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Interpretation of Genotype × Environment Interaction for Winter Wheat Yield in Ontario

Weikai Yan* and L. A. Hunt

ABSTRACT

An understanding of the causes of genotype × environment (GE) interaction can help identify traits that contribute to better cultivar performance and environments that facilitate cultivar evaluation. Through subjecting environment-centered yield of a multi-environment trial data to singular value decomposition, the portion of yield variation that is relevant to cultivar evaluation is partitioned into noncrossover and crossover GE interaction, quantified by the first two principal components (PC), respectively. Each PC is a set of genotypic scores multiplied by a set of environmental scores. By relating the PC scores to genotypic and environmental covariates, GE interaction represented by each PC can be interpreted in terms of trait × factor interactions. This strategy was employed in analysis of the 1992 to 1998 Ontario winter wheat (*Triticum aestivum* L.) performance trial data. Results indicated that plant height and maturity were the major genotypic causes of GE interaction, whereas cold temperature in the winter and hot temperature in the summer were the major environmental causes of GE interaction. Positive interactions were found between earlier maturity vs. warmer winters or hotter summers, and between shorter plant height vs. warmer winters or cooler summers. In addition, better resistance to septoria leaf blotch (caused by *Septoria secalis* Prill. & Delacr.) was frequently associated with overall performance. The results of this study should help in determining breeding objectives and for selecting test sites or environments for winter wheat breeding in Ontario.

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An understanding of environmental and genotypic causes GE interaction is important at all stages of plant breeding, including ideotype design, parent selection, selection based on traits, and selection based on yield (Jackson et al., 1996; Yan and Hunt, 1998). Understanding of the causes of GE interaction can be used to establish breeding objectives, identify ideal test conditions, and formulate recommendations for areas of optimal cultivar adaptation.

Numerous methods have been used in the search for an understanding of the causes of GE interaction (van Eeuwijk et al., 1996). These methods can be categorized into two major strategies. The first strategy involves factorial regression analysis of the GE matrix (i.e., the yield matrix after the environment and genotype main effects are removed) against environmental factors, genotypic traits, or combinations thereof (Baril et al., 1995). The second strategy involves correlation or regression analysis which relates the genotypic and environmental scores derived from principal component analysis of the GE interaction matrix to genotypic and environmental covariates.

Frensham et al. (1998) and Vargas et al. (1998, 1999),

Abbreviations: AMMI, Additive Main Effects and Multiplicative Interaction; GE, genotype × environment interaction; GL, genotype × location interaction; PC, principal component(s); MET, multi-environmental trials; SREG, sites regression model.

used methods that belong to the first category. Frensham et al. (1998), when analyzing 10 years of oat (*Avena sativa* L.) evaluation data in Australia, incorporated several genotypic covariates into a mixed model. They indicated that plant type (plant height, kernel type) by environment interaction explained 50% of the observed GE interaction. Vargas et al. (1998) used a partial least square regression procedure in studying the causes of GE interaction in several wheat multi-environment trial (MET) datasets. Their procedure involved partial regression of the GE interaction matrix against some latent variables derived from principal component analysis of various explanatory traits or environmental variables. The partial regression procedure was introduced to avoid the problem of colinearity among large numbers of explanatory variables.

The second strategy is associated with the use of the Additive Main Effects and Multiplicative Interaction model (AMMI) in MET data analysis, which partitions the GE interaction matrix into individual genotypic and environmental scores. The first example was provided by Zobel et al. (1988), who attributed the GE interaction of a soybean [*Glycine max* (L.) Merr.] MET conducted in New York State to interaction between the maturity of the genotypes and the daylength of the locations. A second example was provided by van Oosterom et al. (1993), who concluded that the maturity × drought interaction was responsible for the GE interaction observed in a barley (*Hordeum vulgare* L.) MET conducted in Syria and Africa. Subsequent studies have shown that maturity × drought and heat stress interactions for pearl millet [*Pennisetum glaucum* (L.) R. Br.] in India (van Oosterom et al., 1996), and earliness × cold stress and plant height × drought interactions for wheat in Italy (Annicchiarico and Perenzin, 1994) were responsible for the observed GE interaction. More examples of this category were reviewed in Gauch and Zobel (1996). Van Eeuwijk (1996) proposed a method that imposes the environmental and genotypic covariates on the GE biplot so that some causes of GE interaction can be visualized. The latter procedure was adopted recently by Vargas et al. (1999) in studying the GE causes in a wheat dataset.

