

Genetics of grain amaranths

4. Variation and early generation response to selection in *Amaranthus cruentus* L.

P. Kulakow* and S. Jain

Department of Agronomy and Range Science, University of California, Davis, CA 95616, USA

Received October 18, 1986; Accepted November 27, 1986

Communicated by G. S. Khush

Summary. Two landrace populations of *Amaranthus cruentus* L. were crossed to generate F_2 populations for quantitative genetic analyses of variation. Evidence for significant inbreeding depression in comparisons of F_1 and F_2 generation means suggested some role of nonadditive gene action for days to first anthesis, leaf length, leaf width, petiole length, plant height, panicle length, and panicle weight. A pooled F_2 population was subjected to bidirectional mass selection for time of first anthesis (two cycles) and leaf length (one cycle). Responses to selection were asymmetrical and the second cycle response for anthesis time was smaller than for the first cycle. Overall, selection gains were significant and gave estimates of heritability in the range of 0.35 to 0.66 for anthesis time and 0.08 to 0.19 for leaf length. This suggested a large additive term in the total genetic variance especially for anthesis time where early and late flowering selection lines diverged by 20.5 days.

Correlations between the selected traits (anthesis time, leaf length) and single plant yield or yield components were also studied to evaluate correlated responses to selection. Selection for optimal flowering time in amaranth cultivation areas is very likely to result in rapid yield improvement.

Key words: Amaranth – Selection – Heritability – Mixed Mating – Crop improvement

Introduction

Grain amaranth breeders require preliminary genetic information to aid in the design of genetic improvement schemes.

* Present address: The Land Institute, Salina, KS 67401, USA

Germplasm collections now exist which cover a range of the available genetic variation in three species (*A. cruentus* L., *A. hypochondriacus* L., and *A. caudatus* L.). Earlier work (Hauptli and Jain 1984; Vaidya 1984) has shown that amaranth landraces have high levels of between family variance within populations and of between-population variance within species to suggest that both intra- and inter-population selection would be successful. Hauptli and Jain (1984) observed that plant height, leaf length and days to first anthesis were relatively important contributors to prediction of single plant seed yield with plant height and leaf length having positive correlations with yield while anthesis time was negatively correlated with both yield and plant height. This suggested that earliness would be an effective selection criterion for developing short stature, high yielding varieties. Given appropriate values of heritability and genetic correlations, along with efficient screening procedures, such indirect predictors of yield may produce higher correlated increases in yield than selection for yield directly.

Since grain amaranth species have a mixed mating system with the capability of controlling pollinations both genetically and mechanically, a range of plant breeding methods can be utilized that combine features of classical selfed and outcrossed systems (Jain et al. 1986). Choice of optimal breeding methods depend on factors such as heritabilities of selection criteria, the relative importance of nonadditive genetic variance, and the efficiency of selection systems in terms of time, labor, and cost.

This paper reports a detailed study of variability and early generation response to selection in an interpopulation cross in *A. cruentus*. The objective of this study was to measure response to mass selection in a population generated from crossing two genetically diverse parental populations. In another paper (Jain and Kulakow, in prep) we will discuss response to recurrent selection within landrace populations based on the natural mixed mating system.

Materials and methods

Two geographically distinct accessions of *A. cruentus* were chosen for crossing in order to maximize differences between

populations within the species. UC87 was collected by Dr. H. Hauptli from a farm near San Martin Jilotepeque, Chimaltenango, Guatemala (Hauptli et al. 1979). UC192 was an introduction from Tanzania which had been grown out several times in Davis, California to increase seed. Both populations have been utilized separately in intrapopulation selection experiments (Ayiecho 1985; Vaidya and Jain 1986).

Individual greenhouse-grown plants from UC192 and UC87 were crossed pairwise using unemasculated green (rr) UC192 plants as seed parents and red (R-) UC87 plants as pollen parents. Plants were bagged together before flowering to control pollination, and the dominant red seedling color allele (R) was used to identify F_1 plants (Kulakow et al. 1985). This crossing method produced a large quantity of F_1 seed for each cross; the selfed F_1 plants produced the F_2 generation during the winter of 1982.

