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# Genotype by Environment Interaction Effects on Starch Content and Digestibility in Potato (*Solanum tuberosum* L.)

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**ABSTRACT:** Biochemically, starch is composed of amylose and amylopectin but can also be defined by its digestibility rates within the human intestinal tract, i.e., rapidly digested (RDS), slowly digested (SDS), or resistant (RS). The relative ratio of these starch components is the main contributor to differences in the glycemic index (GI) of carbohydrate sources. This study evaluated the digestible starch profile of 12 potato genotypes comprising elite breeding lines and commercial varieties in six environments, with the optimal profile defined as low RDS and high SDS. Genotype by environment interaction (GEI) analysis found significant ($p = 0.05$) genotypic and environmental effects for all digestibility rate components; however, interaction effects were only significant for SDS. Optimal starch profiles were identified for two genotypes, CV96044-3 and Goldrush. The desirable starch profile in these potato cultivars can be exploited in breeding programs for the improvement of starch profile and other important characteristics such as high yields and disease resistance.

**KEYWORDS:** *starch, rapidly digestible starch, resistant starch, biplot, genotype by environment interaction, stability*

## INTRODUCTION

The potato is the third most important food crop in the world[1,2] and a rich source of carbohydrates.[3] Throughout the growing season, the plant translocates sugars produced from photosynthesis to the tubers.[4] The sugars move into the tuber and are incorporated into chains of starch, either as the straight chain amylose or branched chain amylopectin.[5]

The process of starch accumulation is expected to be profoundly dependent on the genotype and environmental conditions. Similar to other important agronomic traits, genotype (G), environment (E), and genotype by environment interaction (GEI) effects can be important to understanding the biochemistry and physiology behind starch development. GEI are common for multigene traits, such as starch content, and are important to understanding underlying sources of variation. Temperature, pH, and nutrient levels are important for maintaining plant health and subsequent starch accumulation (yield) throughout the growing season.[6] Yamaguchi et al.[7] found a positive relationship between tuber growth and starch accumulation. Optimal temperatures for tuber bulking and starch content in tubers were established between temperatures of 15 and 21 °C. Higher yields were found in potato plants that experienced short days and cool night temperatures compared to long days and warm nights.[8] Short days with warm night temperatures produced low yields, indicating the importance of temperature on tuber formation and, subsequently, starch accumulation.[9] Ingram and McCloud[10] found temperatures of 14−16 °C to be optimal for tuber formation.

Soil type and moisture levels affect soil temperature and starch content. Kincaid et al.[11] found that sprinkler irrigation used to mitigate unfavorable soil temperatures can result in higher yields and greater starch content. Soil type can affect water availability and plant productivity.[12] Clay soils have the greatest water holding capacity, followed by silt, loam, and sand soils.

Amylopectin typically makes up 70−80% of the available starch in the tuber,[13] with the remaining being amylose. The ratio of amylopectin and amylose is under enzymatic control. One enzyme, granule-bound starch synthase (GBSS), is responsible for amylose production and at least six enzymes are involved with amylopectin production, accounting for the greater abundance of amylopectin. Amylopectin has four starch synthase (SS) enzymes (named SS I−IV) and at least two branching enzymes (BEs). In addition to these enzymes, GBSS is also able to elongate amylopectin chains.

A different suite of enzymes control starch degradation.[5] There are three enzymes that work in concert to break down straight chain starches: $\alpha$-amylase, $\beta$-amylase, and $\alpha$-glucosidase. There are also debranching enzymes to break down branch points in amylopectin. Not only is amylose more difficult to degrade than amylopectin, there are more enzymes working on the degradation of amylopectin than amylose, contributing to differences in digestion rate of these two starch fractions. The tightly coiling of amylose creates resistance to breakdown.[5]

In the human diet, the effect of a starch rich food like potato is measured by the glycemic index (GI).[14] The GI is a measure of the body's blood sugar level in response to ingested carbohydrates. It is measured by monitoring blood glucose

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levels for a three-hour period after ingestion. The GI value of the tested food is expressed as a percentage of a standard food product (glucose). A higher GI value presents a more rapid entry of a larger quantity of glucose from test food into the bloodstream. The blood sugar response to the food we eat is pivotal to intestinal health and weight gain in later life. Research has linked high GI foods to type II diabetes mellitus (TIIDM) and other chronic heart issues.[15−18] Lowering the GI in our diet has been shown to increase weight loss, improve blood pressure, and decrease risk of cardiovascular disease.[19,20] Nutritionists often recommend foods to help moderate blood sugar levels to lower the risks of adverse health conditions.

