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COMBINING ABILITY IN FORAGE SORGHUM HYBRIDS (1)

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ABSTRACT - Two cross-classified hybrid forage sorghum [*Sorghum bicolor* (L.) Moench] experiments were conducted at Mead, NE: Experiment 1 (3 females x 8 males), in 1973-75, and Experiment 2 (13 females x 2 males), in 1974-75. Data were collected on plant height, days to bloom, forage yield, percent dry matter (DM), percent protein, and *in vitro* dry matter disappearance (IVDMD) in both experiments and percent Brix in Experiment 1. Differences among hybrids averaged over females or over males were significant for each trait in one parental group or the other in each test except IVDMD in Test 1 and DM in Test 2. All traits were significant for hybrid entries in both tests. Interactions of traits with years were often significant and, with the few degrees of freedom in F-tests, contributed to the nonsignificance of yield among females in Test 1 and males in Test 2. Genetic ratios indicated that general combining ability often was relatively high for days to bloom, height, DM, and forage yield; and was of some importance for IVDMD and Brix. Specific combining ability was most important for protein. Correlations among traits indicated that high forage yield often was positively correlated with tall height and late maturity; was negatively correlated with DM, protein, and IVDMD; and was not associated with Brix.

KEY WORDS: *Sorghum bicolor* (L.) Moench, forage yield, dry matter,

INTRODUCTION

Sorghum [*Sorghum bicolor* (L.) Moench] is grown as a forage and pasture crop on about 1.2 million hectares in the United States (KOEHN, 1976), with most of the production utilized by beef and dairy animals. The crop is particularly important in the Great Plains where nearly all

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of the production comes from F_1 hybrids, but small amounts of three-way crosses and varieties also are planted (HARVEY, 1977). Hybrid forage sorghums followed closely the advent of hybrid grain sorghums in the 1950's but, except for sorghum x sudangrass hybrids, were accepted more slowly. Reasons for this included the sometimes questionable yield advantages, often questionable forage quality advantages, and initially a difficulty in producing hybrid seed using one or both tall parental stocks that were not adapted to mechanical harvest. However, most of these problems were overcome, and trials from Texas (QUINBY and MARION, 1960), Nebraska (DREIER *et al.*, 1965), and Kansas (OVERLEY, 1965) demonstrated yield advantages of certain hybrid genotypes and, in many instances, quality attributes as good or better than those exhibited by conventional forage sorghum cultivars.

Seed production problems have been alleviated through the use of female and male parents that carry complementary height genes. NB6229, a selection from the cross of Early Hegari x Club Kafir and carrying the height factors $Dw_1 dw_2 Dw_3 dw_4$, was the first experiment station R-line release designed to be crossed with $dw_1 Dw_2 dw_3 dw_4$, $Dw_1 Dw_2 dw_3 dw_4$, or $dw_1 Dw_2 Dw_3 dw_4$ females to give tall F_1 's (WEBSTER *et al.*, 1977). Other $Dw_1 dw_2 Dw_3 dw_4$ types were developed in Kansas and Nebraska by Ross (unpublished data). The latter lines were primarily used in the experiments reported here.

The research was undertaken to identify superior forage sorghum parents and hybrids arising from a practical breeding program and to extract information that will allow appropriate choices of procedures for an effective breeding program. The genetic nature of several quantitative traits was determined through study of complete sets of hybrids made with several females and males. Though genetic combining ability studies have been reported in grain sorghum (CROOK and CASADY, 1974; FINKNER *et al.*, 1976) or cited (ECKEBIL *et al.*, 1977) using essentially the Design II experiment of COMSTOCK and ROBINSON (1952), a paucity of information exists on similar research with hybrid forage sorghum.

The few experiments to date on combining ability in forage sorghum (BLUM, 1968; GREWAL and PARODA, 1974; TARUMOTO 1969; 1971) indicated that general combining ability (GCA) was more important than specific combining ability (SCA) for most characters, particularly those related to yield, but all of the experiments had the limitation of being grown in only one environment or were based on data from only a few plants. Moreover, most of the hybrid forage sorghums in these earlier experiments

were made with combine-height grain sorghum female parents. The hybrids used in the research reported here involved all sorgho derivatives with one exception.

