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Heritability Estimates for Forage Yield, In Vitro Dry Matter Digestibility, Crude Protein, and Heading Date in Indiangrass [1]

K. P. Vogel, H. J. Gorz, and F. A. Haskins[2]

ABSTRACT

Space-planted populations derived from 'Holt' and 'Oto' indiangrass, *Sorghastrum nutans* (L.) Nash, were used to obtain heritability estimates for forage yield, in vitro dry matter digestibility (IVDMD), crude protein, and heading date and to determine their genotypic correlations. Heritability estimates were determined by variance component analyses and by parent-progeny regression. Average narrow sense heritability estimates for the two populations were 0.43, 0.42, and 0.50, for forage yield, IVDMD, and protein, respectively. Narrow sense heritability estimates for heading date were 0.90 or larger. Genotypic correlations of yield and IVDMD were negative for the Holt population but were positive, although low, for the Oto population in 1976. Protein and IVDMD had positive genotypic correlations for both populations. Heading date was positively correlated with yield but was negatively correlated with IVDMD and protein.

Additional index words: *Sorghastrum nutans*, Forage quality, Quantitative genetics.

INDIANGRASS, *Sorghastrum nutans* (L.) Nash, is a warm-season cross-pollinated perennial grass that is native to the prairies and plains of the United States, where it is used for summer grazing and prairie hay. The chromosome number of indiangrass is 2n = 40, and its meiotic behavior is normally that of a diploid (Riley and Vogel, 1979). Although several cultivars of indiangrass have been released, there is little published information on the genetics of this species.

The purpose of our research was to obtain heritability estimates for forage yield, in vitro dry matter digestibility (IVDMD), protein content, and heading date and to determine the relationship among these traits.

Heritability estimates for forage yield and quality have been reported previously for several warm-season grasses. Ross et al. (1975) reported heritability estimates of 0.68 and 0.72, respectively, for forage yield and IVDMD in big bluestem, *Andropogon gerardi* Vitm. Newell and Eberhart (1961) used several methods to determine the heritability of various traits in switchgrass, *Panicum virgatum* L. Their heritability estimates ranged from 0.05 to 0.74 for forage yield and from 0.27 to 0.90 for forage quality, which was estimated by a rating index. Heritabilities of

0.51 to 0.80 for leaf protein percentage in sand luestem, *Andropogon hallii* Hack, were reported by Kneebone (1958). Burton and Monson (1972) reported heritabilities ranging from 0.27 to 0.69 for dry matter digestibility of bermudagrass, *Cynodon dactylon* (L.) Pers., for seasonal averages of two to four clippings; and Quesenberry et al. (1978) reported broad sense heritabilities of in vitro organic matter digestibility in rhodesgrass, *Chloris gayana* Kunth, of 0.14 and 0.42 for 2- and 6-weeks regrowth, respectively.

MATERIALS AND METHODS

The indiangrass population used in this study and the field plot procedures have been described previously (Vogel et al., 1980a). In brief, two indiangrass populations derived from the cultivars 'Holt' and 'Oto' were used. Holt was developed by mass selection from ecotypes collected in northeast Nebraska, while Oto, which is 20 days later in maturity than Holt, was developed by mass and progeny selection from ecotypes collected in southeast Nebraska and northeast Kansas (Hanson, 1972). In 1973, space-planted populations of Holt and Oto were sampled at panicle emergence for IVDMD and for crude protein. Open-pollinated seed was harvested from individual plants of the two isolated populations. In 1974, a twice-replicated, space-planted, half-sib progeny nursery was established at Mead, Nebr., from 41 Holt and 150 Oto parent plants. Within each cultivar, approximately one-sixth of these parent plants were selected for each of the following traits: high IVDMD, low IVDMD, high protein, low protein, early heading, and late heading. In this selection process, attention was given only to the trait being selected. For example, protein content or heading date was not considered when selecting plants for IVDMD. Consequently, we believe the selected parent plants approximate a random sample of the original cultivars. In 1975, two ramets of the parental clones, similar in size to the plants established the previous year, were transplanted into the same nursery. A family plot consisted of a parental ramet and four progeny plants.

