Quantitative Studies in Two Grain Amaranth Populations Using
Two Selection Methods

By

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ABSTRACT

A population of Amaranthus cruentus (UC87) and another of A. hypochondriacus (UC99) were subjected to S1 (selfed) family analysis of genetic variation for plant height, plant weight, head length, head weight, threshing percentage, seed yield:height ratio, days to flowering, 500 seed weight, harvest index and seed yield per plant during the summer of 1982. Mass and recurrent S1 selections were initiated on the two populations for yield:height ratio and harvest index. These selections were advanced to second generation by mass selection in the summer of 1983. The S1 selection was also done for plant weight in UC87 and days to flowering in UC99. All generations of these selection experiments were evaluated together during the summer of 1984.

Population UC87 had significant variation for threshing percentage, 500 seed weight and harvest index as indicated by S1 family analysis. High direct and indirect selection gains indicated presence of additive and additive x additive effects. This was confirmed for harvest index by component variance estimates. There were signs of overdominance in S1 selections.

Population UC99 had significant genotypic variation for all traits except plant weight, head length and head weight. High direct and correlated selection gains indicated high additive and additive x additive effects. This was also confirmed by the genetic component estimates for yield:height ratio and harvest index. Realized gains from mass selection were higher than their expected values and the gains from S1 selection. Gains from the second cycle mass selection were lower than gains from the first

cycle mass selection. These observations were attributed to the heterogeneity of UC99, which most likely involved competition, natural selection and higher homozygosity levels. In both populations mass selection was more efficient than S1 selection. This suggested a greater role of additive than the dominance component of variation.

Based on correlation coefficients and multiple stepwise regression, the best yield predictors were plant height, head weight, threshing percentage and yield:height ratio. Harvest index was an important predictor for the yield of UC99 original population in 1984 only. Yield:height ratio was the most consistent predictor; the path-coefficient analyses indicated that most other variables influenced yield through yield:height ratio. Head weight was also an important indirect path for some predictors.

INTRODUCTION

The grain amaranths, described to have originated in the
Incan Andes and Guatemala (Sauer, 1950), belong to the Amaran-
thaceae family which has at least 60 known species. They are
ubiquitously distributed across the tropical world either as a
grain crop in Central and South America and southern Asiatic
countries, or as a vegetable crop in Central and South America,
southern Asia and Africa. Domesticated as a grain crop by the
Aztecs over 4,000 years ago, their use as a grain crop has been
restricted to isolated regions. Among the presently cultivated
grain types are Amaranthus caudatus, A. cruentus and A.
hypochondriacus.

While amaranth cultivation has declined (Sauer, 1967; Early,
1977; Feine, 1979), Thiesen et al. (1978) described it as a
potential health food and cash crop on marginal lands. Sanchez-
Marroquin et al. (1979) also pointed out its industrial and
animal feed potential. Amaranth seed is rich in lysine and
methionine which are wanting in many food grains, and is about 15
percent high quality protein, 60 percent easily digestible
carbohydrates and fairly high in well composed lipids (Betschart
et al., 1979; Carlsson, 1979; Senft, 1979).

To counteract the declining cultivation and to promote its
utilization the present amaranth research interests are focused
on various aspects of its improvement including germplasm collec-
tion, genetic studies, agronomic practices, seed yield and
nutritional quality improvement of both grain and vegetable
amaranths. Other than U.S.A., a number of Third World countries

including Guatemala, Kenya, Nigeria and India have initiated pilot research programs for the improvement and utilization of amaranths.

Variation studies on grain amaranth collections in Davis have revealed conflicting variation patterns. Though a few landraces were noted to be mixtures of homozygous genotypes, allozyme studies revealed little variation in a number of populations (Hauptli and Jain, 1978, 1984; Jain et al., 1980). However, substantial variation has been noted for quantitative traits in a number of populations. For example, Hauptli et al. (1979) and Jain et al. (1979) reported variation for morphological traits in amaranth populations from Central and South America and India respectively. Similarly, Hauptli and Jain (1980) reported substantial variation for yield-related traits like flowering time, plant height, inflorescence length, harvest index and seed yield in an amaranth population originally obtained from Tanzania.

Though variation in amaranth populations for yield related traits is presently becoming evident few studies have been done to investigate the components of genetic variation. However, detailed knowledge on type of gene action is essential for designing breeding programs. Though amaranths have monoecious inflorescences, they are presently classified with such crops like sorghum and cotton which basically self-pollinate, with variable amounts of outcrossing (Allard, 1960; Simmonds, 1979). In such crops additive and additive x additive effects are known to be predominant (Matzinger, 1963; Sprague, 1966; Dudley and

Moll, 1969).

One problem frequently facing plant breeders in quantitative genetic studies is use of appropriate mating and environmental designs that provide reliable genetic component estimates. Dudley and Moll (1969) compared various mating designs and suggested that the most preferable design is the simplest one that will provide the required information. Choice of mating design is influenced by the ease with which the breeding system of a crop can be manipulated. Selfing species are particularly problematic due to difficulties in making crosses. However, populations of a number of selfing and predominantly selfing crops like soybeans and sorghum are presently crossed with the aid of male sterility genes (Doggett and Eberhart, 1968; Brim and Stuber, 1973; Jan-orn et al., 1976; Eckebil et al., 1977). This makes it easy to plan powerful mating designs that give detailed information on type of gene action. While the breeding system in grain amaranths is not yet completely understood, genetic manipulation of its sexuality is yet unresolved though there are reports of male sterility (I. Peters, unpublished). Under such situations simultaneous use of different selection designs may give an insight into the type of gene action. Gains from different selection methods are known to be affected by varying proportions of genetic variance components. For example, mass selection in a highly inbred population benefits from additive and additive x additive effects only, while selection methods in which a hybrid generation is used as the selection will be influenced by additive, dominance and epistatic effects. It is

with this in mind that two selection methods, mass selection and S1 selection, were used in this study.

Crop yield was first defined in terms of its related traits by Engledow and Wadham (1923). Thereafter, many studies have been focused on analysis of yield in terms of its components or related traits like plant height, biomass yield and harvest index. In crops like sorghum studies have been focused on threshing percentage, head weight, days to bloom, plant height and seed weight (Hadley et al., 1965; Graham and Lessman, 1966; Eckebil et al., 1977). Similarly, in small cereals like wheat and barley yield analysis studies have considered seed number per head, seed weight, head size, tiller number, plant weight, and harvest index (Singh and Stoskopf, 1971; Yap and Harvey, 1972; Park et al., 1977; Ayiecho and Onim, 1983). Few studies have been reported in grain amaranths which relate seed yield to other traits except those of Hauptli and Jain (1980, 1984). In the present study plant height and weight measurements, harvest index, threshing percentage, seed yield:height ratio, seed weight and days to flowering were assessed for their influence on seed yield per plant using simple correlations, multiple stepwise regression and path-coefficient analyses. Stepwise regression has been described by Neter and Wasserman (1974) and Draper and Smith (1981) as a useful method for discriminating among a multiple of potentially useful predictors. Path-coefficient analysis was first proposed by Wright (1923) for understanding how various predictors interact. It was recently discussed at greater length by Li (1975).

Thus the objectives of this study were as follows:

1. To study the quantitative genetics of traits subjected to mass and S1 selections, and use the information obtained to speculate on the quantitative genetics of other traits and other amaranth populations.

2. To study the possibility of amaranth population improvement by the two selection methods. The two methods were compared to find which one could lead to better exploitation of variation in amaranth populations.

3. To identify potentially useful quantitative predictors for amaranth seed yield.

MATERIALS AND METHODS

Materials for this study were developed from two grain amaranth populations, namely, UC87 (Amaranthus cruentus) and UC99 (A. hypochondriacus). The latter is a highly heterogeneous population believed to be a mixture of two subspecies. One component of this mixture comprises of typical A. hypochondriacus plants. The other component is closer to A. cruentus and is faster growing, earlier flowering and less susceptible to Phythium and lodging.

The two populations were subjected to a genetic variation study by planting 48 S1 families from each population in a two-replicate completely randomized block design in the summer of 1982 at Davis. Two selection methods, mass and S1 selection, were also initiated on the two populations as described below.

Mass Selection

Each population was planted in a 34 by 30 meter plot consisting of 34 rows. Between and within row spacings were one meter and 15 cm respectively. Excluding the outer row on either side, the plot was subdivided in to 24 subplots, each four rows by nine meters, to simulate Gardner's (1961) gridding system. Data were taken from seven random subplots, by sampling 20 plants per subplot, giving a total of 140 plants for each population. Mature individual plants were scored for plant size traits, namely: plant height, plant dry weight, head length and head dry weight; seed production efficiency parameters, namely: threshing percentage, seed yield:height ratio, harvest index, and seed yield per plant. Seed size was estimated in terms of 500 seed

weight from each plant. The top 21 plants, three per subplot, were selected (15 percent selection pressure) for harvest index and seed yield:height ratio. Equal amounts of seed from the 21 selected plants were bulked to form the selected accessions for each of these two traits.

Maintaining the same field design and selection technique, the two selections in each population, mass selection for harvest index and mass selection for seed yield:height ratio, were planted in summer of 1983 and a second cycle of selection carried on.

S1 Family Analysis and S1 Selection

For each of the two populations the 48 S1 families were planted in a two-replicate completely randomized block design. Spacings between and within rows were one meter and 15 cm, respectively. The 48 S1 families were scored for days to flowering, in addition to the above mentioned traits. Four plants per replicate for each family were used to obtain data on which variation analysis and selection were based. The family means, based on these plants, were used in selecting the seven best families (approximately 15 percent selection pressure) for harvest index and seed yield:height ratio in each population. Similar selection was done for total plant weight in UC87 and for days to flowering in UC99. For each of these four traits remnant S1 seed of the selected seven best families was planted for intermating in the glasshouse during winter of 1983. The cross seeds were bulked in equal proportions to make up the selected accessions for each trait.

In summer of 1983 the S1 selections for harvest index and seed yield:height ratio in each population were subjected to one cycle of gridded mass selection as described above.

Comparative Evaluation

The following nine selections for each population were subjected to an evaluation trial with the original population as a check in a four-replicate completely randomized block design in summer of 1984 at Davis.

1. S1 selection for total plant weight (plant weight S1) for UC87 or S1 selection for days to flowering (days to flowering S1) for UC99.

2. First mass selection cycle for harvest index (harvest index M1).

3. Second mass selection cycle for harvest index (harvest index M2).

4. S1 selection for harvest index (harvest index S1).

5. Mass selection following S1 selection for harvest index (harvest index S1-M1).

6. First mass selection for seed yield:height ratio (seed yield:height M1).

7. Second mass selection for seed yield:height ratio (seed yield:height M2).

8. S1 selection for seed yield:height ratio (seed yield:-height S1).

9. Mass selection following S1 selection for seed yield:-height ratio (seed yield:height S1-M1).

Between and within row spacing were maintained. For each

entry data was taken on 19 plants for the UC87 and 17 plants for
the UC99 from each replicate. Data was taken on the same traits.
The 500 seed weight was assessed for harvest index selections and
original populations only.

Statistical Analyses

The S1 families were evaluated by a random analysis of
variance model to assess the extent of variation in each popula-
tion. The 1984 selection evaluation experiments were also
subjected to a similar analysis. Duncan's multiple range test
was used to compare the means from the 1984 experiments.

Apart from correlations among the traits, stepwise regres-
sion and path-coefficient analyses were used to assess the
interaction and importance of different traits with respect to
their effects on seed yield per plant using data from the control
population and second cycle mass selection for harvest index.
The analyses were done on Borroughs 7800 computer. The traits
were subjected to multiple stepwise regression and a maximum of
four traits selected as the best seed yield indicators were used
in path analysis.

Selection response data were used to estimate components of
genetic variation as below.

S1 selection predicted again =

$$\frac{k^* \sigma^2 G_{S1}}{\sigma P_{S1}}$$

This was expressed as percentage of the original population
mean.

$\sigma^2 G_{S1}$ = genotypic variation estimate from S1 family analysis.

σP_{S1} = phenotypic standard deviation from S1 family analysis.

k* = selection differential corrected for effective population size using an extension of Table XX of Fisher and Yates (1963) as given in Hallauer and Miranda (1981).

Broad sense heritability, h^2_{S1} =

$$\frac{\sigma^2 G_{S1}}{\sigma^2 P_{S1}}$$

Realized heritability from S1 testing selection,

$$h^2_{RS1} = \frac{\%\ realized\ S1\ selection\ gain}{\%\ S1\ selection\ differential}$$

Realized heritability from mass selection,

$$h^2_{RM} = \frac{\%\ realized\ mass\ selection\ gain}{\%\ mass\ selection\ differential}$$

Mass selection predicted gain =

$$\frac{k(\sigma^2 G_{S1})2F}{\sigma P_o(1+F)}$$

σP_o = phenotypic standard deviation for the original population bulk based on a sample of 140 plants.

$$F = \frac{1-t}{1+t}$$

t = outcrossing rate estimate. This was estimated for UC99 in this study. In case of UC87 an average t estimate of 0.31 obtained by Jain et al. (1982) for A. cruentus was assumed because inflorescence coloration which was being used to estimate t in this study was noted to show signs of multi-loci segregation

in UC87. There was a high degree of phenotypic expression overlap as a result of such segregation.

