant defense responses to environmental abiotic stress is well-documented (*35*). Therefore, with regard to the putative stress-induced variations in the polyamine metabolism on one hand and the variations observed in the phenylpropanoid pathway on the other hand, fluctuations of concentrations in hydroxycinnamic acid amides obtained here upon drought exposure are not surprising. Further studies are yet needed to confirm a hypothetical involvement of these two molecules in drought stress tolerance. From a human nutrition perspective, dietary polyamines are of great interest, not only for their participation in human cell growth and proliferation (particularly important for the digestive tract) (*36*) but also for their potential bioactive properties when conjugated with dihydrocaffeoyl (*37*). To our knowledge, no data are available concerning the antioxidant or health-promoting properties of caffeoyl-putrescine or *p*-CHA.

The levels of both phenolic polyamine conjugates decreased after storage. Significant effects of drought on *p*-CHA and caffeoyl-putrescine were still evident for Guincho Negra, whereas the differences were not significant anymore for the other cultivars following storage.

Drought Impact on Vitamin C. Drought stress did not significantly affect the vitamin C content in harvest potato tubers, except for the cultivar Guincho Negra, which significantly increased its content by 39% upon drought (**Table 3**). This stability or increase is an important nutritional finding, as potato is a notably recognized source of vitamin C in the human diet (*9*). Depending on the genotype and on the year of cultivation, increased, decreased, or unchanged levels of vitamin C in potato tubers grown under drought stress have been reported by Delgado et al. (*26*). Similarly, reductions in vitamin C concentrations in response to drought have been observed in sunflower (*38*), whereas increases have been shown in tomato fruits (*39*), strawberry fruits (*40*), and sorghum (*38*).

The mean poststorage values for control and drought-exposed tubers (974 and 835 μg g^{-1} DW, respectively) were notably lower than the mean harvest values (1135 and 1260 μg g^{-1} DW, respectively). Interestingly, losses during storage were cultivar-dependent as well as irrigation condition-dependent (significant storage-by-genotype and storage-by-irrigation interactions) (**Table 4**). SS-2613 was affected neither by storage nor by drought in terms of vitamin C. By contrast, Sipancachi and Huata Colorada showed decreased total ascorbate levels following storage in both irrigation conditions. Interestingly, whereas the storage had no effect on the vitamin C content in tubers of Guincho Negra and Sullu grown under normal conditions, significant losses were observed when tubers had been subjected to drought stress during growth. This suggests that drought stress during growth led to an increased consumption of ascorbate during storage, corroborating the hypothesis of an accelerated aging process and, thereby, an increased production of ROS due to drought stress conditions.

Drought Impact on Carotenoid Compounds. The carotenoid profile of Andean potato tubers was described in a previous study (*13*), which reported lutein as the predominant carotenoid compound, followed by violaxanthin, neoxanthin, zeaxanthin, antheraxanthin, and β-carotene. The HPLC-DAD analysis performed herein on the five cultivars for carotenoids (**Table 3**) revealed significant differences in terms of quantity between irrigation conditions, although the carotenoid patterns were similar in terms of chemical composition. Similarly to polyphenols, the carotenoid contents were affected by the drought stress treatment in a cultivar-dependent manner (**Tables 3** and **4**). In general, levels of total carotenoids were not affected by the deficit of irrigation in the cultivar Sipancachi, whereas modified concentrations upon drought were revealed in SS-2613 (+49%), Guincho Negra (+54%), Huata Colorada (+61%), and Sullu (−17%). Dietary lutein, zeaxanthin, and β-carotene have been of particular interest for their health-promoting properties. Lutein and zeaxanthin have been well-known for their protective effect against age-related macular degeneration, a major cause of blindness in the elderly (*6*). β-Carotene has exhibited a vitamin A activity, an important property as vitamin A deficiency has remained a major public health concern worldwide. Interestingly, drought stress induced an increase of lutein and β-carotene levels in SS-2613, Guincho Negra, and Huata Colorada. Zeaxanthin concentrations were weakly affected by drought exposure: Only the high carotenoid-containing cultivar Huata Colorada presented higher values in drought-stressed tubers. In tomato, drought stress induced increased or decreased amounts of lycopene to an extent depending on genotype, whereas β-carotene and xanthophylls were not affected (*39*).

