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Cultivar Evaluation and Mega-Environment Investigation Based on the GGE Biplot

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ABSTRACT

Cultivar evaluation and mega-environment identification are among the most important objectives of multi-environment trials (MET). Although the measured yield is a combined result of effects of genotype (G), environment (E), and genotype × environment interaction (GE), only G and GE are relevant to cultivar evaluation and mega-environment identification. This paper presents a GGE (i.e., G + GE) biplot, which is constructed by the first two symmetrically scaled principal components (PC1 and PC2) derived from singular value decomposition of environment-centered MET data. The GGE biplot graphically displays G plus GE of a MET in a way that facilitates visual cultivar evaluation and mega-environment identification. When applied to yield data of the 1989 through 1998 Ontario winter wheat (*Triticum aestivum* L.) performance trials, the GGE biplots clearly identified yearly winning genotypes and their winning niches. Collective analysis of the yearly biplots suggests two winter wheat mega-environments in Ontario: a minor mega-environment (eastern Ontario) and a major one (southern and western Ontario), the latter being traditionally divided into three subareas. There were frequent crossover GE interactions within the major mega-environment but the location groupings were variable across years. It therefore could not be further divided into meaningful subareas. It was revealed that in most years PC1 represents a proportional cultivar response across locations, which leads to noncrossover GE interactions, while PC2 represents a disproportional cultivar response across locations, which is responsible for any crossover GE interactions. Consequently, genotypes with large PC1 scores tend to give higher average yield, and locations with large PC1 scores and near-zero PC2 scores facilitates identification of such genotypes.

M ULTIPLE-ENVIRONMENT TRIALS are conducted annually throughout the world by various breeding institutions and seed companies. The primary goal is usually to identify superior cultivars for the target region. A secondary, but important, goal is to develop understanding of the target region and, in particular, to determine if the target region can be subdivided into different mega-environments. Investigation of mega-environments, which has been an important issue of much MET research, is a prerequisite for meaningful cultivar evaluation and recommendation (Yan and Hunt, 1998). Mega-environments have been defined in different ways. Taking a global perspective of wheat breeding, CIMMYT defined a mega-environment as "a broad, not necessarily contiguous area, occurring in more than one country and frequently transcontinental, defined by similar biotic and abiotic stresses, cropping system requirements, consumer preferences, and, for convenience, by volume of production"(Braun, 1996). Based on this definition they identified 12 wheat mega-environments worldwide (Braun et al., 1996). Gauch and Zobel (1996, 1997), pointing out that the need for growing different cultivars in different regions is due to the existence of GE interaction, defined a mega-environment as a portion of a crop species' growing region with a homogeneous environment that causes some genotypes to perform similarly. Using a maize (*Zea mays* L.) MET dataset, Gauch and Zobel (1997) presented a "which wins where" methodology for identifying mega-environments.

Winter wheat regions in North America, and throughout the world, are typically divided into a number of subregions for cultivar recommendation purposes. Often this is based on traditional thinking (on geographical, climatic, or administrative factors) rather than on available MET data, presumably due to lack of appropriate analytical methods. For example, the winter wheat growing region in Ontario is traditionally divided into four subareas based on yearly Corn Heat Units (CHU). Area I in this classification encompasses much

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Abbreviations: AMMI, Additive Main Effect and Multiplicative Interaction Effect; CHU, Corn Heat Units; E, environment main effect; G, genotypic main effect; GE, genotype × environment interaction; GGE, G plus GE; GGL, G plus GL; GL, genotype × location interaction; L, location main effect; MET, multiple environment trials; OCCC, Ontario Cereal Crops Committee; OWWP, Ontario winter wheat performance trials; PC, principal component(s); SREG, sites regression; SVD: singular value decomposition.

of southern Ontario, Area II and IV, western Ontario, and Area III, eastern Ontario, with the greatest CHU being in Area I and the least in Area IV, which has higher elevations than the other areas. Based on the belief that these subareas are sufficiently different, and thus require different wheat cultivars for optimum performance, each year the Ontario winter wheat performance (OWWP) trial data are summarized separately for each area (Publication no. 296 OMAFRA). However, it is not known if these subareas truly reflect differential winter wheat adaptations.

The work reported here was undertaken to address the question of mega-environment identification using Ontario MET data and a biplot technique. Because the technique is not widely known, our first objective is to present the GGE biplot methodology to graphically summarize the effects of G and GE interaction, and to address the question of "which won where" in a MET dataset. The second objective is to use the GGE biplot technique to examine the possible existence of different mega-environments in the Ontario winter wheat growing region.

MATERIAL AND METHODS

Data Source

Information for each year from 1989 to 1998 was taken from the database maintained at the University of Guelph for the OWWP trials. These trials are sponsored by the Ontario Ministry of Agriculture, Food and Rural Affairs, the Ontario Wheat Producers Marketing Board, and the sponsors of the varieties, to provide information to the Ontario wheat growers about the performance of the available winter wheat cultivars. Each year from 10 to 33 winter wheat cultivars currently grown in the Province along with newly registered or introduced varieties are grown at 9 to 14 locations representing four purportedly different growing areas. At each location a randomized complete block design with four to six replicates is used. Planting date, planting density, and management are according to protocols outlined by the Ontario Cereal Crops Committee (OCCC). Between heading and harvest, trials are inspected by OCCC to determine if requirements are met. For approved trials, three to six replicates are harvested and used in the data summary, depending on locations. Harvest area per plot ranged from 3.0 to 3.5 m². In addition to yield, several phenological (date of heading, date of maturation), agronomic (winter survival, plant height, lodging), and pathological (leaf rust [*Puccinia recondita* f. sp. *tritici* Roberge ex Desmaz.], stem rust [*P. graminis* f. sp. *tritici* Eriks. & E. Henn.], powdery mildew [*Erysiphe graminis* DC. f. sp. *tritici* Ém. Marchal], septoria [*Septoria tritici* Roberge ex Desmaz.], fusarium head blight [*Fusarium graminearum* Schwabe or *Gibberella zeae* (Schwein.) Petch], barley dwarf virus, glume blotch [*S. nodorum* Berk. in Berk. & Broome]) traits are recorded at all or some of the locations. Kernel weight, seed specific weight, and protein content are determined at some or all locations. Average yield at each location, along with the recorded traits, are summarized and published by OCCC (Publication no. 296, OMAFRA). For the purpose of this study, replicated yield data from 1993 to 1998 (except 1995) were collected from the OWWP cooperators. Replicated yield data of 1993 and 1994 were collected previously by Dr. H.M. Haji.

