GENETIC ANALYSIS OF GERMINATION AND JUVENILE GROWTH OF SORGHUM (*Sorghum bicolor* (L.) Moench) AT DIFFERENT TEMPERATURES

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by

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B. S., University of Sierra Leone, 1981

A MASTERS'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Genetics

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1985

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TABLE OF CONTENTS

LIST OF TABLES

ACKNOWLEDGEMENTS

Any form of investigation can never be a one man's achievement. I, therefore, wish to express my sincere thanks to my late major professor, Dr. Dan M. Rodgers for his directions and for making my stay at Kansas State University an enjoyable learning experience, though he could not live to reap his share of the praises. Special thanks also go to my current advisor, Dr. P. Bramel-Cox, for her directions and constructive criticisms during the final phase of my thesis. Last, but not the least, I would also like to thank the other members of my Graduate Committee, Dr. R. L. Vanderlip and Dr. W. T. Schapaugh, Jr. for their timely advice whenever it was needed most.

I. GENETIC ANALYSIS OF GERMINATION OF SORGHUM (*Sorghum bicolor* (L.) Moench) AT DIFFERENT TEMPERATURES.

ABSTRACT

Germination of sixty-six F1 sorghum (Sorghum bicolor (L.) Moench) hybrids and their parents was evaluated for temperature response at ten temperatures, 5, 7.5°C and between 10 and 45°C at 5°C interval in the laboratory. Results indicated that germination rate was slightly heterotic between 10 and 40°C but highly heterotic at 5, 7.5 and 45°C. Most of the genetic variation for germination rate in the hybrids was due to specific combining ability (SCA) and general combining ability (GCA) of the female parents. The superior general combiners for germination rate across temperatures were Tx623 and W. D. Kaoliang for females and males, respectively. Two superior specific hybrids (Tx3042 x D. D. Feterita and Tx623 x D. D. Feterita) were identified for germination rate at low temperatures. The superior hybrid between warm and high temperatures was Tx2749 x Tx415. Thus, the enhancement of germination rate could be achieved if very careful selection was placed on the female parent and if selection was based upon many testers to identify specific combiners which responded better to temperature changes.

Introduction

Sorghum, Sorghum bicolor, (L.) Moench, can be grown in a wide range of climatic regions. Nevertheless, temperature is a major uncontrollable climatic factor which delimits its production areas and limits its yield (Miller, 1982). In the U. S., sorghum may be planted in soils warm enough for germination but prior to germination, colder weather may lower the soil temperature below the threshold for germination for a day to a week or more(Nordquist, 1971). Conversely, poor crop establishment due to impeded germination at high soil temperatures have been very common in the semi-arid tropics, especially in Africa where soil temperatures at planting as high as 68°C have been recorded (Peacock, 1977; 1982). The breeding of sorghum genotypes that would rapidly germinate and establish under such adverse temperature conditions would not only boost its production in marginal production areas, but would also expand its adaptation into more northernly latitudes, higher altitudes, and regions subject to high temperatures at the start of the growing season.

Thomas and Miller (1979) and Miller (1982) reported that the minimum temperature for germination of sorghum varied between 4.6 to 16.5°C. Several researchers have found that the optimum temperature for germination ranged from 21 to 35°C (Martin et al., 1935; Stickler et al., 1962; Stoffer and Van Riper, 1963; Kanemasu et al., 1975; Aisien and Ghosh, 1978). Peacock (1982) reported the lethal

high temperature for germination varied from 40 to 48°C. Wilson et al. (1982) reported significant genetic variation in germination and emergence of sorghum under high soil temperatures but there was a significant genotype x temperature interaction for the genotypes tested. Nordquist (1971) found significant genetic variation for germination, emergence and seedling growth under cold temperatures but tolerance at each of these stages was independent.

The specific objectives of this study were to estimate heterosis, evaluate the relative importance of general and specific combining ability and correlate line and topcross performance for germination at a number of different temperatures.

Materials and Methods

Breeding Materials

The experimental materials included six A-lines (females) adapted to the U. S., eleven diverse R-lines (males), and their F1 hybrids developed in a Design II mating scheme in the summer of 1983. The parents are described in Table 1. The sixty-six hybrids and their parents were evaluated in germination experiments in the laboratory.

Germination Experiments

Seeds were sterilized with 0.03% silver nitrate ($AgNO_3$) solution for four minutes, washed with 0.13% of sodium chloride (NaCl) solution to remove excess $AgNO_3$, re-sterilized with 20 % chlorox solution for five minutes, and washed with four rinses of double distilled water before drying under sterile conditions. All sterilizing solutions contained 0.01% Nonidet (wetting agent).

Two replicates of fifteen seeds per entry were germinated in petri dishes with moist Whatman No.1 filter papers at 7.5 and at 5°C intervals between 5 and 45°C in a completely randomized design in a Precision temperature incubator. Filter papers were kept moist with distilled water which had equilibrated at the treatment temperature. Germination was recorded when emergence of the radicle was visible. Germinated seeds per day were cummulated until the experiment was terminated. Rate index, a measure of the speed of germination and a modification of the coefficient

of velocity (Scott et al, 1984), was calculated as follows:

Rateindex = 100(summation of:((cummulative germination/ day)/BVN)/No. of days accumulated by those germinated seeds),

where BVN = base viable number calculated by averaging total germination over a temperature range of 15 to 35°C. A high rate index indicated a greater germination in a shorter time.

Statistical Analysis

Separate analyses of variance were calculated for individual temperatures for rate index and a combined analysis (McKintosh, 1983) was also calculated to test the significance of genotype x temperature interaction. Parents and checks were not included in the analyses of combining ability. All effects in the models were considered fixed. At some temperatures there was heterogeneity of error variance for the parents and hybrids, thus a separate parent error mean square was used to test the significance of the parents, a hybrid error mean square was used to test the significance of the hybrids and the pooled error mean square was used to test the significance of parents vs hybrids. The significance of the genotype x temperature interaction was tested using the pooled error mean square for the combined analysis.

The average mid-parent heterosis of the hybrids was obtained as follows:

$$\text{Heterosis} = \frac{\text{X hybrids} - (\text{X males} + \text{X females})/2}{(\bar{X}\ \text{males} + \bar{X}\ \text{females})/2}$$

Significance of this estimate of mid-parent heterosis was determined from a single degree of freedom comparison in the analysis of variance. Significance of average high parent heterosis was determined using a least significant difference (LSD) (Cox et al., 1984) between the high parent mean and the hybrid mean. This LSD was:

$$LSD_{0.05} = t_{0.05}((1/rb + 1/ra)MSe)^{1/2},$$

where $t_{0.05}$ was the tabular value of t at the 5% level of significance with the appropiate degrees of freedom, r equalled the number of replications, b equalled the number of entries in a hybrid mean, a equalled the number of entries in a parental mean and MSe was the pooled error mean square.