In 1982, the original parental accessions along with F_1 and F_2 generations from three crosses were grown in a summer field nursery. Entries were planted on June 5 in a randomized complete block design with three replications. Plots consisted of single 3 m rows spaced 76 cm apart. Each block included five rows of each parental accession, one row of each F_1 population, and six rows of each F_2 population. At planting, rows were seeded densely and thinned to 15 cm within row spacing three weeks after planting. Each plant was scored for the time of first anthesis expressed as the number of days after planting. Between 58 and 62 days after planting the central ten plants within each row were measured for the following traits: midseason plant height (designated plant height 1), leaf length, leaf width, and petiole length of the largest leaf.

In 1983, a similar planting was made on June 10 using F_1 and F_2 generations from four crosses, two of which had been planted in 1982. The field design was the same as in 1983 with one row of each F_1 population and five rows of each F_2 population in each block. Scoring was as before with leaf and plant height measurements made between 55 and 58 days after planting. Additional characters included mature plant height (designated plant height 2), panicle length, and panicle weight. Panicle weight, which includes both weight of seeds and flower parts, is highly correlated with single plant yield (Ayiecho 1985).

The original F_2 seed from all five crosses grown in 1982 and 1983 was pooled to form a control population, designated as F_2 -CO. Bidirectional selection for days to first anthesis and leaf length independently was initiated by bulking an equal amount of seed from five plants selected from each of the six blocks grown over two years. Plants with the highest and lowest scores were selected to initiate selection in both directions. Each of the four selected populations (EARLY-C1, LATE C1; High leaf length, Low leaf length) comprised a bulk of 30 plants representing a selection intensity of 2.8%.

The four selected populations (C1) and F_2 -CO were evaluated in 1984 using a randomized complete block design with four replications. All plants were scored as in 1982 along with panicle weight at maturity. A second cycle of selection for days to first anthesis was made using the first cycle populations (EARLY-C1 and LATE-C1) to continue the bidirectional selection. An equal amount of seed from eight plants selected in each of the four replications was bulked to give a total of 32 selected plants (C2) or a 6.3% selection intensity.

Both C1 and C2 populations, selected for days to first anthesis, and F_2 -CO were evaluated in 1985 using the same experimental design as the previous year. Days to first anthesis was scored on all plants. Mature plant height, panicle length, and individual plant seed yield were scored on 16 random plants in each replication.

Data from each year were analyzed using an analysis of variance. Multiple comparisons of means were made using pair-

wise *t*-tests for each character that showed significant treatment differences in the analysis of variance. Simple correlation coefficients were calculated to describe associations between characters. Stepwise multiple regression was used on the 1983 data to determine which combination of characters provided the best predictor of panicle weight. The standard equation for response to selection, $h^2 = R/iS_p$, was used to calculate realized heritabilities where h^2 is the realized heritability, R is the response to selection, i is the standardized selection differential, and S_p is the phenotypic standard deviation.

Results

Means and standard deviations of characters measured in 1982 and 1983 are given in Table 1. UC192 was significantly different from UC87 for days to first anthesis, petiole length, and plant height. UC192 was later flowering, had longer petioles, and was taller than UC87. The larger variances for UC192 indicated that selection would be successful within the population; however, the predominance of later flowering plants, tall plant height, and poor head types relative to UC87 indicated that combining characteristics of the two populations would produce a more agronomically suitable base population to carry out selection.

A comparison among the five biparental crosses between UC192 and UC87, evaluated in 1983 and 1984, provided several observations. First, there were significant differences among crosses indicating that the parents used to make crosses within the parental populations were genetically different. Second, comparisons of standard deviations, coefficients of variation, and ranges for each character indicated that the F_2 generation had a larger variance than the corresponding F_1 generation. Finally, for each character measured, the F_1 mean differed from the F_2 mean in a systematic way indicating inbreeding depression in F_2 generation; each F_1 was earlier flowering than its corresponding F_2 , and for other characters too, the F_1 generation had a higher value than the F_2 except for panicle length in 1983. Pairwise comparisons of F_1 and F_2 means using pooled F_1 and F_2 variance estimates appropriate for each generation were significant at the 95% confidence level in 44 out of 48 comparisons within crosses. Table 2 gives the percentage depression of F_2 means relative to the respective, F_1 's. At complete homozygosity the expected inbreeding depression would be greater than that observed in the F_1 and F_2 comparisons. The largest amount of inbreeding depression was for panicle weight with F_2 means 13.6% to 30.5% lower than the corresponding F_1 means. Pooled F_1 and F_2 means also indicated inbreeding depression on a population basis for all characters except panicle length.

