

Stability and Broad-Sense Heritability of Mineral Content in Potato: Potassium and Phosphorus

C. R. Brown · K. G. Haynes · M. Moore · M. J. Pavek ·
D. C. Hane · S. L. Love · R. G. Novy

Published online: 27 June 2013
© Potato Association of America 2013

Abstract In the study of nutritional variability in potato it is desirable to know the present range of expression and genetic potential for increase. Potato breeding lines and varieties in two separate trials were evaluated for potassium and phosphorus content by wet ashing and Inductively Coupled Argon Plasma Emission Spectrophotometer analysis. Stability and broad-sense heritability were determined. Among genotypes, potassium content ranged from 1.85 and 2.49 % DW while phosphorus content ranged from 0.16 to 0.34 % DW over both trials. Genotype by environment interactions were significant in the Tri-State and Western Regional Red/Specialty (WR-R/SP) trials for both potassium and phosphorus, while environments were not. Genotype was a significant source of variation for both minerals in the WR-R/SP trial only. In the Tri-State trials, 7 and 4 of ten clones were unstable before and after removal of environmental heterogeneity, respectively, for

potassium content, and 5 and 4 genotypes were unstable before and after removal of environmental heterogeneity, respectively, for phosphorus. In the WR-R/SP Trials, 7 and 3 of 13 clones were unstable before and after removal of environmental heterogeneity, respectively, for potassium content, and 3 and 4 genotypes were unstable before and after removal of environmental heterogeneity, respectively, for phosphorus. Broad sense heritability was low for both potassium and phosphorus in the Tri-State Russet-Skin Trials but high for both potassium and phosphorus in the WR-R/SP Trials. Although potato is a minor contributor of phosphorus to the human diet, it is an important source of potassium. Adult males and females receive 12 % of the Recommended Dietary Allowance of potassium from 100 g of potato. Estimates of broad-sense heritability from these two trials suggest that genotypes with higher levels of both potassium and phosphorus can be selected from within the Red/Specialty market class, but not from within the Tri-State russet class. An increase in potassium content in the potato, for which the daily need in the human body is so high, could be a boon to human health.

C. R. Brown (✉)
USDA/Agricultural Research Service, Prosser, WA 99350, USA
e-mail: chuck.brown@ars.usda.gov

K. G. Haynes
Genetic Improvement of Fruits and Vegetables Laboratory, USDA/
Agricultural Research Service, Beltsville, MD 20705, USA

M. Moore
Agri-Northwest, Plymouth, WA 99346, USA

M. J. Pavek
Department of Horticulture and Landscape Architecture,
Washington State University, Pullman, WA 99164, USA

D. C. Hane
Department of Crop Science, Oregon State University, HAREC,
Hermiston, OR 97838, USA

S. L. Love
AREC, University of Idaho, Aberdeen, ID 83210, USA

R. G. Novy
USDA/Agricultural Research Service, Aberdeen, ID 83210, USA

Resumen En el estudio de la variabilidad nutricional en papa es deseable conocer la amplitud actual de expresión y potencial genético para aumentarla. Se evaluaron líneas avanzadas y variedades en dos ensayos separados para el contenido de potasio y fósforo por análisis de cenizas húmedas y por Espectrofotómetro de Emisión de Plasma de Acoplamiento Inductivo de Argón. Se determinaron la estabilidad y la amplitud de la heredabilidad. El contenido de potasio varió de 1.85 a 2.49 % de peso seco (PS) entre genotipos, mientras que el contenido de fósforo fluctuó de 0.16 a 0.34 % PS en ambos ensayos. Las interacciones genotipo-medio ambiente fueron significativas en los ensayos Tri-Estatales y Regionales del Oeste de las especialidades rojas (WR-/R/SP) para ambos elementos, mientras que los ambientes solos no lo fueron. El genotipo fue una fuente significativa de variación para ambos minerales solamente

en el ensayo WR-R/SP. En los Ensayos Tri-Estatales, 7 y 4 de diez clones fueron inestables antes y después de eliminar la heterogeneidad ambiental, respectivamente, para el contenido de potasio, y 5 y 4 genotipos fueron inestables antes y después de eliminar la heterogeneidad ambiental, respectivamente, para fosforo. En los ensayos WR-R/SP, 7 y 3 de 13 clones fueron inestables antes y después de eliminar la heterogeneidad ambiental, respectivamente, para el contenido de potasio, y 3 y 4 genotipos fueron inestables antes y después de quitar la heterogeneidad ambiental, respectivamente, para fosforo. La amplitud de la heredabilidad fue baja para ambos elementos en los ensayos Tri-Estatales de piel tipo russet (corrugada), pero alta para ambos minerales en los ensayos de WR-R/SP. Aún cuando la papa contribuye poco en fosforo de la dieta humana, es una fuente importante de potasio. Los adultos hombres y mujeres reciben 12 % de los requerimientos de la dieta recomendados de potasio por cada 100 g de papa. Las estimaciones de la amplitud de la heredabilidad de estos dos ensayos sugieren que los genotipos con los niveles más altos, tanto de fosforo como de potasio, se pueden seleccionar de entre la clase de mercado de especialidad/roja, pero no de los de clase russet del Tri-Estatal. Un aumento en el contenido de potasio en la papa, del cual la necesidad diaria en el cuerpo humano es tan alta, pudiera ser de un gran beneficio para la salud humana.