The GCA and SCA variance components were calculated from the respective mean squares for males, females and males x females and their expected mean squares (Beil and Atkins, 1967). The standard errors of the estimates were calculated as described by Lothrop et al. 1985. GCA and SCA effects for an individual male or female parent and the SCA effects of their crosses for germination were obtained, and positive values tested for significance with a one tailed t-test using the method of Ross et al. (1983).

Simple phenotypic correlations using line and topcross means were calculated to compare line and topcross performance of the parents for each temperature.

Results and Discussion

Separate analyses of variance for germination rate for each temperature are presented in Table I-2. There was significant variation within both the parents and hybrids. The variation within the A-lines was not significant between 20 and 40°C. Significant differences were not found within R-lines at 20, 25, and 35°C. The A-lines differed significantly from the R-lines at the extremely low temperatures (5 and 7.5°C), and at 30 and 40°C. The variation within the hybrids was significant at all temperatures, as was its components, females, males, and their interaction. The hybrids differed significantly from their parents at all temperatures except 30°C. There were also significant female x temperature, male x temperature and male x female x temperature interactions (Table I-3). Wilson et al. (1982) observed significant changes among the mean ranks of sorghum genotypes in their ability to germinate and emerge under different temperature treatments. Their findings agreed with the results of this study. Both the results of the separate analysis and the combined analysis indicated significant variation in the hybrids and the parents of this study for the ability to germinate over a range of temperatures.

Heterosis

Germination rate in the F1 hybrids was slightly heterotic between 10 and 40°C but highly heterotic at extreme temperatures (Table I-4). At the low temperatures,

5 and 7.5°C, the parental means were significantly different and there was significant mid-parent and high parent heterosis. The high parent heterosis was 55 and 59% at 5 and 7.5°C, respectively. At moderate temperatures of 10, 15 and 20°C, the parents did not differ significantly but there was significant heterosis. At 25°C, the optimum temperature for germination rate in the males, neither the parents nor the parents and their hybrids differed significantly but at 30°C, the optimum temperature for both the females and the hybrids, the parents differed significantly and while the heterosis was significant, it was not very large. At both 35 and 40°C, there was no significant high parent heterosis even though the mid-parent heterosis was significant at both temperatures and the parents differed at 40°C. The highest mid and high parent heterosis occurred at 45°C but at this temperature, the parents did not differ significantly. Thus, in this experiment with 17 parents, heterosis for germination rate could be explained by partial or complete dominance at two or more loci in the parents.

Genetic Variance

Most of the genetic variation for germination rate at all temperatures was due to SCA and GCA(females) (Table I-5). GCA(females) was of much greater importance, based upon its variance components as a percentage of the total genetic variance, at 15, 20, 25, and 40°C. At these temperatures, SCA accounted for a greater proportion of the variance than GCA(males). At 5 and 45°C, the two extreme temperatures, the

three components accounted for nearly equal proportions of the total variance. These GCA(females) and SCA components were nearly equivalent only at one temperature, 10°C. The SCA component accounted for the greatest proportion of the total genetic variance at three temperatures, 7.5, 30 and 35°C, but the relative importance of the two GCA components were different at the different temperatures.

In comparison to the GCA of females, the variation due to GCA of the males had little significance despite their greater diversity. Consequently, as a result of the greater importance of GCA(females) and SCA, the enhancement of germination rate would require very careful selection of the female parent and the use of many testers to identify specific combiners which would give a better temperature response.

GCA and SCA Effects

Prior to this experiment , none of the female lines had been specifically identified as either cold or heat tolerant at germination, yet Tx623, Ks9 and Ks24 had positive GCA effects over all temperatures, at high temperatures and at low temperatures, respectively (Table I-6). Six of the male parents, Man64, 76BTP6-2, 76BTP15-1, 76BT54-3, W. D. Kaoliang and C. B. Kaoliang were specifically identified as cold tolerant lines. None of these male parents had positive GCA effects at 5°C and only Man64 was positive at 7.5°C (Table I-7). Yet, positive GCA effects at both of these temperatures were found in D. D.

Feterita, a Southern African type and Tx415, a R-line developed in Texas.

From 10 to 45°C, all the males had at least one positive GCA effect except Ks53 and Tx415, and two of the cold tolerant lines (76BTP6-2, and 76BTP15-1). The two cold tolerant Kaoliangs were positive in the greatest number of temperatures in this range. Tx430 had a positive effect only at 45°C. No male parent was positive over all temperatures, indicating no relationship in one genotype between low and high temperature tolerance.

In this study, there was no relationship between the specific adaptation of the parents to temperature and their general combining ability in hybrid combinations. This was also found in SCA effects of specific hybrid combinations (Table I-8). At the cold temperatures, 5 to 15°C, seven hybrid combinations had positive SCA effects at all these temperatures, but only three of those which were significant involved a specifically identified cold tolerant line as one parent. This equalled the number of hybrids which involved the good low temperature general combiners, D. D. Feterita, Tx415 and Tx623.

At least one high general combiner at hot temperatures was involved in all but two of the hybrids with positive SCA effects at hot temperatures. These were the two hybrids with Tx2749 as the female. One hybrid, Ks9 x C. B. Kaoliang, involved a cross of two high general combiners at that temperature. Six of the hybrids had as the male parent a

previously selected cold tolerant line.

In conclusion, the hybrids with positive significant SCA effects had at least one parent with positive GCA effects within the range of that temperature class except Tx2479 x MN73X1, Tx2479 x Tx415 and Ks66 x Tx430 at the cold and warm temperatures. Despite this relationship, only about 10% of all the hybrids at the ten temperatures had positive significant SCA effects over a temperature range.

Miller (1982) found a correspondence between tropical adaptation and low temperature germination. In this study, one parent Tx623, showed this relationship. In general, there was no relationship between the adaptation or specific selection of a parent per se and its characterization as a high general combiner or the specific effects of its hybrids.