Although strategies may differ in overall appropriateness, different methods usually lead to the same or similar conclusions for a given dataset. For example, Baril et al. (1995) compared factorial regression and AMMI score-based analysis for a potato (*Solanum tuberosum* L.) dataset and came to the same conclusion that the interaction between maturity and cold or drought stress explained the GE interaction for potato yield. Using the method of Van Eeuwijk (1996), the partial least square regression method, and the factorial regression method, Vargas et al. (1999) also arrived at similar conclusions. Thus, it appears that it is the quality of data, rather than the method of analysis, that is more limiting to the understanding of GE interaction.

The term *GE interaction* commonly refers to yield variation that cannot be explained by the genotype main effect (G) and the environment main effect (E). For cultivar evaluation, however, both G and GE must be considered simultaneously. Using a sites regression model (SREG), Yan et al. (2000) combined G and GE, denoted as G + GE or GGE, and repartitioned this into noncrossover GE interaction and crossover GE interaction. The term *GE interaction* will be hereafter used to denote this combination. Understanding the causes of noncrossover and crossover GE interaction would help develop an understanding of the genotypic characteristics that contribute to a superior cultivar, and the environmental factors that can be manipulated to facilitate selection for such cultivars.

This research was undertaken to investigate the environmental and genotypic causes of crossover and noncrossover GE interactions in Ontario winter wheat performance trials and to determine if commonly measured traits and weather data from such trials can be used to improve understanding of the observed GE interaction.

MATERIALS AND METHODS

Data Source and Structure

Data from the 1992 to 1998 Ontario winter wheat performance trials were used in this study. Each year, 10 to 33 cultivars were tested at 8 to 15 locations representing the winter wheat growing region in Ontario. At each location, a randomized complete block design with four to six replicates was used. In addition to yield, several agronomic (date of heading, date of maturation, winter survival, plant height, lodging) and pathological traits {i.e., leaf rust [caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D.M. Henderson], stem rust (caused by *Puccinia graminis* Pers.: Pers. f. sp. *tritici* Eriks. & E. Henn.), powdery mildew (caused by *Erysiphe graminis* DC. f. sp. *tritici* Em. Marchal), septoria leaf blotch, fusarium head blight (caused by *F. graminearum* Schwabe, Group II), glume blotch [caused by *Stagonospora nodorum* (Berk.) E. Castell. & Germano], and barley yellow dwarf (BYD) virus [caused by barley yellow dwarf virus (BYDV)]} were recorded at all or some of the locations. The genotypic values for each trait were obtained by averaging over locations where data were available.

Meteorological records for monthly average minimum temperature, average maximum temperature, and total precipitation at each location in each year were obtained from Environment Canada, which is based in Toronto, and were used as environmental covariates. For locations where weather data were not available, data from a nearby station were used. Principal component analysis on the monthly weather conditions across 84-year-location combinations revealed close associations between the monthly minimum and maximum temperatures. Consequently, only the monthly minimum temperatures were used in the analysis.

Quantification and Interpretation of GE Interaction

Although the data were highly unbalanced in terms of genotype × year and location × year combinations, they were balanced in terms of GL combinations each year. Thus, the yearly multi-location trial data were subjected to analysis using a SREG model with two PC (Yan et al., 2000)

$$Y_{ij} - \beta_j = \sum_{n=1}^{2} \lambda_n \xi_{in} \eta_{jn} + \varepsilon_{ij} \quad [1]$$

where Y_{ij} is the average yield of Genotype *i* at Location *j*, β_j is the average yield of all cultivars at Location *j*, λ_n is the singular value for principal component PC n, ξ_{in} and η_{jn} are the scores for Genotype *i* and Location *j* on PC n, respectively, and ε_{ij} is the residual associated to Genotype *i* in Environment *j*. Since the environment's (location) main effect is removed before PC analysis, the model contains only G and GE effects. The analysis partitions G + GE into PC, each consisting of a set of genotypic scores multiplied by a set of environmental scores and assumes a structure of G × E. This G × E structure allows interpretation of GE interaction in terms of genotypic trait × environmental factor if the genotypic and environmental PC scores can be related to genotypic and environmental covariates. Only two PC, PC1 and PC2, are retained in the model because such a model tends to be the best model for extracting patterns and rejecting noise from the data. In addition, PC1 and PC2 can be readily displayed in a two-dimensional biplot so that the interaction between each genotype and each environment can be visualized (Yan et al., 2000).