The concept of carbohydrate digestion and GI invokes a classification system that is different from quantifying amylose and amylopectin content. Starch can also be classified by levels of digestibility.[21] In this classification, starch can be broken down into three components: rapidly digestible (RDS), slowly digestible (SDS), and resistant (RS) starch. RDS and SDS represent the portion of starch digested within the first 20 min and 21−120 min postingestion, respectively. All remaining starches (RS) are undigested until they reach the large intestine. Because of the resistant structure of amylose, more of the RS component is expected to be composed of amylose rather than amylopectin. The rapid breakdown of amylopectin molecules means it is more prevalent in RDS and SDS fractions. The rate of digestibility of starch has been termed the "digestible starch profile".[21]

Because of public concern of high GI level foods and potential health implications, it is important to produce a potato genotype with a specific and stable starch profile compatible with lower GI foods. GEI effects have strong implications on heritability and the ability to breed and select for superior genotypes.[22] Field evaluation over time at several locations is important for distinguishing repeatable and nonrepeatable GEI effects.[23] Without GEI analysis, it would be difficult to make positive gains in selection.[24] The key to the development of new genotypes is the stability in genotypic response, which can be defined three ways: static, dynamic, and residual mean square regression.[25] In scenarios where GEI are prominent, dynamic stability is most commonly observed where genotypic responses parallel the environmental responses. Dynamic stability stems from the ability to adjust to environmental conditions and is commonly used in breeding programs for production gains.[26]

Six environments (three locations over two years) and 12 genotypes (eight advanced breeding lines and four commercially available cultivars) were examined in this study. The breeding lines were selected based on preliminary fiber analysis exemplifying higher fiber content.[27] Some breeding lines also had previous sensory perception data on texture after cooking, which was predicted to correspond to different starch profiles.

Ultimately, the goal is to develop potato genotypes with suitable digestible starch profiles with low RDS content and higher SDS or RS content which is referred to as the "best profile". For health issues, the total starch (TS) value is not as important as the profile of starch components, but the higher the TS, the more valuable the potato because of the increase in dry matter. Examining the G, E, and GEI effects will assist in the development of potatoes with better starch profiles. The addition of a new cultivar of potato to the commercial marketplace with improved starch profile allows for greater choice and flexibility for consumers when choosing produce that contributes to a healthier diet. This study had the following objectives: (i) to elucidate the starch profile of potato genotypes, (ii) to determine the stability, G, E, and GEI effects for starch components, and (iii) to relate starch profile to GI and human health.

## MATERIALS AND METHODS

The six environments have been previously described in Bach et al.[28] The six environments were located in southern Ontario in 2009 and 2010 and had different temperature profiles, precipitation patterns, and soil types. Simcoe exhibited hotter and dryer conditions with poor moisture retaining soils. Elora had moderate temperatures and precipitation with silt loam soils. Alliston represented close to optimal conditions for potato production, with moderate temperatures, regular irrigation, and silt loam soils: a soil type with good moisture holding capacity. The trials were arranged in a randomized complete block design (RCBD) with 12 potato genotypes and four replications. Of the 12 genotypes, eight were elite breeding lines and four were commercial varieties. The breeding lines were selected for their high fiber qualities at the Potato Research Centre in Fredericton, New Brunswick, and the Lethbridge Research Centre, Alberta, Canada. The genotypes were: CV96044-3, FV12272-3, WV5475-1, F03031, F05035, F04037, F05081, F05090, Atlantic, Goldrush, Norland, and Russet Burbank. Following harvest, the potatoes samples were prepared by boiling, freezing, freeze-drying, and milling with a 1 mm sieve to produce fine potato flour for starch analysis.

**Safety.** All starch analysis required lab coat, gloves, and eye protection to perform. Some chemicals used were hazardous when exposed, and relevant precautions were taken (i.e., fumehood) to ensure safe handling.

**Digestible Starch Analysis.** Digestible starch measurements were made using the Englyst et al.[21] method scaled to 100 mg samples with minor modifications. Guar gum was not added. Tubes were equilibrated with 0.5 M sodium acetate buffer (pH 5.2), and the water bath had a speed of 200 strokes per minute. Starch digestions were stopped in 1.0 mL of 50% ethanol with a further dilution of 3.0 mL of $ddH_2O$ before centrifugation. Incubation with glucose oxidase peroxidise (GOPOD) reagent was conducted at 37 °C for 10 min, and absorbance values were read at 540 nm.

Taking into account the adjustment for glucose to anhydro-glucose conversion that occurred in the starch samples, the following equation was used to convert the absorbance into a percentage of the total dry weight of each sample (eq 1).

$$\frac{\text{sample abs}_{540} - y\text{intercept}}{\text{slope}} \times \frac{5}{0.1} \times \frac{4.1}{0.1} \times \frac{1}{1000} \times \frac{100}{\text{sample weight} \times \text{dry matter}} \times \frac{162}{180} \quad (1)$$

**Total Starch (TS) Analysis.** TS was calculated using an in-house protocol modified from the Megazyme Total Starch Kit (Megazyme, AA/AMG). The protocol follows the American Association for Clinical Chemistry (AACC) Method 76.13 and the Association of Official Agricultural Chemists (AOAC) Official Method 996.11. Tubes were incubated in boiling water for 12 min, and centrifugation was done at 5000 rpm for 10 min. GOPOD incubation was conducted at 37 °C for 10 min before taking absorbance values at 540 nm.

