Genotype × Storage Environment Interaction and Stability of Potato Chip Color: Implications in Breeding for Cold Storage Chip Quality

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ABSTRACT

Potato (*Solanum tuberosum* L.) genotypes exhibit significant variation for chip color across different storage regimes. Lines that maintain light chip color after long postharvest storage durations and low storage temperatures are desirable to the potato industry. Since storage regimes vary among growers and processors, lines that exhibit stable chip performance across various storage regimes have a high probability of commercial success. The objective was to test if treating storage regimes as "environments," analyzing genotype × storage environment interactions, and applying stability statistics can help identify desirable chip processing lines. To examine this, chip color of 47 breeding clones and six standard varieties was evaluated across eight storage environments. Chip color data was analyzed using stability metrics as well as stability-adjusted selection indices. The effects of genotype, storage environment, and genotype × environment on chip color were significant, explaining 47, 24, and 17% of total variance, respectively. Types I, II, and III stable lines were identified through stability analyses. Type I stability was significantly correlated with mean chip color. The most desirable lines were identified under long and cold storage environments. Using Type I stability and stability-adjusted indices, this study identified breeding clones for advancement, including W5840-4, W6484-5, and W6929-1, which outperformed standard chipping varieties for chip quality and stability.

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Abbreviations: AMMI, additive main effect and multiplicative interaction; b_i, Eberhart and Russell's regression coefficient; G×E, genotype × environment; HARS, Hancock Agricultural Research Station; PC, principal component; P_i, superiority of the *i*th line; RARS, Rhinelander Agricultural Research Station; s^2_{di}, line *i*'s deviation from regression; s^2_i, line *i*'s mean sum of squares of departure from regressions; σ^2_i, Shukla's stability variance; YS_i, Kang's selection index.

Potatoes are the foremost vegetable crop in the United States and fourth most important food crop in the world. Over 50% of the U.S. potato crop is used by the processing industry to make chips, french fries, and other processed products (USDA Economic Research Service, 2012). Nearly 90% of processing potatoes produced in the United States are harvested in the fall and stored in climate controlled rooms until they are needed for processing (USDA, 2012). Potatoes are best stored at low temperatures (just above freezing) and high relative humidity (98%) environments, which decrease sprouting, shrinkage, and storage disease problems (Pringle et al., 2009). Unfortunately, in response to low-temperature storage environments, most potato varieties accumulate reducing sugars through physiological processes known as cold-induced sweetening and senescent sweetening (Coffin et al., 1987; Sowokinos, 2001). This sugar accumulation has undesirable impacts on fry and chip color, as these reducing sugars undergo a nonenzymatic Maillard reaction with free amino acids when potatoes are fried in hot oil, resulting in a darkened product (Roe et al., 1990; Shallenberger et al., 1959). This is a serious problem for the processing industry because dark colored

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potato chips are unacceptable to the consumer and can contain elevated levels of acrylamide (C_3H_5NO), a byproduct of the Maillard reaction and a potential human health risk (Mottram et al., 2002; Foot et al., 2007). Because of this, the potato processing industry desires varieties that accumulate low amounts of sugar and produce light colored potato chips after cold storage.

Over the past few decades, potato breeding programs have made slow but significant progress in developing varieties that accumulate lower reducing sugars and produce lighter chip color following cold storage (Love et al., 1998). Breeders have also investigated the effect of growing environments and storage regimes on chip quality traits. Tai and Coleman (1999) were able to demonstrate a significant effect of growing location and storage temperature on potato chip color and in some cases detected significant genotype × environment (G×E) interactions. More recently, Affleck et al. (2012) and Agblor and Scanlon (2002) showed that variance for french fry color and tuber sugar content are significantly affected by growing environments, storage duration, and their interaction. These findings are important for potato breeders to consider when designing their chipping trials since many in-season and postharvest environmental factors influence and interact with the fry color of potato genotypes. Since storage regimes vary among growers and processors, lines with stable performance across various storage regimes would have a high probability of commercial success.

There are a number of stability analyses that have been developed to analyze G×E interactions in quantitative traits (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Shukla, 1972). The approaches of Finlay and Wilkinson (1963) and Eberhart and Russell (1966) rely on joint regression analysis while Shukla's (1972) stability variance ranks genotypic variance after the environmental effects are removed. These analyses are most often applied to yield data across multiple growing locations but can be applied to almost any trait or type of environment. Stability analyses have been successfully applied to many crops and traits including maize (*Zea mays* L.) yield, soybean [*Glycine max* (L.) Merr.] isoflavone content, and grain quality in wheat (*Triticum aestivum* L.) (Kang and Gorman, 1989; Murphy et al., 2009; Peterson et al., 1992). In potato, these approaches have been applied to tuber specific gravity and carotenoid content among others (Haynes et al., 1995, 2010). This type of approach can also be useful to potato breeders who want to identify lines that can fry well across a range of cold storage regimes that potato growers, processors, and researchers may use.

There are three distinct types of stability that are typically characterized by stability analyses (Bernardo, 2002). Type I stability, or static stability, is present when the value or score of a line does not change across environments. Type II stability, or dynamic stability, is present when the performance of a line changes across environments but in constant proportion with the changing population mean at each environment (Piepho, 1996). Type III stability concerns the precision of the estimate of a line's performance. It is a measure of how much the true value for a line deviates from the value predicted by linear regression over all environments. Eberhart and Russell (1966) developed a joint regression approach that can be used to characterize types I, II, and III stability (Bernardo, 2002). Shukla's (1972) method can be used to further characterize Type II stability. Gauch (1992) developed an additive main effect and multiplicative interaction (AMMI) biplot method that can characterize the effects of each environment and provide a graphical representation of the stability of each line based on principal component (PC) analysis. Often, the stability and overall performance of a certain trait are independent of each other, so selection on one or the other criteria can be ineffective for simultaneous improvement (Lin and Binns, 1988; Kang, 1993). Lin and Binns (1988) developed a method that generates a genotypic superiority estimate that is helpful to rank lines based on both stability and performance. Kang (1993) described an index for simultaneous selection on yield (or any other trait) and stability to help breeders avoid selecting unstable lines or stable-but-mediocre lines.

