Title: Vitamin B_1 content in potato: effect of genotype, tuber enlargement, and storage, and estimation of stability and broad-sense heritability

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Abstract

Thiamine pyrophosphate (vitamin B_1) is an essential nutrient in the human diet, and is often referred as the energy vitamin. Potato contains modest amounts of thiamine. However, the genetic variation of thiamine concentrations in potato has never been investigated. In this study, we determined thiamine concentrations in freshly-harvested unpeeled tubers of fifty-four potato clones, the majority of them originating from the Pacific Northwest Potato Development Program. Tubers from thirty-nine clones were collected from four different environmental conditions. Thiamine concentrations ranged from 292 to 1317 ng g^{-1} fresh weight, which gives a good estimate of the genetic variation available in *Solanum tuberosum* ssp. *tuberosum.* Thirteen clones/varieties contained >685 ng g^{-1} fresh weight and four had >800 ng g^{-1} fresh weight over multiple harvests, indicating that these genotypes would contribute a significant amount of thiamine in the diet (>10% of the Recommended Daily Allowance based on a 175- or 150-g serving, respectively). Broad-sense heritability for thiamine content was calculated as 0.49 with a 95% confidence interval of 0.21–0.72, suggesting that genetic variation accounted for about 50% of the observed variation. There were significant clone and clone x environment effects. After accounting for environmental variation, 25 clones were unstable across environments. Tubers harvested at a mature stage late in the growing season had higher amounts of thiamine than tubers harvested at a young stage early in the season. Storage at cold temperature did not lead to significant thiamine loss; instead, thiamine concentrations slightly increased during storage in some genotypes. These results suggest that increasing the concentration of thiamine in potato is feasible and that all potato varieties may one day be a significant source of thiamine in the human diet.

Introduction

Potato is an important component of the diet of worldwide populations, especially in Europe and North America, and per capita consumption is rapidly growing in Africa and Latin America. Thus, potato contributes a significant portion of the total daily intake of several essential dietary nutrients such as vitamin B_1 (Augustin 1975), vitamin C (Love and Pavek 2008), folate (Konings et al. 2001), vitamin B_6 (Planells et al. 2003), and polyphenols (Brat et al. 2006), to cite only a few. The proportion of nutrients originating from potato is generally calculated based on food composition databases, from which it is usually difficult to retrieve information about the potato variety, the growing conditions, post-harvest treatments, and exact processing and cooking methods. Meanwhile, many new varieties have been released on the market in the last twenty years, and new varieties have started to replace the often used reference variety Russet Burbank. Unfortunately, nutritional data on newly released varieties are usually available for only a few nutrients such as vitamin C, sugars, and starch, and complete nutrient profiles of these new varieties are often missing. This lack of information makes it difficult to determine the full extent of potato contribution to a healthy diet. The emergence of nutritional genomics, nutrigenetics, and personalized nutrition (Muller and Kersten 2003) emphasizes the need to fill this gap. McCabe-Sellers and colleagues (McCabe-Sellers et al. 2009) pointed out that one of the challenges that dietitians will be facing for personalized dietary recommendations to be a success is the availability of more complete food component databases, i.e., food composition based on genotype and growth conditions. The lack of complete nutritional profiles on newly-released varieties and breeding clones also limits the ability of potato researchers to breed for nutritional enhancement.

Thiamine pyrophosphate (vitamin B_1), the active form of thiamine, is an enzymatic cofactor for several thiamine-dependent enzymes involved in glucose metabolism, the Krebs cycle, and branched-chain amino acid biosynthesis (Goyer 2010). Thiamine helps to promote healthy nerves, improves mood, strengthens the heart, and decreases heartburn (Fardet 2010). It also is an antioxidant (Huang et al. 2010, Lukienko et al. 2000). A cross-sectional study of 2,900 Australian men and women, 49 years of age and older, found that those in the highest quintile of thiamine intake were 40% less likely to have nuclear cataracts than those in the lowest quintile (Cumming et al. 2000). In addition, a recent study of 408 U.S. women found that higher dietary intakes of thiamine were inversely associated with five-year change in lens opacification (Jacques et al. 2005). High dose thiamine therapy may also help reverse microalbuminuria in patients with type 2 diabetes (Rabbani et al. 2009). Severe thiamine deficiency leads to a lethal disease known as beriberi which is still very common in numerous developing countries where the main food source is low in thiamine and rich in carbohydrates (Lonsdale 2006, Rindi 1996). Although severe thiamine deficiency is very rare in industrialized countries, marginal deficiency remains a real health concern (deCarvalho et al. 1996, Harper 2006, Lonsdale 2006). These data suggest that developing crops with increased thiamine content could have a positive impact on human health, and as a highly-consumed vegetable worldwide, potatoes with high thiamine content would be a great delivery vehicle for increased thiamine intake.

Current nutritional data indicate that thiamine is in relatively low concentrations in commonly-consumed potato varieties, ranking potatoes in the lower range amongst plant foods (a medium-sized russet potato contains 8% of the Recommended Daily Allowance (RDA) of thiamine as shown in the USDA Nutrient Database (Bodner-Montville et al. 2006)). However, only a handful of potato varieties have been analyzed for their thiamine content, and the extent of

thiamine variation in *Solanum tuberosum* ssp. *tuberosum* remains unknown. Here, we report on thiamine variation in different modern potato genotypes and on the stability and inheritance of thiamine content. The effects of tuber development and storage were also studied.

Materials and Methods

Chemicals and Reagents

Thiamine hydrochloride (No. T4625) and taka-diastase (No. 86247 – 100 units mg^{-1}) were from Sigma-Aldrich. Difco™ thiamine assay medium LV (No. 280810) (TAM-LV) and Lactobacilli Broth AOAC (No. 90004-120) were from Becton, Dickinson, and Company (Sparks, MD).

Bacteria

Lyophilized cultures of *Lactobacillus viridescens* (ATCC™ 12706) were obtained from the American Type Culture Collection (Manassas, VA). Stock cultures were prepared by stab inoculation on Lactobacilli Broth supplemented with agar. After 24 h at 30°C, cultures were kept in duplicate in the refrigerator. Transfers were made at monthly intervals.

