

GENOTYPE-ENVIRONMENT INTERACTION STUDY  
OF BERMUDAGRASS YIELD

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## CHAPTER I

### INTRODUCTION

Genotype-environment interactions can pose serious problems in forage crop cultivars because such crops are grown over a diverse range of climatic, edaphic, and management conditions with multiple cuttings each season. Such interactions occur when two or more genotypes fail to respond consistently in relation to one another and under different environmental conditions. Therefore, it is important for the breeder to adequately sample the environments under which his potential new cultivars are expected to be grown. The importance and relative magnitudes of the various interactions can help the plant breeder determine the number and distribution of test environments needed to adequately characterize the agronomic performance of breeding lines or new cultivars within a geographic area or time period or both. Those environments are commonly subdivided into years and locations with replicated field trials in each. Thus, the breeder must determine and use the best combination of those variables in testing his material.

Bermudagrass [Cynodon dactylon (L.) Pers.] is a major warm-season, sod-forming grass, the cultivars generally being vegetatively propagated and thus constituting single

genotypes. The existing evidence for genotype-environment interactions in bermudagrass yield can be expressed by a contrast of the differences between the cultivars Suwannee, Midland, and Coastal. Suwannee was developed for use on extremely sandy soils, where it is superior to Coastal. It is characterized by being superior in productivity and efficiency of nutrient and water use on deep sand. Midland differs from Coastal and Suwannee in having more winterhardiness and thus is superior to them in forage yield where winter temperatures are more severe. However, if Coastal, Midland, and Suwannee are grown in warmer climates where cold hardiness is not a major factor then Coastal and Suwannee will nearly always out yield Midland. Therefore, these three cultivars indicate definite evidence that genotype-environment interactions occur in bermudagrass.

The current breeding objective of the bermudagrass improvement program is to develop cultivars which are high yielding and, hopefully, have better nutritive value than current cultivars. In order to achieve this objective, crosses are made between the winterhardy (temperate types) bermudagrasses with moderate to low nutritive value and the non-winterhardy (tropic types) bermudagrasses which have the high nutritive value. Progeny from such crosses are usually intermediate between the parents in level of winterhardiness and other important characteristics. In order to adequately evaluate these progeny, one needs information pertaining to



the extent of genotype-environment interaction that will likely occur when testing these materials.

The primary purpose of this research was to assess the importance of genotype-environment interactions in bermudagrass yield, therefore, reducing the difficulties in adequately planning and interpreting further evaluation experiments. Results from these performance tests should also exhibit the relative merits of the tested strains compared to released cultivars and to each other.

Chapters II, III, IV, and V will be presented in a form acceptable to the Crop Science Society of America for publication in its journal, Crop Science.<sup>1</sup>

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<sup>1</sup>Fuccillo, D. A., and R. C. Dinauer (co-chairmen). 1976. Handbook and style manual for ASA, CSSA, and SSSA publications. Crop Sci. Soc. Am., Madison, Wisc.

## CHAPTER II

### ABSTRACT

Eleven bermudagrass [Cynodon dactylon (L.) Pers.] clones were tested in replicated experiments at four locations in Oklahoma over a 3-year period (1974 through 1976). Yield data from these clones were used to study genotype-environment interactions. Mean yield for each clone, averaged over locations, differed widely from year to year and over years.

A nonsignificant mean square and small variance component for the clones by years interaction suggested minimal effects of years on relative yields of bermudagrass. Significance at the 0.05 probability level and a variance component intermediate in size for the clones by locations interaction suggested intermediate effects of locations on relative yielding ability. The highly significant mean square and large variance component for the clones by locations by years interaction indicated that testing in a number of environments is necessary to reliably estimate relative yield performance in bermudagrass, but it indicates nothing about how those experiments should be distributed over years and locations.

The mean yield responses of the 11 bermudagrass clones, averaged over years, had regression coefficients not significantly different from unity. However, there was considerable variation within and over years for the standard deviation ( $\bar{s}_d$ ) of residuals about the regression line for the clones tested. This measure of variation revealed specific instances of yield instability which presumably results from genotype-environment interaction.

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Additional index words: Cynodon dactylon (L.) Pers.,  
Yield stability, Regression analyses.

