GENOTYPE × ENVIRONMENT INTERACTION STUDY OF BERMUDAGRASS YIELDS IN OKLAHOMA

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Gentoype × environment (GE) interactions were studied using forage yield data from 11 bermudagrass [*Cynodon dactylon* (L.) Pers.] genotypes agronomically evaluated for 3 years (1974 through 1976) at each of four Oklahoma locations. Mean squares, estimated variance components, and regression analysis were used to draw conclusions.

The first-order genotype × year (GY) interaction had a statistically nonsignificant ($P > .05$) mean square and a relatively small variance component ($\hat{\sigma}^2_{GY} = 0.11$). The mean square and the variance component attributable to the genotype × location (GL) interaction effect were respectively, significant ($P < .05$), and of intermediate magnitude ($\hat{\sigma}^2_{GL} = 0.33$). The genotype × replication in location GR(L) and the second-order genotype × location × year (GLY) interactions had highly significant ($P < .01$) mean squares and large variance components ($\hat{\sigma}^2_{GR(L)} = 0.73$, $\hat{\sigma}^2_{GLY} = 0.64$).

The results emphasized the considerable magnitude of GE interactions and the necessity for multiple environment testing through time and space to characterize relative genotypic differences. The nonsignificant mean square and the relatively small variance component attributable to the effect of years indicates that the duration of testing is less important than the number of locations at which the testing is conducted.

Regression analysis gave some indication of, but did not elucidate, relative genotypic yield stability across environments. It was very useful, however, in ascertaining specific instances of genotypic instability.

INTRODUCTION

The failure of two or more genotypes (cultivars, lines, strains, etc.) to respond similarly to an environment (genotype × environment interaction) complicates their agronomic evaluation and characterization with respect to relative performance potential and usefulness. Such genotype × environment (GE) interactions prevent the extrapolation of results of agronomic evaluations from one location to another, thus requiring expensive trials at multiple locations. Knowledge of the magnitudes of GE interactions and of the various sources of variation in GE interactions, such as the genotype × year or the genotype × location, is useful in decision-making regarding the amount of testing necessary through time (years) and space (locations) to accurately measure relative genotypic performance (1-5). Additionally, regression analyses methods have been devised to measure the stability of performance, or general adaptation, of individual genotypes across varying environments in an effort to provide meaningful biological explanation of GE interactions (6, 7).

The Oklahoma Agricultural Experiment Station supports an extensive bermudagrass [*Cynodon dactylon* (L.) Pers.] breeding improvement program having as its principal goal the transfer of higher nutritive value from unadapted tropical species to adapted types with high yield potential. In such a program selected genotypes must be thoroughly compared to existing cultivars and their geographic areas of adaption should be described prior to release for public use. In Oklahoma, bermudagrass is used over a wide range of climatic and edaphic conditions ranging from the semi-arid western regions to the more humid regions of the east. The temperature differential across the state is of major importance since bermudagrass genotypes often differ in winterhardiness and it is primarily this trait which dictates the latitude to which they can be successfully utilized.

The studies reported herein assess the importance of GE interactions in bermuda-

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grass forage yields in Oklahoma, estimate the relative magnitudes of the components of GE interactions, and draw conclusions regarding evaluation procedures in the state.

MATERIALS AND METHODS

The data used in the yield analyses are from four cultivars and seven experimental genotypes of bermudagrasses grown for 3 years (1974-1976) at each of four Oklahoma locations near Altus, Chickasha, Mangum, and Muskogee. The experimental strains were from the Oklahoma Agricultural Experiment Station bermudagrass breeding project and carried the designations S-13, S-29, S-54, S-24, SS-16, SS-27, and S-78. The cultivars were 'Midland', 'Hardie', 'Oklan', and 'Alicia'. All represent single plants that have been clonally propagated and will henceforth be referred to as genotypes except where a distinction is made between cultivars and experimental lines.

The test locations were selected to sample the climatic and edaphic conditions likely to be encountered in growing bermudagrass throughout the state. Mangum, in the southwestern portion of Oklahoma, is characterized by semiarid conditions and has a Meno sandy loam soil, a member of the loamy, mixed, thermic Aquic Arenic Haplustalfs. Altus, also in the southwest, is likewise characterized by semi-arid conditions but some supplemental irrigation water was applied during dry periods. That location has a complex soil series of Tillman clay loam, a member of the fine, mixed, thermic Typic Paleustolls and Hollister clay loams, a member of the fine, mixed, thermic Pachic Paleustolls. Chickasha, in central Oklahoma, represents a moderate rainfall area and has a Reinach silt loam soil, a member of the coarse-silty, mixed, thermic Pachic Haplustolls. Muskogee, in eastern Oklahoma, represents a relatively high rainfall area and has a Taloka silt loam soil, a member of the fine, mixed, thermic Mollic Albaqualfs.