Taking into account the adjustment for free glucose to anhydro-glucose that occurred in the starch samples, the following equation was used to convert absorbance into a percentage of the total dry weight of each sample (eq 2).

$$\text{sample abs}_{540} \times \frac{50}{50\ \mu\text{g glucose abs}_{540}} \times \frac{100}{0.1} \times \frac{1}{1000} \times \frac{50}{\text{sample weight} \times \text{dry matter}} \times \frac{162}{180} \quad (2)$$

**Statistical Analysis.** Data was analyzed in SAS v9.2[29] using the general linear model procedure to partition variances into an analysis of variance (ANOVA) and Spearman correlative statistics.[30] The

independent location/year combinations were classified as individual environments. The mean of duplicate samples were used for SAS analysis. The treatment effect was divided into three components: G, E, and GEI effects by the following equation:

$$Y_{ijk} = \mu + \alpha_i + b_j + \alpha b_{ij} + \beta_{jk} + \varepsilon_{ijk} \quad (3)$$

where $Y_{ijk}$ is the average value of the dependent variable of genotype $i$ in environment $j$ in the $k$th block, $\mu$ is a common value to all data points, $\alpha_i$ is the effect of the $i$th genotype. $b_j$ is the effect of the $j$th environment, $ab_{ij}$ is the effect of the $i$th genotype by the $j$th environment, $\beta_{jk}$ is the block effect at the $j$th environment in the $k$th block, and $\varepsilon_{ijk}$ is the residual error term.

Stability analysis was performed with the GGE biplot analysis software from Yan et al.[31] The GGE biplot model is as follows:

$$Y_{ij} = \mu + \beta_j + \lambda_1\xi_{i1}\eta_{1j} + \lambda_2\xi_{i2}\eta_{2j} + \varepsilon_{ij} \quad (4)$$

where $Y_{ij}$ is the average value of the dependent variable of genotype $i$ in environment $j$. $\beta_j$ is the average value of the dependent variable of environment $j$. $\lambda_1$ and $\lambda_2$ are the singular values of the first and second largest principal components: PC1 and PC2. $\xi_{i1}$ and $\xi_{i2}$ are the eigenvectors for PC1 and PC2 of genotype $i$. $\eta_{1j}$ and $\eta_{2j}$ are the eigenvectors for PC1 and PC2 of environment $j$. All remaining effects for genotype $i$ in environment $j$ fall into the residual term $\varepsilon_{ij}$.

Biplots were assembled as described by Yan and Kang[26] and constructed using the GGE biplot software.[31] The biplot is a visual representation of stability and stability parameters. Each biplot displays primary and secondary effects, also called the principal component 1 (PC1) and 2 (PC2). PC1 and PC2 represent the G and GEI, respectively. G effects are on the $x$-axis and represent the mean performance of the trait for each genotype. GEI effects on the $y$-axis represent the stability and genotypic adaptation to environments.[31] Highest mean values fall on the positive end of PC1, and lowest mean values have negative values. For all traits, high stability factor is a valuable quality. High stability across environments is reflected in a small PC2. Genotypes that are stable over all environments fall very close to the PC2 origin, while genotypes that are highly variable are on the extreme positive or negative ends of PC2.

Relationships between locations are visualized by the angle between their vectors.[26] The correlation coefficient is represented by the cosine of the angle between vectors. Small angles have positive correlations nearing $r = 1$, right angles have no correlation, and angles approaching 180° have negative correlations nearing $r = -1$.

## RESULTS AND DISCUSSION

**Total Starch (TS).** The significant E (location × year) effect warranted further analysis (Table 1) and is displayed visually on the biplot (Figure 1). The location vectors had different directions and the orders for 2009 and 2010 were different, explaining the location × year interaction effects. There were two causes for the significant location × year effect for TS. First, there was a greater range of values in 2010 compared to 2009 (Table 2). Second, although most starch values exhibited change over a small range (83−89%), the superior genotypes changed in different environments. Alliston showed a significant increase in TS values from 2009 to 2010 ($p$ = 0.0012). Of the three locations, Elora had significantly higher TS values compared to Simcoe and Alliston ($p$ = 0.0399) in both years. A larger range of TS values would be an indication of higher variability in starch components. Biplot analysis separated the six environments into three clusters (Figure 1). The inability to repeat TS performance in locations over time highlights the significance of the location × year effect.

Of the 12 genotypes, CV96044-3 and WV5475-1 had the highest TS values (90.2 and 88.0%, respectively) and high stability, especially compared to genotypes like F05035 and F03031 (87.2 and 86.1%, respectively) (Figure 1). Norland had below average TS levels and was highly variable across the six environments. The biplot aligns Norland with environment Simcoe 2009, indicating its narrow adaptability to that specific environment. CV96044-3 and WV5475-1 clustered together with Simcoe 2010, Alliston 2009, and Elora 2009, indicating these environments behaved similarly and these two genotypes

**Table 1. Analysis of Variance for Total Starch, Rapidly Digestible Starch, Slowly Digestible Starch and Resistant Starch from 12 Potato Genotypes Grown at Six Environments[a]**

| | | sums of squares | | | |
|---|---|---|---|---|---|
| source | *df* | total starch | rapidly digestible starch | slowly digestible starch | resistant starch |
| environment | 5 | 518** | 518** | 12.0** | 1290** |
| location | (2) | 142 | 18.4** | 2.63 | 91.1 |
| year | (1) | 16.1 | 473** | 9.10** | 844 |
| location × year | (2) | 366** | 25.4** | 0.24 | 354** |
| block (environment) | 18 | 1660** | 82.4** | 20.3* | 1940** |
| genotype | 11 | 521 | 67.8** | 13.5* | 639 |
| environment × genotype | 55 | 1550 | 30.2 | 38.4 | 1630 |
| location × genotype | (22) | 514 | 9.45 | 12.7 | 571 |
| year × genotype | (11) | 505 | 10.7 | 8.34 | 479 |
| location × year × genotype | (22) | 523 | 9.67 | 17.5 | 572 |
| $R^2$ | | 0.41 | 0.90 | 0.43 | 0.45 |

[a] *,** denotes significant at $p$ = 0.05 and $p$ = 0.01, respectively.