Bermudagrass [Cynodon dactylon (L.) Pers.] is a long-lived perennial, warm-season, sod-forming species belonging to the grass subfamily Eragrostoideae. It was probably introduced into the southern United States by 18th century immigrants and rapidly spread throughout this geographic area. Once considered to be a "cotton patch" weed, it now occupies millions of acres of southern pastureland. Widespread acceptance of the species began only recently in the 1940s with the advent of improved cultivars having the following characteristics: high production potential, ability to withstand close grazing, wide adaptability to different soils and climatic conditions, and ability to propagate vegetatively.

The primary purpose of this research was to assess the importance of genotype-environment interactions in bermudagrass yield in Oklahoma, thereby providing a basis for estimating the minimum number of test environments (years and locations) needed to adequately characterize the agronomic performance of experimental strains and new cultivars. The current breeding objective of the bermudagrass improvement program is to develop cultivars which are high yielding and, hopefully, have better nutritive value than current cultivars. The extremely variable environmental conditions which prevail in Oklahoma as one progresses from east to west provides the necessary test environments for which this breeding objective can be implemented.

## CHAPTER III

### REVIEW OF LITERATURE

The extent of occurrence, the nature, and the importance of genotype-environment interactions have been reviewed most recently by Hill (5) and earlier by Comstock and Moll (3). The latter review summed up the impact of genotype-environment interactions by the following statement:

Because genetic facts are inferred from observations on phenotype, because selection is based on phenotype, and because there is a potential contribution of genotype-environment interaction effects to phenotype of all quantitative characters; genotype-environment interaction is in some way involved in most problems of quantitative genetics and many problems of plant breeding.

Forage yield data from 14 alfalfa (Medicago sativa L.) cultivars tested for 3 years at five Oklahoma locations were used by Taliaferro et al. (9) to study genotype-environment interactions in this species. They found nonsignificant mean squares and small variance components for the first-order, i.e., cultivar by location and cultivar by year, interactions suggesting minimal effects of locations and years on relative yields. The second-order, i.e., cultivar by location by year, interaction was large and highly significant, indicating that cultivar by environment interactions in alfalfa yield were attributable to factors other than years and locations. Their results indicated the

necessity for testing in multiple environments, but did not indicate how those tests should be distributed over years and locations.

Murray and Verhalen (8) analyzed the performance of 11 cotton (Gossypium hirsutum L.) cultivars grown at three locations in Oklahoma for 3 years and found a very large and significant cultivars by locations mean square for yield suggesting that the state be subdivided in some manner for testing and breeding purposes. The second-order components for yield and fiber coarseness were large and significant; those interactions could not be attributable to locations or years. Comparisons of variance components led to the same inferences as those obtained from examination of mean squares. Interactions for the other traits studied were not significant, were small, or both.

Karwasra, et al. (7) measured herbage yield of 10 genotypes of yellow sweet clover (Melilotus parviflora Desf.) over a 4-year period at one location. Genotypes interacted significantly with environments, and a large portion of those interactions was attributable to a linear function of environmental means. No association was exhibited between mean green fodder yield and the parameters of stability (b and  $s_d^{-2}$ ). Prediction of mean performance was made using all the genotypes studied in a number of environments and also using only one stable genotype. Mean performance of most genotypes was predicted within the limits of sampling

error. Use of a stable genotype was found to be very useful for the purpose of predication.

Five populations of cocksfoot (Dactylis glomerata) were studied by Breese (1) at two locations over 2 years. Forage yields, averaged over replicates, showed that yields were affected by time, place, and system of harvesting and that large differences were present between the populations. All main effects were highly significant compared with replicates error mean square in the analysis of variance. The populations also interacted significantly with all environmental effects. The major part of the population by environment variance was explained by differences between slopes of their respective linear regressions. The regressions also provided a means of accurately predicting relative performance over a wide range of environments and could be used to simplify varying relationships between parents and offspring under changing conditions. The analyses also provided further evidence on differences between populations for stability of response as measured by regression.

