

Genetic Variation for Potato Tuber Micronutrient Content and Implications for Biofortification of Potatoes to Reduce Micronutrient Malnutrition

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Abstract Micronutrients are crucial to healthy growth and development, yet a large proportion of the world's population suffers from micronutrient deficiencies. Biofortification of staple foods has tremendous potential to alleviate these deficiencies. Potato production in developing countries is increasing rapidly, and therefore, biofortification of potatoes for essential micronutrients may be feasible. The purpose of this study was to determine the amount of genetic variation for micronutrient content in potato germplasm. Eighteen potato clones, consisting of 'Atlantic' and 17 4x-2x hybrids between *S. tuberosum* and diploid hybrids of *S. phureja*-*S. stenotomum*, were grown in three locations (NC, VA, NJ) 2 years (2001, 2002). Samples of tuber tissue were analyzed for copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn). There were significant differences among clones for Cu, Fe, Mn and Zn. Clone x environment interactions were significant for Cu and Zn. Broad-sense heritability and its 95 % confidence interval for Cu was 0.65 (0.50–0.89); Fe was 0.49 (0.27–0.84); Mn was 0.84 (0.82–0.96); and Zn was 0.82 (0.73–0.94). Genetic variation for these four

micronutrients is large, suggesting that the micronutrient content of potatoes can be improved through breeding.

Resumen Los micronutrientes son cruciales para el crecimiento y desarrollo sanos, aun cuando una gran proporción de la población mundial sufre por deficiencias de micronutrientes. La biofortificación de alimentos básicos tiene un potencial tremendo para aliviar estas deficiencias. La producción de papa en países en desarrollo esta aumentando rápidamente, por lo tanto, la biofortificación de papa con micronutrientes esenciales puede ser factible. El propósito de este estudio fue determinar la cantidad de variación genética para el contenido de micronutrientes en germoplasma de papa. Diez y ocho clones de papa, consistentes en "Atlantic" y 17 híbridos 4x-2x entre *S. tuberosum* e híbridos diploides de *S. phureja*-*S. stenotomum* se cultivaron en tres localidades (NC, VA, NJ) en dos años (2001–2002). Se analizaron las muestras del tejido de tubérculo para cobre (Cu), hierro (Fe), manganeso (Mn) y zinc (Zn). Hubo diferencias significativas entre los clones para Cu, Fe, Mn, y Zn. Las interacciones clon x medio ambiente fueron significativas para Cu y Zn. La heredabilidad en amplio sentido y su intervalo de confianza de 95 % para Cu fue de 0.65 (0.50–0.89); el de Fe fue de 0.49 (0.27–0.84); el de Mn fue de 0.84 (0.82–0.96); y para Zn fue de 0.82 (0.73–0.94). La variación genética para estos tres micronutrientes es grande, lo que sugiere que el contenido de micronutrientes en papas puede mejorarse mediante mejoramiento genético.

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Introduction

Since the mid-1980s there has been increasing awareness of micronutrient malnutrition, also known as Hidden Hunger.

The wide-scale adoption of cereal crops during the Green Revolution displaced much of the local production of fruits, vegetables and legumes, which are the chief sources of micronutrients for most people (Welch et al. 1997). The three basic strategies to improve micronutrient nutrition, namely, supplements, food fortification, and the development of nutritionally enhanced crop cultivars, have all been shown to be effective. However, economic will and lack of infrastructure often hamper the distribution of supplements and fortified food. On the other hand, the breeding and subsequent production of nutritionally enhanced crop cultivars is a more stable and economically viable solution for enhancing the nutritional status of many people. Both scientists and policy experts agree that breeding micronutrient-enhanced plants (biofortification) is economically feasible (Welch et al. 1997; Bouis 2000, 2002) and a more viable long-range solution than supplementation or fortification through industrial processes. Interest in breeding micronutrient-enhanced plants has been increasing at the beginning of the 21st century (Bouis 2000; Welch 2002; Welch and Graham 2002; Bouis 2002; Nestel et al. 2006; Mayer et al. 2008).

In response to these micronutrient deficiencies, the CGIAR Micronutrients Project was established with an objective to assemble a package of tools that plant breeders could use to produce mineral- and vitamin-dense cultivars. This project focused on wheat, rice, maize, beans, and cassava for iron, zinc, and vitamin A (Bouis, et al. 1999). In 2004, the HarvestPlus Challenge Program (<http://www.harvestplus.org>) was launched for biofortification research on beans, cassava, maize, pearl millet, rice, sweet potato, and wheat for iron, zinc and vitamin A. Research resulting from these programs suggests that there is adequate genetic variation in maize for zinc (Ortiz-Monasterio et al. 2007), but less so for iron (Banziger and Long 2000; Long et al. 2004); in wheat for zinc and iron (Cakmak et al. 1999; Monasterio and Graham 2000); and, in rice for zinc and iron, although the positive correlations with phytate may reduce their bioavailability (Graham et al. 1999).