Although several studies have evaluated genotypic variation of chip color in response to cold storage temperature, previously published studies have not analyzed the combined effect of different storage temperatures and durations on potato chip color. The concept of chipping stability across storage environments has been presented before by Loiselle et al. (1990), who concluded that selection for chipping stability is less important than selection for overall chip quality. Whereas the Loiselle study reached this conclusion after evaluations across three storage regimes, the present study examines if the importance of chipping stability is greater when evaluated across more storage environments. An objective of the present study was to determine the relative effect of storage environments on potato chip color and the variation due to genotypes and G×E interactions across a larger set of storage environments (8) and to analyze chipping stability with a number of metrics. Five stability analyses were applied to characterize the stability of chip color performance (Eberhart and Russell, 1966; Shukla, 1972; Lin and Binns, 1988; Gauch, 1992; Kang, 1993).

The chip processing industry requires potato chip varieties that exhibit predictable light chip color throughout the storage period. The long term storage ability of potato varieties has been investigated (Glynn and Sowokinos, 2010, 2011, 2012). Glynn and Sowokinos (2010) have proposed a classification of genotypes in which Class A types can be chipped acceptably from 5.5°C at 3 and 7 mo, Class B types can be chipped at 7.2°C at 3 and 7 mo but not at 5.5°C, and Class C types cannot be chipped at either temperature. The stability methods used in this study can be additional tools to help potato breeders classify chip performance and select the best chippers for short, intermediate, and long cold storage while avoiding type I and II selection errors. Stability measures could avoid misclassification of breeding clones that may arise from underestimation of G×E effects.

The current study presents an analysis of the response of potato chip color in a group of 53 potato genotypes subjected to eight storage environments. Specific storage temperature and duration combinations were treated as distinct storage environments. The primary objectives of this study were to evaluate the effectiveness of applying stability measures to potato chip storage data to identify lines that exhibit the three stability types and to identify lines that exhibit superior chipping performance across storage environments.

MATERIALS AND METHODS

Plant Material and Field Experiment

Forty-seven tetraploid advanced breeding clones were selected from progenies produced by crosses between chipping potato germplasm in the Wisconsin potato breeding program. The crosses were made in 2003 at the Rhinelander Agricultural Research Station (RARS) of the University of Wisconsin. The lines were grown from true seed in the greenhouses at RARS in 2003 and in single hill plots at RARS in 2004. Tubers were bulked and maintained at RARS in subsequent years before being entered into the 2007 replicated trial at Hancock Agricultural Research Station (HARS) of the University of Wisconsin. In addition to the 47 breeding clones, six well-characterized standard chipping cultivars, including 'Atlantic', 'Dakota Pearl', 'MegaChip', 'Pike', 'Snowden', and 'White Pearl', were evaluated as the checks.

These 53 materials were grown in a randomized complete block design with three replications at HARS in 2007. Each plot consisted of 20 plants in a 6.1-m row, with 0.9 m spacing between rows. All plots were grown using standard agronomic practices for potato production in Wisconsin.

Storage and Chip Color Evaluation

A fixed-effects linear model was used to estimate the proportion of variance explained (R^2) by genotype, storage temperature and duration, and the interactions. The PROC GLM procedure of the SAS software (version 9.2; SAS Institute, 2008) was used to obtain the ANOVA. The fixed-effect linear regression model was

$$\begin{aligned} Y_{ijkl} &= \mu + \alpha_i + \beta_j + \delta_k + (\beta\delta)_{jk} \\ &\quad + (\alpha\beta)_{ij} + (\alpha\delta)_{ik} + (\alpha\beta\delta)_{ijk} + \varepsilon_{ijkl}, \end{aligned}$$

in which μ is the population mean, α_i is the main effect of the *i*th genotype, β_j is the main effect of the *j*th storage temperature, δ_k is the main effect of the *k*th storage duration, $(\beta\delta)_{jk}$ is the interaction of the *j*th temperature and *k*th duration, $(\alpha\beta)_{ij}$ is the interaction of the *i*th genotype and *j*th temperature, $(\alpha\delta)_{ik}$ is the interaction of the *i*th genotype and *k*th duration, $(\alpha\beta\delta)_{ijk}$ is the interaction of the *i*th genotype in the *jk*th temperature and duration, and ε_{ijkl} is the residual error.

This model was simplified by combining storage temperature and duration into a single "environmental" main effect, considering each temperature–duration combination a distinct storage environment, to analyze the broader environment and G×E effects. The simplified model was

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk},$$

in which μ is the population mean, α_i is the main effect of the *i*th genotype, β_j is the main effect of the *j*th storage environment, $(\alpha\beta)_{ij}$ is the interaction of the *i*th genotype and *j*th environment, and ε_{ijk} is the residual error. Both models were assembled in a single ANOVA table. After fitting the model, outliers were identified as observations with studentized residuals greater than 3.0. As a result, 19 of the 1264 observations were removed from the analysis. The assumptions of normality and equal variance of the residuals were tested, and a log transformation of the scalar chip color scores was performed to improve both aspects of the model. Analysis of variance on the log-transformed data was then repeated with the above models.

Stability and Performance Analyses

Separate stability analyses were performed using the methods of Eberhart and Russell (1966) and Shukla (1972). Eberhart and Russell's stability analysis was conducted on the raw chip color data in SAS (version 9.2; SAS Institute, 2008) using code developed by Piepho (1999). Shukla's (1972) stability variance and Kang's (1993) selection index (YS_i) were calculated from the log-transformed chip color data using the agricolae package in R (Mendiburu, 2012; R Development Core Team, 2011). The cultivar superiority measure (superiority of the *i*th line [P_i]) was calculated according to Lin and Binns's method (1988). The AMMI biplot, based on PC analysis, was produced in R using the agricolae and klaR packages (Weihs et al., 2005) to produce a graphical indicator of stability performance.