## CHAPTER IV

### MATERIALS AND METHODS

In 1973 nine experimental strains and four cultivars of bermudagrass were established in tests at five Oklahoma locations (Altus, Chickasha, Lahoma, Mangum, and Muskogee). The tests at those locations were conducted to compare the performance of the experimental strains and cultivars with that of 'Midland', the most widely used bermudagrass cultivar in Oklahoma. Forage yield data from seven of those strains and all four of the cultivars harvested for 3 years (1974 through 1976) at four of the locations were used in the present study to examine genotype-environment interactions. The strains were from the OSU bermudagrass breeding project and carried the experimental designations S-13, S-54, S-24, S-29, SS-16, SS-27, and S-78 (listed as entries 3, 4, 5, 7, 9, 11, and 12, respectively). The cultivars were 'Midland', 'Hardie', 'Oklan', and 'Alicia' (listed as entries 1, 2, 6, and 13, respectively). Two experimental strains (entries 8 and 10) were deleted from the study due to a lack of winterhardiness and to low persistence following the year of establishment. The Lahoma location was omitted because of a lack of winterhardiness of a majority of the clones tested.



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 semi-arid moisture conditions and has a Meno sandy loam, a member of the loamy, mixed, thermic Aquic Arenic Haplustalfs. Altus, also in the southwest, is likewise characterized by semi-arid moisture conditions; but some supplemental irrigation water is available in dry periods. That location has a complex series of Tillman clay loam, a member of the fine, mixed, thermic Typic Paleustolls and Hollister clay loam, a member of the fine, mixed, thermic Pachic Paleustolls. Chickasha, in central Oklahoma, represents a moderate rainfall area and has a Reinach silt loam, 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, a member of the fine, mixed, thermic Mollic Albaqualfs.

The field plot design at each location was a randomized, complete block with four replications. Plots consisted of an area 1.83 X 6.10 m, and initial plant spacing within plots was 0.62 m for the 10 plants established per plot. The tests were uniformly fertilized each year with nitrogen fertilizer ranging in amounts from approximately 134.5 to 179.4 kg/ha actual N at the different locations. The nitrogen was applied in split applications, the first being applied in April and second in late June or July. Forage yields were measured by

harvesting and weighing a 0.92 X 5.49 m cutting swath from the center of each plot. Samples of the harvested forages were taken for moisture determination, 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 (3) and modified to fit a perennial crop by Taliaferro et al. (9) was used to separate the components of variance. A random effects model was used assuming a random sampling of clones, 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 (2) method for deciding upon the appropriate F-test and calculation of degrees of freedom was used for the data (Table II).

Because the analysis of variance indicated the presence of significant genotype-environment interactions, a joint regression analysis as outlined by Eberhart and Russell (4) 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 clones grown at a particular location in a particular year and subtracting from that quantity the mean of all clones over all environments. The regression of mean yield on

environmental index was obtained for each clone within and over years. A regression coefficient ( $b$ ) and a standard deviation ( $\bar{s}_d$ ) of residuals were also calculated. The regression coefficient measures the increase in mean yield of a clone per unit increase in environmental index. The standard deviation of residuals about the regression line measures how well predicted response agrees with that actually observed and includes genotype-environment interactions. A stable genotype, as described by Eberhart and Russell (4), has a regression coefficient of unity ( $b = 1.0$ ) and deviations from regression as small as possible ( $\bar{s}_d = 0.0$ ).

## CHAPTER V

### RESULTS AND DISCUSSION

#### Analyses of Variance and Estimates of Variance Components

Mean yield for each clone, averaged over locations, differed significantly from year to year and over years as indicated in Table I. Relative rankings of individual clones varied only slightly from year to year. The check cultivar Midland (entry 1) was the third-ranked yielder overall; whereas, the experimental strain S-13 (entry 3) and the cultivar Hardie (entry 2) were consistently equal or superior to it in yield. Cultivars Oklan (entry 6) and Alicia (entry 13) were low yielders during the first growing season; but each succeeding year, they increased in productivity relative to the other clones. The relative performances of clones by locations over years are presented in Figure 1; the cultivars and strains in that figure are listed by their respective entry numbers, and the locations are listed in order from left to right representing a decreasing availability of moisture. The mean yields at those locations averaged over clones and years were significantly different (i.e., 7.33, 6.91, 6.65, and 5.55 metric tons/ha for Muskogee, Altus, Chickasha, and Mangum, respectively).