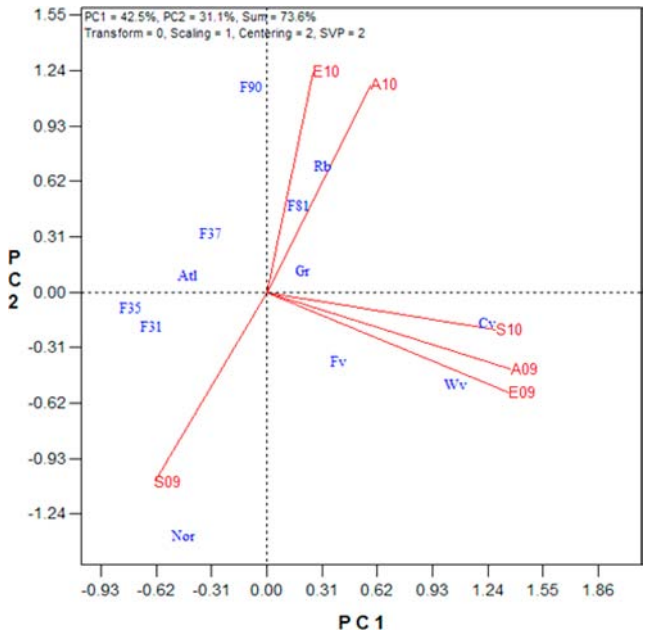


**Figure 1.** GGE biplot for total starch (TS). Locations include Simcoe 2009 (S09), Elora 2009 (E09), Alliston 2009 (A09), Simcoe 2010 (S10), Elora 2010 (E10), and Alliston 2010 (A10). Genotypes include CV96044-3 (Cv), FV12272-3 (Fv), WV5475-1 (Wv), F03031 (F31), F05035 (F35), F04037 (F37), F05081 (F81), F05090 (F90), Atlantic (Atl), Goldrush (Gr), Norland (Nor), and Russet Burbank (Rb).


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Table 2. Least Square Means of Total Starch (TS), Rapidly Digestible Starch (RDS), Slowly Digestible Starch (SDS), and Resistant Starch (RS) from 12 Potato Genotypes Grown at Six Environments Expressed on a Percent Dry Weight Basis[a]