All test plats were planted in the spring of 1973. The field plot design at each location was a randomized complete block with four replications. The grass in individual plots was started by transplanting ten greenhouse-grown plants approximately 0.62 m apart in a 6-m long row. The laterally spreading, sod-forming grasses were restricted to plots measuring approximately 1.83 × 6.10 m. All plots were fully covered by grass by the end of the 1973 growing season. During each year of the 3-year test period all plots received two applications of nitrogen fertilizer. The first application was made in April and the second in late June or July. The yearly total amounts of actual elemental nitrogen applied to the respective tests varied between locations from approximately 134 to 179 kg/ha. Forage yields were measured by harvesting and weighing material from a 0.92 × 5.49 m swath from the center of each plot. Samples of the harvested forages were taken for determination of moisture content, and these data were then used to convert yields to a dry matter basis. Yield data within a year were summed over cuts to give total seasonal production figures on which the analyses herein were conducted.

A conventional analysis of variance based on that outlined by Comstock and Moll (2) and modified to fit a perennial crop by Taliaferro *et al*. (8) was used to separate the components of variance. A random-effects model was used assuming a random sampling of genotypes, locations, years, etc. Unbiased estimates of the genetic and environmental components of variance were obtained by equating the expected mean squares with those calculated from the experiment. Cochran's (9) method for deciding upon the appropriate F-test and calculation of degrees of freedom was used.

Because the analysis of variance indicated the presence of significant GE interactions, a joint regression analysis as outlined by Eberhart and Russell (6) was used to determine whether the interactions were a linear function of the additive environmental component. An environmental index was calculated by taking the means of all genotypes grown at a particular location in a particular year and subtracting from that quantity the mean of all genotypes over all environments. The regression of mean yield on environmental index was obtained for each genotype within and over years. The regression coefficient (*b*) measures the increase in mean yield of a genotype per unit increase in environmental index. The standard deviation ($\bar{s}_d$) of residuals about the regression line measures how well predicted response agrees with that actually observed and includes GE

TABLE 1. *Mean dry matter yield performance (metric tons/ha) of bermudagrass genotypes by year over the four locations.*

Genotype	1974	Rank	1975	Rank	1976	Rank	Avg.
S-13	5.47	1	10.92	1	8.41	1	8.27
Hardie	4.87	2	10.00	2	7.39	5	7.42
Midland	4.73	3	9.71	3	7.41	4	7.28
Oklan	4.23	7	9.26	5	8.22	2	7.24
Alicia	4.09	8	9.34	4	7.52	3	6.98
S-54	4.58	5	8.87	6	6.40	6	6.62
S-24	4.56	6	8.69	8	5.46	10	6.24
S-29	3.66	9	8.83	7	5.72	7	6.07
SS-16	4.63	4	7.67	10	5.53	9	5.94
SS-27	3.13	11	7.29	11	5.70	8	5.37
S-78	3.41	10	7.77	9	4.61	11	5.26
Avg.	4.31		8.94		6.58		6.61

TABLE 2. *Mean dry matter yield performance (metric tons/ha) of bermudagrass genotypes by location over the three years.*

Genotype	Muskogee	Rank	Altus	Rank	Chickasha	Rank	Mangum	Rank	Avg.
S-13	6.49	10	9.85	1	8.38	1	8.36	1	8.27
Hardie	9.04	2	7.54	3	6.82	4	6.27	3	7.42
Midland	9.64	1	7.20	4	6.91	3	5.39	7	7.29
Oklan	7.06	7	6.74	7	7.88	2	7.27	2	7.24
S-54	7.37	5	7.01	6	6.72	5	5.38	6	6.62
Alicia	7.63	4	7.57	2	6.65	6	6.09	4	6.49
S-24	7.09	6	7.03	5	6.36	8	4.47	9	6.24
S-29	6.81	8	6.38	8	6.64	7	4.45	10	6.07
SS-16	7.89	3	5.75	9	4.88	11	5.26	8	5.95
SS-27	6.56	9	5.18	10	5.67	10	4.08	11	5.37
S-78	5.06	11	4.02	11	6.27	9	5.71	5	5.27
Avg.	7.33		6.57		6.65		5.70		

