Published online August 28, 2017

RESEARCH

Reliability of Measurement and Genotype × Environment Interaction for Potato Specific Gravity

Yi Wang,* Lance B. Snodgrass, Paul C. Bethke, Alvin J. Bussan, David G. Holm, Richard G. Novy, Mark J. Pavek, Gregory A. Porter, Carl J. Rosen, Vidyasagar Sathuvalli, Asunta L. Thompson, Michael T. Thornton, and Jeffrey B. Endelman*

ABSTRACT

Specific gravity (SpGr) is often used to measure the processing quality of potato (*Solanum tuberosum* L.) tubers for French fries or potato chips because of its strong correlation with dry matter content and ease of measurement. For French fry processing genotypes, the desirable range for mean SpGr is typically 1.080 to 1.095, and a small variance around the mean is essential for product uniformity. Two multi-year, multi-location trials were conducted to investigate the genetics of SpGr in elite russet germplasm. Consistent with earlier studies, the mean SpGr was measured with high repeatability within each environment: the median plot-basis value was 0.83 for a national trial with six locations and 3 yr. In contrast, the median repeatability of the SD between tubers was only 0.21. Thus, multi-environment trials are needed to identify genotypes with a narrow SpGr distribution. Finlay–Wilkinson stability analysis of the mean SpGr established one genotype as an outlier: when best linear unbiased predictions were regressed on the environment means, this genotype had a regression coefficient of 2.1, compared with 0.4 to 1.4 for the others. The genetic correlation between environments showed a consistent regional pattern in mean SpGr over the years. There was a higher mean correlation between environments within the Pacific Northwest (0.97), Upper Midwest (0.91), and Northeast (0.85) than between environments from the different regions (0.35–0.78). Although breeding for national adaptation is an attractive idea, our results suggest that genetic gain may be easier to achieve at the regional level.

Y. Wang, Kimberly Research and Extension Center, Univ. of Idaho, Kimberly, ID 83341; Y. Wang, L.B. Snodgrass, P.C. Bethke, and J.B. Endelman, Dep. Horticulture, Univ. of Wisconsin, Madison, WI 53706; P.C. Bethke, USDA–ARS Vegetable Crops Research Unit, Madison, WI 53706; A.J. Bussan, Wysocki Produce Farms, Plainfield, WI 54966; D.G. Holm, Dep. Horticulture and Landscape Architecture, San Luis Valley Research Center, Colorado State Univ., Center, CO 81125; R.G. Novy, USDA–ARS Small Grains and Potato Germplasm Research Unit, Aberdeen, ID 83210; M.J. Pavek, Dep. Horticulture, Washington State Univ., Pullman, WA 99164; G.A. Porter, School of Food and Agriculture, Univ. Maine, Orono, ME 04469; C.J. Rosen, Dep. Soil, Water, and Climate, Univ. Minnesota, St. Paul, MN 55108; V. Sathuvalli, Hermiston Agricultural Research and Extension Center, Oregon State Univ., Hermiston, OR 97838; A.L. Thompson, Dep. Plant Sciences, North Dakota State Univ., Fargo, ND 58108; M.T. Thornton, Parma Research and Extension Center, Univ. of Idaho, Parma, ID 83660. Received 3 Dec. 2016. Accepted 27 Feb. 2017. *Corresponding authors (wongyie@gmail.com, endelman@wisc.edu). Assigned to Associate Editor Duli Zhao.

Abbreviations: BLUP, best linear unbiased prediction; FA2, second-order factor analytic; FW, Finlay–Wilkinson; h^2, broad-sense heritability; HH, hollow heart; NAT, National Agronomic Trial; PNW, Pacific Northwest; SpGr, Specific gravity; WRT, Wisconsin Russet Trial.

The specific gravity (SpGr) of potato (*Solanum tuberosum* L.) tubers is highly correlated with tuber dry matter and starch content (Vanasse et al., 1951), and since SpGr is easier to measure than these traits, it is widely used to estimate the culinary and processing quality of potatoes (Greenwood et al., 1952; Young et al., 1964). High-SpGr potatoes are better suited for frying, chipping, dehydration, baking, and mashing, and low-SpGr potatoes are usually used for boiling, canning, roasting, and potato salad.

Specific gravity is typically measured on a sample of many tubers to estimate the mean value for a single source. Mean SpGr is

Published in Crop Sci. 57:1966–1972 (2017).
doi: 10.2135/cropsci2016.12.0976

commonly determined by the water displacement method, in which the weight of the sample is recorded in air and in water, and SpGr is calculated as the weight in air divided by the difference between the weight in air and the weight in water. The target range of SpGr for French fry processing potatoes is typically 1.080 to 1.095 (Wang et al., 2015).