Potato Material

During the 2009 season, seed tubers from forty-six genotypes were planted in twelve- or twenty-two-hill plots at the Hermiston Agricultural Research and Extension Center (HAREC), Hermiston, OR. Tubers were harvested early and late during the season (Table 1). For three genotypes, tubers were harvested at two additional dates during the mid-season (Table 1). Tubers from plants located on the edges of the plot were not harvested. Two tubers from three plants (=3 replicates) for each genotype were harvested by hand, washed with water, air-dried, cut lengthwise (bud end to stem end) in halves, quarters, or sixteen, and two wedges (one from each of the two tubers) were chopped, frozen immediately in liquid nitrogen, and stored at -80°C. So these wedges contain tuber tissue representative from all parts of the tuber (bud end, stem end, center, skin) in proportions representative of a whole tuber. Samples were blended into fine powder in a Waring blender kept cold with liquid nitrogen.

In 2010, forty-one genotypes which were grown in 2009 plus eight additional genotypes were again planted at HAREC in ten-hill plots. Tubers were harvested early and late during the season (Table 1) and processed as described above. Parts of the samples were freeze-dried for dry matter content determination (Table 2 in parenthesis). Tubers from six of these varieties were also acquired from test plots grown at Warden, WA.

For the storage experiment, tubers which were harvested on 18 August 2010 were stored at 7°C for one to three months without sprout inhibitor. Moisture loss was determined by weight difference before and after storage.

Thiamine Assay

Thiamine Assay Standards

Thiamine hydrochloride stock solution was prepared by mixing 150 mg thiamine HCl in 10 ml of 0.05 N HCl, and its concentration was determined by spectrophotometry (extinction molar coefficient at 246 nm = 14,200). Standards containing 2 to 50 μg l^{-1} were prepared by diluting the thiamine stock solution in 0.2 N Na-acetate pH 4.5.

Thiamine extraction

Thiamine was extracted by combining acid digestion and enzymatic hydrolysis. This two-step extraction procedure breaks protein complexes thereby effectively liberating thiamine from the sample matrix, and converts phosphorylated thiamine (thiamine can be found as mono- or di-phosphate esters) to free thiamine form (Lebiedzinska et al. 2007, van de Weerdhof et al. 1973). Fresh potato sample (0.5 g) was added to 10 ml 0.1 N HCl in glass tubes (25 x 150 mm) and autoclaved for 15 min at 121°C. After cooling at room temperature, pH was adjusted to 4.5 by adding 1 ml of 2 N Na-acetate for optimal enzymatic hydrolysis (Bui 1999, Ollilainen et al. 1993, Pearson et al. 1967, Sims and Shoemaker 1993). Taka-diastase which has phosphatase, amylase and protease activities (Ndaw et al. 2000) was prepared at 5 mg ml^{-1} in 0.2 N Na-acetate pH 4.5. Two milliliters of taka-diastase were added to the samples. After 18 h at 37°C, samples were transferred to 15-ml Falcon tubes, placed on ice, and centrifuged in a swinging bucket rotor at 2,700 g for 5 min at 4°C to pellet debris. The supernatants were transferred to new Falcon tubes and volumes were adjusted to 13 ml with 0.2 N Na-acetate pH 4.5. Recovery of thiamine was determined by spiking three potato samples before extraction with a known amount of thiamine standard. Recovery values were between 106 and 109%.

Microbiological Assay

Thiamine concentrations were measured by using a microbiological assay employing *L. viridescens* grown in thiamine deficient medium. Our assay was based on the procedure used by Bui (1999) with a few modifications. This method remains a method of choice for measuring thiamine in food samples. Indeed, it is simple, fast, low cost, very sensitive, and can be performed in any standard laboratory without the need for expensive equipment such as HPLC. The *L. viridescens* inoculum was grown from stab stocks in 10 ml Lactobacilli Broth for ca. 18 h at 30°C, centrifuged in a swinging bucket rotor at 2,700 g for 10 min at 4°C, and washed three times in sterile 0.9% NaCl. Bacterial cells were finally resuspended in 0.9% NaCl at a concentration equivalent to an optical density of ca. 0.3 at 600 nm. The final assay medium was prepared by mixing 8.4 g TAM-LV with 193 ml deionized water and was filter-sterilized (0.45 μm). The final assay solution was prepared by mixing ca. 120 μl bacterial inoculum with 40 ml of final assay medium. Blank solution was obtained without adding bacteria.

Aliquots of 295 μl of final assay medium or blank solution were added to each of the 96 wells of microtiter plates. Equal volumes (5 μl) of thiamine standards, potato extracts, or blank (0.2 N Na-acetate pH 4.5) were then added into the wells. Plates were incubated at 30°C for ca. 18 h. After mixing each well with an 8-channel micropipettor, bacterial growth was measured at 650 nm on a BioTek Instrument EL 311 SX microplate autoreader and analyzed with the KCJr EIA application software. Thiamine concentrations were calculated by reference to a standard curve using known amounts of thiamine, and are the average of two technical measurements performed on at least one extract from each of three independent biological samples. Polynomial

or linear equations were the best curve fittings for the thiamine calibration and were solved by using the Maple 13 software (Maplesoft, Waterloo, ON).

Statistical Analysis

Thiamine concentrations from two data sets were analyzed. The first data set consisted of thirty-nine clones evaluated in four environments, an early (immature tubers) and full-season (mature tubers) harvest at Hermiston in 2009 and 2010. The second data set consisted of six clones evaluated from three full-season harvests, Hermiston in 2009 and 2010, and Warden in 2010.

Thiamine concentration was analyzed by both the mixed models and general linear models procedures in SAS (version 9.2, Cary, NC). Variance components estimated from the mixed models procedure were used to estimate broad-sense heritability (H) as the ratio of the genotypic (σ^2_G) to total phenotypic variance: $H = \sigma^2_G / ((\sigma^2_G + (\sigma^2_{GE}/e) + (\sigma^2_{error}/re))$ (Nyquist 1991), where σ^2_{GE} = genotype x environment variance, r = number of replications and e = number of environments. An exact confidence interval for H was calculated (Knapp et al. 1985) utilizing the mean squares (MS) from the general linear models procedure, with an upper confidence interval of $1-[(MS_{genotype}/MS_{genotype\ x\ environment})\ F_{(1-\alpha/2;\ df2,df1)}]^{-1}$ and a lower confidence interval of $1-[(MS_{genotype}/MS_{genotype\ x\ environment})\ F_{(\alpha/2;\ df2,df1)}]^{-1}$ where df2 and df1 refer to the degrees of freedom associated with genotype x environment and genotype, respectively.

To evaluate the genetic stability of each potato genotype, the genotype x environment interaction was partitioned into stability variance components (σ^2_i) assignable to each genotype (Shukla 1972), using the interactive matrix language procedure written by Kang (1989) in SAS. An environmental index for each environment was calculated by subtracting the grand mean thiamine content over all environments from the mean thiamine content for each environment. Heterogeneity due to this index was removed from the G x E interaction and the remainder was partitioned into s^2_i assignable to each potato genotype.

