Relationships Between Yield and Mineral Concentrations in Potato Tubers

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Abstract. There is concern that modern cultivars and/or agronomic practices have resulted in reduced concentrations of mineral elements essential to human nutrition in edible crops. Increased yields are often associated with reduced concentrations of mineral elements in produce, and a number of recent studies have indicated that, when grown under identical conditions, the concentrations of several mineral elements are lower in genotypes yielding more grain or shoot biomass than in older, lower-yielding genotypes. Potato is a significant crop, grown worldwide, yet few studies have investigated whether increasing yields, through agronomy or breeding, affects the concentrations of mineral elements in tubers. This article examines the hypothesis that increasing yields, either by the application of mineral fertilizers and/or by growing higher-yielding varieties, leads to decreased concentrations of mineral elements in tubers. It reports that the application of fertilizers influences tuber elemental composition in a complex manner, presumably as a consequence of soil chemistry and interactions between mineral elements within the plant, that considerable variation exists between potato genotypes in the concentrations of mineral elements in their tubers, and that, like in other crops, higher-yielding genotypes occasionally have lower concentrations of some mineral elements in their edible tissues than lower-yielding genotypes.

MINERAL ELEMENTS REQUIRED BY HUMANS

Humans require at least 22 mineral elements for their well-being (White and Broadley, 2005a). These can all be supplied by an appropriate diet. However, it is estimated that over 60% of the world's six billion people are iron (Fe)-deficient, over 30% are zinc (Zn)-deficient, 30% are iodine (I)-deficient, and $\approx 15\%$ are selenium (Se)-deficient (Welch and Graham, 2002; White and Broadley, 2005a). Deficiencies of calcium (Ca), magnesium (Mg), and copper (Cu) are also common in both developed and developing countries. This situation has been attributed to sourcing produce from land with low mineral phytoavailability, eating crops with inherently low tissue mineral concentrations, and/or consuming the refined foods of civilization. In particular, it appears that the occurrences of Fe-deficiency anemia, Zn-deficiency disorders, and Ca-deficiency disorders have increased dramatically in populations changing from traditional diets dominated by pulses, vegetables, and fruits to diets dominated by cereals (Graham et al.,

2001; Welch and Graham, 2002), whose tissue concentrations of these elements appear to be constrained by an ancient evolutionary heritage (Broadley et al., 2004, 2007; White and Broadley, 2003). In practical terms, mineral malnutrition can be addressed through supplementation, food fortification, well-chosen dietary diversification, and/or increasing mineral concentrations in edible crops (biofortification). The biofortification of crops through application of mineral fertilizers, combined with breeding varieties with an increased ability to acquire mineral elements, is advocated as an immediate agronomic strategy both to increase mineral concentrations in edible produce and to improve yields on infertile soils (White and Broadley, 2005a).

MINERAL COMPOSITION OF POTATOES

Potatoes are an excellent source of carbohydrates, vitamins, and minerals. A single medium-sized potato weighing 200 g fresh weight (FW) can provide $\approx 26\%$ of the U.S. Dietary Reference Intake (DRI) of Cu; 17% to 18% of the DRI of potassium (K), phosphorus (P), and Fe; and 5% to 13% of the DRI of Zn, Mg, and manganese (Mn) (Table 1). Potatoes are generally not rich in Ca but can be a valuable source of trace elements such as Se and I if fertilized appropriately (Broadley et al., 2006b). Furthermore, because potato tubers have relatively high concentrations of organic compounds that stimulate the absorption of mineral micronutrients by humans such as ascorbate (vitamin C), protein cysteine and various organic and amino acids (U.S. Department of Agriculture, Agricultural Research Service, 2006) and low

concentrations of compounds that limit their absorption such as phytate [0.11% to 0.27% dry matter (DM); Frossard et al., 2000; Phillippy et al., 2004] and oxalate (0.03% DM; Bushway et al., 1984), the bioavailability of mineral elements in potatoes is potentially high.