These major projects have virtually ignored potato, *Solanum tuberosum* L., which has high quality protein, composed of all the essential amino acids necessary in the human diet. In addition, a small potato (148 g serving) provides 7 % of kcal for a 2,000 kcal diet and delivers more than 10 % Daily Value (DV) of folate, manganese, magnesium and phosphorus, and more than 20 % DV of potassium, vitamin C and vitamin B-6 (<http://nutritiondata.self.com/facts/vegetables-and-vegetable-products/2770/2>, accessed 2/10/12). Potatoes are also a good source of fiber. On a per acre basis, potatoes provide more dry matter and protein per unit growing area than do cereal crops (Bamberg and del Rio 2005). In the decade between 1990–1992 and 2000–2002, potato production increased around the world, with

the biggest increases occurring in the developing world: on average consumption increased by 47 % in Africa and Asia, by 41 % in Central American, by 37 % in Polynesia, by 29 % in the Middle East, by 27 % in Central Asia, and by 10 % in South America, (FAO 2010).

Micronutrient malnutrition is a serious problem in both developed and developing countries, with iron deficiency the most common and widespread nutritional disorder worldwide (WHO 2011). Over 30 % of the world's population is anemic, many due to iron deficiency. The World Health Organization (2011) reported that in developing countries 50 % of pregnant women and 40 % of preschool age children are estimated to be anemic. In the U.S., 9 % of toddlers and 9–11 % of adolescent girls and women of childbearing age were found to be iron deficient (Looker et al. 1997). Iron deficiency has negative effects on immune function, cognitive development, temperature regulation, energy metabolism, and work performance (Dallman 1986).

Zinc deficiency was first recognized in the 1960s in young Egyptian men and was characterized by stunted growth and delayed sexual maturation (Prasad et al. 1963). Zinc is needed for growth, normal development, DNA synthesis, immunity, neurosensory function and plays a functional role in many zinc-containing proteins and a large number of zinc-dependent enzymes (Wood 2000). A study by Walker et al. (2009) attributed 4.4 % of deaths among children under 5 years in developing countries to zinc deficiency, with the highest death rates in Africa (5.3 %) and Asia (3.7 %).

Copper, an antioxidant (Chan et al. 1998) required by the central nervous system (LaFontaine et al. 2010), helps regulate blood pressure and pulse, influences bone formation and skeletal mineralization (Palacios 2006), plays a role in heme synthesis (Ames et al. 2005) and promotes wound healing (Berger and Chioloro 1995). Copper deficiency is characterized by loss of appetite, anemia, infection, edema, and arthritis.

Manganese is a key component of several enzymes, notably manganese superoxide dismutase—the principal antioxidant in mitochondria, and activates other enzymes involved in carbohydrate, amino acid, and cholesterol metabolism (Food and Nutrition Board 2001). Manganese deficiencies result in skeletal deformation and inhibit the production of collagen in wound healing (Keen and Zidenberg-Cherr 1996).

Micronutrient analyses of potato have focused primarily on Fe and Zn. Fe content of potato varieties reportedly ranges from 2.8 to 158 mg kg⁻¹ (True et al. 1978; Warman and Havard 1998; Burgos et al. 2007; Brown et al. 2010; Rivero et al. 2003; Andre et al. 2007), with concentrations among the landraces of South America two to three times greater than in the cultivated varieties in the U.S. and Europe. Burgos et al. (2007) reported significant differences

among Andean potato varieties grown at two locations, whereas, Brown et al. (2010) found significant differences among potato selections in only one of three regional trials. Burgos et al. (2007) reported significant genotype \times environment interactions for Fe, and Brown et al. (2010) reported significant genotype \times environment interactions for Fe in two of their three regional trials. Estimates of the amount of genetic variation for Fe content vary greatly. We calculated broad-sense heritability as 0.93 from Burgos et al. (2007) analyses. Brown et al. (2010) obtained estimates of 0, 0.64 and 0.76 for their three regional trials. Although Fe content in the varieties studied by Burgos et al. (2007) appeared to be fairly stable, Brown et al. (2010) reported that in the two regional trials where genotype \times environment interactions were significant, slightly more than half of the genotypes were unstable.

