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Stability and Broad-Sense Heritability of Mineral Content in Potato: Copper and Sulfur

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Abstract Sulfur and copper are important for human health. Sulfur deficiency is rare, but may occur in the elderly. However, a large percentage of the U.S. population is deficient in copper. The purpose of this study was to determine the range of values for sulfur and copper available in advanced potato germplasm and varieties and estimate how much genetic variation exists for these two elements. Potato breeding lines and varieties in three multisite trials were evaluated for copper and sulfur content by wet ashing and Inductively Coupled Argon Plasma Emission Spectrophotometer analysis. Stability and broad-sense heritability were determined. Among genotypes, copper content ranged from 2.0 to 4.5 $\mu\text{g}\cdot\text{g}^{-1}$ DW. This

was a 2.25-fold difference. In these three trials, environment was never significant, while genotype by environment interactions were always significant. Genotype was significant in two of the regional trials. Broad-sense heritabilities were estimated to be 0.0, 0.93 and 0.51 for the Tri-State, Western Regional Russet and Western Regional Red/Specialty trials, respectively. Among genotypes, sulfur content ranged from 991 to 1488 $\mu\text{g}\cdot\text{g}^{-1}$ DW. The highest value was 50 % higher than the lowest. In these three trials, environment was never significant, while genotype x environment interactions were always significant. Genotype was significant in two of the regional trials. Broad-sense heritabilities were estimated to be 0.53, 0.68 and 0.88, for Tri-State, Western Regional Russet, and Western Regional Red/Specialty trials, respectively. For both sulfur and copper, selection in the Western Regional Russet and Western Regional Red/Specialty trials is likely to lead to an increase in content. Selection for sulfur in the Tri-State would result in a gain as well. These results suggest that genetic improvements could be made to potato to enhance the concentrations of these minerals.

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Resumen El azufre y el cobre son importantes para la salud humana. La deficiencia en azufre es rara, pero se puede presentar en la tercera edad. No obstante, un gran porcentaje de la población de los EUA es deficiente en cobre. El Propósito de este estudio fue determinar la amplitud de valores para azufre y cobre disponibles en germoplasma avanzado de papa y en variedades, y estimar cuanta variación genética existe para estos dos elementos. Se evaluaron líneas de mejoramiento de papa y variedades en tres ensayos multi-sitio para el contenido de cobre y azufre por análisis de ceniza húmeda y por Espectrofotómetro de Inducción de Emisión Acoplada de Plasma de Argón. Se determinaron la estabilidad y la heredabilidad de amplio sentido. Entre genotipos, el contenido de cobre varió de 2.0 y 4.5 $\mu\text{g}\cdot\text{g}^{-1}$ DW. Esto fue una diferencia de 2.25 veces. En estos tres ensayos, el medio

ambiente nunca fue significativo, mientras que las interacciones genotipo-medio ambiente siempre fueron significativas. El genotipo tuvo significancia en dos de los ensayos regionales. Las heredabilidades de amplio sentido se estimaron en 0.0, 0.93, y 0.51 para los ensayos Tri-Estatal, Russet Regional del Oeste, y Rojas/Especiales Regional del Oeste, respectivamente. Entre los genotipos, el contenido de azufre varió de 991 a 1488 $\mu\text{g-g}^{-1}$ DW. El valor más alto fue 50% mayor que el más bajo. En estos tres ensayos el ambiente nunca fue significativo, mientras que las interacciones genotipo x medio ambiente siempre lo fueron. El genotipo fue significativo en dos de los tres ensayos regionales. Las heredabilidades de amplio sentido se estimaron en 0.53, 0.68, y 0.88 para los ensayos Tri-Estatal, Russet Regional del Oeste, y Rojas/Especiales Regional del Oeste, respectivamente. Tanto para azufre como para cobre, la selección en Russet Regional del Oeste, y Rojas/Especiales Regional del Oeste, es probable que conduzca hacia un aumento en su contenido. La selección para azufre en el Tri-Estatal pudiera también resultar en ganancia. Estos resultados sugieren que los mejoramientos genéticos pudieran hacerse en la papa para aumentar las concentraciones de estos minerales.