In 1976, data were collected on every plant in the nursery while in 1977 data were collected only from 30 Oto families that had high yields in 1976 for both parents and progenies. Complete data sets used in the statistical analyses were available from 36 Holt families, 147 sets of Oto parents and 146 sets of Oto progenies in 1976. On the heading date (the number of days after 30 June when five or more panicles had emerged from the boot), the tillers bearing the first five panicles were cut 5 cm above the base of the plant. These tillers were used for IVDMD and protein analyses. The Tilley and Terry (1963) method was used to determine the IVDMD percentage and the Kjeldahl procedure was used to determine crude protein content (A.O.A.C., 1960).

The parent and progeny data were analyzed using conventional analyses of variance and covariance procedures. The data for 1976-1977 were analyzed as a split plot in time. Individual progeny plants within a plot were analyzed as subsamples. The methods described by Gardner (1963) for separating variances into their genetic and environmental components were used.

Table 1. Equations used to calculate heritabilities, genotypic and phenotypic correlations, and expected gain from selection.

Equation number	Parameter estimated	Equation†
1	Heritability on a phenotypic mean basis for parental clones for 1 year.	$H = \sigma^2_g/(\sigma^2_g + \sigma^2_e/r)$
2	Heritability on a phenotypic mean basis for parental clones for 2 years.	$H = \sigma^2_g/(\sigma^2_e/ry + \sigma^2_{gy}/y + \sigma^2_{gr}/r + \sigma^2_g)$
3	Heritability on a phenotypic mean basis for half-sib progeny for 1 year.	$H = \sigma^2_g/(\sigma^2_w/rw + \sigma^2_e/r + \sigma^2_g)$
4	Heritability on a phenotypic mean basis for half-sib progeny for 2 years.	$H = \sigma^2_g/(\sigma^2_w/wry + \sigma^2_e/ry + \sigma^2_{gy}/y + \sigma^2_{gr}/r + \sigma^2_g)$
5	Heritability on a single plant basis for parental clones for 1 year.	$H = \sigma^2_g/(\sigma^2_g + \sigma^2_e)$
6	Heritability on a single plant basis for parental clones for 2 years.	$H = \sigma^2_g/(\sigma^2_g + \sigma^2_{gy} + \sigma^2_{gr} + \sigma^2_e)$
7	Heritability on a single plant basis for half-sib progeny for 1 year.	$H = 4 \cdot \sigma^2_g/(\sigma^2_g + \sigma^2_e + \sigma^2_w)$
8	Heritability on a single plant basis for half-sib progeny for 2 years.	$H = 4 \cdot \sigma^2_g/(\sigma^2_g + \sigma^2_e + \sigma^2_w + \sigma^2_{gy} + \sigma^2_{gr})$
9	Heritability estimated by parent-progeny regression.	$H = 2b_{op}$
10	Realized heritability.‡	$H = 2[(\overline{\overline{X}}os - \overline{\overline{X}}o)/\overline{\overline{X}}o]/[\overline{X}ps - \overline{X}p)/\overline{X}p]$
11	Phenotypic correlations§	$r_{ij} = Mpij/\sqrt{MSii \cdot MSjj}$
12	Genotypic correlations¶	$rg_{ij} = \sigma g_{ij}/\sqrt{\sigma^2_{g_{ii}} \cdot \sigma^2_{g_{jj}}}$
13	Gain from selection††	$Gs = [(i \cdot \sigma p \cdot H)/\overline{X}] \times 100$

† r = replications, g = genotypes, y = years, w = plants within a plot, σ^2_g = genetic variance among parental clones or one-fourth the additive genetic variance among the half-sib progenies, σ^2_e = environmental variance among plots within replications for 1 year's results and the genotype × year × rep interaction variance for 2 year's data, σ^2_y = variance among years, σ^2_{gy} = genotype × year interaction variance, σ^2_{gr} = genotype × rep interaction variance, σ^2_{yr} = year × rep interaction variance, σ^2_w = variance among plants within plots.   ‡ $\overline{\overline{X}}os$ = mean of offspring of selected parents, $\overline{\overline{X}}o$ = offspring grand mean, $\overline{X}ps$ = mean of selected parents, $\overline{X}p$ = grand mean of parents.   § MPij = mean product of the ith and jth trait, Ms_{ii} and MS_{jj} = mean squares of the ith and jth trait, respectively.   ¶ σg_{ij} = genetic covariance of the ith and jth trait, $\sigma^2_{g_{ii}}$ and $\sigma^2_{g_{jj}}$ = the genetic variance of the ith and jth trait.   †† i = standardized selection differential for a selection intensity of 10%, σp = phenotypic standard deviation of progeny, H = heritability estimate, X = progeny mean.