HISTORICAL VARIATION IN MINERAL CONCENTRATIONS IN EDIBLE HORTICULTURAL PRODUCTS

Mayer (1997) drew attention to a possible decline in the mean DM content and mean concentrations of Ca, Cu, Mg, and sodium (Na) in raw vegetables and Cu, Fe, K, and Mg concentrations in fresh fruits available in the United Kingdom between the 1930s and 1980s. Subsequently, White and Broadley (2005b) expressed the concentrations of mineral elements in U.K. produce on a DM basis to remove any effects of tissue hydration and confirmed that the mean concentrations of Cu, Mg, and Na in the DM of vegetables and the mean concentrations of Cu, Fe, and K in the DM of fruits available in the United Kingdom had decreased significantly between the 1930s and the 1980s. White and Broadley (2005b) also analyzed comparable data from the United States and observed that the mean Ca, Cu, and Fe concentrations in the DM of vegetables and the mean concentrations of Cu, Fe, and K in the DM of fruits had decreased significantly since the 1930s. Both these publications used geometric means and *t* tests to support their conclusions. At the same time, Davis et al. (2004) used medians and sign (quantile) tests to conclude that the moisture-adjusted concentrations of Ca, Fe, and P in horticultural

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Table 1. The mineral content of 200 g fresh weight of potatoes and its contribution to the U.S. Dietary Reference Intake (DRI).^z

	DRI	US potatoes	UK potatoes	Percent DRI
N (mg)	NS		660	—
S (mg)	NS		60	—
K (mg)	4700	850	720	18
Cl (mg)	2300		132	—
Ca (mg)	1000	22	10	2.2
P (mg)	700	118	74	17
Na (mg)	1500	12	14	0.8
Mg (mg)	420	45	34	11
Fe (mg)	8	1.4	0.8	18
Zn (mg)	11	0.6	0.6	5.5
Mn (mg)	2.3	0.3	0.2	13
Cu (µg)	900	231	160	26
I (µg)	150	37	6	25
Se (µg)	55	0.8	2	1.4

^zMineral contents are means of four potato varieties available in the United States (unspecified varieties, flesh, and skin; U.S. Department of Agriculture, Agricultural Research Service, 2006) or the United Kingdom (Desiree, King Edwards, Maris Piper, and Pentland Crown varieties, flesh only; Food Standards Agency, 2002) with the exception of US potato iodine, which was taken from True et al. (1978). The DRI values are those for a 31- to 50-year-old male (National Academy of Sciences, 2004).

NS = not specified.

produce available in the United States had declined between 1950 and 1999. Davis (2006) noted that the conclusion of declining mineral concentrations in produce depended critically on the statistical method used, observing that nonparametric tests indicated that only Cu and Na concentrations in the DM of vegetables and the concentrations of no minerals in the DM of fruits available in the United Kingdom had decreased significantly between the 1930s and the 1980s. Nevertheless, the observation that similar changes in the geometric mean and median concentrations of mineral elements in vegetables have occurred in both the United Kingdom and United States, which share similar historical horticultural and consumer practices, suggests that this phenomenon might be a consequence of the adoption of modern varieties and/or agronomic practices (White and Broadley, 2005b). Unfortunately, none of the studies mentioned provide sufficient data to determine whether mineral concentrations of any single vegetable or fruit have altered significantly over time either in the United Kingdom or in the United States. Ultimately, different varieties and/or cultivation practices must be compared directly under the same environmental conditions to determine whether mineral concentrations in a particular crop have been affected by changing cultivars or agricultural practices (Broadley et al., 2006a; Davis, 2006; Davis et al., 2004).