Keywords ICAPES · Breeding · RDA · Germplasm · Human nutrition

Introduction

Potassium exists as a univalent cation for which uptake is highly related to metabolic activity. It is highly mobile in plants between and within cells and is transported long distance in the xylem and phloem. It is important in carbohydrate metabolism, protein synthesis, and cell elongation. Nearly all potassium is located intracellularly (Epstein and Bloom 2004). Next to nitrogen, potassium is the mineral most needed for plant growth (Marschner 1995). In one instance of a potato crop in Washington State with exceptionally high yields of 82 t-ha⁻¹, potassium comprised 0.4 % of tops and tubers. That crop took up 370 kg K per hectare, which exceeded the 325 kg of nitrogen it took up (Roberts and McDole 1985). Plants are essentially potassium accumulators, building up levels in the cytosol much higher than in the soil medium. Such high concentrations are necessary for the role of enzyme co-factor (Epstein and Bloom 2004). Potassium influences yield, tuber quality, specific gravity, susceptibility to blackspot bruise, sugar level, and storability (Westermann 1993).

White et al. (2009) found no correlation of potassium concentrations and yield of diverse cultivars. Blackspot bruise of potato was negatively correlated with potassium

content in the tubers (Vertregt 1968). Potassium is an important component of the human diet. The daily need for potassium is quite high at 4,700 mg per day for adults (National Research Council 1989). Having a blood serum potassium of between 3.7 and 5.2 mEq/L is necessary for healthy electrolyte balance (<http://www.nlm.nih.gov/medlineplus/ency/article/003484.htm>; Mount and Zandi-Nejad 2008). Unlike potassium, phosphorus is not reduced in plants but persists in the oxidized form. After uptake, predominantly as H₂PO₄⁻, it can remain inorganic, be esterified into sugar phosphates or be combined into the energy-rich pyrophosphate. Phosphorus has a prominent structural role in nucleic acids. In a potato crop yielding 18 t-ha⁻¹ 22.3 kg per hectare was taken up by tops and tubers with 18.5 kg comprising the tubers. Potato tubers contain generally 0.25 % dry wt phosphorus (Lorenz and Vittum 1980). The RDA for phosphorus is from 800 to 1,200 mg for adults (National Research Council 1989). Phosphorus is the second most abundant element in the human body on a dry basis due to its abundance in the bones.

The purpose of this study is to determine a range of genotypic means over multiple environments, stability, and broad-sense heritability of potassium and phosphorus contents of 23 breeding lines and varieties.

Materials and Methods

Field Experiments Potato genotypes in two distinct trials were planted at different locations in 2004. The 7 (4 for the Tri-State and 3 for the Western Regional Red/Specialty) locations and associated crop management are described in 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 medium-sized undamaged 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 Potassium and phosphorus contents were transformed to the natural logarithm for all statistical analyses and back-transformed for presentation of means. Variance components for each source of variation were estimated from the mixed models procedure in SAS (version 9.1, Cary, NC); 5, 4, 6, and 2 outliers were removed from the Tri-State potassium, Western Regional Red/Specialty potassium, Tri-State phosphorus, and Western Regional Red/Specialty Trial phosphorus data sets, respectively. All effects were considered random. Normality of the residuals

from the analysis of the transformed data was verified by examination of the box plot and normal probability plot using the univariate procedure in SAS. 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 $1 - [(MS_1/MS_2) F_{(1-\alpha/2; df_2, df_1)}]^{-1}$, while the lower confidence interval is $1 - [(MS_1/MS_2) F_{(\alpha/2; df_2, df_1)}]^{-1}$, where MS_1 = mean squares for genotype and MS_2 = mean squares for genotype \times environment. These mean squares were obtained from the type III mean squares from the general linear models procedure in SAS.