Keywords ICAPES · Breeding · RDA · Germplasm · Human nutrition

Introduction

Sulfur plays an important role in plant nutrient uptake, chlorophyll production, stress and pest resistance, and carbohydrate synthesis (Epstein and Bloom 2004; Marschner 1995; Westermann 1993). The need for sulfur in fertilization regimes of potato has been documented in numerous studies. Rykbost et al. (1993) showed that a fertilizer regime including 22 kg-ha^{-1} sulfur was the highest yielding treatment for Russet Burbank under the short season conditions of Klamath Basin in Oregon. Pavlista (2013) recommends a similar level of amendment. Sulfur containing fertilizers should be added when soil levels are under 5 ppm. Irrigation water may have significant amounts of sulfur. Also effective in control of certain diseases, Davis et al. (1974) showed that application of gypsum or elemental sulfur at a rate of 672.5 kg-ha^{-1} resulted in a reduction by 53 % of tubers thrown out of grade due to common scab blemishing. Sulfur is not used alone by the human body. It occurs in association with the vitamins thiamin and biotin and as part of the sulfur-containing amino acids methionine, cysteine, and taurine. However, deficiencies of sulfur have not been defined (Groff and S.S. Gropper 2000).

Copper is almost never identified as deficient in soils for potato production (Kelling 1981). In the human body copper functions in conjunction with several metalloenzymes that act

as oxidases to achieve the reduction of molecular oxygen. Copper is essential to human health. In the United Kingdom it is recommended that adults intake 1.2 mg/day. (http://www.copper.org/consumers/health/papers/cu_health_uk/cu_health_uk.html.)

The objectives of this study were to determine the concentration of sulfur and copper currently available in advanced potato germplasm under growing conditions in the Pacific Northwestern U.S. (and Texas) and estimate how much of the variation in this germplasm is under genetic control.

Materials and Methods

Field Experiments Potato genotypes in three distinct trials were planted at different locations in 2004. The locations (four for the Tri-State, 6 for the Western Regional Russet, 3 for the Western Regional Red/Specialty Trials) and associated crop management have been described by Brown et al. (2010; 2011). Each trial had a different array of genotypes. Field trials were planted as randomized complete blocks, with four blocks. Plots consisted of 20 plants. Tubers were harvested mechanically and packaged out of the field and shipped to Prosser, WA. They were stored at 10 ° C for 30 days at 85 % relative humidity. Three tubers from each plot were sliced, not peeled, dried, and ground to powder as a composite sample. Preparation of samples and analysis was described in Brown et al. (2010; 2011).

Statistical Analysis Copper content was transformed to the natural logarithm for all statistical analyses and back-transformed for presentation of means. Sulfur content values were not transformed. Variance components for each source of variation were estimated from the mixed models procedure in SAS (version 9.1, Cary, NC). Broad-sense heritability (H) was estimated as the ratio of the genotypic (σ^2_G) to total phenotypic variance, $H = \sigma^2_G / ((\sigma^2_{\text{error}/re}) + (\sigma^2_{G \times E/e}) + \sigma^2_G)$ (Holland et al. 2003), where r = number of replications and e = number of environments. Knapp et al. (1985) determined the exact confidence interval for H. The upper confidence interval is $1 - [(MS_1/MS_2) F_{(1-\alpha/2; df2, df1)}]^{-1}$, while the lower confidence interval is $1 - [(MS_1/MS_2) F_{(\alpha/2; df2, df1)}]^{-1}$, where MS_1 = mean squares for genotype and MS_2 = mean squares for genotype x environment. These mean squares were obtained from the type III mean squares from the general linear models procedure in SAS.

To evaluate the genetic stability of each potato genotype, the genotype x environment interaction (G x E) was partitioned into stability variance components (σ_1^2) assignable to each genotype (Shukla 1972), using a program written for the interactive matrix language procedure in SAS (Kang 1989). An environmental index for each environment was calculated

by subtracting the grand mean over all environments from the mean for each environment. Heterogeneity due to this index was removed from the G x E interaction and the remainder was partitioned into s_i^2 assignable to each potato genotype, and constitutes variance not explained by removal of environmental effects.

