

# Genotype by environment interaction effects on fibre components in potato (*Solanum tuberosum* L.)

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**Abstract** Increasing awareness of heart health and disease prevention has led consumers to more proactive grocery food choices. Fibre and its associated health benefits remains an important area of research given the current interest in food, nutrition, and health. To position the potato as a good source of fibre, breeding efforts have focused on developing cultivars and germplasm with high fibre content. The current study examined eight elite potato clones and four commercial cultivars (checks) across six environments (three locations over two years) for their total dietary fibre (TDF), neutral detergent fibre (NDF), and soluble fibre (SF) content. Genotype by environment interaction (GEI) and stability analysis were conducted with SAS and GGE Biplot software.

Significant genotypic (G), environmental (E) and GEI effects were found. The six environments differed in temperature and moisture levels, which were linked to levels of NDF and TDF. Some genotypes had high levels of stability for fibre content. GGE biplot analysis found no significant mega-environments for fibre components. Two elite clones (CV96044-3 and F05081) were identified as high fibre sources (13.3 and 14.4 %, respectively) compared to the other elite clones and commercial cultivars (e.g., Russet Burbank: 11.7 %). These lines may also be suitable as parents with high fibre and stability to breed into backgrounds with other desirable qualities.

**Keywords** Soluble fibre · Neutral detergent fibre · Total dietary fibre · Biplot · Genotype by environment interaction · Stability

## Abbreviations

ANOVA	Analysis of variance
DRI	Daily recommended intake
E	Environment
G	Genotype
GEI	Genotype by environment interaction
LDL	Low density lipoprotein
NDF	Neutral detergent fibre
NDO	Non-digestible oligosaccharide
RCBD	Randomized complete block design
RS	Resistant starch
SF	Soluble fibre
TDF	Total dietary fibre

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## Introduction

The potato (*Solanum tuberosum* L.) is the third most important crop grown in the world today for human consumption—surpassed only by rice and wheat—and is the most important non-cereal crop (CIP 2011). In 1983, worldwide annual potato production was 264 million tonnes but by 2008, that figure exceeded 325 million tonnes—nearly a 25 % increase—establishing potato as an important crop worldwide for fresh and processed industries (FAOSTAT 2008). Despite this, Canadian consumption declined 27 % from 1996 to 2005 (Agriculture and Agri-Food Canada 2007). This movement towards reduced potato consumption has negatively impacted the potato industry, and plant breeding efforts have been made to improve the health benefits of potatoes.

Today's consumers are increasingly more proactive in making healthier food choices. Gilbert's (2000) functional food trend report, which has summarized a decade of research, has found that shoppers believe foods are a source of functional nutrition for health benefits and disease prevention. Piché and Garcia (2001) found health considerations to be one of the top three factors when purchasing food at the grocery store and consumers wanted more information on healthy food choices. This information can come from dietitians and health professionals, but can also come through mainstream media communication. Although the latter form of communication can be misinformed, it is still capable of driving consumer trends.

For many years, heart health has been on the minds of the public. In recent years, gastrointestinal health has become increasingly more prevalent as a research area but also of interest to the consumer, as evidenced by the prevalence of words such as prebiotic and probiotic—all targeting the fibre aspect of our diets (Reid 2004; Schley and Field 2002; Thomas et al. 2011; Wallace et al. 2011). Although potatoes are not commonly seen as an important source of fibre, previous research has found high fibre content in potatoes (8.5 %), especially the skin (22.5 %) (Mullin and Smith 1991). Camire et al. (1993) also found dried potato peels to be 50 % dietary fibre, underscoring the importance of retaining peels when cooking.

When assessing foods that contribute to human health, high fibre content is desirable. A review by Camire et al. (2009) highlighted the positive benefits of potatoes on human health. The United States Food

and Drug Administration set a daily recommended intake (DRI) of at least 25 g of fibre each day, but it is estimated that most Canadians consume less than 50 % of the DRI (Alberta Health Services 2010a; Elleuch et al. 2011). Potatoes are a good source of dietary fibre containing a high proportion of insoluble fibre located in the skin (Camire et al. 1993; Mullin and Smith 1991). The development of potatoes with high and stable fibre levels would be a valuable marketing tool for table stock potatoes, and contribute to dietary improvements where potatoes are part of a staple diet.

Dietary fibre is broken down into two components: soluble (SF) and insoluble fibre—also called neutral detergent fibre (NDF) (Stephen and Cummings 1980). SF is important for heart health by helping reduce the “bad” cholesterol—i.e., low density lipoprotein (LDL) and blood sugar levels (Alberta Health Services 2010b). SFs can also help reduce constipation. NDFs are important for removing toxic waste within the colon and promoting regularity (Elleuch et al. 2011). Non-lignified fibres have been shown to play a role in reducing cholesterol levels (Lazarov and Werman 1996). These are especially important when trying to combat issues such as coronary heart disease, diabetes and obesity (Elleuch et al. 2011). Both components of fibre are important and achieving fibre content of equal NDF and SF contribution is ideal.

