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Effects of Genotype × Environment Interaction on Agronomic Traits in Soybean

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ABSTRACT

Genotype × environment interaction influences the market value of soybean [*Glycine max* (L.) Merr.] protein, oil, and fatty acid traits. The objectives of this research were (i) to evaluate agronomic trait performance and stability of soybean genotypes in individual environments and across environments; and (ii) to evaluate the relationship of test environments for selecting superior genotypes within the mega-environment for soybean production in the southern region of Wisconsin. A total of 68 soybean genotypes were selected from University of Wisconsin soybean evaluation trials and grown at four locations in 2003 and 2004. Soybean genotypes, grown in trials with conventional and Roundup Ready herbicide treatments were analyzed for yield, protein, oil, and the fatty acid components palmitic acid, stearic acid, oleic acid, linoleic acid, and linolenic acid. Repeatability estimates among genotypes ranged from 0.27 to 0.98 with yield and the fatty acid component linolenic acid being the most sensitive to environment effects. Superior genotypes could be consistently selected for yield, protein, oil, and fatty acid components using biplot analysis and stability estimates. Among locations in the southern region in Wisconsin, Arlington provides unique information for soybean fatty acid evaluations, but similar information about soybean yield, protein, and oil with Janesville or Lancaster. So, if soybean fatty acid is not important then Arlington could be dropped as a test site.

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Abbreviations: ARL, Arlington, WI; CN, conventional; E, environment; G, genotype; GE, genotype × environment; GL, genotype × location; GY, genotype × year; GYL, genotype × year × location; JAN, Janesville, WI; LAN, Lancaster, WI; MET, multi-environment trials; RAC, Racine, WI; RR, Roundup Ready.

Soybean [*Glycine max* (L.) Merr.] is an important crop worldwide, especially in eastern Asia. The interaction between genotype and environment results in significant differences in the performance of genotypes when evaluated in different locations (Gauch and Zobel, 1997). To understand the effects of genotype and environment on soybean performance, soybean multi-environment trials (MET) are conducted every year around the world to assist in the identification of superior genotypes and the evaluation of environment relationships, such as determining mega-environments (Yan et al., 2000).

Rao et al. (2002) tested 12 soybean genotypes and found significant genotype × year × location (GYL) effects for grain yield. Fehr (2003) analyzed protein content and found that genotype × environment (GE) interaction has no significant effects on soybean protein components. Several studies have investigated the effects of environments on fatty acids of soybean (Cherry, 1985; Schnebly and Fehr, 1993). These studies reported that higher environmental temperatures reduced linolenic and increased oleic concentration of soybean, and indicated that year effects had significant impact on fatty acid composition. Primomo et al. (2002) investigated GE interaction for soybean fatty acids and found that

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genotype × year (GY) interaction was significant for all fatty acids, but genotype × location (GL) and GYL effects were only significant for oleic, linoleic, and linolenic acids.

GGE Biplot analysis is a powerful tool to visually analyze MET data and understand complex GE interactions (Gauch, 2006). Using biplot methods, genotypes can be evaluated for their performance, stability, and adaptation in individual environments and across environments (Yan and Rajcan, 2003). Simultaneously, environment relationships can be evaluated and mega-environment can be set up by using biplots (Yan et al., 2000).

There have been few examples in the literature describing the use of biplot methods to evaluate GE interaction for soybean yield and quality traits. Yan and Rajcan (2002) graphically displayed the relationship between soybean agronomic traits with genotype and environment in Ontario. Lee (2003) analyzed the effects of year, location and genotype on soybean isoflavones and concluded that environmental effects (Y and YL), as well as GE effects (GY and GYL) were the most important sources of variation for the content of soybean isoflavones. Zhang et al. (2005) used biplot methods to analyze 100 soybean genotypes in Virginia to select the highest yielding and most stable genotypes in different maturity groups.

The objectives of this research were (i) to evaluate agronomic trait performance and stability of soybean genotypes in individual environments and across environments; and (ii) to evaluate the relationship of test environments for selecting superior genotypes within the mega-environment for soybean production in the southern region of Wisconsin. This analysis was undertaken to evaluate how well traditional university test sites were providing variety performance information to farmers.