MATERIALS AND METHODS

Experiment 1 consisted of 24 F_1 hybrids made from crossing 8 male lines to 3 sterile (A) lines. Experiment 2 consisted of 26 hybrids from 2 males crossed to 13 A lines. Females included the common grain sorghum CK60, dominant for one height gene ($dw_1 Dw_2 dw_3 dw_4$), and the released forage lines KS5 and N4692, dominant for two unidentified height genes. N48 is an experimental line also dominant for two genes. The remaining females were CK60 x sorgho derivatives having the same height as CK60 and Early Hegari (EH) x sorgho derivatives with the same height as EH ($Dw_1 dw_2 Dw_3 dw_4$). Males were mostly EH x sorgho derivatives that restored fertility in crosses and were $Dw_1 dw_2 Dw_3 dw_4$ in height. The exception was Rox, a cultivar that does not restore fertility, is $Dw_1 Dw_2 Dw_3 dw_4$, and has been used to an extent in forage sorghum hybrids (HARVEY, 1977).

Both sets of hybrids were grown under dryland conditions at the University of Nebraska Field Laboratory, Mead, Ne, in 1973-75 (Experiment 1) and in 1974-75 (Experiment 2). The experimental design in both cases was a randomized complete block with three replications. From a two-row plot with rows 0.76 m apart and plants 15 cm apart in the row, one row either 3.0 or 4.5 m long, depending on full plant stands, was harvested for yield and analyzed for quality factors. The second row was left standing for lodging observations that are not reported here.

The data collected on a plot basis from both experiments were as follows:

1. Days from planting until most of the plants were in 50% bloom.
2. Average plant height to the tips of the panicles.
3. Percent dry matter (DM) based on three to five whole plants from each plot at harvest.
4. Percent protein of whole-plant materials estimated by the Kjeldahl method.
5. *In vitro* dry matter disappearance (IVDMD) based on the method of TILLEY and TERRY (1963).
6. Forage yield adjusted to 30% dry matter. Several harvest dates were used according to maturity of genotypes to simulate normal field harvest dates.
7. Brix as the percent solids in juice samples from three or four stalks per plot at harvest measured with a hand refractometer (Experiment 1 only).

Analyses of variance were made for each trait with the entry source of variation partitioned into females, males, and females x males. The entry x year interactions were partitioned into females x years, males x years, and females x males x years. Mean squares were equated to their expected values and solved for components estimating the variance among the fixed effects in the corresponding sources of variation.

Genetic ratios (GR) were estimated as follows:

$$GR1 = \frac{\theta_f^2}{\sigma_e^2/RMY + \sigma_{fm}^2/MY + \theta_{fm}^2/M + \sigma_{fy}^2/Y + \theta_f^2} = \frac{\theta_f^2}{\theta_{Pf}^2}$$

$$GR2 = \frac{\theta_m^2}{\sigma_e^2/RFY + \sigma_{fmy}^2/FY + \theta_{fm}^2/F + \sigma_{my}^2/Y + \theta_m^2} = \frac{\theta_m^2}{\theta_{pm}^2}, \text{ and}$$

$$GR3 = \frac{\theta_{fm}^2}{\sigma_e^2/R Y + \sigma_{fmy}^2/Y + \theta_{fm}^2} = \frac{\theta_{fm}^2}{\theta_{pfm}^2}, \text{ where the symbol } \theta^2 \text{ indicates fixed effects and } \sigma^2 \text{ indicates random effects.}$$

GR1 and GR2 estimate general combining ability (GCA) and GR3 estimates specific combining ability (SCA) based on females, males, and females x males, respectively. The symbols θ_f^2 , θ_m^2 , σ_{fy}^2 , σ_{my}^2 , θ_{fm}^2 , σ_{fmy}^2 , and σ_e^2 are the components for females, males, females x years, males x years, females x males, females x males x years, and error respectively; the symbol θ_p^2 with the appropriate subscript is analogous to an estimate of phenotypic variance. Divisions with F, M, Y, and R indicate the number of observations on females, males, years, and replications. The above symbol designations for components are similar to those of SNEDECOR and COCHRAN (1967) who used k instead of θ for fixed effects.