It has been hypothesized that increasing yields has resulted in decreased concentrations of mineral elements in produce because of a “dilution effect” caused by plant growth rates exceeding the ability of plants to acquire these elements (Jarrell and Beverly, 1981) that is impacted by both environmental and genetic factors (Davis, 2005; Davis et al.,

2004). It has long been appreciated that environmental factors accelerating plant growth rates such as higher temperatures, light intensity, and irrigation often result in reduced concentrations of macronutrient elements in plant tissues (Jarrell and Beverly, 1981), and a number of recent studies have shown that the concentrations of various mineral elements are lower in higher-yielding genotypes (Davis et al., 2004; Garvin et al., 2006; Monasterio and Graham, 2000). Monasterio and Graham (2000) observed a strong linear relationship between year of release and grain yield and negative trends between grain Fe, Zn, and P concentrations and date of release in a historical set of 26 bread wheat cultivars grown together at two locations over 3 years. Similarly, in a study of 14 U.S. hard red winter wheat varieties grown together at two locations, Garvin et al. (2006) observed negative relationships between seed Fe, Zn, and Se concentrations and both grain yields and date of release, although the extent to which this effect manifested itself was influenced by the environment. Strong negative relationships between seed P and sulfur (S) and grain yields were also observed in these field trials (Garvin et al., 2002). In leafy vegetables, Farnham et al. (2000) found strong negative relationships between head weight and Ca and Mg concentrations among 27 broccoli genotypes, and Broadley et al. (2008) observed weak negative relationships between shoot biomass and shoot Ca concentrations among genotypes of *Brassica oleracea* var. *gongylodes* (kohlrabi) and var. *sabauda* (Savoy cabbage) and between shoot biomass and shoot Mg concentrations among genotypes of *B. oleracea* var. *acephala* (kale/collards) and var. *gongylodes* (Broadley et al., 2008). This article examines the effects of fertilizer applications on the concentrations of mineral elements in potato tubers, the extent of genetic variation in the concentrations of mineral elements in potato tubers, and the hypothesis that increased yields, produced either by the application of mineral fertilizers and/or by growing higher-yielding varieties, lead to decreased concentrations of mineral elements in potato tubers.

EFFECTS OF FERTILIZER APPLICATION ON TUBER MINERAL CONCENTRATIONS

Yields of potatoes have increased significantly over the last 50 years as a result of the widespread use of fungicides, fertilizers, and irrigation. The application of mineral fertilizers to the potato crop accelerates plant growth and increases tuber yield (e.g., Allison et al., 2001a, 2001b, 2001c; Birch et al., 1967; Eppendorfer et al., 1979; Harris, 1992; Johnston et al., 1986; Neeteson and Wadman, 1987; Simmons and Kelling, 1987; Trehan and Sharma, 2003; White et al., 2005). It is evident that applying nitrogen (N) fertilizers increases tuber N concentrations (e.g., Augustin, 1975; Eppendorfer et al., 1979; Harris, 1992; Sen Tran and Giroux, 1991),