Results

Copper

The analysis of the Tri-State trials included four environments in the Pacific Northwest: one in Aberdeen, ID; one in Hermiston, OR; and, an early and late harvest in Othello, WA (Table 1). Clonal mean for copper content over all environments ranged from 2.8 to 3.9 $\mu\text{g}\cdot\text{g}^{-1}$ DW, the higher being 139 % of the lowest value. Genotypes and environments were not significant while genotype x environment (G x E) interaction was. Six clones showed significant G x E and five were unstable after removal of environmental heterogeneity. Notably, varieties Russet Burbank and Ranger Russet, the first and third most grown varieties in the US, did not show significant G x E.

The Western Regional Russet trials were carried out at six locations (Kimberly, ID; Springlake, TX; Hermiston, OR; and, an early and late harvest in Othello, WA.) (Table 2). Genotypes and G x E were significant for copper content with a range of 2.5–4.5 $\mu\text{g}\cdot\text{g}^{-1}$ DW. The highest genotype mean value was 225 % higher than the lowest mean. Five genotypes

showed significant G x E interaction and these five remained unstable after removal of environmental heterogeneity.

The Western Regional Red/Specialty trial was grown in three environments in the Pacific Northwest (Table 3). Both genotypes and G x E were significant while environments were not. The lowest value was 2.6 $\mu\text{g}\cdot\text{g}^{-1}$ DW and the highest level was 4.1 $\mu\text{g}\cdot\text{g}^{-1}$ DW or 158 % over the lowest value. Eight of the 13 genotypes had significant G x E and five remained unstable after removal of environmental heterogeneity.

Broad-sense heritabilities for copper were estimated as 0.0, 0.93, and 0.51, for the Tri-State, Western Regional Russet, and Western Regional Red/Specialty Trials, respectively (Table 7).

Sulfur

Sulfur content was measured in the Tri-State in four environments (Table 4). Environments and genotypes were not significant but G x E was. Contents ranged from 1195 to 1488 $\mu\text{g}\cdot\text{g}^{-1}$ DW or 124 % of the lower value. Four genotypes displayed significant G x E and four were unstable after removal of the environmental heterogeneity.

Sulfur was measured from six environments from the Western Regional Russet Trial. Environments were not significant while genotypes and G x E were significant (Table 5). The values of sulfur ranged from 1169 to 1408 $\mu\text{g}\cdot\text{g}^{-1}$ or a spread of 120 % over the lower limit. Eight of 13 genotypes showed significant G x E, and five remained unstable after removal of environmental heterogeneity.

Table 1 Copper content ($\mu\text{g}\cdot\text{g}^{-1}$ DW) by trial location and overall, G X E variance (σ_i^2) and residual (s_i^2) after removal of environmental heterogeneity in the Tri-state Trials

Genotype	TS-H ¹	TS-A ²	TS-OE ³	LT-OL ⁴	Genotype mean	σ_i^2	s_i^2
A95409-1	4.6	3.5	2.8	4.7	3.9		**
A96023-6	3.6	3.1	2.7	3.6	3.3	*	*
A96095-3	3.1	3.9	3.0	3.4	3.4		
A96104-2	3.0	3.7	3.9	2.9	3.4	**	**
A98295-3TE	3.7	2.9	3.6	3.6	3.4	**	
AO96164-1 ^a	3.3	3.7	2.8	4.3	3.5	*	*
AOA95154-1 ^b	2.5	4.1	2.7	3.2	3.1	*	
AOA95155-7	2.0	4.9	3.1	3.3	3.3	**	**
Ranger russet	2.6	3.4	2.8	2.6	2.8		
Russet burbank	2.7	2.9	3.0	2.9	2.9		
Location mean	3.1	3.6	3.1	3.5			

* = $P < 0.05$, ** = $P < 0.01$, significance level of variances σ_i^2 , and s_i^2

¹ Hermiston, OR

² Aberdeen, ID

³ Othello, WA (early harvest)

⁴ Othello, WA (late harvest)

^a subsequently named 'Sage Russet'

^b subsequently named 'Clearwater Russet'

Table 2 Copper content ($\mu\text{g g}^{-1}$ DW) by trial location and overall, G X E variance (σ^2_i) and residual (s^2_i) after removal of environmental heterogeneity in the Western regional russet trials