Existing lines were used in the experiment to generalize about a hypothetical « population », and it is realized that statistical treatment as a random model is not entirely appropriate and that qualifications are necessary. However, the application of population improvement to sorghum is of potential importance and warrants at least a preliminary look at the quantitative genetic information that might exist in forage sorghum, particularly in the absence of very much data on the subject.

RESULTS AND DISCUSSION

Differences among parental lines used in the experiment were known to exist and are reflected in the mean hybrid performance values according to females or according to males (Table 1 and 2). Differences among hybrids averaged over one parental group were statistically significant for all traits except IVDMD in Experiment 1 and DM in Experiment 2, but this does not preclude differences among the parental lines *per se*. Female x year and male x year interactions were statistically significant for most traits in one test or the other and most often for bloom date and plant height.

Though performance of hybrids averaged over females or over males is considered, performance of individual hybrids also is important. Wide differences existed among the hybrids in these tests, but the data are too voluminous to present for each F_1 so only maximums, minimums, and means are shown in Tables 1 and 2. The ranges imply the extent of variability in the parental stocks and have some bearing on the possible improvement of specific characters. The widest ranges were for yield in both experiments and Brix in Experiment 1; the narrowest range was for IVDMD in Experiment 1.

Yield and Brix also had the highest coefficients of variability (CV),

TABLE 1 Mean performance of hybrid forage sorghums based on their parental lines and ranges of individual hybrids grown at Mead, NE, in 1973-75, (Experiment 1).

Group or hybrid (1)	Trait						
	Bloom	Height	DM	Protein	IVDMD	Forage yield	Brix
	days	cm		%		metric tons/ha	%
<i>Female mean</i>							
CK60	78	192	30.8	7.4	61.1	36.2	11.4
N4692	86	229	28.8	6.9	60.3	43.3	12.6
KS5	86	227	28.8	6.8	60.8	43.5	13.7
LSD (0.05)	8	36	1.4	NS	NS	NS	NS
<i>Male mean</i>							
EH-Sart	97	259	27.6	6.7	60.2	49.3	14.0
EH-W. Collier	83	204	29.0	7.4	61.1	36.4	9.9
EH-W. Sourless	80	209	30.2	7.2	61.0	40.4	10.4
EH-Rex	84	211	30.2	7.4	60.1	39.1	11.5
EH-Atlas	82	205	30.6	7.1	60.9	38.2	13.9
EH-Rox	80	216	31.1	6.7	60.5	42.1	13.4
EH-Rox	83	213	28.9	6.7	60.9	44.0	13.7
Rox	83	215	28.1	7.1	61.2	38.4	14.0
LSD (0.05)	4	14	1.3	0.5	NS	3.2	2.1
<i>Hybrid</i>							
Maximum	114	310	37.7	9.3	69.3	65.5	19.9
Minimum	67	125	23.0	5.2	53.8	18.8	3.5
Mean	84	216	29.5	7.1	60.7	41.0	12.6
LSD (0.05)	6	25	1.7	0.8	2.0	6.6	3.7
Experiment CV (%)	2.5	5.4	5.3	7.6	2.9	14.6	14.5

NS Nonsignificant.

(1) CK60 is $dw_1 Dw_2 dw_3 dw_4$. N4692 and KS5 are $dw_1 Dw_2 Dw_3 dw_4$ or $Dw_1 Dw_2 dw_3 dw_4$. Early Hegari (EH) derivatives are $Dw_1 dw_2 Dw_3 dw_4$. Rox is a B line and is $Dw_1 Dw_2 Dw_3 dw_4$.

around the 15% level. CV's under 8% were obtained for the quality-related factors of DM, protein, and IVDMD and were 2-5% for height and bloom.

