Stability of Expression and Concentration of Ascorbic Acid in North American Potato Germplasm

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Additional index words. Solanum tuberosum, vitamin C, biplot analysis

Abstract. Ascorbic acid (vitamin C) is an essential nutrient in the human diet and potatoes are a valuable source. As a first step in breeding for potatoes (Solanum tuberosum L.), with higher levels of ascorbic acid, 75 clones from 12 North American potato-breeding programs were evaluated for concentration, and 10 of those for stability of expression. Trials were grown in Idaho, Oregon, and Washington in 1999 and 2000, tubers sampled, and ascorbic acid quantified. There were significant differences among clones and clone by environment interaction was also significant. Concentration of ascorbic acid of the clones was continuously distributed over a range of 11.5 to 29.8 mg/100 g. A subgroup of 10 clones was analyzed using an additive main effects and multiplicative interaction (AMMI) model, to diagnose interaction patterns and measure clone stability. The first two principal component axes accounted for over 80% of the variability. Bi-plot analysis showed ‘Ranger Russet’ to be highly unstable across the environments tested. A plot of Tai’s stability statistics found six of the 10 clones to be stable for ascorbic acid expression. Appropriate evaluation methods for ascorbic acid concentration must involve multi-year testing.

Ascorbic acid is important in the human diet as an essential vitamin and as an antioxidant. Potatoes are a valuable source of ascorbic acid for people living in the United States. A single 148-g uncooked potato provides 45% of the average adult Daily Value of ascorbic acid (Pennington and Wilkening, 1997). This is a lower value than for such fruits and vegetables as bell peppers (Capsicum annum L.), cabbage (Brassica oleracea L.), broccoli (Brassica oleracea L.), strawberries (Fragaria xananasana Duch.), and kiwifruit [Actinidia delicosa (A.Chev) Liang and Ferguson], but compares favorably with tomatoes (Lycopersicon esculentum Mill.) and most citrus (Citrus sp.) fruits, and is higher than for most other common commodities (Pennington and Wilkening, 1997). Given the high consumption rate for potatoes, 180 g per day in the United States in 1999 (National Potato Council, 2001), potatoes are one of the most important sources of ascorbic acid in the human diet.

Cooking reduces the nutritive value of potatoes and has a direct impact on the ascorbic acid concentration in consumed foods. Analysis of ascorbic acid in potato after various methods of preparation has been the subject of numerous studies. Published reten-

Acknowledgments. The authors would like to thank the following respondents for parental breeding stocks. Requests for parental breeding stocks were made to all major public breeding programs in North America with the intent of sampling the most commonly used genetic resources. Each breeder was asked for predominantly utilized parental clones (commonly used term in pota-

tatoes for both released cultivars and breeding germplasm) from their program. Respondents included breeders in Colorado (submitted 5 clones for evaluation), Idaho (U.S. Dept. of Agriculture, Agricultural Research Service USDA/ARS1) (6), Maine (5), Maryland (USDA/ARS) (5), Michigan (5), Minnesota (6), New Brunswick (6), New York (5), North Dakota (7), Texas (2), and Wisconsin (5). Fourteen additional clones were obtained from the USDA/ARS Germplasm Enhancement program in Wisconsin. Also, four clones,
Tubers used for ascorbic acid measurements were produced in trials grown at Aberdeen, Idaho; Corvallis, Ore.; and Othello, Wash., in 1999 and 2000. Each trial within a site consisted of two replications of five hills, arranged as a randomized complete block. Cultural practices at each location were typical of those used by local producers.

Five tubers from each plot were harvested at each location were typical of those used by local producers.

Table 1. Average ascorbic acid concentration in tubers of 75 clones collected from North American potato breeding programs.