Variance estimates were used in heritability estimates, while covariances among traits were used to determine phenotypic and genotypic correlations between traits.

Heritability estimates were calculated by several methods, as shown in Table 1. Variance component estimates were used to provide estimates of heritability in the broad sense among parental clones (Equations 1, 2, 5, and 6) and in the narrow sense for half-sib progenies (Equations 3, 4, 7, and 8). Heritabilities were calculated on both a phenotypic mean and an individual plant basis as described by Allard (1964) and Hanson (1963). The genetic variance among half-sib families is equal to about one-fourth the additive genetic variance (Gardner, 1963) and is multiplied by four to obtain a heritability estimate on an individual plant basis (Equations 7 and 8). Parent-progeny regression (Equation 9) also was used to obtain heritability estimates. Because environmental covariances caused regression of offspring on parents in the same replication to yield inflated heritability estimates (Vogel et al., 1980a), regression of off-spring means in replication 1 on parents in replication 2, and vice versa, were used to obtain heritability estimates with environmental covariances minimized. The regression coefficient is multiplied by 2 to obtain heritability estimates when half-sib means are regressed on parents (Falconer, 1960).

Realized heritability estimates (Equation 10) also were calculated for IVDMD, protein and heading date. The equation used to calculate realized heritability was described by Newell and Eberhart (1961). Parental clones with high IVDMD, high protein, or late maturity, and the half-sib progenies of these clones, were used as the selected parents and offspring for the realized heritability estimates. Since half-sib progenies were used to obtain realized heritability, the parent-progeny ratio was multiplied by two.

Phenotypic and genotypic correlations (Equations 11 and 12) among traits were determined as described by Falconer (1960). Phenotypic correlations were based on mean squares and mean products from the analyses of variance and covariance, while genotypic correlations were calculated from genetic variances and covariances obtained by separation of mean squares and mean products into their genetic and environmental components.

Expected gain from selection (Equation 13) was calculated from the phenotypic standard deviation of the progeny and the heritability estimate determined by parent-progeny regression. The assumptions were that the progenies represented a population of spaced plants and that 10% of the plants for each trait were selected for transplanting into a polycross nursery. The gain from selection is divided by the overall population mean to express gain from selection as a percentage of the mean.

RESULTS AND DISCUSSION

In 1976 there was considerable variation in forage yield for parents and progenies derived from the Holt and Oto populations (Table 2). Mean forage yields for the parental clones in 1976 for both populations were smaller than the mean forage yields of the progenies. The difference in yield between the parents and the progenies was probably due to the parent clones having been transplanted into the nursery 1 year later than the progenies. The yields differed despite attempts to equalize plant sizes at the time the parent clones were transplanted in 1975. The 2-year mean yields of the parents and progenies of the 30 families harvested in 1976 and 1977 were similar. Differences in the yields of Oto and Holt can be attributed in part to differences in maturity.

The means and ranges for IVDMD, protein, and heading date for the parents were similar to those of the progenies for all three data sets (Table 2). In 1976, the Holt population had slightly higher IVDMD and protein values than the Oto population and was 20 days earlier in maturity.

There were significant differences among the Holt parental clones for IVDMD, protein, and heading date, and among the Holt half-sib progenies for yield, protein, and heading date (Table 2). In 1976, there were significant differences among both the Oto parents and progenies for yield, IVDMD, protein, and heading date. For the 30 Oto families harvested in both 1976 and 1977, there were significant differences among the parents for IVDMD, protein, and heading date. Among the Oto progenies for 1976 and 1977, there was a significant difference only for heading date.

Years were a significant source of variation in all traits among the selected Oto progenies for 1976 and 1977 and for protein and heading date among the parents. The genotype × year effect, however, was significant only for heading date among the parents and for protein content among the progenies.