For each mature-tuber environment, cluster analyses using the unweighted pair group method by arithmetic averages (Romesburg 1990) on mean thiamine content were run from the set of 39 clones in which immature and mature tubers were evaluated and also on the set of 6 clones in which only mature tubers were evaluated. Because of significant clone x environment interactions, cluster analyses on mean clonal thiamine content were run by location. For the two locations that evaluated mature-tubers from 39 clones (Table 5A) four clusters were delineated, and for the three locations that evaluated six varieties (Table 5B) three clusters were delineated. Based upon examination of mean clonal thiamine content within each cluster, clusters were defined as being composed of clones with very high (for the 39 clones data set only), high, intermediate, and low thiamine content. For example, of the 39 mature-tuber clones evaluated for thiamine content from Hermiston in 2009 and 2010 (Table 5A), the very high cluster in 2009, which consisted only of POR01PG10-1, was defined by 1215 ng g^{-1} FW, but the very high cluster in 2010, which consisted of All Blue and Umatilla Russet, was defined by 929-932 ng g^{-1} FW. A similar pattern was observed for the high, intermediate, and low clusters in Hermiston 2009 and 2010. In all cases, the ranges in these categories were lower in 2010 than in 2009, corresponding to the fact that thiamine content was lower in Hermiston 2010 than Hermiston 2009. In short, the definition of high, intermediate, and low thiamine content clusters is in relationship to the thiamine content of all clones at that location and not to some minimum threshold value. At the beginning of the clustering procedure, every observation (n) is in a cluster by itself, resulting in n clusters. In agglomerative hierarchical clustering, the closest two clusters

merge, resulting in n-1 clusters. Then, the next closest two clusters merge, resulting in n-2 clusters. The procedure continues until eventually only one cluster remains. The decision on how many clusters to define is rather arbitrary and based on what makes biological sense and a 'large' drop in R-square values for each step in the clustering history, although what constitutes a large drop is subjective.

Statistical analysis of thiamine concentrations in potato tubers of different developmental age and during storage were carried out with single-factor analysis of variance (ANOVA) and Tukey HSD test using the VassarStats website (http://faculty.vassar.edu/lowry/VassarStats.html). Student's *t* test was used to compare young and mature tubers and average thiamine concentrations in 2009 and 2010.

Results

Effect of genotype, development, and storage

We measured thiamine concentrations in 54 potato clones from all market classes. Twenty clones were russet-skinned potatoes, seven were white, and 27 were colored-skinned potatoes (reds, yellows, purples). The majority of the clones were from the Pacific Northwest breeding program and comprised both released varieties and advanced breeding lines. Both young and mature potatoes were harvested because these two types represent different market classes. Thiamine concentrations ranged between 292 and 871 ng g^{-1} FW and 474 and 1317 ng g^{-1} FW in young and mature tubers, respectively (Table 2). Average thiamine concentrations were significantly ($P<0.01$) lower in 2010 than in 2009 in both young (453 *vs.* 617 ng g^{-1} FW) and mature (643 *vs.* 860 ng g^{-1} FW) tubers. Although thiamine content of potatoes was reported to increase with increasing nitrogen fertilization (Augustin 1975), total nitrogen input in our fields was the same in both years (Table 1) and cannot explain the differences observed. Pools of thiamine in plants are known to be responsive to abiotic stress such as cold, heat, and high light (Goyer 2010), but examination of weather data did not indicate any major differences in temperature or solar radiation between the two growing seasons. Therefore, other environmental factors not identified here must have had an effect on thiamine content. For most of the varieties analyzed, mature tubers contained larger amounts of thiamine than young tubers in each year (Table 2). In 2009, the sharpest increase in thiamine concentrations occurred between the June and July harvests (Figure 1), a time of rapid tuber enlargement (see Table 1 for average weights), except for Russet Burbank for which it occurred between the July and August harvests. Tubers harvested two weeks after vine-kill had higher thiamine concentrations than those harvested just before vine-kill, except for Russet Burbank, although it was not significant in the case of Ranger Russet. While a slight increase of dry matter in mature tubers compared to young tubers was generally observed (Table 2), this alone could not explain the large changes observed in thiamine concentrations between those two developmental stages, suggesting that a significant physiological change such as an increase in thiamine biosynthesis exists as tubers are enlarging. These results also indicate that all vitamins do not follow the same concentration pattern during tuber enlargement as for instance, folate concentrations, which were reported to be higher in young than in mature tubers (Goyer and Navarre 2009).

Mature tubers from 13 clones contained more than 685 ng g^{-1} FW of thiamine (Table 2, bolded) in both 2009 and 2010, and therefore would potentially qualify as a "good source" (over 10% of the RDA according to the U.S. Food and Drug Administration labeling guidelines) of

thiamine based on a 175-g raw serving. These included eight russet-skinned clones, three with purple skin and flesh (All Blue, Purple Pelisse, POR01PG10-1), one with purple skin and yellow flesh (POR01PG45-5), and one with yellow skin and flesh (POR02PG26-5). Four of them (two russets and two purple clones) would also be a good source of thiamine based on a 150-g raw serving which is the average potato size that Americans would ingest if consumed on a daily basis (the current annual potato consumption per capita in the United States is *ca.* 54 kg). None of the young tubers consistently contained enough thiamine to qualify as a good source of thiamine, although some of these tubers contained more than 685 ng g^{-1} FW of thiamine in 2009.

We examined whether there was any thiamine loss when tubers were stored at 7°C (45°F) for a few months. In general, there was no or very little loss of thiamine during storage (Figure 2). Actually, in the case of Purple Pelisse and Red La Soda, there was a slight increase in thiamine content after two or three months of storage which could only be partially due to water losses (6% and 7% water loss after two months, respectively). These results are in agreement with previous studies which showed that thiamine content increased in tubers stored at 7°C (45°F) for up to 8 months (Augustin 1975, Augustin et al. 1978a).