TABLE I  
 MEAN PERFORMANCE BY YEARS AND OVER YEARS FOR THE  
 BERMUDAGRASS CLONES OVER LOCATIONS

Test Entry Number	Cultivar or Strain	Dry Matter Yield, Metric Tons/ha							
		1974	Rank	1975	Rank	1976	Rank	Avg	Rank
3	S-13	5.47	1	10.92	1	8.41	1	8.27	1
2	Hardie	4.87	2	10.00	2	7.39	5	7.42	2
1	Midland	4.73	3	9.71	3	7.41	4	7.28	3
6	Oklan	4.23	7	9.26	5	8.22	2	7.24	4
13	Alicia	4.09	8	9.34	4	7.52	3	6.98	5
9	S-54	4.58	5	8.87	6	6.40	6	6.62	6
4	S-24	4.56	6	8.69	8	5.46	10	6.24	7
7	S-29	3.66	9	8.83	7	5.72	7	6.07	8
5	SS-16	4.63	4	7.67	10	5.53	9	5.94	9
12	SS-27	3.13	11	7.29	11	5.70	8	5.37	10
11	S-78	3.41	10	7.77	9	4.61	11	5.26	11
	LSD 0.05	0.76		0.87		1.09		0.72	
	CV	25.14		13.97		23.66		26.94	

Mean squares and estimates of variance components relevant to the study of genotype-environment interactions are presented in Tables II and III, respectively. Expected mean squares for this analysis have been given previously by Taliaferro et al. (9). The clones, clones by locations by years, and clones by replications in locations mean squares were highly significant. Significance at the 0.05 probability level and a variance component estimate about half that for the three sources listed above for the clones by locations interaction suggest intermediate effects for such interactions on the comparative yielding ability of bermudagrass clones. Consequently, it can be tentatively concluded that all environments analyzed in this experiment were of some value in determining genotypic differences among the individual clones. Some thought might also be given toward subdividing the state for breeding and testing purposes. Consideration of Figure 1 will show that entries 1 and 2 did very well in a high rainfall environment, but less well where water became more limiting; whereas, entries 3 and 6 (especially 3) were markedly superior to the other clones under more limited moisture conditions. A statistically nonsignificant mean square and small variance component for the clones by years interaction suggest minimal effects of that interaction on yielding ability. One could have predicted such a result from the relatively consistent rankings among clones from year to year over locations (Table I). From these data, one might conclude that bermudagrass could be adequately

TABLE II  
 MEAN SQUARES RELEVANT TO THE STUDY OF  
 GENOTYPE-ENVIRONMENT INTERACTION

Source	Dry Matter Yield metric tons/ha	
	df	Mean Square
Clones (C)	10	41.28**
C X Locations (L)	30	9.74*
C X Years (Y)	20	5.32
C X L X Y	60	3.56**
C X Replications (R) in L	120	3.17**
Error (e)	240	0.99

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

TABLE III  
 VARIANCE COMPONENT ESTIMATES AND THEIR  
 STANDARD ERRORS FOR YIELD

Component	Dry Matter Yield metric tons/ha	
	Estimate	$\bar{s}_d$
$\sigma_C^2$	0.62	0.39
$\sigma_{CL}^2$	0.33	0.37
$\sigma_{CY}^2$	0.11	0.11
$\sigma_{CLY}^2$	0.64	0.16
$\sigma_{CR \text{ in L}}^2$	0.73	0.14
$\sigma_e^2$	0.99	