RESULTS

PC1 and PC2 Represent Noncrossover and Crossover GE Interaction

In all years, the location PC1 scores were of the same sign or near zero (results not shown). Thus, they were arbitrarily assigned a positive value so that the genotypic PC1 scores were positively correlated with the average yield or main effects of the genotypes. Location PC1 scores taking only positive values implies that the yield due to PC1-based GL interaction, which was the product between the PC1 score of a genotype and the PC1 score of a location, is always higher for genotypes with a larger PC1 score. For the same reason, the differences among genotypes in yield due to PC1 were always greater at locations with a larger PC1 score. Thus, PC1 represents a noncrossover GL interaction or a proportionate genotype response (P.L. Cornelius, 1999, terminology suggested in a personal communication).

Unlike PC1, the PC2 scores of genotypes and locations took both positive and negative values. Consequently, a genotype that has large positive PC2-based interactions with some locations must have large negative interactions with some other locations. Thus, PC2 presented a disproportionate genotype response (P.L. Cornelius, personal communication, 1999), which was the major source of variation for any crossover GL interaction. This disproportionate genotype response is referred to as crossover GL interaction for convenience.

Causes of GE Interaction Represented by PC1

PC1 and Genotypic Covariates

For all years except 1996, near perfect correlation coefficients were obtained between the genotypic PC1 scores and the genotype main effect (i.e., the average yield of the genotypes across locations; Table 1). The genotypic PC1 scores can therefore be interpreted as representing the genotype main effects. This near perfect correlation provides a basis for the GGE biplot constructed from PC1 and PC2 to be used for visual identification of both superior cultivars and ideal test environments (Yan et al., 2000).

Correlation coefficients between genotypic PC1 scores and the genotypic covariates varied with years (Table 1). First, significant correlation between PC1 scores (hence average yield) and winter survival, heading and maturity dates, and plant height occurred only in some years. Second, the correlations were positive in some years and negative in others. As a result, no simple conclusions can be drawn with regard to these traits. Lodging score was not associated with genotypic PC1 scores in any of the years.

Negative correlations were found between genotypic PC1 scores and genotypic response to disease pressure. In particular, septoria leaf blotch ratings showed significant negative correlations with PC1 scores in five out of seven years, indicating that better resistance to this disease consistently contributed to superior cultivar performance. The positive correlation between PC1 scores and fusarium head blight scores in 1994, which suggests higher average yield for more susceptible cultivars, might reflect the fact that some conditions such as high moisture during heading favor both wheat growth and fusarium head blight development. The negative corre-

Table 1. Correlation coefficients between genotype PC1 scores and agronomic traits and disease incidence ratings.

Trait	1992	1993	1994	1995	1996	1997	1998
Number of genotypes	**10**	**18**	**15**	**14**	**23**	**28**	**33**
				Correlation with average yield			
Yield	**1.00****	**0.99****	**0.98****	**0.95****	**0.82****	**0.99****	**1.00****
				Correlation with agronomic traits			
Winter survival	**0.07**	**0.32**	**0.15**	**−0.04**	**−0.46***	**0.43***	**–**
Heading date	**−0.13**	**−0.00**	**0.19**	**−0.48***	**0.11**	**−0.19**	**−0.63****
Maturity date	**0.02**	**–**	**0.30**	**−0.19**	**0.45***	**−0.26**	**−0.56****
Height	**−0.64***	**−0.03**	**0.76****	**−0.54***	**−0.25**	**−0.25**	**−0.45****
Lodging score	**−0.20**	**0.27**	**0.29**	**−0.27**	**−0.21**	**0.15**	**−0.04**
				Correlation with disease scores			
Barley yellow dwarf	**–**	**−0.65****	**–**	**−0.15**	**−0.12**	**–**	**−0.78****
Fusarium head blight	**–**	**−0.06**	**0.54***	**–**	**−0.40***	**0.23**	**–**
Glume blotch	**–**	**–**	**−0.67****	**0.37**	**–**	**0.01**	**–**
Leaf rust	**0.05**	**−0.07**	**0.05**	**−0.34**	**−0.36***	**−0.42***	**0.15**
Powdery mildew	**0.01**	**0.33**	**−0.03**	**−0.11**	**0.33**	**−0.31**	**−0.64****
Septoria leaf blotch	**0.11**	**−0.66****	**−0.77****	**−0.53****	**−0.50***	**−0.66****	**−0.01**
Stem rust	**0.38**	**−0.57***	**–**	**−0.07**	**–**	**−0.15**	**–**

*** Significant at 0.05 probability level.**
**** Significant at 0.01 probability level.**

Table 2. Correlation coefficients between PC1 scores and monthly minimum temperatures and precipitation.