Variation in SpGr among tubers from the same source can be extensive (Sayre et al., 1975). The variance of SpGr in a bulk sample can be measured using the water displacement method on individual tubers (Edgar, 1951), but for commercial lots in the processing industry, it is more common to use a set of tanks containing brine solutions spanning a range of densities. Starting at the tank with the highest SpGr solution, tubers are passed from one tank to the next; when a tuber sinks, its SpGr falls in between the value for that tank and the previous one (Young, 1962).

Excessive SpGr variation between tubers is of concern for processors because of its potential effect on the consistency of the final product, particularly the texture of French fries (Kleinkopf et al., 1987). The ideal French fry should have a crisp outer crust with a soft mealy interior (Agblor and Scanlon, 2002). Excessive SpGr variation within the raw product often leads to textural defects associated with over- or underprocessing. Overprocessed fries typically have hard shells and hollow interiors, whereas underprocessed fries are excessively wet or firm inside.

To be successful, new French fry processing genotypes must meet the SpGr target across a range of environments. Environmental effects can be caused by geographical variation, year-to-year variation, and variations in cultural practices. For a complex, quantitative trait such as SpGr, efficient genotype development depends on an understanding of the reliability of the phenotyping method, both within one environment (i.e., repeatability) and across multiple environments (i.e., broad-sense heritability [h^2] or reliability). The reliability of measuring mean SpGr by water displacement has been frequently reported and is generally high (Henninger et al., 2000; Wang et al., 2015). Wang et al. (2015) reported that the genotype × location and genotype × year variances for mean SpGr were <20% of the main effect for genotype in a national trial of fry processing russet potatoes spanning five locations and 3 yr.

Since the study of Wang et al. (2015) was unreplicated within environment, there was limited opportunity to investigate the geographic pattern of genotype × location interactions. Regional patterns have been investigated for potato yield and quality in other countries (Affleck et al., 2008; Paget et al., 2015), but our understanding of this topic on a national scale in the United States is largely anecdotal. Therefore, the main goals of this study were (i) to determine the reliability of methods for measuring the mean and SD of the SpGr distribution, (ii) to assess the SpGr stability of new elite processing genotypes across environments, and (iii) to determine whether there is a consistent contribution of genotype × environment to mean SpGr across the major potato production regions in the United States.

MATERIALS AND METHODS

Field Trials

Results from two different multi-environment trials are presented: the National Agronomic Trial (NAT) and the Wisconsin Russet Trial (WRT). In the NAT, russet potato genotypes were grown at six locations from 2013 to 2015: University of Idaho Parma Research and Extension Center (Parma, ID), University of Maine Aroostook Research Farm (Presque Isle, ME), University of Minnesota Sand Plain Research Farm (Becker, MN), Oregon State University Hermiston Agricultural Research and Extension Center (Hermiston, OR), Washington State University Othello Research Station (Othello, WA), and University of Wisconsin Hancock Agricultural Research Station (Hancock, WI). Planting occurred between late March and mid-May to match local commercial practices. Seed spacing was between 23 and 36 cm, and row spacing was either 86 or 91 cm, depending on the location. Tuber harvests at all locations were conducted between mid-September and early October. Crop production strategies applied in each year at each trial location were based on best management practices recommended by local extension personnel and were consistent across years.

A total of 21 genotypes (Supplemental Table S1) were planted during the 3-yr NAT, including the standard variety Russet Burbank. The entry list included elite fry processing genotypes from potato breeding programs in Colorado, Idaho, Maine, North Dakota, Oregon, and Wisconsin, as well as a few recently released cultivars. Within each year, the same entries were tested in all locations, but the design of the NAT was unbalanced across years, as lackluster entries were withdrawn after 1 yr of testing, and entries with outstanding performance were included for all 3 yr. There were 15, 10, and 10 entries tested in 2013, 2014, and 2015 respectively, with five common genotypes evaluated in all 3 yr. Genotypes from Idaho and Oregon breeding programs were not planted in Maine because of phytosanitary restrictions on breeder seed tuber importation. In this study, a year–location combination is termed as an environment; therefore, there are 18 environments in the NAT. In each environment, a randomized complete block design was used, with three or four replications (plots) per entry, depending on location.

The WRT results are based on three Wisconsin locations, evaluated across 2 yr (2014–2015). One of the locations was the University of Wisconsin Hancock Agricultural Research Station, and the other two were commercial farms in Coloma and Nekoosa, all within the Central Sands region (soil series Plainfield sand [mixed, mesic Typic Udipsamments]). Seed spacing was 30 cm and row spacing was 91 cm, with 15 seed pieces per plot and three replications (plots) per environment (randomized complete block design). There were 26 russet genotypes in the trial, nine of which were tested in both years and the remainder in only 1 yr (Supplemental Table 2). Within year, the same entries were tested in all three locations.