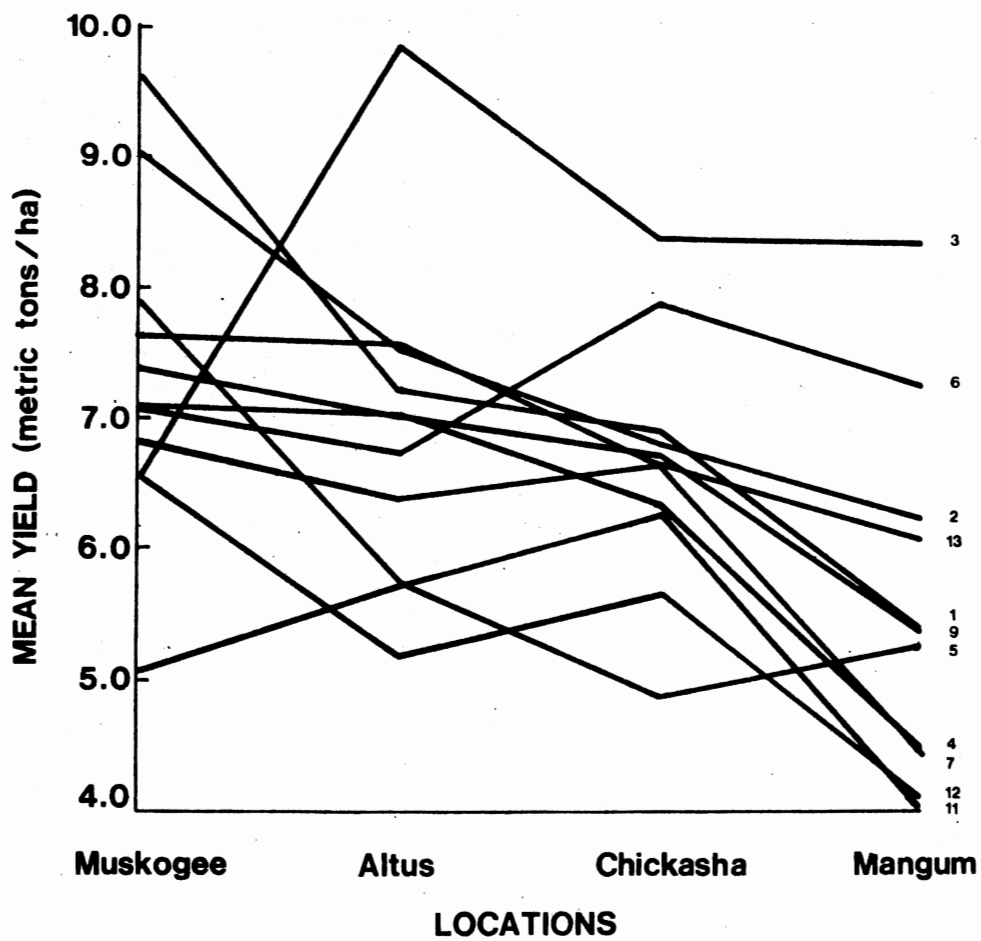


Figure 1. Forage Yield Among Bermudagrass Clones by Locations Over Years

evaluated in Oklahoma by testing for a minimum of 2 years (3 years if one includes the year of establishment). Consequently, the commonly observed problem of plot invasion in long-term experiments of this sort and the resulting competition caused by more aggressive clones of bermudagrass would be less troublesome if the test period could be shortened to fewer growing seasons. The highly significant mean square and large variance component for the three factor interaction indicates that testing in multiple environments is essential to reliably estimate relative yield performance, but it says nothing as to how those tests should be distributed over years and locations. The first-order interactions discussed above would imply that locations should be emphasized more than should years. Since replications remain static over years in a perennial crop such as bermudagrass, the clones by replications in location variance component was included in these calculations. As Taliaferro et al. (9) noted for yield of alfalfa in Oklahoma, the highly significant mean square for this interaction indicates that the magnitude of yield differences between clones varied significantly from replication to replication. The significant mean square and large variance component for clones implies that differences among clones were of such magnitude that some progress could be achieved merely by basing selections on overall means of the clones. For example, S-13, Hardie, and Midland consistently did well and would be judged the better clones regardless of how the data were scrutinized. In contrast,

SS-27 and S-78 were consistently poor in performance, and no breeder would hesitate to eliminate them from consideration for release.

#### Regression Analyses

The mean yield responses of the 11 bermudagrass clones averaged over years and locations had regression coefficients not significantly different from 1.0 as shown in Table IV. Within years over locations, only S-54 (1975), S-24 (1976), S-29 (1974, 1975, 1976), and SS-27 (1975) had regression coefficients significantly different from unity. As described earlier, a desirable clone should have a high mean performance, a regression coefficient close to 1.0, and a standard deviation from regression near zero. According to Joppa et al. (6), regression coefficients larger than 1.0 may indicate either better than average response to high yield environments or worse than average response to low yield environments. The cultivar Midland with a regression coefficient (b) of  $1.14 \pm 0.14$  had better than average yields at all but Mangum, the environment with the least available moisture. However, Hardie ( $b = 1.10 \pm 0.10$ ), Alicia ( $b = 1.07 \pm 0.16$ ), and S-29 ( $b = 1.11 \pm 0.08$ ) had regression coefficients which deviated from the above criteria by either having better than average or worse than average responses at most locations. On the basis of the regression coefficients over years and locations and their standard errors, strains S-54 with a mean rank of 6 and S-29 with a mean rank