Stability, cluster analysis, and heritability

Thirty-nine clones were grown in four environments. Broad-sense heritability was calculated for this group of clones as 0.49 with a 95% confidence interval of 0.21–0.72. Genotype x environment interactions were significant for thiamine content. Closer inspection revealed that the thiamine content of six clones (Highland Russet, Klamath Russet, Mazama, POR02PG37-2, POR03PG80-2, Russet Burbank) was stable both before and after removal of environmental heterogeneity (Table 2). Among this group, Highland Russet had the highest average thiamine content of 691 ng g^{-1} FW and clustered in the high and intermediate thiamine variety-groups in 2009 and 2010, respectively (Table 5). Eight clones (A97066-42LB, AmaRosa, Crimson Red, Dark Red Norland, POR01PG10-1, Purple Majesty, Purple Pelisse, Russet Norkotah) were stable after removal of environmental heterogeneity. Among this group, POR01PG10-1 and A97066-42LB had the highest average thiamine contents of 762 and 776 ng g^{-1} FW, respectively. POR01PG10-1 clustered in the very high and high thiamine variety-groups in 2009 and 2010, respectively. A97066-42LB clustered in the intermediate and high thiamine variety-groups in 2009 and 2010, respectively. The remaining 25 clones were unstable both before and after removal of environmental heterogeneity. Among this group, Premier Russet and AOA95155-7 had the highest average thiamine contents of 779 and 795 ng g^{-1} FW, respectively, both clustering in the intermediate and high thiamine variety-groups in 2009 and 2010, respectively. From the wide ranges in thiamine content in these three groups it appears that thiamine content and the stability of that thiamine content are independent, that is, high (and low) concentrations of thiamine can be found in clones which are stable for thiamine content across environments, and in clones which are unstable.

We measured thiamine concentrations in mature tubers from six varieties which were harvested from a third location (Warden, WA) (Table 3) and used those data along with the data on mature tubers from Hermiston to estimate broad-sense heritability. Broad-sense heritability was calculated as 0.64 with a 95% confidence interval of -0.44–0.95. Once again, genotype x environment interactions were significant. Three clones were stable both before and after removal of environmental heterogeneity, including Premier Russet, which contained relatively high amount of thiamine over the three years (Tables 3 and 5), and three were unstable both

before and after removal of environmental heterogeneity. With these data, it is not possible to say that the higher estimate of broad-sense heritability on mature tubers (H=0.64) is significantly different than on the data involving immature and mature tubers (H=0.49) because of the wide confidence intervals, particularly for the data from mature tubers only. Nevertheless, both estimates suggest that substantial genetic variation exists for thiamine content.

Discussion

The purpose of this study was to comparatively evaluate the thiamine content of different modern potato clones, identify high thiamine material, if any, and estimate genetic stability and heritability. The range of thiamine concentrations in mature potatoes reported in this paper was larger than those reported by the USDA Nutrient Database (710 to 820 ng g^{-1} FW) and by Augustin (1978a) (620 to 900 ng g^{-1} FW after conversion from dry weight data, assuming a 20% dry matter content), the latter report having used only a handful of varieties. Given the relatively large population used in this study, our data give a good estimation of the genetic variability available in *Solanum tuberosum* ssp. *tuberosum* for thiamine. Although genotypes which had the highest thiamine concentrations throughout the two Hermiston growing seasons were russets and purples, there seems to be no correlation between skin/flesh color and thiamine content as some russeted (e.g., Klamath Russet) and purple (e.g., OR00068-11) clones had more modest amounts of thiamine. The highest thiamine concentration was found in a red skin/yellow flesh clone (A999331-2RY). Additional data will be needed to confirm whether this clone contains relatively large amount of thiamine throughout the growing seasons.

Several of the clones analyzed here would provide over 10% of the RDA based on a medium size serving and would potentially qualify as good source of thiamine. Although our analyses were done on raw potatoes, thiamine retention during home cooking preparation is high, 95% and 88% for microwaved and boiled unpeeled potatoes, respectively (Augustin et al. 1978b). This is particularly interesting since two clones which had high thiamine content are specialty potatoes (All Blue and POR01PG10-1) which are destined for home cooking preparation. An All Blue potato would still qualify as a good source of thiamine after oven-baking, the most destructive cooking method reported for thiamine (86% retention). Two other clones (Owyhee Russet and GemStar Russet) are dual-purpose varieties suitable for both fresh market and processing. Thiamine retention during French fry processing is also relatively high. For instance, absolute retention in small fries was reported as 88% during blanching and 91% during deep-fat frying of frozen potato fries (Augustin et al. 1979). As thiamine content slightly increased during storage (this study and previous reports (Augustin 1975, Augustin et al. 1978a)), thiamine losses during processing and cooking could be partially offset by prior storage.

Broad-sense heritability was moderate (0.49 and 0.64), indicating that about 50% of the variation is due to genetic variation, and hence, breeding for thiamine enhancement should be possible. There was some discrepancy about the stability of individual clones between the two sets of data analyzed for the varieties Russet Burbank, Red Sunset, and Premier Russet (Tables 2 and 3). Whether these discrepancies are due to physiological differences among immature and mature tubers from one data set and mature tubers from the second data set, or due to sample size (and hence precision) (39 clones in the data set of immature and mature tubers *vs.* 6 clones in the mature tuber data set) remains to be seen. If differences in gene expression exist between immature and mature tubers, they would be confounded with environmental effects in the larger data set in this study. The differences in the number of clones analyzed in the two data sets (39

vs. 6) may also partially explain the differences in the results of the stability analyses. As expected, the amount of unexplained variation (error variance) was greatest in the larger (10,097), rather than the smaller (8,713) data set (Table 4). However, the critical F-value for significance testing was smaller (more degrees of freedom) for the data from the larger data set (F=3.00739), than from the smaller data set (F=3.10516). Interestingly, these two factors (differences in error variances and critical F-values) resulted in lower threshold values for determining significance in the smaller data set.

These results suggest that breeding to enhance thiamine content in *S. tuberosum* germplasm is feasible. Decisions on which parental materials to use in future breeding efforts or which clones merit release as new varieties are based on many factors. When the relative performance of genotypes varies across environments, genotype x environment interactions are said to be present. The presence of these interactions impedes breeding progress. Ideally, clones that perform well across different environments are desired. The clustering and stability analyses of this study reveal the difficulty of identifying such clones. For example, Premier Russet and Umatilla Russet showed significant genotype x environment interaction, yet, both performed as well as or better than the mean of all clones in each location (Figure 3). The difference being, in the case of Premier Russet, when environmental heterogeneity was removed, it became stable (in terms of the graph the line for Premier Russet roughly paralleled the line for the overall mean), whereas, even with the removal of environmental heterogeneity, Umatilla Russet remained unstable (in terms of the graph the line for Umatilla Russet did not parallel the line for the overall mean). However, both clones were ranked in the high or intermediate thiamine clusters in all three environments (Table 5B). In this example, we would favor Premier Russet over Umatilla Russet, but either of these would be preferable to Crimson Red or Red Sunset. The reason for preferring Premier Russet over Umatilla Russet is that in another environment, there is a higher probability that the variability in Umatilla Russet may result in it underperforming the mean (similar to Russet Burbank in environment H2010 since removal of environmental heterogeneity did not result in stability). In addition, identified high-thiamine genetic materials from other *Solanum* species (Goyer, unpublished) could be used to further enhance the breeding effort.

