HERITABILITY OF *IN VITRO* DRY MATTER DIGESTIBILITY IN BERMUDAGRASS

By

BOBBY RAY MCGEHEE

Bachelor of Science in Agriculture
Texas Tech University
Lubbock, Texas
1956

Master of Science
Oklahoma State University
Stillwater, Oklahoma
1970

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
DOCTOR OF PHILOSOPHY
December, 1974

HERITABILITY OF IN VITRO DRY MATTER

DIGESTIBILITY IN BERMUDAGRASS

Thesis Approved:

Charles M Taliaferro
Thesis Adviser

Lavoy J. Croy

J. C. Lynd

Wayne W. Huffine

Robert D Morrison

N N Durham
Dean of the Graduate College

ACKNOWLEDGEMENTS

I wish to express sincere gratitude to Drs. C. M. Taliaferro and L. I. Croy for their guidance and constructive criticisms while conducting this research. Appreciation is extended to other members of my committee, Dr. W. W. Huffine, Dr. J. Q. Lynd, and Dr. R. D. Morrison for their encouragement and guidance during my studies.

Sincere gratitude is likewise given to Dr. Floyd Horn of the Ft. Reno Research Station for his assistance in conducting this research and to Dr. R. W. McNew for his able advice.

I am especially indebted to Dr. Ralph S. Matlock and the Department of Agronomy, Oklahoma State University, for the financial assistance which enabled me to continue my education. Grateful acknowledgement is also extended to the Department of Agronomy for the use of their facilities in conducting this research.

I am especially grateful to my wife, Mary Ann, and daughters, Catherine and Celia, for their patience, unselfishness, and encouragement during the course of my studies and the preparation of this dissertation.

I also wish to thank Mrs. Marianne Pool and Mrs. Lavonne Beard for typing the draft copy of this dissertation. I also would like to thank Mrs. Betty Simpson for typing the final copy of this dissertation.

To my instructors, fellow students, and countless others, too numerous to mention, I express my sincere thanks.

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CHAPTER I

INTRODUCTION

The science of plant breeding depends on a population with genetic variation for the traits chosen for improvement and on the ability to identify the desirable genotypes in the population. This implies that the means must be available to evaluate a sufficient number of the individuals within the population for the traits in question in order to adequately sample the genotypes present. Most forage plant breeding efforts in the past have been directed toward improving yield rather than quality simply because the means were not available to accurately measure the quality of forage samples from a large number of genotypes. This situation has changed, however, with the development of precise but inexpensive laboratory techniques for estimating quality using only a few grams of forage (2, 8). Forage plant breeders now have the tools to evaluate individual plants for forage quality and select genotypes with the desired traits.

As valuable as these tools are, it must be recognized that only the phenotypes of the individuals are being measured while the purpose of a breeding program is to identify genotypes. This fact has been embodied into the concept of heritability which seeks to proportion the observed variation in phenotypes in a population into that due to genetic differences between the individuals and that due to the different environments to which the individuals may have been exposed.

The agronomic traits of bermudagrass (Cynodon L. C. Rich) have been markedly improved by plant breeding and efforts are now being made to improve its forage quality. Although many of the problems associated with characterizing and measuring forage quality of bermudagrass have been overcome, a basic knowledge of the proportion of the observable variation in quality traits that is due to genetic differences is lacking. The objective of this study was to estimate the heritability of one of the traits associated with forage nutritive value, in vitro dry matter digestibility, thereby supplying some of this basic knowledge.

CHAPTER II

LITERATURE REVIEW

The development (25) and refinement (26) of the *in vitro* technique for measuring apparent digestibility (dry-matter disappearance) of small forage samples provided forage breeders with a tool to improve forage quality through breeding. These techniques enable breeders to classify the relative digestibility of large numbers of individual plants within a species and to identify the more desirable genotypes in the populations with which they are working.

The validity of this laboratory technique as a measurement of relative dry matter digestibility has been established by several workers. Cooper et al. (8) reported that estimates of digestibility obtained by the *in vitro* technique showed a high correlation ($r = .95$) with the corresponding *in vivo* results. Wurster et al. (27) also found *in vitro* dry matter digestibility (IVDMD) to be highly correlated ($r = .89$) with *in vivo* digestion data and concluded that the two stage process of IVDMD gives the best overall laboratory measure of the digestibility that takes place in the rumen. Duble et al. (9) reported significant correlation ($r = .78$) between animal performance as measured by average daily gain and IVDMD. Marten, Goodrich, and Schmid (18, 22) evaluated chemical and biological laboratory methods for determining quality of corn and sorghum silage and concluded that the two stage *in vitro* technique was superior to chemical tests and was the procedure most highly

correlated with *in vivo* digestibility. Kamstra et al. (13) found a high correlation (r = .95) between *in vivo* and *in vitro* digestibility of forage from smooth bromegrass (*Bromus inermis* Leyss.) synthetics grown under field conditions. They failed, however, to find the expected digestibility differences in the field grown forage of the synthetics that they found in space-planted progeny of crosses of the genotypes used to make the synthetics. This lack of correspondence between the spaced plant and field results was attributed to unknown factors affecting digestibility under field conditions.

Several workers that have reported genetic variation for IVDMD within grass species have also estimated the proportion of this genetic variation to the total observed variation. Cooper et al. (8) found significant variation in IVDMD between individual genotypes and families of ryegrass (*Lolium perenne* L.) and orchardgrass (*Dactylis glomerata* L.). Estimates of the repeatability of IVDMD between two successive cuts of the families were .44 for ryegrass and .53 for orchardgrass. Heritability estimates derived from parent-progeny correlation gave little information in the ryegrass families because of the small amount of variation in the mid-parent values. In the orchardgrass families, however, the heritability estimates were .52 for one cut and .53 for the other, indicating that there was sufficient genetic variation within the species for utilization by the plant breeder.

Burton et al. (2) used the nylon-bag technique to screen large numbers of bermudagrass (*Cynodon dactylon* (L.) Pers.) parents and hybrids for dry matter digestibility (NBDMD). They found that genotype was a highly significant variable in all dry matter digestibility trials in which bermudagrass genotypes were compared. This screening

program resulted in the release of 'Coastcross-1" (4) which was more digestible than other bermudagrass varieties. The per acre live weight gains of steers grazing Coastcross-1 in replicated grazing trials exceeded those of steers grazing Coastal bermuda by as much as 50%.