Grading and Measurement of Specific Gravity

In both trials, after mechanical harvest at each location, tubers were culled for external defects such as growth cracks, knobs, misshapes, greening, and disease (USDA-AMS, 1983). Remaining tubers were then graded for yield and size. After grading, 20 marketable tubers weighing between 170 and 283 g were randomly picked from each plot and measured individually for SpGr. In the NAT, each tuber was weighed in air and under water, and SpGr was calculated as (weight in air)/(weight in air − weight in water). In addition, the incidence of internal defect hollow heart (HH) was measured by cutting open 10 tubers per plot. In the WRT, seven brine tanks were prepared with 56 L of NaCl solution in the density range of 1.050 to 1.098, with increments of 0.008. The amount of NaCl dissolved in each tank was based on Hilderbrand (1993) and verified with a hydrometer. The SpGr of the tanks was checked daily and adjusted accordingly. Twenty tubers from each plot were individually passaged from high to low SpGr, stopping when the tuber sank. The SpGr for each tuber was recorded as the SpGr in the tank where it sank plus 0.004, which is the midpoint between the tank in which the tuber sank and the next higher tank. This formula was also used for tubers that sank in the first tank or did not sink in any tank (which was very rare). In both trials, the mean and SD of SpGr for the 20 tubers were computed from the individual tuber measurements for each plot in each trial.

Data Analysis

Variance components within each environment were calculated using the following linear model and the PROC MIXED function in SAS (version 9.4; SAS Institute, 2015):

$$P_{ij} = \mu + G_i + B_j + \varepsilon_{ij} \quad [1]$$

where μ is the intercept and G_i, B_j, and ε_{ij} are the random effects for genotype, block, and residuals, respectively. Broad-sense heritability (h^2) within each environment on a per-plot basis was calculated as $h^2 = \sigma^2_G/(\sigma^2_G + \sigma^2_e)$, where σ^2_G and σ^2_e are the variance components for genotype and residual error, respectively.

For the analysis of the NAT as a multi-environment trial, several approaches were used depending on the goal. To obtain best linear unbiased predictions (BLUPs) for each genotype, averaged across all environments (results shown in Fig. 1), the following linear model was used:

$$P_{ijkr} = \mu + G_i + Y_j + L_k + \mathrm{YL}_{jk} + B_{r(jk)} + \mathrm{GY}_{ij} + \mathrm{GL}_{ik} + \mathrm{GYL}_{ijk} + \varepsilon_{ijkr} \quad [2]$$

where μ is the intercept and G_i, Y_j, L_k, and $B_{r(jk)}$ are random effects for genotype, year, location, and block, respectively. The index i takes on values 1…21 for genotype, j = 1...3 for year, k = 1…6 for location, and r is block within environment. The entry-basis h^2 across the 18 environments in the NAT was calculated as $h^2 = \sigma^2_G/(\sigma^2_G + \sigma^2_{GY}/3 + \sigma^2_{GL}/6 + \sigma^2_{GYL}/18 + \sigma^2_e/65)$, where σ^2_G, σ^2_{GY}, σ^2_{GL}, σ^2_{GYL}, and σ^2_e are the variance components for genotype, genotype × year, genotype × location, genotype × year × location, and residual error, respectively (Holland et al., 2003). The residual error variance was divided by 65 because this was the average number of total plots per entry in the trial.

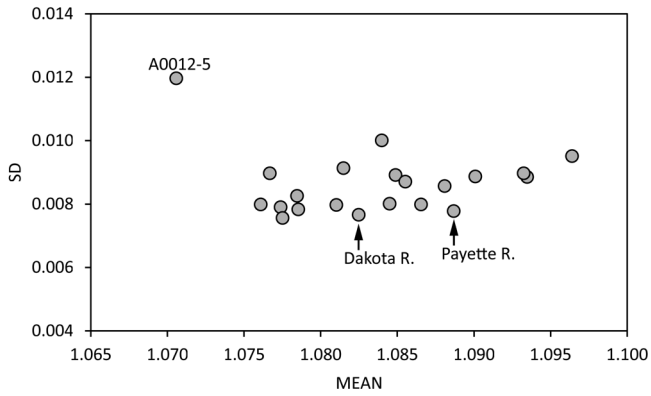

Fig. 1. Relationship between the mean (*x*-axis) and SD (*y*-axis) of the specific gravity distribution for russet potato genotypes in the National Agronomic Trial. The A0012-5 genotype is undesirable because of its low mean and high SD, whereas two of the named varieties (Dakota R. and Payette R.) performed well with low SD and mean specific gravity in the target range.