Dynamic stability occurs when the performance of a genotype changes across environments in proportion to the population mean at each environment (Piepho 1996). For example, if the same genotypes were evaluated in three environments, with average yields of all genotypes in the first and second environments being 200 % and 150 %, respectively, of yields in a third environment, a stable genotype would have average yields in the first and second environments of 200 % and 150 %, respectively, of yields in the third environment. To evaluate the stability of each potato genotype in these studies, the genotype \times environment interaction ($G \times E$) was partitioned into stability variance components (σ^2_i) 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 $G \times E$ interaction and the remainder was partitioned into s^2_i assignable to each potato genotype, and constitutes variance not explained by removal of environmental effects Fig. 1. Least significant differences for comparing genotypic mean K or P over all environments at $P = 0.05$ were calculated when the genotype source of variation from the mixed models procedure was significant.

Results and Discussion

In the Tri-State trials, ten clones were grown in four environments in the Pacific Northwest: one in Aberdeen ID, one in Hermiston OR, and an early and late harvest in Othello WA. Potassium content ranged from 2.01 to 2.37 %. Neither environments (E) nor genotypes (G) were significant sources of variation for potassium, while $G \times E$ was. Both Russet Burbank and Ranger Russet, the most widely grown and the third most widely grown varieties in North America, respectively, did not display significant $G \times E$. Only one

other clone, AOA95154-1, did not display significant $G \times E$. For these three stable clones, K was highest in the late Othello harvest, as it was for the overall location; followed by Hermiston; then the early Othello harvest; and, finally, K was lowest at the Aberdeen site. In contrast, seven clones displayed significant $G \times E$ and four of these remained unstable after removal of environmental heterogeneity (Table 1). In two cases, K was higher in one location than would have been expected based on the environmental means: A96023-6 and AO96164-1 were higher in Hermiston than in the late harvest Othello location. In three cases, K was lower in one location than would have been expected based on the environmental means: A95409-1, A96095-3 and A98295-3TE were lower in the early Othello harvest than in Aberdeen. In two cases, the difference in K between locations was less than expected: for AOA95155-7, K was very similar in Hermiston and Aberdeen; for A96104-2, was very similar in Hermiston and the early Othello harvest.

In the Western Regional Red/Specialty trial, 13 clones were grown in three environments in the Pacific Northwest. For potassium, genotypes and $G \times E$ were significant, but environments were not (Table 2). Six clones were stable across these three environments: All Blue, BTX1544-2, CO94165-3, NDA5507-3, VC0967-2, and Yukon Gold. Seven clones showed significant $G \times E$ and three remained unstable after removal of environmental heterogeneity (Table 2). In two cases, the lowest K values were found in Mount Vernon, not Aberdeen: A96741-2R and VC1015-7. In the other five cases, the instability was a result of relative proportional differences among locations: A96741-1R, AO93487-2R, CO93037-6R, CO94183-1, and VC1002-3. Potassium ranged between 1.85 and 2.5 %. The highest level was 36 % higher than the lowest. A graphic demonstration of the partition of $G \times E$ is shown in Fig. 1 for four genotypes. Lack of significant $G \times E$ was displayed by “All Blue” which tracks the environmental mean calculated over all genotypes. Significant $G \times E$ (σ^2_i) and significant remainder left after removal of $G \times E$ heterogeneity (s^2_i), is shown for A96741-2R, which is unstable. Genotypes A96741-1R and AO93487-2R show significant $G \times E$ but are not unstable after removal of heterogeneity due to environment.

Phosphorus content of clones in the Tri-State trials was analyzed over four environments. The genotype \times environment interaction was significant, but genotypes and environments were not. Three clones were stable across these environments: A95409-1, A96095-3, and AO96164-1. Five and four clones were unstable before and after removal of environmental heterogeneity, respectively (Table 3). Of these, two were unstable both before and after removal of environmental heterogeneity: A98295-3TE and AOA95155-7. Phosphorus contents averaged over environments ranged from 0.28 to 0.34 % DW.

Table 1 Potassium content (percent DW) by trial location and overall, significance of the contribution each genotype makes to the G×E variance before (σ^2_i) and after (s^2_i) removal of environmental heterogeneity in the Tri-state Trials