applying P fertilizers increases tuber P concentrations (Allison et al., 2001a; Alvarez-Sánchez et al., 1999; Hammond and White, 2005; Rocha et al., 1997; Simpson, 1962; Trehan and Sharma, 2003), applying K fertilizers increases tuber K concentrations (Addiscott, 1976; Allison et al., 2001b; Harris, 1992; Maier, 1986), and applying Ca or Mg fertilizers increases tuber Ca (Bamberg et al., 1993, 1998; Clough, 1994; Karlsson et al., 2006; McGuire and Kelman, 1984, 1986; Simmons and Kelling, 1987) and Mg concentrations (Allison et al., 2001c), respectively. In addition, the application of these fertilizers can also affect the concentrations of other mineral elements in tubers. For example, although the application of N fertilizers often has little effect on tuber K, Ca, and Mg concentrations, it can lead to a decrease in tuber Fe and P concentrations (Allison et al., 2001c; Augustin, 1975; Harris, 1992; Simpson, 1962), the application of P fertilizers can increase tuber N and Mg concentrations but may reduce tuber Mn concentrations (Hammond and White, 2005), the application of K fertilizers often, but not always, increases tuber Mg but reduces tuber Ca and P concentrations (Addiscott, 1974, 1976; Allison et al., 2001c; Maier, 1986), and the application of Ca fertilizers generally reduces tuber Mg concentrations but can increase tuber P, S, and K concentrations (Clough, 1994; Simmons and Kelling, 1987). These effects are the result not only of complex interactions between mineral elements in the soil and their consequences for uptake by plants, but also of the effects of tissue mineral composition on the redistribution of elements within the plant. Taken together, these studies indicate that tuber mineral concentrations depend greatly on the phytoavailability of different mineral elements to the crop. Indeed, tuber mineral concentrations vary significantly with location (True et al., 1978) allowing mineral profiling of tubers to be used to verify the regional origin of produce (Anderson et al., 1999; Casañas Rivero et al., 2003; Di Giacomo et al., 2007; Padín et al., 2001). In addition, it has been observed that tuber P, S, K, Mg, Fe, molybdenum, and Cu concentrations are often higher in organically grown potatoes, whereas tuber N and Mn concentrations are higher in conventionally grown potatoes (Warman and Havard, 1998; Wszelaki et al., 2005). Thus, the complex interactions between minerals in the soil together with interactions between mineral elements in their uptake and distribution within the plant suggest that the differences in tuber mineral concentrations observed under contrasting fertilization regimes are unlikely to be the result of a simple dilution effect resulting from increased yields per se.

Other environmental factors impacting tuber yields include irrigation and elevated CO₂ concentrations. Increasing yield through irrigation appears to have little effect on tuber N or K concentrations but can increase tuber P concentration and reduce tuber Ca and Mg concentrations (Asfary et al., 1983; Simpson,

1962). Increasing yield through elevated CO₂ has been found to reduce the concentrations of N, K, and Mg in tubers at crop maturity (Fangmeier et al., 2002). These studies suggest that increased tuber yield can be associated with a reduction in the concentrations of some, but not all, mineral elements in the tubers.

GENETIC VARIATION IN TUBER MINERAL CONCENTRATIONS

There is considerable genetic variation in tuber mineral concentrations both between and within *Solanum* species (Table 2). Tuber Ca, Fe, and Zn concentrations have been shown to vary significantly between *Solanum* species grown under identical conditions (Andre et al., 2007; Bamberg et al., 1993, 1998). Among the *Solanum* species, *S. gourlayi* and *S. microdontum* had the highest tuber Ca concentrations, whereas *S. kurtzianum*

and *S. tuberosum* had the lowest tuber Ca concentrations when supplied with ample Ca (Bamberg et al., 1993). Although the skin generally has a greater Ca concentration than the flesh (Ereifej et al., 1998; McGuire and Kelman, 1984, 1986; Wszelaki et al., 2005), differences in tuber Ca concentration between *Solanum* species do not appear to be associated simply with differences in skin-to-flesh ratios (Bamberg et al., 1993). Andre et al. (2007) observed a strong relationship between tuber Ca and Fe concentrations and a weak but significant correlation between Zn and Fe concentrations among 74 Andean landraces. They observed that some genotypes from the Ajanhuiri group had exceptionally high tuber Ca and Fe concentrations and that tuber size explained ≈13% of the variability in tuber Fe concentrations. When grown under identical conditions, *S. tuberosum* genotypes have been shown to differ in tuber N (Augustin, 1975; Fitzpatrick et al.,