For genotype × environment analysis of the NAT, each year–location was coded as one of 18 environments, and the following linear model was used:

$$P_{ijk} = \mu + E_j + B_{k(j)} + G_{ij} + \varepsilon_{ijk} \quad [3]$$

In Eq. [3], the index i takes on values 1…21 for genotype, j = 1...18 for environment, and k is block within environment. Equation [3] models observations using an intercept (μ), a fixed effect for environment (E_j), a random effect for block [$B_{k(j)}$], and a multi-variate normal random effect for genotype (G_{ij}) with separable covariance $I_{21\times21} \otimes \Sigma_{18\times18}$. A second-order factor-analytic (FA2) model was used for the genetic covariance between environments $\Sigma = \boldsymbol{\lambda}\boldsymbol{\lambda}^{\mathrm{T}} + \psi$, where $\boldsymbol{\lambda}$ is an 18 × 2 matrix of environmental loadings and ψ is an 18 × 18 diagonal residual variance matrix (Smith et al., 2001). The factor loadings in $\boldsymbol{\lambda}$ were rotated according to the procedure in Cullis et al. (2010) to create a uniplot, which displays the relationships between environments geometrically. Variance components were estimated by restricted maximum likelihood using SAS PROC MIXED. For the Finlay–Wilkinson (FW) analysis (Finlay and Wilkinson, 1963), the genotype BLUPs for each environment (G_{ij} in Eq. [3]) were regressed onto the environment means (E_j in Eq. [3]), using the lm function in R (R Development Core Team, 2015).

RESULTS

Across the 18 environments in the NAT, broad-sense heritability (h^2) on a plot basis of the mean SpGr ranged from 0.58 to 0.94, with a median of 0.83. The h^2 of the SD within each plot ranged from 0.00 to 0.74, with a median of 0.21 (Table 1). For the six environments in the WRT, h^2 for the mean SpGr ranged from 0.82 to 0.93, with a median of 0.90, and h^2 of the SD ranged from 0.00 to 0.27, with a median of 0.14 (Table 2). Consequently, there was a clear trend that the mean of the SpGr distribution was measured with much higher reliability than the SD, by both the water displacement and brine tank methods.

Table 1. Broad-sense heritability on a plot basis for the mean and SD of the specific gravity distribution in the National Agronomic Trial, using the water displacement method.

	Mean			SD		
Site	2013	2014	2015	2013	2014	2015
ID	0.88	0.94	0.89	0.10	0.49	0.32
ME	0.66	0.88	0.80	0.49	0.00	0.61
MN	0.92	0.82	0.89	0.74	0.06	0.41
OR	0.58	0.69	0.86	0.00	0.00	0.00
WA	0.69	0.92	0.72	0.09	0.50	0.00
WI	0.80	0.82	0.83	0.38	0.00	0.37

Table 2. Broad-sense heritability on a plot basis for the mean and SD of the specific gravity distribution in the Wisconsin Russet Trial, using the brine tank method.

	Mean		SD	
Site	2014	2015	2014	2015
Coloma	0.88	0.93	0.27	0.14
Hancock	0.89	0.92	0.14	0.27
Nekoosa	0.92	0.82	0.00	0.06

Figure 1 shows the BLUPs for the SpGr mean (entry basis $h^2 = 0.95$) and SD (entry basis $h^2 = 0.81$) of the 21 genotypes in the NAT, across all 18 environments. The outlier genotype in the top left of the figure is A0012-5, which had a low mean and high SD—both undesirable. After removing this outlier, the mean and SD showed a modest correlation of $r = 0.46$ ($p = 0.04$). Recent variety releases Dakota Russet and Payette Russet had overall mean SpGr in the target range 1.080 to 1.095 and SD at the lower end of the population (7.7×10^{-3} and 7.8×10^{-3}, respectively).

The stability of the mean SpGr across the 18 environments in the NAT was analyzed using the Finlay–Wilkinson (FW) method. The results of the regression of the genotype BLUPs on environment means are shown in Table 3. With the exception of A0012-5, the regression coefficients ranged from 0.4 to 1.4. A coefficient of 0 indicates static stability (i.e., the SpGr of the potato genotype was constant across environments), whereas a coefficient of 1 indicates dynamic stability (i.e., the SpGr of the potato genotype tracked the population mean across environments). Genotype A0012-5, which was identified in Fig. 1 as having the largest SD within environment, also had the most variable mean SpGr across environments, with a regression coefficient of 2.1. The location averages for each genotype in Table 3 are provided to illustrate the stability results. For example, A0012-5 had values of 1.083, 1.086, 1.048, 1.080, 1.073, and 1.059 at Idaho, Maine, Minnesota, Oregon, Washington, and Wisconsin, respectively. After removing A0012-5, there was no significant correlation between the FW regression coefficient and overall SD ($r = -0.05$, $p = 0.8$).