RESULTS

Environments with lower temperature and longer storage regime resulted in higher mean chip color score and a larger variance of color score (Table 1; Fig. 1). The storage environments partitioned into six significantly different groups by Fisher's LSD. Analysis of variance and the plot of temperature and duration indicated that both factors and their interaction significantly affected chip color (Table 2; Fig. 1).

Analysis of Variance

Analysis of variance identified significant variation of potato chip color due to genotype, storage environment, and genotype × storage interaction. According to the fixed effects model, genotype explained 24% of the variation, environment explained 47% of the variation, and G×E explained 17% of the variation (Table 2). The partition of environmental variation showed temperature explained 25%, duration explained 16%, and the temperature × duration interaction explained 5% of the total variation (Table 2).

Table 1. Potato chip color score of tubers from 53 genotypes fried after storage at eight different environments. Chip color was scored on a 1 to 10 scale (1 indicates lightest). Mean score of all genotypes, best and worst score irrespective of genotype, and standard deviation of chip color scores are presented.

Storage environment	Temp (°C)	Duration (months)	Mean score (1–10)[†]	Best score	Worst score	Standard deviation
1	5.5	3	3.38 e	2.33	6.40	1.06
2	5.5	5	6.43 b	3.27	9.87	2.19
3	5.5	6	6.73 a	3.17	10.00	2.03
4	5.5	9	6.72 a	3.17	9.80	2.05
5	8.3	3	3.08 f	2.13	4.50	0.76
6	8.3	5	3.51 e	2.37	7.37	1.38
7	8.3	6	4.12 d	2.40	8.53	1.62
8	8.3	9	5.43 c	2.30	9.40	2.02

[†] Letters indicate groupings based on Fisher's LSD; means with the same letter are not significantly different.

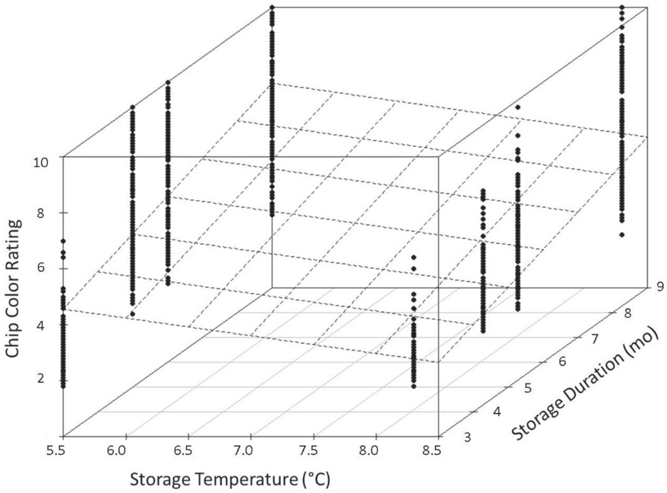

Figure 1. Three-dimensional scatter plot with a fitted regression plane of chip color rating of 53 potato genotypes fried after storage at two storage temperatures and four storage durations.

Table 2. Analysis of variance of potato chip color score of 53 potato genotypes evaluated after eight storage environments[†] consisting of four storage durations and two temperatures based on a fixed-effects linear regression model. Factors indented indicate subfactors of the main effects factors. Chip color was rated on a 1 to 10 scale and the ANOVA was performed on a log transformation of the data.

Source of variation	df	SS[‡]	MS[§]	R^2
Genotype	52	55.90	1.08***	0.24
Storage environment	7	110.97	115.85***	0.47
Duration	3	59.94	19.98***	0.25
Temperature	1	38.13	38.13***	0.16
Duration × temperature	3	12.93	4.31***	0.05
Genotype × storage	364	40.31	0.11***	0.17
Genotype × duration	156	22.87	0.15***	0.10
Genotype × temperature	52	7.82	0.15***	0.03
Genotype × duration × temperature	156	9.58	0.06***	0.04
Error	821	29.32	0.04	0.12

*** Significant at the 0.001 probability level.

[†] Storage environments: 3 mo at 5.5°C, 3 mo at 8.3°C, 5 mo at 5.5°C, 5 mo at 8.3°C, 6 mo at 5.5°C, 6 mo at 8.3°C, 9 mo at 5.5°C, and 9 mo at 8.3°C.

[‡] SS, sum of squares.

[§] MS, mean square.

Stability Analyses

The results of the stability analyses are presented in Table 3. Eberhart and Russell's (1966) regression coefficient (b_i) identified lines that exhibit Type I stability. The b_i for the 53 genotypes ranged from 0.20 to 1.76, centered around 1, with a standard deviation of 0.36. The six check varieties in this study exhibited poor Type I stability, with the exception of White Pearl, which had $b_i = 0.71$, significantly lower than 1 (Table 3). The b_i for Dakota Pearl demonstrated Type II stability while Pike, MegaChip, Atlantic, and Snowden demonstrated poor Type II stability, with b_i's significantly higher than 1 (Table 3). Three breeding lines (W6929-1, W6484-5, and W6598-2) had the lowest b_i, which indicates their chip color scores do not change much in absolute terms across all storage environments (Type I stability). The b_i also identified breeding lines that exhibit Type II stability. Five lines, namely W6602-2, W5800-5, W6599-2, W6407-3, and W6854-1, exhibited similar response to storage environments as the population mean ($b_i \approx 1.0$) (Table 3). Lines exhibiting Type III stability were identified by Eberhart and Russell's (1966) line *i*'s deviation from regression (s^2_{di}) and Shukla's (1972) line *i*'s mean sum of squares of departure from regressions (s^2_i) stability statistics. The most Type III-stable lines according to s^2_{di} and s^2_i were W6390-2 and White Pearl (Table 3). W6602-2 had the fourth lowest deviation from its regression-predicted scores (s^2_{di}), making it a Type II and Type III stable line. W6484-5 had the eighth lowest s^2_{di}, making it a Type I and Type III stable line.