Locations and genotypes in the OWWP trials varied each

year, resulting in highly unbalanced year × genotype and year × location data, although the yearly genotype × location data were largely balanced. Ten cultivars were common to trials from 1989 to 1993, 13 cultivars were common to trials from 1996 to 1998, and seven cultivars were tested in most or all of the 10 yr. A total of 52 cultivars were tested in at least one of the 10 yr.

Model and Biplot Selection

To make possible the display in a single graph of the performance of each genotype at each location, the biplot technique developed by Gabriel (1971) was used. Through singular value decomposition (SVD), a $g \times e$ matrix of mean yield of g cultivars in e environments can be approximated as the product of a genotype matrix and an environment matrix, so that the yield of genotype i at environment (location) j, Y_{ij}, is approximated as

$$\hat{Y}_{ij} = \sum_{n=1}^{r} \lambda_n \xi_{in} \eta_{jn} \qquad (\lambda_1 \geq \lambda_2 \geq \lambda_3 \dots \geq \lambda_r) \qquad [1]$$

where r is the number of PCs required to approximate the original data, with $r \leq \min(g,e)$; λ_n is the singular value of PCn, the square of which is the sum of squares explained by PCn. ξ_{in} and ξ_{jn} are the ith genotype score and the jth environment score, respectively, for PCn. The SVD allows the $g \times e$ table of means to be displayed in a plot having g points for the genotypes plus e points for the environments. Each genotype is represented by a point, called a marker, defined by the genotype's scores on all PCs, and each environment is represented by a marker defined by the environment's scores on all PCs. Such a plot is called a biplot because both the genotypes and the environments are plotted in a single plot. Biplots can be multidimensional, but two-dimensional biplots, using only the first and the second PCs, are most common, both for biological reasons as well as for easy comprehension. To achieve symmetric scaling between the genotype scores and the environment scores, Eq. [1] is usually written in the form:

$$\hat{Y}_{ij} = \sum_{n=1}^{r} \xi_{in}^* \eta_{jn}^* \qquad [1a]$$

where $\xi_{in}^* = \lambda_n^{0.5} \xi_{in}$ and $\eta_{jn}^* = \lambda_n^{0.5} \eta_{jn}$.

The mean yield of genotype i in environment j is commonly described by a general linear model

$$\hat{Y}_{ij} = \mu + \alpha_i + \beta_j + \phi_{ij} \qquad [2]$$

where μ is the grand mean, α_i is the main effect of ith genotype, β_j is the main effect of jth environment, and ϕ_{ij} is the interaction between genotype i and environment j. Deletion of α_i and/or β_j or all of $\mu + \alpha_i + \beta_j$ allows variation explainable by the deleted term(s) to be absorbed into the ϕ_{ij} term. It is the matrix of ϕ_{ij} values that is subjected to SVD. Subjecting the ϕ_{ij} in Eq. [2] to SVD results in the Additive Main effects and Multiplicative Interaction (AMMI) model (Gauch, 1988; Zobel et al., 1988).

We use the sites regression (SREG) model (Cornelius et al., 1996; Crossa and Cornelius, 1997) obtained from Eq. [2] by deleting the α_i term and subjecting the ϕ_{ij} (which are now environment-centered yields) to SVD. Explicitly,

$$\phi_{ij} = \hat{Y}_{ij} - \mu - \beta_j = \sum_{n=1}^{r} \xi_{in}^* \eta_{jn}^* \qquad [3]$$

A biplot based on Eq. [3] contains only G plus GE, and will be characterized as a GGE biplot. In contrast, a biplot based on SVD of ϕ_{ij} in Eq. [2] contains only GE interaction and can be referred to as a GE biplot. Kempton (1984) applied the

GE biplot in an analysis of a wheat MET, and the GGE biplot to a wheat variety × fungicide study.

The SREG model can have an environment-standardized version

$$(\hat{Y}_{ij} - \mu - \beta_j)/z_j = \sum_{n=1}^{r} \xi_{in}^* \eta_{jn}^* \qquad [3a]$$

where z_j is either the phenotypic standard deviation among cultivar means within environment j (Fox and Rosielle, 1982; DeLacy et al., 1996; McLaren, 1996; Cooper et al., 1997), or the standard error of a cultivar mean within environment j (Crossa and Cornelius, 1997). The latter is preferred when replicated data are available since it removes any environment to environment heterogeneity of error variances. The environmental centered SREG (Eq. [3]) was used here since not all replicated data were available.

Considering that test locations are basic units of mega-environments, and that the genotype × year and the location × year data were highly unbalanced, the GL relation was the focus of analysis. Starting from 1989, the yearly GL data were analyzed using Eq. [3] and a GGL biplot constructed using the first two PCs. The yearly results were then collectively summarized and interpreted.