TABLE 3. *Mean squares relevant to the study of genotype × environment interactions.*

Source	Dry matter yield (metric tons/ha) df	Mean square
Genotypes (G)	10	41.28**
G × Locations (L)	30	9.74*
G × Years (Y)	20	5.32
G × L × Y	60	3.56**
G × Replications (R) in L	120	3.17**
Error (e)	240	0.99

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

interactions. A stable genotype, as described by Eberhart and Russell (6), has a regression coefficient of unity ($b = 1.0$) and deviations from regression as small as possible ($\bar{s}_d = 0.0$).

RESULTS

Yield, Analyses of Variance, and Estimates of Variance Components. Mean genotypic yields, averaged over locations, differed significantly ($P < .01$) during each test year and over test years. There was only slight variation in the relative rankings of individual genotypes from year to year (Table 1). The mean yields of geno-

TABLE 4. *Variance component estimates and their standard errors for yield.*

Component	Dry matter yield (metric tons/ha) Estimate	$\bar{s}_d$
G	0.62	0.39
GL	0.33	0.37
GY	0.11	0.11
GLY	0.64	0.16
GR(L)	0.73	0.14
e	0.99	

types at the respective locations, averaged over years, also differed significantly ($P < .05$), but there was considerably more variation in the relative rankings of individual genotypes from location to location, as compared to that from year to year (Table 2).

Mean squares and estimates of variance components relevant to the study of GE interactions are given in Tables 3 and 4, respectively. Mean squares associated with the GR(L) and GLY interactions were highly significant ($P < .01$). The GL and GY interactions had respectively, significant ($P < .05$) and nonsignificant ($P > .05$) mean squares.

The variance component estimate for $\hat{\sigma}^2_{GY}$ was relatively small (0.11) compared to estimates for the other components. The estimate for the $\hat{\sigma}^2_{GL}$ component was of intermediate size (0.33) while the estimates for the $\hat{\sigma}^2_{G}$, $\hat{\sigma}^2_{GR(L)}$ and $\hat{\sigma}^2_{GLY}$ components were large (0.62, 0.73 and 0.64, respectively) and were exceeded only by the error component $\hat{\sigma}^2_{e}$ (0.99).

Regression Analysis

Regression coefficients and their standard errors for the 11 genotypes are listed in Table 5. With yields averaged over locations and years, all genotypes had regression coefficients within two standard errors of unity (1.0). For location yields, averaged over years, several genotypes had regression coefficients differing from unity by more than two standard errors.

The standard deviation of residuals about the regression line vary considerably within and over locations (Table 6). The genotypes could be arbitrarily divided into low, intermediate, and high groups based on their standard deviation of residuals. The genotypes S-29, S-54, Hardie, and SS-27 had relatively low standard deviations. Genotypes S-24, S-78, Midland, Alicia, and SS-16 had standard deviations of intermediate magnitude while genotypes Oklan and S-13 had relatively high standard deviations. Specific instances of genotypic instability, based on significant yield deviations from a 95% confidence interval set about the

TABLE 5. *Regression coefficients and their standard errors for forage yields of the bermudagrass genotypes over years.*

Genotype	Test location				Over Locations
	Altus	Chickasha	Mangum	Muskogee	
S-13	1.25 ± 0.02	1.21 ± 0.18	1.42 ± 0.68	0.39 ± 0.05	0.98 ± 0.26
Hardie	1.05 ± 0.16	0.93 ± 0.06	1.35 ± 0.14	1.22 ± 0.10	1.10 ± 0.10
Midland	1.32 ± 0.09	0.99 ± 0.02	1.03 ± 0.09	0.97 ± 0.14	1.14 ± 0.14
Oklan	1.06 ± 0.65	1.30 ± 0.45	1.23 ± 0.57	0.50 ± 0.34	1.02 ± 0.22
Alicia	0.94 ± 0.94	1.14 ± 0.11	0.66 ± 0.15	1.68 ± 0.46	1.07 ± 0.16
S-54	0.79 ± 0.56	0.90 ± 0.17	1.24 ± 0.12	1.02 ± 0.15	0.98 ± 0.09
S-24	1.33 ± 0.45	0.88 ± 0.10	0.78 ± 0.51	0.82 ± 0.14	0.98 ± 0.12
S-29	1.32 ± 0.08	1.05 ± 0.15	0.87 ± 0.04	1.25 ± 0.19	1.11 ± 0.08
SS-16	0.47 ± 0.19	0.62 ± 0.31	0.61 ± 0.31	0.93 ± 0.37	0.69 ± 0.17
SS-27	0.91 ± 0.01	0.98 ± 0.06	0.66 ± 0.25	1.09 ± 0.67	0.96 ± 0.11
S-78	0.58 ± 0.27	1.01 ± 0.11	1.13 ± 0.40	1.14 ± 0.26	0.97 ± 0.13