1969; Rexen, 1976), K (Brown et al., 2005; Ereifej et al., 1998; Tekalign and Hammes, 2005; Van Marle et al., 1994; Workman and Holm, 1984), P (Dampney et al., 2002; Ereifej et al., 1998; Randhawa et al., 1984; Tekalign and Hammes, 2005; Trehan and Sharma, 2003), S (Tekalign and Hammes, 2005), Ca (Ereifej et al., 1998; Karlsson et al., 2006; McGuire and Kelman, 1986; Randhawa et al., 1984; Tekalign and Hammes, 2005; Tzeng et al., 1990; Van Marle et al., 1994), Mg (Allison et al., 2001c; Ereifej et al., 1998; Randhawa et al., 1984; Tekalign and Hammes, 2005), Fe (Brown et al., 2005; Ereifej et al., 1998; Randhawa et al., 1984), Zn (Brown et al., 2005; Ereifej et al., 1998; Randhawa et al., 1984; Tekalign and Hammes, 2005), Cu (Ereifej et al., 1998; Randhawa et al., 1984; Tekalign and Hammes, 2005), and Mn concentrations (Brown et al., 2005). Systematic differences in tuber K, Mg, Fe, Zn, Cu, and Mn concentrations

Table 2. Variation in tuber mineral concentrations among *Solanum* genotypes in diverse trials.^z

Element	Genotypes	N	Trial	Concn (mean ± sd)	Reference
N	<i>S. tuberosum</i> varieties	33	Field, low N	13.2 ± 2.1	Rexen (1976)
N	<i>S. tuberosum</i> varieties	33	Field, high N	15.8 ± 2.6	Rexen (1976)
N	<i>S. tuberosum</i> varieties	26	Field	11.2 ± 1.8	SCRI, unpublished data
N	<i>S. tuberosum</i> breeding lines	73	Field	17.9 ± 2.3	Fitzpatrick et al. (1969)
N	<i>S. tuberosum</i> breeding lines	10	Field	19.9 ± 2.6	Fitzpatrick et al. (1969)
K	<i>S. tuberosum</i> varieties	10	Field	13.8 ± 1.7	Ereifej et al. (1998)
K	<i>S. tuberosum</i> varieties	4	Field	24.9 ± 3.5	Tekalign and Hammes (2005)
K	<i>S. tuberosum</i> varieties	26	Field	21.3 ± 1.5	SCRI, unpublished data
P	<i>S. tuberosum</i> varieties	10	Field	2.32 ± 0.65	Ereifej et al. (1998)
P	<i>S. tuberosum</i> varieties	3	Glasshouse	2.97 ± 0.45	Trehan and Sharma (2003)
P	<i>S. tuberosum</i> varieties	4	Field	2.85 ± 0.38	Tekalign and Hammes (2005)
P	<i>S. tuberosum</i> varieties	26	Field	1.34 ± 0.16	SCRI, unpublished data
S	<i>S. tuberosum</i> varieties	4	Field	2.38 ± 1.84	Tekalign and Hammes (2005)
S	<i>S. tuberosum</i> varieties	26	Field	1.07 ± 0.13	SCRI, unpublished data
Ca	<i>Solanum</i> species	21	Glasshouse, low Ca	0.45 ± 0.14	Bamberg et al. (1993)
Ca	<i>Solanum</i> species	21	Glasshouse, high Ca	1.52 ± 0.47	Bamberg et al. (1993)
Ca	Andean landraces	74	Field	0.50 ± 0.17	Andre et al. (2007)