Burton and Monson continued this screening and testing program and used the data to estimate heritabilities for dry matter digestibility (DMD) of bermudagrass (5). Forage samples were collected from multiple harvests of 148 bermudagrass selections that were evaluated in three clipping tests conducted over an eight year period. DMD was measured by either the nylon bag or in vitro technique. Broad sense heritability estimates were derived using the method developed for replicated clonal material (1). Annual average heritability estimates calculated from the analysis of variance of all DMD measurements for a single year ranged from .27 to .78. The authors felt that these estimates had more significance than more variable and somewhat larger values derived from individual harvests within each test. The variation in DMD of F_1 hybrids involving the same parents indicated that several genes controlled this character and that the parents were heterozygous for them. Multiple factor inheritance with little if any dominance was indicated.

Christie and Mowat (7) found significant differences in IVDMD among clones of orchardgrass and bromegrass and estimated the percent genotypic variances (broad sense heritabilities) for this trait. They estimated that approximately 74% of the variation in IVDMD among the orchardgrass clones was due to the differences in the genotypes. The percent genotypic variances among bromegrass clones in the digestibilities of different plant fractions and whole plants ranged from 60.2% to 73.1%.

Carlson et al. (6) studied the variation in percentage of IVDMD in fall-saved forage from 20 clonally propagated reed canarygrass (Phalaris arundinacea L.) genotypes and their topcross progeny. Broad sense heritability estimates ranged from .51 to .80 among clonal means and from .06 to .66 among progeny means. Narrow sense heritability estimates based on the regression of progeny means on clonal means ranged from .30 to 1.31 with a value of .55 being considered as the best estimate.

Ross et al. (21) investigated the genetic variation for IVDMD in a six-parent diallel cross of smooth bromegrass. A heritability estimate of 1.06 was obtained by doubling the regression of array means on the corresponding parental means. They concluded that there was a high additive genetic effect for this character and that significant initial progress, by mass selection for digestibility, should be possible within the population investigated. They also concluded that genotypes with superior digestibility could be selected in smooth bromegrass and that production of a synthetic variety having higher digestibility should be possible.

Sleper et al. (23) also used a six-parent diallel cross to investigate the inheritance of digestibility of smooth bromegrass as measured by the acid-pepsin dry matter disappearance (APDMD) technique (15). The digestibility of the whole forage was evaluated for two years and that of the plant parts for one year. Forage was harvested on two sampling dates within each year and data were analyzed as first and second harvest APDMD of whole forage over two years and the APDMD of plant parts from a single cutting of one year. Differences in APDMD among progenies were highly significant for both sampling dates

averaged over years and were consistent, with no progeny by year interaction. Broad and narrow sense heritability estimates were calculated from the genetic parameters estimated by the mean squares of the analysis of variance. Broad sense heritability values were .86, .87, and .84 for the first harvest, second harvest, and leaf blades only, respectively, with these narrow sense estimates being .67, .64, and .78. The workers noted that these heritability estimates should be evaluated with caution because of the small number of parents used, but that progress in selecting for APDMD in the material should be possible.

CHAPTER III

MATERIALS AND METHODS

The genotypes used in this study were parental and progeny clones of bermudagrass (Cynodon) selections that were part of a more comprehensive Cynodon breeding program at Oklahoma State University (Table I). The taxonomic classification was according to that proposed by Harlan et al. (11, 12). Genotypes used as parents included direct accessions and previously selected hybrids that had resulted from crosses of accessions. Parental plants were crossed in the fall of 1969 by Mr. William L. Richardson using a previously described technique (20). Seed from these crosses were germinated in the greenhouse the following spring then seedling plants were transferred to individual clay pots.

All parents and progenies were grown outside during the summer of 1970 in 16 inch clay pots filled with silt loam soil. Water and a balanced fertilizer were uniformly applied to the pots in sufficient quantities to maintain vigorous plant growth. The plants were clipped periodically to remove excess growth and to encourage complete establishment of the seedling plants within the pots. All pots of grass were transferred to the greenhouse October 17, 1970 where uniform applications of water and fertilizer were continued.

The system of analyzing plant material from potted plants growing in a greenhouse was used as a method of reducing variation in in vitro dry matter digestibility (IVDMD) due to environment. Preliminary tests

TABLE I

CYNODON PLANTS USED AS PARENTS TO FORM THE BASIC POPULATION FOR HERITABILITY ESTIMATES

Oklahoma Accession Number	Taxon	Origin
8152	C. dactylon var. afghanicus	Herat, Afghanistan
8153	C. dactylon var. afghanicus	Khanabad, Afghanistan
8795	C. dactylon var. dactylon	Khandahar, Afghanistan
8800	C. dactylon var. afghanicus	Khandahar, Afghanistan
9945a	C. dactylon var. dactylon	Elazig, Turkey
9945c	C. dactylon var. dactylon	Elazig, Turkey
9946	C. dactylon var. dactylon	Athens, Greece
10000	C. dactylon var. dactylon	Cambirene, Senegal
10123	C. dactylon var. coursii	Lake Alaotra, Malagasy
10125	C. dactylon var. coursii	Lake Alaotra, Malagasy
10127	C. dactylon var. coursii	Ambatondrozaba, Malagasy
10153	C. dactylon var. dactylon	Union of South Africa
10254a	C. dactylon var. elegans	Darhan, Union of S. Africa
10287	C. dactylon var. coursii	Salisbury, Rhodesia
10306	C. dactylon var. coursii	Lake Alaotra, Malagasy
10311	C. dactylon var. dactylon	Trombay, India
10351	C. dactylon var. elegans	Boekenhoutspruit, Union of S. Africa
10360	C. dactylon var. elegans	Boesmanskop, Union of S. Africa
10385	C. dactylon var. elegans	Pretoria, Union of S. Africa
10416a	C. aethiopicus	Dar Es Salaam, Tanzania
10421	C. nlemfuensis var. robustus	Ghana
10429	C. dactylon var. coursii	Ampasikely, Malagasy
10452	C. dactylon var. coursii	Lake Alaotra, Malagasy
10561	C. nlemfuensis var. robustus	Tengenu, Tanzania
11129	C. dactylon var. elegans	Zambia, Zambia
11657	C. dactylon var. dactylon	Berlin, Germany
0-1097b	Cynodon (species unknown)	Unknown
52	Cynodon (species unknown)	Unknown
57	Cynodon (species unknown)	Unknown
NT-67-2	Cynodon (species unknown)	Unknown
BL-22-27	Cynodon (species unknown)	Unknown
10466a	Cynodon (species unknown)	Unknown
7R	Cynodon (species unknown)	Unknown
85	Cynodon (species unknown)	Unknown
NK-37	Cynodon (species unknown)	Northrup-King & Co.

using this system have revealed close correlation between differences in IVDMD of forage harvested from bermudagrass lines grown in the field and differences between the same lines grown in a greenhouse (24). Smaller absolute differences in IVDMD were detected among the lines grown in pots, indicating that variation due to environment was reduced. This system is being further evaluated as a more economical way to screen large numbers of bermudagrass selections for relative IVDMD.