Simple phenotypic correlations were compared for F_1 and F_2 generations. In most cases, correlations were significantly different from zero and moderate to high in magnitude. The pattern of correlations was similar among

Table 1. Summary of means and standard deviations for UC192, UC87, F₁ and F₂ populations grown in 1982 and 1983. Sample sizes were approximately 160 for UC192 and UC87; 30 for each F₁ generation; and 150 for each F₂ generation

Population		Days to first anthesis		Leaf length		Leaf width		Petiole length		Plant height 1		Plant height 2	Panicle length	Panicle weight
		1982	1983	1982	1983	1982	1983	1982	1983	1982	1983	1983	1983	1983
UC192	Mean	66.8	—	19.5	—	8.9	—	14.8	—	177.5	—	—	—	—
	St dev	6.9	—	3.4	—	1.8	—	3.3	—	26.0	—	—	—	—
UC87	Mean	63.1	—	19.1	—	9.2	—	10.1	—	163.0	—	—	—	—
	St dev	2.4	—	2.4	—	1.3	—	1.5	—	20.7	—	—	—	—
F ₁ -1	Mean	57.8	56.2	20.8	25.4	10.0	11.6	13.8	15.4	180.5	185.8	223.0	43.7	94.1
	St dev	2.1	1.1	2.5	3.6	1.1	1.6	1.8	1.8	23.1	28.0	26.7	9.6	43.8
F ₂ -1	Mean	62.5	59.3	19.9	23.6	9.4	10.4	13.1	15.0	164.3	173.1	214.3	39.6	69.0
	St dev	5.7	3.8	3.1	2.9	1.4	1.5	2.2	2.0	24.6	24.4	31.8	9.7	34.7
F ₁ -2	Mean	60.7	—	20.5	—	9.8	—	12.0	—	204.7	—	—	—	—
	St dev	1.9	—	2.9	—	1.6	—	2.0	—	26.3	—	—	—	—
F ₂ -2	Mean	64.8	—	19.2	—	9.3	—	11.6	—	175.5	—	—	—	—
	St dev	6.0	—	3.2	—	1.7	—	2.5	—	36.9	—	—	—	—
F ₁ -3	Mean	58.2	57.0	21.5	26.4	10.6	12.4	13.6	15.2	188.0	195.9	235.7	38.8	93.3
	St dev	2.4	1.3	2.9	3.8	1.6	1.8	2.3	1.6	22.8	27.7	33.5	9.1	53.8
F ₂ -3	Mean	59.8	58.7	20.5	22.8	9.9	10.8	13.1	14.3	172.4	165.7	208.0	37.4	64.7
	St dev	3.9	2.6	3.1	3.1	1.8	1.6	2.3	1.9	24.3	26.5	30.3	10.3	33.2
F ₁ -4	Mean	—	61.0	—	24.4	—	11.6	—	15.6	—	191.0	245.3	32.0	82.1
	St dev	—	1.1	—	2.6	—	1.2	—	1.6	—	22.5	22.9	6.9	35.4
F ₂ -4	Mean	—	61.9	—	22.5	—	10.7	—	14.7	—	174.7	225.4	34.0	70.9
	St dev	—	3.6	—	3.5	—	1.7	—	2.1	—	28.0	31.0	10.2	40.0
F ₁ -8	Mean	—	58.9	—	25.8	—	11.7	—	16.3	—	195.0	240.3	36.9	91.1
	St dev	—	3.4	—	3.0	—	1.5	—	1.8	—	26.0	28.2	9.9	32.4
F ₂ -8	Mean	—	60.0	—	23.0	—	10.6	—	14.2	—	154.5	209.9	35.8	67.7
	St dev	—	3.4	—	3.0	—	1.5	—	1.8	—	26.0	28.2	9.9	32.4
F ₁ -all	Mean	58.9	58.2	20.9	25.5	10.1	11.8	13.1	15.4	191.5	191.5	235.6	37.9	90.0
	St dev	2.5	2.4	2.8	3.4	1.5	1.5	2.2	1.6	26.1	26.7	29.4	9.8	43.4
F ₂ -all	Mean	62.2	60.0	19.9	23.0	9.5	10.6	12.6	14.5	170.0	169.3	214.3	36.6	68.0
	St dev	5.6	3.6	3.1	3.2	1.7	1.6	2.4	2.0	25.5	26.6	31.0	10.2	35.2