Additive genetic variance estimate:

$$\sigma_A^2 = (\frac{1+F}{2F})\ h_{RM}^2\ \sigma^2 P_{S1}$$

Nonadditive variance estimate:

$$\sigma^2_{NA} = \sigma G_{S1}^2 - \sigma_A^2$$

RESULTS

Quantitative Variation

A.   Quantitative Variation in UC87

Data on variation analysis are presented in Tables 1 and 2.
The S1 family analysis for this population shows that only
threshing percentage, 500 seed weight and harvest index had
significant variation among families (Table 2). There were no
significant variations in plant size traits (plant height, plant
weight, head length and head weight), seed yield:height ratio and
seed yield per plant. With the exception of threshing percentage
and 500 seed weight there were large family-replicate interaction
effects. High coefficient of variation values were also observed
for plant weight, head weight, seed yield:height ratio and seed
yield per plant. A few families were noted to be segregating for
head coloration.

Components of variation, heritability estimates and expected
selection gains are given in Table 3. Broad sense heritability
estimates show that only threshing percentage, 500 seed weight
and harvest index had some detectable genetic variation. Expect-
ed gains are based on the same methods: mass selection from a
population of size $\geq$ 140 and S1 selection from 48 families, with
intensity of approximately 15 percent. Harvest index had the
highest expected gain estimate. Other traits had evidently no
genetic variation as per method used, hence no expected gains.

B.   Quantitative Variation in UC99

The UC99 population was generally more variable for metric
traits than UC87 though plant size traits had no significant

Table 1. Means, standard errors and coefficient of variation estimates for the original populations (1982).

Trait	UC87			UC99		
	Mean	S.E.	C.V.	Mean	S.E.	C.V.
Plant height (cm)	174.6	1.7	0.11	202.2	1.70	0.10
Plant weight (gm)	141.6	5.7	0.47	158.4	5.90	0.44
Head length (cm)	45.2	0.56	0.15	41.5	0.85	0.24
Head weight (gm)	66.2	2.30	0.41	62.6	2.70	0.52
Threshing %	51.8	0.52	0.12	36.9	0.60	0.19
Seed yield:height	0.1887	0.0049	0.30	0.1134	0.0053	0.55
500 seed weight (gm)	0.2316	0.0011	0.06	0.4077	0.0027	0.08
Harvest index	0.2502	0.0041	0.19	0.1501	0.0047	0.37
Seed yield per plant (gm)	33.6	1.10	0.38	23.2	1.20	0.59

N = 140 for each population.

Table 2. S1 family analysis of variance for UC87 (1982).

Trait	df	Blocks 1	Families 47	Interaction 47	Error 288	Mean	C.V.
			Mean squares				
Plant height (cm)		1899.00	1744.79	1933.83**	22.70	174.7	0.09
Plant weight (gm)		6200.00	6093.09	11014.81**	2256.11	145.2	0.33
Head length (cm)		101.10	65.80	61.70**	24.60	44.9	0.11
Head weight (gm)		1445.00	807.55	1501.11**	356.99	66.5	0.28
Threshing %		89.10**	37.71**	21.96	16.6	53.3	0.08
Seed yield:height		0.0082	0.00475	0.00489**	0.0021	0.1984	0.23
Days to flowering		9.37	16.98	14.77**	2.39	59.8	0.036
500 seed weight (gm)		0.00103**	0.00038**	0.0001	0.0009	0.2379	0.040
Harvest index		0.0013	0.007**	0.0035**	0.0011	0.2533	0.13
Seed yield per plant (gm)		729.40	229.74	384.94**	90.01	35.2	0.27

* P = 0.05, ** P = 0.01

Table 3. Heritability, expected selection gain and components of variation estimates for UC87.

Trait	$^2P_{S1}$	$^2G_{S1}$	Broad sense h^2_{S1}	Expected % Gain(1)	Expected % Gain(1)	Realized h^2 (1)	(2)	^2_A*	$^2_{NA}$**
Plant height	1933.83	0	0	0	0				
Plant weight	11014.81	0	0	0	0	0.50			
Head length	64.10	0.53	0.008	0.19	0.23				
Head weight	1501.11	0	0	0	0				
Threshing %	29.84	7.88	0.26	2.62	4.19				
Seed yield:height	0.00489	0	0	0	0	0.55	0.87		
Days to flowering	15.84	1.11	0.07		-0.72				
500 seed weight	0.00024	0.00014	0.60	5.05	5.88				
Harvest index	0.0053	0.0018	0.34	15.96	15.10	0.30	0.78	0.0020	-0.0002
Seed yield per plant	0.38494	0	0	0	0				

S1 = Denotes estimates from S1 families.
(1). Denotes estimates for mass selection
(2). Denotes estimates for S1 selection.
*   Includes pure additive and additive x additive effects.
**   Includes pure dominance and dominance epistasis.

variation according to S1 family (Tables 1 and 4). Significant variations were noted for the seed production efficiency parameters (threshing percentage, seed yield:height ratio and harvest index), days to flowering, 500 seed weight and seed yield per plant. Days to flowering was also noted to be highly variable. One family was observed to be segregating for days to flowering and plant height; namely, dwarf early flowering vs. tall late flowering; and another for marbling of head coloration. A few families showed more profuse branching with big plants, small heads and low seed yields. Apart from being large with small heads, such branched plants were late flowering. Excessive height and Pythium attack lead to lodging in some families.

Apart from plant height every trait had substantial exploitable genetic variation as can be seen in Table 5. Threshing percentage, days to flowering, 500 seed weight and harvest index had the highest genetic variation as can be noted from broad sense heritability estimates. Accordingly, expected selection gains were fairly high for all traits except plant weight and head weight. Expected gain for plant height S1 selection was rather low.

Direct Response to Selection

A. Direct Response to Selection in UC87

The means for the selections and the control check are presented in Table 6. The analysis of variance among these entries are presented in Table 7 and Duncan's multiple range test in Figure 1. Though the analysis of variance tests indicate significant differences among the entries for plant weight, no

Table 4. S1 family analysis of variance for UC99 (1982).

		Mean squares					
		Blocks	Families	Interaction	Error		
Trait	df	1	47	47	288	Mean	C.V.
Plant height (cm)		2420.00	2036.00	1510.57**	189.28	186.1	0.07
Plant weight (gm)		12297.00	7174.49	7841.77**	2535.27	150.4	0.34
Head length (cm)		16.70	183.10	113.92**	31.89	39.7	0.14
Head weight (gm)		2301.00	1245.98	1115.11**	366.22	58.2	0.33
Threshing %		26.90	106.03**	37.00	21.00	32.1	0.14
Seed yield:height		0.0041	0.0066**	0.0030**	0.0010	0.1028	0.31
Days to flowering		24.50	231.58**	18.40	17.85	74.6	0.06
500 seed weight (gm)		0.0036**	0.0031**	0.0009	0.0005	0.4095	0.017
Harvest index		0.0008	0.0057**	0.00111**	0.0007	0.1299	0.21
Seed yield per plant (gm)		318.00	274.69*	163.70**	43.88	19.4	0.34

* P = 0.05, ** P = 0.01

Table 5. Heritablity, expected selection gain and components of variation estimates for UC99.

Trait	$\sigma^2 P_{S1}$	$\sigma^2 G_{S1}$	Broad sense h^2_{S1}	Expected % gain(1)	Expected % gain(2)	Realized h^2 (1)	(2)	σ^2_A*	σ^2_{NA}**
Plant height	1773.29	262.72	0.16	9.30	5.19				
Plant weight	841.77	0	0	0	0				
Head length	148.51	34.59	0.23	11.75	11.06				
Head weight	740.67	65.44	0.09	4.57	6.39				
Thresing %	71.52	34.52	0.48	18.58	19.14				
Seed yield:height	0.00478	0.0018	0.38	35.99	39.18	0.88	0.27	0.0047	-0.0029
Days to flowering	124.99	106.59	0.85		-19.77		0.18		
500 seed weight	0.00199	0.0011	0.54	12.10	9.32				
Harvest index	0.00338	0.0023	0.67	38.70	47.11	1.02	0.75	0.0035	-0.0012
Seed yield per plant	219.20	55.25	0.25	24.45	29.85				

S1 Denotes estimates from S1 families.
(1). Denotes estimates for mass selection.
(2). Denotes estimates for S1 selection.
*   Includes pure additive and additive x additive effects.
**   Includes pure dominance and dominance epistasis.

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Table 6. Means from selection evaluation experiments for UC87 (1984).

Selection criterion and method	Plant height	Plant weight	Head length	Head weight	Threshing %	Seed yield: height	Days to flowering	500 seed weight	Harvest index	Seed yield per plant
	(cm)	(gm)	(cm)	(gm)				(gm)		(gm)
Control population	201.3	127.2	52.7	54.6	39.4	0.1006	65.2	0.2277	0.1668	21.1
Plant weight, S1	204.6	146.8	51.1	62.2	40.8	0.1211	65.0		0.1724	24.9
Harvest index, M1	198.2	143.1	54.5	65.5	39.9	0.1254	63.3	0.2142	0.1809	25.2
Harvest index, M2	199.5	153.0	52.1	72.3	43.1	0.1483	62.1	0.2273	0.2007	30.3
Harvest index, S1	194.3	120.2	50.4	54.8	42.1	0.1149	64.9	0.1989	0.1907	22.4
Harvest index, S1-M1	204.2	149.8	55.3	69.7	40.9	0.1298	64.1	0.2282	0.1902	27.1
Seed yield:height M1	215.7	166.7	57.0	73.2	38.3	0.1238	64.9		0.1625	27.2
Seed yield:height M2	208.7	160.7	57.2	76.9	41.6	0.1502	62.0		0.1958	31.8
Seed yield:height S1	191.0	129.0	51.5	59.6	41.9	0.1248	64.0		0.1911	23.9
Seed yield:height S1-M1	193.1	140.4	54.5	66.3	41.2	0.1386	63.8		0.1960	26.9

S1 = Cycle 1 of S1 selection.
M1 = Cycle 1 of mass selection.
M2 = Cycle 2 of mass selection.

Table 7. Analysis of variance for selection evaluation experiments (1984).

Source	df	Plant height	Plant weight	Head length	Head weight	Threshing	Seed yield height	Days to flowering	Seed weight	Harvest index	Seed yield per plant
JC 81											
Blocks	3	18104.37**	50739.35**	347.65*	9215.17**	32.01	0.0439**	44.53**	0.01853*	0.0234**	2418.96**
Selections	9	4271.45**	16107.11**	397.37	465.50	130.84	0.0177**	83.84**	0.01210*	0.0134**	820.73**
Interaction	27	972.30**	7375.66**	233.30**	2013.77**	91.45**	0.0134	13.57**	0.00341**	0.0033**	312.65**
Error	720	306.21	4285.27**	94.00	1038.85	42.15	0.0027	4.77	0.00143	0.0012	131.08
JC 99											
Blocks	3	6416.34**	55384.59**	131.62	6210.90**	547.82**	0.0809**	332.06**	0.00154	0.0253**	4536.70**
Selections	9	8184.63**	35049.01**	321.18	16403.61**	3420.75**	0.1143**	698.36**	0.04740**	0.1343**	6495.85**
Interaction	27	1075.64**	894.68**	157.90**	2888.28**	154.39**	0.0110**	46.97**	0.00343**	0.0075**	1150.73**
Error	640	430.74	458.55	82.09	1682.71	100.35	0.0037	24.31	0.00233	0.0010	355.42

*t = .05, **t .01 = 9.84

Note: df for 500 seed weight are 1, 3, 12 and 640 respectively for JC 81,
3, 8, 12 and 320 respectively for JC99

Figure 1. Duncan's multiple range test for selection
          means of UC87 (1984).