Representative lines for each type of stability were chosen to plot performance over the storage index (Fig. 2). Type I stability is demonstrated by W6929-1, which has a nearly flat regression line. Type II stability is represented by W5800-5, which has a slope nearly identical to the fitted population mean across the eight storage environments. Type III stability is demonstrated by W6390-2, which has minimal deviation of true scores from those predicted by regression. Snowden did not exhibit any of the stability types. Figure 3 demonstrates the lack of Type I stability observed for the check varieties across the different storage environments. The slopes of the regression lines in Fig. 2 and Fig. 3 are the b_i parameters as calculated according to Eberhart and Russell (1966).

Selection Indices

The superiority index P_i as described by Lin and Binns (1988) and the simultaneous YS_i according to Kang (1993) were able to rank the 53 lines considering both chip performance and stability (Table 3). The most superior line, ranked by P_i, was W6484-5 followed by W5840-4, W6929-1, and W6598-2. Each of these lines also ranked in

Table 3. Mean chip color score across all environments, Lin and Binns (1988) superiority measure (superiority of the *i*th line [P_i]), Eberhart and Russell's (1966) regression coefficient (b_i) and deviation from regression sum of squares (*i*'s deviation from regression [s^2_{di}]), and Shukla's (1972) stability variance (σ^2_i) and mean sum of squares departure from regression (line *i*'s mean sum of squares of departure from regressions [s^2_i]) for 53 potato lines evaluated across eight storage environments, arranged in order of mean chip color.

	Mean score	Lin and Binns superiority		Eberhart and Russell stability				Shukla stability			
Line	(1–10)	P_i	Rank	b_i	Rank	s^2_{di}	Rank	σ^2_i	Rank	s^2_i	Rank
W6484-5	3.05	0.04	1	0.26	2	0.13	8	0.220	36	0.009	6
W5840-4	3.18	0.05	2	0.50	5	0.14	10	0.151	25	0.012	8
W6929-1	3.42	0.06	3	0.20	1	0.13	9	0.234	37	0.006	3
W6598-2	3.53	0.1	5	0.44	3	0.33	17	0.168	27	0.025	11
W7312-1	3.69	0.09	4	0.49	4	0.01	5	0.133	22	0.009	5
White Pearl	3.69	0.12	6	0.71	13	0.08	2	0.080	9	0.002	2
W6803-3	3.83	0.15	9	0.66	11	0.41	23	0.106	16	0.041	16
W6929-3	3.83	0.15	8	0.53	7	0.45	22	0.154	26	0.029	12
W6822-2	3.87	0.18	10	0.85	19	0.20	13	0.053	4	0.013	9
W6390-2	3.89	0.14	7	0.62	8	−0.02	1	0.095	12	0.002	1
W6483-5	3.97	0.20	11	0.83	17	0.11	6	0.056	5	0.011	7
W6822-4	3.99	0.22	13	0.91	23	0.17	11	0.043	1	0.014	10
W6822-3	4.12	0.22	12	0.68	12	0.40	20	0.106	15	0.038	15
W6323-6	4.16	0.34	20	0.73	14	1.04	49	0.215	34	0.183	39
W6483-4	4.16	0.33	18	0.63	10	1.12	50	0.269	39	0.254	44
W7279-5	4.19	0.24	14	0.84	18	0.51	26	0.181	30	0.124	30
W6929-2	4.26	0.27	16	0.80	15	0.50	25	0.079	8	0.051	18
W6571-3	4.36	0.42	22	0.96	25	0.98	48	0.186	32	0.199	40
W6484-2	4.39	0.26	15	0.62	9	0.06	3	0.093	10	0.007	4
W5800-5	4.42	0.36	21	1.04	31	0.53	28	0.062	6	0.071	21
W5941-3	4.55	0.3	17	0.50	6	0.34	18	0.129	21	0.031	13
W6602-2	4.57	0.34	19	0.97	26	0.07	4	0.096	13	0.052	19
W7279-8	4.66	0.45	23	1.05	33	0.85	44	0.117	19	0.138	35
W6599-2	4.70	0.54	26	1.00	30	1.45	53	0.317	43	0.371	49
W5955-1	4.79	0.6	33	1.43	45	0.72	37	0.181	29	0.163	37
W6609-3	4.81	0.5	25	0.91	24	0.78	40	0.127	20	0.138	34
W6483-1	4.83	0.49	24	1.04	32	0.66	34	0.093	11	0.110	27
W6390-5	4.85	0.64	36	0.86	21	1.27	51	0.500	48	0.560	52
W6444-2	4.90	0.57	29	1.17	36	0.68	35	0.073	7	0.087	24
W5963-2	4.92	0.58	32	0.85	20	1.32	52	0.299	41	0.338	48
W6529-1	4.97	0.58	31	1.20	38	0.69	36	0.098	14	0.105	26
W6803-2	5.00	0.55	28	1.16	35	0.32	16	0.045	3	0.053	20
Dakota Pearl	5.09	0.58	30	0.97	27	0.59	31	0.116	18	0.129	31
W6387-3	5.17	0.75	37	1.25	39	0.75	38	0.273	40	0.319	47
W6407-3	5.18	0.62	34	0.99	29	0.77	39	0.137	23	0.162	36
W5948-2	5.19	0.55	27	0.83	16	0.52	27	0.044	2	0.038	14
W6854-1	5.26	0.63	35	0.99	28	0.61	32	0.115	17	0.136	33
W5939-4	5.43	0.93	39	1.49	49	0.91	45	0.658	52	0.622	53
W6387-4	5.48	0.85	38	1.18	37	0.92	47	0.216	35	0.249	43
Snowden	5.55	0.99	41	1.64	51	0.57	30	0.300	42	0.178	38
W6393-1	5.75	0.99	40	1.46	47	0.41	21	0.184	31	0.136	32
Pike	5.86	1.01	42	1.44	46	0.53	29	0.323	44	0.208	41
W6036-1	5.95	1.08	43	1.52	50	0.23	14	0.147	24	0.043	17
W5885-3	6.25	1.18	45	1.40	44	0.27	15	0.193	33	0.075	22
W8138-2	6.39	1.17	44	0.87	22	0.81	42	0.255	38	0.290	45
W6388-3	6.56	1.45	47	1.40	43	0.91	46	0.482	47	0.459	51
W6850-3	6.57	1.49	48	1.70	52	0.34	19	0.549	50	0.091	25
W6387-7	6.70	1.5	49	1.36	42	0.80	41	0.506	49	0.444	50
W6591-1	6.79	1.41	46	1.14	34	0.18	12	0.169	28	0.111	28
W6040-6	6.81	1.64	53	1.76	53	0.12	7	0.978	53	0.082	23
Atlantic	6.89	1.61	52	1.46	48	0.64	33	0.375	45	0.116	29
MegaChip	6.92	1.56	50	1.34	41	0.49	24	0.579	51	0.245	42
W5916-1	6.95	1.59	51	1.29	40	0.85	43	0.434	46	0.305	46