The biplots and data in Table 1 were based on the published cell means, but the model tests in Table 2 were based on the replicated data. Since not all replicates were available, and since the number of replicates varied from three to six depending on the test locations, the values in Tables 1 and 2 do not exactly match.

RESULTS

Analysis of Variance

Results of analyses of variance for the yearly data are presented in Table 1, which gives an overall picture of the relative magnitudes of the G, L, and GL variance terms. Location was always the most important source of yield variation, accounting for 73 to 90% of the G + L + GL, except in 1998 when it accounted for 53%. Genotype × location was equal to or greater than G in nine of the 10 yr. The large yield variation due to L, which is irrelevant to cultivar evaluation and mega-environment investigation (Fox and Rosielle, 1982; Gauch and Zobel, 1996), justifies selection of SREG as the appropriate model for analyzing the MET data. The large GL, relative to G, suggests the possible existence of different mega-environments. The PC1 and PC2 derived by subjecting the location-centered yield to SVD were significant for all years except 1994, as indicated by the F_{GH2} statistics (Cornelius, 1993; Cornelius et al., 1996) (Table 2). In 1994, only PC1 was significant. The PC1 and PC2 together, which make up a GGL biplot, explained from 60 to 85% of the total G + GL (Table 2).

The GGL Biplot

A two-dimensional, symmetrically scaled GGL biplot graphically approximates the location-centered yield data (Fig. 1). For a specific genotype at a specific location, the location-centered yield is approximated by the product of the genotypic PC1 score by the location PC1 score, plus the product of the genotypic PC2 score by the location PC2 score. Geometrically, this is the length

Table 1. Genotype (G), location (L) and genotype × location (GL) variance terms for yield for the Ontario Winter Wheat Performance Trials, 1989 to 1998.

Year	Source	df	SS†	% of G + L + GL
1989	L	8	87.39	82.7
	G	9	6.26	5.9
	GL	72	11.98	11.3
1990	L	6	46.36	83.1
	G	9	3.42	6.1
	GL	54	5.98	10.7
1991	L	8	121.08	90.7
	G	9	3.80	2.8
	GL	72	8.67	6.5
1992	L	9	65.07	78.4
	G	9	9.11	11.0
	GL	81	8.79	10.6
1993	L	8	117.90	73.2
	G	17	22.12	13.7
	GL	136	21.03	13.1
1994	L	10	83.84	80.3
	G	13	6.20	5.9
	GL	130	14.41	13.8
1995	L	13	166.10	84.8
	G	13	6.65	3.4
	GL	169	23.13	11.8
1996	L	8	272.71	85.7
	G	22	10.59	3.3
	GL	176	34.91	11.0
1997	L	8	360.62	82.7
	G	27	35.85	8.2
	GL	211	39.84	9.1
1998	L	7	119.77	53.1
	G	32	72.51	32.1
	GL	224	33.37	14.8

† SS is sums of squares.

of the location vector (the absolute distance from the plot origin to the marker of the location) multiplied by the length of the genotype vector (the absolute distance from the plot origin to the marker of the genotype) and by the cosine of the angle between them (Kroonenberg, 1995). This property allows the following information to be readily visualized: (i) the similarity and difference among the locations in their differentiation of the genotypes, (ii) the similarity and difference among the genotypes in their response to the locations, and (iii) the nature (positive vs. negative) and magnitude of the interaction between any genotype and any location.

Comparing the Performance of Different Genotypes at a Location

Figure 1A illustrates graphic comparison of the relative performance of all genotypes at location NN (see Table 3 for full location names). This is done by first drawing a straight line passing through the plot origin and the marker of location NN, then drawing a perpendicular to this line from each genotype marker. The location-centered yield of each genotype at this particular location is the length of the location vector (always positive) multiplied by the length of the projection of each genotype onto the location vector (can be positive or negative). Therefore the relative yield of the genotypes can be compared simply by the length of their projections. In this example, cultivar AC RON had the highest yield at NN, followed by 'Augusta', 'Harmil',

Table 2. F_{GH2} statistics of the first two principal components for the 1993, 1994, 1996, 1997, and 1998 Ontario Winter Wheat Performance trials. Analysis after Cornelius (1993) and Cornelius et al. (1996).

	λ^2	% of G + GL	u_1¶	MS	h_2§ (df)	Error variance	Error df	F_{GH2}	$P > F$
1993									
PC1	25.10	58.90	42.09	0.60	75.73	0.067	483	8.93	0.0000
PC2	8.16	19.10	38.17	0.21	66.60	0.067	483	3.20	0.0000
1994									
PC1	8.95	53.00	35.45	0.25	61.46	0.066	378	3.85	0.0000
PC2	2.64	15.70	31.64	0.08	53.09	0.066	378	1.27	0.1051
1996									
PC1	13.4	35.2	47.40	0.30	86.0	0.056	617	5.03	0.0000
PC2	10.7	23.5	43.30	0.20	75.9	0.056	617	4.41	0.0000
1997									
PC1	39.36	57.50	56.20	0.70	104.65	0.063	695	11.07	0.0000
PC2	12.10	17.70	51.88	0.23	93.41	0.063	695	3.69	0.0000
1998									
PC1	70.64	70.60	61.89	1.14	116.84	0.046	818	24.80	0.0000
PC2	15.10	15.10	57.45	0.26	104.84	0.046	818	5.71	0.0000

¶ u_1 is the numerator df for computing the mean square [MS = $(\lambda^2)/u_1$].
§ h_2 is the numerator df for computing the P value.