There were significant female x male interactions for height and forage yield in both experiments, for days to bloom and Brix in Experiment 1, and for DM in Experiment 2. These interactions can be expected because not all males and females interact similarly in hybrid combinations despite general trends that might exist for GCA. The only nonsignificant female x male interactions were for protein and IVDMD. The ranges for these traits were

TABLE 2 - Mean performance of hybrid forage sorghums based on their parental lines and ranges of individual hybrids grown at Mead, NE, in 1974-75, (Experiment 2).

Group or hybrid (1)	Trait					Forage yield metric tons/ha
	Bloom	Height	DM	Protein	IVDMD	
	days	cm		%		
<i>Female mean</i>						
CK60	88	187	31.0	7.3	62.7	36.0
N4692	98	231	29.9	6.6	61.1	49.1
N48	99	231	28.4	6.2	61.9	45.7
KS5	87	198	30.7	6.7	62.4	38.6
CK-Tracy	92	207	29.6	6.6	63.4	42.6
CK-W. Collier	91	187	31.1	7.2	62.5	38.5
CK-W. Sourless	92	187	28.8	7.4	63.0	39.1
CK-W. Sourless	94	191	31.0	7.0	62.3	38.8
CK-Ellis	97	200	31.1	6.9	63.0	42.5
CK-Atlas	98	222	29.1	6.5	59.6	49.5
EH-Sart	97	126	31.4	7.5	63.4	32.9
EH-W. Collier	95	150	29.8	7.2	61.8	38.3
EH-Atlas	100	153	30.0	6.5	64.0	42.3
LSD (0.05)	7	33	NS	0.8	3.2	11.3
<i>Male mean</i>						
EH-Sart	104	205	29.0	6.8	61.4	45.2
EH-Rox	85	175	31.3	7.0	63.4	37.0
LSD (0.05)	NS	NS	NS	NS	NS	NS
<i>Hybrid</i>						
Maximum	115	297	40.5	8.7	70.0	78.0
Minimum	73	95	22.3	4.9	34.1	16.6
Mean	95	190	30.1	6.9	62.4	41.1
LSD (0.05)	10	48	4.1	0.9	4.2	13.4
Experiment CV (%)	1.9	4.2	7.9	7.3	4.4	16.0

(1) CK60 and CK derivatives are $dw_1 Dw_2 dw_3 dw_4$. N4692, N48, and KS5 are $dw_1 Dw_2 Dw_3 dw_4$ or $Dw_1 Dw_2 dw_3 dw_4$. Early Hegari (EH) derivatives are $Dw_1 dw_2 Dw_3 dw_4$.

narrower.

Significant female x male x year interactions existed only for bloom and height (both experiments) and Brix (Experiment 1). This is related to the diverse growing seasons involved, particularly to the rainfall received. Total precipitation for each of the 3 years was: 1973, 88 cm; 1974, 53 cm; and 1975, 49 cm. Though 1974 and 1975 were dry years, the drought

TABLE 3 - Quantitative genetic estimates of agronomic and quality traits from two hybrid forage sorghum experiments at Mead, NE, in 1973-75 (Experiment 1) and 1974-75 (Experiment 2).