There is limited knowledge of the physiology behind fibre bulking in potatoes. Biochemical pathways for starch granule production are under strong genetic control, regulated by starch synthases, as is fibre synthesis (Jane et al. 1994). However, most traits are influenced by the environment. It is important from a breeding perspective to develop potato genotypes that have predictable performance for traits of interest with minimal genotype by environment interaction (GEI) (Lin et al. 1986; Tai 2007).

Many compounds contribute to the classification of dietary fibre (Buttriss and Stokes 2008). From celluloses and lignins to non digestible oligosaccharides (NDOs) and resistant starches (RS), each component responds differently depending on the genotype and environment. The presence of GEI strengthens the importance of this concept of genotypic and environmental effects (Cotes et al. 2002; Tai 2007). With multiple biochemical pathways and enzymes driving the production of fibre components, each genetic combination of enzymes will respond in a unique

way to environmental conditions. The current study used six environments (three locations over two years) involving a range of temperature and moisture levels to study interaction effects on potato fibre content.

In this study, the goal was to examine the variability of genotype and environment on fibre profile in selected potato genotypes with the intent of identifying potato genotypes with fibre profiles high in TDF with relatively equal amounts of NDF and SF. The specific objectives of this study were:

1. to elucidate the fibre profiles of selected potato genotypes, and
2. to determine the magnitude of stability, genotypic (G), environmental (E) and GEI effects for the fibre profile.

## Materials and methods

### Field trials

Twelve potato genotypes were grown in six environments in Ontario to measure the G, E and GEI effects. The locations used were Simcoe Research Station, Elora Research Station and a private farm in Alliston, Ontario in 2009 and 2010. The soil types were a Scotland sand soil at Simcoe, Conestoga silt loam soil at Elora and silt loam soil at Alliston. Only Alliston received supplemented irrigation during the season, therefore total moisture levels varied at each location with Alliston receiving the greatest and most consistent amount. Differences in latitude and lake effect of each environment also resulted in differing average temperature profiles throughout the field season—typically Simcoe was the warmest, followed by Alliston and Elora.

Trials were conducted with 12 potato genotypes in a randomized complete block design (RCBD) with four replications. Four commercial cultivars were used as checks (i.e., Atlantic, Goldrush, Norland, and Russet Burbank); the remaining eight were elite clones from the Agriculture and Agri-Food potato breeding program in Fredericton, New Brunswick (i.e., CV96044-3, F03031, F05035, F04037, F05081, F05090, FV12272-3 and WV5475-1).

Plots at Elora and Alliston were 5.0 m long with 0.89 m row spacing. Plots at Simcoe were 5.0 m long with 1.0 m row spacing. Plots contained 48 row entries (12 genotypes by four replications), excluding guard

rows. Spacing between plants was 25 cm with the exception of Russet Burbank which was spaced at industry standards of 46 cm. Plots were planted by hand at the end of May.

In furrow applications of Admire (imidacloprid 21.4 % at 7.5–12 mL 100 m<sup>-1</sup>) and Quadris (azoxystrobin 22.9 % at 4–6 mL 100 m<sup>-1</sup>) were applied with a backpack sprayer. Plots were fertilized with 20:10:10 NPK at 1000 kg ha<sup>-1</sup>. Pre-emergence herbicides were also sprayed after planting: Dual Magnum (s-metolachlor 83.7 % at 1.5 L ha<sup>-1</sup>) and Sencor 480 (metribuzin 480 g L<sup>-1</sup> at 1.75 L ha<sup>-1</sup>). Fungicides were applied to foliage as required throughout the growing season. The fungicides included Curzate (cymoxanil 60 % at 225 g ha<sup>-1</sup>), Dithane DG 75 (mancozeb 75 % at 1.35–1.6 kg ha<sup>-1</sup>) and Bravo 500 (chlorothalonil 40.4 % at 2 L ha<sup>-1</sup>). The insecticide Decis (deltamethrin 5.67 % at 150 mL ha<sup>-1</sup>) was also sprayed as required.

Plots were harvested by hand or by single row digger from mid-September to mid-October. Potatoes were stored in a 15 °C refrigerated trailer until transported to the University of Guelph for processing. The potatoes were boiled, frozen, freeze dried, milled into flour with a 1.0 mm sieve and then used for fibre analysis.

### Fibre analysis

Two biochemical assays were performed to determine the fibre profile: a total dietary fibre (TDF) assay, and a second to determine the insoluble fibre—known as NDF. The SF was calculated as the difference between TDF and NDF.