'Delaware', 'Harus', 'Zavitz', 'Annette', 'Karena', 'Rebecca', and 'Ena'. Note that the thick broken line that is perpendicular to the vector of location NN and passes through the origin separates the cultivars with higher than average yield from those with lower than average yield at NN.

Comparing the Relative Performance of a Genotype at Different Locations

Figure 1B compares the relative performance of Rebecca at all locations. This is done by first drawing a straight line passing the plot origin and the marker of cultivar Rebecca, then drawing perpendiculars to this straight line from the location markers. The performance of Rebecca at different locations, relative to other genotypes, is compared by the length of the location projections. Thus, Rebecca performed well at locations WK and WE, followed by at EA, MH, LN, ID, RN, BH, NN, and HW. Again, the thick broken line that is perpendicular to the Rebecca vector and passes through the origin separates the locations at which Rebecca was above average from those at which Rebecca was below average.

Comparing the Performance of Two Genotypes at All Locations

Based on the same principle, the performance of two genotypes can be easily compared on the GGL biplot. To compare two cultivars, here cultivars AC Ron and Rebecca in Fig. 1C, first connect their markers by a straight line; then draw a perpendicular line that passes through the plot origin. This perpendicular divides the locations into two groups, each of these two cultivars yielding better than the other at locations with markers on its side of the perpendicular, and vice versa. Thus, Rebecca yielded better than AC Ron at WE, WK, and MH, while AC Ron yielded better at the other locations (namely NN, HW, BH, RN, ID, LN, and EA). The perpendicular through the origin represents virtual locations at which AC Ron and Rebecca would yield the same.

Winning Genotypes and Mega-Environment Identification

On each biplot, some corner or vertex genotypes, which are the most responsive ones, can be visually identified. These are either the best or the poorest genotypes at some or all locations; they can be used to identify possible mega-environments. The corner genotypes for the 1992 dataset were AC Ron, Rebecca, Ena, and Harmil (Fig. 1D). By connecting the markers of these corner genotypes a polygon is formed. By drawing perpendiculars to each side of the polygon passing through the origin, the locations are divided among several sectors, each with a different corner cultivar. In Fig. 1D, the locations are divided between two sectors. The first sector contains locations WE, WK, and MH, with cultivar Rebecca being the winner. The other locations make up the second sector, cultivar AC Ron being the winner. With Rebecca winning at three locations and AC Ron at seven locations, AC Ron gave higher average yield across the locations. Cultivar Delaware was located at an intermediate point on the line connecting AC Ron and Rebecca; therefore, it performed intermediately between AC Ron and Rebecca at all locations. The two other corner cultivars, Harmil and Ena, were the poorest-yielding cultivars. They located far away from the markers of all locations, reflecting the fact that they yielded poorly at all locations. Cultivars within the polygon were less responsive to the locations than the corner cultivars.

If mega-environments are defined by different winning cultivars (Gauch and Zobel, 1997), Fig. 1D suggests the existence of two mega-environments for winter wheat in Ontario, namely the Rebecca-winning niche and the AC Ron-winning niche. However, such a subdivision can be regarded only as a suggestion insofar as it is based solely on one year's data.