Table 2. Inbreeding depression (measured in percent of F₁ means) for all F₁ versus F₂ comparisons from five pairwise crosses between UC192 and UC87

Cross	Days to first anthesis		Leaf length		Leaf width		Petiole length		Plant height 1		Plant height 2	Panicle length	Panicle weight
	1982	1983	1982	1983	1982	1983	1982	1983	1982	1983	1983	1983	1983
1	-8.1**	-5.5**	4.3**	7.3**	6.0**	10.3**	5.1**	2.6**	8.4**	6.7**	3.9**	9.4**	26.7**
2	-6.8**	—	6.3**	—	5.1**	—	3.3	—	14.3**	—	—	—	—
3	-2.7**	-3.0**	4.7**	13.6**	6.6**	12.9**	3.7*	5.9**	8.3**	15.4**	11.8	3.6	30.7**
4	—	-1.5**	—	7.8**	—	7.8**	—	5.8**	—	8.5**	8.1**	3.0*	13.6**
8	—	-3.6**	—	10.9**	—	9.4**	—	7.2**	—	15.6**	12.7**	3.4	25.7**
Total	-5.6**	-3.1**	4.8**	9.8**	5.9**	10.2**	3.8*	5.8**	10.8**	11.6**	9.0**	3.4	24.4**

**, * = F₁ mean is significantly different from F₂ mean at $P=0.01$ and $P=0.05$, respectively, using a pairwise *t*-test with unequal variances. Appropriate pooled variance estimates from F₁ and F₂ populations were used

Table 3. Simple phenotypic correlations for pooled F₂ data grown in 1983. Only correlations that were significantly different from zero at $P=0.05$ are presented

	Days to first anthesis	Leaf length	Leaf width	Petiole length	Plant height 1	Plant height 2	Panicle length
Leaf length	-0.15						
Leaf width	-	0.69					
Petiole length	0.09	0.49	0.50				
Plant height 1	-0.33	0.63	0.55	0.40			
Plant height 2	-	0.66	0.63	0.55	0.88		
Panicle length	-0.50	0.54	0.41	0.22	0.65	0.60	
Panicle weight	-0.20	0.70	0.62	0.34	0.70	0.70	0.65

Table 4. The order of independent variables entered in stepwise multiple regression for prediction of panicle weight based on pooled F₂ data from 1983

1. Analysis of eight independent variables with five measured at flowering and three at maturity

Variable	Order entered	Model r^2
Plant height 2	1	0.49
Leaf length	2	0.59
Stem height	3	0.64
Leaf width	4	0.65
Plant height 1	5	0.66

2. Analysis of five independent variables evaluated at flowering

Variable	Order entered	Model r^2
Plant height 1	1	0.49
Leaf length	2	0.60
Leaf width	3	0.61
Petiole length	4	0.62

crosses and generations. The relationship between characters is summarized in Table 3 for pooled F₂ data obtained in 1983. Many of the characters reflect plant size differences and are consequently highly correlated. Leaf size measurements were correlated with plant height which was also correlated with panicle length. Although plant height measured both at flowering and maturity had a 0.70 correlation with panicle weight, a yield increase associated with increasing plant height is likely to increase lodging and reduce harvest index. Leaf length also showed a high correlation with panicle weight indicating that this simple measure of leaf size may be used to increase seed yield. Moreover, earliness (= fewer days to first anthesis) showed a positive correlation with panicle weight.