### Total Dietary Fibre

The TDF assay was done through enzymatic and gravimetric methods using a kit from Sigma Aldrich (Sigma Aldrich TDF100A) with minor modifications. The modifications were as follows: one blank instead of two was used during each experiment and protein analysis by Kjeldahl nitrogen analysis was not conducted. The percent dry weight of TDF was calculated using the following formulas:

$$\text{Residue weight} = W_2 - W_1 \quad (1)$$

$$\text{Ash weight} = W_3 - W_1 \quad (2)$$

$$\text{Blank} = \text{residue weight}_{\text{blank}} - \text{ash weight}_{\text{blank}} \quad (3)$$

$$\%TDF = \frac{\text{residue weight}_{\text{sample}} - \text{ash weight}_{\text{sample}} - \text{blank}}{\text{sample weight}} \times 100 \quad (4)$$

Let  $W_1$  be the Celite + crucible weight,  $W_2$  be the residue + Celite + crucible weight, and  $W_3$  be the ash + Celite + crucible weight.

### Neutral Detergent Fibre

The ANKOM 200 Fibre Analyzer is an automated instrument specifically designed for NDF analysis (ANKOM Technology, Macedon, NY). Using the ANKOM 200, 24 samples were analyzed simultaneously with the specially designed filter bags (ANKOM Technology F57). Analysis was conducted according to the ANKOM recommended method (NDF Method 13) with minor modifications. The modifications were as follows: filter bags were not soaked in acetone before drying. The percent dry weight NDF was determined from the following two equations where  $W_1$  was the filter bag weight,  $W_2$  was the sample weight, and  $W_3$  was the dried bag weight after analysis. Fibre was analyzed on replications 2 and 3 from each of the six environments.

$$\text{Blank bag correction}(C_1) = \frac{W_3(\text{blank})}{W_2(\text{blank})} \quad (5)$$

$$\% NDF = \frac{W_3 - (W_2 \times C_1)}{W_2} \times 100 \quad (6)$$

In 2009, the TDF and NDF assays were done as duplicate assays to account for technical errors. In 2010, duplicate assays were deemed unnecessary due to the lack of significant differences between duplicate runs.

### Statistical analysis

Analysis of variance (ANOVA) and Spearman correlative statistics were conducted using SAS v9.2 (SAS 2009). Each location/year combination was classified as an individual environment. When available, the mean of duplicate samples from 2009 were used for SAS analysis. The model statement for the ANOVA broke the treatment down into three components: G, E and GEI effects:

$$Y_{ijk} = \mu + \alpha_i + b_j + \alpha b_{ij} + \beta_{jk} + \varepsilon_{ijk} \quad (7)$$

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  $i^{\text{th}}$  genotype,  $b_j$  is the effect of the  $j$ th environment,  $\alpha b_{ij}$  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 (2001). Biplot analyses (Yan and Kang 2003) were used to measure the association between traits, genotypes and their stability. The environment standardized and centred GGE biplot model is as follows:

$$Y_{ij} = \mu + \beta_j + \lambda_1 \xi_{i1} \eta_{1j} + \lambda_2 \xi_{i2} \eta_{2j} + \varepsilon_{ij} \quad (8)$$

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  $\varepsilon_{ij}$ .

In the biplots, the measure of relationship among locations is visualized by the angle between their vectors (Yan and Kang 2003). The best environments are characterized by large primary effects and low secondary effects. The correlation coefficient is represented by the cosine of the angle between vectors. Small angles indicate a positive correlation approaching  $r = 1$ , right angles indicate no correlation and angles approaching  $180^\circ$  indicate negative correlations approaching  $r = -1$ . Genotypes are distributed across the biplot based on their overall stability and performance. High performing genotypes fall on the right hand side and low performing genotypes on the left. Highly stable genotypes fall near the x-axis. Biplots were assembled as described by Yan and Kang (2003). Biplots were constructed using the GGE biplot software (Yan 2001).

### Results

The analysis of variance for dietary fibre components is presented in Table 1. The data were presented by location and year due to the presence of significant interactions (Table 2). Although the fibre profile is important for its role in gastrointestinal health, the

**Table 1** Analysis of variance and broad sense heritability for total dietary fibre, neutral detergent fibre and soluble fibre from 12 potato genotypes grown at six environments (three locations over two years)

Source	df	Sums of squares		
		Total dietary fibre	Neutral detergent fibre	Soluble fibre
Block (Environment)	6	56.0**	5.50**	48.0**
Genotype	11	93.8**	21.2**	75.2**
Environment	5	43.4**	74.9**	19.2**
Location	(2)	22.9**	25.3**	0.559
Year	(1)	3.62*	35.8**	16.6**
Location × year	(2)	16.8**	13.8*	1.98
Genotype × environment	55	45.3	21.6*	41.0**
Genotype × location	(22)	12.1	11.6*	13.2
Genotype × year	(11)	10.2	3.34	11.9**
Genotype × location × year	(22)	23.0*	6.64	15.9
Error	66	37.0	16.5	26.7
$R^2$		0.87	0.88	0.87
$H^2$		0.88	0.52	0.72

\*,\*\*Denotes significance at  $p = 0.05$  and  $p = 0.01$ , respectively

total amount of fibre is more important (Elleuch et al. 2011). Potatoes are not commonly considered a good source of fibre, therefore one of the objectives of this research was to examine fibre levels in several potato genotypes. The “best profile” was defined as a potato with high amounts of TDF and roughly equivalent portions of NDF and SF.