Finally, this study reflects the kind of efforts needed to improve crop composition databases. The USDA Nutrient Database for Standard Reference (Bodner-Montville et al. 2006) and the International Network of Food Data System (Butrum and Young 1984) are major repositories of food composition data. However, these databases usually do not provide information for crop varieties over multiple growing seasons. The International Life Sciences Institute Crop Composition Database (Alba et al. 2010, Ridley et al. 2004) is currently filling this gap for corn, cotton, and soybeans. As McCabe-Sellers et al. (2009) said, "Knowledge of variance in food composition for given foods and given varieties of selected foods will be critical to the development of databases that can estimate or assess consumption sufficient for the study of nutrigenomics in humans." Indeed, reliable nutritional data on foods are critical for future nutritional research, nutrition labeling, and plant breeding.

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Table 1 Production practices for the potato material used in this study

Location	Planting date	Harvest date (no. days)	Storage	Tuber size range and (average) in grams	Lb/acre N	P	K	S	B
Hermiston 2009	April 23	June 17, 18 & 25 (55)	No	3 - 54 (16)	275	80	200	40	2
		July 17 (85)	No	47 - 216 (110)					
		August 17 (116)	No	142 - 334 (206)					
		August 31 & Sept 1 (129)	No	50 - 731 (226)					
		Sept 17 (147)	No	214 - 888 (360)					
Hermiston 2010	April 14	June 21 & 23 (69-71)	No	2 - 161 (34)	275	80	200	40	2
		August 18, 19 & 20 (126-128)	No	17 - 387 (123)					
Warden 2010	April 26	July 7 (72)	No	43 - 201 (84)	294	273	359	140	2
		Sept 14 (141)	No	105 - 702 (246)					

Table 2 Thiamine concentrations and genetic stability in young and mature tubers in clones grown in 2009 and 2010 in Hermiston, OR.

Clone/Variety[a]	Thiamine concentrations (ng g^{-1} FW ± SE)				Genetic stability[e]		
	Young 2009	Mature 2009	Young 2010	Mature 2010	σ^2_i	s^2_i	Outcome
A00286-3Y	410 ± 23	997 ± 67**[b]	292 ± 16 (19)[c]	584 ± 50 (21)**	**	**	Unstable
A96814-65LB	543 ± 17	960 ± 68**	486 ± 22 (21)	635 ± 65 (26)	**	**	Unstable
A97066-42LB	663 ± 19	**787 ± 22***	789 ± 43 (-)	**866 ± 37 (28)**	**	ns	GxE
A99331-2RY	624 ± 21	1317 ± 34**	-[d]	-	-	-	-
Abnaki	475 ± 21	626 ± 55**	-	-	-	-	-
Achirana	545 ± 17	941 ± 26**	-	-	-	-	-
All Blue	619 ± 45	**1097 ± 22****	423 ± 30 (16)	**929 ± 19 (22)****	**	**	Unstable
Alturas	583 ± 20	885 ± 37**	314 ± 23 (19)	494 ± 17 (22)**	**	**	Unstable
AmaRosa	514 ± 32	655 ± 9**	413 ± 17 (19)	494 ± 45 (22)	**	ns	GxE
AOA95155-7	871 ± 35	**884 ± 36**	670 ± 39 (17)	**756 ± 53 (19)**	**	**	Unstable
AOR00681-15	644 ± 21	998 ± 55**	-	-	-	-	-
Atlantic	-	-	604 ± 19 (21)	513 ± 15 (20)**	-	-	-
Blazer Russet	688 ± 27	712 ± 24	487 ± 20 (19)	588 ± 20 (17)**	**	**	Unstable
Classic Russet	602 ± 37	946 ± 24**	375 ± 31 (18)	578 ± 39 (18)**	**	**	Unstable
Clearwater Russet	599 ± 26	961 ± 12**	372 ± 26 (22)	558 ± 23 (19)**	**	**	Unstable
Crimson Red	656 ± 39	546 ± 26	479 ± 53 (20)	561 ± 31 (28)	**	ns	GxE
Dark Red Norland	564 ± 21	953 ± 47**	394 ± 11 (20)	538 ± 24 (20)**	**	ns	GxE
Defender	607 ± 24	**1031 ± 41****	378 ± 16 (17)	**780 ± 55 (18)****	**	*	Unstable
Gem Russet	643 ± 30	958 ± 10**	487 ± 10 (20)	656 ± 32 (20)**	**	**	Unstable
GemStar Russet	840 ± 32	**959 ± 58**	473 ± 12 (18)	**814 ± 22 (29)****	**	**	Unstable
Highland Russet	640 ± 26	992 ±31**	451 ± 22 (20)	680 ± 32 (21)**	ns	ns	Stable
IdaRose	-	-	473 ± 25 (17)	617 ± 65 (28)	-	-	-
Ivory Crisp	-	-	606 ± 22 (18)	627 ± 35 (18)	-	-	-
Klamath Russet	483 ± 17	646 ± 33**	366 ± 13 (22)	494 ± 41 (19)*	ns	ns	Stable
Mazama	589 ± 23	800 ± 57**	410 ± 29 (20)	548 ± 76 (20)	ns	ns	Stable
Modoc	578 ± 19	766 ± 40**	446 ± 15 (16)	438 ± 20 (19)	*	**	Unstable
OR00068-11	669 ± 27	671 ± 22	448 ± 32 (23)	598 ± 32 (26)**	**	*	Unstable
OR04036-5	-	-	470 ± 13 (18)	619 ± 24 (16)**	-	-	-
OR04131-2	-	-	477 ± 33 (19)	475 ± 8 (18)	-	-	-
Owyhee Russet	577 ± 26	**975 ± 42****	414 ± 19 (19)	**814 ± 108 (19)****	**	**	Unstable
PA96RR1-193	496 ± 37	661 ±64*	425 ± 33 (20)	627 ± 37 (22)**	**	**	Unstable
POR01PG10-1	636 ± 37	**1215 ± 91****	346 ± 8 (17)	**854 ± 76 (22)****	**	ns	GxE
POR01PG1-6	660 ± 52	635 ± 76	344 ± 9 (20)	503 ± 36 (16)**	**	**	Unstable
POR01PG45-5	642 ± 37	**865 ±40****	493 ± 75 (24)	**746 ± 14 (28)****	*	**	Unstable
POR02PG26-5	590 ± 19	**973 ± 26****	407 ± 8 (19)	**698 ± 19 (24)****	**	*	Unstable
POR02PG37-2	658 ± 45	896 ± 27**	446 ± 10 (20)	636 ± 86 (20)	ns	ns	Stable
POR03PG23-1	523 ± 27	805 ± 45**	339 ± 11 (15)	535 ± 24 (22)**	**	*	Unstable
POR03PG80-2	620 ± 26	970 ± 29**	442 ± 11 (17)	618 ± 26 (25)**	ns	ns	Stable
Premier Russet	856 ± 36	**795 ± 23**	562 ± 37 (19)	**906 ± 74 (23)****	*	**	Unstable
Purple Majesty	538 ± 33	892 ± 37**	363 ± 13 (19)	572 ± 32 (20)**	*	ns	GxE
Purple Pelisse	680 ± 42	**716 ± 22**	479 ± 37 (19)	**706 ± 14 (16)****	**	ns	GxE
Ranger Russet	508 ± 66	**1041 ± 60****	467 ± 22 (20)	**701 ± 42 (21)****	**	**	Unstable
Red LaSoda	754 ± 29	867 ± 138	495 ± 118 (15)	588 ± 31 (19)*	-	-	-
Red Sunset	732 ± 60	519 ± 24*	493 ± 26 (20)	474 ± 13 (17)	**	**	Unstable
Russet Burbank	510 ± 37	808 ± 43**	324 ± 19 (19)	518 ± 60 (20)*	ns	ns	Stable
Russet Norkotah	515 ± 40	633 ± 65	433 ± 35 (23)	492 ± 22 (22)	**	ns	GxE
Shepody	465 ± 16	811 ± 44**	403 ± 20 (18)	674 ± 55 (18)**	**	**	Unstable
Superior	-	-	312 ± 19 (17)	496 ± 28 (16)**	-	-	-
TerraRosa	635 ± 38	1001 ± 47**	430 ± 30 (20)	563 ± 41 (29)**	**	**	Unstable
Umatilla Russet	428 ± 18	**728 ± 9****	423 ± 28 (18)	**932 ± 36 (24)****	**	**	Unstable
Wallowa Russet	460 ± 17	673 ± 49**	-	-	-	-	-
Willamette	-	-	471 ± 18 (17)	719 ± 39 (21)**	-	-	-
Yukon Gem	-	-	460 ± 31 (19)	753 ± 38 (21)**	-	-	-
Yukon Gold	432 ± 27	635 ± 22**	356 ± 42 (18)	497 ± 22 (22)*	-	-	-