Genotype	TS-H ^a	TS-A ^b	TS-OE ^c	TS-OL ^d	Genotype Mean	σ^2_i	s^2_i
A95409-1	2.34	1.65	1.45	2.59	2.01	**	**
A96023-6	2.69	1.62	2.05	2.61	2.24	**	**
A96095-3	2.12	1.83	1.81	2.53	2.07	*	ns
A96104-2	2.21	1.78	2.19	2.60	2.20	**	**
A98295-3TE	2.43	1.57	1.43	2.63	2.02	**	**
AO96164-1 ^e	2.87	1.72	1.89	2.63	2.28	**	ns
AOA95154-1 ^f	2.21	1.70	1.87	2.67	2.11	ns	ns
AOA95155-7	2.16	2.15	2.29	2.88	2.37	**	ns
Ranger Russet	2.39	1.69	1.72	2.58	2.10	ns	ns
Russet Burbank	2.22	1.63	1.70	2.63	2.05	ns	ns
Location Mean	2.36	1.73	1.84	2.64			

ns not significant

^a Hermiston, OR

^b Aberdeen, ID

^c Othello, WA (early harvest)

^d Othello, WA (late harvest)

^e Subsequently named ‘Sage Russet’

^f Subsequently named ‘Clearwater Russet’

Table 2 Potassium content (percent DW) by trial location and overall, significance of the contribution each genotype makes to the G×E variance before (σ^2_i) and after (s^2_i) removal of environmental heterogeneity in the Western Regional Red/Specialty Trials

Genotype	W/R/SP-H ^a	W/R/SP-A ^b	W/R/SP-M ^c	Genotype Mean	σ^2_i	s^2_i
A96741-1R	2.70	1.76	2.11	2.19	**	ns
A96741-2R	2.96	2.30	2.21	2.49	*	**
AO93487-2R ^d	2.32	2.01	2.15	2.16	*	ns
All Blue	2.25	1.79	1.89	1.98	ns	ns
BTX1544-2	2.45	1.77	2.09	2.10	ns	ns
CO93037-6R	2.71	1.83	2.19	2.24	*	ns
CO94165-3 ^e	2.17	1.76	1.88	1.94	ns	ns
CO94183-1 ^f	2.18	1.64	2.09	1.97	*	**
NDA5507-3 ^g	2.39	1.98	2.25	2.21	ns	ns
VC0967-2	2.31	1.77	1.98	2.02	ns	ns
VC1002-3	2.83	1.89	2.18	2.30	*	ns
VC1015-7	2.55	2.10	1.97	2.20	**	**
Yukon Gold	2.09	1.67	1.79	1.85	ns	ns
Environment Mean	2.45	1.87	2.06			
LSD (0.05)				0.11		

ns not significant

^a Hermiston, OR

^b Aberdeen, ID

^c Mount Vernon, WA

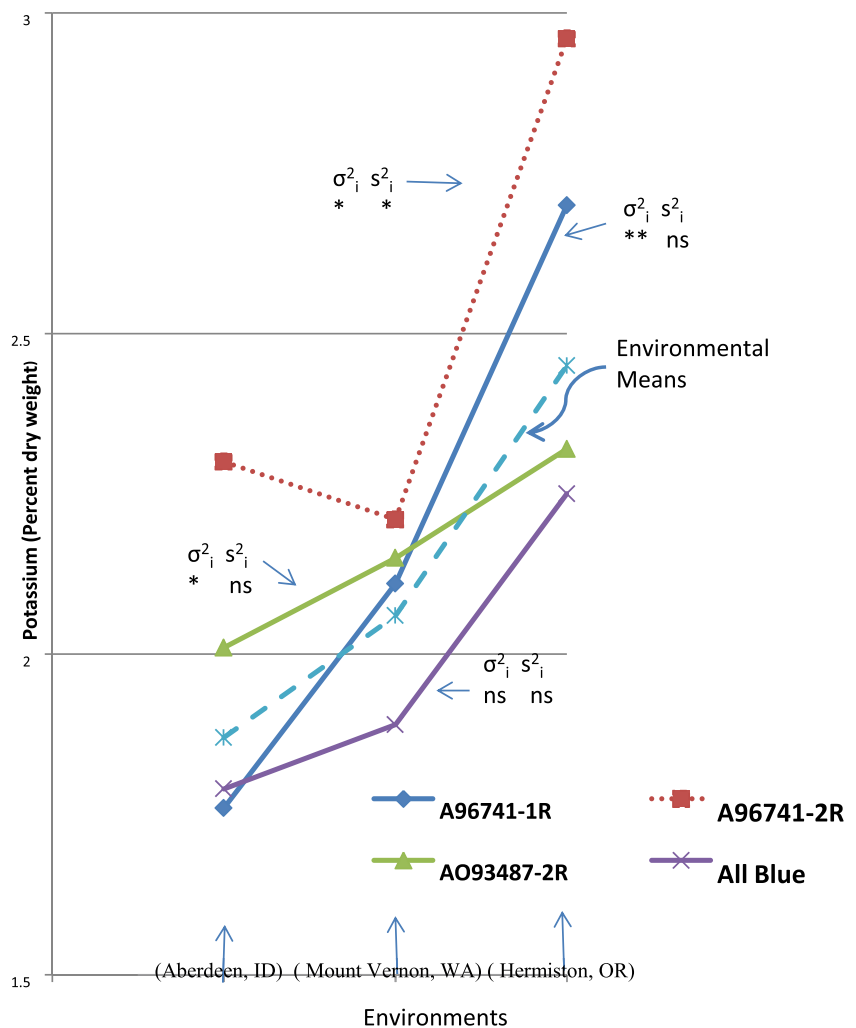
^d Subsequently named ‘Red Sunset’