The clones of grass were uniformly clipped two inches above the soil and all plant material harvested on December 26, 1970, February 1, 1971, March 10, 1971, April 7, 1971, and May 5, 1971. Plant material used for analysis was that harvested on the last four cutting dates.

Plant material was uniformly dried at 65° C immediately after harvesting then ground with a Wiley mill to pass through a 2mm screen. Ground samples were stored at 22° C until the last clipping was ground, then all samples were reground to pass through a 40 mesh screen.

Four different laboratory digestion runs were made to measure the samples for IVDMD by a modification of the method described by Tilley and Terry (26). Digestion runs #1 and #2 were made in a forage evaluation laboratory of the Agronomy Department at Oklahoma State University. Runs #3 and #4 were made in a similar laboratory at the Fort Reno Research Station, El Reno, Oklahoma. Duplicate measurements were made on each sample within each digestion run and the mean of these measurements used as the IVDMD value of the sample. This resulted in four IVDMD values for each clone (one sample from each of four cuts). The selection of samples to be measured in a given digestion run was determined by the grouping of the parents and progenies as described in

the following paragraphs and by the limitation of a maximum of 480 digestion units per run.

Regression

Narrow sense heritability estimates of IVDMD were derived by parent-progeny regression using IVDMD values from laboratory runs #1, #2, and #3. These estimates were made from twelve different family groups which consisted of two or more unrelated parental lines (the regression parents) and the progenies that had resulted from crossing the lines with a single other unrelated line (the group parent) (Table II). Some regression parents served as pollen parents and some served as seed parents in these crosses. Numbers of progenies from these individual crosses ranged from 1 to 14.

Heritability estimates were derived by doubling the coefficient calculated from the regression of IVDMD of progenies on IVDMD of the regression parent within each of these separate family groups according to the method described by Lush (16). Pooled regression coefficients from various combinations of family groups were obtained by summing the sum of products of the deviations (Σxy) and the sum of squares (Σx^2) from the individual regression calculations of each family group in the given combination (19):

$$\text{pooled regression coefficient} = \frac{\Sigma\Sigma xy}{\Sigma\Sigma x^2} .$$

These pooled regression coefficients were also doubled to estimate the heritability:

$$h^2 = 2 \times \text{pooled regression coefficient} .$$

TABLE II

FAMILY GROUPS FORMED TO ESTIMATE HERITABILITY BY PARENT-PROGENY REGRESSION

Group No.	Measured for IVDMD In Digestion Run	Parents		Type Parent	No. Progenies
		Group	Regression		
1	R1	(10123x10287)			
			X 57	♂	6
			X (10561x10125)	♂	1
2	R1	10311-1			
			X "NK-37"	♂	3
			X (8800x10421)	♂	13
			X 57	♂	8
3	R1	10311-2			
			X (8800x10421)	♂	2
			X (10000x10153)	♂	4
			X 57	♂	1
4	R1	"NK-37"			
			X (10000x10153)	♀	2
			X 10311-2	♀	3
5	R1	(10306x10153)-2			
			X (8800x10421)	♂	1
			X 10311-2	♀	4
6	R2	(9946x8152)			
			X 10311-1	♂	1
			X (10306x10153)-1	♂	8
			NT-67-2	♂	2
			X (10561x10125)	♂	4
			X (10254ax10429)	♂	3
			8795	♂	1
7	R2	8152			
			X 10351	♂	3
			X 10360	♂	6
			X 10385	♂	6
			X (10254ax10429)	♂	1
			X (10466ax8795)	♀	8
8	R3	(10561x10125)			
			X (10000x10153)	♂	4
			X (10416ax11129)	♂	1

TABLE II (CONTINUED)

Group No.	Measured for IVDMD In Digestion Run	Parents		Type Parent	No. Progenies
		Group	Regression		
9	R3	NT-67-2			
			X "NK-37"	♂	14
			X (10416ax11129)	♀	1
			X 11657	♀	4
10	R3	8153			
			X (10306x10153)-1	♀	1
			X (9945ax10127)	♀	2
			X (10254ax7R)	♀	2
			X BL-22-27	♀	2
			X 52	♀	1
11	R3	(10254ax10429)			
			X 52	♀	1
			X (10416ax11129)	♀	3
12	R3	8795			
			X 0-1097b	♀	2
			X 9945c	♂	2

The varying numbers of progenies per regression parent in these groups made it necessary to weight these numbers in computing the regression coefficients within each family group and to express the heritability estimates as a range of values. This was done by: (a) repeating the IVDMD of the regression parent with that of each of its progeny in the regression calculation and (b) regressing the mean IVDMD of all progenies of a regression parent on the IVDMD of that parent. These two methods were used with the assumption that an unbiased estimate of regression would fall somewhere between the resulting values. According to Kempthorne and Tandon (14), the first method is valid if the correlation between progenies of a parent is zero while the second method is valid if the correlation among these progenies is one. They pointed out that, in most populations with heterozygous parents, the real situation is intermediate to these two extremes with the correlation usually nearer to zero.

Sib Analysis

The population used to estimate heritability by sib analysis consisted of 24 progenies from three half-sib families. Each half-sib family consisted of two full-sib families of four progenies each (Table III). The analysis was made using the procedure described by Falconer (10) with the phenotypic variance of the progenies being divided into its observational components using the form shown in Table IV. Phenotypic values of the progenies were mean IVDMD of samples from four cuts, therefore the estimates were the heritability of mean IVDMD.