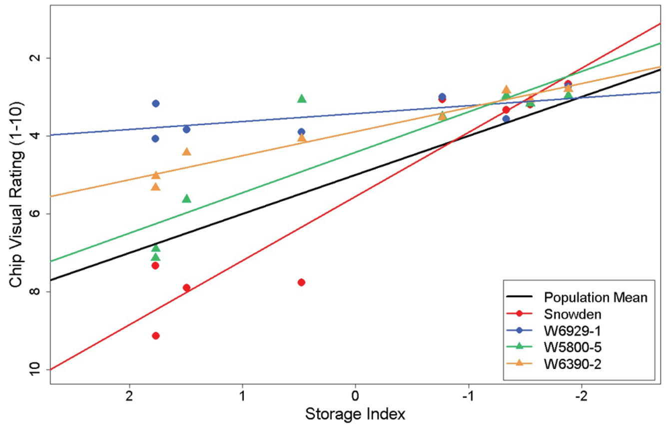

Figure 2. Regression lines of chip color over the storage index for selected potato breeding clones that exhibit types I (W6929-1), II (W5800-5), and III (W6390-2) stability, standard variety Snowden, and the mean response of 53 genotypes across eight storage environments. Chip color is rated according to the Snack Food Industry scale (1 indicates lightest and 10 indicates darkest) and each storage regime is plotted across the storage index by its deviation from the grand mean of chip color rating, which is set to 0. A positive storage index indicates an unfavorable environment with a darker mean chip score and a negative index indicates a favorable environment with a lighter mean score. The regression slopes are equivalent to Eberhart and Russell's regression coefficient (b_i) as described by Eberhart and Russell (1966).

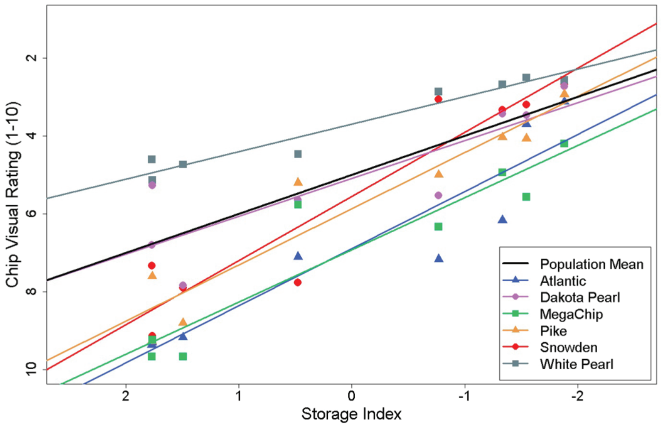

Figure 3. Regression lines of chip color over the storage index for six standard potato varieties and the mean response of 53 genotypes across eight storage environments. Chip color is rated according to the Snack Food Industry scale (1 indicates lightest and 10 indicates darkest) and each storage regime is plotted across the storage index by its deviation from the grand mean of chip color rating, which is set to 0. A positive storage index indicates an unfavorable environment with a darker mean chip score and a negative index indicates a favorable environment with a lighter mean score. The regression slopes are equivalent to Eberhart and Russell's regression coefficient (b_i) as described by Eberhart and Russell (1966).

the top seven of the YS_i, and the top ranked line according to YS_i was also W6484-5. In general, the lines that ranked highest for the selection indices also had the highest Type I stability. Both measures were in agreement for the worst performing genotypes, with the check lines Atlantic and MegaChip ranking near the bottom (Table 3).

Rank Correlations for Stability Measures

Spearman's pairwise rank correlation tests showed some stability measures to be highly correlated with each other when applied to the chip color data (Table 4). The s^2_{di} and s^2_i stability parameters of Eberhart and Russell (1966) and Shukla (1972) were highly correlated ($r = 0.88$). However, b_i was not correlated with Shukla's stability variance (σ^2_i) ($r = 0.42$), unlike the findings in other stability studies (Murphy et al., 2009). The b_i was correlated with mean chip color ($r = 0.85$) (Table 4). These results indicate that the lines within this testing population that demonstrate Type I stability also tend to have good overall performance. Superiority P_i and simultaneous YS_i were highly correlated with each other ($r = -0.98$). Both measures were also very highly correlated with mean chip performance ($r = 0.98$) (Table 4).