^e Subsequently named ‘Purple Majesty’

^f Subsequently named ‘Mountain Rose’

^g Subsequently named ‘Yukon Gem’

Fig. 1 Graphical illustration of types of interaction of genotypes over three environments derived from Table 2. Lack of $G \times E$ (σ^2_i) is characterized by close parallelism with the average of all genotypes at each environment while significant $G \times E$ is deviation from that. A96741-2R has significant $G \times E$ and s^2_i , while “All Blue” is not significant for either component. (*ns* not significant, $*P < 0.05$, $**P < 0.01$). AO93487-2R and A96741-2R do not have significant remainders (s^2_i) after removal of environmental heterogeneity



Phosphorus contents in the Western Regional Red/Specialty trial were obtained from three environments (Table 4). Genotypes and $G \times E$ were significant while environments were not. Seven clones were stable across environments: A96741-1R, AO93487-2R, BTX1544-2, CO94183-1, VC0967-2, VC1002-3, and Yukon Gold. Three and five genotypes were unstable before and after removal of environmental heterogeneity, respectively. Only two of these were unstable both before and after removal of environmental heterogeneity: CO94165-3 and NDA5507-3. The phosphorus content of CO94165-3 was higher than expected in Aberdeen, and NDA5507-3 was lower than expected in Aberdeen based on environmental means. The genotype means averaged over the three environments ranged from 0.16 to 0.27 %, the upper value reaching 69 % more than the lower value (Table 4).

Broad-Sense Heritability

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. Broad-sense heritabilities for potassium content and their 95 % confidence intervals were 0.20 (−1.06, 0.78) and 0.81 (0.45, 0.93), for the Tri-State and Western Regional Red/Specialty Trials, respectively. Broad-sense heritabilities for phosphorus content and their 95 % confidence intervals were 0.33 (−0.74, 0.82) and 0.81 (0.49, 0.93) for the Tri-State and Western Regional Red/Specialty Trials, respectively (Table 5). From these results it may be surmised that the selection applied to the Western Regional Red/Specialty trial for increased phosphorus and potassium content would succeed while the Tri-State does not possess sufficient genetic variation to result in a gain. Broad-sense heritability is applicable to vegetatively propagated crops in the sense that, when significant, it predicts gain by selection within a group of genotypes that are clonally fixed from this generation into the next. Gain in a selected subset is predicted to occur in proportion to the relative magnitude of the genetic variance versus total phenotypic variance. Selection among clones will result in highest gain where H is highest, e.g. for

Table 3 Phosphorus content percent DW by trial location and overall, significance of the contribution each genotype makes to the G×E variance before (σ^2_i) and after (s^2_i) removal of environmental heterogeneity in the Tri-state Trials

Genotype	TS-H ^a	TS-A ^b	TS-OE ^c	LT-OL ^d	Genotype Mean	σ^2_i	s^2_i
A95409-1	0.37	0.20	0.27	0.40	0.31	ns	ns
A96023-6	0.44	0.19	0.30	0.43	0.34	ns	*
A96095-3	0.35	0.18	0.29	0.40	0.30	ns	ns
A96104-2	0.33	0.21	0.29	0.37	0.30	**	ns
A98295-3TE	0.38	0.13	0.20	0.42	0.28	**	**
AO96164-1 ^e	0.39	0.18	0.27	0.46	0.33	ns	ns
AOA95154-1 ^f	0.34	0.21	0.29	0.39	0.31	*	ns
AOA95155-7	0.31	0.24	0.31	0.44	0.33	**	**
Ranger Russet	0.36	0.19	0.32	0.39	0.32	ns	*
Russet Burbank	0.37	0.14	0.26	0.44	0.30	**	ns
Environment Mean	0.36	0.19	0.28	0.41			

ns not significant

^a Hermiston, OR

^b Aberdeen, ID

^c Othello, WA (early harvest)

^d Othello, WA (late harvest)

^e Subsequently named ‘Sage Russet’

^f Subsequently named ‘Clearwater Russet’