Five heritability estimates were derived by using the observational components of variance as estimates of the causal components of the

TABLE III

POPULATION USED TO ESTIMATE HERITABILITY BY SIB ANALYSIS

Parents Common to half-sib families	Parents of full-sib families	Progenies	
10311-1	(10561x10125)	4 full-sibs	8 half sibs
	57	4 full-sibs	
8152	10360	4 full-sibs	8 half sibs
	10385	4 full-sibs	
NT-67-2	"NK-37"	4 full-sibs	8 half sibs
	77	4 full-sibs	

TABLE IV

FORM OF SIB ANALYSIS USING MEAN IVDMD FOR PHENOTYPIC VALUES

Source of Variation	d. f.	Composition of Mean Squares
Among half-sib families	h - 1	$\sigma_P^2 + p\sigma_F^2 + pf\sigma_H^2$
Between full-sib families within half-sib families	h(f - 1)	$\sigma_P^2 + p\sigma_F^2$
Among progenies of full-sub families	hf(p - 1)	σ_P^2

Where:

h	= no. of half-sib families	= 3	
f	= no. of full-sib families in each half-sib family	= 2	
p	= no. of progenies in each full-sib family	= 4	
σ_H^2	= variance among means of half-sib families		= $\frac{1}{4}V_A$
σ_F^2	= variance between full-sib families within each half-sib family		= $\frac{1}{4}V_A + \frac{1}{4}V_D$
σ_P^2	= variance among progenies of full-sib families		= $\frac{1}{2}V_A + \frac{3}{4}V_D + V_E$
σ_T^2	= $\sigma_H^2 + \sigma_F^2 + \sigma_P^2$ = total phenotypic variance		= $V_A + V_D + V_E$

total phenotypic variance and calculating the following proportions of genetic variation:

$$\frac{4\sigma_H^2}{\sigma_T^2} = \frac{V_A}{V_P}$$

$$1 - \frac{\sigma_P^2 - 2\sigma_H^2}{\sigma_T^2} = \frac{V_A + \frac{1}{4}V_D}{V_P}$$

$$\frac{2(\sigma_H^2 + \sigma_F^2)}{\sigma_T^2} = \frac{V_A + \frac{1}{2}V_D}{V_P}$$

$$1 - \frac{\sigma_P^2 - 2\sigma_H^2}{\sigma_T^2} = \frac{V_A + \frac{3}{4}V_D}{V_P}$$

$$\frac{4\sigma_F^2}{\sigma_T^2} = \frac{V_G}{V_P}$$

The causal components shown to be estimated by the observational components ignored the variance effects caused by epistasis and linkage. Causal components of variance were symbolized by:

V_P	phenotypic
V_G	genotypic ($V_A + V_D$)
V_A	additive
V_D	dominance
V_E	environmental

The effect of multiple measurements on heritability estimates was demonstrated by an additional analysis that used the IVDMD of the samples from each cut as four phenotypic values of each progeny. This made possible the partitioning of the total phenotypic variance into an

additional component due to the variation in IVDMD of samples from different cuts of a single progeny (Table V). The estimates derived from this analysis were the heritability of IVDMD of forage from a single cut.

Repeatability

The repeatabilities of IVDMD measurements of samples from the four successive cuts were estimated from each of the four laboratory digestion runs using the procedure described by Falconer (10). Analyses of the variances of the IVDMD measurements of unrelated lines (Table VI) within each of the digestion runs partitioned these variances into their within-line and between-line components (Table VII). The ratio of the between-line component to the total phenotypic variance measured the correlation between repeated measurements of the same line and estimated the repeatability of the measurements of IVDMD. These estimates expressed the proportions of the variances of single measurements that were due to permanent differences, both genetic and environmental, between individual unrelated lines. The within-line variance was due to temporary circumstances associated with the separate cuts while the between-line components of variance contained the genetic variance confounded with the portion of environmental variance due to the general environment, i.e. the environmental variance contributing to the between-line component and arising from permanent or non-localized circumstances. These repeatabilities were considered as upper limits of the heritability of IVDMD in populations where the phenotypic variance included variation in IVDMD of samples from separate cuts.

TABLE V

FORM OF SIB ANALYSIS USING FOUR PHENOTYPIC VALUES PER PROGENY

Source of Variation	d. f.	Composition of Mean Squares
Among half-sib families	h - 1	$\sigma_C^2 + c\sigma_P^2 + cp\sigma_F^2 + cpf\sigma_H^2$
Between full-sib families within half-sib families	h(f - 1)	$\sigma_C^2 + c\sigma_P^2 + cp\sigma_F^2$
Among progenies of full-sib families	hf(p - 1)	$\sigma_C^2 + c\sigma_P^2$
Among cuts of each progeny	hfp(c - 1)	σ_C^2

Where:

h = no. of half-sib families = 3

f = no. of full-sib families in each half-sib family = 2

p = no. ofprogenies in each full sib family = 4

c = no. of cuts of each progeny = 4

σ_H^2 = variance among means of half-sib families = $\frac{1}{4}V_A$

σ_F^2 = variance between full-sib families within each half-sib family = $\frac{1}{4}V_A + \frac{1}{4}V_D$

σ_P^2 = variance among progenies of full-sib families

σ_C^2 = variance among samples from different cuts of each progeny } = $\frac{1}{2}V_A + \frac{3}{4}V_D + V_E$

$\sigma_T^2 = \sigma_H^2 + \sigma_F^2 + \sigma_P^2 + \sigma_C^2$ = total phenotypic variance = $V_A + V_D + V_E$

TABLE VI

LINES USED TO ESTIMATE REPEATABILITY FROM EACH DIGESTION RUN

Digestion Run			
R1	R2	R3	R4
10123x10287	10351	"NK-37"	85x9953
10452	10360	10416ax11129	10123x10287
10561x10125	10385	77	10452
"NK-37"	10254ax10429	10306x10153	10561x10125
8800x10421	10466ax8795	9945ax10127	10311-1
10311-2	10311-1	10254ax 7R	10306x10153
10000x10153	10306x10153	BL-22-27	NT-67-2
	NT-67-2	52	10416ax11129
	10561x10125	10254ax10429	"NK-37"
		8795	8800x10421
		0-10976	9945ax10127
		9945c	BL-22-27
		10561x10125	52
			10254ax10429
			10351
			10360
			10385
			10466ax8795

TABLE VII

FORM OF ANALYSIS USED TO PARTITION THE PHENOTYPIC VARIANCE OF IVDMD OF SAMPLES FROM FOUR SUCCESSIVE CUTS

Source of Variation	d.f.	Composition of Mean Square
Between lines	$\ell - 1$	$\sigma_W^2 + 4\sigma_B^2$
Among cuts of each line	$\ell(4 - 1)$	σ_W^2

Where:

ℓ = no. of lines sampled

4 = no. of cuts of each line

σ_B^2 = variance between means of lines

σ_W^2 = variance among cuts within each line

$\sigma_B^2 + \sigma_W^2 = \sigma_T^2$ = total phenotypic variance

And:

$$\text{Repeatability} = \frac{\sigma_B^2}{\sigma_T^2}$$

CHAPTER IV

RESULTS AND DISCUSSION

IVDMD Measurements

Mean IVDMD percentages, standard deviations, and coefficients of variation of samples from each of the four cuts (C1 - C4) measured in duplicate in each of the four laboratory runs (R1 - R4) are given in Tables VIII, IX and X. Means of samples measured in the different runs ranged from 52.1% (R2) to 67.7% (R4) with the mean IVDMD of all samples being 61.3%. Means of samples from different cuts fell within a relatively narrow range (59.8% to 62.4%) as did most of the means of samples from different cuts measured in the same run. One exception was the samples from C1 measured in R2 which had a mean IVDMD at least five percentage points less than the samples from the other three cuts. The standard deviation and coefficient of variation of this group of samples were also larger than these parameters in other groups of samples.