[a] In bold and bordered are genotypes which would provide at least 10% of the Recommended Daily Allowance based on a 175-g or 150-g serving, respectively, of mature tuber in both years 2009 and 2010. [b] Significant difference between young and mature tubers at two-tailed $P<0.01$ (**) or $P<0.05$ (*) as determined by Student t test. [c] Percentage dry matter is indicated in parenthesis. [d] -, not available. [e] (*), (**), and (ns), respectively, indicate that the genotype makes a significant ($P=0.05$), highly significant ($P=0.01$), or no significant contribution to the genotype (G) x environment (E) interaction before (σ^2_i) or after (s^2_i) removal of the environmental heterogeneity. Stable=genotypes that were stable both before and after removal of environmental heterogeneity; Unstable=genotypes that were unstable both before and after removal of environmental heterogeneity; GxE=genotypes were unstable before removal of environmental

heterogeneity but stable after removal of environmental heterogeneity, or stable before removal of environmental heterogeneity but unstable after removal of environmental heterogeneity.

Table 3 Thiamine concentrations and genetic stability in mature tubers in clones from three different harvests.

Variety	Thiamine concentrations (ng g^{-1} FW)			Genetic stability[b]		
	Hermiston 2009	Hermiston 2010	Warden 2010	σ^2_i	s^2_i	Outcome
Crimson Red	546 ± 26	561 ± 31 (28)[a]	735 ± 12 (20)	ns	*	GxE
Premier Russet	795 ± 23	906 ± 74 (23)	958 ± 62 (24)	ns	*	GxE
Ranger Russet	1041 ± 60	701 ± 42 (21)	824 ± 71 (29)	**	**	Unstable
Red Sunset	519 ± 24	474 ± 13 (17)	649 ± 20 (19)	ns	ns	Stable
Russet Burbank	808 ± 43	518 ± 60 (20)	914 ± 34 (24)	**	ns	GxE
Umatilla Russet	728 ± 9	932 ± 36 (24)	808 ± 37 (21)	**	**	Unstable

[a] Percentage dry matter is indicated in parenthesis. [b] See Table 2.

Table 4 Mean squares and estimates of the variance component

Source	DF		Mean squares		Estimate of the variance component	
	Exp 1[a]	Exp 2	Exp1	Exp 2	Exp 1	Exp 2
Environment	3	2	7054635	222689	29599	3121
Rep (environment)	8	6	28165	13619	232	409
Genotype	38	5	228223*[b]	309237	4912*	11323
Genotype*environment	114	10	110335**	105432*	16706**	16120*
Error	772	84	10097	8713	10097	8713
Corrected total	935	107				

R-square		Coeff var		Thiamine mean	
Exp 1	Exp 2	Exp 1	Exp 2	Exp 1	Exp 2
0.845	0.810	15.820	12.655	635	737

[a] Exp 1 refers to data set from Table 2, Exp 2 refers to data set from Table 3. [b] Significance for 5% (*) and 1% (**) levels.

Table 5 Distribution of clones/varieties into clusters with very high (VH), high (H), intermediate (I) and low (L) mean thiamine content of mature tubers for (A) set of 39 clones (from Table 2) and (B) set of 6 clones (from Table 3) based on the results of cluster analyses.