Comparison of Line and Topcross Performance

Parental lines did not generally have a significant positive linear relationship with their topcross performance(Table I-9) except at 5°C. This lack of a consistent relationship between per se and topcross performance was expected with the significant male x female interaction across all ten temperatures. Thus, the performance of a line per se at a given temperature between 5 and 45°C was unrelated to the performance of its hybrid.

Summary

The performance of sixty-six F1 hybrids of sorghum and their seventeen parents evaluated at ten laboratory temperatures showed that germination rate was slightly heterotic between 10 and 40°C but highly heterotic at extreme temperatures (for both mid and high parent heterosis). The results from both the performance of the parents and their F1 hybrids indicated that heterosis could be accounted for by partial or complete dominance at two or more loci in the parents.

Most of the genetic variation for germination rate between 5 and 45°C was accounted for by GCA of the female and SCA. GCA(males) had very little significance despite the greater diversity of the males. Thus, the enhancement of germination rate at different temperatures would require careful selection of the female and the use of many testers in evaluation tests to identify specific combiners that would give better temperature response.

No relationship was found between low and high temperature germination response nor between the specific adaptation of parents to temperature and their general combining ability in hybrid combinations. Thus, the mean performance of a line at a given temperature was not indicative of its hybrid performance. In conclusion, genotypes would need to be subjected to evaluation tests at the given temperature conditions in hybrid combination.

Table I-1. Descriptions of female and male parents used in the study of germination at ten temperatures.

Line	Description
Female	
Ks9	A line derived from Schrock x Ellis.
Ks24	A line derived from Spur Feterita-Western Blackhull[3] x Redbine-60.
Ks66	Elite breeding line.
Tx623	Tropically adapted line derived from B3197 x SC170-6
Tx2749	Selection from Redlan x Ks30 for greenbug resistance. Ks30 was a Sorghum bicolor var. bicolor x var. virgatum cross.
Tx3042	Selection from Redbine 60 x Ks30 for greenbug resistance. Ks30 was a Sorghum bicolor var. bicolor x var. virgatum cross.
Male	
Man64	Dwarf cold tolerant line from CIMMYT, Mexico.
76BTP6-2	" " " " " " " .
76BTP15-1	" " " " " " " .
76BT54-3	" " " " " " " .
W. D. Kaoliang	Dwarf Chinese cold tolerant line.
C. B. Kaoliang	" " " " " .
D. D. Feterita	A southern African-type R-line.
Ks53	A kafir-type R-line derived from 43W29[2] x Ks7
MN73X1	A R-line developed in Minnesota.
Tx415	A R-line developed from Tx3078 x Tx09.
Tx430	A tropically adapted line derived from Tx2536 x SC170-6.

Table I-2. Analysis of variance for germination rate of six female and eleven male inbred parents and their sixty-six F1 hybrids incubated at ten temperatures in the laboratory.

		Temperature (°C)									
		5	7.5	10	15	20	25	30	35	40	45
Source	df	Mean square									
Genotypes	82	12.77**	93.49**	472.75**	322.21**	1276.73**	783.96**	442.30**	288.9**	1018.85**	1862.66**
Parents(P)	16	3.33**	18.46**	654.49**	350.37**	745.38	244.57	947.10**	523.13	1916.11**	605.41**
A-line(A)	5	4.37**	18.82**	696.14**	495.84**	1115.96	506.81	416.60	178.56	136.12	970.47**
R-line(R)	10	2.41**	14.98*	679.00**	312.48**	634.62	137.86	1039.85**	696.70	2198.09**	472.47**
A vs R	1	7.34**	51.44**	201.16	1.99	0.01	0.48	2672.13**	510.28	7996.23**	119.58
Hybrids(H)	65	14.03**	105.80**	358.08**	279.76**	1153.53**	925.93**	185.55**	213.61**	595.58**	1899.28**
Females(F)	5	65.46**	385.42**	1973.88**	1892.10**	6945.10**	4951.51**	208.67**	572.96**	3380.92**	6908.45**
Males(M)	10	24.61**	100.32**	236.12**	185.29**	1463.43**	1264.14**	314.24**	311.42**	484.77**	3721.56**
M X F	50	6.76**	78.93**	220.89**	137.42**	512.40**	455.73**	150.30*	158.11*	339.21**	1033.90**
P vs H	1	82.17**	493.47**	5018.61**	2630.90**	17786.11**	185.83	9054.03**	1368.72**	14175.35**	19598.80**
Error											
Parent	16	0.46	4.19	90.47	68.29	432.81	328.53	204.04	319.15	243.62	117.42
Hybrid	66	2.61	10.38	73.72	48.55	259.17	135.84	86.70	89.81	100.10	317.14
P vs H	1	3.03	1.61	419.34	28.24	118.46	311.92	1.55	166.53	66.47	97.23
Pooled	83	2.22	9.14	82.08	52.08	289.85	169.93	109.56	135.09	126.82	274.64

*, ** $P < 0.05$ and 0.01, respectively.

Table I-3. Combined analysis of variance for germination rate of sixty-six F1 hybrids of sorghum at ten temperatures in the laboratory.

Source	df	Mean square
Males(M)	10	2433.08**
Females(F)	5	13514.59**
M x F	50	633.80**
Temperature(T)	9	515869.79**
M X T	90	630.31**
F X T	45	1537.99**
M X F X T	450	273.32**
Residual	660	112.40

*, ** $P \leq 0.05$ and 0.01, respectively.

Table I-4. Means of parental lines, mid-parents, hybrids and average heterosis for germination rate at ten temperatures.

Temperature(°C)	Male	Female	Mid-parent	Hybrid	Mid-parent heterosis
	--- Rate index ---				-- %--
5	1.0	2.0	1.5	3.1	106.7
7.5	1.8	4.4	3.1	7.0	125.8
10	41.1	46.6	43.8	55.8	27.1
15	79.6	79.1	79.4	89.3	12.5
20	108.2	107.6	107.9	133.9	24.1
25	153.7	153.5	153.6	156.3	1.8
30	149.2	167.7	158.5	174.0	9.8
35	129.6	138.4	134.0	140.3	4.7
40	98.0	130.1	114.1	132.2	15.9
45	16.9	20.7	18.8	45.2	140.4

Table I-5. Estimates of variance components, standard errors and components expressed as percentages of the total genetic variance (parenthesis) for germination rate of sixty-six F1 hybrids of sorghum at ten temperatures.