To ensure that the stability analysis was not biased by the presence of HH internal defects, which can lead to underestimation of SpGr, the relationship between mean SpGr and HH incidence at the plot level was inspected across all entries and specifically for A0012-5 (Supplemental Fig. S1). In neither case was there evidence that HH was a confounding factor.

The genetic correlation between the 18 environments of the NAT was estimated using a FA2 model. The results are shown as a uniplot in Fig. 2, in which each environment is displayed with a four-digit code (state + year) within the unit circle (radius = 1). The squared distance of each point from the origin equals the proportion of the total genetic variance captured by the FA2 model for that environment. Most of the environments lie very close to the circle, indicating that the FA2 model is a good parsimonious approximation to an unstructured covariance matrix. The most significant departure was with Maine 2013 (ME13), for which the FA2 model only captured 54% of the variance.

Figure 2 shows a remarkably tight grouping of the 3 yr for each location, which indicates that the rank ordering of the genotypes at one location was consistent over time, relative to the other locations. The grouping of the locations was also consistent on a regional level, with the six trial locations falling into three groups: (i) the Pacific Northwest (PNW) (Idaho, Oregon, and Washington), (ii) the Upper Midwest (Minnesota and Wisconsin), and (iii) the Northeast (Maine). The average correlation between the environments within each region was high (0.97 for PNW, 0.91 for Upper Midwest, and 0.85 for Northeast), whereas the average correlation between the regions ranged from 0.35 between the Northeast and Midwest to 0.78 between the PNW and other two regions (Table 4).

DISCUSSION

As a proxy for dry matter content, tuber SpGr is one of the most important traits for selecting suitable potato genotypes for the French fry and potato chip processing markets. The ideal range for SpGr is typically 1.080 to 1.095 for the fry processing potatoes; values outside this range are undesirable for several reasons, including higher processing costs (e.g., energy costs to remove excess water, increased oil uptake, and associated oil replacement costs with low SpGr, decreased product recovery), quality problems with the raw product (e.g., bruising), or quality

Table 3. Comparison of the mean specific gravity stability for entries in the National Agronomic Trial. The first six columns of data are the site averages for each genotype, followed by the national average (overall mean). The Finlay–Wilkinson regression coefficient and SE were calculated from a regression of the genotype best linear unbiased prediction vs. environment mean across all 18 environments. The last column contains the national average for the SD of the gravity distribution, which measures stability within an environment.

Genotype	ID	ME	MN	OR	WA	WI	Overall mean	Regression coefficient (SE)	Overall SD ($\times 10^{-3}$)
AOR06070-1KF	1.095	1.093	1.098	1.087	1.092	1.094	1.093	0.4 (0.4)	9.0
A03921-2	1.101	1.097	1.094	1.096	1.095	1.095	1.096	0.7 (0.2)	9.5
AF4342-3	1.099	1.093	1.092	1.095	1.093	1.092	1.093	0.7 (0.2)	8.9
A06084-1TE	1.077	1.082	1.083	1.072	1.076	1.078	1.078	0.8 (0.3)	8.3
AO01114-4	1.088	1.089	1.086	1.080	1.084	1.085	1.086	0.8 (0.1)	8.7
Russet Burbank	1.077	1.080	1.080	1.074	1.075	1.077	1.078	0.9 (0.2)	7.6
A02138-2	1.086	1.088	1.085	1.081	1.082	1.083	1.084	0.9 (0.1)	8.0
A02424-83LB	1.090	1.090	1.088	1.087	1.086	1.086	1.088	0.9 (0.1)	8.6
AC96052-1RU	1.080	1.083	1.077	1.078	1.077	1.075	1.079	0.9 (0.1)	7.8
AF4296-3	1.077	1.082	1.077	1.076	1.075	1.075	1.077	0.9 (0.1)	7.9
A0073-2	1.091	1.090	1.085	1.085	1.086	1.085	1.087	0.9 (0.1)	8.0
Payette Russet	1.094	1.091	1.087	1.086	1.089	1.087	1.089	1.0 (0.1)	7.8
AO00057-2	1.089	1.090	1.082	1.083	1.084	1.082	1.085	1.0 (0.1)	8.9
AC00395-1RU	1.095	1.095	1.085	1.091	1.089	1.087	1.090	1.0 (0.1)	8.9
Easton	1.077	1.082	1.079	1.070	1.075	1.076	1.077	1.0 (0.2)	9.0
Mountain Gem Russet	1.077	1.082	1.077	1.070	1.075	1.075	1.076	1.1 (0.1)	8.0
W6234-4rus	1.083	1.088	1.080	1.078	1.079	1.078	1.081	1.1 (0.1)	8.0
AC99375-1RU	1.089	1.089	1.078	1.086	1.083	1.080	1.084	1.2 (0.1)	10.0
Dakota Russet	1.086	1.089	1.079	1.079	1.081	1.079	1.082	1.2 (0.1)	7.7
W8152-1rus	1.086	1.091	1.072	1.081	1.080	1.076	1.081	1.4 (0.3)	9.1
A0012-5	1.083	1.086	1.048	1.080	1.073	1.059	1.071	2.1 (0.7)	12.0
Overall mean	1.087	1.088	1.082	1.082	1.082	1.081	1.084	1.0	8.6