Genotype	1-WR-K ¹	2-WR-S ²	3-ERT-H	4-WR-A ⁴	5- WR-OE ⁵	6- WR-OL ⁶	Genotype mean	σ^2_i	s^2_i
A92030-5	5.0	4.8	3.5	3.6	3.1	3.2	3.9	**	*
A92294-6	4.3	3.9	2.6	3.3	3.6	3.3	3.5		
A9304-3	4.3	4.3	3.1	3.8	3.8	2.8	3.7		
A9305-10 ^a	6.9	6.8	3.0	3.9	3.8	2.8	4.5	**	*
A93157-6LS ^b	5.4	3.7	2.8	3.2	4.5	2.8	3.7		
A95109-1 ^c	5.4	4.3	3.4	3.2	4.2	3.1	3.9		
AC92009-4	5.7	4.7	2.6	4.3	5.2	3.3	4.3		
AC93026-9	5.5	4.3	3.1	4.3	3.9	3.4	4.1		
AO96160-3 ^d	5.6	4.7	2.8	3.9	3.2	2.9	3.8		
ATX92230-1	5.8	5.5	3.4	3.3	4.5	3.3	4.3		
CO93001-11	4.8	3.4	2.9	3.2	2.8	3.5	3.4	**	**
CO94035-15 ^e	4.1	2.7	1.4	2.7	2.2	1.6	2.5	**	*
PA95A11-14	2.6	1.9	1.0	1.6	3.4	1.3	2.0	**	**
Location mean	5.0	4.2	2.7	3.4	3.7	2.9			

* = $P < 0.05$, ** = $P < 0.01$, significance level of variances σ^2_i and s^2_i

¹ Kimberly, Idaho

² Springlake, Texas

³ Early Harvest, Hermiston, Oregon

⁴ Aberdeen, Idaho

⁵ Early Harvest, Othello, Washington

⁶ Late Harvest, Othello, Washington

^{a/} Subsequently named ‘Alpine Russet’

^{b/} Subsequently named ‘Premier Russet’

^{c/} Subsequently named ‘Classic Russet’

^{d/} Subsequently named ‘Owyhee Russet’

^{e/} Subsequently named ‘Mesa Russet’

In the Western Regional Red/Specialty trial, genotypes and G x E were significant while the environments were not (Table 6). Sulfur values ranged from 991 to 1445 $\mu\text{g g}^{-1}$ DW or 146 % of the lower value. Six genotypes demonstrated significant G x E and five of these remained unstable after removal of environmental heterogeneity.

Broad-sense heritabilities for sulfur were estimated as 0.53, 0.68, and 0.88, for the Tri-State, Western Regional Russet, and Western Regional Red/Specialty Trials, respectively (Table 7).

Discussion

Broad-sense heritability refers to the ratio of all genetic variation to total phenotypic variation. It is therefore not a predictor of expected gain from sexual breeding and selection, but rather a predictor of change effected by selection among the clonally propagated individuals in that population. The broad sense heritabilities derived for both copper and sulfur from the

three trials were all significantly greater than zero, with the exception of copper in the Tri-State Trial (Table 7). The group of genotypes in the Western Regional Russet Trial and the Western Regional Red/Specialty would offer the best prospect of change in response to selection for copper and sulfur, respectively. The copper and sulfur contents reported here are in conformity with summaries in Rastovski and A. van Es (1987) and Woolfe (1987). Subar et al. (1998) found that white fleshed potatoes provide 9 % of copper in the US population. Ma and Betts (2000) found that daily copper intakes for adults over 60 years of age in the US are 1.3 mg for men and 1.0 mg for women (Food and Nutrition Board, Institute of Medicine 2001; National Research Council 1989) values that would indicate deficiency. In their study, potatoes comprised 22 % of the sources of copper in the elderly population. Milne (1998) found that at the levels of intake of copper determined in men, only 30 to 40 % is absorbed. This points to copper deficiency both by generalized insufficient intake and poor absorption. One of the most important roles of copper together with zinc is in the metalloenzyme superoxide