Genotype × Storage Environment Variance: Additive Main Effect and Multiplicative Interaction Biplot

The AMMI biplot approach clustered genotypes and environments together according to the first two PCs of multiplicative (genotype × storage environment) variance (Fig. 4). The first two PCs explained 71.2% of the G×E variance. Principal component 1 was correlated with the chip color means across environments ($r = -0.96$) while PC2 was highly correlated with b_i across genotypes ($r = -0.97$) (Table 4). Shorter-duration storage environments clustered together as did middle-duration environments with lower temperature. Environments in close proximity to the y axis contributed the least to the multiplicative variance while environments far from the origin contributed the most to the variance.

DISCUSSION

The present study evaluated the potato chip color and chipping stability of genotypes subjected to a number of storage environments. The results reinforce that storage environments have an important effect on the color of potato chips fried out of storage and that potato genotypes respond differentially to storage regimes (Loiselle et al., 1990; Tai and Coleman, 1999). Genotype × storage environment interaction had a large effect on the variation observed in chip quality evaluations (Table 2). Certain lines exhibited chip color stability across a range of storage durations and temperatures while the chip quality of others was highly variable across storage conditions (Fig. 2 and 3).

The stability measures of Eberhart and Russell (1966) and Shukla (1972) were able to quantify and rank the chip color stability of the lines in this trial (Table 3); however, these models only measure stability without considering

Table 4. Matrix of pairwise Spearman's rank-based correlations between mean chip color score, Lin and Binns (1988) superiority index (superiority of the ith line [Pi]), Kang's (1993) selection index (YSi), Eberhart and Russell' (1966) stability regression coefficient (b_i) and regression deviation sum of squares (i's deviation from regression [s^2_{di}]), Shukla's (1972) stability variance (σ^2_i) and interaction sum of squares (line *i*'s mean sum of squares of departure from regressions [s^2_i]), and additive main effect and multiplicative interaction principal component (PC) 1 and PC2 calculated for 53 potato genotypes evaluated across eight storage environments.

	Lin and Binns	Kang	Eberhart and Russell		Shukla		AMMI	
	P_i	YS_i	b_i	s^2_{di}	σ^2_i	s^2_i	PC1	PC2
Mean	0.98***	0.98***	0.85***	0.36**	0.50***	0.62***	0.17 ns†	−0.87***
P_i		−0.98***	0.88***	0.43**	0.58***	0.69***	0.11 ns	−0.90***
YS_i			−0.85***	−0.41**	−0.62***	−0.68***	−0.16 ns	0.87***
b_i				0.30*	0.42**	0.56***	0.14 ns	−0.97***
s^2_{di}					0.43**	0.88***	−0.15 ns	−0.36**
σ^2_i						0.66***	−0.23 ns	−0.48***
s^2_i							−0.10 ns	−0.61***
PC1								−0.01ns

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

†ns, not significant (at $p > 0.05$).

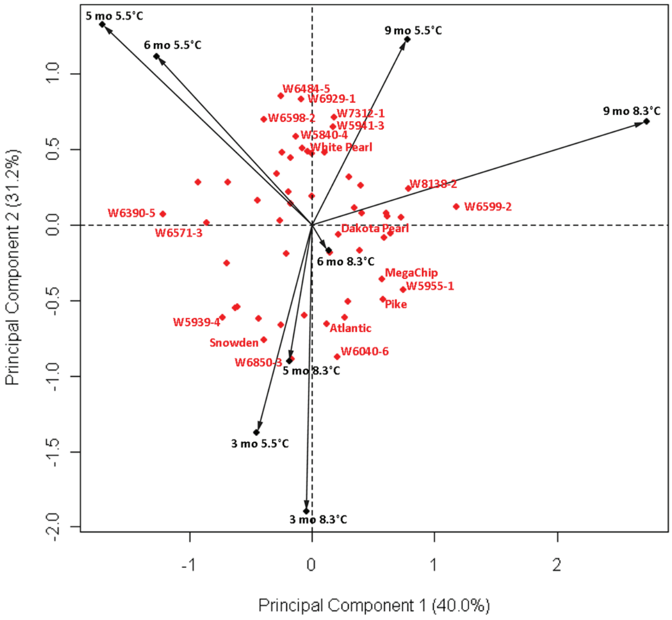

Figure 4. Additive main effects and multiplicative interaction biplot of the first two principal components that explain variation for mean potato chip color rating (1 indicates lightest and 10 indicates darkest) of 53 potato genotypes evaluated after eight storage environments. Select genotypes are labeled.

performance. The use of the combined stability-performance indices of Kang (1993) and Lin and Binns (1988) attempted to address this. Since in this trial, average chip color was directly correlated with b_i ($r = 0.85$), the use of performance-adjusted indices did not significantly change the rank of lines or improve the identification of top performers (Tables 3 and 4). Hence, it unnecessary to use performance-adjusted selection indices to aid selection, as the most stable lines generally had the lowest mean color scores. The five most Type I stable lines were also the five lines with the lightest mean chip color (Table 3). Although they did not improve selection efficiency in this instance, the application of selection indices P_i and YS_i are often useful to minimize type II error when making selections. In cases such as Loiselle et al. (1990), in which some lines chip stably but poorly across environments, these indices can prevent them from being selected based on stability alone.

In the AMMI biplot, the stable lines clustered together around the *y* axis and above the *x* axis (Fig. 4). The AMMI biplot was helpful for visualizing the scope of G×E within a population to identify groups of superior genotypes and useful storage regimes for testing. A picture of the similarity or dissimilarity of genotypes to each other can be gained by looking at the distance between any two genotypes. Genotypes that clustered near the origin exhibited Type II stability while genotypes that fell above the *x* axis had more Type I stability. Genotypes furthest from the *x* origin were the least Type III stable while those closest generally had the most Type III stability (Fig. 4).