problems with the processed product (e.g., undesirable French fry texture).

For any quantitative trait in any crop, there is variation between the harvested "units" (e.g., grains, tubers, fruits), even within a nominally homogeneous environment. The within-plot variance, however, is rarely a phenotypic trait used by plant breeders. Even for potato, where tuber-to-tuber variation in SpGr is a well-known problem for the French fry processing industry (hence, its routine measurement via the brine tank method at processing plants), this trait is not measured in the US public breeding programs. The results of this study provide some justification for the status quo, as h^2 for the SD of the SpGr distribution within a plot was four to six times lower than the plot mean (Tables 1 and 2), regardless of whether SpGr was measured by water displacement or brine tanks. Using the median h^2 values from the NAT, one would need to measure the SD on 16 plots to equal the heritability of one plot for the mean SpGr. Alternatively, measuring more tubers per plot would be another way to improve the reliability of SD estimates.

Although 16 is not a reasonable number of replications within a single environment, 16 plots of data are readily obtained through cooperative regional or national trials. Although the NAT was short lived (it was tied to a federal grant), there is continued support for US national trials in the fry processing (Wang et al., 2015) and chip processing markets. In the National Fry Processing trial, there are currently five locations with two replicates per site, for a total of 10 plots $yr^{-1,}$ and in the chip processing trial, there are currently nine locations with two replicates per site for returning entries.

Even though SD could be measured with sufficiently high h^2 in these national trials, it is not clear that the additional effort of measuring each tuber would be justified. This is because a genotype that exhibits high tuber-to-tuber variation in one environment may be expected to show more variation in the plot means across environments (i.e., lower stability as quantified through the FW method). The results for genotype A0012-5 supported this expectation, as it was the only genotype with exceptionally high SD within a plot (Fig. 1) and the highest FW regression coefficient (Table 3). Among the remaining genotypes in the NAT, there was no significant correlation between the within-plot and between-environment measures of stability, but we believe this was due to the selected nature of the population. In this study, a number of new genotypes, including Payette Russet, Mountain Gem Russet, Easton, and Dakota Russet, showed good dynamic stability of mean SpGr (Table 3), which should prove attractive to the French fry processing industry. Our conclusion is that breeders can effectively select for the needs of the potato industry by