	1992	1993	1994	1995	1996	1997	1998
Number of locations	9	7	9	13	9	8	8
				Correlation with monthly average minimum temperature			
October	−0.56	−0.22	−0.35	0.61*	−0.59*	−0.20	0.61
November	−0.52	−0.10	−0.44	0.66*	0.06	0.09	0.67*
December	−0.53	0.14	−0.65*	0.70**	0.07	0.04	0.77*
January	−0.40	0.28	−0.71*	0.78**	0.02	0.23	0.80*
February	−0.48	0.20	−0.65*	0.50*	−0.08	0.51	0.64*
March	−0.44	−0.18	−0.72*	0.48	−0.52	0.47	0.57
April	−0.43	−0.51	−0.54	0.35	−0.66*	0.26	−0.02
May	−0.78*	−0.69*	0.00	0.17	−0.54	0.18	−0.06
June	−0.67*	−0.71*	−0.31	0.45	−0.64*	−0.17	−0.41
July	−0.64*	−0.27	−0.05	0.32	−0.73*	0.27	−0.08
				Correlation with monthly total precipitation			
October	−0.38	0.70*	0.39	0.35	−0.28	−0.37	0.60
November	0.07	0.83**	0.49	−0.50*	0.63*	−0.21	−0.54
December	−0.03	0.61	0.41	0.04	0.10	−0.15	0.58
January	0.14	0.31	0.28	−0.15	0.32	−0.46	−0.33
February	0.16	0.14	−0.04	0.29	0.22	−0.14	0.36
March	−0.16	−0.51	−0.30	0.27	−0.33	−0.01	−0.15
April	0.25	−0.26	−0.24	0.49*	0.73*	−0.40	−0.04
May	0.48	−0.35	0.42	−0.02	0.71*	0.53	0.68*
June	0.68*	0.51	−0.59*	−0.09	0.36	0.44	−0.67*
July	0.19	0.37	0.51	−0.42	0.11	−0.30	0.32

* Significant at 0.05 probability level.
** Significant at 0.01 probability level.

lation between PC1 scores and winter survival in 1996, which suggests lower average yield for cultivars with better winter survival, might have resulted from compensations among yield components.

PC1 and Environmental Covariates

The correlation coefficients between the location PC1 scores and the monthly weather conditions are presented in Table 2. No consistent association was observed between PC1 scores and the environmental covariates. In general, four different types of associations existed between environmental PC1 scores and the temperature conditions. The first type showed a negative correlation between PC1 scores and summer (May–August) temperatures (1992, 1993, and 1996). The second type showed a negative correlation between PC1 and winter (December–March) temperatures (1994). The third type showed a positive correlation between PC1 and winter temperatures (1995 and 1998), and the fourth showed no relation between PC1 and temperature (1997). For precipitation, no associations were significant for the winter months (December–March), but some significant associations (both positive and negative) were found for the pre-winter (October–November) and the post-winter months (April–June).

Genotypic Trait vs. Environmental Factor Interactions Represented by PC1

GE interaction of yield must be explained at the level of trait × environmental-factor interactions. Such information for PC1 can be drawn from joint examination of Tables 1 and 2, which is summarized in Table 3. For example, in 1992, shorter cultivars tended to have greater PC1 scores and hence higher average yield (Table 1). Such genotypes should be more favored by, and most easily identified at, locations with greater PC1 scores, which was associated with cooler summer (May–July) temperatures and more June precipitation (Table 2). The interpretation is that in 1992, shorter stature interacted positively with cooler summer temperatures to give higher yields (Table 3). Similarly, in 1994, Tables 1 and 2 suggest that tall stature interacted positively with colder winter (December–March) temperatures and less June precipitation. In 1995 and 1998, early maturity and/or short stature interacted positively with warmer

Table 3. Genotypic trait by environmental factor interaction suggested by PC1.