                    Key to Figure 1

1.   Control population.

2.   Plant weight S1 selection.

3.   Harvest index first cycle mass selection (M1).

4.   Harvest index second cycle mass selection (M2).

5.   Harvest index S1 selection.

6.   Harvest index first cycle mass selection following S1
     selection (S1-M1).

7.   Seed yield:height ratio first cycle mass selection (M1).

8.   Seed yield:height ratio second cycle mass selection.

9.   Seed yield:height ratio S1 selection.

10. Seed yield:height ratio mass selection following S1
     selection (S1-M1).
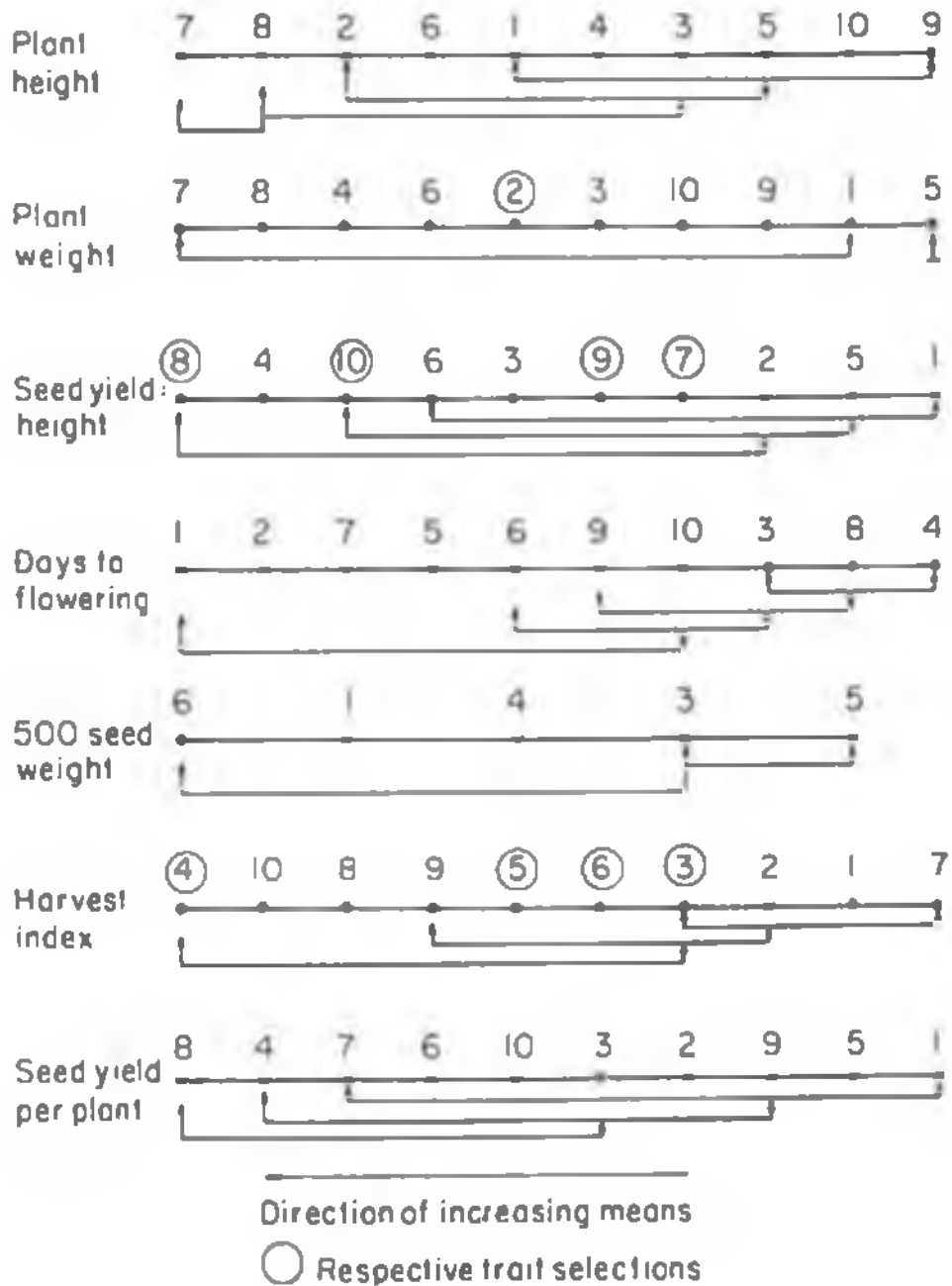
significant response was observed when it was selected for as revealed by Duncan's multiple range test. There was a gain of 15.4 percent from S1 selection for this trait (Appendix 1). There were significant differences among the entries for both seed yield:height ratio and harvest index indicating significant response. Though mass selection seemed more effective in increasing seed yield:height ratio over the two generations with an average gain of 24.6 percent (Table 8 and Figure 2), its cumulative gain was not significantly different from that of S1 selection combined with mass selection as noted from Duncan's multiple range test. Both were significantly different from the control population. Mass selection was also slightly more effective in increasing harvest index over the two generations. The 14.3 percent cumulative gain from S1 and mass selection combination was all realized in the S1 selection generation.

Data presented in Table 3 show that no genetic variation was noted for plant weight, yet high realized heritability of 0.50 was obtained, indicating that S1 family analysis failed to reveal all the variation in the population. Seed yield:height ratio also had realized heritability of 0.55 and 0.87 from mass and S1 selections respectively. In case of harvest index realized heritability from mass selection (0.34) was close to broad sense heritability estimate (0.30), indicating high additive and additive x additive epistasis. This was also reflected by closeness of expected and observed S1 selection gains for this trait. Additive variance estimate for this trait was 0.0020 with zero or negative nonadditive estimate. However, realized herita-

Table 8. Average percentage gains from selections (1984).

Selection criterion and method	Plant height	Plant weight	Head length	Head weight	Threshing %	Seed yield: height	Days to flowering	Seed weight	Harvest index	Seed yield per plant
UC 87										
Harvest index M1+M2	0	10.2	1.8	16.2	4.7	23.7	-2.3	0	10.2*	21.8
Harvest index S1+S1-M1	0.7	8.9	2.6	13.9	3.4	14.5	-0.9	0.11	7.2*	14.2
Seed yield:height M1+M2	3.6	15.5	4.3	20.4	2.7	24.6*	-1.9		8.7	25.3
Seed yield:height S1+S1-M1	0	5.2	1.8	10.8	3.1	18.9*	-1.0		8.8	13.8
UC 99										
Harvest index M1+M2	8.3	19.3	4.8	33.9	35.1	57.8	-6.1	8.0	47.0*	60.0
Harvest index S1+S1-M1	8.3	22.8	5.5	28.5	33.3	44.7	-4.4	4.7	36.4*	50.7
Seed yield:height M1+M2	5.3	13.7	3.9	24.7	34.7	44.5*	-5.0		44.4	45.6
Seed yield:height S1+S1-M1	6.6	17.7	6.7	25.3	31.3	40.6*	-4.8		36.2	44.4

M1 = Cycle 1 of mass selection.
M2 = Cycle 2 of mass selection.
S1 = Cycle 1 of S1 selection.

* = Direct response.

Figure 2. Percentage cumulative direct and indicrect
          selection gains in seed yield:height ratio
          and harvest index of UC87 (1984).
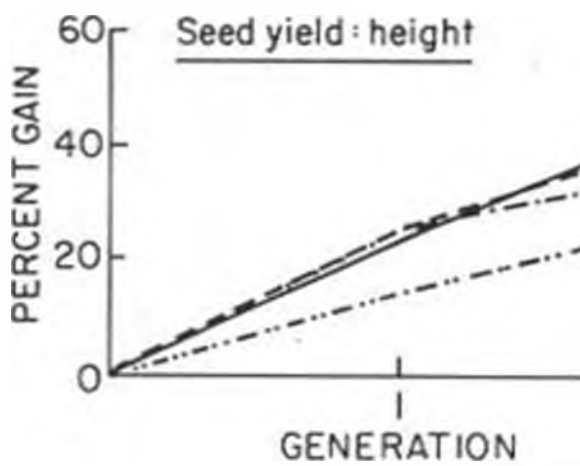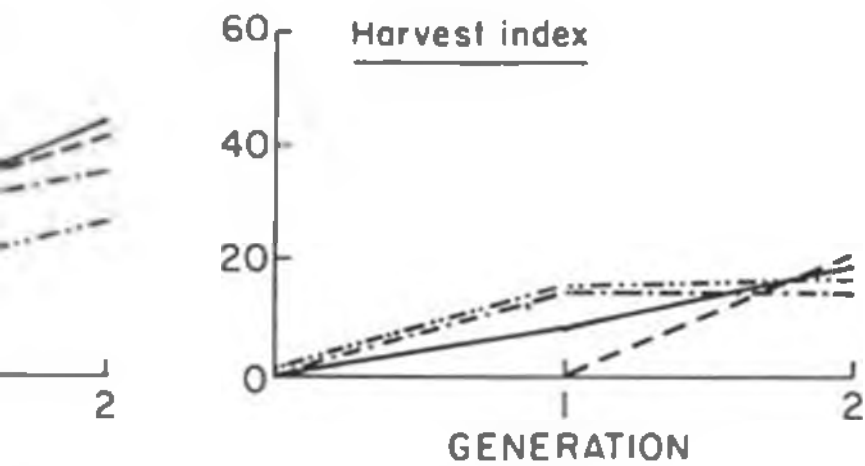
Seed yield : height

PERCENT GAIN

60

40

20

0

GENERATION

60 — Harvest index
40
20
0

GENERATION

——— Direct ; mass selection
—·—·— Direct ; SI - mass selection
——— Indirect ; mass selection
······· Indirect ; SI - mass selection

bility from S1 selection was much higher (0.78) reflecting overdominance.

B.   Direct Response to Selection in UC99

The analysis of variance for the selection evaluation experiments is presented in Table 7. Duncan's multiple range tests among the selections is given in Figure 3. The selections were significantly different for all the directly selected traits. The S1 selection was directly effective for harvest index only as indicated by Duncan's multiple range test. The average percentage gains from selection and means are presented in Tables 8 and 9 respectively. Response to S1 selection for days to flowering is also given in Appendix 1. Average gain from the two generations of mass selection for seed yield:height ratio was 44.5 percent with over 80 percent of the gain being realized in the first generation (Figure 4). The S1 selection gave a lower response, though when followed by mass selection the gain was much increased. Gains from harvest index selection followed similar trends (Figure 4). Nearly all the gain was realized in the first cycle of the two mass selection cycles. Gain from the S1 selection was significantly less than gain from the first mass selection generation as indicated by Duncan's multiple range test.

Realized heritability estimates are presented in Table 5. Realized heritability estimates from mass selection were much higher than their broad sense estimates. Realized gains from first cycle mass selections were also much higher than the expected values. However, with the exception of harvest index,

Figure 3.   Duncan's multiple range test for selection
              means of UC99 (1984).