Variance for chip color was significantly lower in storage regimes that were favorable for potato chip quality (Table 1). Figure 1 demonstrates how the scores clustered closer together at warmer temperature and shorter duration environments and spread out after longer durations or at lower temperature. Due to this, the most desirable genotypes were only clearly discernible from less-desirable genotypes in the harsher storage environments. This suggests that breeding efforts for high quality cold chippers should give priority to chipping evaluations that follow long postharvest storage regimes (i.e., 6–9 mo) at low temperatures (i.e., 5.5°C) to maximize phenotypic variation.

When making selections for potato chip color from long storage, elimination of clones with poor overall performance but Type I stability is a necessary first step. Second, among clones with good chip performance, preference should be given to the most Type I stable lines such as W6484-5 (Table 3). These will perform dependably in favorable storage environments and significantly outperform Type II stable lines in harsh environments. Lines that exhibit Type II storage stability (such as W6483-1) should generally be eliminated from programs emphasizing cold and long storage chip quality. This is because although they perform predictably around the population mean across storage regimes, they are susceptible to the negative effects of cold and long duration storage. Lines that have a b_i value greater than 1 should especially be avoided since these will be least adapted to the harsh target environments.

Traits such as chip color stability require a different interpretation than traditional selection for yield stability as proposed by Eberhart and Russell (1966). Improving stability in complex traits such as yield across a range of growing environments generally requires selection of lines with high means and with b_i values close to 1 (Blum, 1988; Bernardo, 2002). Trait superiority is often independent of trait stability, and while it is desirable to have lines that are superior in both favorable and unfavorable environments, achieving this is difficult for most traits (Bernardo, 2002). For many of these complex traits, it is rare to find lines that exhibit favorable Type I stability; it is much more common to find a Type I stable line that performs near or below average for the trait of interest. Therefore, for many of these traits it has been recommended to select Type II stable lines that outperform in relative proportion to each environment's mean (Blum, 1988; Bernardo, 2002).

The situation for selecting desirable storage-adapted potato chipping lines involves concerns that are not present in the standard stability-selection program. In most of the circumstances that consider trait stability, it has been measured across essentially random growing environments. In the present study, the environments in question are applied postharvest and are selected and controlled by the researcher. In the commercial setting, these environments are under control of the various growers and processors who store potatoes preprocessing. When applying stability-selection criteria in a way that is useful for the potato chip industry, little concern should be given to how well a line performs under a trait-favorable (short duration and warmer) storage environment. Growers and processors are interested in lines that can store well for longer durations at cold temperatures, which are unfavorable environments for chip color, necessitating the selection of lines that exhibit light chip color and Type I stability. While this stability-selection approach differs from the yield stability approach, it is well suited to selection for processing potatoes that meet industry requirements. These results suggest that breeders can use stability analysis as a tool to identify lines that exhibit commercially desirable storage characteristics. As mentioned before, storage regimes vary among potato growers and processors; therefore, lines with stable chipping performance across various storage regimes would have a high probability of commercial success. This recommendation agrees with Thill and Peloquin (1995) and Hayes and Thill (2003) who emphasize a selection regime that evaluates across a range of storage durations and temperatures to ensure adaptability to a range of storage conditions.

Among the breeding clones and commercial checks in this study, the most favorable genotypes were W6929-1, W6484-5, and W5840-4, which were the top three lines for both mean chip color and P_i (Table 3). Importantly, these lines also demonstrated remarkable Type I stability, in the 90th percentile among the 53 lines. All three were also in the 75th percentile for Type III stability, calculated with Eberhart and Russell (1966) or Shukla's (1972) method.

Among the commercial check varieties used, White Pearl exhibited the best performance. It demonstrated high Type III stability and a low mean chip color but with b_i within one standard deviation of the population-mean regression coefficient, a sign of Type II stability (Table 3). This suggests that White Pearl can be expected to perform predictably within a particular storage regime, but its performance will vary across different storage conditions. Dakota Pearl also demonstrated Type II stability, responding similarly to the various storage environments as the population mean (Fig. 3). The other four commercial check varieties tested ranked in the bottom 25% for performance and Type I stability, including Atlantic and Snowden, cultivars that currently are used extensively in the processing industry (Table 3). The chipping performance observed for Snowden, Dakota Pearl, and Atlantic indicated that chip quality of these varieties is highly influenced by the storage environment. These varieties have been previously classified as Class A chipping varieties that can chip acceptably after 7 mo of storage 5.5°C (Glynn and Sowokinos, 2010, 2011, 2012). Results presented here indicate these varieties do not always exhibit the stable chipping performance of the Class A group. Advanced breeding clones in this study can outperform the industry standards for chip color across a range of storage conditions and can better fit the Class A type. As more stable chipping varieties are developed, the processing industry should benefit from increased flexibility in managing storage regimes and frying schedules as they supply processed potato products to consumers year-round. Robust stability analyses using procedures described here can be essential tools for breeders to better identify the best performing chip clones for the industry.

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References

Affleck, I., J.A. Sullivan, R. Tarn, and R. Yada. 2012. Stability of eight potato genotypes for sugar content and french fry quality at harvest and after storage. Can. J. Plant Sci. 92:87–96. doi:10.4141/cjps2011-066

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

Bernardo, R. 2002. Breeding for quantitative traits in plants. 2nd ed. Stemma Press, Woodbury, MN.

Blum, A. 1988. Plant breeding for stress environments. CRC Press, Boca Raton, FL.

Coffin, R.H., R.Y. Yada, K.L. Parkin, B. Grodzinski, and D.W. Stanley. 1987. Effect of low temperature storage on sugar concentrations and chip colour of certain processing potato cultivars and selections. J. Food Sci. 52:639–645. doi:10.1111/j.1365-2621.1987.tb06692.x

Eberhart, S.A., and W.A. Russell. 1966. Stability parameters for comparing varieties. Crop Sci. 6:36–40. doi:10.2135/cropsci1966.0011183X000600010011x

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

Foot, R.J., N.U. Haase, K. Grob, and P. Gonde. 2007. Acrylamide in fried and roasted potato products: A review on progress in mitigation. Food Addit. Contam. 24:37–46. doi:10.1080/02652030701439543

Gauch, H.G. 1992. Statistical analysis of regional field trials: AMMI analysis of factorial designs. Elsevier, Amsterdam, Netherlands.