Table 3 Copper content ($\mu\text{g g}^{-1}$ DW) by trial location and overall, G X E variance (σ^2_i) and residual (s^2_i) after removal of environmental heterogeneity in the Western Regional Red/Specialty Trials

Genotype	W/SP/R-H ¹	W/S/SP/R-A ²	W/SP/R-M ³	Genotype Mean	σ^2_i	s^2_i
A96741-1R	4.4	3.9	4.1	4.1	*	
A96741-2R	3.3	4.6	4.2	4.0	**	**
AO93487-2R ^a	3.1	4.2	4.0	3.8	**	**
All Blue	2.6	2.4	3.9	3.0		
BTX1544-2	3.7	2.2	4.3	3.4	**	*
CO93037-6R	3.4	3.9	4.6	4.0		
CO94165-3 ^b	2.8	2.2	3.1	2.7		
CO94183-1 ^c	3.9	2.5	4.6	3.7	*	*
NDA5507-3 ^d	3.1	1.8	5.0	3.3	**	
VC0967-2	3.0	2.7	4.1	3.3		
VC1002-3	3.5	3.3	4.8	3.9		
VC1015-7	3.9	2.5	3.4	3.2	**	**
Yukon gold	2.2	1.9	3.7	2.6	*	
Location mean	3.3	2.9	4.1			

* = $P < 0.05$, ** = $P < 0.01$, significance level of variances σ^2_i , and s^2_i

¹ Hermiston, OR

² Aberdeen, ID

³ Mount Vernon, WA

^a subsequently named 'Red Sunset'

^b subsequently named 'Purple Majesty'

^c subsequently named 'Mountain Rose'

^d subsequently named 'Yukon Gem'

Table 4 Sulfur content ($\mu\text{g g}^{-1}$ DW) by trial location and overall, G X E variance (σ^2_i) and residual (s^2_i) after removal of environmental heterogeneity in the Tri-state trials

Genotype	TS-H ¹	TS-A ²	TS-OE ³	LT-OL ⁴	Genotype mean	σ^2_i	s^2_i
A95409-1	1340	977	1373	1610	1325	**	**
A96023-6	1538	1078	1561	1755	1483	**	**
A96095-3	1322	1321	1571	1736	1488		
A96104-2	1145	1335	1871	1408	1439	**	**
A98295-3TE	1280	1122	1619	1417	1360		
AO96164-1 ^a	1100	1000	1470	1482	1263		
AOA95154-1 ^b	1246	1198	1537	1486	1367		
AOA95155-7	1227	1354	1408	1593	1396	**	
Ranger Russet	1046	1093	1398	1244	1195		*
Russet Burbank	1194	1044	1416	1561	1303		
Environment Mean	1244	1152	1522	1529			

* = $P < 0.05$, ** = $P < 0.01$, significance level of variances σ^2_i , and s^2_i

¹ Hermiston, OR

² Aberdeen, ID

³ Othello, WA (early harvest)

⁴ Othello, WA (late harvest)

^a subsequently named 'Sage Russet'

^b subsequently named 'Clearwater Russet'

Table 5 Sulfur content ($\mu\text{g g}^{-1}$ DW) by trial location and overall, G X E variance (σ^2_i) and residual (s^2_i) after removal of environmental heterogeneity in the Western regional russet Trials

Genotype	1-WR-K	2-WR-S ²	3-ERT-H	4-WR-A ⁴	5- WR-OE ⁵	6- WR-OL ⁶	Genotype Mean	σ^2_i	s^2_i
A92030-5	1135	1426.0	1314.0	1077.0	1200.0	1367.0	1253	*	
A92294-6	1040	1160.0	1035.0	1064.0	1372.0	1194.0	1203	**	**
A9304-3	1172	1379.0	1080.0	1157.0	1458.0	1330.0	1233	**	**
A9305-10 ^a	1103	1348.0	1081.0	1085.0	1445.0	1152.0	1231		
A93157-6LS ^b	1197	1401.0	1139.0	1103.0	1449.0	1273.0	1298	**	*
A95109-1 ^c	1196	1442.0	1198.0	979.0	1824.0	1378.0	1326		
AC92009-4	1119	1201.0	1128.0	1307.0	1586.0	1558.0	1293		
AC93026-9	1144	1212.0	1199.0	1238.0	1608.0	1221.0	1313	*	*
AO96160-3 ^d	1334	1433	1160.0	1319.0	1528.0	1360.0	1357	**	
ATX92230-1	1202	1441	1339.0	1085.0	1470.0	1617.0	1408		
CO93001-11	1243	1580	1289.0	1138.0	1561.0	1932.0	1383		
CO94035-15 ^e	1137	1291	1290.0	1251.0	1470.0	1415.0	1309	**	**
PA95A11-14	1112	1263	1143.0	1081.0	1220.0	1197.0	1169	*	
Location Mean	1164	1352	1184.2	1144.9	1476.2	1384.2			