Winter Wheat Mega-Environments in Ontario

The GGL biplots for the other 9 yr were similarly constructed and are not presented. Each year the locations fell into different groups but the pattern of the
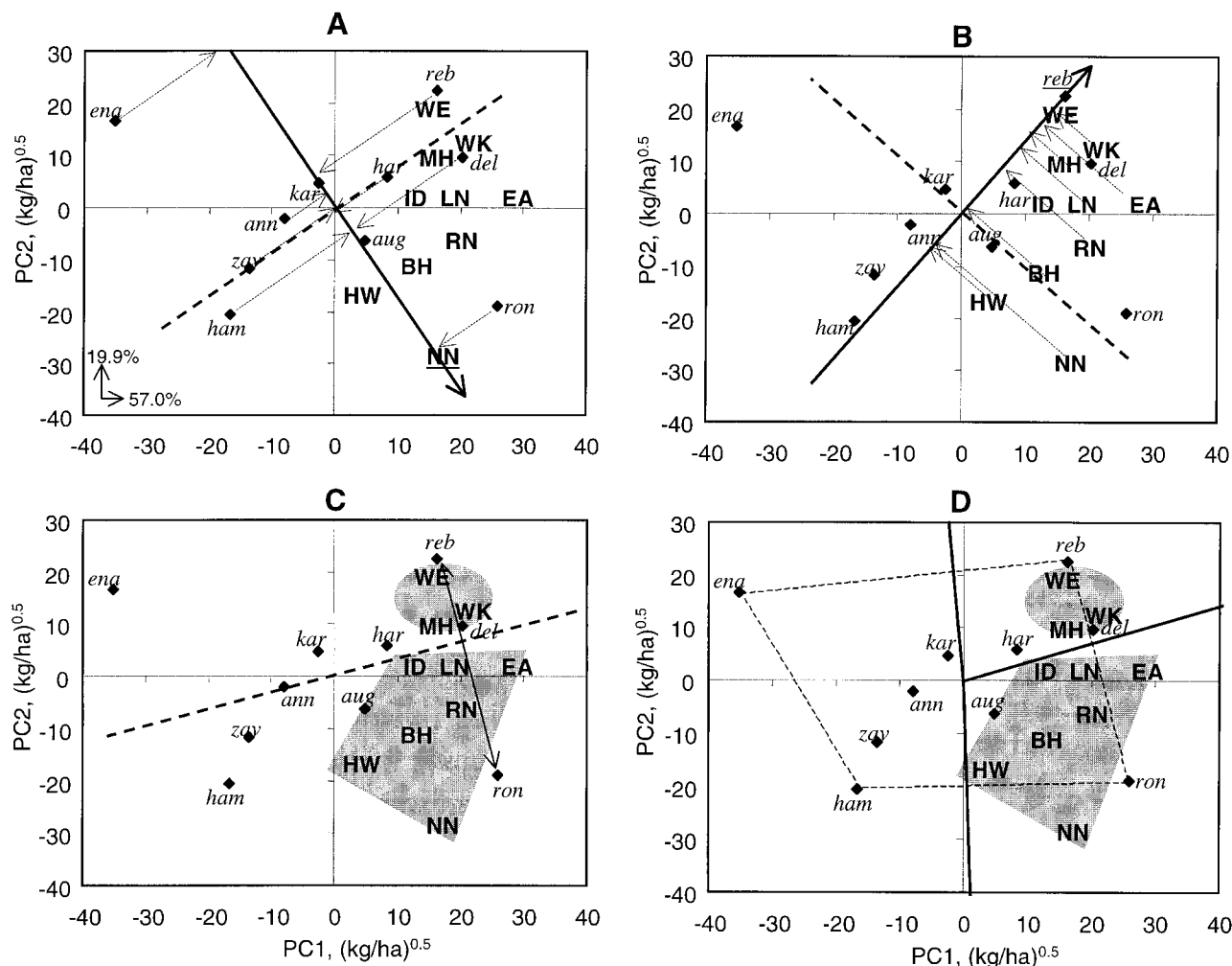
Fig. 1. The GGL biplot based on the 1992 Ontario winter wheat performance trial data. (A) Comparison of the genotypes at a given location, (B) comparison of the performance of a given genotype at different locations, (C) comparison of two genotypes at each and all locations, and (D) mega-environments and their winning cultivars. The full cultivar names are Ann = Annete, Aug = Augusta, Del = Delaware, Ena = Ena, Ham = Harmil, Har = Harus, Kar = Karena, Reb = Rebecca, Ron = AC Ron, and Zav = Zavitz. The full location names are BH = Bath, CA = Centralia, EA = Elora, GH = Guelph, HN = Harriston, HW = Harrow, ID = Inwood, KE = Kemptville, LN = London, MH = Morpeth, NN = Nairn, OA = Ottawa, RN = Ridgetown, WE = Woodslee, WK = Woodstock, WP = Winthrop.

location groupings varied across years. In most cases, the suggested mega-environments based on the location grouping did not correspond with the traditional area divisions (Table 3). However, examination of the yearly location groupings revealed that the eastern Ontario location OA tended to be grouped separately from the majority of other locations (1989, 1993, 1994, 1995, 1996, and 1998). It was always grouped with another eastern Ontario location KE (1993–1995 and 1997). This suggests that the two eastern Ontario locations, OA and KE, form a single mega-environment, which is different from the other locations (Table 3).

The GGL biplots based on multi-year data (Fig. 2 and 3) seem to support this suggestion. Ten cultivars were common to trials in 1989 to 1993 and 12 locations were used in the test for at least two of the 5 yr. The GGL biplot based on the averaged 10 cultivar by 12 location data separated the two eastern Ontario locations OA and KE from the other locations (Fig. 2). Similarly, 21 cultivars were common to trials in 1996 to 1998 and eight locations were used in the test for at

least two of the 3 yr. The GGL biplot based on the averaged 21 cultivar by 8 location data separated OA from the other locations (Fig. 3). Location WE was separated from other locations in Fig. 2 but this was not repeated in Fig. 3. Likewise, locations ID and RN were separated from other locations in Fig. 3, but this was not seen in Fig. 2. Thus, there are two winter wheat mega-environments in Ontario: the eastern Ontario mega-environment represented by OA and KE, and the western and southern Ontario represented by other locations.

The eastern Ontario mega-environment, traditionally called Area III, constitutes only a small portion of the total Ontario winter wheat–growing area. The western and southern Ontario mega-environment constitutes the main body of the Ontario winter wheat–growing region, which was traditionally divided into three subareas (Area I, II, and IV). Although the yearly biplots indicate clear crossover GL interactions among locations representing the three subareas, the pattern of the location groupings varied across years. In most cases, the

Table 3. Yearly winning cultivars and their winning locations in the Ontario winter wheat performance trials, 1989 to 1998.

Year	Winning cultivars	Location groupings†
1989	Delaware	OA
	AC Ron & Zavit	MH‡, WK, NN, ID, HW, LN
	Harmill	RN, EA
1990	Delaware	KE‡, NN, RN, EA
	Zavit	LN
	AC Ron	BH, WK
1991	Karena	EA‡
	Augusta	WE
	Zavit	KE, MH, HW, RN
	AC Ron	WK, BH, NN
1992	Rebecca	WK, MH, WE
	AC Ron	EA‡, NN, RN, LN, ID, BH, HW
1993	Zavit	OA, KE‡
	Fundulea	BH‡, EA‡, HN, LN, WP, NN, RN
1994	Marilee	OA‡, KE‡, HW‡, BH
	Rebecca	RN, LN, NN, EA, WP
		HW‡, WE‡,
1995	Freedom	RN, GH, WK, WP, NN, EA, LN, CA
	Delaware	OA, KE, HN, ID
1996	Delaware	OA
	2533	EA‡, WK, CA, HW
	2510 & Freedom	LN, ID, RN
	Dynasty	WE
1997	TW93	WE‡, OA, KE, EA, WK, NN
	2540	RN‡, HN, ID
1998	2560	RN‡, WE, ID, NN
	64914	HN, WK, EA
	PRC8	OA