Table 2. Means and ranges of yield, IVDMD, protein, and heading date in indiangrass parental clones and half-sib families.

| Population | Trait | Mean ± SD† | | Range | | Progeny phenotypic standard deviation§ |
		Parents	Progenies	Parents	Progenies	
Holt 1976	Yield (g/plant)	358 ± 172	606** ± 185	50 – 606	366 – 935	220
	IVDMD (%)	37.4* ± 2.0	36.9 ± 3.9	32.4– 40.9	33.5– 39.8	2.7
	Protein (%)	6.0** ± 0.6	6.0** ± 0.7	5.0– 8.0	4.7– 6.8	0.8
	Date‡	42** ± 3	44** ± 8	23 – 59	26 – 60	12
Oto 1976	Yield	659** ± 188	916** ± 289	232 –1,136	522 –1,244	248
	IVDMD	36.5** ± 2.2	36.1* ± 3.4	31.2– 44.0	33.0– 41.7	2.5
	Protein	5.4** ± 0.8	5.2** ± 0.7	4.0– 7.7	4.3– 6.0	0.8
	Date	62** ± 2	64** ± 6	42 – 76	54 – 76	7
Oto 1976–1977	Yield	707 ± 188	779 ± 304	532 –1,045	619 – 959	322
	IVDMD	39.0* ± 2.0	39.1 ± 2.6	36.1– 44.3	36.0– 42.7	3.7
	Protein	5.6* ± 0.5	5.6 ± 1.1	4.4– 7.3	4.9– 6.2	0.9
	Date	61** ± 4	61** ± 8	53 – 72	53 – 73	8

*,** Indicate that in the analyses of variance, genotypic effects were significant at the 0.05 and 0.01 levels of probability, respectively. † SD = $\sqrt{}$error mean square for genotypes. ‡ Days from June 30 to heading. § As used in Table 1, Equation 13.

Table 3. Heritability estimates and expected gain from selection for yield, IVDMD, protein, and heading date in indiangrass parental clones and their progenies.

Population and trait	Heritability estimates						Expected gain from selection
	Phenotypic mean basis		Individual plant basis		Parent-progeny regression	Realized heritability	
	Parent	Progenies	Parent	Progenies			
	H_b‡	H_n‡	H_b	H_n	H_n		
Holt 1976:							
	(1)†	(3)	(5)	(7)	(9)	(10)	(13)
Yield	0.28	0.79	0.17	1.32	0.38		24.2
IVDMD	0.48	0.16	0.32	0.20	0.34	0.16	4.3
Protein	0.55	0.74	0.38	1.09	0.82	0.30	20.5
Date	0.97	0.91	0.93	2.34	1.42	1.71	
Oto 1976:							
	(1)	(3)	(5)	(7)	(9)	(10)	(13)
Yield	0.42	0.41	0.27	0.48	0.16		7.6
IVDMD	0.52	0.30	0.36	0.40	0.28	0.38	3.4
Protein	0.38	0.52	0.23	0.48	0.22	0.44	5.7
Date	0.96	0.81	0.92	1.52	0.92	1.01	
Oto 1976–1977:							
	(2)	(4)	(6)	(8)	(9)		
Yield	0.32	0.20	0.14	0.14	0.30		
IVDMD	0.73	0.74	0.36	0.71	0.66		
Protein	0.75	0.16	0.43	0.12	0.44		
Date	0.85	0.80	0.70	1.34	1.14		

† Numbers in parentheses refer to the equations, listed in Table 1, that were used to determine the heritability estimates.
‡ H_b and H_n refer to heritability in the broad and narrow sense, respectively.

Heritability estimates for a trait within a population varied depending upon the method used for calculation (Table 3). There were no consistent trends among the estimates obtained by the various methods. In some cases heritability estimates determined by parent-progeny regression were higher than those determined by variance components, and in some cases they were lower. Broad sense heritability estimates for the parental clones were often lower than the narrow sense heritability estimates for the half-sib progenies. The progenies were established a year earlier than the parents and establishment differences among the parent plants resulted in more environmental variation among the parent clones than among the half-sib families, which in turn resulted in low broad sense heritability estimates.

The 30 Oto families evaluated over the 2 years were families in which both parents and progeny performed well in 1976. The 1976–1977 heritability estimates determined by parent-progeny regression are probably the most reliable because selected families were used.