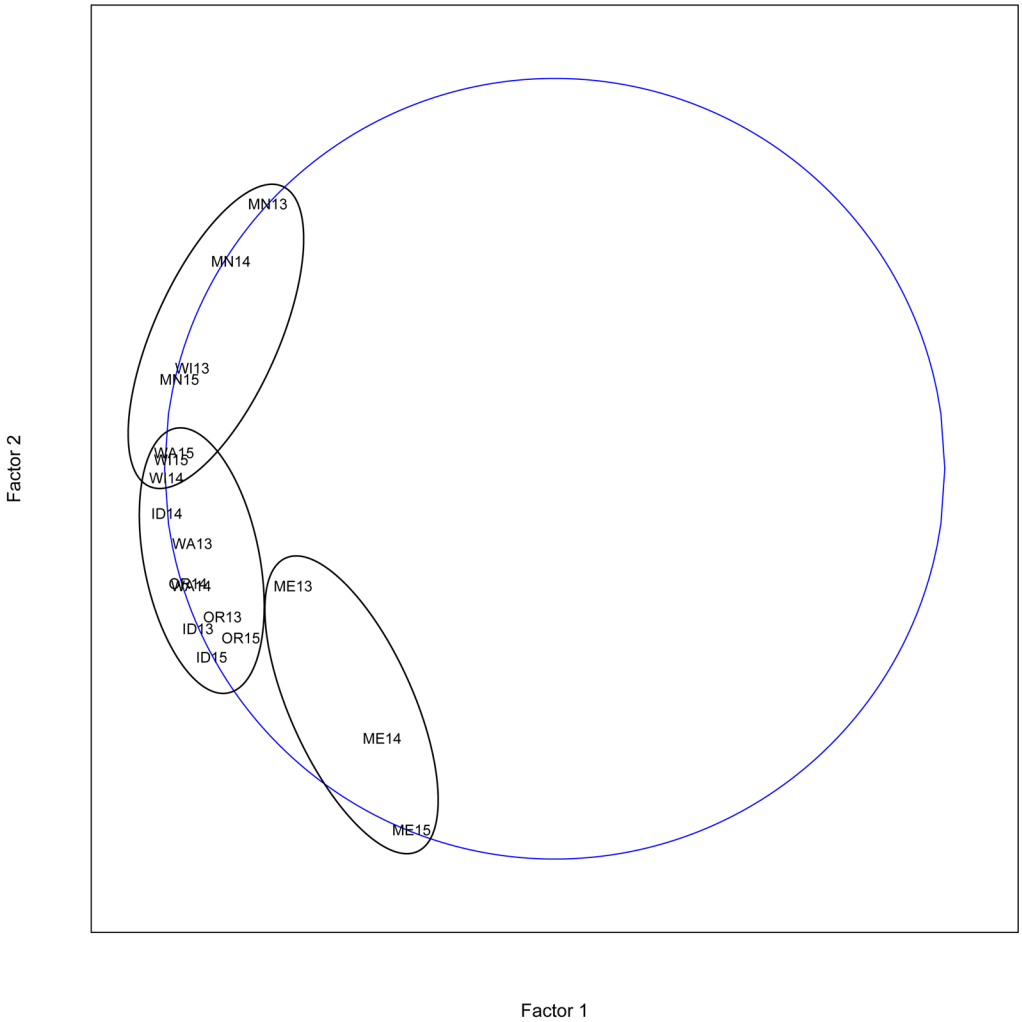

Fig. 2. Uniplot representation of the genotype × environment interaction for the mean specific gravity in the National Agronomic Trial, based on a second-order factor-analytic model. Uniplots are scaled to the unit circle, with the cosine of the angle between two environments equal to the genetic correlation (only approximately for points in the interior of the circle; Cullis et al., 2010). Each environment is coded as the combination of a site (OR, ME, WI, ID, MN, WA) and a year (13, 14, 15). Ellipses are added to illustrate the regional grouping of environments.

focusing on mean SpGr, provided that the stability of this trait is assessed in multi-environment trials.

To maximize return on the public and private investment in the national processing trials, they should be designed efficiently. This is the first study to clearly demonstrate consistent US regional differences for the ranking of potato genotypes with respect to SpGr. Previously, it was well known that some locations (e.g., Wisconsin) typically produce tubers with lower SpGr than other locations (e.g., Maine; see Table 3), but the grouping of environments shown in Fig. 2 reflects the ordering of the genotypes, not simply the population mean. Although geographically the Midwestern locations of Wisconsin and Minnesota are in the middle of the United States, from a genetic perspective, the PNW locations (Oregon, Washington, and Idaho) appear to occupy the "middle" space of US environments (Fig. 2). Identifying which physical characteristics of the environments are responsible for this phenomenon will help translate our statistical genetic results into a better understanding of potato physiology and ultimately phenotype prediction, which is an area of active research in other major crops (Heslot et al., 2014; Jarquín et al., 2014). We conclude that all three regions contribute unique information and should be retained in national trials, but if the pattern observed for SpGr holds up for other traits, there could be an opportunity to reduce the number of locations (or replicates within location) for the PNW and Midwestern regions.

Table 4. Average genetic correlation within (on-diagonal) and between (off-diagonal) regions in the National Agronomic Trial. Pacific Northwest: ID, OR, and WA; Upper Midwest: MN and WI; Northeast: ME.

	Pacific Northwest	Upper Midwest	Northeast
Pacific Northwest	0.97	0.78	0.78
Upper Midwest		0.91	0.35
Northeast			0.85

Supplemental Material Available

Supplemental material for this article is available online.

Acknowledgments

The authors thank all the individuals involved in the NAT and WRT for laboratory and field work assistance. Financial support for the NAT was provided by the Potatoes USA, potato grower associations at the state level, several fry processing companies, and the USDA-NIFA-Specialty Crop Research Initiative (Grant no. 2011-51181-30629). Financial support for the WRT was provided by grants from the Wisconsin Potato

and Vegetable Growers Association and Specialty Crop Block Grants (12-001, 13-007) from the Wisconsin Department of Agriculture, Trade and Consumer Protection.