Ca	<i>Solanum gourlayi</i>	18	Glasshouse, low Ca	0.37 ± 0.12	Bamberg et al. (1998)
Ca	<i>Solanum gourlayi</i>	18	Glasshouse, high Ca	1.69 ± 0.49	Bamberg et al. (1998)
Ca	<i>Solanum kurtzianum</i>	10	Glasshouse, low Ca	0.17 ± 0.03	Bamberg et al. (1998)
Ca	<i>Solanum kurtzianum</i>	10	Glasshouse, high Ca	0.93 ± 0.52	Bamberg et al. (1998)
Ca	<i>Solanum microdontum</i>	8	Glasshouse, low Ca	0.26 ± 0.05	Bamberg et al. (1998)
Ca	<i>Solanum microdontum</i>	8	Glasshouse, high Ca	1.87 ± 0.63	Bamberg et al. (1998)
Ca	<i>Solanum phureja</i>	38	Field	0.50 ± 0.10	SCRI, unpublished data
Ca	<i>S. tuberosum</i> varieties	10	Field	1.04 ± 0.31	Ereifej et al. (1998)
Ca	<i>S. tuberosum</i> varieties	4	Field	0.61 ± 0.08	Tekalign and Hammes (2005)
Ca	<i>S. tuberosum</i> varieties	5	Field, low Ca	0.18 ± 0.05	Karlsson et al. (2006)
Ca	<i>S. tuberosum</i> varieties	5	Field, high Ca	0.22 ± 0.06	Karlsson et al. (2006)
Ca	<i>S. tuberosum</i> varieties	26	Field	0.39 ± 0.09	SCRI, unpublished data
Mg	<i>S. tuberosum</i> varieties	10	Field	1.34 ± 0.13	Ereifej et al. (1998)
Mg	<i>S. tuberosum</i> varieties	3	Field, 4 N rates	0.98 ± 0.08	Allison et al. (2001c)
Mg	<i>S. tuberosum</i> varieties	4	Field	1.38 ± 0.14	Tekalign and Hammes (2005)
Mg	<i>S. tuberosum</i> varieties	26	Field	1.04 ± 0.11	SCRI, unpublished data
Fe	Andean landraces	74	Field	55.9 ± 18.2	Andre et al. (2007)
Fe	<i>S. tuberosum</i> varieties	10	Field	114 ± 32.0	Ereifej et al. (1998)
Fe	<i>S. tuberosum</i> varieties	4	Field	56.2 ± 3.98	Tekalign and Hammes (2005)
Fe	<i>S. tuberosum</i> varieties	26	Field	75.7 ± 76.9	SCRI, unpublished data
Zn	Andean landraces	74	Field	11.3 ± 7.8	Andre et al. (2007)
Zn	<i>S. tuberosum</i> varieties	10	Field	20.4 ± 4.2	Ereifej et al. (1998)
Zn	<i>S. tuberosum</i> varieties	4	Field	16.6 ± 3.7	Tekalign and Hammes (2005)
Zn	<i>S. tuberosum</i> varieties	26	Field	11.3 ± 2.2	SCRI, unpublished data
Cu	<i>S. tuberosum</i> varieties	10	Field	14.6 ± 6.85	Ereifej et al. (1998)
Cu	<i>S. tuberosum</i> varieties	4	Field	20.0 ± 1.51	Tekalign and Hammes (2005)
Cu	<i>S. tuberosum</i> varieties	26	Field	3.72 ± 0.70	SCRI, unpublished data
Mn	<i>S. tuberosum</i> varieties	10	Field	7.80 ± 1.40	Ereifej et al. (1998)
Mn	<i>S. tuberosum</i> varieties	4	Field	3.78 ± 0.56	Tekalign and Hammes (2005)
Mn	<i>S. tuberosum</i> varieties	26	Field	5.78 ± 0.57	SCRI, unpublished data