There is less variation in potatoes for Zn than Fe. Zn content of potatoes has been reported to range from 2 to 37 mg kg⁻¹ (True et al. 1978; Warman and Havard 1998; Rivero et al. 2003; Andre et al. 2007; Burgos et al. 2007; Brown et al. 2011). With the exception of one variety from *S. x chaucha* (Rivero et al. 2003) all other potato germplasm has been found to contain <29 mg kg⁻¹ Zn.

Cu and Mn contents of potato tubers are low relative to other minerals. True et al. (1978) obtained an average value of 1.93 mg kg⁻¹ FW Cu for nine varieties grown in various locations in the U.S. with a range from 0.87 to 3.27 mg kg⁻¹, and an average value of 2.53 mg kg⁻¹ FW Mn with a range from 1.43 to 6.99 mg kg⁻¹. Warman and Havard (1998) found no difference in tuber Cu content between conventional and organically grown tubers of the variety ‘Superior’, which ranged from 4.0 to 4.8 mg kg⁻¹, nor in Mn content, which ranged from 2.8 to 7.2 mg kg⁻¹. Rivero et al. (2003) reported that Cu content ranged from 7.2 to 11.2 mg kg⁻¹ and Mn content ranged from 1.02 to 2.14 mg kg⁻¹ in three species/subspecies grown in Europe.

The purposes of this study were to 1) estimate the proportion of phenotypic variation attributable to genetic variation (broad-sense heritability) for micronutrient content, 2) determine the importance of genotype \times environment interactions on micronutrient content, and 3) determine the stability of micronutrient content in potato.

Materials and Methods

Eighteen potato clones, consisting of ‘Atlantic’ and 17 tetraploid clones resulting from 4x-2x hybrids between tetraploid *S. tuberosum* and diploid hybrids of *S. phureja*-*S. stenotomum*, were grown for 2 years (2001, 2002) in three locations (Plymouth NC, Painter VA, Bridgeton NJ) for a total of six environments. The parentage of the 4x-2x clones

is given in Table 1. Planting, harvest dates, and soil types for each environment are given in Table 2. These clones were originally selected for their resistance or susceptibility to internal heat necrosis as part of a study to determine if tuber mineral status differed among resistant and susceptible clones (Sterret et al. 2006).

A two-factor factorial study (18 clones \times 2 rates of CaSO₄) was planted as a randomized complete block design with three replicates in each environment. Half the plots received no CaSO₄, while in the other half, 448 kg ha⁻¹ was applied as an in-furrow treatment over the seedpieces at planting. Each plot consisted of 20 hills spaced 0.23 m within the row at each location. Tubers from each plot were mechanically harvested and sized into groups. Pith tissue samples from ten clean tubers 64–83 mm in diameter from each plot were obtained using a No. 9 cork borer to obtain a longitudinal section. Tissue cores were sliced and dried at 60 C for tissue analysis. These tissue samples were shipped to A & L Labs, Richmond, VA to be ground and analyzed for Cu, Fe, Mn, and Zn. Tuber tissue was prepared for analyses by microwave assist open nitric/hydrochloric acid digestion using closed vessel microwave digestion (CEM Mars 5) then determined by inductively coupled plasma spectrometry (Mills and Jones 1996).

Since there were no differences among the calcium treatments, nor interactions involving calcium treatments for the four micronutrients analyzed, all sources of variation involving calcium treatments were ignored. Cu, Fe, Mn and Zn concentrations were transformed using the natural logarithm prior to analyses to conform to normality. Clone, clone

Table 1 Parentage of the 17 4x-2x (*S. tuberosum* \times *S. phureja*-*S. stenotomum*) hybrids evaluated for tuber mineral content in Plymouth NC, Painter VA, and Bridgeton NJ in 2001 and 2002

Clone	Female parent	Male parent
BTD0054-3	B0169-56	BD016-2
BTD0060-3	B0220-14	BD016-2
BTD0060-9	B0220-14	BD016-2
BTD0063-8	B0220-14	BD040-3
BTD0070-1	B9955-11	BD019-4
BTD0073-1	Superior	BD042-2
BTD0088-2	Atlantic	BD011-1
BTD0104-1	B0566-5	BD042-2
BTD0105-2	B0566-5	BD043-3
BTD0111-1	B0172-22	BD016-2
BTD0112-3	B0172-22	BD067-4
BTD0114-1	B0587-9	BD040-3
BTD0118-5	B1066-47	BD040-3
BTD0120-2	K7-8	BD031-2
BTD0124-5	B0925-4	BD033-3
BTD0127-3	B0806-13	BD040-3
BTD0128-5	B0808-3	BD040-3