Paired comparisons of IVDMD of samples measured in two or more digestion runs indicated that all differences between the runs compared with each other were significant except those between R3 and R4 (Table XI). These significant differences in measurements between runs were expected but the low mean IVDMD and higher standard deviation of the samples measured in R2 indicated a larger than expected variation in the digestion process of this run. The same basic technique was used

TABLE VIII

MEAN PERCENT IVDMD, STANDARD DEVIATIONS, AND COEFFICIENTS OF VARIATION OF SAMPLES FROM FOUR CUTS MEASURED IN FOUR DIGESTION RUNS

	R1			R2			R3			R4		
	$\bar{X}$	S.D.	C.V.	$\bar{X}$	S.D.	C.V.	$\bar{X}$	S.D.	C.V.	$\bar{X}$	S.D.	C.V.
C1	60.9	2.98	4.89	47.5	5.25	11.05	63.6	3.97	6.24	67.3	3.09	4.59
C2	62.4	2.93	4.69	54.2	3.87	7.14	64.8	4.04	6.23	68.6	3.88	5.65
C3	61.3	2.67	4.35	54.2	3.80	7.01	64.9	3.61	5.56	67.9	3.01	4.43
C4	60.6	2.47	4.07	52.5	4.58	8.72	63.8	3.44	5.39	67.4	2.39	3.54

Mean of all samples--61.3

TABLE IX

MEAN PERCENT IVDMD, STANDARD DEVIATIONS, AND COEFFICIENTS OF VARIATION OF SAMPLES FROM FOUR CUTS

Cut	No. Samples	Mean	S.D.	C.V.
C1	216	59.8	8.34	13.94
C2	217	62.4	6.37	10.20
C3	217	62.1	6.01	9.67
C4	217	61.0	6.33	10.37

TABLE X

MEAN PERCENT IVDMD, STANDARD DEVIATIONS, AND COEFFICIENTS OF VARIATION OF SAMPLES MEASURED IN FOUR DIGESTION RUNS

Cut	No. Samples	Mean	S.D.	C.V.
R1	227	61.3	2.84	4.63
R2	212	52.1	5.18	9.94
R3	224	64.2	3.79	5.90
R4	204	67.7	3.16	4.66

in all four runs, but evidently, some factor in R2 resulted in a digestion process that gave lower IVDMD values.

TABLE XI

COMPARISONS OF IVDMD OF SAMPLES MEASURED IN TWO DIGESTION RUNS

Runs Compared	Number of Paired Comparisons	Difference in Mean % IVDMD
R1 vs. R2	8	9.0**
R1 vs. R3	12	-8.2**
R1 vs. R4	20	-6.5**
R2 vs. R3	20	-14.3**
R2 vs. R4	36	-16.6**
R3 vs. R4	36	-1.4

**Significant at the 1% level.

Regression

Heritability estimates of IVDMD of forage from a single cut that were derived from regression calculations using IVDMD values from each separate cut are given in Table XII. Estimates are from the regression calculations of individual family groups and from the pooled coefficients of the family groups in each digestion run and in all combinations of digestion runs.

TABLE XII

RANGES OF HERITABILITY ESTIMATES DERIVED BY REGRESSION FROM EACH OF FOUR CUTS*

Family Group No.	Run	Cut (harvest) No.			
		C1	C2	C3	C4
1	R1	----	1.72 - 1.73	11.67 - 12.00	2.37 - 2.38
2	R1	.14 - .20	-.15 - .18	-.45 - -.43	.95 - 1.33
3	R1	-.08 - -.05	.86 - .89	.39 - .36	.55 - .60
4	R1	-.74 - -.75	8.50	1.21 - 1.22	-1.62 - -1.65
5	R1	-.43 - -.45	-.12 - -.11	.79	1.61
6	R2	1.08 - 1.19	.38 - .52	.96 - .74	-.76 - -.55
7	R2	.74 - .67	-.21 - -.20	.30 - .52	.41 - -.10
8	R3	1.81 - 1.83	5.56 - 5.54	-3.03 - -3.00	1.75 - 1.78
9	R3	.25 - .85	-.39 - -.10	-.53 - -.54	-1.14 - -1.17
10	R3	.90 - .69	1.64 - 1.62	2.74 - 2.71	1.40 - 1.41
11	R3	.85 - .84	7.75	-.60	1.70 - 1.67
12	R3	-2.61 - -2.59	-8.48 - -8.43	-66.00	28.83 - 29.00
Pooled Combinations					
R1		-.45 - -.49	.55	.33 - .50	.77 - .89
R2		.84 - 1.00	.09 - .32	.41 - .58	-.23 - -.38
R3		.48 - .60	1.08 - 1.19	-.14 - .24	.59 - .76
R1 and R2		.73 - .82	.19 - .39	.38 - .54	.00 - .05
R1 and R3		.31 - .44	.88 - .97	.09 - .38	.65 - .80
R2 and R3		.73 - .82	.38 - .70	.20 - .45	.07 - .25
All Groups		.66 - .71	.41 - .67	.23 - .47	.19 - .37

*Limits of ranges are the h^2 estimates derived by doubling the coefficients from two regression calculations:

1. Repeating IVDMD of regression parent with that of each progeny.
2. Regressing mean IVDMD of all progenies of a regression parent on the IVDMD of that parent.

Estimates from the individual family groups varied widely with 35 of the 47 family group estimates having values in ranges either < 0 or > 1. These extreme values were probably due to the relatively small populations of some of the family groups. The twelve estimates with values between 0 and 1 fell within ranges that had a minimum value of .14 and a maximum value of .96.

Some of the estimates derived from the pooled coefficients also fell within ranges < 0 or > 1 but they did not have the extreme values of the estimates from the individual family groups. This was because the pooled coefficients were, in effect, averages of these individual regression coefficients, weighted according to the size of the family group population. Estimates derived from the pooled coefficients of all family groups were based on the largest total population and should have been the most accurate. The differences between the values of the estimates from the separate cuts were large, however, with a relatively low value (.19-.37) coming from the samples of C4 and a high value (.66-.71) from the samples of C1.