| Cultivar          | Conc (mg/100 g) | Contributing program | Cultivar          | Conc (mg/100 g) | Contributing program |
|-------------------|-----------------|----------------------|-------------------|-----------------|----------------------|
| ND4027-4          | 29.8            | ND                   | ND2225-1R         | 19.6            | ND                   |
| Ranger Russet     | 29.4            | ID                   | Red Companion     | 19.5            | WI                   |
| Yukon Gold        | 29.3            | MI                   | Durango Red       | 19.2            | CO                   |
| Russet Nugget     | 28.7            | TX                   | MN17922           | 19.1            | MN                   |
| A85331-16 (control) | 28.6           | ID                   | EB8109-1          | 19.0            | ME                   |
| Silverton Russet  | 27.0            | O                    | Snowden           | 18.8            | WI                   |
| W1313             | 27.0            | WI                   | WH10392           | 18.8            | WIG                  |
| MN17993           | 26.9            | MN                   | NY115             | 18.5            | NY                   |
| Avon              | 26.5            | MD                   | BO607-33          | 18.4            | MD                   |
| AC87079-3         | 26.3            | CO                   | NY121             | 17.7            | NY                   |
| MN18142           | 26.3            | MN                   | Dakota Rose       | 17.6            | ND                   |
| WH1327            | 26.2            | WIG                  | WH10411           | 17.4            | WIG                  |
| Gem Russet        | 26.1            | ID                   | NY123             | 17.0            | NY                   |
| Shepody           | 25.5            | NB                   | USDA41956         | 16.9            | MD                   |
| F65089            | 25.5            | NB                   | W1099Russ         | 16.8            | WI                   |
| BO692-2           | 25.4            | MD                   | Spartan Pearl     | 16.6            | MI                   |
| Chipeta            | 25.3            | ID                   | W1242             | 16.6            | WI                   |
| Jacqueline Lee    | 23.5            | MI                   | F95203            | 15.8            | NB                   |
| A86102-6          | 23.5            | ID                   | WH10276           | 15.7            | WIG                  |
| AF522-5           | 23.4            | ME                   | WH10214           | 15.7            | WIG                  |
| F73068            | 23.4            | NB                   | B1065-61          | 15.6            | MD                   |
| ND5256-7R         | 23.4            | ND                   | S440              | 15.3            | MN                   |
| Eva               | 23.0            | NY                   | WH10213           | 15.3            | WIG                  |
| MN18714           | 22.9            | MN                   | MSG227-2          | 15.0            | MI                   |
| ND24470-7         | 22.3            | ND                   | Cherry Red        | 14.9            | CO                   |
| MSB076-2          | 22.1            | MI                   | WH10438           | 14.5            | WIG                  |
| WH1325            | 22.1            | WIG                  | WH1302            | 14.5            | WIG                  |
| W1321             | 21.8            | WIG                  | CS7324-4          | 14.3            | ME                   |
| Dakota Pearl      | 21.6            | ND                   | WH10470           | 13.9            | WIG                  |
| Ivory Crisp       | 21.4            | ID                   | S438              | 13.7            | MN                   |
| W20136            | 20.0            | ME                   | A79141-3 (control)| 13.3            | ID                   |
| F66041            | 20.7            | NB                   | WH10469           | 13.0            | WIG                  |
| WH10234           | 20.1            | WIG                  | A8792-11 (control)| 11.5            | ID                   |
| A84118-3          | 20.0            | ID                   |                   |                 |                      |

The ANOVA of the multiplicative interaction was completed and principal component analyses (PCA) performed. In addition, biplot analysis of the G × E interaction was used to interpret the underlying structure (Bradu and Gabriel, 1978; Gabriel, 1971; Zobel et al., 1988). Scaling of the PCA axes was achieved by multiplying each axis by the square root of its respective singular value. Finally, genotypic stability and range of performance was assessed using Tai’s (1971) regression-based procedures.
Variance analysis revealed a highly significant genotype effect for ascorbic acid concentration among the 75 clones, a highly significant environment effect among the six location/years, and a highly significant genotype × environment interaction among clones. The concentration for clones within each of the other eleven breeding programs ranged from relatively high levels of ascorbic acid to relatively low. The similarity of ascorbic acid concentration of breeding clones from one program to another is not surprising because public breeders have not systematically selected for higher levels. However, it appears that every program has parental germplasm that may be useful for improving ascorbic acid concentration.

The WIG clones represent a unique grouping among those evaluated. They consist of hybrids or progeny of hybrids of Solanum tuberosum ssp. tuberosum crossed with a variety of wild species, including Solanum tuberosum ssp. andigena, S. raphanifolium, S. sucrensis, S. acaule, S. albicans, S. gourlayi, S. brevidens, S. chacoense, S. boliviense, S. tarijense, and S. phureja. Fourteen of these hybrid-derived clones were evaluated—a higher number than from any other program. A wide range of species-related materials were included with intent to determine whether any of these wild species have potential to contribute genes for high ascorbic acid to the cultivated potato germplasm base. As a group, these clones were lower in ascorbic acid than their domestic counterparts, with a breeding program average of 17.2 mg/100 g. Ten of the 14 clones were below the median of the 75 clones evaluated, and only one (WH1327) was in the top third. Although this group of species-derived germplasm is small, these results suggest that genes for high ascorbic acid concentration are not common among the related wild species used to create these hybrids.
Screening provided evidence for genetic variability for ascorbic acid concentration among North American clones. Theoretically, this should provide the potential to intercross superior parents, select appropriate new gene combinations, and hopefully identify progeny populations with transgressive individuals.

**GxE analysis.** The contribution to variance for genotype, environment, and the GxE interaction within the subset of 10 clones is found in Table 4. The largest contributor to variance in the ANOVA model was genotype with 56% of the total sums of squares. This was twice as high as the contribution of environment, with 29%. There was also a significant GxE interaction, although the amount of variation attributed to the interaction was only 10% of the total. This variance structure provides some critical insights into possible breeding behavior of the ascorbic acid trait. Because the largest proportion of the variation is due to genotype, heritability of this trait is probably high and good breeding progress can be expected. This was confirmed by a computation of broad sense heritability, based on the ANOVA. For this subset of 10 clones the heritability was 0.92. This estimate of heritability is likely inflated by the inclusion of high and low concentration clones in the subset. For the entire group of 75 clones, the broad sense heritability was 0.71.