	Variance component		
Temperature (°C)	GCA(males)	GCA(females)	SCA
5	1.83±0.84	2.86±1.59	2.08±0.68
	(27.0)	(42.2)	(30.7)
7.5	7.47±3.42	17.05±9.36	34.28±7.79
	(12.7)	(29.0)	(58.3)
10	13.53±8.10	86.37±48.0	73.59±22.56
	(7.8)	(49.8)	(42.4)
15	11.40±6.34	83.79±45.98	44.44±14.14
	(8.2)	(60.0)	(31.8)
20	100.36±49.90	303.91±168.75	126.61±54.94
	(18.9)	(57.2)	(23.9)
25	94.03±43.05	218.89±120.31	159.95±46.18
	(19.9)	(46.3)	(33.8)
30	18.96±10.67	5.54±5.07	31.79±16.51
	(33.7)	(9.8)	(56.5)
35	18.47±10.67	21.96±13.94	34.15±17.31
	(24.8)	(24.9)	(45.8)
40	32.06±16.55	149.13±82.15	119.56±34.35
	(10.7)	(49.5)	(39.8)
45	283.70±126.69	299.61±167.87	358.38±104.97
	(30.1)	(31.8)	(38.1)

*, ** $P \leq 0.05$ and 0.01, respectively.

Table I-6. Estimates of GCA effects for germination rate of six female inbred parents of sixty-six F1 hybrids of sorghum at ten temperatures.

	Temperature (°C)									
Female	5	7.5	10	15	20	25	30	35	40	45
Ks9	-0.7	-3.9	5.2*	12.1*	19.8*	18.4*	4.0*	6.1*	8.7*	14.7*
Ks24	1.4*	6.2*	8.6*	0.0	-3.2	5.3*	-2.2	3.1	5.4*	-2.0
Ks66	-2.2	-3.5	-12.9	-6.0	-20.8	2.7	-3.8	-7.2	-24.1	-29.4
Tx623	2.4*	3.9*	8.7*	6.9*	22.6*	5.6*	3.5*	3.6*	7.1*	19.9*
Tx2749	0.6*	-0.1	0.7	0.9	-3.3	-6.0	2.2	-4.0	-2.0	-8.1
Tx3042	-1.5	-2.5	-10.2	-14.1	-15.0	-25.6	-3.4	-1.7	5.2*	4.9
SE	0.3	0.7	1.8	1.5	3.4	2.5	2.0	2.0	2.1	3.8

* Positive values significantly different from zero.

Table I-7. Estimates of GCA effects for germination rate of eleven male inbred parents of sixty-six F1 hybrids of sorghum at ten temperatures.

	Temperature (°C)									
Male	5	7.5	10	15	20	25	30	35	40	45
MAN64	-0.1	2.3*	1.3	-1.3	-18.0	-9.0	5.6*	5.0*	5.7*	-5.6
76BTP6-2	-0.7	-4.0	1.5	-4.3	-9.4	0.9	1.7	-7.6	-0.3	3.1
76BTP15-1	-0.6	-0.8	-6.7	-5.6	1.5	-7.1	-4.3	4.0	-2.3	-5.9
76BT54-3	-1.0	0.4	-2.0	5.1*	-1.2	2.4	-1.6	-6.1	6.5*	-11.3
W. D. Kaoliang	0.7	-1.1	3.5	7.8*	19.7*	20.4*	6.9*	6.2*	11.9*	21.8*
C. B. Kaoliang	-0.7	-3.0	8.6*	1.0	12.9*	13.8*	1.8	3.0	-0.9	20.2*
D. D. Feterita	2.7*	3.4*	1.9	-1.9	4.3	8.7*	-5.5	-0.8	-2.4	-12.2
Ks53	0.6	4.2*	-6.0	0.7	-8.0	-8.2	-7.0	-3.0	-7.3	-21.0
MN73X1	-1.0	-2.5	-3.9	-1.7	8.4*	-8.1	6.6*	-6.5	-7.2	-20.3
Tx415	2.3*	3.3*	0.9	-2.3	-7.6	-5.4	-5.4	4.7	-7.4	0.2
Tx430	-1.0	-2.3	1.4	2.3	-1.5	-8.6	1.5	0.9	4.2	31.5*
SE	0.5	0.9	2.5	2.0	4.6	3.4	2.7	2.7	2.9	5.1

* Positive values significantly different from zero.

Table 1-8. Hybrids with positive SCA effects for germination rate for three subgroups of ten temperatures.

Hybrid	Temperature (°C)									
	5	7.5	10	15	20	25	30	35	40	45
	Cold				Warm				Hot	
Ks9 X C. B. Kaoliang	-	-	-	-	-	-	-	-	10.0	18.8*
Ks9 X Tx415	0.3	1.4	13.2*	7.6	-	-	-	-	-	-
Ks24 X 76BT54-3	0.0	11.1*	3.1	7.3	37.2*	9.3	4.8	9.4	-	-
Ks66 X MAN64	2.1*	0.1	8.2	11.3*	3.4	25.0*	4.2	6.7	19.0*	0.8
Ks66 X W. D. Kaoliang	2.6*	4.2*	3.9	2.7	-	-	-	-	-	-
Ks66 X Tx430	0.8	3.1	13.4*	4.1	22.5*	16.0*	5.1	3.8	14.4*	4.8
Tx623 X 76BTP6-2	-	-	-	-	-	-	-	-	11.0	42.4*
Tx623 X 76BTP15-1	-	-	-	-	-	-	-	-	5.6	51.7*
Tx623 X D. D. Feterita	0.1	16.4*	12.2*	8.4*	-	-	-	-	-	-
Tx623 X Tx430	-	-	-	-	8.3	13.4*	4.3	1.9	-	-
Tx2749 X W. D Kaoliang	-	-	-	-	23.0*	12.6	0.2	7.5	-	-
Tx2749 X MN73X1	-	-	-	-	-	-	-	-	23.4*	20.9*
Tx2749 X Tx415	-	-	-	-	17.0*	13.4*	12.5*	5.7	18.9*	66.6*
Tx3042 X 76BTP6-2	-	-	-	-	-	-	-	-	12.9*	23.7*
Tx3042 X D. D. Feterita	3.5*	4.8*	17.6*	9.5*	-	-	-	-	-	-
SE	1.1	2.3	6.1	4.9	11.4	8.2	6.6	6.7	7.1	12.6

* Positive SCA effects significantly different from zero.
\- Negative SCA effects.

Table I-9. Phenotypic correlation coefficients between parental lines and topcross performance for germination rate at ten temperatures.