Table 4 Phosphorus content (percent DW) by trial location and overall significance of the contribution each genotype makes to the G×E variance before (σ^2_i) and after (s^2_i) removal of environmental heterogeneity in the Western Regional Red/Specialty Trials

Genotype	WR/R/SPR-H ^a	WR/R/SPR-A ^b	WR/R/SP-M ^c	Genotype mean	σ^2_i	s^2_i
A96741-1R	0.41	0.19	0.19	0.24	ns	ns
A96741-2R	0.41	0.24	0.21	0.27	ns	*
AO93487-2R ^d	0.34	0.21	0.22	0.25	ns	ns
All Blue	0.29	0.18	0.18	0.21	*	ns
BTX1544-2	0.32	0.16	0.16	0.20	ns	ns
CO93037-6R	0.37	0.17	0.20	0.24	ns	*
CO94165-3 ^e	0.25	0.17	0.14	0.18	**	**
CO94183-1 ^f	0.33	0.18	0.18	0.22	ns	ns
NDA5507-3 ^g	0.32	0.13	0.21	0.21	**	**
VC0967-2	0.32	0.18	0.17	0.21	ns	ns
VC1002-3	0.36	0.17	0.18	0.22	ns	ns
VC1015-7	0.35	0.21	0.18	0.23	ns	*
Yukon Gold	0.25	0.12	0.14	0.16	ns	ns
Environment Mean	0.33	0.18	0.18			
LSD (0.05)				0.03		

ns not significant

^a Hermiston, OR

^b Aberdeen, ID

^c Mount Vernon, WA

^d Subsequently named ‘Red Sunset’

^e Subsequently named ‘Purple Majesty’

^f Subsequently named ‘Mountain Rose’

^g Subsequently named ‘Yukon Gem’

Table 5 Broad-sense heritabilities (H) of potassium and phosphorus content in the Tri-State and Western Regional Red/Specialty

	Tri-State	Western Regional Red/Specialty
Potassium		
H	0.33	0.81
Upper CI	0.82	0.93
Lower CI	-0.74	0.49
Phosphorus		
H	0.20	0.81
Upper CI	0.78	0.93
Lower CI	-1.06	0.45

CI confidence interval

potassium and phosphorus in the Western Regional Red/Specialty trials.

Potassium accumulation by plant genotypes may be a component of drought resistance. This has been demonstrated in wheat in the instance of the “or” gene that controls higher potassium uptake (Richards 2006). Wheat cultivars with homozygous “or” (it is recessive) yield consistently more under drought conditions than those lacking this genetic configuration. A protective effect is also found in tomato genotypes where higher potassium uptake is associated with resistance to salinity (Ghazi 2000). It is debatable whether potato utilizes osmotic adjustment to resist drought with Vos and Haverkort (2007) denying its existence and most prominently Levy et al (2013) rebutting and stating that there is evidence of osmotic adjustment in response to drought. Increasing potassium uptake might provide more drought tolerance to potato.

The potassium and phosphorus contents reported here are in conformity with summaries in Rastovski and van Es (1987) and Woolfe (1987). Subar et al. (1998) found that white-fleshed potatoes provide 2.1 % of the total phosphorus in the US consumers’ diet and 8.5 % of the total potassium. The RDA for phosphorus is 700 mg per day. Thus a 100 g portion of potato supplies about 10 mg or 1.4 % of the daily need. Phosphorus is, therefore, of limited importance because so little of the RDA is supplied by the potato. On the other hand, only 25 % of the phosphorus is found in the form of phytic acid that can impede the absorption of iron, calcium and zinc by the human gastrointestinal tract. Small grains and food legumes, in contrast, have at least three times as high a percentage of phosphorus in the form of phytic acid (Quick and Li 1976; Woolfe 1987).

Potatoes are an important source of potassium. One hundred grams of potato (fresh weight, cooked) can supply 1/8 of the RDA of an adult (National Research Council 1989). Bamberg et al. (2007) found tuber levels approaching 4 % dry weight in cultivated potato Groups *Phureja* and *Stenotomum*. The breeding lines and cultivars measured in this study 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.