| | Simcoe 2009 | | | | Simcoe 2010 | | | |
|---|---|---|---|---|---|---|---|---|
| genotype | TS (%) | RDS (%) | SDS (%) | RS (%) | TS (%) | RDS (%) | SDS (%) | RS (%) |
| CV96044-3 | 88.3a* | 8.8a | 2.8a | 76.8a | 94.8a | 5.5a | 1.8a | 87.5a |
| FV12272-3 | 88.0a | 9.4a | 2.3a | 76.3a | 91.3a | 5.5a | 1.3a | 84.5a |
| WV5475-1 | 87.0a | 10.3a | 1.2a | 75.5a | 91.9a | 6.7a | 1.6a | 83.6a |
| F03031 | 88.7a | 8.9a | 2.1a | 77.7a | 82.2a | 6.7a | 1.5a | 74.0a |
| F05035 | 89.3a | 10.3a | 1.4a | 77.6a | 87.0a | 6.3a | 1.8a | 78.9a |
| F04037 | 86.9a | 11.0a | 2.0a | 74.0a | 81.6a | 7.5a | 1.3a | 72.8a |
| F05081 | 87.4a | 9.3a | 2.1a | 75.9a | 88.2a | 6.7a | 1.7a | 79.8a |
| F05090 | 86.4a | 9.5a | 1.9a | 75.1a | 83.3a | 6.4a | 1.6a | 75.3a |
| Atlantic | 88.3a | 9.3a | 2.6a | 76.4a | 85.4a | 6.0a | 1.7a | 77.6a |
| Goldrush | 88.1a | 8.8a | 2.9a | 76.4a | 84.5a | 5.8a | 1.8a | 76.9a |
| Norland | 89.2a | 9.7a | 1.7a | 77.8a | 82.7a | 6.0a | 1.3a | 75.4a |
| Russet Burbank | 87.0a | 10.6a | 1.2a | 75.1a | 87.5a | 6.5a | 1.5a | 79.5a |
| ***mean*** | ***87.9*** | ***9.7*** | ***2.0*** | ***76.2*** | 86.7 | 6.3 | 1.6 | 78.9 |
| | Elora 2009 | | | | Elora 2010 | | | |
| genotype | TS (%) | RDS (%) | SDS (%) | RS (%) | TS (%) | RDS (%) | SDS (%) | RS (%) |
| CV96044-3 | 90.7a | 8.7a | 1.6a | 80.3a | 90.5a | 7.2b | 1.3ab | 82.0a |
| FV12272-3 | 89.3a | 9.4a | 1.9a | 78.0ab | 88.4a | 7.2b | 1.6ab | 79.6a |
| WV5475-1 | 89.8a | 10.4a | 1.0a | 78.5ab | 84.7a | 8.1ab | 1.2b | 75.6a |
| F03031 | 88.1a | 9.7a | 1.1a | 77.3ab | 87.1a | 7.9ab | 1.4ab | 77.9a |
| F05035 | 87.9a | 10.2a | 2.1a | 75.6b | 88.3a | 8.6a | 0.7b | 79.0a |
| F04037 | 88.8a | 9.9a | 1.4a | 77.5ab | 87.8a | 8.1ab | 1.4ab | 78.3a |
| F05081 | 88.7a | 9.2a | 2.7a | 76.8ab | 91.0a | 6.9b | 1.5ab | 82.6a |
| F05090 | 88.2a | 8.8a | 2.3a | 77.1ab | 90.1a | 7.9ab | 1.2b | 81.0a |
| Atlantic | 88.5a | 9.2a | 2.5a | 76.9ab | 90.2a | 7.5ab | 1.2b | 81.5a |
| Goldrush | 89.1a | 9.3a | 1.6a | 78.1ab | 85.8a | 7.2b | 1.1b | 77.6a |
| Norland | 89.0a | 9.8a | 1.3a | 78.0ab | 79.8a | 7.5ab | 1.5ab | 71.1a |
| Russet Burbank | 88.7a | 9.8a | 1.4a | 77.5ab | 90.1a | 7.6ab | 2.7a | 79.8a |
| ***mean*** | ***88.9*** | ***9.5*** | ***1.7*** | ***77.6*** | ***87.8*** | ***7.6*** | ***1.4*** | ***78.8*** |
| | Alliston 2009 | | | | Alliston 2010 | | | |
| genotype | TS (%) | RDS (%) | SDS (%) | RS (%) | TS (%) | RDS (%) | SDS (%) | RS (%) |
| CV96044-3 | 85.5a | 8.3a | 1.7a | 75.5a | 91.4a | 6.1a | 1.6a | 83.7a |
| FV12272-3 | 85.1a | 9.4a | 1.8a | 74.0a | 84.3a | 5.8a | 2.1a | 76.4a |
| WV5475-1 | 86.1a | 9.8a | 1.4a | 74.8a | 87.3a | 8.2a | 1.1a | 77.9a |
| F03031 | 84.5a | 9.1a | 1.8a | 73.6a | 85.7a | 6.9a | 1.0a | 77.9a |
| F05035 | 83.8a | 10.6a | 1.1a | 72.1a | 86.8a | 7.1a | 1.4a | 78.3a |
| F04037 | 84.3a | 10.3a | 2.6a | 71.4a | 87.3a | 7.2a | 1.7a | 78.4a |
| F05081 | 84.7a | 9.5a | 2.0a | 73.1a | 89.3a | 6.7a | 1.8a | 80.9a |
| F05090 | 84.5a | 9.1a | 1.9a | 73.5a | 94.5a | 7.1a | 1.4a | 86.1a |
| Atlantic | 84.1a | 8.6a | 2.5a | 73.0a | 85.1a | 7.0a | 1.6a | 76.6a |
| Goldrush | 85.2a | 8.7a | 1.3a | 75.2a | 94.9a | 6.5a | 1.4a | 87.0a |
| Norland | 84.8a | 9.7a | 1.3a | 73.9a | 82.2a | 6.8a | 1.5a | 73.8a |
| Russet Burbank | 85.0a | 10.0a | 2.0a | 73.0a | 92.9a | 7.4a | 1.2a | 84.3a |
| ***mean*** | ***84.9*** | ***9.4*** | ***1.8*** | ***73.6*** | ***88.4*** | ***6.9*** | ***1.5*** | ***80.1*** |

[a]*Means with the same letters within a column and location are not significantly different at $p = 0.05$ based on a Tukey's test.

had similar performance and were best adapted to a broader range of environments.

**Rapidly Digestible Starch (RDS).** The G and E effects were significant for RDS (Table 1). All E effects were significant, with year contributing the largest portion of variation based on magnitude of the sums of squares (SS). Visually, this is illustrated by genotypes widely dispersed across the biplot (Figure 2). In 2009, the RDS values for the three environments were separated only by a ~15° angle, indicating a high degree of similarity.

Genotypes differed in the amount of RDS, and response to years was not consistent, some genotypes responding with an increase in RDS, others with a decrease. In 2010, the differences between environments were greater and associated with generally higher temperatures during the growing season (data not shown). This change highlighted the significance of years on the differential RDS production in these genotypes. Although there were significant differences in RDS between years, the same genotypes tended to rank higher. In the absence of genotypic crossover effects, interaction effects are expected to be small, which was observed.