### Total Dietary Fibre

TDF had significant G, E and GEI effects (Table 1) for environment and its components. The GEI effects arose from genotype × location × year effects, which were illustrated in the biplot (Fig. 1). The two field seasons from an individual location did not have overlapping vectors, indicating their different performances. The wide distribution of genotypes along the x-axis contributes to the G effect. The GEI effects—through the genotype × location × year interaction—were illustrated by the large angle of vectors and the crossover ranking of locations and genotypes from one field season to the other.

Mega-environment analysis was also conducted on the biplot to distinguish environments that performed distinctly different from others (Yan and Kang 2003). The analysis grouped all six environments into the same mega-environment due to the similar behaviour of TDF.

TDF values ranged from 10.8 to 15.0 %. The overall average TDF value was 12.7 % and the most stable genotype with the highest average TDF was F05081 (14.4 %). CV96044-3, a genotype previously shown to have an exceptional starch profile (data not shown), performed well with high stability and an above average amount of TDF (13.3 %), while F05090 and Russet Burbank had low amounts of TDF (11.8 and 11.7 %, respectively). The lack of stability in F04037 contributed to the spread of environments on the biplot (Fig. 1).

### Insoluble Fibre (NDF)

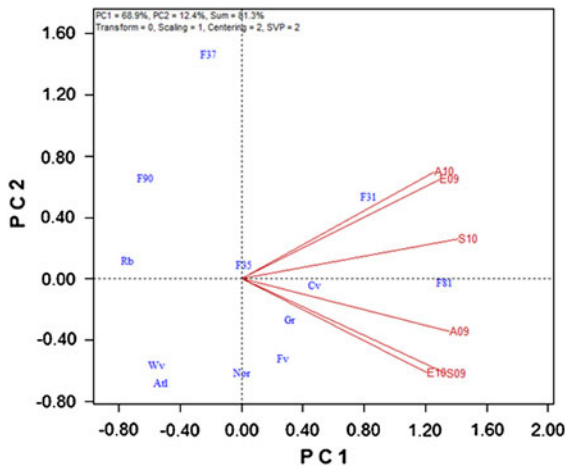
NDF values ranged from 2.1 to 6.5 %. The ANOVA table for NDF showed significant G, E and GEI effects (Table 1). Environmental variation was attributed to significant year, location and location × year interactions. Genotype × location interaction effects were significant, indicating crossover effects among locations. A genotype that had higher NDF levels in one location had the lowest NDF value in another location (CV96044-3 at Simcoe and Alliston; Table 2). The biplot (Fig. 2) showed location × year interactions, where Alliston and Simcoe reversed orders in comparison to Elora from 2009 to 2010.

The proportion of NDF was relatively stable among all locations in 2009 (3.1–3.4 %) but environmental

**Table 2** Means of fibre components: total dietary fibre (TDF), neutral detergent fibre (NDF), and soluble fibre (SF), from 12 potato genotypes grown at six environments (three locations over two years) expressed on a percent dry weight basis