MATERIALS AND METHODS

Plant Materials

Data were obtained from Wisconsin soybean trials conducted in the southern region in 2003 and 2004. Experiments were conducted at four locations: Arlington (ARL), Janesville (JAN), Lancaster (LAN), and Racine (RAC). The soil type at RAC is an Ashkum silty clay loam (fine, mixed, superactive, mesic Typic Endoaquoll), and the soil type at ARL and JAN is a Plano silt loam (fine-silty, mixed, superactive, mesic Typic Argiudoll), and at LAN has a Fayette silt loam (fine-silty, mixed, superactive, mesic Typic Hapludalf).

Recommended practices for commercial production were used to establish, maintain and harvest experimental plots. Herbicide treatment included conventional herbicide (CN) and Roundup herbicide (RR). The herbicide treatments varied by location and weed pressure. Both herbicide treatments at ARL and LAN had metolachlor, 2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl)acetamide (Dual, Syngenta, Wilmington, DE) and imazethapyr, 2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-5-ethyl-3-pyridinecarboxylic acid (Pursuit, BASF, Research Triangle Park, NC), applied preplant incorporated, while at JAN and RAC, no herbicide was applied before planting. Following planting in the RR herbicide treatment, one application of glyphosate, *N*-(phosphonomethyl)glycine (Roundup), was applied post emergence. In the CN herbicide treatment, various tank mixtures of quizalofop, (±)-2-[4-[(6-chloro-2-quinoxalinyl)oxy]phenoxy]propanoic acid (Assure, DuPont, Wilmington, DE); cloransulam, 3-chloro-2-[[(5-ethoxy-7-fluoro[1,2,4]triazolo[1,5-*c*]pyrimidin-2-yl)sulfonyl]amino]benzoic acid, (Firstrate, DOW, Indianapolis, IN); thifensulfuron, 3-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl] amino]sulfonyl]-2-thiophenecarboxylic acid (Harmony and Pinnacle, DuPont), and/or imazethapyr were tank mixed and applied. Sixteen soybean genotypes were treated with CN herbicides and 52 soybean genotypes treated with RR herbicide were selected.

The experimental design was blocked and randomized for herbicide treatment with four replications at ARL, JAN, and RAC, and three replications in LAN. Soybean genotypes were randomized within herbicide treatment. Grain yield was converted to Mg ha^{-1} at 130 g kg^{-1} moisture.

Grain Composition Analyses

At harvest, a 500-g soybean sample was collected from each plot and analyzed for composition. Protein and oil concentration in soybean seed was determined using a near-infrared reflectance whole grain analyzer (Foss Infratec 1241 grain analyzer; Foss Tecator AB, Hoganas, Sweden). Standardization and calibration equations were conducted by the Grain Quality Laboratory at Iowa State University. Five 100-g subsamples were scanned for each soybean sample. The mean percentage for protein and oil in each soybean sample was calculated. Check samples were run after every 100 samples to assure analysis accuracy and precision consistency.

Fatty acid composition (palmitic acid [16:0], stearic acid [18:0], oleic acid [18:1], linoleic acid [18:2], and linolenic acid [18:3]) was analyzed by gas chromatography (Shimadzu GC-2010; Shimadzu Corporation, Kyoto, Japan). Five seeds per sample were analyzed and mean percentage was calculated. A reference standard containing known amounts of fatty acid components (Nu-chek-prep, Inc., Elysian, MN) was run every 50 samples to assure analysis accuracy and precision.