Total carotenoid contents decreased following storage at 10 °C, which is in general agreement with the work of Griffiths et al. (*41*). They also demonstrated that lutein was the most stable carotenoid compound, as it was in this work. Interestingly, β-carotene concentrations also remained stable or increased poststorage. As β-carotene has rarely been reported in potato tubers (*13*), this was the first time that this observation was described. Interestingly, differences in carotenoid contents between drought-stressed and well-watered tubers were reduced following storage.

Drought Impact on Vitamin E. α-Tocopherol was the only vitamin E compound identified in native potato tubers (*13*). Drought stress did not affect the α-tocopherol contents in Sipancachi and Guincho Negra, while a significant increase was observed in SS-2613 (+40%) and Huata Colorada (+104%) (**Table 3**). In contrast, in Sullu, α-tocopherol concentrations decreased upon drought stress (−37%), following the same behavior than total carotenoids. In plants in general, tocopherol levels were elevated in response to a variety of abiotic stresses, including drought (*42*). However, variations of α-tocopherol concentrations due to drought stress crucially depended on the severity of the stress, the stress sensitivity of the species, and the presence of alternative mechanisms of antioxidant protection (*8*). There has been strong evidence that high dietary vitamin E intake is beneficial to health (*43*), suggesting an interest in the consumption of tubers from native cultivars.

Unchanged (SS-2613, Sipancachi, and Guincho Negra) or increased (Huata Colorada and Sullu) α-tocopherol contents were recorded following storage. Increases were also reported

by Spychalla and Desborough (*44*) during the storage of potato tubers for 40 weeks at two different temperatures (3 and 9 °C). Furthermore, after 4 months of storage, the impact of drought was not significant anymore in any cultivars.

Drought Impact on Hydrophilic Antioxidant Capacity. The reducing capacity of the yellow-fleshed tubers from SS-2613 and Sipancachi was not affected by drought. In contrast, the values were significantly lower for the drought-exposed purple- and red-fleshed tubers from Guincho Negra and Sullu (−44 and −32%, respectively) and significantly higher for the tubers from Huata Colorada under drought conditions (+104%). The peroxyl radical scavenging capacity (ORAC assay) followed the same trend than the Folin−Ciocalteu assay (correlation coefficient between both measurements $r = 0.98$).

As expected from the polyphenol concentrations determined by HPLC, significant decreases of the reducing capacity of the potato hydrophilic extracts following storage were measured in SS-2613, Sipancachi, and Sullu. Following storage, the effects of drought were less pronounced. Indeed, differences observed at harvest between control and drought-exposed tubers from Huata Colorada and Sullu were reduced poststorage to a nonstatistically significant level. As a result, after 4 months of storage, only the tubers from Guincho Negra were significantly affected by drought in terms of reducing capacity. H-ORAC values showed similar patterns than the ones from the Folin−Ciocalteu assay concerning the drought-by-storage effects.

The three most colored cultivars, Guincho Negra, Sullu, and Huata Colorada, were the most affected by drought stress in terms of dietary antioxidants. Polyphenol contents in Guincho Negra and Sullu, which both contained anthocyanins in the flesh, changed in a similar manner under drought exposure. The overall phenylpropanoid production pathway decreased in their harvest tubers upon drought. The reduced polyphenol concentrations led to a partial loss of their antioxidant potential, that is, their health-promoting value. This may also have serious consequences on the marketable quality of both cultivars. First, Guincho Negra has been proposed as a promising source of natural colorant for the industry thanks to its high content in petanin, an acylated anthocyanin presenting high color intensity and high stability (*13*). However, a drastic decrease of the occurrence of this anthocyanin appeared after drought exposure. For Sullu, the disappearance of the red vascular ring in the flesh (**Figure 2**) may decrease its aesthetic appeal and therefore its market value. In contrast, drought induced an increase of polyphenol compounds in the purple-skinned and yellow-fleshed tubers from Huata Colorada and, in turn, of its health-promoting value. The polyphenol analysis revealed indeed higher 5-CQA, caffeic acid, kaempferol-3-*O*-rutinoside, and total anthocyanin contents in the drought-stressed tubers as compared to their control counterparts.