TABLE IV  
 REGRESSION COEFFICIENTS AND THEIR STANDARD ERRORS BY YEARS AND OVER YEARS  
 FOR THE BERMUDAGRASS CLONES OVER LOCATIONS

Cultivar or Strain	1974	1975	1976	Over Years
S-13	1.11 ± 0.48	-0.86 ± 2.72	-0.16 ± 0.70	0.98 ± 0.26
Hardie	1.29 ± 0.22	0.35 ± 1.00	1.02 ± 0.38	1.10 ± 0.10
Midland	1.35 ± 0.58	1.81 ± 0.98	1.34 ± 0.56	1.14 ± 0.14
Oklan	1.13 ± 0.49	-0.56 ± 1.02	0.74 ± 0.97	1.02 ± 0.22
Alicia	0.96 ± 0.36	1.88 ± 1.12	0.63 ± 0.68	1.07 ± 0.16
S-54	1.09 ± 0.37	0.28 ± 0.28	1.41 ± 0.27	0.98 ± 0.09
S-24	0.99 ± 0.01	1.88 ± 1.02	1.44 ± 0.15	0.98 ± 0.12
S-29	0.76 ± 0.11	2.39 ± 0.20	1.13 ± 0.06	1.11 ± 0.08
SS-16	0.97 ± 0.23	0.94 ± 1.12	0.58 ± 0.97	0.69 ± 0.17
SS-27	0.68 ± 0.22	1.71 ± 0.24	1.49 ± 0.45	0.96 ± 0.11
S-78	0.68 ± 0.43	1.19 ± 0.97	1.38 ± 0.39	0.97 ± 0.13

of 8 in the 11 bermudagrass clones analyzed were the most stable genotypes. They did relatively poorly, but they were consistent in that performance over years and locations.

Considerable variation within and over years for the standard deviation ( $\bar{s}_d$ ) of residuals about the regression line was detected (Table V). The data were arbitrarily divided into low, intermediate, and high groups based on their standard deviations of residuals. Experimental strains S-54, S-29, and SS-27 and the cultivar Hardie had relatively low deviations. Strains S-24, SS-16, and S-78 and the cultivars Midland and Alicia had intermediate deviations while strain S-13 and the cultivar Oklan had relatively high deviations. Specific instances of instability were apparently related to large deviations at one to three locations in a particular year, based on significant deviations from a 95% confidence interval set about the regression line for each clone. An example for a cultivar was the large standard deviation of Oklan in 1976 which was itself directly attributable to large deviations at the Chickasha, Mangum, and Muskogee locations. An example for an experimental strain was S-13 in 1975 which had a large standard deviation traceable to the Altus, Mangum, and Muskogee locations.

As discussed by Eberhart and Russell (4), the phenotypic expression of a particular population in a specific environment depends on three genotypic parameters: the mean expression, the linear response to environment, and the residual deviations from regression. The latter two parameters

TABLE V

STANDARD DEVIATION OF RESIDUALS ABOUT THE REGRESSION  
LINE BY YEARS AND OVER YEARS FOR THE BERMUDAGRASS  
CLONES OVER LOCATIONS

Cultivar or Strain	1974	1975	1976	Over Years
S-13	1.14	2.93	1.70	1.97
Hardie	0.51	1.07	0.93	0.74
Midland	1.37	1.05	1.36	1.05
Oklan	1.15	1.10	2.36	1.61
Alicia	0.84	1.21	1.65	1.18
S-54	0.87	0.30	0.65	0.68
S-24	0.01	1.09	0.36	0.92
S-29	0.26	0.22	0.15	0.59
SS-16	0.53	1.20	2.35	1.27
SS-27	0.52	0.26	1.09	0.82
S-78	1.02	1.04	0.95	1.00

dictate the relative phenotypic expressions of vegetatively propagated bermudagrass clones. Consequently, utilization of those parameters in the evaluation process will further increase the precision of relative determination of yield and stand persistence and their related factors of winter-hardiness, drought tolerance, and reactions to disease and insect pests.

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