† The full location names are BH = bath, CA = Centralia, EA = Elora, GH = Guelph, HN = Harriston, HW = Harrow, ID = Inwood, KE = Kemptville, LN = London, MH = Morpeth, NN = Nairn, OA = Ottawa, RN = Ridgetown, WE = Woodslee, WK = Woodstock, WP = Winthrop.
‡ Locations with larger PC1 scores give better discrimination of the cultivars.

mega-environments suggested by the location groupings did not correspond with the subarea divisions (Table 3). Thus, the western and southern Ontario winter wheat–growing region cannot be further divided into meaningful subareas. Rather, it should be regarded as a single mega-environment with unpredictable crossover GE interactions. This conclusion was supported by analysis of variance of the 10-yr data involving 16 locations and 52 genotypes (Table 4). The year main effect accounted for 31.1% of the total yield variation; the year × location interaction accounted for 37.9% of the total variation. Clearly, the year-related effect dominated the yield variation. When the genotype × year (1.9%) and the genotype × location × year interaction (5.1%) are also taken into account, the year-related effects explained 76% of the total yield variation. The location main effect was the third largest source of yield variation (11.2%). The GL interaction (5.8%), which is the basis for any mega-environment differentiation, was overridden by the much larger location × year interaction (37.9%).

Axes of the GGL Biplot: Crossover vs. Noncrossover Genotype × Location Interactions

Genotype × Location Interaction Due to Proportionality of Cultivar Response across Locations

In all GGL biplots examined, the environmental PC1 scores of the locations take, or can be made to take,
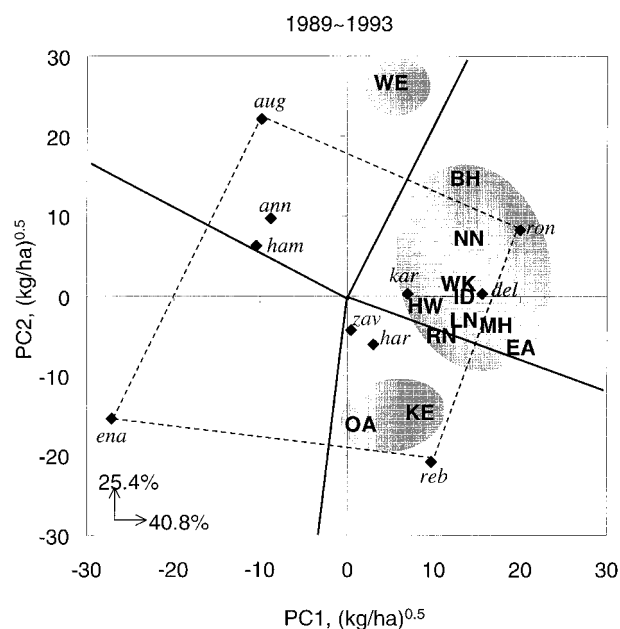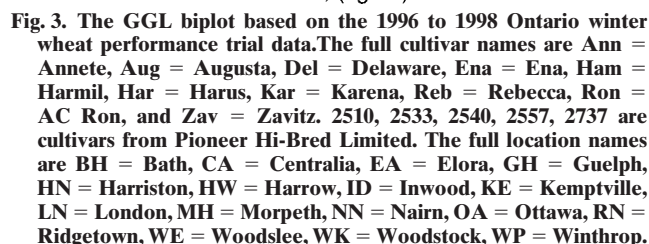

Fig. 2. The GGL biplot based on the 1989 to 1993 Ontario winter wheat performance trial data. The full cultivar names are Ann = Annete, Aug = Augusta, Del = Delaware, Ena = Ena, Ham = Harmil, Har = Harus, Kar = Karena, Reb = Rebecca, Ron = AC Ron, and Zav = Zavitz. The full location names are BH = Bath, CA = Centralia, EA = Elora, GH = Guelph, HN = Harriston, HW = Harrow, ID = Inwood, KE = Kemptville, LN = London, MH = Morpeth, NN = Nairn, OA = Ottawa, RN = Ridgetown, WE = Woodslee, WK = Woodstock, WP = Winthrop.

only positive or near-zero values. This implies that a genotype with a larger PC1 score (compared with other genotypes) would have a greater PC1 yield component at all locations. Moreover, the yield advantage of a genotype with a larger PC1 score becomes greater at locations with larger PC1 scores. Thus, a genotype with a larger PC1 score has a greater average yield, as evidenced by the near-perfect correlation coefficients between the genotypic PC1 scores and the genotype mean yield across locations (results not shown). A further implication is that cultivars with greater PC1 scores, hence higher average yield, are more easily identified at locations (environments) with larger PC1 scores. That all location PC1 scores are positive allows PC1 in the GGL biplot to be interpreted as representing proportional genotype yield differences across locations, which leads to a noncrossover GE interaction. The same implication was previously exploited by Crossa and Cornelius (1997) in a scheme for clustering environments. They indicated that yield predictions from the SREG model with PC1 as the only principal component included will not display any crossover GE interactions provided that the environment PC1 scores are all of like sign.