* = $P < 0.05$, ** = $P < 0.01$, significance level of variances σ^2_i and s^2_i

dismutase. The functioning of this enzyme is the first line of defense against the toxicity engendered by reactive oxygen species. Although rare, diets devoid of copper or zinc would severely hamper this catalytic process (Johnson and Giulivi

2005). On the other hand there is evidence of copper accumulation in brain tissue accompanying the development of Alzheimer's Disease (Singh et al. 2013). Sulfur does not have a Recommended Daily Allowance established nor is

Table 6 Sulfur content ($\mu\text{g g}^{-1}$ DW) by trial location and overall, G X E variance (σ^2_i) and residual (s^2_i) after removal of environmental heterogeneity in the Western regional red/specialty trials

Genotype	W/SP/R-H ¹	W/S/SP/R-A ²	W/SP/R-M ³	Genotype mean	σ^2_i	s^2_i
A96741-1R	1561	1537	1236	1445	**	**
A96741-2R	1540	1508	1177	1408		
AO93487-2R ^a	1521	1467	1071	1353		
All Blue	960	1092	921	991		
BTX1544-2	1256	1210	1009	1158		
CO93037-6R	1285	1175	1155	1205	**	*
CO94165-3 ^b	1101	1062	877	1013	**	**
CO94183-1 ^c	1288	1234	1024	1182	**	**
NDA5507-3 ^d	1166	1229	1041	1145		
VC0967-2	1370	1448	1066	1294	*	
VC1002-3	1301	1081	943	1108	**	**
VC1015-7	1439	1189	894	1174		
Yukon Gold	1250	1322	1032	1201		
Location Mean	1310	1273	1034			

* = $P < 0.05$, ** = $P < 0.01$, significance level of variances σ^2_i and s^2_i

¹ Hermiston, OR

² Aberdeen, ID

³ Mount Vernon, WA

^a subsequently named 'Red Sunset'

^b subsequently named 'Purple Majesty'

^c subsequently named 'Mountain Rose'

^d subsequently named 'Yukon Gem'

Table 7 Broad-sense heritabilities (H) and their confidence intervals (CI) of copper and sulfur content in the Tri-State, Western Regional Russet and Western Regional Red/Specialty trials

	Tri-state	Western regional russet	Western regional red/specialty
	Copper		
H	0	0.93	0.51
Upper CI	NA	0.97	0.82
Lower CI	NA	0.84	0.43
	Sulfur		
H	0.53	0.68	0.88
Upper CI	0.87	0.89	0.96
Lower CI	0.22	0.31	0.68

deficiency perceived as commonly limiting to nutritional health. Potato is not a particularly good source of sulfur. Certain food legumes, nuts, small grains, spinach and fried onions are higher (Masters and McCance 1939). However, increases in content in potato could be achieved by selection if a benefit were found in future nutritional studies. Copper nutritional needs have been estimated by depletion/repletion studies. For infants, potatoes could be a significant source of copper supplying 40 % of daily needs of children 7 to 12 months old up to 2 years old in a 100 gram FW sample. Taken as a whole, there is a reason to recommend potato with higher values of copper in that it might reduce the shortage of intake in US populations.

These breeding lines represent a small fraction of the total variation to be accessed in potato germplasm and a more thorough survey of the Cultivated Collection of the International Potato Center or of wild accessions in the USDA/ARS Potato Germplasm Collection of Sturgeon Bay, Wisconsin, might provide a greater range to choose from.

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