Statistical Analysis

Independent analyses were conducted for each of the agronomic traits of yield, protein, oil, and fatty acid composition. The analysis of variance was obtained using PROC GLM in SAS (SAS Institute, 1996). Restricted maximum likelihood (REML) estimates of the variance components were obtained using PROC MIXED in SAS (SAS Institute, 1996). Years, locations, and replications were considered random effects, whereas genotype was considered a fixed effect. Conventional and RR trials were analyzed separately. Because genotype was considered as a fixed effect in this experiment, heritability estimates could not be calculated; rather estimates of repeatability were determined. Repeatability is dependent on the genotypes evaluated as well as the environments in which they were evaluated. When genotypes are randomly sampled from a defined reference population, repeatability is termed broad-sense heritability or coefficient of genetic determination. Repeatability is the ratio of variance

within individuals to variance between individuals and sets an upper limit to heritability (Falconer and Mackay, 1996). Repeatability estimates were calculated by the formula:

$$r = \left[(V_G) / \left(V_G + \frac{V_{GY}}{y} + \frac{V_{GL}}{l} + \frac{V_{GYL}}{yl} + \frac{V_E}{ryl} \right) \right] \quad [1]$$

where V_G, V_{GY}, V_{GL}, V_{GYL}, and V_E refer to variance due to genotype, genotype × year, genotype × location, genotype × year × location, and error, respectively (Lorenz and Coors, 2008; Gravois and Bernhardt, 2000). Coefficients y, l, and r refer to the number of years, locations, and replications per location per year, respectively (Cooper and Hammer, 1996; Falconer and Mackay, 1996).

The correlation among genotype ranks at different locations was estimated using Spearman's rank correlation analysis. Stability parameters were estimated by regressing the genotypic means in each location on an environmental index, according to the method by Eberhart and Russell (1966). The environmental index was estimated as the mean of all genotypes at a specific location minus the grand mean. The GGE biplot method (Yan and Kang, 2003) was used to study the GE interaction relationship among locations.

RESULTS AND DISCUSSION

Analysis of Variance

In the CN trial, the Y effect was significant for yield, oil, palmitic, and linolenic acid (Table 1). The L effect was significant only for palmitic acid. The YL interaction was significant for protein, stearic, oleic, linoleic, and linolenic acids. Genotypic effects were significant for all agronomic traits. For GE interaction effects, the GY interaction was significant for oil, palmitic, oleic, linoleic and linolenic acids; the GL interaction was nonsignificant for all traits; the GYL interaction was significant for yield, protein, oil, oleic, and linoleic acids.

In the RR trial, Y effect was significant for oil, palmitic, and linolenic acids. Similar to the CN trial, both L and GL interactions were nonsignificant for all traits in the RR trial. The YL, G, and GY interactions were significant for all traits. The GYL interaction was significant for yield, protein, oil, and oleic, linoleic, and linolenic acids.

Repeatability of Soybean Traits

Repeatability indicates the effect of nongenetic factors on phenotypic variance. The smaller repeatability is, the larger the GE component will be. Yield and linolenic acid were the least repeatable (most sensitive) to environment effects, although yield was not consistent between trials (Table 2). Repeatability of yield was high in the CN trial (0.93) but was very low (0.27) in RR trial. One possible reason is recent differences in breeding effort between CN and RR genotypes. Another possible reason for high yield repeatability in the CN trial is that there are high proportions of food-grade soybean genotypes in the CN trial compared to the RR trial. Food grade soybean genotypes, which contain high protein content, may be stable and less sensitive to environment effects for yield (Rao et al., 2002).

In the CN trial, repeatability of yield was similar to protein and oil. In both CN and RR trials, protein and oil had similar repeatability as the saturated fatty acid components palmitic and stearic acid. Unsaturated fatty acids (oleic, linoleic, and linolenic acids) had lower repeatability in both trials with linolenic acid always the lowest of all fatty acids. The interactions GY and GYL were major sources of variation for lowering repeatability of yield and the unsaturated fatty acids oleic, linoleic, and linolenic. In both trials, there were no significant GL interactions for any measurement.

In both trials, Spearman rank correlations among four locations were more consistent and higher for protein, oil, and palmitic, stearic, oleic, and linoleic acids than grain yield and linolenic acid (data not shown). High correlation indicated that significant GE interactions did not result from genotype rank changes, but rather from relative performance differences for these traits across the different locations. For yield, ARL, JAN, and LAN had higher correlations ($r \geq 0.7$) with each other but lower correlation with RAC ($r \leq 0.60$) in both herbicide treatments, indicating that ARL, JAN, and LAN could provide similar rank order for yield, but RAC would provide different rank information because of GE interaction.