Effect of Drought on Glycoalkaloid Contents. Glycoalkaloid concentrations as well as the α-chaconine/α-solanine ratios are reported in **Table 3**. Total glycoalkaloids in tubers from control plants are lower than the acceptable limit for human consumption [200 mg glycoalkaloids kg^{-1} fresh weight or around 1000 $\mu g\ g^{-1}$ of DW (*45*)]. Contents are not affected by the drought treatment in tubers from Sullu and Sipancachi. Total glycoalkaloid values for SS-2613, Guincho Negra, and Huata Colorada are, however, 3.3-, 3.9-, and 2.4-fold higher in the drought-exposed tubers as compared to the control ones. As a consequence, drought-stressed tubers from Guincho Negra are not acceptable anymore for human consumption. Peeling may, however, remove 75−97% of total glycoalkaloids in potato tubers (*46*). Differences between cultivars with regard to the ratios α-chaconine/α-solanine have been reported (*46*, *45*). α-Chaconine appears in numerous in vitro and animal studies to be more toxic than α-solanine (*45*); it is desirable to have this ratio as low as possible. Our values are in general agreement with the literature (0.82−2.62) (*45*). The drought treatment did not appear to influence the ratios between the two glycoalkaloids. Although Guincho Negra showed high total glycoalkaloid levels after drought exposure, it presents a low relative amount of the highly toxic molecule α-chaconine (48%; ratio of 1.07).

Increases due to drought that were observed at harvest were still significant following storage for SS-2613, Guincho Negra, and Huata Colorada. Storage tended to increase the concentrations of antinutrients such as glycoalkaloids, with the most pronounced increases occurring in the outer tuber layers (*45*). In this study, the behavior of Sullu in terms of glycoalkaloids was of particular interest. While storage had no effect on well-watered tubers, an important increase in glycoalkaloids was noticed in tubers subjected to drought during growth. This suggested that the potentially accelerated physiological age induced by drought stress may play a role in determining the levels of glycoalkaloids.

Conclusion. It is generally recognized that drought affects the potato plant and reduces tuber yield as well as tuber size. The present study has investigated for the first time from a human nutrition perspective the fate of both dietary antioxidants and glycoalkaloids in potato tubers grown under field drought conditions. Potato responses to drought stress are complex with levels of antioxidants showing increases, decreases, or remaining stable, depending on the genotype and kind of antioxidant. Under drought, variations of health-promoting compounds are associated with increased or stable levels of glycoalkaloids. Storage at 10 °C for 4 months tends to decrease the concentration of all dietary antioxidants, except for α-tocopherol and aromatic amino acids, and reduce the drought-induced variations observed at harvest.

The increase of oxidative stress (generation of ROS) induced by the drought exposure might be responsible for the modifications of antioxidant contents, which relied mainly on the cultivar stress sensitivity. These variations could be due to (i) changes of the expression level of the genes coding for enzymes involved in the antioxidant biosynthetic pathway, alterations of the activity of the same enzymes, or an increase of the consumption of the antioxidant itself due to an overproduction of ROS that the plant cannot cope with (resulting in decreased antioxidant levels). Further research is needed to clearly understand at which level the regulation of their content occurs. It is also conceivable that the limited carbohydrate supply from the foliage to the sink organ (tuber) during drought exposure plays a role in this regulation.

ABBREVIATIONS USED

CIP, International Potato Center; ROS, reactive oxygen species; ANOVA, analysis of variance; ORAC, oxygen radical absorbance capacity; *p*-CHA, *p*-coumaroyl-hydroxy-agmatine; CQA, caffeoyl quinic acid; 5-CQAE, 5-caffeoyl quinic acid equivalent; MS, mass spectrometer; TE, Trolox equivalent; DW, dry weight; HPLC, high-performance liquid chromatography; DAD, diode array detector.

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