                          Key to Figure 3

1.   Control population.

2.   Days to flowering S1 selection.

3.   Harvest index first cycle mass selection (M1).

4.   Harvest index second cycle mass selection (M2).

5.   Harvest index S1 selection.

6.   Harvest index first cycle mass selection following S1
       selection (S1-M1).

7.   Seed yield:height ratio first cycle mass selection (M1).

8.   Seed yield:height ratio second cycle mass selection (M2).

9.   Seed yield:height ratio S1 selection.

10.   Seed yield:height ratio first cycle mass selection following
       S1 selection (S1-M1).

Plant height

| 6 | 3 | 10 | 4 | 8 | 7 | 5 | 2 | 9 | 1 |

Plant weight

| 6 | 3 | 4 | 10 | 8 | 7 | 5 | 9 | 2 | 1 |

Head weight

| 4 | 6 | 3 | 10 | 8 | 7 | 5 | 2 | 9 | 1 |

Threshing %

| 4 | 7 | 8 | 6 | 10 | 3 | 5 | 2 | 9 | 1 |

Seed yield₁ height

| 4 | 6 | ⑧ | ⑩ | ⑦ | 3 | 5 | ⑨ | 2 | 1 |

Days to flowering

| 9 | 1 | 5 | ② | 6 | 3 | 10 | 7 | 8 | 4 |

500 seed weight

| 3 | 4 | 6 | 5 | 1 |

Harvest index

| ④ | 8 | 7 | ⑥ | 10 | ③ | ⑤ | 2 | 9 | 1 |

Seed yield per plant

| 4 | 6 | 8 | 10 | 3 | 7 | 5 | 2 | 9 | 1 |

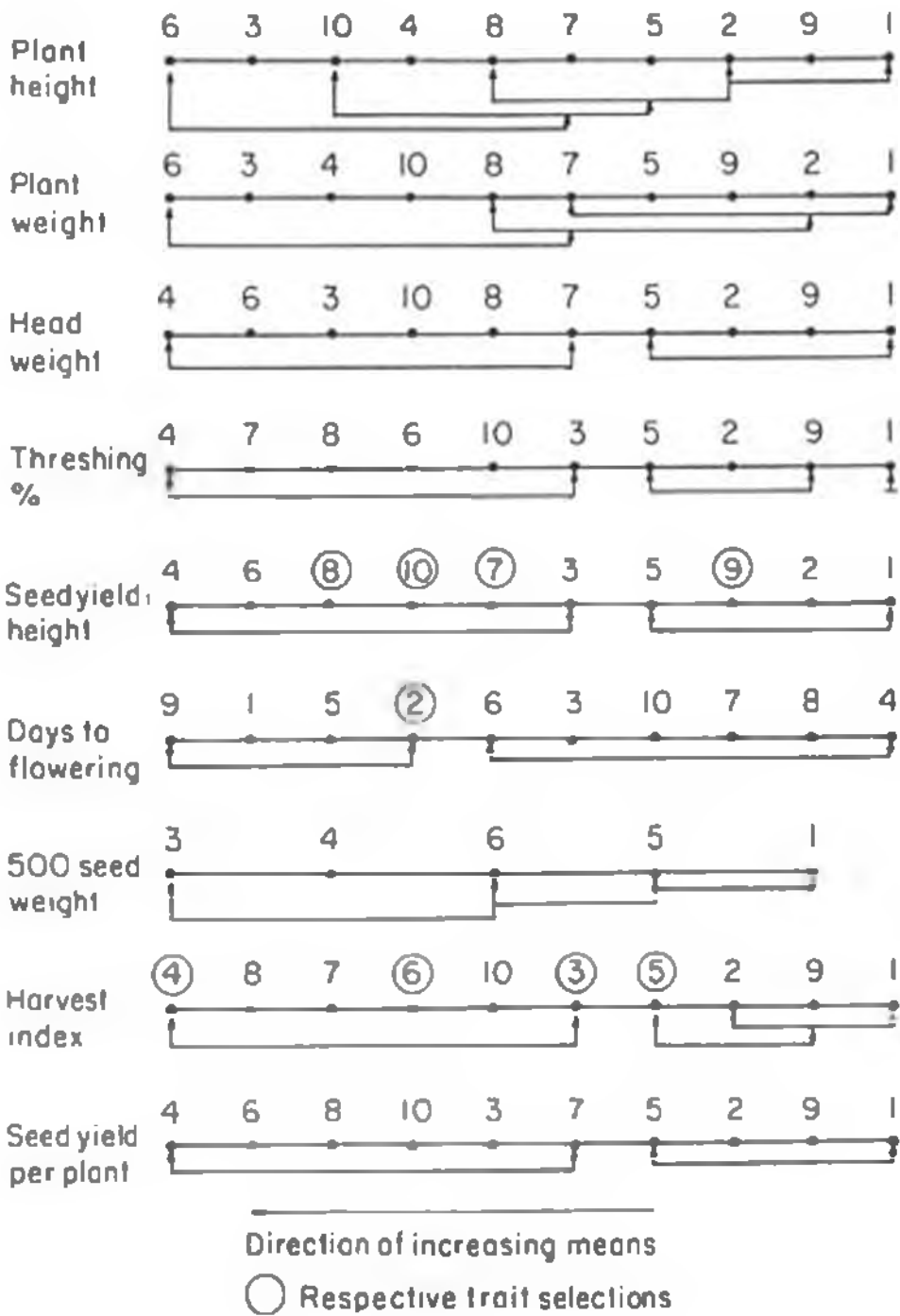———————— Direction of increasing means

◯ Respective trait selections

Figure 4. Percentage cumulative direct and indirect
selection gains in yield:height ratio and
harvest index of UC99 (1984).
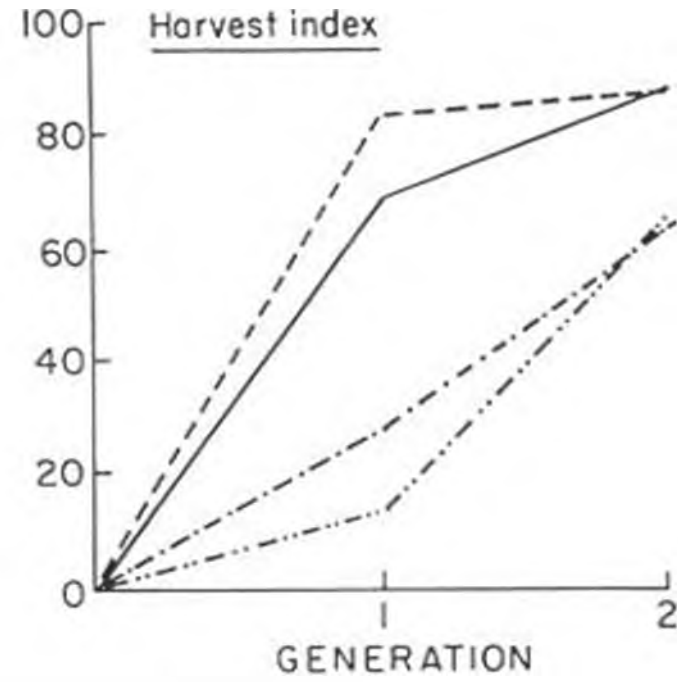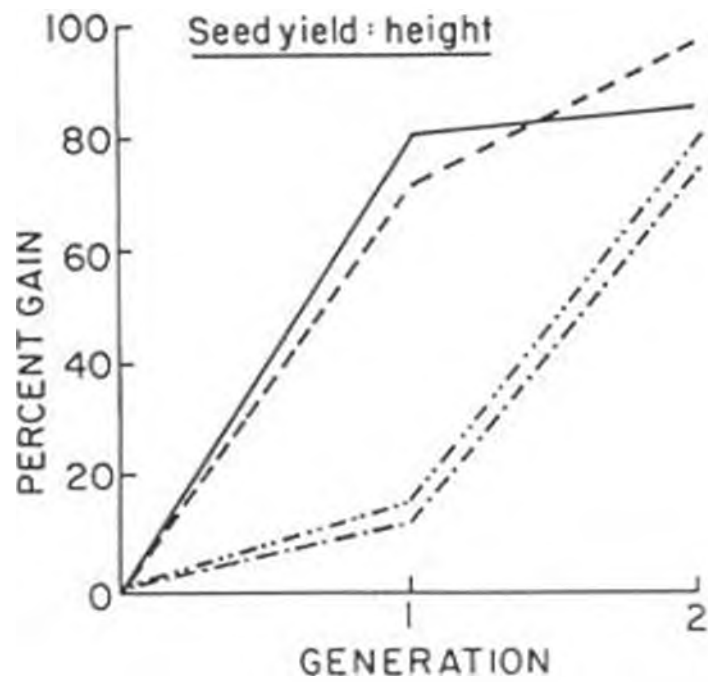
PERCENT GAIN

Seed yield : height

Harvest index

GENERATION

GENERATION

———— Direct ; mass selection

—·—·— Direct; SI- mass selection

———— Indirect ; mass selection

—··—··— Indirect ; SI- mass selection

Table 9. Population means for UC99 (1984).

Selection criterion and method	Plant height	Plant weight	Head length	Head weight	Threshing %	Seed yield: height	Days to flowering	500 seed weight	Harvest index	Seed yield per plant
Control population	192.4	137.1	48.9	60.9	27.0	0.1016	65.8	0.3950	0.1242	21.6
Days to flowering S1	200.6	141.8	54.3	65.4	32.1	0.1131	64.4		0.1499	24.2
Harvest index M1	224.3	190.0	53.6	91.7	43.0	0.1750	60.0	0.4580	0.2095	40.0
Harvest index M2	214.4	187.0	53.3	102.2	45.9	0.2190	57.8	0.4418	0.2410	47.5
Harvest index S1	209.9	148.8	51.2	65.7	35.4	0.1172	64.7	0.4104	0.1581	25.5
Harvest index S1-M1	224.4	199.6	54.3	95.6	44.9	0.1922	60.0	0.4322	0.2147	43.6
Seed yield:height M1	211.8	169.8	49.2	85.5	45.7	0.1833	59.5		0.2276	39.4
Seed yield:height M2	212.6	174.0	52.7	91.0	45.2	0.1920	59.3		0.2345	41.3
Seed yield:height S1	196.4	147.2	53.0	64.2	31.3	0.1140	66.5		0.1408	23.7
Seed yield:height S1-M1	218.0	185.5	55.5	91.7	43.8	0.1844	59.5		0.2140	40.8

S1 = Cycle 1 of S1 selection.
M1 = Cycle 1 of mass selection.
M2 = Cycle 2 of mass selection.

realized heritabilities from S1 selection were all lower than
their broad sense estimates. Similarly, S1 selection gains were
also lower than their expected values.

Comparisons between the S1 and the first cycle mass selec-
tions suggest underdominance. However, the genetic component
estimates for seed yield:height ratio and harvest index show lack
of nonadditivity or negative nonadditive variance.

Indirect Response to Selection

A.   Indirect Response to Selection in UC87

Correlated responses for seed yield:height ratio, harvest
index, days to flowering and seed yield per plant are presented
in Table 8, Appendix 1, Figures 2, 5, and 6. They followed
similar trends as direct gains, with two generations of mass
selection having slightly greater impact than S1 and mass selec-
tion having slightly greater impact than S1 and mass selections
combined. Indirect gain in seed yield per plant was one of the
objectives of this study. One generation of S1 selection for
plant weight lead to 18 percent gain in seed yield per plant
(Appendix 1). The two generations of mass selection for both
seed yield:height ratio and harvest index significantly shifted
seed yield per plant as indicated by Duncan's multiple range test
(Figure 1). Though substantial, indirect gains in head length,
head weight and threshing percentage were not significant, hence
not presented. However, increased seed yield among the selec-
tions may be attributed, among other factors, to increased head
weight which correlated strongly to plant weight, seed yield:-
height ratio and seed yield per plant. There were reciprocal

Figure 5. Percentage indirect selection gains in days
           to flowering (1984).

GENERATION

PERCENT GAIN

UC87

—————— Harvest index mass selection

—·—·— Harvest index SI - mass selection

— — — Seed yield : height mass selection

···—···— Seed yield : height SI - mass selection
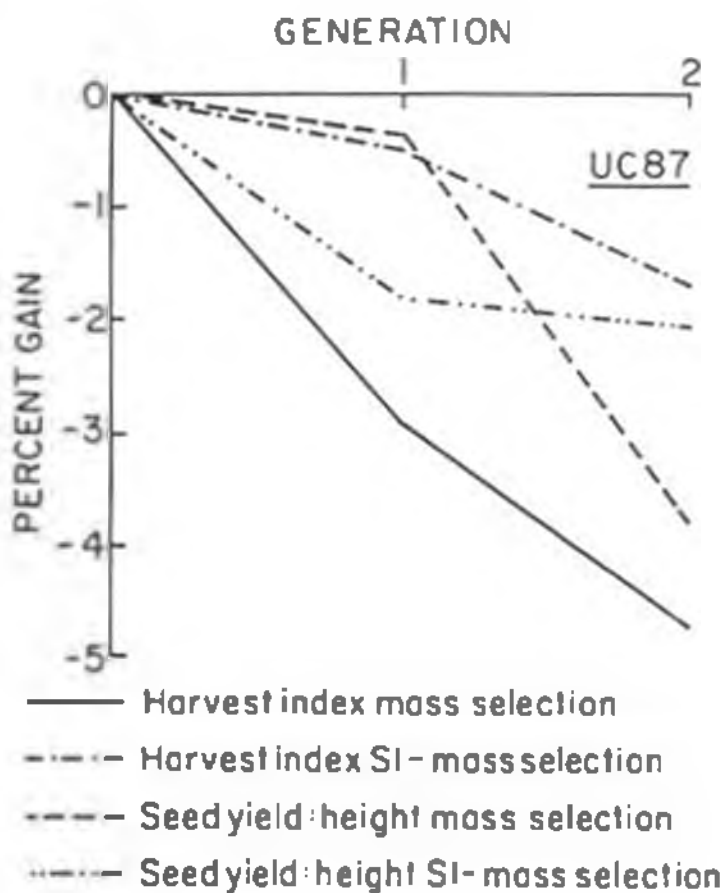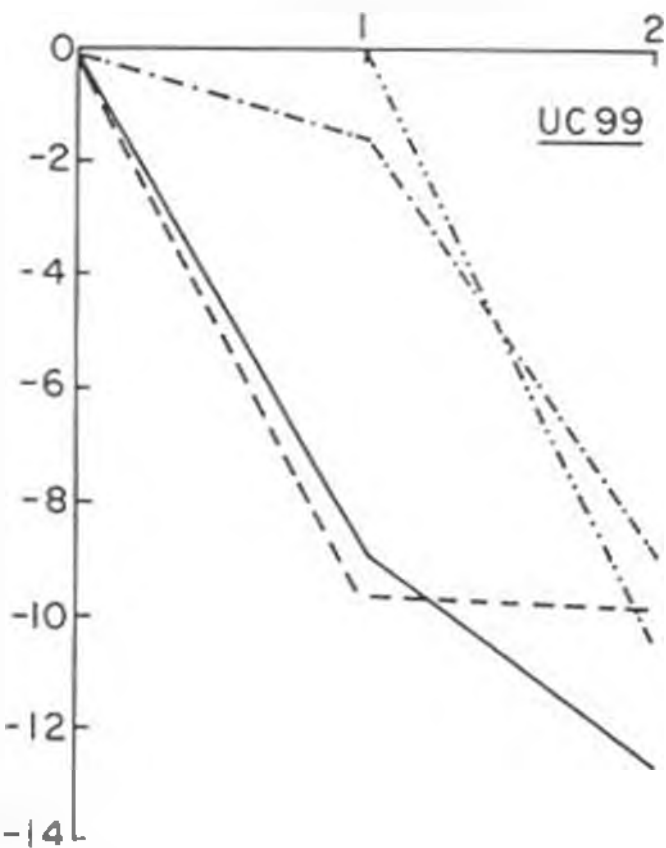
GENERATION

UC 99

Figure 6.   Percentage cumulative indirect selection
gains in seed yield per plant (1984).