Temperature (°C)	Correlation coefficient(r)	
	Male	Female
5	0.60*	0.81*
7.5	0.75**	0.41
10	-0.42	0.77
15	0.19	0.34
20	0.23	0.54
25	0.15	0.72
30	-0.06	0.21
35	-0.26	-0.06
40	-0.23	0.24
45	0.15	0.14

*, ** Significantly different from zero at the 0.05 and 0.01 probability level, respectively.

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II. GENETIC ANALYSIS OF JUVENILE GROWTH OF SORGHUM(*Sorghum bicolor* (L.) Moench) AT DIFFERENT TEMPERATURES.

Abstract

Sixty-six F1 hybrids and their parents were evaluated for juvenile growth temperature response in growth chamber experiments at four day/night temperatures and in the field. Results indicated that juvenile growth was highly heterotic at all temperature regimes and in the field, yet was largely predictable by general combining ability. GCA(males) accounted for a greater proportion of the total genetic variance than GCA due to females and SCA. The Kansas breeding lines, as a male or female, did not have any significant GCA effect. Most of the significant GCA effects across temperature regimes were observed in the exotic and Texas lines (W. D. Kaoliang, C. B. Kaoliang, Man64 and 76BTP15-1 for males and Tx2749 and Tx3042 for females). Evidence of significant genotype x temperature interaction was detected in this study. GCA was relatively more stable to changes in enviroment than SCA. There was no parallel trend between line and topcross performance. The correlation of results obtained for juvenile growth under low temperature regime and field results was fairly high and significant (r=0.60). Thus, juvenile cold temperature response could be evaluated in the growth chamber with a fairly high measure of precision.

Introduction

Metabolic processes in sorghum, Sorghum bicolor (L.) Moench, are affected by enviromental stresses whose overall effects are often manifested as decreased yields (Christiansen, 1978; Lyons et al., 1979; Levitt, 1980; Raper and Kramer, 1983). Temperature stress occurs under field conditions and cannot be easily manipulated, thus it is a major factor limiting sorghum production (Peacock, 1982). In the U. S., sorghum is planted in soils warm enough for germination but colder weather may occur post-emergent and impede the early growth of the crop (Nordquist, 1971). In the semi-arid tropics, particularly in areas of Africa, the early part of the growing season, which has high solar radiation, is often associated with very high temperatures (Peacock, 1982).

In the Poaceae, developmental rates in the absence of water and nutrient stresses have been shown to be largely governed by temperature (Johnson, 1967; Downes, 1968; McCree and Davis, 1974; Troughton et al., 1974; Watts, 1974; Peacock, 1976; Gallager, 1979; Peacock, 1982). Breeding sorghum for enhanced temperature response in the juvenile stage would not only boost its production under adverse conditions but would also expand its adaptation into more northernly latitudes, higher altitudes, and regions of extremely high temperatures.

Genetic variation for sorghum leaf growth rate in relation to temperature was large (Quinby et al., 1973).

Genetic variation for chilling sensitivity (Bagnall, 1979) and both heat and dessication tolerance (Sullivan and Blum, 1970; Sullivan and Ross, 1979) have also been reported. Paull et al. (1979) found inheritance of chilling sensitivity within the sorghum species to be largely additive and under polygenic control.

Hence, the objectives of this study were to estimate heterosis, evaluate the relative importance of general and specific combining ability and correlate line and topcross performance for juvenile growth at a number of temperature regimes.

Materials and Methods

Breeding Materials

The experimental materials included six A-lines (females) adapted to the Great Plains of the U. S., eleven diverse R-lines (males), and their F1 hybrids developed in a Design II mating scheme. The parents are described in Table 1. The sixty-six F1 hybrids, and their parents were evaluated for juvenile temperature response in the growth chamber and in the field.

Growth Chamber Experiments

Juvenile growth of the sixty-six F1 hybrids and their parents was evaluated in the growth chamber in a randomized complete block design with six replications of single plants. There were four day/night temperatures of 17/9°C, 25/17°C, 33/25°C and 41/33°C in a photoperiod regime of fourteen hours light and ten hours dark. Seeds were sterilized with 0.03% silver nitrate ($AgNO_3$) solution for four minutes, washed with 0.13% sodium chloride solution (NaCl) to remove excess $AgNO_3$, re-sterilized with 20% commercial Chlorox solution for five minutes, and washed with four rinses of double distilled water before drying under sterile conditions. All sterilizing solutions contained 0.01% Nonidet (wetting agent).

Seeds were oversown in the dark in pure vermiculite contained in Super Cell Cone-Tainers mounted on crates and partially submerged in acrylic coated metal troughs where the containers were watered through capillary action

with modified Hoagland's solution (half strength) (Hoagland and Arnon,1950). At the two-leaf stage, each container was thinned to a single plant of approximately the same height and vigor before the temperature treatment was initiated. The single plant shoots were harvested and oven-dried at 60°C for 72 hours when a check hybrid (Wheatland x Tx2536) reached the six-leaf stage. Shoot dry matter (biomass) was measured.

Field Study

The field cold tolerance study was conducted at the Kansas State University Ashland Research Farm with the same experimental materials as in the growth chamber experiments. The soil at the Ashland site was Haynie very fine sandy loam (coarse-silty, mixed, mesic, mollic udefluvent). The soil and air temperatures during the experimental period are presented in Table II-2. Captan treated seeds were planted under rainfed conditions on 28 April, 1984 in a randomized complete block design with three replications. Plots with 3m long single rows with 0.76m between rows, were oversown and thinned at the two leaf-stage to thirty plants per plot giving a plant population of approximately 130,000 plants/ha. The biomass above ground was harvested on 6 June, 1984 when the check hybrid reached the six-leaf stage, then oven-dried at 60°C for 72 hours and weighed.

Statistical Analysis

Biomass was analyzed separately for individual temperature regimes in the growth chamber and for the field.

A combined analysis of variance (McKintosh, 1983) of genotypes over temperatures was performed to test for the significance of genotype x temperature interaction for the growth chamber experiments. Parents and checks were not included in the analysis for combining ability in both experiments. All effects in the models were considered fixed. At some temperatures there was heterogeneity of error variance for the parents and the hybrids, thus a separate parent error mean square was used to test the significance of the parents, a hybrid error mean square was used to test the significance of the hybrids and the pooled error mean square was used to test the significance of parents vs hybrids. The significance of the genotype x temperature interaction was tested using the pooled error mean square for the combined analysis.