Table 2 Planting and harvest dates, and soil type for 18 potato clones evaluated for tuber Cu, Fe, Mn and Zn content in six mid-Atlantic environments

Location	Year	Planting date	Harvest date	Soil type
Plymouth, NC	2001	14 March	17 July	Portsmouth fine sandy loam
Painter, VA	2001	9 April	16 July	Bojac sandy loam
Bridgeton, NJ	2001	20 April	20 August	Aura loam
Plymouth, NC	2002	20 March	27 July	Portsmouth fine sandy loam
Painter, VA	2002	25 March	22 July	Bojac sandy loam
Bridgeton, NJ	2002	17 April	19 August	Aura loam

x environment, and error variance components were estimated from the mixed models procedure in SAS (version 9.2, Cary, NC) and used to estimate broad-sense heritability (H) as the ratio of genetic to phenotypic variance (Nyquist 1991). Exact confidence intervals for H were calculated using the formulas derived by Knapp et al. (1985). The mean squares needed to calculate these confidence intervals were obtained from the type III mean squares from the general linear models procedure in SAS. Where significant clone x environment interactions were found, the genetic stability of each clone before and after removal of environmental heterogeneity was determined using an interactive matrix language procedure in SAS written by Kang (1989). An environmental index for each environment was calculated by subtracting the grand mean over all environments from the mean for each environment. For Cu, Fe, Mn and Zn the back-transformed means are shown in all tables and figures, however, stability analyses were run on the natural logarithm transformed values.

Results and Discussion

There were no significant differences among environments for tuber Fe, Mn, Cu, or Zn content (Table 3). Average Fe, Mn, Cu, and Zn contents were 47, 10.2, 9.9, and 20.0 mg kg⁻¹, respectively.

There were significant differences among clones for Fe content (Table 3). Average Fe content in the clones ranged from 42 to 52 mg kg⁻¹ (Table 4). One clone had an Fe content significantly greater than ‘Atlantic’ (46 mg kg⁻¹); the remaining clones were not significantly different than ‘Atlantic’. Brown et al. (2010) reported a much wider range in Fe content, 17 to 64 mg kg⁻¹, for 33 clones grown over three trials in the Pacific Northwest; however, unlike our study, they found no significant differences among clones for Fe content in two of the three trials reported therein. There was no significant clone x environment interaction for Fe content in our study (Table 3), whereas, Burgos et al.

Table 3 Estimates of the variance components from the mixed models analysis of ln(Fe), ln(Mn), ln(Cu) and ln(Zn), broad-sense heritability (H), and the upper and lower confidence intervals for H ($P=0.95$)

Variance components	ln(Fe)	ln(Mn)	ln(Cu)	ln(Zn)
Environment	0.01235	9.9598	0.01150	0.04423
Rep(environment)	0.00861*	5.1782*	0.00346*	0.00005
Clone	0.00294*	1.3788**	0.00551*	0.01056**
Clone x environment	0.00208	9.0636	0.00532**	0.00588**
Error	0.04926	0.04695	0.03694	0.03185
Broad-sense heritability	0.49	0.84	0.65	0.82
Lower confidence interval	0.27	0.82	0.50	0.73
Upper confidence interval	0.84	0.96	0.89	0.94

*, ** Significant at the 5 % and 1 % levels, respectively

(2007) found significant genotype x environment interactions among Andean potatoes grown at two locations and Brown et al. (2010) found significant clone x environment interactions in two of their three trials. Broad-sense heritability for Fe content in these clones was estimated as 0.49 with a 95 % confidence interval of 0.27 to 0.84, as compared to estimates of 0.00, 0.64, and 0.73 that Brown et al. (2010) reported for the Tri-state, Western Regional Russet, and Specialty/Red Trials, respectively, and 0.93 which we calculated from the data analyses in Burgos et al. (2007). With the exception of the Tri-State estimate (Brown et al. 2010), most reports agree that the proportion of genetic

Table 4 Mean iron and manganese (mg kg⁻¹ DW) content of 18 clones grown in Plymouth NC, Painter VA, and Bridgeton, NJ in 2001 and 2002