Heritability estimates derived by regression calculations using IVDMD values from all cuts in a single estimate are given in Table XIII. The estimates given are from the regression calculations of individual family groups and from pooled coefficients of combinations of family groups.

Sets of estimates were derived from regression coefficients calculated by three methods:

(1) Using the mean IVDMD of samples from the four cuts as the phenotypic value of each genotype in a single regression calculations.

TABLE XIII

RANGES OF HERITABILITY ESTIMATES DERIVED BY REGRESSION USING IVDMD OF SAMPLES FROM ALL CUTS*

Family Group No.	Run	Calculation Methods		
		1	2	3
1	R1	2.91 - 2.88	.85 - .99	1.88 - 1.89
2	R1	.20 - .27	-.21 - .11	-.06 - .05
3	R1	.49 - .56	.51 - .48	.50
4	R1	.14 - .16	-.42 - -.32	.09
5	R1	.83 - .84	.09 - .44	.60 - .61
6	R2	-.03 - .48	.73 - .72	.29 - .60
7	R2	.45 - .47	.85	.37 - .36
8	R3	2.02 - 2.10	1.07 - 1.50	2.51 - 2.52
9	R3	-.41 - -.28	-.30 -.32	-.43 - -.36
10	R3	1.75 - 1.69	1.33 - 1.30	1.47 - 1.33
11	R3	-1.14	1.04 - .92	.98 - .97
12	R3	-10.01 - -10.13	-1.40 - -1.39	-3.60 - -3.57
Pooled Combinations				
R1		.49 - .62	.12 - .30	.39 - .48
R2		.33 - .47	.80 - .79	.34 - .43
R3		.50 - .84	.36 - .70	.43 - .71
R1 and R2		.37 - .52	.68 - .67	.35 - .45
R1 and R3		.50 - .77	.25 - .55	.41 - .63
R2 and R3		.40 - .67	.69 - .76	.37 - .55
R2 and R3		.41 - .66	.61 - .68	.37 - .53

*Limits of ranges are the h^2 estimates derived by doubling the coefficients from two regression calculations:

1. Repeating IVDMD of regression parent with that of each progeny.
2. Regressing mean IVDMD of all progenies of a regression parent on the IVDMD of that parent.

(2) Using four IVDMD values (one from each cut) for each genotype in a single regression calculation.

(3) Pooling the sum of products of the deviations and the sum of squares from four (one for each cut) separate regression calculations.

The estimates derived by method 1 are heritability of mean IVDMD while those derived by methods 2 and 3 are heritability of IVDMD based on a single cut.

Although all three methods of calculating the coefficients tended to remove some of the variation among IVDMD of samples from four cuts, many estimates from individual family groups were in ranges with values < 0 or > 1. The individual estimates from the families measured in R3 were especially extreme with all but one of them being in ranges with values < 0 or > 1. In most families, the estimate calculated by method 3 was intermediate to the estimates derived by the other two calculation methods.

Estimates from pooled coefficients of the seven combinations of family groups were all within ranges with values $\geq .12$ and $\leq .84$. Minimum values of these estimates ranged from .12 to .79 with the maximum values being between .30 and .84.

Each calculation method gave different ranges of values for estimates derived from pooled coefficients of a given combination of family groups. For each of the seven combinations, however, the range from method 1 has higher values than the range from method 3 and these two generally agreed more closely with each other than with the range from method 2. The range from method 3 had a higher value than the range from method 2 only in the three combinations that did not include

families measured in R2. Method 2 resulted in relatively high values for estimates from the four combinations that included families measured in R2 and low values for estimates from the other three combinations. This relationship was reversed, however, for the pooled estimates calculated by methods 1 and 3; the four combinations that included families measured in R2 gave estimates with lower values than the combinations of families measured in R1 and R3.

According to Lush (17), if a trait can be measured repeatedly over a period of time, the heritability fraction of that trait increases as the number of measurements increases. The heritability estimates calculated by method 1, therefore, were expected to have higher values than the estimates from methods 2 and 3. The relatively high values of estimates calculated by method 2 and the low values calculated by methods 1 and 3 from the families measured in R2 was the reverse of what was expected and may have been the result of the large amount of variation in the measurements made in that run.

The most valid heritability estimate should have come from the pooled coefficients of the combinations of all family groups because that combination represented the largest population. The families measured in R2 should be excluded, however, because of the possible inaccuracy of their IVDMD measurements. The best heritability estimates from regression, therefore, are probably from the combination of families measured in R1 and R3. This would give an estimate of heritability of mean IVDMD in the range of .50-.77. The best estimate would probably be in the lower part of this range and have an approximate value of .53. An estimate of heritability of single cut IVDMD would be more difficult to approximate but would probably be between .28 and .44.

Sib Analysis

The mean squares and variance components from the sib analysis using mean IVDMD for the phenotypic values are given in Table XIV. Theoretically, the variance among means of half-sib families (σ^2_H) should have been less than the variance between full-sib families within each half-sib family (σ^2_F) because the causal component estimated by σ^2_H did not contain any variance due to dominance deviations. Similarly, the relationship between the values of the heritability estimates derived from these variance components was the reverse of what was expected (Table XV). The lowest value estimated the ratio with the most genetic variance and the highest value the ratio with the least. The values of estimates of ratios with the additive variance plus portions of the dominance variance were intermediate to these two extremes but their relation to each other was also the reverse of what was expected.

A value of .76 as an estimate of the heritability of IVDMD is not extremely high when the fact is considered that heritability differs between populations. This estimate is questionable, however, when compared to the broad sense heritability estimate from the same population of .11. This reverse relationship in values was probably the result of a lack of precision in the estimates due to a relatively small number of families and of progenies per family.