The average mid-parent heterosis of the hybrids was calculated as follows:

$$\text{Heterosis} = \frac{\bar{X}\ \text{hybrids} - (\bar{X}\ \text{males} + \bar{X}\ \text{females})/2}{(\bar{X}\ \text{males} + \bar{X}\ \text{females})/2}$$

Significance of this estimate of mid-parent heterosis was determined from a single degree of freedom comparison in the analysis of variance. Significance of average high parent heterosis was determined using a least significant difference (LSD) (Cox et al., 1984) between the high parent and the hybrid mean. This LSD was:

$$LSD_{0.05} = t_{0.05}((1/rb + 1/ra)MSe)^{1/2},$$

where $t_{0.05}$ was the tabular value of t at the 5% level of significance with the appropiate degrees of freedom, r equalled the number of replications, b equalled the number of entries in a hybrid mean, a equalled the number of entries in a parental mean and MSe was the pooled error mean square.

The GCA and SCA variance components were calculated from the respective mean squares for males, females and males x females and their expected mean squares (Beil and Atkins,1967). The method of estimating standard errors of the GCA and SCA estimates were obtained as described by Lothrop et al. (1985). GCA effects for an individual male or female parent and the SCA effects of their cross were estimated and positive GCA and SCA effects were tested for significance with a one-tailed t-test using the method of Ross et al. (1983).

Simple phenotypic correlations were calculated using line and topcross means for both experiments to compare line and topcross performances of the parents. A correlation of entry means from the lowest growth chamber temperature regime and the field was calculated.

Results

Growth Chamber and Field Experiments

The analysis of variance for juvenile growth (Table II-3) found significant variation among parents and hybrids at all temperature regimes and for the field cold tolerance study. There was only significant variation within A-lines at 25/17°C. There were significant differences among the R-lines at all temperature regimes and in the field. The A-lines did not differ significantly from the R-lines at 17/9°C and in the field. The significant variation found in the hybrids at all temperature regimes was due to all three components, males, females, and the interaction between the two. In all cases, the hybrids significantly differed from their parents. The combined analysis of variance found significant males x temperature, females x temperature and males x females x temperature interactions (Table II-4).

Heterosis

Juvenile growth was highly heterotic at all temperature regimes and in the field (Table II-5). Maximum heterosis (160%) was obtained at day/night temperatures of 25/17°C. In all cases, the average performance of the hybrids significantly exceeded the average performance of the high parent.

Genetic Variance

Most of the genetic variation for temperature response for juvenile growth was due to GCA of the male parent in both experiments (Table II-6). The GCA of males accounted

for a greater proportion of the total genetic variance than the GCA due to females. The SCA component was greater than the GCA(females) component at the lowest temperature regime but these two components were nearly equivalent at two other temperature regimes (25/17°C and 41/33°C) and in the field. At 33/25°C, the SCA component accounted for 0% of the total genetic variance.

GCA and SCA Effects

Only two of the female parents, Tx2749 and Tx3042 (Table II-7) had significant, positive GCA effects across temperature regimes. Only one female (Tx2749) had a significant, positive GCA effect in the field. The three Kansas lines did not have any significant GCA effect for juvenile growth. Four superior general combiners across temperature regimes and in the field were identified among male parents (Table II-8), W. D. Kaoliang, C. B. Kaoliang, Man64 and 76BTP15-1. These parents also had positive significant GCA effects. All four parents had been identified prior to this study as cold tolerant genotypes.

Only about 6% of all hybrid-temperature combinations had significant, positive SCA effects (Table II-9). The greater proportion of these involved at least one parent identified earlier as a good general combiner at that temperature regime or in the field. Tx2749 x 76BTP15-1, a high GCA x high GCA hybrid, had positive significant SCA in three of the four temperature regimes while Tx3042 x C. B. Kaoliang, another high GCA x high GCA hybrid, was

significant in two temperature regimes. Of the male parents, C. B. Kaoliang was involved in the greatest number of hybrids with significant positive SCA effects while both Tx2749 and Tx3042, high GCA females, were involved in most of the significant positive SCA effect hybrids.

Comparison of Line and Topcross Performance

Significant correlation between lines *per se* and their topcross performance (Table II-9) was found only at temperatures regimes of 25/17°C for male parents and 33/25°C for the female parents.

The correlation coefficient(r) for results obtained at the lowest temperature regime in the growth chamber and the field cold tolerance study was 0.60.

Discussion

Response of juvenile growth to different temperature regimes in the growth chamber and cool temperatures in the field was highly variable. Only at one temperature regime was there significant variation within the A-line parents, which were representative of elite breeding lines, while there was significant variation within the R-line parents for all temperature regimes and in the field. Thus the response of the diverse male parents was more variable than the elite female parents.

Among the females, only two of the Texas breeding lines had significant GCA effects across temperature regimes. These lines were derived from exotic germplasm x adapted line crosses. None of the Kansas breeding lines used as either male or female parents had significant GCA effects. Among males, the Chinese cold tolerant lines and two of the four cold tolerant lines from CIMMYT gave consistent significant GCA effects across temperature regimes and in the field. Thus, to improve the juvenile temperature response of adapted, high yielding sorghum hybrids, there is need to introduce exotic germplasm with known cold tolerance.

Juvenile growth was highly heterotic, yet was largely predictable by GCA. A wide range of gene effects could have been responsible for the heterosis expressed by the hybrids at the different temperature regimes and in the field (Jinks and Jones, 1958).

About two thirds of the total genetic variance was accounted for by GCA of the male parent. The variance component of GCA due to females and SCA contributed very little to the total genetic variance except at the lowest temperature regime where SCA accounted for more variability than GCA of females.

Rankings of GCA effects could be useful in choosing lines to develop cold tolerant populations. The preponderance of GCA of the male indicated that the best approach to improve juvenile growth temperature response would be to use S1 line selection in a population developed not only from adapted elite lines but exotic germplasm with a known temperature response.

Superior specific combiners for low temperature response in the controlled environment were generally not significantly positive in the field. One possible explanation for this could be because the variance component due to SCA was highly sensitive to changes in the environment. The cold temperatures in the field were not as severe as in the growth chamber. This could have caused differential cold temperature response among certain parental combinations under field conditions. Pethani and Kapoor (1984) studying combining ability and its interaction with environments for grain yield in pearl millet also noted that the variance component due to SCA was highly subject to changes in environments unlike the variance component due to GCA.