Parameter estimated (1)	Trait						
	Bloom	Height	DM	Protein	IVDMD	Forage yield	Brix
<i>Genotypic component</i>							
<i>Expt. 1</i>							
θ_f^2	22.70	324.91	1.248	0.0510	0.085	12.42	0.579
θ_m^2	24.90	241.29	1.249	0.0751	0.000	13.33	1.878
θ_{fm}^2	3.84	123.63	0.204	0.8072	0.102	6.23	1.479
<i>Expt. 2</i>							
θ_f^2	4.44	869.30	0.000	0.0542	0.517	4.28	—
θ_m^2	167.13	401.51	2.364	0.0115	1.342	26.90	—
θ_{fm}^2	9.84	23.18	1.770	0.1002	0.000	12.16	—
<i>Genetic ratio</i>							
<i>Expt. 1</i>							
$\theta_f^2 / \theta_{Pf}^2$	0.84	0.77	0.90	0.24	0.58	0.72	0.54
$\theta_m^2 / \theta_{Pm}^2$	0.86	0.77	0.80	0.20	0.00	0.80	0.66
$\theta_{fm}^2 / \theta_{Pfm}^2$	0.56	0.75	0.43	0.93	0.23	0.61	0.50
<i>Expt. 2</i>							
$\theta_f^2 / \theta_{Pf}^2$	0.30	0.85	0.00	0.32	0.32	0.18	—
$\theta_m^2 / \theta_{Pm}^2$	0.98	0.84	0.92	0.47	0.64	0.80	—
$\theta_{fm}^2 / \theta_{Pfm}^2$	0.48	0.08	0.65	0.60	0.00	0.53	—
<i>Stability ratio</i>							
<i>Expt. 1</i>							
$\theta_f^2 / (\theta_f^2 + \sigma_{fy}^2)$	0.69	0.58	0.84	0.23	0.80	0.53	0.62
$\theta_m^2 / (\theta_m^2 + \sigma_{my}^2)$	0.83	0.84	0.73	0.72	0.00	1.00	1.00
$\theta_{fm}^2 / (\theta_{fm}^2 + \sigma_{fmy}^2)$	0.34	0.61	1.00	0.91	1.00	1.00	0.31
<i>Expt. 2</i>							
$\theta_f^2 / (\theta_f^2 + \sigma_{fy}^2)$	0.87	1.00	0.00	0.48	0.37	0.21	—
$\theta_m^2 / (\theta_m^2 + \sigma_{my}^2)$	0.98	0.82	1.00	1.00	0.51	0.73	—
$\theta_{fm}^2 / (\theta_{fm}^2 + \sigma_{fmy}^2)$	0.32	0.04	1.00	0.67	0.00	0.62	—

(1) θ_f^2 , θ_m^2 , θ_{fm}^2 , σ_{fy}^2 , σ_{my}^2 , and σ_{fmy}^2 are the variance for females, males, females x males, females x years, males x years, and females x males x years, respectively. θ_p^2 is the « phenotypic » variance for females, males, or females x males, as appropriate.

pattern was different due to distribution of rain and to temperature extremes that further influenced results.

A low female x male x year interaction is valuable to plant breeders in that confidence is gained to rank hybrid combinations for different traits in

repeated experiments. Fortunately, bloom and height are among the least difficult traits with which to work, and generally a limited amount of data will allow satisfactory classification. The interactions may have little bearing on the heritability of a character which relates more to the progress that can be expected through breeding. In grain sorghum both height and bloom are known to be highly heritable, whereas yield often has low heritability (JAN-ORN *et al.*, 1976).

Component analyses (Table 3) supplemented the mean square data through extraction of quantitative-type genetic information and indicated phenotypic and genetic influences. An examination of θ_f^2 and θ_m^2 in Table 3 shows that they were generally higher than θ_{fm}^2 for bloom date and height. They tended to be higher for yield and dry matter but lower for protein. Trends were not always clear for remaining traits.

GCA was computed for female and for male gene action, and SCA was computed for female x male gene action. On the whole, GCA seemed most important for bloom and height, DM, and yield; was of some importance for IVDMD and Brix; and was of little importance for protein. Negative components, assumed to be zero, caused divergent results with respect to IVDMD in both experiments and to DM in Experiment 2. GCA values exceeded SCA values for Brix in Experiment 1, largely due to the male component.

When θ_f^2 and θ_m^2 were considered in relation to their year interaction components, σ_{fy}^2 and σ_{my}^2 , stability ratios as computed by KAMBAL and WEBSTER (1965) were most pronounced for date of bloom. The θ_{fm}^2 ratio was high for height in Experiment 2 but not Experiment 1. In general, male components tended to be more stable than female components in both experiments, and both sometimes showed moderate stability for DM, protein, and yield.