Soybean Agronomic Traits Stability and Which-Won-Where

Yield is directly related to soybean market value. Yield in the RR trial was more sensitive to GE interaction than the other agronomic traits as calculated by repeatability (Table 2). Therefore, predicting grain yield or picking superior genotypes according to yield is more challenging and better accomplished using MET.

Stability describes the degree of similarity of a genotype's performance to an estimated or predicted level (Becker, 1988). The regression coefficient (b) describes the linear response of a genotype across different environments; the deviation from regression describes the performance consistency (Eberhart and Russell, 1966). Higher regression values (>1.0) describe higher sensitivity to environmental change and better performance in good environments, but worse than average performance in bad environments. Lower regression coefficients (<1.0) describe lower sensitivity to environmental change and better performance in poor environments, but worse than average performance in good environments. When a regression coefficient (b) is close to 0, it indicates stable performance of a genotype across environments, whereas when a b value is close to 1, it indicates that the genotype behaves similarly to the average across all environments.

For soybean grain yield in the CN trial (Fig. 1A), 3 of the 16 soybean genotypes (8, 11, and 13) yielded greater

Table 1. Mean squares from analysis of variance of yield, protein, oil, and fatty acid compositions for soybean genotypes in Wisconsin's southern region during 2003 and 2004.

Source†	df	Yield	Protein	Oil	Palmitic	Stearic	Oleic	Linoleic	Linolenic
Conventional trial									
Y	1	35.08*	37.14	293.8**	50.84**	15.09	21.21	0.61	267.8**
L	3	2.38	24.97	17.42	6.48*	7.22	80.55	51.17	9.19
YL	3	2.24	45.02**	2.64	0.30	6.58**	28.67*	20.58*	6.77**
Replication/YL	22	1.15	5.76	1.34	0.48	0.42	6.27	5.95	0.35
G	15	2.76**	61.94**	10.75**	10.86**	4.81**	53.69**	43.50**	1.80*
GY	15	0.16	1.34	0.61*	0.46**	0.14	9.20**	8.55**	0.70**
GL	45	0.22	1.01	0.35	0.15	0.14	2.89	2.22	0.18
GYL	45	0.24**	0.86**	0.27**	0.12	0.17	3.53**	2.71**	0.19
Error	291	0.09	0.28	0.09	0.13	0.16	1.77	1.43	0.14
Roundup Ready trial									
Y	1	165.09	138.94	1198.72**	101.83**	189.85	16.30	18.26	1041.61*
L	3	11.50	109.27	137.30	13.52	17.52	545.20	291.88	64.07
YL	3	21.80**	140.40**	21.71**	2.46**	56.59**	249.33**	151.93**	35.62**
Replication/YL	22	0.97	7.93	1.99	0.29	0.20	4.59	4.77	0.22
G	51	0.55**	30.70**	5.43**	6.43**	5.13**	132.77**	103.48**	3.30**
GY	51	0.39**	1.82**	0.41*	0.50**	0.46**	16.71**	14.63**	0.75**
GL	153	0.22	0.56	0.31	0.25	0.23	5.10	3.68	0.26
GYL	153	0.20**	0.61**	0.25**	0.23	0.19	7.04**	5.43**	0.22*
Error	1094	0.12	0.34	0.15	0.19	0.18	2.25	1.83	0.17

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

†Y, year; L, location; G, genotype.

Table 2. Estimates of variance components and repeatability for yield, protein, oil, and fatty acid composition of soybean genotypes in the southern region of Wisconsin evaluated in 2003 and 2004.