Glynn, M., and J. Sowokinos. 2010. Advanced potato breeding clones: Storage and processing evaluation. Valley Potato Grower. 75(199):12–16.

Glynn, M., and J. Sowokinos. 2011. Advanced potato breeding clones: Storage and processing evaluation. Valley Potato Grower. 76(207):8–12.

Glynn, M., and J. Sowokinos. 2012. Advanced potato breeding clones: Storage and processing evaluation. Valley Potato Grower. 77(215):10–14.

Hayes, R.J., and C.A. Thill. 2003. Genetic gain from early generation selection for cold chipping genotypes in potato. Plant Breed. 122:158–163. doi:10.1046/j.1439-0523.2003.00776.x

Haynes, K.G., B.A. Clevidence, D. Rao, B.T. Vinyard, and J.M. White. 2010. Genotype × environment interactions for potato tuber carotenoid content. J. Am. Soc. Hortic. Sci. 135:250–258.

Haynes, K.G., D.R. Wilson, and M.S. Kang. 1995. Genotype × environment interaction for specific-gravity in diploid potatoes. Crop Sci. 35:977–981. doi:10.2135/cropsci1995.0011183X003500040007x

Kang, M.S. 1993. Simultaneous selection for yield and stability in crop performance trials: Consequences for growers. Agron. J. 85:754–757. doi:10.2134/agronj1993.00021962008500030042x

Kang, M.S., and D.P. Gorman. 1989. Genotype × environment interaction in maize. Agron. J. 81:662–664. doi:10.2134/agronj1989.00021962008100040020x

Lin, C.S., and M.R. Binns. 1988. A superiority measure of cultivar performance for cultivar × location data. Can. J. Plant Sci. 68:193–198. doi:10.4141/cjps88-018

Loiselle, F., G.C.C. Tai, and B.R. Christie. 1990. Genetic components of chip color evaluated after harvest, cold storage, and reconditioning. Am. Potato J. 67:633–646. doi:10.1007/BF03043449

Love, S.L., J.J. Pavek, A. Thompson-Johns, and W. Bohl. 1998. Breeding progress for potato chip quality in North American cultivars. Am. J. Potato Res. 75:27–36. doi:10.1007/BF02883514

Mendiburu, F. 2012. agricolae: Statistical procedures for agricultural research. R package version 1.0-9. Institute for Statistics and Mathematics of Wirtschaftsuniversität Wien, Vienna, Austria. http://cran.r-project.org/web/packages/agricolae/index.html (accessed 31 Oct. 2012).

Mottram, D.S., B.L. Wedzicha, and A.T. Dodson. 2002. Acrylamide is formed in the Maillard reaction. Nature 419:448–449. doi:10.1038/419448a

Murphy, S.E., E.A. Lee, L. Woodrow, P. Seguin, J. Kumar, I. Rajcan, and G.R. Ablett. 2009. Genotype × environment interaction and stability for isoflavone content in soybean. Crop Sci. 49:1313–1321. doi:10.2135/cropsci2008.09.0533

Peterson, C.J., A.W. Gromacher, P.S. Baenziger, and R.A. Graybosch. 1992. Genotype and environment effects on quality characteristics of hard red winter wheat. Crop Sci. 32:98–103. doi:10.2135/cropsci1992.0011183X003200010022x

Piepho, H.-P. 1996. Analysis of genotype-by-environment interaction and phenotypic stability. In: M.S. Kang and H.G. Gauch, editors, Genotype by environment interaction. CRC Press, Boca Raton, FL. p. 151–174.

Piepho, H.-P. 1999. Stability analysis using the SAS system. Agron. J. 91:154–160. doi:10.2134/agronj1999.00021962009100010024x

Pringle, B., C. Bishop, and R. Clayton. 2009. Potatoes postharvest. CAB International, Cambridge, MA.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/ (accessed 31 Oct. 2012).

Roe, A.M., R.M. Faulks, and J.L. Belsten. 1990. Role of reducing sugars and amino acids in fry colour of chips from potatoes frown under different nitrogen regimes. J. Sci. Food Agric. 52:207–214. doi:10.1002/jsfa.2740520207

SAS Institute. 2008. SAS for Windows 9.2. SAS Institute, Cary, NC.

Shallenberger, R.S., O. Smith, and R.H. Treadway. 1959. Food color changes: Role of the sugars in the browning reaction in potato chips. J. Agric. Food Chem. 7:274–277. doi:10.1021/jf60098a010

Shukla, G.K. 1972. Some statistical aspects of partitioning genotype-environmental components of variability. Heredity 29:237–245. doi:10.1038/hdy.1972.87

Sowokinos, J.R. 2001. Biochemical and molecular control of cold-induced sweetening in potatoes. Am. J. Potato Res. 78:221–236. doi:10.1007/BF02883548

Tai, G.C.C., and W.K. Coleman. 1999. Genotype × environment interaction of potato chip color. Can. J. Plant Sci. 79:433–438. doi:10.4141/P98-109

Thill, C.A., and S.J. Peloquin. 1995. A breeding method for accelerated development of cold chipping clones in potato. Euphytica 84:73–80. doi:10.1007/BF01677559

USDA Economic Research Service. 2012. Vegetables and pulses data: Potatoes. USDA Economic Research Service, Washington, DC. http://www.ers.usda.gov/topics/crops/vegetables-pulses/potatoes.aspx (accessed 9 Nov. 2012).

Weihs, C., U. Ligges, K. Luebke, and N. Raabe. 2005. klaR: Analyzing German business cycles. In: D. Baier, R. Decker, and L. Schmidt-Thieme, editors, Data analysis and decision support. Springer-Verlag, Berlin, Germany. p. 335–343.