Year	Traits associated with greater PC1 scores (higher average yield)	Favorable environmental factors
1992	Shorter	Cooler summer; high precipitation in June
1993	Less BYDV, septoria leaf blotch, and stem rust	More October and November precipitation; cooler summer
1994	Taller; less glume blight and septoria leaf blotch	Colder winter; less precipitation in June
1995	Earlier/shorter	Warmer winter
1996	Later/winterhardier	Cooler summer; more precipitation in April and May
1997	Less septoria blotch	–
1998	Earlier/shorter	Warmer winter
1993-1997	Better resistance to septoria leaf blotch	–

winters. In 1996, later maturity or better winterhardiness interacted positively with cooler summer temperatures.

Thus, although the relation between genotypic traits or environmental factors and PC1 scores varied dramatically over years, the trait × factor interaction patterns were relatively consistent. The underlying causes of the GE interaction revealed by PC1 can be summarized as: 1) earlier maturity interacted positively with warmer winters and hotter or drier summers, whereas later maturity interacted positively with colder winters and cooler summers; and 2) taller stature interacted positively with colder winters and hotter summers, whereas shorter stature interacted positively with warmer winters and cooler summers. Different combinations of these two traits resulted in different GE interaction patterns. In general, early and tall cultivars are favored by hotter and drier summers, early and short cultivars are favored by warmer winters, late and tall cultivars are favored in colder winters, and late and short cultivars are favored in cooler summers. The interaction between plant height and winter temperatures was previously reported by Thomas et al. (1993) who, based on analysis of winter wheat yield trials in western Canada, revealed associations between plant height and yield that tended to be positive following cold winters, but negative following warm winters. Although the association between low temperature tolerance and vernalization genes has been well established (Fowler et al., 1999), the genetic association between low temperature tolerance and plant height is much less clear.

Causes of GE Interaction Represented by PC2

PC2 and Genotypic Covariates

The genotypic PC2 scores were significantly correlated with one or more of the agronomic traits in all years. PC2 was correlated with winter survival scores in 1993; with heading dates in 1993, 1996 and 1998; with plant height in 1992, 1993, 1997 and 1998; and with lodging scores in 1993, 1995, and 1997 (Table 4). Thus, depending on years, these traits caused some cultivars to perform *relatively* better at some locations but poorer at others. An increase or decrease in the levels of expression of these traits would, therefore, improve the specific adaptation of the genotypes to certain environments, but it is unlikely to lead to improved overall cultivar performance. To reduce crossover GE interaction, the levels of these traits should be optimized, as opposed to being maximized or minimized.

Significant correlation coefficients were obtained between genotypic PC2 scores and one or more disease scores in some years (Table 4). Leaf rust ratings were more frequently associated with PC2 scores than other diseases.

PC2 and Environmental Covariates

PC2 scores were negatively correlated with winter temperatures in 1993 and 1998 and with temperatures in all months in 1995 (Table 5), suggesting large differential genotypic responses to winter (December–March) or post-winter temperatures. Such differential responses were not apparent in 1992 and 1996, and were only marginally significant in 1994 and 1997.

There was no consistent trend over years regarding the association between PC2 scores and monthly precipitation (Table 5). PC2 was significantly associated with precipitation in every month from November through June, except March, in one or more years. There also were significant associations in four out of seven years between PC2 and precipitation in June. Therefore, precipitation in June, which usually coincides with the beginning of the winter wheat grain-filling period in Ontario, was a frequent factor leading to crossover GE interaction. The sign of the correlation coefficients is meaningless unless it is considered jointly with the genotypic traits as discussed below.

Genotypic Trait vs. Environmental Factor Interactions Represented by PC2

Joint examination of Tables 4 and 5 allows interpretation of the GE interaction represented by PC2 in terms of trait × factor interaction (Table 6). In 1992, taller cultivars, which were more resistant to stem rust, were favored by less precipitation in June, indicating that taller cultivars are more tolerant to drought during grain

Table 4. Correlation coefficients between genotype PC2 scores and agronomic traits and disease incidence ratings.