^zEach trial comprised N genotypes grown under identical conditions. Tuber concentrations of N, K, P, S, Ca, and Mg are given in g/kg dry matter. Tuber concentrations of Fe, Zn, Cu, and Mn are given in mg/kg dry matter.

Table 3. Relationships between the concentrations of mineral elements in tubers and tuber yield among N genotypes of *Solanum tuberosum* in diverse trials.^z

Element	Gradient	Intercept	N	R ²	P	Units (y)/(x)	Reference
N	-3.59 ± 2.48 E-05	13.5 ± 1.62	26	0.080	0.161	(g/kg DM)/(kg FW/ha)	SCRI, unpublished data
K	6.80 ± 6.10 E-02	29.7 ± 11.4	8	0.171	0.308	(g/kg FW)/(quintals/ha)	Randhawa et al. (1984)
K	-3.37 ± 1.93 E-04	36.5 ± 6.84	4	0.603	0.223	(g/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
K	2.13 ± 2.13 E-05	20.0 ± 1.39	26	0.040	0.328	(g/kg DM)/(kg FW/ha)	SCRI, unpublished data
P	-1.66 ± 0.87 E-03	0.70 ± 0.16	8	0.380	0.104	(g/kg FW)/(quintals/ha)	Randhawa et al. (1984)
P	-1.37 ± 0.48 E-03	4.44 ± 0.53	3	0.890	0.215	(g/kg DM)/(mg/plant)	Trehan and Sharma (2003)
P	-4.16 ± 1.51 E-05	4.29 ± 0.53	4	0.791	0.111	(g/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
P	5.20 ± 1.96 E-06	1.00 ± 0.13	26	0.227	0.014	(g/kg DM)/(kg FW/ha)	SCRI, unpublished data
S	-2.13 ± 0.57 E-05	9.75 ± 2.01	4	0.875	0.065	(g/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
S	0.53 ± 1.84 E-06	1.11 ± 0.12	26	0.003	0.777	(g/kg DM)/(kg FW/ha)	SCRI, unpublished data
Ca	-1.13 ± 1.54 E-03	0.45 ± 0.29	8	0.082	0.492	(g/kg FW)/(quintals/ha)	Randhawa et al. (1984)
Ca	-6.57 ± 4.78 E-06	0.84 ± 0.17	4	0.485	0.303	(g/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
Ca	-0.69 ± 1.27 E-06	0.43 ± 0.08	26	0.012	0.594	(g/kg DM)/(kg FW/ha)	SCRI, unpublished data
Mg	0.35 ± 4.66 E-04	0.16 ± 0.09	8	0.001	0.943	(g/kg FW)/(quintals/ha)	Randhawa et al. (1984)
Mg	-1.42 ± 0.43 E-05	1.17 ± 0.06	3	0.915	0.189	(g/kg DM)/(kg DM/ha)	Allison et al. (2001c)
Mg	-1.24 ± 0.89 E-05	1.81 ± 0.31	4	0.492	0.299	(g/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
Mg	-0.56 ± 1.58 E-06	1.07 ± 0.10	26	0.005	0.727	(g/kg DM)/(kg FW/ha)	SCRI, unpublished data
Fe	-1.99 ± 3.40 E-02	10.1 ± 6.33	8	0.054	0.580	(mg/kg FW)/(quintals/ha)	Randhawa et al. (1984)
Fe	-0.96 ± 3.41 E-04	59.5 ± 12.1	4	0.038	0.805	(mg/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
Fe	0.48 ± 1.09 E-03	45.1 ± 71.4	26	0.008	0.665	(mg/kg DM)/(kg FW/ha)	SCRI, unpublished data
Zn	0.44 ± 4.67 E-02	5.27 ± 8.69	8	0.001	0.928	(mg/kg FW)/(quintals/ha)	Randhawa et al. (1984)
Zn	-4.21 ± 1.29 E-04	31.2 ± 4.56	4	0.842	0.082	(mg/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
Zn	-1.05 ± 3.15 E-05	11.9 ± 2.05	26	0.005	0.741	(mg/kg DM)/(kg FW/ha)	SCRI, unpublished data
Cu	5.75 ± 6.76 E-02	-4.52 ± 12.6	8	0.108	0.427	(mg/kg FW)/(quintals/ha)	Randhawa et al. (1984)
Cu	-1.04 ± 1.09 E-04	23.6 ± 3.86	4	0.311	0.443	(mg/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
Cu	3.10 ± 0.78 E-05	1.74 ± 0.51	26	0.399	0.0005	(mg/kg DM)/(kg FW/ha)	SCRI, unpublished data
Mn	-3.09 ± 4.39 E-05	4.85 ± 1.55	4	0.199	0.554	(mg/kg DM)/(kg FW/ha)	Tekalign and Hammes (2005)
Mn	1.78 ± 8.21 E-06	5.67 ± 0.54	26	0.002	0.830	(mg/kg DM)/(kg FW/ha)	SCRI, unpublished data

^zA linear relationship ($y = mx + c$) was assumed between the concentration of a mineral element in the tuber (y) and tuber yield (x), and SES on gradients (m) and intercepts (c), correlation coefficients (R²), and probability that the gradient is zero (P) were calculated.

have also been observed between potato varieties obtained commercially (Casañas Rivero et al., 2003; Di Giacomo et al., 2007). It is likely, therefore, that tuber mineral concentrations can be manipulated genetically through commercial breeding programs.