Genotype × Location Interaction Due to Disproportionality of Cultivar Response across Locations

In contrast to PC1, the location PC2 takes both positive and negative values. Consequently, it is impossible for a genotype to have large positive PC2 interactions with all locations. If it has large positive interactions

Fig. 3. The GGL biplot based on the 1996 to 1998 Ontario winter wheat performance trial data.The full cultivar names are Ann = Annete, Aug = Augusta, Del = Delaware, Ena = Ena, Ham = Harmil, Har = Harus, Kar = Karena, Reb = Rebecca, Ron = AC Ron, and Zav = Zavitz. 2510, 2533, 2540, 2557, 2737 are cultivars from Pioneer Hi-Bred Limited. The full location names are BH = Bath, CA = Centralia, EA = Elora, GH = Guelph, HN = Harriston, HW = Harrow, ID = Inwood, KE = Kemptville, LN = London, MH = Morpeth, NN = Nairn, OA = Ottawa, RN = Ridgetown, WE = Woodslee, WK = Woodstock, WP = Winthrop.

Table 4. Analysis of variance of the 1989 to 1998 Ontario Winter Wheat Performance trial yield data.

Source	df	Type III SS†	MS	F	% of total
Location (L)	15	207.7	13.9	118.9***	11.20
Genotype (G)	51	130.2	2.6	21.9***	7.02
GL	520	108.3	0.2	1.8***	5.84
Year (Y)	9	576.5	64.1	549.9***	31.08
GY	109	35.8	0.3	2.8***	1.93
LY	70	702.4	10.0	86.1***	37.87
GLY	805	93.8	0.1	–	5.06
Total	1579	1854.7			100.00

*** Significant at 0.001 level of probability.
† SS is sum of squares.

GGL biplots for each of the 10 yr are labeled with "‡" in Table 3. Among all 16 locations involved in the 10 yr of testing, location EA was identified as a better location for cultivar evaluation for four of the 10 yr. Other locations that were identified as a better testing location include KE (three out of 6 yr), RN (two out of 10 yr), HW (two out of 7 yr), WE (two out of 6 yr), BH (one out of 5 yr), OA (one out of 7 yr), and MH (one out of 3 yr). The other eight locations were not identified as a good testing location in any of the years.

Under limited resources and the need to conduct cultivar evaluation in a limited number of environments, the better locations will be those with high values of the PC1 and small values of PC2. The locations so selected should constitute a sample of environments that adequately cover the range of environmental conditions of the target geographical region.

DISCUSSION

Strengths of the GGE Biplot

This analysis demonstrates that the GGE biplot is a useful tool for the analysis of yearly MET data. Based on a drawn-to-scale, two-dimensional GGE biplot, the similarities and differences among environments in their discrimination of the genotypes, the similarities and differences among the genotypes in their response to the environments, and the nature and magnitude of interaction between any genotype and any environment can be readily visualized. Moreover, by adding some supplemental lines to the biplots, the best cultivars and their respective winning environments become evident. A GGE biplot thus facilitates both mega-environment identification and cultivar evaluation.

The validity of the GGE (or GGL) biplot can be inferred by the bulk of evidence from applying the AMMI model. Upon reviewing the application of AMMI in MET data analysis in recent years, Gauch and Zobel (1996) concluded that in 70% of the cases, $AMMI_1$ (with one multiplicative term) is the best model, and for the rest, $AMMI_2$ (with two multiplicative terms) is the best. A best model is considered to best capture the pattern but reject the noise contained in the data (Gauch, 1988; Piepho, 1994; Cornelius et al., 1993, 1996). From both theory and actual calculation, a two-dimensional GGE biplot based on $SREG_2$ always uses an intermediate number of degrees of freedom and explains an interme-

with some of the locations (due to a large genotypic PC2 score of same sign), it must simultaneously have large negative interactions with some other locations. Thus PC2 summarizes the most important sources of variation of a MET that lead to disproportionate genotype yield differences across locations. If this disproportionality is sufficiently severe, it can lead to the net combined effects of PC1 and PC2 revealing crossover GE interactions. The GGL biplots clearly demonstrate crossover GL interactions for all years. For example, Fig. 1C shows AC Ron is better than Rebecca at locations above the dashed line and Rebecca better than AC Ron below it. It is the crossover GL interaction involving the better cultivars that leads to mega-environment differentiation.

Better Locations for Cultivar Evaluation

In case of random GL interaction, a GGL biplot displays the tested genotypes in terms of average yield across locations (approximated by the genotype PC1 scores) and yield stability (represented by the genotype PC2 scores). Thus, high- and stable-yielding genotypes should have large PC1 scores but near-zero PC2 scores. These genotypes are most easily identified at locations with large PC1 scores and near-zero PC2 scores. For example, EA was such a location in 1992 (Fig. 1). The better testing locations visually identified based on the

diate portion of G + GE variation between $AMMI_1$ and $AMMI_2$. Thus, a GGE biplot should always be close to the best model. Using the simplified method suggested in Gauch and Zobel (1996) to estimate the pattern vs. noise contained in the data, it was revealed that the best model was $SREG_2$ for 1993, 1994, and 1998 and $SREG_3$ for 1996 and 1997. Thus, in many cases a GGE biplot displays the location-centered yield data not only graphically, but also more accurately than the raw data. The merit of using a GGE biplot would be increasingly manifest as more genotypes are tested in more environments and as the GE interaction pattern becomes more complicated.