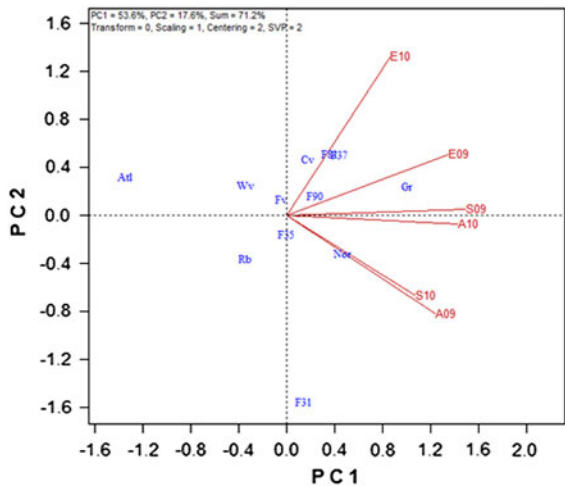
Genotype	TDF (%)	NDF (%)	SF (%)	TDF (%)	NDF (%)	SF (%)
	Simcoe 2009			Simcoe 2010		
CV96044-3	14.1ab*	3.7ab	10.4ab	14.0a	5.0ab	9.0a
FV12272-3	13.1abc	3.1bc	10.0ab	13.7a	5.4ab	8.3a
WV5475-1	12.1abc	3.1bc	9.0abc	12.6a	5.2ab	7.4a
F03031	13.3abc	3.6ab	9.7ab	14.9a	5.9ab	9.1a
F05035	12.8abc	3.5abc	9.2abc	13.7a	5.6ab	8.1a
F04037	10.9c	3.5abc	7.3b	13.8a	5.1ab	8.7a
F05081	14.3a	3.8ab	10.5a	14.9a	5.2ab	9.7a
F05090	11.7bc	3.5abc	8.2bc	12.8a	4.1b	8.7a
Atlantic	12.3abc	2.6c	9.7ab	12.5a	4.0b	8.5a
Goldrush	13.1abc	4.4a	8.7abc	14.7a	6.5a	8.2a
Norland	12.4abc	3.3bc	9.1abc	14.1a	5.6ab	8.5a
Russet Burbank	11.7bc	3.0bc	8.7abc	12.9a	5.6ab	7.3a
<b>Mean</b>	<b>12.7</b>	<b>3.4</b>	<b>9.2</b>	<b>13.7</b>	<b>5.3</b>	<b>8.5</b>
	Elora 2009			Elora 2010		
CV96044-3	12.6bcd	3.2ab	9.4bc	11.6ab	3.7a	7.9bcd
FV12272-3	12.7bcd	3.1ab	9.6bc	12.3ab	3.9a	8.4bcd
WV5475-1	11.6 cd	3.0ab	8.6c	11.1b	3.5a	7.6 cd
F03031	13.9ab	3.0ab	10.9ab	12.1ab	2.1a	10.1a
F05035	11.8bcd	2.9ab	9.0c	12.0ab	3.3a	8.7abcd
F04037	13.5abc	3.9a	9.6bc	11.3b	3.8a	7.5 cd
F05081	15.0a	3.3ab	11.7a	13.5a	4.0a	9.5ab
F05090	11.6 cd	3.5a	8.2c	10.8b	3.4a	7.4d
Atlantic	11.4d	2.3b	9.1c	12.2ab	3.0a	9.1abc
Goldrush	12.9bcd	3.6a	9.3c	12.5ab	4.3a	8.2bcd
Norland	11.1d	2.9ab	8.2c	12.7ab	3.9a	8.8abcd
Russet Burbank	11.8 cd	3.0ab	8.8c	10.9b	3.0a	7.9 cd
<b>Mean</b>	<b>12.5</b>	<b>3.1</b>	<b>9.4</b>	<b>11.9</b>	<b>3.5</b>	<b>8.4</b>
	Alliston 2009			Alliston 2010		
CV96044-3	13.4a	2.9a	10.5a	14.2a	4.7a	9.5ab
FV12272-3	13.5a	3.6a	9.9a	12.6a	3.5a	9.1ab
WV5475-1	12.8a	2.8a	10.0a	11.0a	3.7a	7.3b
F03031	13.8a	3.9a	9.9a	14.5a	4.1a	10.4a
F05035	11.9a	3.1a	8.8a	13.7a	4.2a	9.5ab
F04037	11.6a	3.4a	8.2a	13.4a	4.3a	9.1ab
F05081	14.1a	3.3a	10.8a	14.7a	4.3a	10.4a
F05090	11.3a	3.8a	7.5a	13.0a	4.7a	8.3ab
Atlantic	11.5a	2.4a	9.1a	11.7a	2.7a	9.1ab
Goldrush	12.5a	3.6a	8.9a	12.4a	4.6a	7.8ab
Norland	12.2a	4.0a	8.3a	12.7a	5.4a	7.4b
Russet Burbank	11.4a	3.2a	8.2a	11.3a	3.4a	7.9ab
<b>Mean</b>	<b>12.5</b>	<b>3.3</b>	<b>9.2</b>	<b>12.9</b>	<b>4.1</b>	<b>8.8</b>

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



**Fig. 1** GGE biplot for total dietary fibre (TDF) at locations in Ontario, Canada: Simcoe 2009 (S09), Elora 2009 (E09), Alliston 2009 (A09), Simcoe 2010 (S10), Elora 2010 (E10) and Alliston 2010 (A10) for genotypes: 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)

changes in 2010 at Simcoe and Alliston (5.3 and 4.1 %, respectively) led to significant changes in the NDF values ( $p < 0.0001$ ), confirming the year effect as the largest contributor of environmental variation (Table 1).