Clone	Fe	Mn
Atlantic	46.3	8.3
BTD0054-3	48.3	12.9
BTD0060-3	51.1	9.4
BTD0060-9	50.7	10.2
BTD0063-8	51.7	10.6
BTD0070-1	42.8	11.9
BTD0073-1	46.1	10.1
BTD0088-2	41.5	9.8
BTD0104-1	43.7	9.0
BTD0105-2	44.4	7.8
BTD0111-1	49.4	11.0
BTD0112-3	48.4	10.8
BTD0114-1	44.2	9.9
BTD0118-5	43.0	10.3
BTD0120-2	46.8	9.3
BTD0124-5	53.0	12.2
BTD0127-3	48.2	10.2
BTD0128-5	47.9	10.3
Mean	46.9	10.2
LSD (0.05)	5.1	1.4

Table 5 Mean copper (mg kg⁻¹ DW) content of 18 clones grown in Plymouth NC, Painter VA, and Bridgeton, NJ in 2001 and 2002, and the stability before (σ_1^2) and after (s_1^2) removing environmental heterogeneity

Clone	NC2001	NC2002	VA2001	VA2002	NJ2001	NJ2002	Mean	σ_1^2	s_1^2
Atlantic	9.0	11.3	11.0	8.0	8.0	8.0	9.2	*	**
BTD0054-3	9.2	7.2	11.5	7.0	10.5	9.7	9.2	**	**
BTD0060-3	10.2	9.8	13.0	8.7	10.8	8.4	10.2	ns	*
BTD0060-9	10.2	6.8	11.5	7.2	8.3	8.0	8.7	**	**
BTD0063-8	9.3	10.2	13.5	9.2	11.2	9.3	10.4	ns	ns
BTD0070-1	7.2	8.3	12.0	8.0	10.5	11.0	9.6	*	*
BTD0073-1	8.7	10.3	11.8	8.7	9.3	8.8	9.6	ns	ns
BTD0088-2	8.2	9.8	11.3	9.3	8.8	9.1	9.4	ns	ns
BTD0104-1	8.2	11.0	11.2	8.2	10.3	10.7	9.9	ns	ns
BTD0105-2	9.2	9.8	9.8	8.0	11.0	8.8	9.4	ns	ns
BTD0111-1	10.5	10.5	14.3	10.3	11.0	12.0	11.4	ns	ns
BTD0112-3	11.0	10.2	11.7	11.3	9.3	10.2	10.6	*	ns
BTD0114-1	8.5	11.0	13.2	8.8	10.0	10.3	10.3	ns	ns
BTD0118-5	6.7	9.0	11.9	8.3	8.2	8.3	8.7	ns	ns
BTD0120-2	7.7	9.7	12.2	10.0	9.0	9.2	9.6	ns	ns
BTD0124-5	9.5	13.4	13.2	10.5	11.3	11.5	11.6	ns	ns
BTD0127-3	7.7	12.0	13.5	10.8	9.8	11.2	10.8	*	*
BTD0128-5	7.2	11.3	11.7	9.5	10.7	11.7	10.3	**	**
Mean	8.8	10.1	12.1	9.0	9.9	9.8	9.9		

*, ** Significant at the 5 % and 1 % level, respectively
 ns not significant

variation to total phenotypic variation for iron ranges from moderate to high.

There were significant differences among clones for Mn content (Table 3). Average Mn content in the clones ranged from 7.8 to 12.9 mg kg⁻¹ (Table 4), which is slightly higher than either True et al. (1978) (1.43–6.99 mg kg⁻¹) or Warman

and Havard (1998) (2.8–7.2 mg kg⁻¹) reported. Thirteen clones had a significantly higher Mn content than ‘Atlantic; the other four clones were not significantly different than ‘Atlantic’. Broad-sense heritability for Mn content was estimated as 0.84 with a 95 % confidence interval of 0.82 to 0.96, indicating that the genetic variation for Mn content is very high.

Table 6 Mean zinc (mg kg⁻¹ DW) content of 18 clones grown in Plymouth NC, Painter VA, and Bridgeton, NJ in 2001 and 2002, and the stability before (σ_1^2) and after (s_1^2) removing environmental heterogeneity