In this study, there was generally no consistently significant, positive linear relationship between parental lines and their topcross performance at different temperature regimes suggesting that parental lines must be tested for temperature response in hybrid combinations using a number of testers to evaluate their potential for specific temperature adaptation. The results obtained for cold temperature response at the lowest temperature regime in the growth chamber and field for juvenile growth were related (r=0.60). Thus, juvenile cold temperature response could be measured with a fairly high precision in the growth chamber, especially for parental selection or S1 line selection in the development or improvement of a cold tolerant population.

Table II-1. Descriptions of female and male parents used in the study of juvenile growth in the growth chamber and in one field study.

Line	Description
Female	
Ks9	A line derived from Schrock x Ellis.
Ks24	A line derlved from Spur Feterita-Western Blackhull[3] x Redbine-60.
Ks66	Elite breeding line.
Tx623	Tropically adapted line derived from B3197 x SC170-6
Tx2749	Selection from Redlan x Ks30 for greenbug resistance. Ks30 was a Sorghum bicolor var. bicolor x var. virgatum cross.
Tx3042	Selection from Redbine 60 x Ks30 for greenbug resistance. Ks30 was a Sorghum bicolor var. bicolor x var. virgatum cross.
Male	
Man64	Dwarf cold tolerant line from CIMMYT, Mexico.
76BTP6-2	" " " " " " " .
76BTP15-1	" " " " " " " .
76BT54-3	" " " " " " " .
W. D. Kaoliang	Dwarf Chinese cold tolerant line.
C. B. Kaoliang	" " " " " .
D. D. Feterita	A southern African-type R-line.
Ks53	A kafir-type R-line derived from 43W29[2] x Ks7
MN73X1	A R-line developed in Minnesota.
Tx415	A R-line developed from Tx3078 x Tx09.
Tx430	A tropically adapted line derived from Tx2536 x SC170-6.

Table II-2. Average minimum and maximum soil and air temperatures during the experimental period (28 April - 6 June, 1984) at Ashland Research Farm.*

	Temperature (°C)	
Type	Min	Max
Air	10.2	22.3
Soil	14.0	23.1

*Courtesy of the Evapo-transpiration Laboratory of Kansas State University, Manhattan, Kansas.

Table II-3. Analysis of variance for juvenile growth of six female and eleven male inbred parents and their sixty-six F1 hybrids grown at four day/night temperatures in the growth chamber and in one field study.

		Temperature regime (°C)				
		17/9	25/17	33/25	41/33	Field
Source	df	Mean square				
Replications	5	0.014	1.204**	0.416*	0.320**	3.023**(2)@
Genotypes	82	0.510**	1.788**	0.596**	0.390**	0.244**
Parents(P)	16	0.319**	0.208**	0.163*	0.092**	0.097**
A-lines(A)	5	0.039	0.307**	0.043	0.021	0.042
R-lines(R)	10	0.459**	0.169*	0.201*	0.084**	0.031**
A vs R	1	0.311	3.488**	0.384*	0.535**	0.033
Hybrids(H)	65	0.510**	1.778**	0.616**	0.397**	0.189**
Males(M)	10	1.744**	5.587**	2.617**	1.723**	0.625**
Females(F)	5	0.703*	5.235**	0.818**	0.630**	0.341**
M X F	50	0.244**	0.670**	0.176	0.108**	0.087*
P vs H	1	3.593**	27.745**	6.189**	4.718**	6.137**
Error						
Parents	80	0.084	0.070	0.086	0.018	0.024(32)@
Hybrids	325	0.120	0.287	0.172	0.064	0.059(130)@
P vs H	5	0.093	0.263	0.182	0.060	0.145(2)@
Pooled	410	0.113	0.244	0.155	0.055	0.054(164)@

*, ** $P \leq 0.05$ and 0.01, respectively.

@ Values in parenthesis indicate degrees of freedom for field study where different from growth chamber experiments.

Table II-4. Combined analysis of variance in juvenile growth of sixty-six F1 hybrids of sorghum grown at four day/night temperatures in the growth chamber.

Source	df	Mean square
Temperature(T)	3	14.653**
Replications/temperature	20	0.608**
Males(M)	10	9.480**
Females(F)	5	4.504**
M X F	50	0.594**
M X T	30	0.731**
F X T	15	0.960**
M X F X T	150	0.201*
Residual	1300	0.161

*, ** $p \leq 0.05$ and 0.01, respectively.

Table II-5. Means of parents, mid-parents, hybrids and average heterosis for juvenile growth in sixty-six F1 hybridsat four day/night temperatures in the growth chamber and in one field study.

	Biomass				
Temperature (°C)	Male	Female	Mid-parent	Hybrid	Heterosis
	---------- g/plant ----------				-- % --
17/9	0.44	0.33	0.39	0.61	58.0
25/17	0.33	0.39	0.36	0.93	160.6
33/25	0.42	0.30	0.36	0.67	88.2
41/33	0.29	0.14	0.22	0.47	123.6
Field	0.63	0.61	0.62	1.02	64.5

Table II-6. Estimates of variance components, standard errors and components expressed as percentages of the total genetic variance(parenthesis) for juvenile growth of sixty-six F1 hybrids at four day/night temperatures and in one field study.

Temperature regime (°C)	Variance component		
	GCA(males)	GCA(females)	SCA
17/9	0.045±0.020	0.008±0.006	0.021±0.008
	(60.8)	(10.8)	(28.4)
25/17	0.147±0.063	0.075±0.042	0.064±0.022
	(51.4)	(26.2)	(22.4)
33/25	0.068±0.030	0.010±0.007	0.000±0.006
	(87.2)	(12.8)	(0.0)
41/33	0.046±0.020	0.009±0.005	0.007±0.004
	(74.2)	(14.5)	(11.3)
Field	0.031±0.014	0.008±0.005	0.009±0.006
	(64.6)	(16.7)	(18.8)

Table II-7. Estimates of GCA effects for juvenile growth of six female inbred parents of sixty-six F1 hybrids grown at four day/night temperatures inthe growth chamber and in one field study.

	Day/night temperature (°C)				
Female	17/9	25/17	33/25	41/33	Field
Ks9	-0.05	-0.48	-0.15	-0.10	0.06
Ks24	-0.14	-0.18	-0.06	0.03	-0.18
Ks66	-0.08	0.12	-0.05	-0.12	-0.04
Tx623	0.06	0.07	0.13	0.00	0.03
Tx2749	0.12*	0.23*	0.03	0.11*	0.12*
Tx3042	0.08*	0.25*	0.12*	0.12*	0.01
SE	0.04	0.07	0.05	0.03	0.04

* Positive values significantly different from zero.