A

Clone/Variety	H2009[1]	H2010[2]
A000286-3Y	H	L
A96814-65LB	H	I
A97066-42LB	I	H
AOA95155-7	I	H
All Blue	H	VH
Alturas	I	L
AmaRosa	L	L
Blazer Russet	L	L
Classic Russet	H	L
Clearwater Russet	H	L
Crimson Red	L	L
Dark Red Norland	H	L
Defender	H	H
Gem Russet	H	I
GemStar Russet	H	H
Highland Russet	H	I
Klamath Russet	L	L
Mazama	I	L
Modoc	I	L
OR00068-11	L	L
Owyhee Russet	H	H
PA96RR1-193	L	I
POR01PG1-6	L	L
POR01PG10-1	VH	H
POR01PG45-5	I	H
POR02PG26-5	H	I
POR02PG37-2	I	I
POR03PG23-1	I	L
POR03PG80-2	H	I
Premier Russet	I	H
Purple Majesty	I	L
Purple Pelisse	L	I
Russet Burbank	I	L
Ranger Russet	H	I
Red Sunset	L	L
Russet Norkotah	L	L
Shepody	I	I
Terra Rosa	H	L
Umatilla Russet	L	VH

B

Variety	H2009[3]	H2010[4]	W2010[5]
Crimson Red	L	L	L
Premier Russet	I	H	H
Ranger Russet	H	I	I
Red Sunset	L	L	L
Russet Burbank	I	L	H
Umatilla Russet	I	H	I

[1] Range in clonal mean thiamine content (ng g^{-1} FW) for clusters defined as L (519-728), I (766-917), H (940-1128), and VH (1215).

[2] Range in clonal mean thiamine content (ng g^{-1} FW) for clusters defined as L (438-598), I (612-706), H (741-906), and VH (929-932).

[3] Range in clonal mean thiamine content (ng g^{-1} FW) for clusters defined as L (519-546), I (728-808), and H (1041).

[4] Range in clonal mean thiamine content (ng g^{-1} FW) for clusters defined as L (474-561), I (701), and H(906-932).

[5] Range in clonal mean thiamine content (ng g^{-1} FW) for clusters defined as L (649-735), I (808-824), and H (914-958).

Figure Captions

Fig. 1 Thiamine concentrations during tuber enlargement and after vine-kill. Tubers were harvested throughout the 2009 growing season from mid-June to the end of September at Hermiston, OR. Plants were vine-killed on September 4th. Samples that share identical letters were not significantly different as determined by ANOVA and Tukey HSD test ($P > 0.05$).

Fig. 2 Thiamine concentrations during cold storage. Tubers were harvested on August 18th 2010 from Hermiston fields and stored for one to three months at 4°C. Samples that share identical letters were not significantly different as determined by ANOVA and Tukey HSD test ($P > 0.05$).

Fig. 3 Thiamine concentrations in mature tubers of Premier Russet, Umatilla Russet, Crimson Red, Red Sunset, Russet Burbank, and Ranger Russet compared to thiamine content of all varieties in each environment based on data from Table 3. H2009, Hermiston 2009; H2010, Hermiston 2010; W2010, Warden 2010.

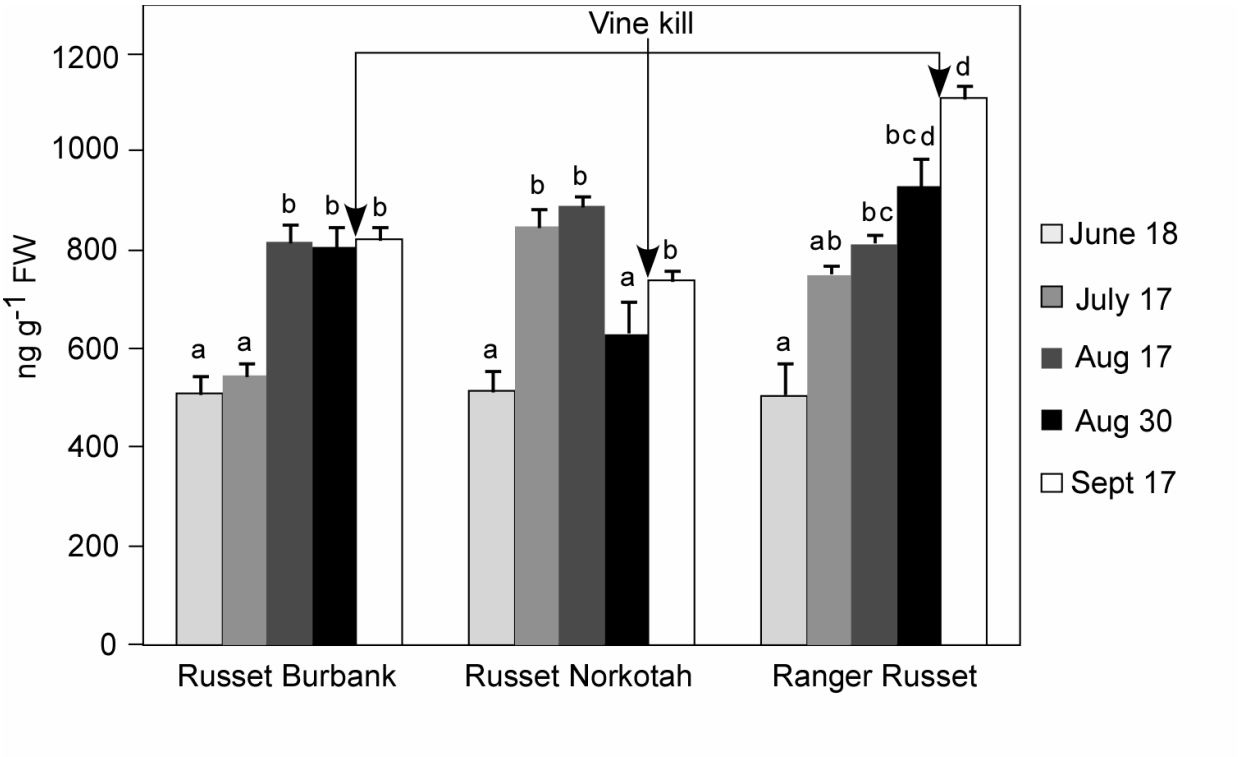
Vine kill
1200
1000
800
600
400
200
0
ng g-1 FW
a
a
b
b
b
a
b
b
a
b
a
ab
bc
bcd
d
Russet Burbank
Russet Norkotah
Ranger Russet
June 18
July 17
Aug 17
Aug 30
Sept 17