Stepwise multiple regression showed that plant height and leaf length were the variables first entered as the best predictors of panicle weight (Table 4). Use of characters measured at the time of flowering resulted in similar r^2 values compared to regression analysis that also included

characters measured at maturity. Choice of selection criteria that are scored before reproduction, followed by intermating or complete selfing only on the selected individuals, would increase the expected response to selection through biparental control. Days to first anthesis was not one of the first variables to enter the regression equation. This indicated that plant size measurements were better predictors of seed yield than the time of flowering. However, some other factors such as higher heritability of flowering time and the potential to increase yield without increasing plant height would support the use of days to first anthesis as a selection criterion.

Response to selection

In 1984, F₂-CO was grown along with the first cycle of bidirectional mass selection for days to first anthesis and leaf length. Means and coefficients of variation (CV) for days to first anthesis, leaf length, plant height at flowering and panicle weight are given in Table 5. The estimates of CV values for days to first anthesis were all less than 10%; but the values ranged for leaf length and plant height 2 to 16% and for panicle weight 68 to 73%. The large CV for panicle weight in 1983 was due to increased variation caused by damage resulting from high winds during the week prior to harvest. Analysis of variance indicated significant differences between populations for each character. The population means of EARLY-C1 and LATE-C1 were both significantly different from F₂-CO for days to first anthesis. Selections for days to first anthesis also showed significant differences from F₂-CO for leaf length, plant height at flowering, and panicle weight. First cycle selections for leaf length had significantly different leaf length means compared to F₂-CO for other characteristics.

In 1985, the first and second cycles of bidirectional mass selection for days to first anthesis were grown along with F₂-CO. Seed yields were depressed in this season due to a severe infestation by leafhoppers, *Empoasca* sp. Means and CV's for days to first anthesis, mature plant height, panicle length, and seed yield are given in Table 6. Each character had a characteristic CV range of 7–7.5%

Table 5. Summary of means^a and coefficients of variation for F₂-CO and first cycle of bidirectional mass selection for days to first anthesis and leaf length, grown in 1984. Approximately 500 plants evaluated per population

Population	Days to first anthesis		Leaf length ^b		Plant height ^b		Panicle weight	
	Mean (days)	C.V. %	Mean (cm)	C.V. %	Mean (cm)	C.V. %	Mean (cm)	C.V. %
EARLY-C1	57.4 a	6.7	22.2 a	15.0	160.8 ab	15.3	45.4 c	70.2
LATE-C1	69.9	8.9	22.6 b	11.7	157.9 a	13.8	30.3 a	72.8
F ₂ -CO	61.3	7.6	23.2 c	15.6	166.1 c	14.2	37.6 b	67.7
High leaf length	61.6 b	9.5	23.7 d	12.6	166.7 c	13.7	36.0 b	72.8
Low leaf length	61.5 b	9.2	21.9 a	14.1	164.0 bc	13.8	36.2 b	72.2

^a For each character, means followed by different letters are significantly different at $P=0.05$ using pairwise t -tests

^b Leaf length and plant height were measured 58–62 days after planting

Table 6. Means^a and coefficients of variation for Cycle 0, Cycle 1 and Cycle 2 bidirectional mass selection for days to first anthesis grown in 1985

Population	Days to first ^b anthesis		Plant height 2 ^c		Panicle length ^c		Panicle yield ^c	
	Mean (days)	C.V. %	Mean (cm)	C.V. %	Mean (cm)	C.V. %	Mean (cm)	C.V. %
EARLY-C2	54.3 a	7.0	186.2 a	15.7	41.3 a	22.0	9.8 a	53.3
EARLY-C1	56.1 b	7.5	204.8 b	11.2	42.1 a	20.2	10.2	39.2
F ₂ -CO	61.1 c	7.2	204.6 b	8.4	37.8 b	20.8	9.0 a	42.1
LATE-C1	69.3 d	7.2	200.6 b	9.2	31.8 c	19.0	6.7 b	46.5
LATE-C2	74.8 e	7.0	203.0 b	8.6	29.2 c	25.2	5.6 b	50.9

^a For each character, means followed by different letters are significantly different at $P=0.05$ using pairwise t -tests

^b Approximately 370 plants evaluated per population

^c 64 plants evaluated per population

for days to first anthesis, 8.4–15.7% for plant height, 19–25.2% for panicle length, and 39.2–53.3% for seed yield. Analysis of variance indicated significant differences between populations for all characters. Pairwise t -tests showed each population to be significantly different for days to first anthesis. Plant height in the EARLY-C2 generation was lower than other populations. Panicle length in both selection cycles for early flowering was greater than F₂-CO, and both selection cycles for late flowering had significantly shorter panicle length. Seed yields of both early selection cycles were greater than F₂-CO although the differences were not significant.