PERCENT GAIN

UC 87

UC 99

GENERATION

GENERATION

———— Harvest index mass selection

—·—·— Harvest index SI - mass selection

———— Seed yield height mass selection

···—···— Seed yield height SI - mass selection
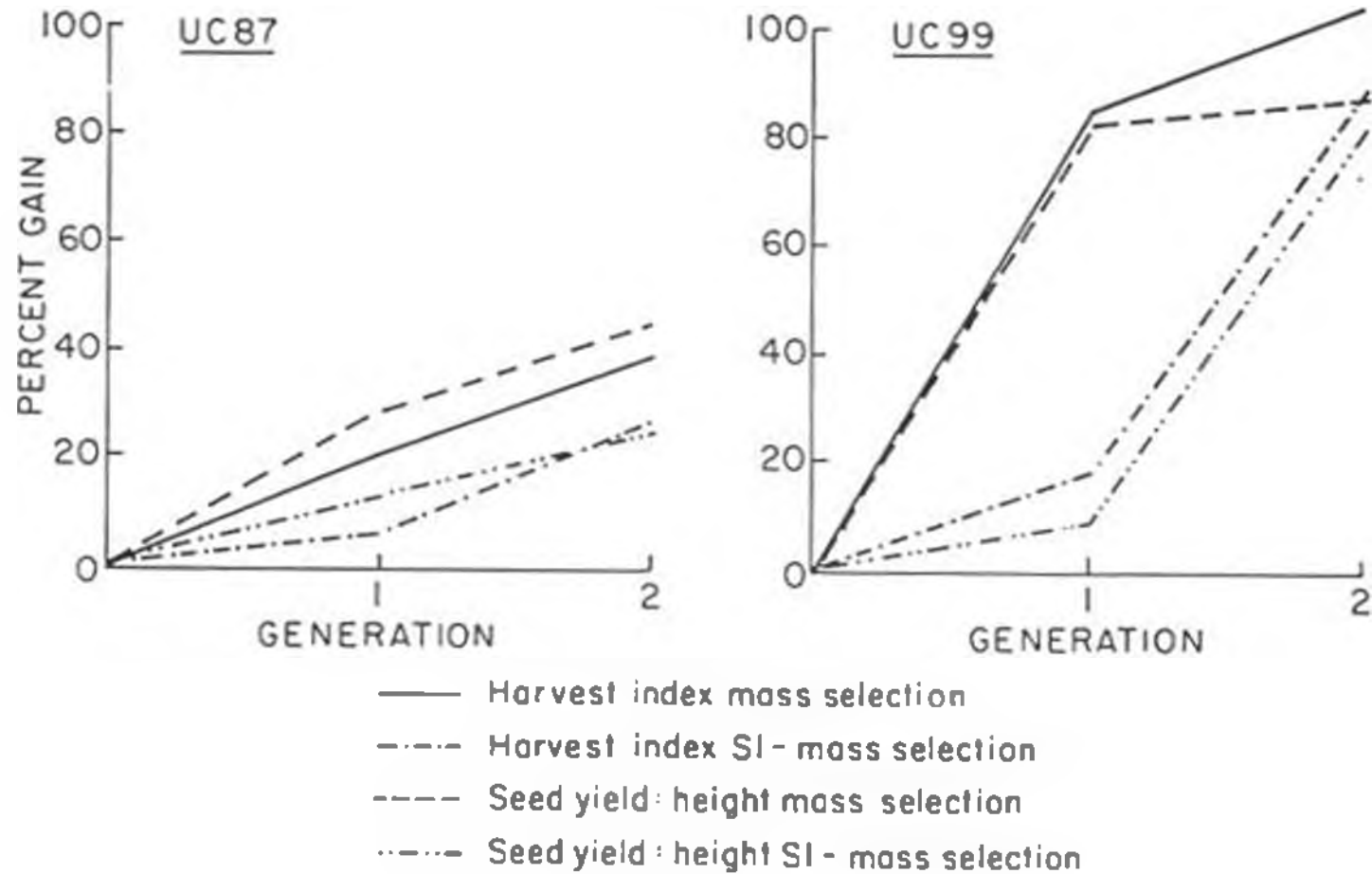
gains in seed yield:height ratio and harvest index when one or the other was selected for.

Only the first and the second generations of straight mass selection for harvest index and the second generation of seed yield:height ratio mass selection flowered significantly earlier than the original population.

B. Indirect Response to Selection in UC99

The analysis of variance among the selections indicated significant differences in all traits except head length (Table 7). With the exception of plant height and plant weight, Duncan's multiple range test placed the selections into two distinct groups; all the S1 selections being grouped together with the control (Figure 3).

Most of the correlated gains were realized in the first generation of mass selection. Along with increased plant size traits there were increased seed production efficiency (Table 8, Appendix 1, Figures 4, 6 and 7). In both cases seed yield:height ratio or harvest index could equally be improved by selecting for one or the other. The most dramatic response was in seed yield per plant which was doubled after two generations of mass selection for harvest index with an average gain of 60.0 percent. Head weight and days to flowering were also significantly changed due to selection for seed yield:height ratio and harvest index (Figures 5 and 7). Cumulative gains in both were largest when mass selection was applied on harvest index.

Phenotypic and Genotypic Correlations

Phenotypic correlation coefficients for the two populations

Figure 7. Percentage indirect selection gains in head
weight and threshing percentage of UC99
(1984).
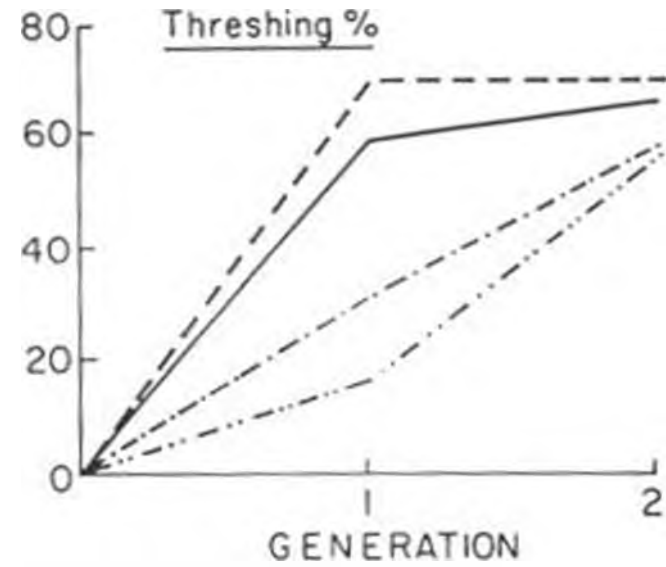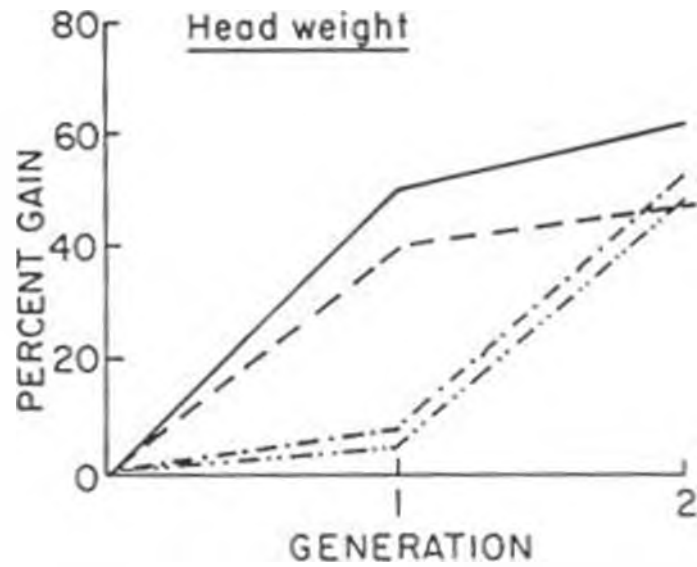
are given in Tables 10, 12 and 13. Genotypic correlations are presented in Table 11. The correlation coefficients were subjected to statistical t tests with $P = 0.05$.

A. Correlations in UC87

In both years plant size traits were strongly and positively correlated among themselves in UC87. With the exception of seed yield:height ratio the seed production efficiency parameters were either negatively or weakly related to plant size traits. For example, heavier plants tended to have low threshing percentages and harvest indices. In 1984 negative association between threshing percentage and plant weight measurements were not statistically significant for the original population. The same was true for the relationships between harvest index and plant size traits. These trends of relationships were maintained in the harvest index selection. Strong associations between seed yield:height ratio and plant size traits indicated that bigger plants were higher yielding. In all cases plant size traits and seed yield:height ratio maintained strong correlations with seed yield per plant with head weight and seed yield:height ratio having the strongest associations. Threshing percentage had no significant correlation with seed yield per plant. Harvest index showed significant but small correlation to seed yield of the original population in 1984 ($r = 0.278$) only. Threshing percentage and harvest index were highly correlated.

Days to flowering had no significant genetic correlation to any trait except seed yield:height ratio, 500 seed weight and harvest index. It tended to be negatively correlated to plant

Table 10. Phenotypic correlations for UC87 and UC99 original populations (1982).

Trait	1	2	3	4	5	6	7	8	9
1 Plant height		0.730	0.728	0.796	-0.268	0.589	0.142^{NS}	-0.446	0.761
2 Plant weight	0.463		0.568	0.833	-0.379	0.611	0.221	-0.533	0.700
3 Head length	0.271	0.409		0.718	-0.280	0.565	-0.035^{NS}	-0.172	0.657
4 Head weight	0.385	0.901	0.603		-0.400	0.788	0.134^{NS}	-0.420	0.858
5 Threshing %	-0.101^{NS}	-0.211	0.288	0.049^{NS}		0.157^{NS}	0.036^{NS}	0.751	0.055^{NS}
6 Seed yield:height	0.212	0.671	0.615	0.898	0.407		0.171	0.033^{NS}	0.967
7 500 seed weight	0.083^{NS}	-0.049^{NS}	-0.145^{NS}	-0.042^{NS}	-0.078^{NS}	-0.038^{NS}		-0.259	0.192
8 Harvest index	-0.138^{NS}	-0.135^{NS}	0.504	0.227	0.872	0.566	-0.074^{NS}		-0.109^{NS}
9 Seed yield per plant	0.330	0.730	0.649	0.932	0.361	0.985	-0.033^{NS}	0.506	

NS, Not significant, P = 0.05

Upper half is UC87
Lower half is UC99

Table 11. Genotypic correlations based on SI family data (1982).

Trait	1	2	3	4	5	6	7	8	9	10
1 Plant height		0.735	0.596	0.623	-0.116^{NS}	0.046	0.209^{NS}	0.376	-0.434	0.574
2 Plant weight	0.674		0.547	0.813	-0.291	0.341	0.169^{NS}	0.145^{NS}	-0.577	0.690
3 Head length	0.375	0.422		0.756	0.113^{NS}	0.537	-0.088^{NS}	-0.207^{NS}	0.090^{NS}	0.772
4 Head weight	0.485	0.870	0.645		-0.051^{NS}	0.738	-0.070^{NS}	-0.170^{NS}	-0.071^{NS}	0.954
5 Threshing %	0.122^{NS}	0.309	0.429	0.529		0.388	-0.175^{NS}	-0.046^{NS}	0.725	0.238^{NS}
6 Seed yield:height	0.127^{NS}	0.610	0.570	0.810	0.755		-0.296	-0.457	0.478	0.832
7 Days to flowering	0.137^{NS}	-0.052^{NS}	-0.746	-0.383	-0.449	-0.489		0.387	-0.405	-0.137^{NS}
8 500 seed weight	0.019^{NS}	0.007^{NS}	-0.274^{NS}	-0.109^{NS}	-0.152^{NS}	-0.077^{NS}	0.273^{NS}		-0.465	-0.189^{NS}
9 Harvest index	-0.099^{NS}	0.130^{NS}	0.597	0.521	0.870	0.741	-0.725	-0.203^{NS}		0.150^{NS}
10 Seed yield per plant	0.405	0.740	0.654	0.937	0.778	0.890	-0.478	-0.133^{NS}	0.732	

NS, Not significant, P = 0.05

UC87 in upper half.
UC99 in lower half.

Table 12. Phenotypic correlations for UC87 original population and harvest index second cycle mass selection (1984).

Trait	1	2	3	4	5	6	7	8	9	10
1 Plant height		0.878	0.684	0.842	-0.228	0.650	-0.165^{NS}	0.662	-0.185^{NS}	0.785
2 Plant weight	0.824		0.733	0.978	-0.172^{NS}	0.836	-0.238	0.641	-0.037^{NS}	0.927
3 Head length	0.533	0.672		0.780	-0.408	0.623	-0.405	0.444	-0.056^{NS}	0.680
4 Head weight	0.719	0.952	0.777		-0.174^{NS}	0.879	-0.264	0.640	0.080^{NS}	0.946
5 Threshing %	-0.087^{NS}	-0.276	-0.344	-0.369		0.112^{NS}	0.240	-0.049^{NS}	0.728	0.082^{NS}
6 Seed yield:height	0.602	0.876	0.672	0.922	-0.086^{NS}		-0.258	0.546	0.378	0.940
7 Days to flowering	0.232	0.012^{NS}	-0.290	-0.142^{NS}	0.137^{NS}	-0.179^{NS}		-0.216^{NS}	0.038^{NS}	-0.242
8 500 seed weight	0.720	0.824	0.679	0.840	-0.178^{NS}	0.766	-0.159^{NS}		0.037^{NS}	0.615
9 Harvest index	-0.255	-0.162^{NS}	0.054^{NS}	-0.006^{NS}	0.550	0.269	-0.356	0.048^{NS}		0.278
10 Seed yield per plant	0.750	0.934	0.714	0.954	-0.127^{NS}	0.970	-0.095^{NS}	0.841	0.153^{NS}	

NS, Not significiant, $P = 0.05$.

UC87 original population in upper half.
UC87 harvest index second cycle mass cycle in lower half.

Table 13. Phenotypic correlations for UC99 original population and harvest index second cycle mass selection (1984).

Trait	1	2	3	4	5	6	7	8	9	10
1 Plant height		0.696	0.550	0.588	0.492	0.569	-0.497	0.500	C.475	0.600
2 Plant weight	0.658		0.426	0.859	0.542	0.838	-0.393	0.571	0.578	0.858
3 Head length	0.312	0.159^{NS}		0.433	0.399	0.448	-0.437	0.401	0.412	0.460
4 Head weight	0.580	0.976	0.212^{NS}		0.643	0.891	-0.480	0.592	0.711	0.902
5 Threshing %	0.052^{NS}	0.331	-0.171^{NS}	0.407		0.816	-0.720	0.826	0.938	0.799
6 Seed yield:height	0.402	0.890	0.065^{NS}	0.944	0.612		-0.578	0.745	0.881	0.997
7 Days to flowering	-0.135^{NS}	-0.400	0.291	-0.413	-0.434	-0.505		-0.671	-0.670	-0.569
8 500 seed weight	-0.094^{NS}	0.248	0.053^{NS}	0.290	0.239	0.296	0.125^{NS}		0.805	0.740
9 Harvest index	0.044^{NS}	0.424	-0.010^{NS}	0.551	0.926	0.732	-0.417	0.311		0.864
10 Seed yield per plant	0.530	0.933	0.132^{NS}	0.972	0.576	0.980	-0.474	0.267	0.691	

NS. Not significant, P = 0.05

Upper half is UC99 original population.
Lower half is UC99 harvest index second cycle mass selectin.

size traits in the original population in 1984. Seed yield per
plant had a small but significant negative correlation with days
to flowering in the original population during 1984. The same
negative associations between plant size traits and days to
flowering was repeated for head length only ($r = -0.290$) in the
harvest index selection. The other correlations were weak except
its correlation to plant height ($r = 0.232$).