Fig. 1

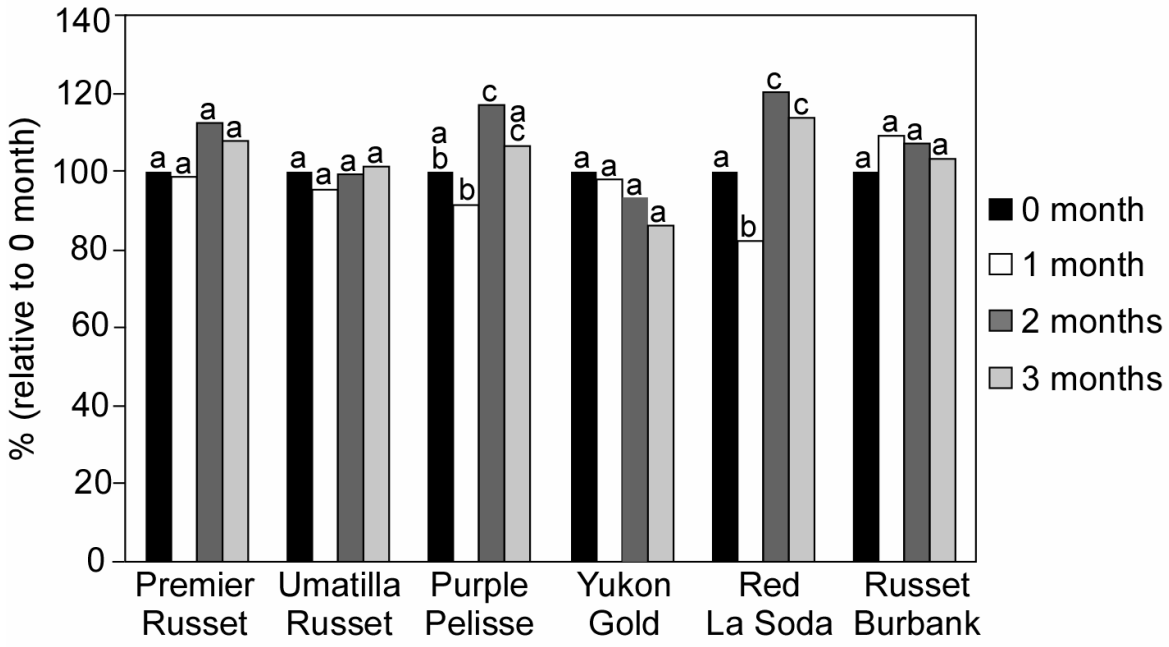
140
120
100
80
60
40
20
0
% (relative to 0 month)
a a a a
a a a a
a b c a
a a a a
a b c c
a a a a
Premier Russet
Umatilla Russet
Purple Pelisse
Yukon Gold
Red La Soda
Russet Burbank
0 month
1 month
2 months
3 months

Fig. 2

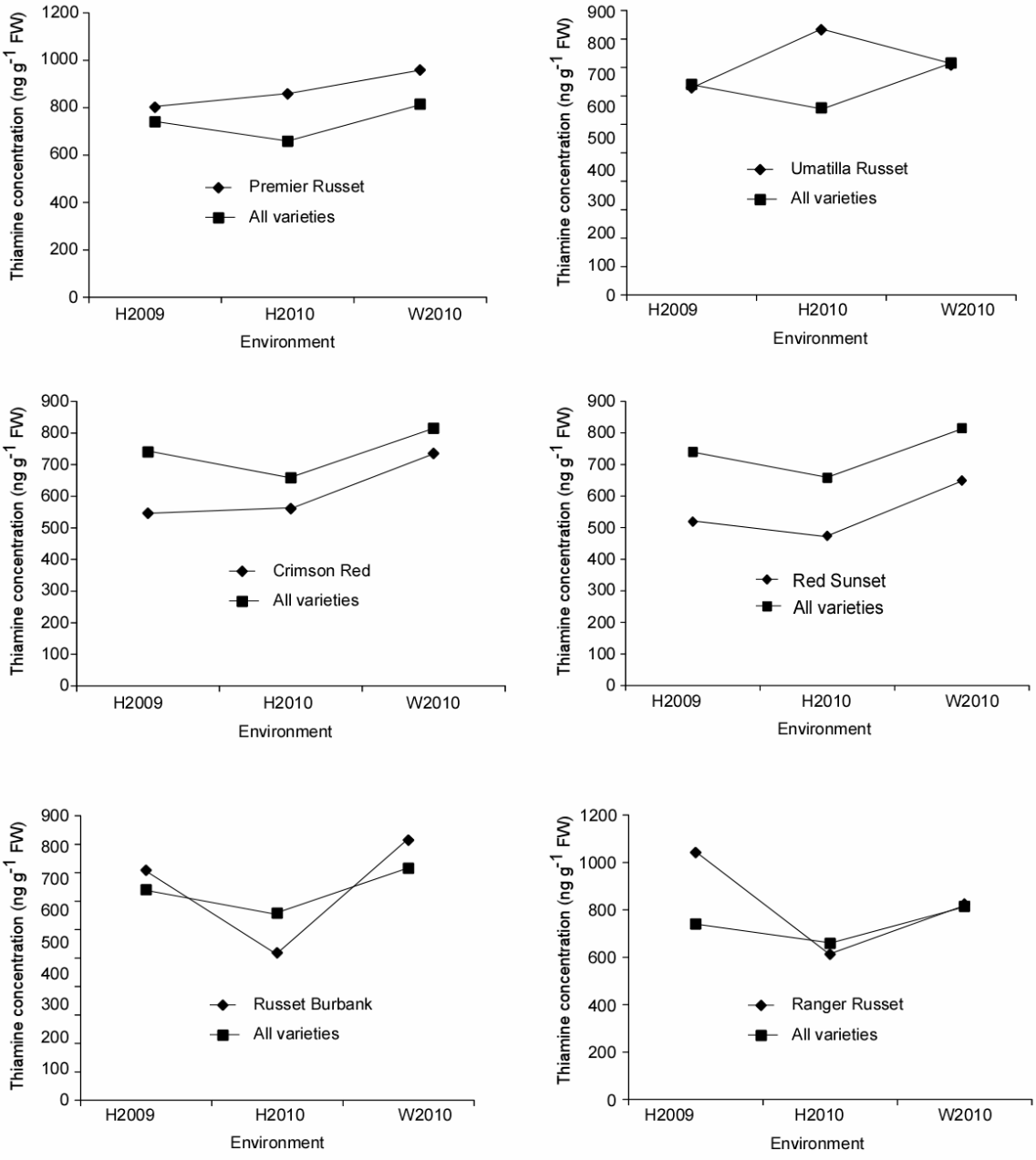
Thiamine concentration (ng g-1 FW)
Environment
H2009
H2010
W2010
Premier Russet
All varieties
Umatilla Russet
All varieties
Crimson Red
All varieties
Red Sunset
All varieties
Russet Burbank
All varieties
Ranger Russet
All varieties

Fig. 3