A summary of the responses to selection observed in 1984 and 1985 is given in Table 7. In all comparisons, the selected populations were significantly different from F₂-CO. The selection responses for late flowering and low leaf length were greater than for selection in the opposite direction, indicating greater proportion of additive genetic variance that would be present for the recessive phenotype of the character. This asymmetry is also consistent with the observed inbreeding depression for both charac-

ters. Response to selection for leaf length was low relative to the response for days to first anthesis. Realized heritability values for high leaf length and low leaf length were 0.08 and 0.19, respectively. Low heritability for leaf length was likely due to a greater environmental variance as indicated by the estimates of CV and lower genetic variation due to a relatively smaller difference between the parental populations.

Selection for days to first anthesis showed a high response to selection in both directions. Selection for early flowering decreased the population mean on an average 5.6% per cycle while selection for late flowering increased the mean by 11.2% per cycle. This corresponded to a change in the population mean compared to F₂-CO of 2.6 standard deviations for two cycles of early selection and 4.8 standard deviations for two cycles of late selection. After two cycles of selection EARLY-C2 and LATE-C2 means diverged by 20.5 days.

An important purpose of selection for time of flowering or a plant size character like leaf length is to determine if selection response indirectly affected seed yield. Simple

Table 7. Summary of response to bidirectional mass selection for days to first anthesis and leaf length (cm)

Population	Selection differential	Selection response		Realized heritability		% gain		Response in units of s.d.	
		1984	1985	1984	1985	1984	1985	1984	1985
EARLY-C2	-5.2	-	-1.8	-	0.35	-	-3.2	-	-2.6
EARLY-C1	-7.9	-4.3	-5.0	0.54	0.63	-7.0	-8.2	-1.5	-1.9
LATE-C1	12.6	8.3	8.2	0.66	0.65	13.5	13.4	2.9	3.0
LATE-C2	11.2	-	5.5	-	0.49	-	7.9	-	4.8
High leaf length	6.4	0.5	-	0.08	-	2.1	-	0.1	-
Low leaf length	-7.2	-1.4	-	0.19	-	-6.4	-	-0.4	-

correlations in the base population indicated that selection for early flowering or high leaf length would increase yield. The low realized heritability for leaf length and the high CV's for panicle weight in 1984 did not indicate any change in seed yield associated with selection for leaf length. Correlation between leaf length and panicle weight ($r=0.54$) in the population selected for high leaf length was highly significant.

Selection for days to first anthesis resulted in significant changes in panicle weight in 1984 with a 20.7% increase in panicle weight for EARLY-C1 and a 19.4% decrease in panicle weight for LATE-C1. In 1985, seed yield was measured directly. Despite the general depression of seed yield for all populations, EARLY-C1 and EARLY-C2 selections had increased single plant yields of 13.3% and 8.8%, respectively, compared to F_2 -CO, but these differences were not statistically significant. LATE-C1 and LATE-C2 selections were significantly lower in yield compared to F_2 -CO, with a yield depression of 25.6% and 37.8% respectively. The lowest yielding LATE-C2 population was 45% below the highest yielding EARLY-C1 population.

Simple correlations between days to first anthesis and panicle weight were significant for both F_2 -CO and EARLY-C1 populations in 1984. The correlation in the EARLY-C1 population was -0.09 compared to -0.24 in F_2 -CO. The decreased correlation would indicate that one cycle of selection for early flowering capitalized on most of the negative correlation between time of flowering and yield in the Davis environment. The mean days to first anthesis would approximate an optimal time of flowering for the planting date and location used in this study. In 1985, EARLY-C1 was highest yielding. This population showed a significant negative correlation of -0.36 with seed yield. The correlation in EARLY-C2, however, was not significant.