Table II-8. Estimates of GCA effects for juvenile growth of eleven male inbred parents of sixty-six F1 hybrids grown at four day/night temperatures in the growth chamber and in one field study.

	Day/night temperature(°C)				
Male	17/9	25/17	33/25	41/33	Field
MAN64	0.29*	0.41*	0.40*	0.19*	0.24*
76BTP6-2	0.19*	-0.25	-0.27	-0.23	0.21*
76BTP15-1	0.21*	0.25*	0.12*	0.16*	0.20*
76BT54-3	-0.21	-0.21	-0.12	-0.12	-0.13
W.D.Kaoliang	0.30*	0.67*	0.27*	0.25*	0.14*
C.B.Kaoliang	0.13*	0.44*	0.48*	0.44*	0.13*
D.D.Feterita	-0.11	-0.31	-0.12	-0.14	-0.24
Ks53	-0.23	-0.22	-0.25	-0.15	-0.18
MN73X1	-0.16	-0.46	-0.12	-0.19	-0.22
Tx415	-0.20	-0.44	-0.25	-0.13	-0.07
Tx430	-0.19	0.15*	-0.10	-0.02	-0.09
SE	0.06	0.09	0.07	0.04	0.05

* Positive values significantly different from zero.

Table II-9. Hybrids with positive SCA effects for juvenile growth for four day/night temperatures in the growth chamber or inthe field.

	Day/night temperature (°C)				
Hybrid	17/9	25/17	33/25	41/33	Field
Ks9 X Tx415	-0.09	0.36*	0.09	0.19	0.23*
Ks9 X 76BTP6-2	0.34*	0.33*	0.03	0.14	-0.20
Ks9 X D. D. Feterita	0.16	0.20	0.06	0.00	-0.23
Ks9 X Ks53	0.04	0.17	0.06	0.00	0.04
Ks24 X 76BT54-3	0.19	0.18	0.00	0.17*	0.07
Ks24 X C. B. Kaoliang	0.45*	0.26	0.46*	0.10	-0.06
Ks66 X C. B. Kaoliang	-0.10	-0.22	-0.29	0.05	0.29*
Ks66 X MN73X1	0.13	0.29	0.33*	0.06	0.00
Tx623 X MAN64	0.10	0.20	0.16	0.12	-0.03
Tx623 X 76BTP6-2	0.01	0.05	0.08	0.04	0.26*
Tx2749 X 76BTP15-1	0.55*	0.35*	0.04	0.18*	0.11
Tx2749 X W. D. Kaoliang	0.15	0.04	0.18	0.06	0.14
Tx2749 X MN73X1	-0.05	-0.18	-0.01	-0.13	0.23*
Tx3042 X W. D Kaoliang	0.12	0.21	0.04	0.04	0.05
Tx3042 X C. B. Kaoliang	0.09	0.78*	0.21	0.20*	0.07
Tx3042 X D. D. Feterita	0.09	0.33*	0.09	0.02	0.49*
SE	0.14	0.22	0.17	0.10	0.14

* Positive SCA effects significantly different from zero.

Table II-10. Phenotypic correlation coefficients between parentallines and topcross performance for juvenile growth at four day/night temperatures in the growth chamber and in one field study.

	Correlation coefficient(r)	
Temperature regime (°C)	Male	Female
17/9	0.46	0.28
25/17	0.61*	0.79
33/25	0.40	0.85*
44/33	0.38	0.75
Field	0.44	0.36

* significantly different from zero at the 0.05 probability level.

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GENETIC ANALYSIS OF GERMINATION AND JUVENILE GROWTH OF SORGHUM (*Sorghum bicolor* (L.) Moench) AT DIFFERENT TEMPERATURES

by

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B. S., University of Sierra Leone, 1981

AN ABSTRACT OF A MASTERS'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Genetics

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1985

Germination and juvenile growth of sixty-six F1 hybrids developed in a Design II mating scheme and their parents were evaluated for temperature response at different temperatures. Rate index (measure of speed of germination) was calculated at 7.5 and at 5°C intervals between 5 and 45°C. Juvenile growth was evaluated in the growth chamber at four day/night temperature regimes of 17/9°C, 25/17°C, 33/25°C and 41/33°C, respectively and in the field. Shoot dry matter (biomass) was measured when a check hybrid (Wheatland x Tx2536) reached the six-leaf stage.

Results indicated that germination rate was slightly heterotic between 10 and 40°C, but highly heterotic outside of this range. Most of the genetic variation for germination rate was due to specific combining ability (SCA), and general combining ability (GCA) of the female parent. The superior general combiners for germination rate across temperatures were Tx623 and W. D. Kaoliang for females and males, respectively. Two superior specific combiners (Tx3042 x D. D. Peterita and Tx623 x D. D. Peterita) were identified for germination rate across temperatures. Juvenile growth was highly heterotic at all temperature regimes and in the field, yet was largely predictable by general combining ability. The greatest proportion of the total genetic variation for juvenile growth was accounted for by the GCA of the male parent. The highest GCA effects for juvenile growth across temperature regimes were identified in the females, Tx3042 and Tx2749, and the males, W. D. Kaoliang

and C. B. Kaoliang, Man64 and 76BTP15-1. Significant genotype x temperature interactions were detected for both germination and juvenile growth temperature response.

There was no general relationship between parental lines and their topcross performance for both germination rate and juvenile growth. The correlation of results obtained for juvenile growth under the lowest temperature regime in the growth chamber and the field results was fairly high and significant (r=0.60). The performance of the genotypes used in this study at different temperatures suggests that heterotrophic and autotrophic growth may be genetically independent.

This study demonstrates that germination rate can be enhanced if very careful selection is placed on the female parent, and many testers are used to identify specific combiners that would give the best temperature response. Juvenile growth could be enhanced at different temperatures by optimizing the temperature response in both parents by introducing exotic germplasm with known temperature response into populations to diversify and increase the genetic variance. Recurrent selection using S1 line selection could be used to select cold tolerant parents to be used to develop high yielding cold tolerant hybrids. In this study, cold tolerance was measured in the growth chamber with a fairly high precision. Thus, selection could be based on the growth chamber measurement where the number of S1 lines evaluated could be larger, the generation time reduced, and

the environment more easily controlled to give stable, reproducible results.