The low contribution of the GxE interaction also lends itself to a conclusion that selection within an environment will probably be effective. But, the fairly high contribution of environment indicates that multiple evaluations over different environments will be needed to accurately quantify ascorbic acid.

Using the AMMI model, the GxE interaction was decomposed into five components (Table 5). The first two components accounted for 81% of the variability in the model, and therefore, only these two were retained. AMMI biplots are shown in Figs. 1 and 2. In Fig. 1, PCA axis 1 is plotted against PCA axis 2, for clones and environments. Clones and environments that have small interactions will appear close to the center of the axes. A79141-3, ‘Yukon Gold’, and ‘Ivory Crisp’, for example, had small interaction effects, while ‘Ranger Russet’ showed the strongest interaction effect of all clones included in the analysis.

The direction of each point from the axes’ center provides important information about the nature of the interaction. When a clone and environment are located on opposite sides of the center, such as with ‘Ranger Russet’ and OR99, it indicates their contributions are opposing to the interaction. In other words, they are negatively correlated. In contrast, ‘Krantz’, ‘Snowden’, ‘Cherry Red’, and A8792-11 are in the same direction as WA99, indicating a positive contribution to the interaction and that these clones should perform well in that environment. The trial locations, as a component of the environments, were not consistent with respect to their direction from the center of the axes.

Fig. 2 depicts PCA axis 1 plotted against average ascorbic acid concentration for all clones and environments. This plot demonstrates that both clones and environments contributed to the variability in the model. In this plot, clones and environments that appear close to the horizontal line, where PCA axis 1 is 0, contribute less to the interaction and are considered more stable. ‘Ranger Russet’ again shows a distinct lack of stability, and ‘Yukon Gold’ and ‘Ivory Crisp’ demonstrate stability. The locations OR99, WA99, ID00, and OR00 show high contributions to the interaction, indicating considerable environmental variation. This suggests that wide environmental variability, and differential response of cultivars, should be anticipated during the process of screening progeny and breeding for elevated levels of ascorbic acid.

Groupings above or below the center line can reveal underlying reasons for the variance structure. In this case, there was no strong pattern with respect to locations, indicating that none of the evaluation sites consistently contribute more to the variability than any other. However, there was a strong pattern with respect to years. The 1999 trials were all grouped below the axis and all but the Washington site in 2000 (which was nearly on the axis) was grouped above the axis. This suggests that year contributes heavily to the GxE interaction and that evaluation across years may be more important for quantifying ascorbic acid than evaluation across locations.

There was a strong agreement between the AMMI biplots and the results of the distribution of Tai’s stability statistics (Fig. 3). For this type of plot, the clones between the two vertical lines and within the parabolic curve (α = 0) are considered to be relatively stable. ‘Ranger Russet’ and A8792-11 showed strong tendencies for instability, lying outside of both bounds. But, the fairly high contribution of environment indicates that multiple evaluations over different environments will be needed to accurately quantify ascorbic acid.

![Biplot](image)

**Fig. 2.** Biplot of principal component analysis (PCA) axis 1 vs. mean ascorbic acid concentration in tubers of 10 selected potato clones grown in Idaho, Oregon, and Washington in 1999 and 2000.

![Diagram](image)

**Fig. 3.** Distribution of Tai’s stability statistics for tuber ascorbic acid concentration of 10 selected potato clones grown in Idaho, Oregon, and Washington in 1999 and 2000. The hyperbola represents a 95% confidence interval for λ = 0; the vertical lines are 95% confidence intervals for λ = 1.
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‘Krantz’, ‘Chipeta’, and A79141-3 were marginally unstable. ‘Yukon Gold’, A85331-16, ‘Ivory Crisp’, ‘Cherry Red’, ‘Snowden’, and ‘Krantz’ showed the best overall relative stability. Biological or morphological differences among the clones that could help explain the basis for stability could not be identified. It did not appear to be related to stress tolerance, maturity class, vine size, or any other obvious plant characteristic (data not presented).

The AMMI analysis demonstrates that these clones differ, not only for ascorbic acid concentration, but also for stability of expression across environments. If a consistently high level of ascorbic acid is to be achieved, both level and stability of expression are important considerations.

From the results of this study, several conclusions concerning the breeding behavior of ascorbic acid can be made: 1) there is adequate variability within North American germplasm to expect the presence of suitable genes to breed for higher ascorbic acid content in potato tubers; 2) North American potato germplasm expresses diversity for stability of expression for ascorbic acid and progeny families derived from this germplasm is likely to do the same; 3) given a high genotype variance, combined with a low G × E interaction and high broad sense heritability, rapid breeding progress can be expected if suitable parents are used; 4) selection within a single location should provide adequate breeding progress; and 5) AMMI analysis suggests that years may be more important than locations in explaining variability and multi-year evaluations are important to properly quantify ascorbic acid.

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