LOWER TUBER MINERAL CONCENTRATIONS ARE SOMETIMES OBSERVED IN HIGHER-YIELDING GENOTYPES

There is some evidence in the literature to suggest that higher-yielding potato genotypes have lower concentrations of mineral elements in their tubers than lower-yielding genotypes when grown in the same environment (Table 3). For example, in studies comparing a small number of genotypes, it has been observed that tuber K (Tekalign and Hammes, 2005), P (Randhawa et al., 1984; Tekalign and Hammes, 2005; Trehan and Sharma, 2003), S (Tekalign and Hammes, 2005), Ca (Randhawa et al., 1984; Tekalign and Hammes, 2005), Mg (Allison et al., 2001c; Tekalign and Hammes, 2005), Fe (Randhawa et al., 1984; Tekalign and Hammes, 2005), Zn (Tekalign and Hammes, 2005), Cu (Tekalign and Hammes, 2005), and Mn (Tekalign and Hammes, 2005) concentrations are lower in higher-yielding varieties than in lower-yielding varieties grown in the same trial, but none of these relationships are statistically robust. Moreover, Randhawa et al. (1984) found nonsignificant positive relationships between tuber FW yield and tuber K, Mg, Zn, and Cu concentrations in their comparison of eight potato varieties.

Recently, a more extensive investigation of genetic variation in concentrations of mineral elements in potato tubers was initiated at the Scottish Crop Research Institute. During this investigation, field trials incorporating 26 commercial potato varieties provided no support for the hypothesis that

higher-yielding varieties have lower concentrations of mineral elements in their tubers than lower-yielding varieties (Fig. 1; Table 3). In these trials, there were no significant relationships between tuber FW yield and tuber N, K, S, Ca, Mg, Fe, Zn, or Mn concentrations, but tuber P ($P = 0.014$) and

Fig. 1. Relationships between tuber mineral concentrations and tuber yield in a core collection of 26 commercial *Solanum tuberosum* varieties trialled in the field at SCRI in 2006. Data are means of two replicate plots each containing eight plants at 40 cm spacing. Yields approximate 32,000 to 92,000 kg fresh weight/ha. Plant husbandry followed local practice. Statistical parameters for linear regressions are presented in Table 3.

Cu concentrations ($P < 0.001$) increased significantly with increasing tuber FW yield. This is possibly the first report in which concentrations of mineral elements in edible produce are significantly positively correlated with yields and suggests that breeding for both increased yields and increased concentrations of mineral elements is feasible.

CONCLUSIONS

The concentrations of mineral elements in potato tubers are influenced by both environmental and genetic factors. One of the most significant environmental factors is the phytoavailability of mineral elements in the soil. The literature contains some evidence to support the hypothesis that increasing tuber yields, either by elevating CO₂ concentrations or by growing higher-yielding varieties, can lead to decreased concentrations of some mineral elements in tubers, but this is not universally observed. A reduction in tuber mineral concentrations might be addressed through appropriate applications of mineral fertilizers. Increasing yields through the application of mineral fertilizers has diverse effects on tuber mineral concentrations depending on the composition of the fertilizer, the soil type, and the crop genotype. Interactions between mineral elements in the soil, and also within the plant, are likely to affect the concentrations of mineral elements in tubers independent of any "yield dilution" phenomenon. Consequently, it should be possible to increase tuber mineral concentrations by combining genotypes that have naturally higher tuber mineral concentrations with appropriate fertilization strategies to deliver more essential minerals to the diet without compromising yield.

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