Neither potassium or phosphorus are identified commonly as resulting in health problems due to insufficiency in the diet. However, the human body maintains potassium in a tight range through the regulatory action of the kidney. Maintenance of a healthy state depends in large part on proper exercise and nutrition including abundant electrolytes which are most available from vegetables (Rodriguez and Ross 1998). Potatoes are often prohibited from the diet of patients with impaired renal function. Bethke and Jansky (2008) showed that cutting potato into small pieces and leaching in water resulted in significant decreases in potassium content, which would aid potassium avoiders in their preparation of potatoes. On the other hand, potatoes are recommended for patients who are losing potassium, at abnormally high rates, to maintain electrolyte balance and to reduce blood pressure. Insufficient potassium in the blood serum can result in coronary arrhythmia. Most importantly, potassium consumption at the RDA levels is an excellent means to counter acidosis. Humans evolved with a diet high in plant foods and rich in potassium-base (e.g. potassium carbonate). Today’s “Western” diet is high in sodium-acid (sodium chloride) and protein (Frassetto et al. 2001). The most important consequences are high blood pressure, and in the aging body, excretion of calcium which is extracted from the bones, leading to osteoporosis. Potassium consumption is negatively correlated to frequency of hip fractures in people aged 60 and above (Leibman 2010). Dietary potassium reduces vascular damage and lowers blood pressure in rats with salt-sensitive hypertension (Kido et al. 2007). Maintenance of potassium homeostasis is an important component of treatment of severe hypertensive heart disease (Packer 1990). Long term positive outcomes with enhanced potassium in the diet include the decrease of morbidity due to heart disease and kidney disease (Demigné et al. 2008; He and MacGregor 2008). High potassium foods are often recommended for temporary potassium deficiency that might accompany rigorous physical activity or other non-chronic causes of low potassium (<http://www.WHfoods.com>). The American population is estimated to be 40 to 60 % deficient in potassium on a daily basis (Ervin et al. 2004). Since potato is a significant source of potassium in the diet of the U.S. consumer, breeding for higher levels may have health benefits. Potato is among the most potassium-dense vegetables. Other plant-derived foods with similarly high potassium include sweet potatoes, bananas, raisins, and lima beans, to name a few (<http://webmd.com/food-recipes/features/potassium>). The broad-sense heritability estimated from the Western Regional Red/Specialty trial indicates that increasing potassium and phosphorus would be feasible in potato. However, this trial is composed of mostly unconventional and red-skinned genotypes

suggesting that a program to increase potassium or phosphorus would have greater progress in this type of germplasm. Since the daily requirement of potassium is so high and the incidence of deficiency so prevalent in the US, breeding for increased potassium in potato, the most consumed vegetable, would probably benefit the general population.