Source†	Yield	Protein	Oil	Palmitic	Stearic	Oleic	Linoleic	Linolenic
Conventional trial								
G	0.095	2.269	0.374	0.387	0.172	1.617	1.278	0.038
GY	0.000	0.035	0.025	0.025	0.000	0.380	0.390	0.036
GL	0.000	0.022	0.011	0.003	0.000	0.000	0.000	0.000
GYL	0.037	0.172	0.054	0.000	0.001	0.412	0.305	0.015
Residual	0.094	0.278	0.091	0.131	0.157	1.782	1.430	0.139
Repeatability	0.93	0.98	0.94	0.97	0.97	0.84	0.82	0.61
Roundup Ready trial								
G	0.005	0.996	0.172	0.203	0.164	3.943	3.021	0.086
GY	0.013	0.084	0.013	0.018	0.019	0.674	0.649	0.036
GL	0.004	0.000	0.007	0.003	0.005	0.000	0.000	0.006
GYL	0.021	0.066	0.029	0.011	0.003	1.030	0.737	0.013
Residual	0.005	0.343	0.147	0.192	0.180	2.266	1.834	0.167
Repeatability	0.27	0.94	0.91	0.92	0.91	0.88	0.86	0.77

†G, genotype; Y, year; L, location.

than one standard deviation above the mean grain yield with 8 and 13 having mean *b* values within one standard deviation of 1; and Genotype 11 having a mean *b* value one standard deviation above 1.

For the RR trial (Fig. 1B), 8 of the 52 soybean genotypes produced one standard deviation above-average grain yield, with Genotypes 27, 30, 31, 35, 36, and 49 having mean *b* values within one standard deviation of 1; Genotype 62 had a mean *b* value one standard deviation above 1; and Genotype 53 had a mean b value one standard deviation below 1.

Biplots effectively identify GE interaction and which-won-where information (Yan et al., 2000). Using biplot methods, genotypes can be evaluated for their performance, stability, and adaptation in individual environments and across environments. Figure 2 indicates which genotype won where for soybean yield in the CN and RR trials. In the CN trial (Fig. 2A), principal components 1 and 2 together explained 81.4% of the observed variation for soybean grain yield. RAC in 2003, JAN in 2003, and ARL in 2003 were in the same sector, with 8 as the highest yielding genotype. LAN in 2003 and 2004, JAN in 2004, and ARL in 2004 were in the same sector, with 11 as the highest yielding genotype. RAC in 2004 was