Compared with AMMI, the GGE biplot presents the genotypic main effect as a multiplicative effect in terms of GE interaction (called the cultivar "primary" effect by Crossa and Cornelius, 1997). Since the PC1 scores of all locations tend to be of the same sign, PC1 presents a noncrossover GE interaction. Because typically the genotypic PC1 scores are highly correlated with genotype main effects, for practical purposes they can substitute for the main effects; however, conceptually the two are quite different. By definition, "genotypic main effect" is a constant genotypic effect in any environment, but yield predictions from PC1 in the GGE biplot for a given genotype are not constant. They vary across environments in direct proportion to the environment PC1 scores. We believe that this proportionality of genotype yield response is more logical and biologically plausible than the concept of additive main effects. Moreover, a unique property of this concept is that locations that facilitate identification of genotypes with greater main effect are simultaneously indicated (locations labeled with "‡" in Table 3). Another strength of the GGE biplot is the differentiation between proportionate and disproportionate cultivar responses and their implications for crossover and noncrossover GE interactions. Understanding of these interactions may be achieved by relating PC1 and PC2 scores to genotypic and/or environmental covariates.

Implications for Future Cultivar Evaluation and Selection

Analysis using the GGE biplot method revealed two winter wheat mega-environments in Ontario: eastern Ontario, which is a small mega-environment, and southern and western Ontario, which makes up the majority of the Ontario winter wheat–growing region. This has several implications for future breeding and cultivar evaluation in Ontario. First, different cultivars should be deployed for the two mega-environments to achieve optimal adaptation. Second, although crossover GL interaction was frequently observed within the southern and western Ontario mega-environments, it could not be effectively exploited due to its unpredictability. The unpredictable annual GL interaction introduces uncertainty (instability) to cultivar performance and therefore should be avoided or minimized through breeding. This must be achieved through cultivar evaluation and selection focusing on genotype main effects or general adaptation. Any measured yield at a given location in a given year is a mixture of the year, location, and genotype main effects plus various interaction effects. Reliable selection for the genotype main effect requires removal of all other unfixable variations, that is, the various year and location related effects. The only way to achieve this is to conduct multiple-location trials in multiple years. The finding that some testing locations may be better than others for cultivar evaluation suggests that the genotypes may be evaluated at fewer but better locations while still achieving the same or even better evaluation.

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Effect of One- and Two-Eared Selection on Stalk Strength and Other Characters in Maize

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ABSTRACT

Prolificacy associated with higher grain yield in maize (*Zea mays* L.) has been widely documented. However, one serious concern is that prolificacy appears associated with poor stalk strength and plant standability. The objective of this research was to compare stalk strength and other agronomic characters of one- and two-eared sub-populations derived from three maize populations (MoSQA(S7-H)C8 × Georgia Cow Corn [ACC]; MoSQB(S8-H)C8 × Georgia Cow Corn [BCC]; SI171). Entries were evaluated by using nine combinations of three levels of nitrogen (N) application (90, 180, and 270 kg ha^{-1} N) and three levels of plant density (35 800, 47 800, and 59 800 plants ha^{-1}). Stalk crushing strength showed significant differences between one- and two-eared subpopulations for ACC and BCC, but it was not significant for SI171. One-eared subpopulations had higher rind penetrometer resistance than two-eared subpopulations for all populations. Two-eared selections generally resulted in poorer root and stalk strength. However, total grain yield of the two-eared subpopulations was significantly higher than that of the one-eared subpopulations for BCC and SI171, but not for ACC. Prolificacy has significant potential as a novel character for grain yield improvement in the future. Selection for prolificacy alone, representing indirect selection for grain yield, would produce undesirable effects on other agronomic characters, especially root and stalk strength. Concurrent improvement for total grain yield, prolificacy, and root and stalk strength by using a standardized, weighted selection index should be used to extract the real benefit of the prolific character.

Maize breeders have succeeded in increasing grain yield of single-ear (non-prolific) types of maize (Troyer, 1999). Additional grain yield gains have occurred through use of improved management systems, especially the greater use of fertilizers and higher plant densities. The trend for grain yield is still upwards, but recent progress may be at a relatively slower rate. This suggests that maize breeders may need to look back into the total maize gene pool and search for a novel trait for grain yield improvement. One of the more attractive traits for grain yield improvement is prolificacy. The prolific trait has a potential for grain yield improvement because (i) the opportunity to enlarge the ear sink (grain yield) is greater when compared with non-prolific genotypes, (ii) at low plant density, prolific genotypes produce more grain per plant than non-prolific genotypes, and (iii) at high plant density, prolific genotypes resist barreness more than non-prolific genotypes. With continuing manipulation of genetic diversity within maize germplasm, introgression of desirable traits, and selection for prolificacy, it is possible that future grain yields of prolific genotypes will surpass those of non-prolific genotypes.

There are a number of reports which indicate the association of greater prolificacy with higher grain yields (Mareck and Gardner, 1979; Moll and Hanson, 1984; Singh et al., 1986; Subandi, 1990; Maita and Coors, 1996). Some researchers reported that grain yields of prolific genotypes were more stable than those of non-prolific genotypes over different environments (Collins et al., 1965; Russell and Eberhart, 1968; Barnes and Woolley, 1969; Miller et al., 1995). Prolific genotypes tended to produce fewer barren plants at higher plant densities than non-prolific genotypes (Russell, 1968; Duvick, 1974). Prior and Russell (1975) found that prolific hybrids out-yielded non-prolific hybrids at low plant density, but they were lower yielding than non-prolific hybrids at high plant density. The data suggested that prolific genotypes compensated with more grain per unit area at low plant density. Inconsistency of grain yield superiority of prolific vs. non-prolific genotypes over different environments might be attributed to genetic background differences of parents or environmental effects.

One concern among maize breeders selecting for prolificacy is that prolificacy seems to have an association with poor stalk strength and plant standability (Lonnquist, 1967; Duvick, 1974; Motto and Moll, 1983; Thomison and Jordan, 1995; Carena et al., 1998). Poor root and stalk strength for a prolific genotype might be caused by competition between root–stalk and ear sinks for

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