The correlations between 500 seed weight and seed yield per
plant tended to follow plant size traits to which it was
positively correlated in 1984. These correlations were not
consistent with 1982 data which were either weak or significant
but smaller. It had significant genetic correlations with plant
height, seed yield:height ratio, days to flowering and harvest
index only.

B.   Correlations in UC99

As can be seen in the lower halves of Tables 10 and 11 and
Table 13, correlations among plant size traits were positive in
UC99 though the magnitudes were lower than those observed for
UC87. In the harvest index selection the correlations between
head length and plant weight and between head length and head
weight were not statistically significant. In this selection
head length was not related to any of the traits except plant
height and days to flowering ($r = 0.312$ and $r = 0.291$ respective-
ly). The rest of the plant size traits had significant associa-
tions with seed yield:height ratio and seed yield per plant in
both years. Seed yield:height ratio also had constant strong
phenotypic correlations to seed yield per plant in all cases ($r >$

0.900). Phenotypic correlations between threshing percentage and plant size traits were less consistent in 1982 than they were in 1984 for the original population. It had strong genetic correlations to all traits except plant height and seed weight. In 1982 it had significant negative and positive phenotypic correlations to plant weight and head length ($r = -0.211$ and $r = 0.288$) respectively. Though it had consistent positive relationships to plant size traits in 1984, its relationships to plant height and head length in the harvest index selection were not significant. In all cases it had positive relationships to seed yield:height ratio, harvest index and seed yield per plant in all cases.

Relationships between days to flowering and other traits show that bigger plants flowered earlier and had higher seed yields. there was no significant genetic relationships between days to flowering and plant height. plant weight and 500 seed weight. Seed weight also had no significant genetic relationship to any trait. However, it had strong phenotypic correlations to all traits in the original population during 1984 season. These relationships were less strong and inconsistent in the harvest index selection.

Stepwise Regression and Path Analysis

A. Stepwise Regression and Path Analysis in UC87

The results of stepwise regression are presented in Table 14. They show that only two traits, plant height and seed yield:height ratio, were responsible for nearly all the variation in UC87 seed yield per plant during 1982 season. Over 90 percent of this variation was attributed to seed yield:height ratio with

Table 14. Stepwise regression for prediction of seed yield in UC87 and UC99.

		UC87		UC99		No. of predictors in the equation
Step	Predictor entered in equation	% Total variation (R^2)	Predictor entered in equation	% Total variation (R^2)	
Original population (1982)						
1	Seed yield:height	93.41	Seed yield:height	97.07		1
2	Plant height	99.06	Plant height	98.62		2
3			Head weight	98.95		3
4			Threshing %	99.15		4
Original population (1984)						
1	Head weight	89.43	Seed yield:height	99.38		1
2	Threshing	95.67	Plant weight	99.53		2
3	Seed yield:height	96.82	Plant height	99.59		3
4	Plant height	97.13	Harvest index	99.62		4
Harvest index M2 (1984)						
1	Seed yield:height	94.21	Seed yield:height	96.14		1
2	Plant height	98.46	Plant height	98.32		2
3	500 seed weight	98.77	Head weight	98.67		3
4	Head weight	98.88	Threshing %	99.00		4

plant height contributing a marginal variation of less than six percent.

The pattern of contribution was not consistently maintained for the original population in 1984. Head weight and threshing percentage contributed 89.43 and 6.24 percent respectively. Seed yield:height ratio and plant height had small marginal effects (marginal R^2 = 1.15 and 0.31 respectively). For the harvest index selection seed yield:height ratio and plant height contributed 98.46 percent with seed yield:height ratio accounting for 94.21 percent of the variation. The 500 seed weight and head weight were the next important predictors (marginal R^2 = 0.31 and 0.11 respectively).

With these major predictors in the equation the three respective prediction equations are as follows:

$Y = -32.53 + 0.189X_1 + 176.20X_4$

$Y + -27.96 + 0.064X_1 + 0.229X_2 + 0.392X_3 + 83.00X_4$

$Y = -28.91 + 0.122X_1 + 0.039X_2 + 177.90X_4 + 24.60X_5$

Where Y = seed yield per plant, X_1 = plant height, X_2 = head weight, X_3 = threshing percentage, X_4 = seed yield:height ratio and X_5 = seed weight.

Path coefficients for UC87 (Table 15 and 16) show that most of the plant height contribution to seed yield per plant was indirect. For example, over a half of its contribution to the seed yield of the original population in 1982 and harvest index selection was through seed yield:height ratio (0.467 and 0.417 respectively). In the original population during 1984 most of its effects were mainly realized through head weight. Most of

Table 15. Direct and indirect path effects of predictor
            variables on seed yield of UC87 original population.

Cause and effect	Path-coefficient
Original population (1982)	
Plant height	
Direct	0.294
Indirect via seed yield:height	0.467
Total	0.761
Seed yield:height	
Direct	0.793
Indirect via plant height	0.173
Total	0.967
Original population (1984)	
Plant height	
Direct	0.110
Indirect via head weight	0.508
Indirect via threshing %	-0.040
Indirect via seed yield:height	0.208
Total	0.785
Head weight	
Direct	0.603
Indirect via plant height	0.092
Indirect via threshing %	-0.030
Indirect via seed yield:height	0.281
Total	0.946
Threshing %	
Direct	0.175
Indirect via plant height	-0.025
Indirect via head weight	-0.105
Indirect via seed yield:height	0.036
Total	0.082
Seed yield:height	
Direct	0.319
Indirect via plant height	0.071
Indirect via head weight	0.530
Indirect via threshing %	0.020
Total	0.940

Table 16. Direct and indirect path effects of predictor variables on seed yield of UC87 second cycle harvest index mass selection (1984).

Cause and effect	Path-coefficient
Plant height	
Direct	0.200
Indirect via head weight	0.077
Indirect via seed yield:height	0.417
Indirect via 500 seed weight	0.055
Total	0.750
Head weight	
Direct	0.107
Indirect via plant height	0.144
Indirect via seed yield:height	0.638
Indirect via 500 seed weight	0.064
Total	0.954
Seed yield:height	
Direct	0.693
Indirect via plant height	0.121
Indirect via head weight	0.099
Indirect via 500 seed weight	0.058
Total	0.970
500 seed weight	
Direct	0.076
Indirect via plant height	0.144
Indirect via head weight	0.090
Indirect via seed yield:height	0.531
Total	0.841

the effects of seed yield:height ratio were direct. However, its effects in the original population during 1984 were mainly via head weight. Head weight effects in the original population were also mostly direct with a little through seed yield:height ratio (0.281). The latter effects were stronger in the harvest index selection. Though threshing percentage had no significant relationships to seed yield per plant it was an important predictor in the original population during 1984 season. Its direct effects were counteracted by negative effects via head weight (-0.105) and plant height (-0.025). Seed weight contribution to the seed yield of harvest index selection was mainly indirect through plant height (0.144) and seed yield:height ratio (0.531).

B.   Stepwise Regression and Path Analysis in UC99

For UC99 seed yield:height ratio was constantly a powerful predictor, contributing not less than 95 percent of the total variation in seed yield per plant. In 1984 it contributed up to 99 percent of seed yield variation in the original population. Other than the original population in 1984 when plant weight was more important (marginal R^2 = 0.15), plant height was the next important predictor. Head weight and threshing percentage were important in 1982 and also for the harvest index selection. Harvest index was important for original population in 1984 with a marginal contribution of R^2 = 0.03.

With these predictors in the equation the three respective equations are:

$$Y = -18.80 + 0.057X_1 + 0.127X_3 + 0.162X_4 + 146.00X_5$$
$$Y = -5.87 + 0.030X_1 + 0.0036X_2 + 224.90X_5 - 13.50X_6$$

$$Y = -35.85 + 0.091X_1 + 0.244X_3 + 0.363X_4 + 103.00X_5$$

Y = seed yield per plant, X_1 = plant height, X_2 - plant weight, X_3 = head weight, X_4 = threshing percentage, X_5 = seed yield:height ratio and X_6 = harvest index.

Path analysis results are presented in Tables 17 and 18. They show that plant height influenced seed yield per plant through head weight and seed yield:height ratio for the 1982 crop and for harvest index selection. In the original population, in 1984, its effects were mainly through seed yield:height ratio. Though head weight affected seed yield of the original population in 1982 mainly through seed yield:height ratio, its effects on seed yield of the harvest index selection were almost equally shared between direct (0.470) and indirect through seed height ratio (0.412). The effects of threshing percentage on grain yield of harvest index selection were realized through three major paths, namely, direct (0.114), through head weight (0.191) and through seed yield:height ratio (0.267). Seed yield:height ratio was the most important indirect path for all the predictors over the two years. Its effects in the original population were mostly direct (0.665 and 1.010 respectively), with some substantial effects (0.269) channelled through head weight in 1982. In the harvest index selection its effects were almost equally shared between direct (0.437) and indirect through head weight (0.444) with small effects through plant height and threshing percentage. Like other predictors, harvest index had large positive effects on seed yield of the original population through seed yield:height ratio. Its direct effects were small and

Table 17. Direct and indirect path effects of predictor
           variables on seed yield of UC99 original population.

Cause and effect	Path-coefficient
Original population (1982)	
Plant height	
Direct	0.082
Indirect via head weight	0.115
Indirect via threshing %	-0.008
Indirect via seed yield:height	0.141
Total	0.330
Head weight	
Direct	0.299
Indirect via plant height	0.032
Indirect via threshing %	0.004
Indirect via seed yield:height	0.597
Total	0.932
Threshing %	
Direct	0.084
Indirect via plant height	-0.008
Indirect via head weight	0.015
Indirect via seed yield:height	0.271
Total	0.361
Seed yield:height	
Direct	0.665
Indirect via plant height	0.018
Indirect via head weight	0.269
Indirect via threshing %	0.034
Total	0.985
Original population (1984)	
Plant height	
Direct	0.041
Indirect via plant weight	0.009
Indirect via seed yield:height	0.575
Indirect via harvest index	-0.025
Total	0.600
Plant weight	
Direct	0.012
Indirect via plant height	0.029
Indirect via seed yield:height	0.846
Indirect via harvest index	-0.031
Total	0.856

Table 17 (continued):

Cause and effect	Path-coefficient

Original population (1984)

Seed yield:height

Direct	1.010
Indirect via plant height	0.024
Indirect via plant weight	0.010
Indirect via harvest index	-0.047
Total	0.997

Harvest index

Direct	-0.053
Indirect via plant height	0.020
Indirect via plant weight	0.007
Indirect via seed yield:height	0.890
Total	0.864

Table 18. Direct and indirect path effects of predictor
variables on seed yield of UC99 second cycle harvest
index mass selection (1984).

	Cause and effect	Path-coefficient
Plant height		
	Direct	0.075
	Indirect via head weight	0.273
	Indirect via threshing %	0.006
	Indirect via seed yield:height	0.175
	Total	0.530
Head weight		
	Direct	0.470
	Indirect via plant height	0.044
	Indirect via threshing %	0.046
	Indirect via seed yield:height	0.412
	Total	0.972
Threshing %		
	Direct	0.114
	Indirect via plant height	0.004
	Indirect via head weight	0.191
	Indirect via seed yield:height	0.267
	Total	0.576
Seed yield:height		
	Direct	0.437
	Indirect via plant height	0.030
	Indirect via head weight	0.444
	Indirect via threshing %	0.070
	Total	0.980

negative. The effects of other predictors through this trait were also small and negative.

DISCUSSION

Quantitative Variation and Response to Selection

This study reveals the presence of exploitable variation in the two amaranth populations, especially UC99 in which broad sense heritability estimates were fairly high. In this population all the traits, except plant weight and head weight, had detectable genetic variation. Though little information is available about its cultivation at the collection site, the heterogeneity of UC99 may be explained by mechanical seed mixing or mixed planting of different cultivars or landraces, a practice which is characteristic of peasant farming. The UC87 population had less variation with an apparent lack of variation for plant height, plant weight, seed yield:height ratio, and seed yield per plant.

Hauptli and Jain (1984) also studied variation for yield related traits in the two populations used in the present study. They noted significant variation for leaf petiole length, plant height, internode length and days to flowering in both populations. The UC87 had no significant variation for seed yield.

Substantial gains from mass and S1 selections in both populations noted in the present study indicate preponderance of additive and additive x additive epistatic effects. This is confirmed by the closeness of expected and observed gains for harvest index S1 selection in UC87. Closeness of realized heritability from mass selection to broad sense heritability also reflects high additive and additive x additive effects for harvest index in UC87. In UC99 realized gains from the first

cycle mass selections were excessively higher than the expected values and the corresponding observed S1 selection gains. This also indicates high additive and additive x additive effects for this population. Such discrepancies may also reflect competition and seasonal effects which are discussed in detail below. Since predominantly selfing species have higher levels of additive and additive x additive than dominance effects (Sprague, 1966; Moll and Stuber, 1974) we can use the results of the present study to speculate that amaranth populations, particularly the landraces which have been shown by allozyme variation analysis to be mixtures of homozygous genotypes, have high levels of additive and additive x additive variation components for most measurement and yield related traits.