References

- Bamberg, J.B., M.W. Martin, and J.P. Palta. 2007. Variation in *Solanum* species' tuber potassium accumulation and its implications for human nutrition. *American Journal of Potato Research* 85: 2 (Abstract).
- Bethke, P.C., and S.H. Jansky. 2008. The effects of boiling and leaching on content of potassium and other minerals in potato. *Journal of Food Science* 75: H80–H85.
- Brown, C.R., K.G. Haynes, M. Moore, M.J. Pavsek, D.C. Hane, S.L. Love, R.G. Novy, and J.C. Miller Jr. 2010. Stability and broad-sense heritability of mineral content in potato: Iron. *American Journal of Potato Research* 87: 390–396.
- Brown, C.R., K.G. Haynes, M. Moore, M.J. Pavsek, D.C. Hane, S.L. Love, R.G. Novy, and J.C. Miller Jr. 2011. Stability and broad-sense heritability of mineral content in potato: Zinc. *American Journal of Potato Research* 88: 238–244.
- Demigné, C., H. Sabboh, M.-N. Horcajada, and V. Coxam. 2008. Contribution of various dietary constituents to the acid base status: interest of animal models of latent metabolic acidosis. *The Open Nutrition Journal* 2: 1–4.
- Epstein, E., and A.J. Bloom. 2004. *Mineral nutrition of plants: principles and perspectives*. NY: Sinauer Associates. 400 pp.
- Ervin, R.B., C.Y. Wang, J.D. Wright, and J. Kennedy-Stephenson. 2004. *Dietary intake of selected minerals for the United States population: 1999–2000. Advance data from vital and health statistics; no. 341*. Hyattsville: National Center for Health Statistics.
- Frassetto, L., R.C. Morris Jr., D.E. Sellmeyer, K. Todd, and A. Sebastian. 2001. Diet, evolution and aging: the pathophysiologic effects of the post-agricultural inversion of the potassium-to-sodium and base-to-chloride ratios in the human diet. *European Journal of Nutrition* 40: 200–213.
- Ghazi, N.A.-K. 2000. Growth, water use efficiency and sodium and potassium acquisition by tomato cultivars grown under salt stress. *Journal of Plant Nutrition* 23: 1–8.
- He, F.J., and G.A. MacGregor. 2008. Beneficial effects of potassium on human health. *Physiologia Plantarum* 133: 725–735.
- Holland, J.B., W.E. Nyquist, and C.T. Cervantes-Martinez. 2003. Estimating and interpreting heritability for plant breeding: an update. *Plant Breeding Reviews* 22: 9–112.
- Kang, M.S. 1989. A new SAS program for calculating stability-variance parameters. *Journal of Heredity* 80: 415.
- Kido, M., A. Katsuyuki, M. Onozato, T. Akihiro, M. Yoshikawa, T. Ogita, and T. Fujita. 2007. Protective effect of dietary potassium against vascular injury in salt-sensitive hypertension. *Hypertension* 51: 225–231.
- Knapp, S.J., W.W. Stroup, and W.M. Ross. 1985. Exact confidence intervals for heritability on a progeny mean basis. *Crop Science* 25: 192–194.
- Leibman, B. 2010. Bad for bones: the latest on food and fractures. Nutrition Action Health Letters. Center for science in the public interest. November pp. 1–7.
- Levy, D., W.K. Coleman, and R.E. Veilleux. 2013. Adaptation of potato to water shortage: irrigation management and enhancement of tolerance to drought and salinity. *American Journal of Potato Research* 90: 186–206.
- Lorenz, O.A., and M.T. Vittum. 1980. Phosphorus nutrition in vegetable crops and sugar beets. In *The role of phosphorus in agriculture*, ed. F.E. Khasawneh, E.C. Sample, and E.J. Kamprath, 737–762. Madison: American Society of Agronomy. 910 pp.
- Marschner, H. 1995. *Mineral nutrition of higher plants*, 2nd ed. New York: Academic. 889 pp.
- Mount, D.B., and K. Zandi-Nejad. 2008. Disorders of potassium balance. In *Brenner and Rector's the kidney*, 8th ed, ed. B.M. Brenner. Philadelphia: Saunders Elsevier. chap 15.
- National Research Council. 1989. *Recommended dietary allowances. Committee on Dietary Allowances. Subcommittee on the Tenth Edition of the RDAs. Committee on Life Sciences*. Washington, DC: National Academy Press. 302 pp.
- Packer, M. 1990. The potential role of potassium as a determinant of morbidity and mortality in patients with systemic hypertension and congestive heart failure. *The American Journal of Cardiology* 65: 45E–51E.
- Piepho, H.-P. 1996. Analysis of genotype-by-environment interaction and phenotypic stability. In *Genotype by environment interaction*, ed. M.S. Kang and H.G. Gauch. Boca Raton: CRC Press.
- Quick, W.A., and P.H. Li. 1976. Phosphorus balance in potato tubers. *Potato Research* 19: 305–312.
- Rastovski, A., and A. van Es. 1987. *Storage of potatoes: post-harvest behaviour, store design, storage practice, handling*. Wageningen: Pudoc. 453 pp.
- Richards, R.A. 2006. Physiological traits used in the breeding of new cultivars for water-scarce environments. *Agricultural Water Management* 80: 197–211.
- Roberts, S., and R. McDole. 1985. Potassium nutrition of potatoes. In *Potassium in agriculture*, ed. R.D. Munson, 779–818. Madison: American Society of Agronomy. 1223 pp.
- Rodriguez, D.J., and M.T. Ross. 1998. Can nutrition and exercise prevent chronic disease states? Getting back to the basics of health care: part 1: nutritional and dietary factors. *Disease Management* 1: 135–149.
- Shukla, G.K. 1972. Some statistical aspects of partitioning genotype-environment components of variability. *Heredity* 29: 237–245.
- Subar, A.F., S.M. Krebs-Smith, A. Cook, and L.L. Kahle. 1998. Dietary sources of nutrients among US adults, 1989 to 1991. *Journal of the American Dietetic Association* 98: 537–547.
- Vertregt, N. 1968. Relation between black spot and composition of the potato crop. *European Potato Journal* 11: 34–44.
- Vos, J., and A.J. Haverkort. 2007. Water availability and potato crop performance. In *Potato biology and biotechnology: advances and perspectives*, ed. D. Vreugdenhil, J. Bradshaw, C. Gebhardt, F. Govers, M.A. Taylor, D.K.L. MacKerron, and H.A. Ross, 333–351. Amsterdam: Elsevier.
- Westermann, D.T. 1993. Fertility management. In *Potato health management*, ed. R.C. Rowe, 77–86. St. Paul: APS Press. 178 pp.
- White, P.J., J.E. Bradshaw, M.F.B. Dale, G. Ramsay, J.P. Hammond, and M.R. Broadley. 2009. Relationships between yield and mineral concentrations in potato tubers. *HortScience* 44: 6–11.
- Woolfe, J.A. 1987. *The potato in the human diet*. Cambridge: Cambridge University Press. 237 pp.