References

Affleck, I., J.A. Sullivan, R. Tarn, and D.E. Falk. 2008. Genotype by environment interaction effect on yield and quality of potatoes. Can. J. Plant Sci. 88:1099–1107. doi:10.4141/CJPS07207

Agblor, A., and M.G. Scanlon. 2002. Effect of storage period, cultivar and two growing locations on the processing quality of French fried potatoes. Am. J. Potato Res. 79:167–172. doi:10.1007/BF02871932

Cullis, B.R., A.B. Smith, C.P. Beek, and W.A. Cowling. 2010. Analysis of yield and oil from a series of canola breeding trials. Part II. Exploring genotype by environment interaction using factor analyis. Genome 53:1002–1016. doi:10.1139/G10-080

Edgar, A.D. 1951. Determining the specific gravity of individual potatoes. Am. Potato J. 28:729–731. doi:10.1007/BF02851328

Finlay, K.W., and G.N. Wilkinson. 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14:742–754. doi:10.1071/AR9630742

Greenwood, M.L., M.H. McKendrick, and A. Hawkins. 1952. The relationship of the specific gravity of six genotypes of potatoes to their mealiness as assessed by sensory methods. Am. Potato J. 29:192–196. doi:10.1007/BF02885340

Henninger, M.R., S.B. Sterrett, and K.G. Haynes. 2000. Broad-sense heritability and stability of internal heat necrosis and specific gravity in tetraploid potatoes. Crop Sci. 40:977–984. doi:10.2135/cropsci2000.404977x

Heslot, N., D. Akdemir, M.E. Sorrells, and J.-L. Jannink. 2014. Integrating environmental covariates and crop modeling into the genomic selection framework to predict genotype by environment interactions. Theor. Appl. Genet. 127:463–480. doi:10.1007/s00122-013-2231-5

Hilderbrand, K.S. 1993. Preparation of salt brines for the fishing industry. Oregon State Univ. Ext. https://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/24998/SGNO221993.pdf?sequence=1 (accessd 19 Oct. 2016).

Holland, J.B., W.E. Nyquist, and C.T. Cervantes-Martínez. 2003. Estimating and interpreting heritability for plant breeding: An update. Plant Breed. Rev. 22:9–111.

Jarquín, D., J. Crossa, X. Lacaze, P. Du Cheyron, J. Daucourt, J. Lorgeou et al. 2014. A reaction norm model for genomic selection using high-dimensional genomic and environmental data. Theor. Appl. Genet. 127:595–607. doi:10.1007/s00122-013-2243-1

Kleinkopf, G.E., D.T. Westermann, M.J. Wille, and G.D. Kleinschmidt. 1987. Specific gravity of Russet Burbank potatoes. Am. Potato J. 64:579–587. doi:10.1007/BF02853760

Paget, M.F., L.A. Apiolaza, J.A.D. Anderson, R.A. Genet, and P.A. Alspach. 2015. Appraisal of test location and genotype performance for the selection of tuber yield in a potato breeding program. Crop Sci. 55:1957–1968. doi:10.2135/cropsci2014.11.0801

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

SAS Institute. 2015. SAS system for Windows. Release 9.4. SAS Inst., Cary, NC.

Sayre, R.N., M. Nonaka, and M.L. Weaver. 1975. French fry quality related to specific gravity and solids content variation among potato strips within the same tuber. Am. Potato J. 52:73–82. doi:10.1007/BF02855128

Smith, A., B. Cullis, and R. Thompson. 2001. Analyzing genotype by environment data using multiplicative mixed models and adjustments for spatial field trend. Biometrics 57:1138–1147. doi:10.1111/j.0006-341X.2001.01138.x

USDA-AMS. 1983. United States standards for grades of potatoes for processing. USDA, Agric. Marketing Serv. https://www.ams.usda.gov/sites/default/files/media/Potatoes_for_Processing_Standard%5B1%5D.pdf (accessed 30 Oct. 2016).

Vanasse, N.A., E.D. Jones, and H.L. Lucas. 1951. Specific gravity: Dry mattter relationship in potatoes. Am. Potato J. 28:781–791. doi:10.1007/BF02851876

Wang, Y., P.C. Bethke, A.J. Bussan, M.T. Glynn, D.G. Holm, F.M. Navarro et al. 2015. Acrylamide-forming potential and agronomic properties of elite U.S. potato germplasm from the National Fry Processing Trial. Crop Sci. 56:1–10.

Young, D.A. 1962. The selection of potato samples for the evaluation of culinary quality. Am. Potato J. 39:14–18. doi:10.1007/BF02912627

Young, D.A., P.W. Voisey, and N. Dixon. 1964. A specific gravity calculator for potatoes. Am. Potato J. 41:401–405. doi:10.1007/BF02908891