Biplot analysis indicated that RDS values at a location varied over years, consistent with a large year effect (Figure 2, Table 1). Of the 12 genotypes tested, CV96044-3 and Goldrush


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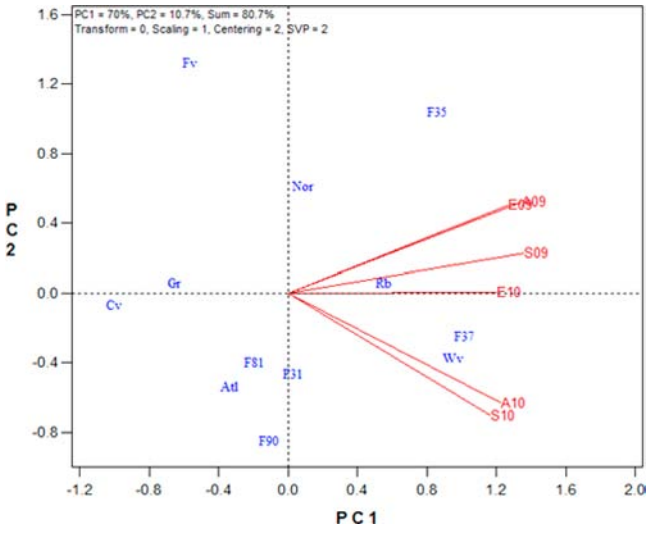


**Figure 2.** GGE biplot for rapidly digestible starch (RDS). Locations include Simcoe 2009 (S09), Elora 2009 (E09), Alliston 2009 (A09), Simcoe 2010 (S10), Elora 2010 (E10), and Alliston 2010 (A10). Genotypes include CV96044-3 (Cv), FV12272-3 (Fv), WV5475-1 (Wv), F03031 (F31), F05035 (F35), F04037 (F37), F05081 (F81), F05090 (F90), Atlantic (Atl), Goldrush (Gr), Norland (Nor), and Russet Burbank (Rb).

consistently produced the lowest amounts of RDS (7.4 and 7.7%, respectively), while WV5475-1, F05035, and F04037 consistently provided the highest RDS values in every environment (8.9, 8.8, and 9.0%, respectively). Considering the "best profile", low amounts of RDS are desirable. Because of their low production of RDS and their high stability, CV96044-3 and Goldrush were seen as promising genotypes for this component of starch.

**Slowly Digestible Starch (SDS).** A significant G and E (year) effect was found for the SDS contents (Table 1), with a larger proportion of the variation attributed to the genotype. This was illustrated in the biplot, where the vectors angles of the 2010 locations were greater compared to the 2009 locations (data not shown). No significant GEI effects were found.

The SDS content was highly variable among the environments where Simcoe and Elora samples produced similar values in 2009 (2.0 and 1.7%, respectively) but were dramatically different in 2010 (1.6 and 1.4%, respectively) ($p = 0.0006$). The biplot shows the vectors of the 2010 locations were at angles of 90° to each other, indicating low correlations. There were large differences between locations over years, highlighting the importance of the location × year effect (Table 1).

Some genotypes were able to maintain very stable SDS values across environments, while other genotypes exhibited a high level of variability. Genotypes on the perimeters of the biplot (F05035, F04037, and FV12272-3) exhibited high instability with a large PC2 and also had average SDS values. Norland, F05090 and CV96044-3 exhibited very stable SDS levels (1.4, 1.7, and 1.8%, respectively). Along with the stability displayed by Norland, these samples produced low amounts of SDS, a highly desired combination.

CV96044-3 had high SDS values and low RDS, fitting the "best profile", while others did not (WV5475-1 with high RDS and low SDS values). Goldrush also had higher SDS content but had a relatively high level of instability.

**Resistant Starch (RS).** RS was the largest starch component and accounted for 71.4 to 87.5% of TS. The ANOVA demonstrated significant E (location × year) effects (Table 1). There was no correlation between 2009 and 2010, as indicated by the 90° angle between vectors. The changes in RS component between all of the environments contributed to the location × year effect. Biplot analysis did not demonstrate any significant mega-environments. The large angles separating environmental vectors and the change in order of locations between years illustrates the location × year effect (Table 2).

There were no mega-environments identified for starch components, however, the starch data tended to group environments based on the growing year, emphasizing the greater importance of testing over multiple years rather than locations. The biplot consistently identified Alliston as similar to other locations, suggesting the removal of this location was possible without losing the power to distinguish between genotypes for stability or performance.

The test environments spanned a broad range of climatic conditions for this region and contributed to a large proportion of variation.[33] Simcoe's warmer temperatures and drought prone sandy soils resulted in considerably reduced tuber growth and yield[33] and an increased SDS content (Table 2). Although the high SDS content is desirable, it must be considered relative to the yield potential. Alliston was considered the best location, with regular irrigation and high levels of management (e.g., pest control). The warm day and low night temperatures were associated with increased tuber production (total tuber number of 199 in Alliston vs 96 in Simcoe) but had slightly lower amounts of SDS (Table 2).[9] Not only did SDS exhibit variability depending on environmental conditions, larger variations in TS content were found in 2010 compared to 2009 (range: 15.1% vs 6.9%, respectively), in part due to the increased temperature differences between the growing seasons. These variations in environmental conditions played an important role in the modification of starch profiles.

Starch is the product of sugar production and starch enzyme activity and is produced during photosynthesis which can be inhibited by adverse environmental conditions such as moisture stress.[4,5] Starch storage begins at tuber initiation and continues until the end of the plant's life cycle. This underscores the importance of adequate moisture levels during the period of tuber growth and explains how the environment can play an important role in starch accumulation.[34] The dry environments (e.g., Simcoe) showed an increased proportion of SDS compared to environments with adequate moisture levels (e.g., Alliston).