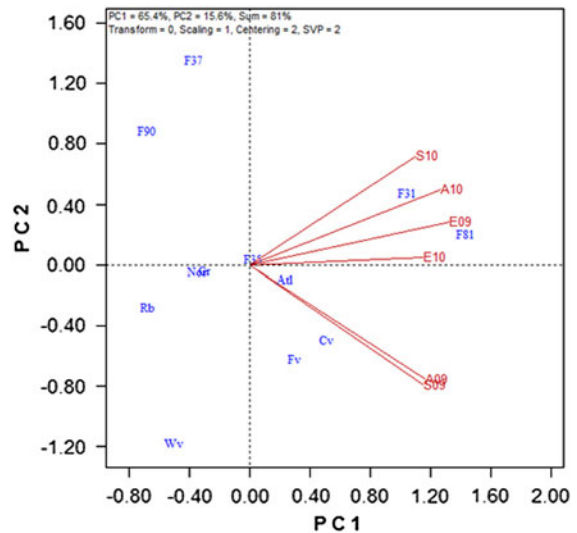
**Fig. 2** GGE biplot for neutral detergent fibre (NDF) at locations in Ontario, Canada: Simcoe 2009 (S09), Elora 2009 (E09), Alliston 2009 (A09), Simcoe 2010 (S10), Elora 2010 (E10) and Alliston 2010 (A10) for genotypes: CV96044-3 (Cv), FV12272-3 (Fv), WV5475-1 (Wv), F03031 (F31), F05035 (F35), F04037 (F37), F05081 (F81), F05090 (F90), Atlantic (Atl), Goldrush (Gr), Norland (Nor) and Russet Burbank (Rb)

No clear mega-environments were found, but the biplot grouped Simcoe 2010 and Alliston 2009 separately from the other four environments, due to largely different NDF values for these two locations (5.3 and 3.1 %, respectively). Goldrush had the highest levels and stable performance. F05081, which had high and stable levels of TDF, had average levels of NDF as well (4.0 %). Contrary to the results for TDF, F05090 had above average NDF content (3.8 %) while Atlantic had low NDF values (2.8 %).

**Soluble Fibre**

SF values ranged from 7.3 to 11.7 %. SF content had significant G, E, and GEI effects (Table 1) and was reflected by the biplot (Fig. 3). In 2009 and 2010, the angle of the location vectors and groups of locations/years highlight the year and genotype effects.

Mega-environment analysis grouped all six environments together, indicating the general repeatability of SF across locations and years (8.4–9.4 %). Although there were significant differences among some environments, years contributed more to variation than locations (Table 1). There was a similar pattern for TDF and NDF.



**Fig. 3** GGE biplot for soluble fibre (SF) at locations in Ontario, Canada: Simcoe 2009 (S09), Elora 2009 (E09), Alliston 2009 (A09), Simcoe 2010 (S10), Elora 2010 (E10) and Alliston 2010 (A10) for genotypes: 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)

Many genotypes, such as F04037 and WV5475-1, had a large variation in SF value (7.3–9.6 and 7.3–10.0 %, respectively). Despite the overall GEI, F05081 had the highest levels of SF of all genotypes in all environments (10.4 %) and was moderately stable in four of the six environments (Fig. 3). The overall profile of F05081 was promising for the production of higher fibre potatoes with a good fibre profile. F05090 and Russet Burbank consistently had the lowest SF levels (8.0 and 8.1 %, respectively) and had poor fibre profiles. Atlantic, a commercial variety, also had high SF levels (9.1 %). Spearman's correlation statistics found TDF to be correlated with NDF ( $r = 0.56$ ,  $p < 0.0001$ ) and SF ( $r = 0.71$ ,  $p < 0.0001$ ). The best fibre profiles were found in F05081 and CV96044-3.

## Discussion

Analyzing potato genotypes to discern fibre profiles and identify significant sources of variation were major objectives for this study. The best fibre profile was defined as high TDF with equal amounts of NDF and SF. In addition to significant G and E effects, some significant GEI effects were found in fibre components.

Biplot analysis clustered all environments together (with the exception of Alliston 2009 and Simcoe 2010 for NDF), denoting the similar performances of the traits in all of the environments. Thus, when testing for fibre, these data suggest only a limited amount of testing is required. The ability to identify optimal environments with the greatest ability to differentiate among genotypes was also utilized by Affleck et al. (2008) in potato French fry colour and Yan and Hunt (2001) for winter wheat yields. The separation of Alliston 2009 and Simcoe 2010 in the NDF component suggests increasing the number of years of analysis rather than locations for analysis may provide a more comprehensive understanding of the GEI and efficient identification of promising selections.

Location, year, and location  $\times$  year effects were significant for TDF and NDF but only year effects were significant in SF. This suggests the year effect was more important than location, reinforcing the mega-environment finding. The location and year effects can be attributed in part to the large differences in water availability among the three chosen locations. Simcoe received less water with higher temperatures and lower management inputs compared to Elora and

Alliston. Elora had moderate temperatures and precipitation with moderate inputs; Alliston had close to optimal temperatures, supplemental irrigation and excellent disease and insect management.