Correlations (Table 4) added to the interpretation of the experiments by showing the interrelationships among the several characters studied. High forage yield was correlated with tall height in both experiments and with late maturity in Experiment 2. These associations were expected based on previous knowledge. High forage yield also tended to be associated with lower dry matter percentage, lower grain protein, and lower IVDMD which in turn was related to late maturity. Brix in Experiment 1 was not associated with any other characters, and the r values were all close to zero.

Several lines were identified which had high GCA for yield and which should be useful in a practical breeding program. These included N48, N4692, and CK-Atlas females and EH-Sart and EH-Rox males. While the six possible hybrids among the above parents exhibited high yield, a few other crosses not involving these lines also warrant further study.

TABLE 4 - Correlation coefficients among agronomic and quality traits from two hybrid forage sorghum experiments at Mead, NE, in 1973-75 (Experiment 1) and 1974-75 (Experiment 2).

Trait	Expt.	Trait					
		Height	DM	Protein	IVDMD	Forage yield	Brix
Bloom	1	0.12	-0.40*	-0.31*	-0.34*	-0.01	0.02
	2	0.64*	-0.62*	-0.24*	-0.46*	0.65*	—
Height	1		-0.60*	-0.39*	-0.68*	0.74*	0.12
	2		-0.63*	-0.34*	-0.47*	0.72*	—
DM	1			0.16	0.26*	-0.21*	0.17
	2			0.03	0.42*	-0.33*	—
Protein	1				0.20*	-0.37*	0.07
	2				0.15	-0.35*	—
IVDMD	1					-0.52*	-0.09
	2					-0.42*	—
Forage yield	1						-0.04
	2						—

* Significant at least at the 0.05 probability level.

From the basic plant breeding viewpoint, the experiments quantified important traits in forage sorghum and implied ways and means of improving them. Though F_1 data indirectly bear upon heritability, a more fundamental approach would be to test families from forage sorghum populations and calculate true heritabilities based on additive gene action. Recombination of the selected families and subsequent testing of the improved cycles would permit comparisons of expected and actual gains. Through recurrent selection techniques, the probability should be increased for ultimate extraction of elite lines. This, in turn, would augment a hybrid-oriented program.

RIASSUNTO

Attitudine combinatoria in ibridi di sorgo da foraggio

Sono stati condotti due esperimenti con ibridi di sorgo da foraggio a Mead, Nebraska: il primo nel 1973-75 (Esperimento 1; 3 femmine per 8 maschi) e il secondo nel 1974-75 (Esperimento 2; 13 femmine per 2 maschi). Sono stati ottenuti dati sull'altezza della pianta, precocità, produzione di foraggio, percento di sostanza secca (DM), percento di proteine e digeribilità in

vitro (IVDMD). Nell'esperimento 1 si è ottenuto anche il percento di residui solidi (Brix). Le differenze medie tra ibridi (medie delle femmine o dei maschi) sono risultate significative in uno o nell'altro dei gruppi parentali, a meno del carattere IVDMD nell'esperimento 1 e DM nel 2. In entrambi gli esperimenti le differenze tra ibridi per tutti i caratteri sono risultate significative. Spesso le interazioni carattere x anni sono apparse significative contribuendo alla non-significatività della produzione, tra femmine nell'esperimento 1 e tra maschi nel 2. L'attitudine combinatoria generale è risultata alta per precocità, altezza della pianta, DM e produzione di foraggio; la stessa è inoltre di una qualche importanza per i caratteri IVDMD e percento di residui solidi. L'attitudine combinatoria specifica è risultata particolarmente importante per il percento di proteine. Le correlazioni tra caratteri indicano che una elevata produzione di foraggio è correlata positivamente con l'altezza della pianta e la tardività e negativamente con DM, % proteine e IVDMD; non è invece associata con il percento di residui solidi.

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