Although single plant yield showed a high positive correlation with plant height, high yielding and tall accessions tend to have severe lodging problems when grown at high plant densities. EARLY-C2 in 1985 had a mature plant height that was 9% lower than F_2 -CO indicating that

some reduction in plant height can be achieved through earlier flowering without decreasing seed yield.

Discussion

In this study, the variation generated in an interpopulation cross between two *A. cruentus* populations of different geographic origin was described. Significant variation was observed for all nine characters measured. Five separate biparental crosses showed significant variation among crosses indicating that the parental populations were variable. Within each cross, the F_2 generation showed increased variability compared to the F_1 .

In most pairwise F_1 - F_2 comparisons, significant inbreeding depression was observed indicating some role of nonadditive gene action. Each character had a characteristic level of inbreeding depression with the greatest levels of up to 30% observed for panicle weight. Similar observations of heterosis and inbreeding depression have been reported for cotton, buckwheat, and sorghum (Meredith 1979; Marshall 1979; Kirby and Atkins 1968). The relative importance of additive and nonadditive variation and its effect on heritabilities of selected characters in grain amaranth requires further study. Large amounts of pseudo- or true over-dominance would argue in favor of development of varieties that maintain significant levels of heterozygosity. Even if dominant gene action accounts for the observed heterosis, early breeding efforts are unlikely to combine most of the favorable dominant genes into one pure line variety. This further argues for the use of heterogeneous and heterozygous varieties.

As grain amaranth breeding programs are established, it will be useful to know which breeding methods and selection criteria will give the greatest short term gains in seed yield. In the long term, it will be important to know what conditions will allow efficient and sustained responses to selection. As a mixed mating crop, a wide range of breeding methods are feasible. Breeding methods in amaranth can vary from pedigree methods that lead to development of pure lines to population improve-

ment schemes that maintain selections in variable bulk populations. Numerous breeding methods are available that combine features of maintenance of selections as lines versus bulks and encourage more or less recombination between selected materials (Simmonds 1979). The mixed mating system of amaranth requires knowledge of natural outcrossing rates to determine the amount of isolation and pollen control needed to achieve a particular breeding system that would vary from selfpollination in the development of pure lines to high outcrossing in the development of random mating populations. F_2 -CO used in this study had mean outcrossing rates of 34%, 21% and 24% in the three successive years 1982, 1983 and 1984 (Jain and Kulakow, in prep.).

The most economical breeding methods for amaranth, at least in its current development as a newly rediscovered crop species, must rely on natural pollination that does not necessarily demand controlled selfing of panicles or enforced cross-pollination. In this study, mass selection was initiated in a pooled F_2 population from five crosses made between UC192 and UC87. In a self-pollinated system, this would be a bulk-pedigree type of breeding method since it relies on selection of individual plants that are propagated as bulk populations. In population improvement terms, this breeding method would be a form of mass selection that practices an intermediate level of parental control depending on the balance of self- and cross-pollination. The response to selection is characterized by increased additive genetic variance due to selfing and continued recombination due to outcrossing. In early generations from a cross, the variation generated from the maximally heterozygous F_1 would often provide enough variation to sustain a selection response in early generations if heritabilities and desirable genotypic correlations are high. For example, Frey (1967) showed that mass selection for high seed width in oats resulted in an sustained increase in seed weight for five generations. Redden and Jensen (1974), however, showed that response to early generation mass selection for tiller number in wheat and barley was enhanced by intercrossing selected plants rather than allowing natural self-pollination. The enhanced response from outbreeding, they argued, was due to breakup of linkage blocks that increased heritability for tiller number. Meredith and Bridge (1971) also argued that intermating will increase the probability of recovering desirable recombinants. Although the mixed mating system in grain amaranth may affect early generation response to selection, it would have even greater role in the long term response to selection in hybrid populations (as used in this study) as well as within landrace populations. Based on population genetic theory and models of artificial selection, in fact, we suggest that mixed selfing and random mating species with outcrossing rates in the range of 10 to 30% offer an optimal population dynamic process of selection based on linked gene systems and certain low levels of recombinant novel variation.