The environmental conditions at each of the three locations provided the basis for differences in fibre content, while the genotype also played an important role, suggesting a gradient for enzyme kinetics in fibre synthesis. Usadel et al. (2004) found reductions in rhamnogalacturonan I (a plant primary cell wall pectin polysaccharide) synthesis with mutant *Arabidopsis* lines, ultimately affecting the SF content. Whetten and Sederoff (1995) discussed the increased lignification (NDF component) of the secondary cell walls brought on by stress, potentially as a defense mechanism against pathogens and predators. This was seen with the higher NDF levels in both Simcoe environments (Table 2). Hu et al. (2009) tested drought stress in drought tolerant and drought sensitive maize plants. The drought-induced proteins were involved in lignin biosynthesis (NDF component) in maize leaves and led to higher lignin content in the drought tolerant plants. This proposed correlation between stress and NDF explains the higher NDF levels at Simcoe (a stress environment) in both years. Although the difference was only 0.1 % in 2009, the three locations were unique in their combination of temperature, moisture level and pathogen risk. Simcoe was considered the location with the highest levels of stress and had the highest TDF levels in both years (average: 12.7 and 13.7 %, respectively) (Table 2). Environmental conditions had their greatest impact at the Simcoe location in 2010 when average temperatures were higher with less rainfall. The environmental conditions at Simcoe in 2010 resulted in a significant increase in NDF (lignin) levels ( $p < 0.0001$ ) (3.4–5.3 %, Table 2), which agree with findings from Hu et al. (2009) and Whetten and Sederoff (1995). The stress levels (i.e., temperature, moisture levels) in Simcoe resulted in higher TDF and NDF levels, which meet the requirements in the “best” fibre profile of high TDF and increased NDF content. The 2010 field season showed a greater amount of variation than 2009 due to the increased stress from warmer temperatures. Elora, with low environmental stresses, had the lowest TDF and NDF levels in both years and a SF value comparable to Simcoe and Alliston, again supporting the higher lignin contents observed by Hu et al. (2009) and Whetten and Sederoff (1995).



The biplots (Figs. 1, 2, 3) indicated F05081 to be highest in TDF and SF levels, and to have higher than average NDF levels and good stability. This was notable across the wide range of environmental conditions for the study. CV96044-3 also exhibited above average levels of each fibre component and good stability throughout. Although Goldrush had higher NDF levels and good stability, the fibre profile was poor due to its lower TDF and SF levels. F05081 and CV96044-3 had the “best” fibre profiles, with high amounts of all fibre components (TDF: 14.4 and 13.3 % NDF: 4.0 and 3.9 %, SF: 10.4 and 9.5 %, respectively). The fibre profile of CV96044-3 is particularly promising because of its desirable starch profile as well (Bach 2012). With an attractive starch and fibre profile, CV96044-3 may serve a dual purpose in the amelioration of GI effects and better gastrointestinal health.

Dietary fibre is composed of several compounds, including cellulose, lignin, pectins and RS (Buttriss and Stokes 2008). SFs include RS and pectin, NDFs include cellulose and lignins. Each of these components is controlled by several different mechanisms in their production, so a more complex system of interaction between the potato genotype and environment is expected (Campbell and Reece 2008; Whetten and Sederoff 1995; Usadel et al. 2004). This was confirmed by the ANOVA tables for fibre components (Table 2) and the presence of GEI. These GEI bring to the forefront a complex mechanism underlying the production of fibre within potato tubers, through interactions between the genotype and the environment.

Genotypic effects significantly contributed to differences in TDF and SF content (Table 2), indicating the potential ability to breed for potatoes with higher TDF and SF content. Broad sense heritability ( $H^2$ ) calculations also indicate the importance of G effects on fibre components (Table 1). NDF was more influenced by the environment than the genotype (Whetten and Sederoff 1995). Since SF is a calculated value, a large source of variation can come from TDF. Although it is highly regulated by genotypic and environmental factors, there are still confounding effects (i.e., drought and high NDF levels) that create complex interaction relationships. The development of high NDF potato genotypes is complicated by the environmental factors, further illustrating the need for testing over a series of years. A larger study may help to improve our understanding of these complex GEI relationships.

The four commercial cultivars used in the study had low (Atlantic and Russet Burbank) or average fibre (Goldrush and Norland) content. F05081 and CV96044-3 were able to outperform these commercial genotypes with improved overall fibre content and the amount of NDF and SF available.

In summary, F05081 and CV96044-3 both had high levels of TDF, NDF, and SF (Figs. 1, 2, 3) but only F05081 was stable. Previous research has found correlations between stress and fibre content, particularly in NDF content (Hu et al. 2009; Whetten and Sederoff 1995). Mega-environment analysis indicated all six environments were part of the same group. These data indicate that further testing for fibre content and profile would benefit from an increase in years over locations.