Higher realized heritability from S1 selection than from mass selection for seed yield:height ratio and harvest index in UC87 reflects overdominance in the F1. The discrepancy between expected and observed mass selection gains for harvest index could be attributed to inaccurate identification of superior plants due to environmental effects, hence, probable need for S1 testing in this population. Though genotypic variation was masked by large-environment interaction effects, family means were good approximations of family genotypic means, leading to response despite apparent low genotypic variation for some traits. Plot subdivision also increased efficiency of mass selection. In UC99 realized gains from S1 selection were lower than their expected values and the corresponding first cycle mass selection gains. This discrepancy between realized and expected

S1 selection gains may also be explained in terms of underdominance operating in the heterozygous F1 derived by intermating the selected families. Linkage and negative epistasis may lead to an apparent underdominance. This would lead to a lower cumulative gain from S1 and mass selection combination than from two generations of straight mass selection. Underdominance due to linkage may be dissipated by a few generations of controlled intermating before selection is enforced. Miller and Rawlings (1967) reported that up to six generations of intermating were needed to reduce bias in variance components due to linkage in cotton. Furthermore, for proper exploitation of additive and additive x additive effects intermating to obtain desirable linkages is necessary. In contrast to the lower gains from S1 selection, realized heritability from S1 selection was higher than broad sense heritability, reflecting overdominance. These observations may also be due to differences in year effects and genotype competition.

Correlated response depends on the degree of genetic correlation between traits (Falconer, 1981; Hallauer and Miranda, 1981). The correlations and the presence of genetic variation for seed yield:height ratio and harvest index explains the correlated gains for seed yield in UC99. Apparent lack of variation in seed yield:height ratio and seed yield, and weak genotypic correlation between harvest index and seed yield per plant, makes correlated gains for seed yield per plant in UC87 difficult to explain. However, family means might have given a good relative assessment of the family genotypic values despite

large genotype environment interactions. The gridding technique was also able to increase the efficiency of mass selection. It is also hypothesized here that selection for harvest index in this population lead to increased seed yield per plant through seed yield:height ratio. In early generations of selection frequencies of major genes interacting with minor genes to affect morphological traits are also likely to be shifted leading to unexpected correlated changes. Changes in covariation always accompany changes in gene frequencies (Bohren et al., 1966). Such changes may create correlations among traits that were not related in the original population, leading to unexpected corre- lated changes. This may also apply if negative and positive effects of genes that cause covariation lead to no net correla- tions in the original population. Clayton et al. (1957) also observed correlated responses in Drosophila between traits that were originally uncorrelated. The environment masking effects may also be extended to covariation, hence, making correlations and correlated gains misleading.

It is known that an increase in harvest index is accompanied by a higher relative increase in seed yield than in dry matter (Donald and Hamblin, 1976). In this study selection for seed yield:height ratio and harvest index lead to higher relative increase in seed yield than plant size traits. While the two traits have indicated their importance for seed yield improvement they can also be improved by selecting for one or the other. This is explained by their genetic association that lead to the large correlated gains.

(1958) illustrated that mass selection is superior to progeny testing selection methods at high heritability values. Following studies on sorghum Doggett (1968) suggested that mass selection may be relatively more efficient than progeny testing selection if one crop is grown per year and facilities are limited. Based on the amount of additive variance to the number of generations per cycle, Empig et al. (1972) also showed in mathematical terms that mass selection would be more efficient. However, if heritability is low progeny testing selection becomes more efficient.

Other than environmental effects masking the genotypic variation, hence low or no heritability for most traits in UC87, sample size of eight plants per family was too small to make the experiment sensitive enough to expose the full variation. The higher the number of individuals contributing to the family mean the closer does the mean approach the genetic merit of the family (Lerner, 1958). The 48 families were also too few to be representative enough to reveal the full variation in a less heterogeneous population like UC87. Inadequate population sampling fails to expose complete variation and may lead to negative variance estimates (Hallauer and Miranda, 1981). The conflicting estimates may also be due to seasonal differences. Selection differentials and gains were obtained in different years. A comparison between original population means in 1982 and 1984 shows large differences between the two years.

Apart from underdominance and environmental effects a number of explanations may also be given for the large differences between observed and expected mass selection gains, and between

observed S1 and mass selection gains for UC99. Since UC99 was a mixture of two plant types mass selection simply sorted the superior faster growing type from the population. The superior type was underrepresented by only two families among the 48 families. However, their progenies comprised the bulk of plants advanced by mass selection from S1 selections. This is also evidence that small population size affected the S1 and mass selection combination more seriously than the straight mass selection in the two populations. Effective population size has been discussed by Kojima (1961), Bliss and Gates (1968), Baker and Curnow (1969) and Rawlings (1970, 1980) as a serious limitation to selection gains. A recent study by Vaidya and Jain (1984) also indicated restricted response to mass selection in grain amaranths due to small population size. In the present study only seven families and 21 plants were selected for each S1 and mass selections respectively. Baker and Curnow (1969) and Rawlings (1970) recommended an effective population size of 30 to 45 with an intensity of 10 percent to avoid undue restriction to selection response. The S1 selection might have suffered a greater bottleneck due to small effective population size leading to a lower cumulative response from the S1 and mass selection combination.

Intergenotypic competition is another factor that could lead to large responses in the heterogeneous UC99. The fast growing plants would suppress the slow growing plants in the original population and in the S1 selections. This would happen within and between selections due to neighbor effect. This would lead

to reduced performance in the original population and the S1 selections, resulting in the dramatic response obtained in mass selections in which the majority of plants shifted to the faster growing, higher yielding type. Graham and Lessman (1966) and Hamblin and Donald (1974) considered this nature of competition between short and tall plants in sorghum and barley respectively.

One of the UC99 mixture components was less adapted due to slow growth, late flowering and susceptibility to Phythium. Wide variation in adaptation in this population is also postulated here as being responsible for the higher observed selection gains as compared to UC87. The UC87 was better adapted with less variation with respect to its adaptation. However, adaptation of UC99 was much improved after one generation of mass selection, leading to the observed dramatic selection gains.

Improved adaptation of UC99 after one generation of mass selection and high degree of homozygosity can be used to explain the reduced gains from the second cycle of mass selection. In this study UC99 wa estimated to have a low outcrossing rate or 0.085. Jain et al. (1982) also reported low outcrossing rates for other A. hypochondriacus populations ranging from 0.035 to 0.14. Such low outcrossing rates result in high degree of homozygosity. In such a case only one generation of mass selection may lead to significant reduction in variation, hence reduced response to subsequent selections. Shifts in frequencies of major genes affecting morphological traits may also have a share in such changes. Thus, response in UC99 is a result of interaction of heterogeneity, natural selection, small effective

population size and high selfing rate.

Correlations and Yield Prediction

The correlation coefficients show that bigger plants had higher seed yield:height ratio and higher seed yields in both populations. In an earlier study on a population of A. cruentus Hauptli and Jain (1980) also found taller plants to be higher yielding than the shorter ones. Increased seed production in bigger plants may be as a result of increased foliage and vegetative parts to support higher seed yield, hence improved source-sink relationships. It is known that dry matter and leaf area are positively related and both relate positively to seed yield (Yap and Harvey, 1972; Thurling, 1974).

The plant size relationships to threshing percentage in UC87 show that as plant size increased the amount of recoverable grain relative to head size decreased. The negative relationships between head size and threshing percentage probably lead to compensating effects on the relationship between threshing percentage and seed yield per plant, leading to the latter relationship being insignificant. Low genotypic correlations between plant size traits and threshing percentage in this population suggest large environmental effects on these covariations. Adams (1967) and Puri et al. (1982) also noted that the plasticity of morphological traits lead to high environmental influence on their covariations. In UC99 higher relative increase in recoverable seed in the head accompanying increased plant size lead to consistent positive relationship between threshing percentage and seed yield per plant.

Harvest index relationships to plant size traits in UC87 indicate that a relatively higher proportion of metabolites was used for vegetative growth than for seed development. While it is normal for bigger plants to have lower harvest indices lack of correlation between plant size and harvest index is known in mixed populations (Donald and Hamblin, 1976). In such a situation effects of genes responsible for positive correlation may be balanced by those responsible for negative correlation. Lower proportional increase in seed yield as compared to increased dry matter is also likely to happen when plants have less stress and competition for resources. Wide within row spacing of 15 cm used in this experiment as compared to closer spacing of 3 cm current- ly recommended for amaranth cultivation is equivalent to low competition conditions. This is comparable to a recent study by Cavagnaro and Jain (ms submitted) who noticed that UC87 had high harvest index under high water stress levels, indicating that in the absence of stress relatively more metabolites were used for vegetative growth than for seed development.

Constant positive relationships between harvest index and seed yield per plant in UC99 indicated that bigger plants did not have their seed yields offset by higher dry matter yields. This applied to the less branched plants which comprised the majority of plants in the population. Highly branched plants had low harvest indices. Similar relationships were reported for grain amaranths by Hauptli and Jain (1978). The strong consistent relationships between harvest index and threshing percentage along with its relationships to head size indicates that as head

size increased a higher proportion of this increase was due to recoverable seed. These relationships make harvest index a favorable selection criterion in UC99.

Relationships involving days to flowering in UC87 show that environment had more influence on it than genetic effects. This makes it an unreliable trait to use for seed yield improvement. However, phenotypic correlations in the original population during 1984 season show that early plants were bigger and higher yielding. The positive genetic relationship between days to flowering and 500 seed weight in this population probably reflects that earlier plants would have higher seed set and, hence, lower seed weight. This is looked at from the point of view of negative relationships between seed number and seed weight known in other crops (Jan-orn et al., 1976; Rao and Ramachandram, 1977; Ayiecho and Onim, 1983). However, this relationship was not reflected in the phenotypic correlations in 1984. Days to flowering seems to be a more useful trait in UC99 than in UC87 because of its stronger negative relationships to the seed production efficiency parameters. Early plants were probably higher yielding because they had enough time for head component development before day length and temperatures changed towards the end of summer season.

An interesting observation was made on the relationship of head length to other traits in UC99. In the original population it had strong relationships to most traits. However, in the harvest index selection it had no relationship to any trait except plant height and days to flowering. This change may be

associated with changes in gene frequencies of major genes that influence head development and other morphological traits.

Correlation coefficients in conjunction with stepwise regression analyses indicate that the best predictors for seed yield per plant in both populations were constantly plant height and seed yield:height ratio. Plant height had been noted in a stepwise regression analysis by Hauptli and Jain (1984) to be one of the best amaranth grain yield predictors. Taller plants have advantage over shorter ones in heterogeneous populations (Graham and Lessman, 1966; Hamblin and Donald, 1974; Wilcox and Schapaguh, 1980). Graham and Lessman (1966) pointed out that differences between yields of short and tall plants is due to differences in micro-environment around the tall and short plants. In breeding programs it is not a good approach to increase plant seed yield by increasing height since this leads to lodging and harvesting problems. It would probably be a better approach to employ dwarfing genes and make height more uniform. One UC99 family was noticed to be segregating for dwarfing genes which could be used to reduce plant height.

Harvest index was another important predictor, particularly for UC99 original population during 1984 season. Harvest index and seed yield:height ratio could be considered as similar traits for assessing plant productivity. This is supported by closeness of their direct and indirect responses when one or the other is selected. The patterns of their relationships to other traits suggest that they may be under slightly different but interacting genetic controls. The components of these ratios, plant height

and plant weight, may be affected by genes with varying degrees of pleiotropism. Path effects for UC99 in 1984 show that harvest index had small but compensating effects for seed yield:height ratio. Literature shows that seed yield:height ratio has never been considered as a potential for plant yield improvement. The present study suggests that it is a ratio worth considering just as much as harvest index which has received much attention recently in plant breeding.

Another common predictor for seed yield per plant except in two cases was head weight (Table 14). Importance of head size has been illustrated in a parallel experiment which yielded significant indirect response to visual mass selection for yield, with a shift toward larger heads (unpub. data of S. K. Jain and D. Bryant). In the present study head weight and seed yield:height ratio had complementary effects in nearly all cases, though the magnitudes of their complementarity varied to some degree (Tables 15 to 18). The most striking of such complementarity was noted for the harvest index selection of UC99 in which the path effects of the two traits were almost equally shared between direct and reciprocal indirect effects. Compensating effects between head weight and threshing percentage noticed for UC87 in 1984 (Table 15) and varied magnitudes of their direct and reciprocal indirect effects on seed yield (Tables 17 and 18) are undesirable. It is known that component compensation will lead to improvement of one trait at the expense of others (Adams, 1967; Adams and Grafius, 1971; McNeal et al. 1978). The correlations between the two traits were also quite

inconsistent in UC87, indicating a large degree of environmental influence. Head weight increase is expected to lead to high seed yield per plant because it contains fertility factor and seed weight which are some of the important plant yield components. Though seed weight relationships to head weight and seed yield were highly inconsistent it was an important predictor for grain yield of harvest index selection in UC87.

Plant weight was an important predictor for the seed yield of the original population in 1984. Its influence may be connected with that of plant height.