Trait	1992	1993	1994	1995	1996	1997	1998
Number of genotypes	10	18	15	14	23	28	33
				Correlation with agronomic traits			
Winter survival	0.12	0.77**	−0.16	−0.02	−0.06	0.26	–
Heading date	−0.11	0.75**	−0.19	0.34	0.61**	−0.03	0.59**
Maturity date	−0.13	–	−0.43	0.25	0.35	−0.32	0.55**
Height	0.66*	0.75**	−0.38	−0.15	0.19	0.55**	0.68**
Lodging score	0.24	0.72**	−0.05	0.88**	0.12	0.46*	0.05
				Correlation with disease scores			
Barley yellow dwarf	–	0.15	–	0.27	0.41*	–	0.19
Fusarium head blight	–	−0.57*	0.44	–	0.20	−0.34*	–
Glume blotch	–	–	0.11	−0.25	–	−0.06	–
Leaf rust	−0.23	0.69**	0.66**	0.40	0.43*	0.37*	0.39*
Powdery mildew	0.09	0.42*	−0.44	−0.52*	−0.30	0.02	−0.26
Septoria leaf blotch	0.06	−0.59**	0.30	−0.12	−0.207	0.15	−0.55**
Stem rust	−0.82**	0.42*	–	0.04	–	0.28	–

* Significant at 0.05 probability level.
** Significant at 0.01 probability level.

Table 5. Correlation coefficients between PC2 scores and monthly minimum temperatures and precipitation.

	1992	1993	1994	1995	1996	1997	1998
Number of locations	9	7	9	13	9	8	8
				Correlation with monthly minimum temperature			
October	0.26	−0.79*	−0.19	−0.68**	−0.324	0.15	−0.92**
November	0.42	−0.91**	0.19	−0.75**	−0.38	−0.21	−0.95**
December	0.14	−0.97**	0.33	−0.72**	−0.38	−0.04	−0.93**
January	−0.08	−0.95**	0.43	−0.70**	−0.45	−0.74*	−0.93**
February	0.10	−0.92**	0.22	−0.77**	−0.47	−0.51	−0.96**
March	−0.02	−0.85**	0.30	−0.81**	−0.28	−0.43	−0.97**
April	−0.14	−0.43	0.20	−0.85**	−0.20	−0.22	−0.61
May	0.38	0.35	−0.30	−0.80**	−0.29	−0.17	−0.48
June	0.31	−0.50	0.13	−0.86**	−0.26	0.27	−0.22
July	0.36	−0.32	−0.73*	−0.80**	−0.11	−0.25	−0.50
				Correlation with monthly total precipitation			
October	0.23	−0.62	−0.21	0.05	0.40	−0.32	0.08
November	0.19	−0.53	−0.32	0.64*	−0.06	−0.28	0.86**
December	0.46	−0.41	0.10	0.12	0.59*	−0.37	−0.51
January	0.19	0.21	0.22	0.60*	−0.23	0.01	0.53
February	0.41	0.08	−0.06	0.35	0.19	−0.20	−0.73*
March	0.48	0.54	0.33	0.10	−0.35	−0.97	0.11
April	0.27	0.47	0.27	0.07	−0.19	−0.17	−0.67*
May	−0.19	0.87**	0.19	0.07	−0.43	−0.36	−0.78*
June	−0.75*	−0.36	0.67*	0.65*	−0.29	−0.28	0.70*
July	−0.31	0.01	−0.11	0.16	0.29	−0.30	−0.48

* Significant at 0.05 probability level.
** Significant at 0.01 probability level.

filling. In 1993, cultivars that were tall, late, or had better winter survival ratings were favored by colder winters, a clear indication that tall and late cultivars were more winterhardy. In 1995, cultivars that experienced more lodging were favored by colder winters and cooler summers. In 1997, tall cultivars were favored by lower temperatures in January. In 1998, late and tall cultivars were favored by colder winters.

The implied causes of GE interaction presented by PC2 were complementary to, or reinforced, those suggested by PC1 (Table 3 and Table 6). The common relationship revealed by both PC1 and PC2 was that late maturity and tall stature interacted positively with cold winters. Alternatively, earlier and shorter cultivars were favored by warmer winters. The trait by factor basis for the interaction represented by PC2 for 1994 and 1996 are not obvious (Table 6).