Temperature profiles can also affect plant growth and enzymatic specificity to alter starch deposition.[35,36] The starch profile (consisting of RDS, SDS, and RS, or as amylose and amylopectin components) is related to the activity of multiple starch synthesis enzymes. Amylose is synthesized by one enzyme, GBSS, while amylopectin is synthesized by at least five enzymes (GBSS, SSes, BEs).[13] Differences in enzyme activity can result in altered ratios of RDS and SDS components, as observed for different genotypes (Table 1). Lafta and Lorenzen[36] report reductions in tuber growth and overall weight at higher temperatures due to reductions in partitioning from shoots to tubers. In addition to cooler temperatures favoring tuber bulking,[37] Yamakawa et al.[38] found high temperatures during the milky stage of rice grain ripening down-regulated starch synthesis genes GBSS and BEs, resulting in a reduction in amylose and long chain amylopectin. Altering the rice ripening temperature conditions resulted in grain weight differences due to a reduction in amylose content.


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Larkin and Park[39] also observed temperature sensitivity of the rice GBSS enzyme and attributed it to genetic polymorphism. A similar study on corn found deficiencies in starch BEs resulted in altered branching patterns and digestibility due to impaired starch utilization.[40] An enzyme kinetic study from Edwards et al.[35] saw marked decreases in enzymatic activity above 25 °C. The temperature sensitivity of these enzymes could account for the differences the starch profiles of tested potatoes in the different environments. Genetic and environmental effects resulting in altered starch profiles in other species suggest a similar genetic mechanism in these tested potato genotypes and could explain the G and E effects.[38−40]

Previous studies have shown night temperatures to be a large factor in tuber bulking.[37] Plants grown at high night temperatures (e.g., Simcoe) had low to no yields due to poor tuber formation which is favored during low night temperatures (e.g., Alliston).[9,41] However, higher temperatures and lower moisture levels appear to result in higher SDS values, a desirable outcome. All tested locations provided different moistures and temperature conditions, contributing to a wide range of TS values for all genotypes (81 to 95%) (Table 2). The environment at Elora exhibited a more moderate temperature profile, contributing to the stability in TS content (Table 2). The large difference in precipitation throughout the 2010 growing season led to changes in the starch profile at Simcoe, with lower average RDS values (2009: 9.7%; 2010: 6.3%) and higher average RS values (2009: 76.2%; 2010: 78.9%). Alliston, which received adequate levels of moisture throughout the growing season due to supplemental irrigation but a warmer 2010 season, also had higher RS levels (2009: 73.6%; 2010: 80.1%). The higher temperatures in all locations in 2010 coincided with reductions in the RDS values (27% lower) (Table 2).

Genotypic differences also contributed to differences in starch profile. Pasty (sticky) and dry (crumbly) textures are linked with low and high DM content, respectively (lower and higher amounts of starch, respectively).[42] This is consistent with TS levels because higher DM content is associated with higher starch. Genotypes previously found to have pasty textures (F05032, F05035, F05081) (personal communication, B. Bizimungu) had lower TS values while potatoes (F05064) with a dry texture had higher TS values (Figure 1).

Much of the potato starch literature focuses on amylose and amylopectin content with an emphasis on the physical, chemical, and enzymatic properties for the food processing industry rather than how starch composition affects potato as a food source.[43] However, a recent study bridged the gap between biochemical composition and in vitro digestion of starches and found a negative relationship between RDS and amylose content in barley grain.[44] Because of the water insoluble nature of amylose, it is assumed to be more resistant to digestion than amylopectin and linked to SDS and RS.[45,46] Although this relationship has long been proposed, few papers have explored the direct relationship until Asare et al.[44] directly linked starch composition and the corresponding physiological effects in humans. Despite elucidating this relationship, timed enzymatic hydrolysis to quantify starch fractions can be a better predictor of dietary contributions compared to amylose and amylopectin content. However, knowing the amylose and amylopectin content may help to explain the physiological effects of starch profiles on humans and could be used in breeding programs as an efficient screening tool during selection.

As a polysaccharide made solely of glucose, starch plays a direct role in blood sugar levels, GI, TIIDM, and overall health in humans. The digestible profile developed by Englyst et al.[21] bears tremendous weight on the discussion of blood glucose and TIIDM. The GI values are known for only two genotypes in this study and are closely related to individual starch profiles. CV96044-3 was shown to have a consistent medium GI value (62 to 65 ± 6) compared to V1255-3, which ranged from medium to high GI (59 to 74 ± 6).[47,48] In this study, CV96044-3 was found to have low RDS levels, which is consistent with the lower GI values observed by Moreira and Wolever.[47,48] Low RDS levels are correlated with low to medium GI values.[32] From a previous report, the GI value of Russet Burbank was 77± 9.[49] This is substantially higher than the GI values for CV96044-3 and V1255-3 reported by Moreira and Wolever.[47,48] On the basis of the current study, the high GI value of Russet Burbank can be explained by the starch profile observed in most test environments (Table 2). With the exception of Elora 2010, Russet Burbank had either the highest or one of the highest RDS values (Table 2: average 8.7%), which would contribute to a rapid release of glucose into the bloodstream, resulting in a high GI. Henry et al.[50] reported on the GI of several potato cultivars in Great Britain and found a wide range of GI values between 56 and 94. The low GI values for CV96044-3, coupled with data reported by Henry et al.,[50] highlights the value in exploring the GI values of a wider array of advanced genotypes in Agriculture and Agri-Food Canada and other breeding programs. The combination of results from Henry et al.[50] and Moreira and Wolever[47,48] strongly suggests that potatoes with a lower GI already exist as commercial cultivars and/or advanced breeding lines. Unfortunately, the Henry et al.[50] study did not include an analysis of the starch profiles for tested cultivars. However, on the basis of the starch profiles developed to date, many genotypes have been identified as potential breeding material for low GI potatoes.