Concluding Remarks and Suggestions for Further Studies

The results of this study showed clearly that mass selection can be used to improve amaranth populations more effectively than SI selection. The two populations were shown to have enough variability for improvement by mass selection if adequate population size is used. Gains from selection suggest presence of exploitable additive and additive x additive genetic effects. Signs of overdominance and underdominance in the SI selections in these populations indicate that before prolonged selection is carried on amaranth populations controlled intermatings for a few generations may be necessary to increase frequencies of desirable linkages.

This has been the first attempt in grain amaranths to uncover genetic components. The problem of components of genetic variation was not clearly solved by the design used here because of the conflicts between high realized heritability from SI selection and low realized gains from SI selection as compared to

high realized gains from mass selection, especially in UC99.
There were also conflicts between lack of genetic variation and
large realized gains in UC87. However, the results of this study
are encouraging and motivating for further investigations. For
such investigations to be fruitful better designs like diallel
cross method with adequate sampling are to be suggested for
further studies. Though there are plans to proceed with selec-
tion the selection evaluation experiments need to be repeated to
confirm the responses, especially in UC87.

Determination of which traits to employ for amaranth seed
yield improvement was one the objectives of this study and a
previous one by Hauptli and Jain (1984). While traits like leaf
length, node number, plant height and days to flowering had been
shown by Hauptli and Jain (1984) as some of the important seed
yield predictors, the present study has expanded the choice of
traits in amaranth breeding, adding seed yield:height ratio, head
weight, threshing percentage and harvest index to the list.
Plant weight and seed weight may also be considered. The
inconsistency of some relationships involving threshing
percentage and 500 seed weight sets questions of environmental
effects which need to assessed in some detail. Such studies on
environmental effects should consider temperature and day length
responses in amaranth populations. These responses are currently
believed to be some of the factors leading to eratic changes in
amaranth performance in Davis. The genetics of these responses
need to be properly understood. Photoperiod studies by Jain,
Hauptli, and Kulakow (unpublished) indicated that amaranth

populations responded differently to day length and temperature treatments. Cavagnaro and Jain (ms submitted) have shown that varying supply of water can have substantial effects on amaranth performance, affecting both dry matter and seed yields. To reach valid conclusions on amaranth yield predictors replicated experiments over environments are necessary. This may solve the problems noticed in this study, namely, lack of genotypic variation as opposed to strong genotypic correlations and strength of some traits as seed yield predictors.

REFERENCES

Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to field bean, Phaseolus vulgaris. Crop Sci. 7:505-510.

Adams, M. W. and J. E. Grafius. 1971. Yield component compensation: alternative interpretations. Crop Sci. 11:33-35.

Allard, R. W. 1960. Principles of Plant Breeding. Wiley, New York and London.

Ayiecho, P. O. and J. M. F. Onim. 1983. Correlations between yield and malting quality in barley. Ind. J. Agric. Sci. 13:342-346.

Baker, L. H. and R. N. Curnow. 1969. Choice of population size and use of variation between replicate populations in plant breeding selection programs. Crop Sci. 9:555-560.

Betschart, A. A., D. W. Irving, A. D. Shepherd, E. L. Wheeler, and R. M. Saunders. 1979. Nutritional studies on Amaranthus hypochondriacus and its milling fractions. Proc. 2nd Amaranth Conf. Rodale Press, Emmaus. p. 59-60.

Bliss, F. A. and C. E. Gates. 1968. Directional selection in simulated populations of self-pollinated plants. Aust. J. Biol. Sci. 21:705-719.

Bohren, B. B., W. G. Hill, and A. Robertson. 1966. Some observations on assymetrical correlated responses to selection. Genet. Res. 7:44-57.

Brim, C. A. and C. W. Stuber. 1973. Application of genetic male sterility to recurrent selection schemes in soybeans. Crop

Sci. 13:528-530.

Carlsson, R.   1979.   Quantity and quality of <u>Amaranthus</u> grain
from plants in temperate, cold and hot, and subtropical
climates--a review.   Proc. 2nd Amaranth Conf.   Rodale Press,
Emmaus.   p. 48-58.

Clayton, G. A., G. R. Knight, J. A. Morris, and A. Robertson.
1957.   An experimental check on quantitative genetic theory.
III.   Correlated responses.   J. Genet. 55:171-180.

Doggett, H.   1968.   Mass selection systems for sorghum.   Crop
Sci. 8:391-392.

Doggett, H. and S. A. Eberhart.   1968.   Recurrent selection in
sorghum.   Crop Sci. 8:119-121.

Donald, C. M. and J. Hamblin.   1976.   The biological yield and
harvest index of cereals as agronomic and plant breeding
criteria.   Adv. Agron. 28:361-405.

Donald, C. M. and J. Hamblin.   1983.   The convergent evolution of
annual seed crops in agriculture.   Adv. Agron. 36:97-143.

Draper, N. and H. Smith.   1981.   Applied Regression Analysis.
2nd ed. Wiley, New York.

Dudley, J. W. and R. H. Moll.   1969.   Interpretation and use of
estimates of heritability and genetic variances in plant
breeding.   Crop Sci. 9:257-262.

Early, D.   1977.   Cultivation and uses of amaranth in
contemporary Mexico.   Proc. 1st Amaranth Seminar, July 29,
1977.   Maxatawny, PA.

Eckebil, J. P., W. M. Ross, C. D. Gardner, and J. W. Maranville.
1977.   Heritability estimates, genetic correlations and

predicted gains from S1 tests in three sorghum random mating
populations. Crop Sci. 17:373-377.

Empig, L. T., C. O. Gardner, and W. A. Compton. 1972.
Theoretical gains from different population improvement
procedures. Univ. Nebraska Agric. Expt. Station Bull. MP26.

Engledow, F. L. and S. M. Wadham. 1923. Plant characters on
yield. J. Agric. Sci. 13:390-439.

Falconer, D. S. 1981. Introduction to Quantitative Genetics.
2nd ed. Longman, London and New York.

Feine, L. B. 1979. An ethnobotanical observation and collection
of grain amaranth in Mexico. Proc. 2nd Amaranth Conf.
Rodale Press, Emmaus p. 111-116.

Fisher, R. A. and F. Yates. 1963. Statistical Tables for
Biological, Agricultural and Medical Research. 6th ed.
Hafner, New York.

Gardner, C. O. 1961. An evaluation of effects of mass selection
and seed irradiation with thermal neutrons on yield of corn.
Crop Sci. 1:241-245.

Graham, D. and K. J. Lessman. 1966. Effects of height on yield
components of two isogenic lines of Sorghum vulgare. Pers.
Crop Sci. 6:372-374.

Hadley, H. H., J. E. Freeman, and E. Q. Javier. 1965. Effects
of height mutants on yield in sorghum. Crop Sci. 5:11-14.

Hallauer, A. R. and J. B. Miranda. 1981. Quantitative Genetics
in Maize Breeding. Iowa State Univ. Press, Ames.

Hamblin, J. and C. M. Donald. 1974. The relationships between
plant form, competitive ability and grain yield in a barley

cross. Euphytica 23:535-542.

Hauptli, H. and S. K. Jain. 1978. Biosystematics and agronomic
potential of some weedy and cultivated amaranths. Theor.
Appl. Genet. 52:177-185.

Hauptli, H.and S. K. Jain. 1980. Genetic polymorphisms and
yield components in a population of amaranth. J. Hered.
71:290-292.

Hauptli, H. and S. K. Jain. 1984. Genetic structure of
landrace populations of New World grain amaranths.
Euphytica (in press).

Hauptli, H. and S. K. Jain. 1985. Genetic variation in
outcrossing rate and correlated floral traits in a popula-
tion of grain amaranth. Genetica (in press).

Hauptli, H., R. L. Lutz, and S. K. Jain. 1979. Germplasm
exploration in Central and South America. Proc. 2nd
Amaranth Conf. Rodale Press, Emmaus. p. 117-122.

Jan-orn, J., C. O. Gardner, and W. M. Ross. 1976. Quantitative
genetics of NP3R random mating grain sorghum population.
Crop Sci. 16:489-496.

Jain, S. K., H. Hauptli, and K. R. Vaidya. 1982. Outcrossing
rate in grain amaranths. J. Hered. 73:71-72.

Jain, S. K., K. R. Vaidya, and B. D. Joshi. 1979. Collection
and evaluation of Indian grain amaranths. Proc. 2nd
Amaranth Conf. Rodale Press, Emmaus. p. 123-128.

Jain, S. K., L. Wu, and K. R. Vaidya. 1980. Levels of
morphological and allozyme variation in Indian amaranths: a
striking contrast. J. Hered. 71:283-285.

Kojima, K. 1961. Effects of dominance and size of population on
    response to mass selection. Genet. Res. 2:177-188.

Lerner, I. M. 1958. The Genetic Basis of Selection. Wiley, New
    York and London.

Li, C. C. 1975. Path Analysis, A primer. Pacific Grove,
    California, Boxwood Press.

Matzinger, D. F. 1963. Experimental estimates of genetic
    parameters and their applications in self-fertilizing
    plants. In Hanson, W. D. and Robinson, H. F. (ed). Statis-
    tical Genetics and Plant Breeding. Publ. 982. Nat. Acad.
    Sci., Nat. Res. Council. Washington D.C. p. 253-276.

McNeal, F. H., C. O. Qualset, D. E. Baldridge, and V. R. Stewart.
    1978. Selection for yield and yield components in wheat.
    Crop Sci. 18:795-799.

Miller, P. A. and J. O. Rawlings. 1967. Breakup of linkage
    blocks through intermating in a cotton breeding population.
    Crop Sci. 7:199-204.

Moll, R. H. and C. W. Stuber. 1974. Quantitative
    genetics--empirical results relevant to plant breeding.
    Adv. Agron. 26:277-314.

Neter, J. and W. Wasserman. 1973. Applied Linear Statistical
    Models. Irwin, Homewood.

Park, D. R., E. Reinbergs, and L. S. P. Son. 1977. Grain yield
    and its components in spring barley under row and hill plot
    conditions. Euphytica 26:521-526.

Puri, Y. P., C. O. Qualset, and W. A. Williams. 1982.
    Evaluation of yield components as selection criteria in

barley breeding. Crop Sci. 22:927-931.

Rao, V. R. and M. Ramachandram. 1977. An analysis of
    association of components of yield and oil in safflower
    (Carthamus tinctorius L.). Theor. Appl. Genet. 50:185-191.

Rawlings, J. O. 1970. Present status of research on long- and
    short-term recurrent selection in finite populations--choice
    of population size. Proc. 2nd Meet. Work. Group Quant.
    Genet., Sec. 22. I.U.F.R.O., Raleigh, N.C. p. 1-15.

Rawlings, J. O. 1980. Long- and short-term recurrent selection
    in finite population--choice of population size. In Corbin,
    F. T. (ed.), Proc. World Soybean Res. Conf. II. Westview
    Press, Boulder.

Sanchez-Marroquin, A., S. Maya, and J. L. Perez. 1979.
    Agroindustrial potential of amaranth in Mexico. Proc. 2nd
    Amaranth Conf. Rodale Press, Emmaus. p. 95-104.

Sauer, J. D. 1950. The grain amaranths: a survey of their
    history and classification. Ann. Missouri Bot. Garden
    37:561-619.

Sauer, J. D. 1967. The grain amaranths and their relatives. A
    revised taxonomy and geographic surveys. Ann. Missouri Bot.
    Garden 54:103-137.

Senft, J. 1979. Protein quality of amaranth grain. Proc. 2nd
    Amaranth Conf. Rodale Press Emmaus. p. 43-47.

Simmonds, N. W. 1979. Principles of Crop Improvement. Longman,
    London and New York.

Singh, J. D. and N. C. Stoskopf. 1971. Harvest index in
    cereals. Agron. J. 63:224-226.

Sprague, G. F. 1966. Quantitative genetics in plant
    improvement. In Frey, K. J. (ed.), Plant Breeding. Iowa
    State Univ. Press, Ames. p. 315-347.

Theisen, A. A., E. G. Knox, F. L. Mann and H. B. Sprague. 1978.
    Possibility of introducing food crops better adapted to
    environmental stress. Washington D.C. Nat. Sci. Founda-
    tion, Report No. NSF/RA-780038.

Thurling, N. 1974. Morphological determinants of yield in
    rapeseed. (Brassica campestris and B. napus). I. Growth
    and morphological characters. Aust. J. Agric. Res. 25:697-
    710.

Vaidya, K. R. and S. K. Jain. Response to mass selection
    for agronomic characters in amaranth. Submitted to Zeitsch.
    Pflanzenz.

Wilcox, J. R. and W. T. Schapaugh. 1980. Effectiveness of
    single plant selection during successive generations of
    inbreeding in soybeans. Crop Sci. 20:809-811.

Wright, S. 1921. Correlation and causation. J. Agric. Res.
    20:557-585.

Yap, T. C. and B. L. Harvey. 1972. Inheritance of yield
    components and morphological traits in barley, Hordeum
    vulgare L. Crop Sci. 12:283-286.

Appendix 1. Percentage gains from S1 selection for plant weight (UC87) and days to flowering (UC99).

	Plant height	Plant weight	Head length	Head weight	Threshing %	Seed yield:height	Days to flowering	Harvest index	Seed yield per plant
UC87									
Plant weight S1	1.6	15.4*	0.0	13.9	3.6	20.4	-0.3	3.4	18.0
UC99									
Days to flowering S1	4.3	3.4	11.0	7.4	1.9	11.3	-2.1*	20.7	12.0

* Direct selection gain.