DISCUSSION

This is the first report in which a SREG model was used to study the causes of GE interaction. The SREG model explains what is commonly called genotype main effects G in terms of a noncrossover GE interaction. Although the genotypic PC1 scores had near-perfect correlations with the genotype main effects, conceptually the two are quite different. Genotype main effect is by definition a constant value for a given genotype across the tested environments, whereas the genotypic PC1 score represents a tendency of the genotypes to respond to the environmental factors represented by the environmental PC1 scores. The yield of the genotype due to PC1 is not the same at all locations; rather, it is in direct proportion to the location PC1 scores. Thus, the SREG model emphasizes the fact that the so-called genotype main effect not only has a genotypic basis, but also is dependent on the environmental conditions. In other words, the so-called genotype main effect is actually a result of GE interaction.

Table 6. Genotypic trait by environmental factor interaction suggested by principal component 2.

Year	Traits associated with greater PC2 scores	Favorable environmental factors
1992	Taller; less stem rust	Less precipitation in June
1993	Harder/taller/later	Colder winter; more precipitation in May
1994	More leaf rust	Higher precipitation in June and lower temperature in July
1995	More lodging	Cooler summer and colder winter
1996	Later	More precipitation in December
1997	Taller	Lower temperature in January
1998	Later/taller	Colder winter

Viewing G in terms of GE has one potential advantage: examination of PC1 scores not only identifies genotypes with better overall performance, but also simultaneously suggests environmental conditions that facilitate identification of these genotypes. Thus, an understanding of the causes of GE interaction in PC1 not only helps identify characteristics that contribute to overall performance, but also helps identify environmental factors that facilitate selection of such characteristics. This advantage is, however, based on the condition that there is a near-perfect correlation between the genotypic PC1 scores and the genotype main effects. In cases where the correlation is much less than perfect (i.e., the 1996 dataset; Table 1), its application would be questionable. To avoid such possible exceptions, an alternative SREG model would involve replacement of PC1 with regressions of environment-centered or standardized yield data on the genotype main effects.

As with most variety trials, genotypes and locations varied each year in the Ontario winter wheat performance trials. This, in addition to the large yearly weather variation, led to different GL interaction patterns across years. Nevertheless, the trait × factor interaction patterns identified in this study were relatively consistent over years. Based on PC1 for 1992, 1994, 1995, 1996, and 1998, interactions existed between traits plant height and maturity and factors winter and summer temperatures. Taller cultivars are favored in colder winters and hotter summers, and earlier cultivars are favored in warmer winters and hotter summers (Table 3). Although these interactions were not obvious for 1992 and 1997 from PC1, they were clearly indicated by PC2 (Table 6). Thus, PC1 and PC2 complementarity indicated that interactions between genotypic effects such as maturity and plant height, and environmental factors such as winter and summer temperatures were the major causes of GE interaction for winter wheat yield in Ontario. This study demonstrates that the SREG model is an effective tool for quantifying and interpreting the GE interaction.

How might this information be used to assist winter wheat breeding and improve cultivar recommendation in Ontario? If the GE interaction patterns were consistent over years, it would be possible to make unambiguous recommendations as to what traits should be improved and under what conditions this can be most effectively achieved. The results indicate that in three of the seven years (1992, 1995, and 1998), shorter and earlier cultivars had higher average yield, particularly in environments with warmer winters or cooler summers (Table 3). Opposite results were obtained in 1994 and 1996, however (Table 3). Thus, the large yearly variation does not allow a simple solution for winter wheat breeding and cultivar recommendation in Ontario. Nevertheless, the conclusion that plant height and maturity are important traits responsible for the observed GE interaction suggests that GE interaction, including both genotype × year interaction and GL interaction, could be reduced by optimizing the levels (i.e., by selecting for intermediate levels) of plant height and maturity. This means that genotypes with extreme levels of plant height or maturity can be discarded with confidence even at early stages of breeding. With respect to environmental factors, since different conditions (cooler summer, warmer winter, or colder winter) were identified to be more effective in identifying superior cultivars for different years, no single environment can be recommended for most effective cultivar evaluation. Rather, cultivar evaluation must be conducted in multiple locations for multiple years to fully sample the target environment (Cooper et al., 1997). Cultivar evaluation in the presence of unpredictable GE interaction is a perennial problem in crop breeding (Bramel-Cox, 1996). To select for superior cultivars, it seems that there is no easier way other than to test widely (Troyer, 1996) and select for both average yield and stability (Lin and Binns, 1994; Kang, 1997). In addition to agronomic traits, resistance to various diseases (septoria leaf blotch in particular), should continue to be top priorities in Ontario winter wheat breeding.

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