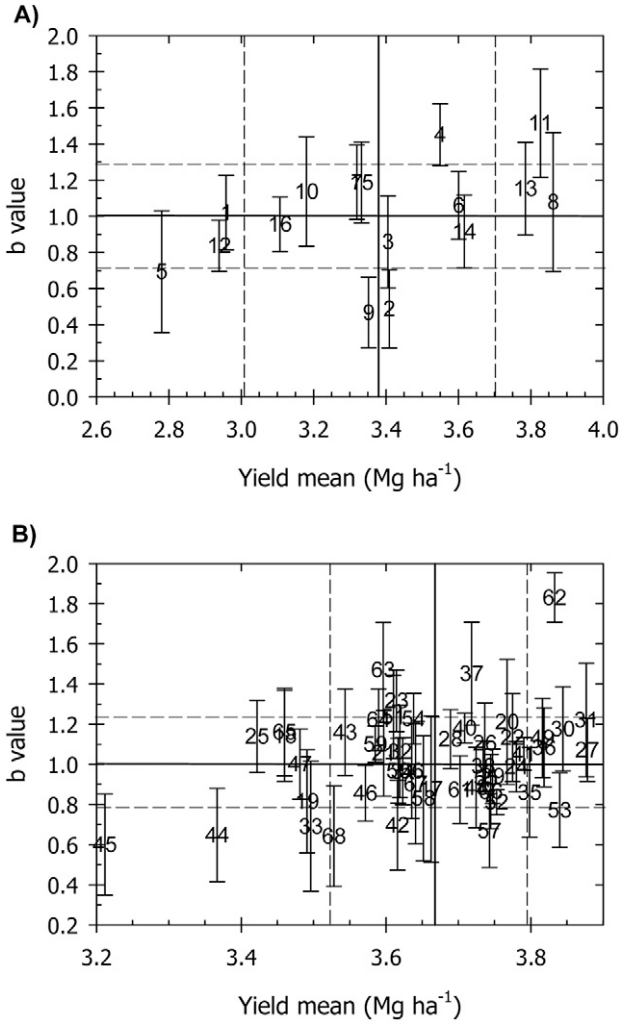

Figure 1. The stability of yield for soybean genotypes in (A) conventional (CN) trial including 16 genotypes, and (B) Roundup Ready (RR) trial including 52 genotypes in the southern region of Wisconsin. Genotype regression coefficients (*b* value) are plotted against their mean grain yield. The *b* value describes the linear response of a genotype across changing environments. The vertical solid line is the grain yield mean. The vertical dashed lines are one standard deviation above and below the mean. The horizontal solid line represents a regression coefficient of average stability (*b* = 1.0). The horizontal dashed lines are one standard deviation above and below the average slope (*b* = 1.0).

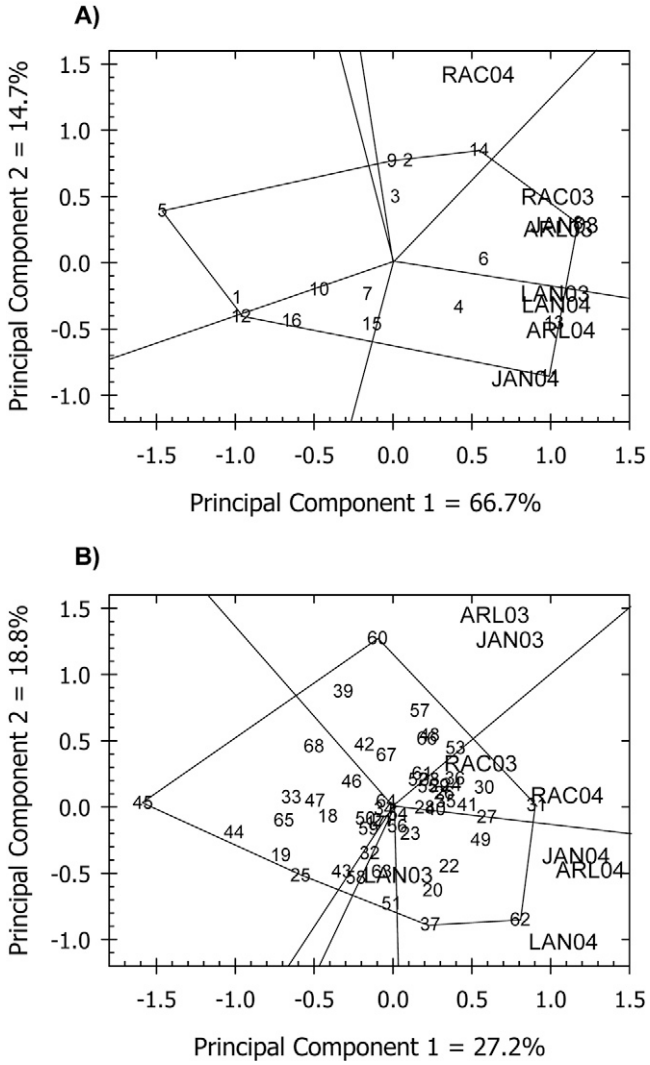

Figure 2. GGE biplot for soybean yield in the (A) conventional (CN) and (B) Roundup Ready (RR) trials in the south region of Wisconsin, showing which genotypes yielded most by location. PC1 and PC2 are first and second principal components, respectively.

grouped individually and Genotype 14 performed the best for grain yield in this sector.

In the RR trial (Fig. 2B), principle components 1 and 2 together explained 46% of the observed variation for soybean grain yield. JAN and ARL in 2003 fell in the same sector, with 60 as the highest yielding genotype. LAN in 2003 and 2004 were grouped together with JAN 2004 and ARL 2004, with 62 as the highest yielding genotype. RAC in 2003 and 2004 were grouped together with 31 as the highest yield genotype. Both which-won-where biplots indicate that LAN provides similar information for soybean yield in both years. ARL and JAN provide different yield information in 2003 and 2004, but they always share the same best set of genotypes.