As observed with the TS values, CV96044-3 had the highest RS values (81.0%) and very stable performance among environments. Not only did it have the highest TS value, it also fit the criteria for the "best profile" previously outlined (TS, 90.2%; RDS, 7.4%; SDS, 1.8%; RS, 81.0%). Although not fitting every criteria, Goldrush also displayed a favorable profile (TS, 87.9%; RDS, 7.7%; SDS, 1.7%; RS, 78.5%) and good stability. With above average TS content and an exceptionally low RDS content, Goldrush also fit some of the aspects of the "best profile". The starch profiles and stability of CV96044-3 and Goldrush are potato genotypes worth noting for further analysis.

There was a significant correlation between TS and RS ($r$ = 0.947, $p < 0.0001$) and a small negative relationship between RDS and RS ($r = -0.32$, $p < 0.0001$). WV5475-1 and CV96044-3 were consistently high in TS (88% and 90%) and RS (78% and 81%).

The large amount of instability in the RDS and SDS contents of Atlantic and Norland (Figure 2) are also indicators of the need to develop newer potato genotypes with stability and a better starch profile for health benefits. If a "healthier" potato is going to be developed and marketed, it will be important for the cultivar to have stable performance for starch profiles over a range of years and locations.

RS was measured as a component of our starch profile, however, current literature suggests RS does not play a role in the fluctuations of blood glucose.[45] Rather, it is more important for the overall health of the colon.[51] The determination of RS is

simple to measure, as it is calculated by subtraction. RDS is the most significant contributor to sudden and adverse changes in blood sugar levels,[32] making it the most important component of starch to monitor. The "best profile" was then modeled with low amounts of RDS and a shift toward higher SDS and RS.

Although genotypic and environmental effects along with small GEI effects (Table 1) are important pieces of information for a breeding program focused on producing a healthier potato, the stability of potato genotypes is equally as important. Affleck et al.[52] emphasized the importance of this for other quality characteristics such as sugar content and French fry color. In our tested genotypes, V1255-3 had large variations in RDS content (Table 2: 8.0−12.0%) and high instability, while CV96044-3 experienced little in variation and strong stability (7.3−7.9%). The stability of starch components in CV96044-3 is noteworthy.

Conventional breeding can be used to develop new potato genotypes with desirable starch profiles, or genetic modification of amylose or amylopectin enzymes can be utilized to create vast changes in starch profiles. Potatoes with modified starch profiles can be used in the fresh market for consumption as a healthy alternative, or utilized in the processing industry with a high proportion of total starches (amylose, amylopectin, or a combination) with desirable rheological properties.

Genotype and environment were the most significant factors contributing to variations in starch profile (Table 1) and not the more unpredictable GEI. Significant year effects were most frequent, indicating the influence of temperature, precipitation, or other climatic factors on starch production. This also highlights the advantages of using multiple years rather than locations as separate environments (Figures 1 and 2) to better conduct GEI studies.

The cultivars used in this study (Atlantic, Norland, and Russet Burbank) were shown to have starch profiles that could be associated with high RDS and undesirable GI values. As a staple food in human diets, it is important to develop a healthier potato. The genotypes with the "best profile" of low RDS and higher SDS or RS components and favorable stability were CV96044-3 and Goldrush (Table 2). Goldrush is commercially available. CV96044-3 had low RDS content, high stability, and shows low environmental interaction (Figure 2). In summary, none of the starch digestibility components were found to have significant GEI, therefore it can be predicted with some accuracy. Most of the variation was attributed to environmental effects, especially location by year interactions, implying a complex effect of temperature and moisture leading to the production of different starch profiles. The identification of an advanced genotype with a good starch profile and corresponding lower GI value is an exciting finding of this study.

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### Notes

The authors declare no competing financial interest.

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## ABBREVIATIONS USED

AACC, American Association for Clinical Chemistry; ANOVA, analysis of variance; AOAC, Association of Official Agricultural Chemists; BE, branching enzyme; dd$H_2O$, double distilled water; E, environment; G, genotype; GBSS, granule-bound starch synthase; GEI, genotype by environment interaction; GI, glycemic index; GOPOD, glucose oxidase peroxidise reagent; GEI, genotype by environment interaction; PC1, principal component 1; PC2, principal component 2; RCBD, randomized complete block design; RDS, rapidly digestible starch; RS, resistant starch; SDS, slowly digestible starch; SS, starch synthase; TIIDM, type II diabetes mellitus; TS, total starch

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