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## References

- Affleck I, Sullivan JA, Tarn R, Falk DE (2008) Genotype by environment interaction effect on yield and quality of potatoes. *Can J Plant Sci* 88:1099–1107
- Agriculture and Agri-Food Canada (2007) Canadian Potato Situation and Trends. [http://www4.agr.gc.ca/resources/prod/doc/misb/hort/sit/pdf/po\\_06\\_07\\_e.pdf](http://www4.agr.gc.ca/resources/prod/doc/misb/hort/sit/pdf/po_06_07_e.pdf). Accessed: 28 June 2011
- Alberta Health Services (2010a) Road to healthy living—fibre fact. <http://www.albertahealthservices.ca/hp/if-hp-tr-en-fibre-facts.pdf>. Accessed 27 June 2011
- Alberta Health Services (2010b) Road to healthy living—healthy eating to lower your LDL cholesterol. <http://www.albertahealthservices.ca/hp/if-hp-tr-en-healthy-eating-to-lower-your-ldl-cholesterol.pdf>. Accessed 27 June 2011
- Bach S (2012) Genotype by environment interaction effects on starch, fibre and agronomic traits in potato (*Solanum tuberosum* L.). Dissertation, University of Guelph
- Buttriss JL, Stokes CS (2008) Dietary fibre and health: an overview. *Brit Nutr Found* 33:186–200

- Camire ME, Zhao J, Violette DA (1993) In vitro binding of bile acids by extruded potato peels. *J Agric Food Chem* 41:2391–2394
- Camire ME, Kubow S, Donnelly DJ (2009) Potatoes and human health. *Crit Rev Food Sci Nutr* 49:823–840
- Campbell NA, Reece JB (2008) *Biology*, 8th edn. Pearson Benjamin Cummings, San Francisco
- CIP, International Potato Center (2011) Potato. <http://www.cipotato.org/potato>. Accessed 11 January 2012
- Cotes JM, Nustez CE, Martinez R, Estrada N (2002) Analyzing genotype by environment interaction in potato using yield-stability index. *Am J Potato Res* 79:211–218
- Elleuch M, Bedigian D, Roiseux O, Besbes S, Blecker C, Attia H (2011) Dietary fibre and fibre-rich by-products of food processing: characterisation, technological functionality and commercial applications: a review. *Food Chem* 124:411–421
- Food and Agriculture Organization of the United Nations (2008) FAOSTAT. <http://faostat.fao.org/>. Accessed 11 January 2012
- Gilbert LC (2000) The functional food trend: what's next and what Americans think about eggs. *J Am Coll Nutr* 19:507S–512S
- Hu Y, Li WC, Xu YQ, Li GJ, Liao Y, Fu FL (2009) Differential expression of candidate genes for lignin biosynthesis under drought stress in maize leaves. *J Appl Genet* 50:213–223
- Jane J-L, Leas S, Zobel H, Robyt J (1994) Anthology of starch granule morphology by scanning electron microscopy. *Starch* 48:S121–S129
- Lazarov K, Werman M (1996) Hypercholesterolaemic effect of potato peels as a dietary fibre source. *Med Sci Res* 9:581–584
- Lin CS, Binns MR, Lefkovitch LP (1986) Stability analysis: where do we stand? *Crop Sci* 26:894–900
- Mullin JW, Smith JM (1991) Dietary fibre in raw and cooked potatoes. *J Food Compos Anal* 4:100–106
- Piché LA, Garcia AC (2001) Factors influencing food-buying practices of grocery shoppers in London, Ontario. *Can J Diet Pract Res* 62:199–202
- Reid K (2004) Gastrointestinal health. The role of pro- and pre-biotics in standard foods. *Aust Fam Physician* 33(4):253–255
- SAS (2009) SAS Institute Inc. v9.2. Cary, North Carolina
- Schley PD, Field CJ (2002) The immune-enhancing effects of dietary fibre and prebiotics. *Br J Nutr* 87:S221–S230
- Stephen AM, Cummings JH (1980) Mechanism of action of dietary fibre in the human colon. *Nature* 284:283–284
- Tai GCC (2007) The canon of potato science: 7. Genotype-by-environment interaction. *Potato Res* 50:231–234
- Thomas F, Hehemann J-H, Rebuffet E, Czjzek M, Michel G (2011) Environmental and gut *Bacteroidetes*: the food connection. *Front Microbiol* 2:93. doi:10.3389/fmicb.2011.00093
- Usadel B, Kuschinsky AJ, Rosso MG, Eckermann N, Pauly M (2004) RHM2 is involved in mucilage pectin synthesis and is required for the development of the seed coat in Arabidopsis. *Plant Phys* 134:286–295
- Wallace TC, Guarner F, Madsen K, Cabana MD, Gibson G, Hentges E, Sanders ME (2011) Human gut microbiota and its relationship to health and disease. *Nutr Rev* 69:392–403
- Whetten R, Sederoff R (1995) Lignin biosynthesis. *Plant Cell* 7:1001–1013
- Yan W (2001) GGE Biplot v6.3
- Yan W, Hunt LA (2001) Biplot analysis of multi-environment trial data. *Genomics and Plant Breed*. CAB Int Quant Gen, New York, pp 289–303
- Yan W, Kang MS (2003) GGE biplot analysis. CRC Press, New York City