Test Site Evaluation

Ideal test locations effectively discriminate genotypes and represent their mega-environment (Yan and Rajcan, 2002). Using biplots, test locations can be classified into three types: (i) locations with low genotype discrimination that should not be selected as test locations; (ii) locations with high genotype discrimination and representative of the mega-environment that are close to ideal and should be chosen for superior genotype selection, when few test locations can be managed due to budget constraints; and (iii) locations with high genotype discrimination that do not represent the mega-environment, which could be used for unstable genotype evaluation (Yan et al., 2007).

To evaluate test locations in the southern region of Wisconsin, biplots were generated for soybean yield

(biplots not shown). All four locations showed high genotype discrimination. According to methods by Blanche and Myers (2006), the mean distance from the ideal location for each test location across 2 yr were calculated to obtain the ideal location information within the southern region of Wisconsin (example for yield in Table 3). In the CN trial, ARL was closest to the ideal location, followed by JAN, LAN, and RAC. In the RR trial, JAN was closest to the ideal location, followed by ARL, LAN, and RAC (Table 3). Biplots for soybean protein, oil, and fatty acids were generated (biplots not shown). All locations showed high genotype discrimination for agronomic traits. Standardized distances were calculated, and the ideal locations for each trait in the southern region were ranked according to the same method above. Some test locations may provide similar information with at least one other test location in the same mega-environment. To identify redundant locations, research costs can be reduced without loss of information to separate and rank genotypes (Yan et al., 2007). In this analysis, since there was no GL interaction, genotypes did not change rank for agronomic traits, but no single location was ideal for yield, protein, oil, and fatty acid components. But, if we are only interested in soybean yield, protein, and oil, without regard to fatty acid component, ARL could be dropped, because it did not provide much unique information.

CONCLUSIONS

Genotype × environment interaction influenced agronomic traits. Some locations were better for testing than others. The repeatability of yield was lower than protein and oil, and unsaturated fatty acids displayed lower repeatability than saturated fatty acids. Like repeatability, among agronomic traits, the ranking correlations of four locations were always lower for yield and linolenic acid, which contain three unsaturated double bonds. These results indicate that yield and unsaturated fatty acid, especially linolenic acid, are more sensitive to GE interaction than other agronomic traits. "Which-won-where" information from biplots and genotype stability provided comprehensive information about features of each genotype across environments. This information makes it efficient to select suitable winning genotypes according to different requirements such as agronomic performance and stability. Location relationships were analyzed by rank correlations and biplot analyses. Ideal locations were ranked for each agronomic trait and herbicide treatment based on genotype discrimination and representation of the mega-environment. According to GGE biplot and location correlation, the uniqueness of each test location was evaluated. There is no redundant location in this mega-environment to test soybean yield, protein, oil, and fatty acid at the same time. But if we only focus on yield, protein, and oil, ARL could be dropped as a test location in the mega-environment without much loss of information.

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Table 3. Standardized distance between actual and ideal locations and ranking of four locations in the southern region by the distance to ideal location for soybean agronomic traits in Conventional and Roundup Ready trials averaged over 2003 and 2004.

Location†	Yield distance	Ranking							
		Yield	Protein	Oil	Palmitic	Stearic	Oleic	Linoleic	Linolenic
Conventional trial									
ARL	0.443	1	2	3	3	3	2	4	4
JAN	0.765	2	1	1	1	1	1	1	2
LAN	1.283	3	3	2	2	4	3	2	1
RAC	1.508	4	3	4	4	2	4	3	3
Roundup Ready trial									
ARL	0.928	2	3	1	4	1	3	2	3
JAN	0.734	1	2	2	2	1	1	1	1
LAN	0.986	3	1	3	1	3	2	3	2
RAC	1.352	4	4	3	3	2	4	4	4

†ARL, Arlington; JAN, Janesville; RAC, Racine; LAN, Lancaster.

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