Two cycles of selection for time of first anthesis resulted in a large selection response with realized heritabilities ranging from 0.35 to 0.66. Response to one cycle of selection for leaf length was significant but with low heritabilities of 0.08 for high leaf length and 0.19 for low leaf length. Days to first anthesis had high enough heritability to be selected in early generations. The decline in the response to selection in the second cycle ($h^2 = 0.35$ to 0.49) compared to the response in the first cycle ($h^2 = 0.54$

to 0.66) indicated an apparently rapid approach to a selection plateau although this would have to be confirmed by further selection cycles. The reduced response could be due to declining genetic variance such as would happen if time of anthesis was controlled by a few major genes. Major gene determination of the time of flowering was shown in another study involving accession UC192 (Kulakow and Jain 1985). The lack of a decline in coefficients of variation for days to first anthesis in the selected versus control cycles did not indicate a decline in variance. Natural selection could oppose selection for delayed flowering because very late flowering plants often fail to produce seed before the autumn season cuts off the growing season. This would not be true for early flowering selections, however, which also showed a decline in selection response.

Early generation response to selection for time of anthesis had the indirect effect of changing panicle weight in 1984 and single plant yield in 1985. Early flowering plants tended to be higher yielding than late flowering plants confirming the earlier observations of Hauptli and Jain (1984). Although the negative correlation of days to first anthesis and single plant yield was only moderate in this cross, compared to high positive correlations between plant size traits like leaf length of plant height and yield, the high heritability of days to anthesis was sufficient to result in a correlated response in single plant yield. This was especially evident in terms of 26% and 38% decreased yield of late flowering selections. Earlier flowering may increase yield due to several interrelated factors including avoidance of cooler fall temperatures, increase of harvest index through reduction in plant height and leaf number, lengthening of the reproductive period, decreased lodging due to decreased plant height, reduction in water use by shortening the growth cycle, and avoidance of the stress of pest infestations and decrease epiphytotics. In any location which is new to grain amaranth cultivation, determination of and mass selection for optimal time of flowering may substantially increase seed yield.

References

- Ayiecho PO (1985) Quantitative studies in two grain amaranth populations using two selection methods. PhD Dissertation, University of California, Davis
- Frey KJ (1967) Mass selection for seed width in oat populations. *Euphytica* 16: 341–349
- Hauptli H, Jain SK (1984) Genetic structure of landrace populations of the New World grain amaranths. *Euphytica* 33: 857–884
- Hauptli H, Jain SK (1985) Genetic variation in outcrossing rates and correlated floral traits in a population of grain amaranth (*Amaranthus cruentus* L.). *Genetica* 66: 21–27
- Hauptli H, Lutz RL, Jain SK (1979) Germplasm exploration in Central and South America. In: Proc 2nd Amaranth Conf, Rodale Press, pp 117–122

- Jain SK, Kulakow PA, Peters I (1986) Genetics and breeding of grain amaranth: Some research tissues and findings. In: Proc 3rd Amaranth Conf. Rodale Press, pp 174–191
- Kirby JS, Atkins RE (1968) Heterotic response for vegetative and mature plant characters in grain sorghum, *Sorghum bicolor* (L.) Moench. Crop Sci 8:335–339
- Kulakow P, Hauptli H, Jain SK (1985) Genetics of grain amaranth. 1. The inheritance of six color characteristics. J Hered 76:27–30
- Kulakow PA, Jain SK (1985) The inheritance of flowering in *Amaranthus* species. J Genet 64:85–100
- Marshall HG (1979) Studies of inbreeding depression, breeding behavior and heterosis in inbred lines of buckwheat. Crop Sci 19:110–114
- Meredith WR (1979) Inbreeding depression in selected F₃ cotton progenies. Crop Sci 19:83–88
- Meredith WR, Bridge RR (1971) Breakup of linkage blocks in cotton, *Gossypium hirsutum* L. Crop Sci 11:695–698
- Redden RJ, Jensen NF (1974) Mass selection and mating systems in cereals. Crop Sci 11:695–698
- Simmonds NW (1979) Principles of crop improvement. Longman, New York
- Vaidya KR (1984) Genetic variation in landrace populations of Indian amaranths. PhD dissertation, University of California Davis
- Vaidya KR, Jain SK (1986) Response to mass selection for plant height and grain yield in amaranth (*Amaranthus* spp.). Z Pflanzenzucht 89: 1–4