Heritability estimates for heading date were very high for both the Holt and Oto populations. Averaged over both populations, narrow sense heritability estimates for forage yield, IVDMD, and protein were 0.43, 0.42, and 0.50, respectively. In calculating the averages, realized heritability values were not used and heritability values greater than one were given a value of one. The average IVDMD and protein heritability values are almost the same as the realized heritability values obtained for the Oto population but are higher than the realized heritability values obtained for the Holt population. The heritability estimates for yield, IVDMD, and protein are similar to those obtained on other warm-season grasses as indicated previously.

Expected gains from selection per cycle in a restricted recurrent selection breeding program (Burton, 1974), with heritability values calculated by parent-progeny regression, are listed in Table 3. Expected gains from selection per cycle from the average narrow sense heritability values listed above in Equation 13 of Table 1 are

Table 4. Genotypic and phenotypic correlations for four traits of indiangrass parental plants (upper values) and their progenies (lower values). Genotypic correlations are above the diagonals, phenotypic correlations are below the diagonals.

Trait	Holt 1976 Yield	IVDMD	Protein	Date	Oto 1976 Yield	IVDMD	Protein	Date	Oto 1976–1977 Yield	IVDMD	Protein	Date
Yield		−0.81	−0.75	0.73		0.27	−0.39	0.22		−0.21	−0.35	0.58
		−0.38	−0.62	0.64		0.18	−0.57	0.53		0.06	−0.39	0.52
IVDMD	−0.32		0.87	−0.66	0.08		0.53	−0.19	−0.18		0.44	−0.14
	−0.20		1.11	−0.74	0.10		0.25	0.24	−0.07		0.26	−0.39
Protein	−0.39*	0.54**		−0.63	−0.14	0.42**		−0.70	−0.33	0.53**		−0.19
	−0.52**	0.55**		−0.82	−0.29**	0.32**		−0.48	−0.23	0.46**		−0.26
Date	0.38*	−0.49**	−0.50**		0.17*	−0.16	−0.42**		0.18	−0.16	−0.15	
	0.58**	−0.33*	−0.70**		0.29**	0.01	−0.32**		0.09	−0.20	0.04	

*,** Indicate significance at the 0.05 and 0.01 levels of probability, respectively, for the phenotypic correlations only.

27, 5, and 12%, respectively, for yield, IVDMD, and protein for the Holt population and 20, 5, and 13%, respectively, for yield, IVDMD, and protein for the Oto population with 1976 data. Based on the average narrow sense heritability estimates these results indicate that selection for a single trait could result in substantial improvement in forage yield and moderate improvement in IVDMD and protein in a recurrent selection breeding program.

Phenotypic correlations for yield and IVDMD were not significant (Table 4). Yield and IVDMD were negatively correlated genotypically in the Holt population for both the parents and progenies. However, in Oto in 1976, genotypic correlations between yield and IVDMD were low but positive. For the Oto families harvested for yield in 1976 and 1977, there was a low but positive genotypic correlation between yield and IVDMD among the progenies. Perry and Baltensperger (1979) reported that for Oto indiangrass the IVDMD of stems was equal to or higher than the IVDMD of the leaves throughout the growing season, and the decline in IVDMD with maturity was similar for both leaves and stems. If it is indeed true that Oto leaves are similar to stems in digestibility, increases in yield brought about by increases in either leaves or stems might not have an adverse effect on IVDMD. In general, yield and protein were negatively correlated both phenotypically and genotypically while IVDMD and protein were positively correlated. Heading date was positively correlated with yield but negatively correlated with IVDMD and protein.

In summary, heritability estimates for forage yield, IVDMD, and protein were low to moderately high in the indiangrass populations evaluated. The low but positive genotypic correlations between yield and IVDMD in the Oto population indicated that selection for either of these traits would not have much effect on the other, i.e., simultaneous selection for both traits would be feasible. In the Holt population, some parents had progenies with above average yields and IVDMD, which indicates that selection for both traits also may be feasible in this cultivar if large enough populations were used. If selection for IVDMD is practiced, some increase in protein content could be expected. A space-planted nursery was used in this study, but the results of Burton (1974) and Vogel et al. (1980b) indicate that the performance of warm-season forage grasses in space-planted nurseries is predictive of their performance in swards. The incon-

sistency among the heritability estimates for a particular trait illustrates that heritability estimates are not absolute but vary according to the method and germplasm used to obtain the estimates.

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