The heritability estimates calculated from the various combinations of the observational components of variance were neither strictly broad sense nor narrow sense estimates because the ratios they represented involved the additive variance plus portions of the dominance variance. These estimates may more accurately depict the relative

TABLE XIV

MEAN SQUARES AND VARIANCE COMPONENTS FROM SIB ANALYSIS USING MEAN IVDMD FOR PHENOTYPIC VALUES

Source of Variation	d.f.	Mean Square
Among half-sib families	2	7.3904
Between full-sib families within each half-sib family	3	2.7325
Among progenies of full-sib families	18	2.3967
Total	23	2.8747

$$\sigma_H^2 = \frac{7.3904 - 2.7325}{8} = .5822 = \tfrac{1}{4}V_A$$

$$\sigma_F^2 = \frac{2.7325 - 2.3967}{4} = .0839 = \tfrac{1}{4}V_A + \tfrac{1}{4}V_D$$

$$\sigma_P^2 = 2.3967 = \tfrac{1}{2}V_A + \tfrac{3}{4}V_D + V_E$$

$$\sigma_T^2 = 3.0628 = V_A + V_D + V_E = V_P$$

TABLE XV

HERITABILITY ESTIMATES FROM SIB ANALYSIS USING MEAN IVDMD FOR PHENOTYPIC VALUES

h^2	=	$\frac{4(.5822)}{3.0628}$	=	.76	=	$\frac{V_A}{V_P}$
H	=	$1 - \frac{2.3967 - 2(.5822)}{3.0628}$	=	.60	=	$\frac{V_A + \frac{1}{4}V_D}{V_P}$
H	=	$\frac{2(.5822 + .0839)}{3.0628}$	=	.43	=	$\frac{V_A + \frac{1}{2}V_D}{V_P}$
H	=	$1 - \frac{2.3967 - 2(.0839)}{3.0628}$	=	.27	=	$\frac{V_A + \frac{3}{4}V_D}{V_P}$
H	=	$\frac{4(.0839)}{3.0628}$	=	.11	=	$\frac{V_A + V_D}{V_P}$

amount of genetic variation in the population, however, because of the averaging effects of combining the variance components.

Using four phenotypic values per progeny in a sib analysis had the effect of increasing the total observed phenotypic variance of the population without changing the variance among full-sib and half-sib families (Table XVI). The resulting values of the estimates of heritability of IVDMD based on a single cut (Table XVII) were approximately half the values of heritability of IVDMD based on a mean of four cuts. (Table XV). This would indicate that selection for IVDMD based on a mean of four cuts would be approximately twice as efficient as selection based on IVDMD of samples from a single cut.

Repeatability

The variance components and repeatabilities of IVDMD measurements of samples from the four successive cuts that were measured in each of the four digestion runs are given in Table XVIII. A relatively large amount of variation in the digestion process of R2 was again indicated by the low repeatability (.22) of the measurements made in that digestion run. The large component of variance arising from variation in IVDMD of samples from different cuts of single lines (σ^2_W) was environmental in origin and probably due to inaccurate IVDMD measurements. This inaccuracy was also the probable cause of the lower percent IVDMD values for samples measured in R2.

Repeatabilities of IVDMD measurements made in the other three digestion runs indicated larger components of variance due to genetic differences. The lowest of these was from R1 where the measurements of

TABLE XVI

MEAN SQUARES AND VARIANCE COMPONENTS FROM SIB ANALYSIS USING FOUR PHENOTYPIC VALUES PER PROGENY

Source of Variation	d.f.	Mean Square
Among half-sib families	2	29.5616
Between full-sib families within each half-sib family	3	10.9300
Among progenies of full-sib families	18	9.5866
Among cuts of each progeny	72	3.7872
Total	95	5.6542

$\sigma^2_H = \frac{29.5616-10.9300}{32} = .5822 = \frac{1}{2}V_A$

$\sigma^2_H = \frac{10.9300-9.5866}{16} = .0839 = \frac{1}{4}V_A + \frac{1}{4}V_D$

$\sigma^2_P = \frac{9.5866-3.7872}{4} = 1.4498$

$\sigma^2_C = 3.7872$

$\sigma^2_P + \sigma^2_C = 5.2370 = \frac{1}{2}V_A + \frac{3}{4}V_D + V_E$

$\sigma^2_T = 5.9031 = V_A + V_D + V_E = V_P$

TABLE XVII

HERITABILITY ESTIMATES FROM SIB ANALYSIS USING FOUR PHENOTYPIC VALUES PER PROGENY

h^2	=	$\frac{4(.5822)}{5.9031}$	=	.39	=	$\frac{V_A}{V_P}$
H	=	$1 - \frac{5.2370 - 2(.5822)}{5.9031}$	=	.31	=	$\frac{V_A + \frac{1}{4}V_D}{V_D}$
H	=	$\frac{2(.5822 + .0839)}{5.9031}$	=	.23	=	$\frac{V_A + \frac{1}{2}V_D}{V_P}$
H	=	$1 - \frac{5.2370 - 2(.0839)}{5.9031}$	=	.14	=	$\frac{V_A + \frac{3}{4}V_D}{V_P}$
H	=	$\frac{4(.0839)}{5.9031}$	=	.06	=	$\frac{V_A + V_D}{V_P}$

seven lines had a repeatability of .58. Measurements of 13 and 18 lines in R3 and R4 had repeatabilities of .70 and .62 respectively.

TABLE XVIII

VARIANCE COMPONENTS AND REPEATABILITIES ESTIMATED FROM ANALYSIS OF PHENOTYPIC VARIANCES OF IVDMD OF SAMPLES MEASURED IN EACH DIGESTION RUN

Run	No. Lines	Variance Component			Repeatability
		σ^2_B	σ^2_W	σ^2_T	
R1	7	5.85	4.29	10.14	.58
R2	9	6.72	23.49	30.21	.22
R3	13	10.72	4.49	15.21	.70
R4	18	8.92	5.46	14.38	.62

The repeatabilities from each of the digestion runs can be used as the upper limits of the estimates of heritability of single cut IVDMD derived by regression. A comparison of these values (Table XIX) indicates that the maximum values of the estimates from the family groups measured in R1 and R3 were either less than or approximately equal to the values of the repeatabilities. The estimates from the families measured in R2, on the other hand, had values above the repeatability, further indicating that heritability estimates based on families measured in R2 are possibly inaccurate.

TABLE XIX

RANGES OF SINGLE CUT HERITABILITY ESTIMATES FROM REGRESSION AND REPEATABILITIES OF IVDMD MEASUREMENTS

Run	Regression Calculation Method		Repeatability
	2	3	
R1	.12 - .30	.39 - .48	.58
R2	.89 - .79	.34 - .43	.22
R3	.36 - .70	.43 - .71	.70

Another repeatability estimate was derived by using the estimates of phenotypic variance from the two sib analyses (Tables XIV and XVI) in the formula from Falconer (10):

$$\frac{V_{P(n)}}{V_P} = \frac{1 + r(n - 1)}{n}$$

Where $V_{P(n)}$ is the variance of phenotypic values which are means of n measurements, V_P is the variance of phenotypic values which are single measurements, and r is the repeatability of the measurements. A repeatability value of .36 was obtained by using 3.0628 and 5.9031 as $V_{P(n)}$ and V_P respectively, and solving for r with n = 4.

With .36 as the upper limit, the most valid estimate of heritability of single cut IVDMD derived by sib analysis would be either .23 or .31 (Table XVII). These values correspond very closely with the regression estimate of heritability of single cut IVDMD (.28 - .44) and indicate that the best estimate from this study would be .28.