Clone	NC2001	NC2002	VA2001	VA2002	NJ2001	NJ2002	Mean	σ_1^2	s_1^2
Atlantic	31.2	19.2	21.0	14.0	12.7	13.0	18.5	**	**
BTD0054-3	29.9	15.5	23.8	12.8	17.5	16.3	19.3	**	**
BTD0060-3	34.8	20.5	28.3	17.3	20.5	17.2	23.1	**	*
BTD0060-9	28.7	18.8	27.0	14.3	15.3	15.5	19.9	**	ns
BTD0063-8	26.1	19.7	25.0	16.7	19.1	16.5	20.5	ns	ns
BTD0070-1	20.3	15.5	23.2	13.2	16.8	16.3	17.6	**	**
BTD0073-1	26.7	24.2	25.8	19.0	18.5	16.9	21.8	**	**
BTD0088-2	23.0	20.3	23.2	16.5	17.7	16.1	19.4	ns	ns
BTD0104-1	23.5	19.7	20.8	14.0	17.7	16.8	18.8	ns	ns
BTD0105-2	22.8	18.5	19.3	14.4	16.5	14.0	17.6	ns	ns
BTD0111-1	25.0	20.0	25.0	16.8	18.7	18.2	20.6	ns	ns
BTD0112-3	28.3	22.0	25.2	18.0	19.5	19.3	22.1	ns	ns
BTD0114-1	22.3	19.5	24.5	13.7	15.3	15.3	18.5	ns	ns
BTD0118-5	22.3	19.5	23.3	14.2	16.3	12.3	18.0	ns	*
BTD0120-2	24.0	19.5	24.5	15.5	17.3	18.7	19.9	ns	ns
BTD0124-5	34.5	28.2	29.0	20.7	19.5	23.3	25.9	**	*
BTD0127-3	27.0	23.5	27.3	18.7	15.6	19.5	21.9	*	*
BTD0128-5	29.0	23.5	27.2	18.3	16.8	21.7	22.8	ns	ns
Mean	26.6	20.4	24.6	16.0	17.3	17.1	20.4		

There were significant differences among clones for tuber Cu content (Table 3). Average tuber Cu content in the clones ranged from 8.7 to 11.6 mg kg⁻¹ (Table 5). The clone with the highest Cu content was only 33 % higher than the lowest. Eight of the clones had a Cu content significantly higher than ‘Atlantic’ (9.2 mg kg⁻¹); the other nine clones were not significantly different than ‘Atlantic’. Our results are in close agreement with Rivero et al. (2003) who reported a range from 7.2 to 11.2 mg kg⁻¹ for three potato species/subspecies grown in Europe, but our results are more than eight times greater than the values reported by True et al. (1978) for nine varieties grown in the U.S. ‘Atlantic’, which was the only cultivar we tested, was not one of the cultivars evaluated by True et al. (1978). The clone x environment interaction was significant for Cu. Ten of the clones were stable for Cu across these six environments both before and after removal of environmental heterogeneity (Table 5). Broad-sense heritability for Cu content was estimated as 0.65 with a 95 % confidence interval of 0.50 to 0.89 (Table 3). We found no reports in the literature estimating broad-sense heritability for tuber Cu content, nor presenting data from which we could estimate H. Our estimate indicates that genetic variation for Cu content is moderately high.

There were significant differences among clones for zinc content (Table 3). Average zinc content in the clones ranged from 18 to 26 mg kg⁻¹ (Table 6). Ten clones had a significantly higher Zn content than ‘Atlantic’; the other seven clones were not significantly different than ‘Atlantic’. Brown et al. (2011) reported a range of 12 to 18 mg kg⁻¹ in their trials, thus our results were slightly higher, but of a similar range. Brown et al. (2011) found no significant differences among clones for Zn content in two of their three trials. The clone x environment interaction was significant for Zn (Table 3). Seven 4x-2x hybrids and ‘Atlantic’ made a significant contribution to the clone x environment interaction both before and after removal of environmental heterogeneity (Table 6). Broad-sense heritability for Zn content in these clones was estimated as 0.82 with a 95 % confidence interval of 0.73 to 0.94, as compared to estimates of 0.29, 0.61, and 0.19 that Brown et al. (2011) reported for the Tri-State, Western Regional Russet, and Specialty/Red Trials, respectively. Our estimate indicates that the genetic variation for Zn content is very high. This was in contrast to the estimates obtained by Brown et al. (2011); however, in two of their three trials they found no significant differences among clones, which would be responsible for their low estimates.

This study suggests that significant genetic variation exists for tuber micronutrient content in potatoes and that genetic variation is a large portion of the total phenotypic variation. Although genetic variation at the tetraploid level is more complex than at the diploid level, our results, in agreement with several other researchers, suggests that it

should be possible to increase the micronutrient value of potato through breeding. Given the widespread growth in potato production worldwide, it makes sense to consider adding potato to the list of foods under consideration for biofortification.

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