TABLE 6. *Standard deviation of residuals about the regression line for forage yields of the bermudagrass genotypes over years.*

Genotype	$\bar{s}_d$				
	Altus	Chickasha	Mangum	Muskogee	Over Locations
S-29	0.21	0.79	0.13	0.49	0.59
S-54	1.51	0.86	0.36	0.40	0.68
Hardie	0.45	0.29	0.45	0.26	0.74
SS-27	0.04	0.31	0.77	1.78	0.82
S-24	1.22	0.53	1.58	0.38	0.92
S-78	0.74	0.55	1.25	0.68	1.00
Midland	0.24	0.08	0.29	0.38	1.05
Alicia	2.54	0.56	0.46	1.21	1.18
SS-16	0.51	1.59	0.98	0.99	1.27
Oklan	1.77	2.31	1.77	0.91	1.61
S-13	0.05	0.95	2.12	0.13	1.97

regression line for each genotype, could be detected at individual locations in individual years.

DISCUSSION

The highly significant mean square and the large variance component estimate for the GLY interaction indicate the necessity for multiple environmental testing if the relative performance of bermudagrass genotypes is to be accurately assessed for a large geographic region. This gives no clues, however, as to how such testing should be distributed through time and space. The magnitudes of the mean squares and variance components for the GY and GL interaction effects suggest that years have considerably less effect than locations on relative yield performance. However, bermudagrass genotypes differ in their ability to persistently maintain good stands and yield potential. Some genotypes, particularly those with intermediate levels of winterhardiness, may perform satisfactorily for a period of time, perhaps a year or two, then begin to deteriorate in stand and yield. This is due apparently to an interaction of the stress brought upon the genotypes by multiple seasonal harvests and natural environmental hazards including freeze damage, drought, and attacking insect or disease pests or both. Genotypes have a threshold tolerance level to these stresses which when surpassed results in stand decline and yield reduction. Consequently, it is necessary to test genotypes for a minimum of 2 years, with any additional years of testing giving greater reliability to the results. However, if a choice has to be made between increasing the number of years of testing beyond 2 (or perhaps 3) and increasing the number of testing locations, our data indicate the latter to be the better choice.

The highly significant mean square and the large variance component for the GR (L) interaction mean that the magnitude of the yield differences between genotypes varied from replication to replication in the individual tests. In the testing of perennial crops such as bermudagrass, replications remain static for the duration of the test and there is consequently some correlation of individual plot yields from year to year. Such correlations tend to cause underestimation of true GE interactions and an overestimation of the true genotypic component. The large GR(L) interaction and error effects are not unusual in tests of this type but are nonetheless disturbing by virtue of their graphic illustration of the amount of variability generated at the submacro- to microenvironmental levels. Since clonal propagules of single genotypes are used to establish plot replicates, the yield variability from such plots should be due entirely to environment or experimental errors (measurement error) or both. The relative size of these effects should conceivably be reduced by using more uniform test environments or more replications or both. From a practical standpoint, however, these measures are frequently either not possible or not feasible. The use of more elaborate experimental designs, e.g. lattices and latin squares, may sometimes prove beneficial in reducing experimental error.

The regression analysis did not elucidate the relative performance stability over environments of genotypes but did pinpoint specific instances of yield instability. On the basis of the standard deviations of residuals about the regression line, the genotypes S-54 and S-29 were the most stable. Though their performance was relatively poor, they were the most consistent over locations and years. Several genotypes had regression coefficients larger than one though they did not differ from one by more than two standard errors. Joppa *et al*. (7) point out that regression coefficients larger than one are indicative of either better than average performance in high-yield environments or worse than average performance in lowyield environments.

From the data presented, we conclude that the large GE interactions for bermudagrass forage yields in Oklahoma mandate multiple environmental testing to elucidate true genotypic yield performance across the state. These tests must be conducted at several locations representing as many of the major climatic and edaphic regions as possible. We believe that the duration of the tests should be at least 3 years including the year of establishment.

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