The relationships between the heritability estimates from the two sib analyses would also indicate that the best estimate of heritability of mean IVDMD derived by sib analysis would be either .43 or .60. These values also correspond very well with .53 as an estimate of heritability of mean IVDMD derived by regression. All of these estimates are between .25 and .78 which was the range of broad sense heritability estimates that Burton and Monson (5) found in their studies.

Selection for IVDMD

Bermuda, as a forage grass, is primarily propagated vegetatively; therefore, most plant breeding efforts to improve it have been directed toward identifying single outstanding plants that can be increased and maintained indefinitely by axexual reproduction. Very little sexual reproduction has been used beyond the production of a single generation of F_1 hybrids that are evaluated for their potential as improved asexual varieties.

The results of this study indicate that there is sufficient genetic variation in IVDMD in bermuda to develop high yielding varieties with improved nutritive value. Although this would require several generations of sexual reproduction, it could probably be accomplished without the tedious and time consuming process of making crosses by hand emasculation. Bermuda, like many other forage grasses, has in its sexual reproductive mechanism a high level of self-incompatibility and is highly cross-pollinated. Hybrid seed could be produced by utilizing this incompatibility with the methods described by Burton (3) or by harvesting seed from open pollinated heads of selected plants grown in close proximity of each other in the field. Plants produced from these

seed could be grown in individual pots in a greenhouse or some other uniform environment and their forage measured for IVDMD. Selection among these plants for high IVDMD would provide the plants to be used as parents for the next cycle of selection. These selection cycles would continue as long as significant progress was being made in increasing IVDMD, then selected plants could be increased by asexual reproduction.

The progress that could be made from at least one IVDMD selection cycle can be predicted by using the heritability and variance estimates from this study. If .53 is accepted as the best estimate of narrow sense heritability and 8.92 (Table XVIII) as the phenotypic variance of mean IVDMD of the parent lines, the increase in IVDMD to be expected by selecting the upper 10% of the lines would be 2.8 digestion percentage units. This rate of increase would result in significant improvement in the nutritive value of bermudagrass forage.

CHAPTER V

SUMMARY AND CONCLUSIONS

Clones of 177 bermudagrass genotypes were grown in 16 inch clay pots under uniform conditions from June, 1970 to June, 1971. Samples of plant material taken from the genotypes on four cutting dates were measured for *in vitro* dry matter digestibility (IVDMD) using an artificial rumen technique and rumen liquor from a fistulated steer. Four laboratory digestion runs were required to measure the samples with duplicate measurements being made of each sample in each digestion run. Estimates of the heritability of IVDMD were derived by parent-progeny regressions and sib analysis from families of clones. Repeatabilities of IVDMD measurements of samples from the four cuts were calculated and used as upper limits of heritability estimates.

Mean IVDMD of all measurements of all samples was 61.3% with the samples measured in run #2 (R2) having the lowest mean IVDMD and those measured in run #4 (R4) the highest. In addition to being the lowest in percent IVDMD, the measurements made in R2 were more variable than the measurements made in the other three runs. The differences between the mean IVDMD of all measurements of the samples from the separate cuts were small, with the lowest mean being 59.8% and the highest 62.4%.

The large differences between the single cut IVDMD heritability estimates derived by regression for each cut indicated that IVDMD data from a single cut was unreliable for estimating heritability and that

selection for IVDMD based on a single cut might not be effective. Estimates derived by regression from data from four cuts appeared to be more reliable than estimates based on one cut. The exceptions to this were the estimates derived from family groups measured in R2 where the single cut IVDMD heritability estimates had values larger than the estimates based on mean IVDMD. This relationship was the reverse of what was expected and indicated that the validity of estimates derived from these families was questionable. The best estimate of heritability of mean IVDMD was from the combination of family groups measured in R1 and R3 and had an approximate value of .53.

The relationship between the values of five heritability estimates derived by sib analysis was the reverse of what was expected and made the validity of these estimates questionable also. This was probably the result of a lack of precision in the estimates due to a relatively small number of families and of progenies per family. A comparison of the estimates derived by sib analysis of single cut IVDMD heritability and mean IVDMD heritability indicated that selection for IVDMD based on a mean of four cuts would be approximately twice as efficient as selection based on IVDMD of samples from a single cut.

The low repeatability of IVDMD measurements made in R2 was another indication of a relatively large amount of variation in the digestion process of that run. The relationship between this repeatability and the single cut IVDMD heritability estimates derived by regression from the family groups measured in R2 also indicated that these estimates were possibly inaccurate. Estimates from family groups measured in R1 and R3, on the other hand, were consistent with the repeatabilities of measurements made in those runs.

Repeatability of the IVDMD measurements of the progeny clones used for sib analysis was calculated from the ratio between the variance of phenotypic values that were means of four measurements and the variance of phenotypic values that were single measurements. This repeatability indicated that the best estimate of single cut IVDMD heritability was .28.

The results of this study indicate that IVDMD in bermudagrass is a heritable trait and that there is sufficient genetic variation among available genotypes to improve this trait by plant breeding. A selection program for IVDMD should be an effective method of increasing the nutritive value of bermudagrass forage.

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VITA

Bobby Ray McGehee

Candidate for the Degree of

Doctor of Philosophy

Thesis: HERITABILITY OF IN VITRO DRY MATTER DIGESTIBILITY IN BERMUDAGRASS

Major Field: Crop Science

Biographical:

Personal Data: Born March 14, 1935, at Lampasas, Texas, the son of Thomas Middleton and Ava Loene McGehee.

Education: Attended elementary school at Lampasas, Texas; graduated from Lampasas High School in May, 1952; received the Bachelor of Science in Agriculture degree with honors from Texas Tech University in May, 1956, with a major in Agronomy (Range option); received the Master of Science degree at Oklahoma State University in July, 1970; completed requirements for the Doctor of Philosophy degree at Oklahoma State University in December, 1974.

Professional Experience: Served as a pilot in the United States Air Force, 1956 to 1959; self-employed in farming at Anton, Texas, 1959 to 1965; manager, West Texas Seed Co., Morton, Texas, 1965 to 1967; graduate research assistant in the agronomy Department of Oklahoma State University, 1967 to 1971; sorghum breeder, McNair Seed Co., Plainview, Texas, 1971 to 1974.

Member of: American Society of Agronomy, Crop Science Society of America, American Genetic Association, Alpha Zeta, Phi Kappa Phi, Phi Eta Sigma, Sigma Xi.