OUTCROSSING AND YIELD PREDICTION STUDIES IN GRAIN AMARANTHS

BY

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DECLARATION

(a) This thesis is my original work and has not been presented for a degree in any other University.

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ABSTRACT

Outcrossing and yield prediction studies were conducted in four populations of grain amaranth, populations 1008 and 1024 (*A. hypochondriacus*) and 1034 and 434 (*A. cruentus*). The studies were conducted at Kabete Campus of the University of Nairobi and National Hortcultural Research Station, Thika during the long rains and the short rains of 1988. A two-replicate alternate-row method where dominant red pigmention parent was planted in the centre with the recessive green pigmentation parent on either side was used. Both intraspecific and interspecific outcrossing rate estimates were determined and utilized to describe the breeding system of grain amaranth species (*A. hypochondriacus* and *A. cruentus*). Quantitative traits, plant height, head length of the mature plant, seed yield per plant, sun dried head weight of the mature plants, days to flowering and days to maturity were used to determine yield predictors in the four grain amaranths.

High intraspecific and interspecific outcrossing rate variations were noted in both the two species with a high ability to outbreeding exhibited by *A. cruentus*. Intraspecific outcrossing rate for the two species oscillated around 10 per cent with interspecific outcrossing rate of about 3.87 per cent. There was sufficiently very high locational and seasonal variations for the outcrossing rate estimates. The probable factors contributing to the variations were believed to be locational, seasonal and pollinator density variations, and genetic structural differences alongside genotype x environment interaction.

Multiple regression and multiple correlation analyses showed that plant height and head length were constantly strongly correlated to seed yield per plant. Head weight offered good prediction levels for seed yield for the

four populations. Days to flowering and days to maturity did insignificantly correlate to seed yield per plant for most of the analyses hence were not regarded important yield predictor variable in the present study.LSD$_{0.05}$ of the means for the six quantitative traits investigated showed variation between the means of the two seasons for some of the traits and variation between the means of the two locations for the four populations used in the present study. Outcrossing and correlation analyses indicated that breeding system of grain amaranths requires further research for the establishment of mating system that would exploit natural pollination for the crop improvement and development.

CHAPTER 1

INTRODUCTION

The grain amaranths, described to have originated in the Central and South America (Sauer, 1977; Grubben and Stolen, 1981) and Guatemala (Sauer, 1950) belong to the Amaranthaceae family which has at least 60 species. It is difficult to ascertain precisely the origin of the various species of the cultivated amaranths because the wild ancestors are pantropical and cosmopolitan weeds (Grubben and Stolen, 1981). Though the grain amaranth was once a major food crop in Central and South American countries it has been neglected probably due to its substitution with other grain crops like maize. The production of the crop was also suppressed by Spanish conquerors in Mexico because it was associated with pagan ceremonies (Sauer, 1950).

There is revived interest in this crop because of its high leaf and seed protein content, nutritious amino acid complement and high digestibility of its protein, possession of the C_4 photosynthetic pathway and the availability of domesticated types with favourable crop morphology (Lexander, 1970; Ruttle, 1976; and Marx, 1977). Compared to the other grain crops, the grain amaranths show superior nutritional traits. The leaves and the seeds have high quality protein with very high lysine and sulfur-containing amino acids which are limiting in both maize and legumes. Therefore it has a potential as a promising cultivated crop and as an organism for genetic and physiological studies. The grain amaranth is useful for genetic studies because of the ease of cultivation, the ability to produce large quantities of seed, and the

existence of three cultivated species (*Amaranthus hypochondriacus*, *A. cruentus* and *A. caudatus*) as well as many related weed species (Kulakow *et al*, 1985). The grain amaranth is also desirable for its wide adaptability coupled with drought tolerance and suitability for marginal areas. Grain amaranths have been described as a potential health food and cash crop on marginal lands (Ayiecho, 1985). Currently, projects have been initiated to improve the crop with respect to varietal development, cultural optimization, harvesting and seed cleaning, uses and market strategy, genetic studies, germplasm collection, agronomic practices, yield and nutritional quality (Kauffman, 1979; Ayiecho, 1985; Gudu and Gupta, 1988a).

Most of the known species of the genus *Amaranthus* are the weedy types. However there are a few cultigens. The weedy types are basically used as pot-herbs in West Africa, India, Taiwan, parts of China and Phillipines. The grain amaranths are grown in India, Central America and Andean region (Sauer, 1977; Grubben and Stolen, 1981). The grain amaranths can be used as breakfast cereal or as ingredients in confectionary biscuits, cakes, candy, flour for making bread and cookies, tortillas, pasta and martapans. The seed can also be popped and consumed directly or used to make candy (Ayiecho *et al*, 1989). The stem can be used for making soups vegetable and leaf protein concentrate.

The present study was prompted by the fact that, the genus *Amaranthus* shows wide variation within and across species (Hauptli and Jain, 1985). This called for studies to understand and appreciate the range of variation in the breeding system of the crop. The breeding system of this crop appears to be very variable, ranging from complete selfing to very high outcrossing rates (Pal, 1972; Simmonds, 1979; and Hauptli and Jain, 1985). The outcrossing rates in this crop have not yet properly been established and documented as

has been done for other crops.

The objectives of the study were as follows:

1. To Estimate intraspecific and interspecific outcrossing rates in grain amaranths by using two populations of A. cruentus and two populations of A. hypochondriacus.

2. To conduct yield prediction studies in grain amaranths by using two populations of A. cruentus and two populations of A. hypochondriacus.

CHAPTER 2

REVIEW OF LITERATURE

2.1.1. Mating system studies in often cross-pollinated crops

Cotton (*Gossypium* spp) and sorghum (*Sorghum* spp) have been classified as often cross-pollinated crop plants (Allard, 1960; and Simmonds, 1979). They are, however, highly self-fertile.

Pope *et al* (1944), using genes for green and red leaf pigmentation in Upland cotton, found natural crossing to occur at distances of upto 1.29 km to leeward, though the amount was only 0.02 per cent as compared with 20.36 per cent within the main field. In a study by Love (1934) percentages of interspecific natural crossing of domestic and introduced cottons in several locations in China following emasculation varied from 1.0 to 27.2 per cent. Afzal and Khan (1950a) also studied natural crossing in *G. hirsutum* and *G. herbaceum* cottons under Punjab conditions, using varieties with marker characters. Percentages of interspecific cross-pollination were less than 1 per cent in each species. In another study Afzal and Khan (1950b) found that the extent of natural crossing in a nursery in which progenies of different strains of cotton were grown side by side approximated 2.0 per cent. Insects of the order Hymenoptera were found to be active pollinators in the Punjab area for two consecutive seasons.

Simpson (1948) indicated that the good yields and wide adaptability of many commercial cotton varieties were partly due to their appreciable heterozygosity maintained by cross-pollination. It also appears that much progress may be made in cotton improvement by intervarietal crossing and subsequent selection. Progeny-selection methods (replicated progeny-row

method of Hutchinson and Panse, mass-pedigree selection and bulked progeny-test selection) and backcrossing have been suggested for cotton improvement (Hutchinson and Manning, 1951).

Inbreeding has been noted to explain yield reduction in cotton (Richmond, 1951). He suggested the following factors as contributing or related to reduction of productivity due to inbreeding

(1) the degree of heterogeneity of the original parent stock

(2) the improbability of accumulating and holding all or most of the favourable yield genes in one homozygous line

(3) mechanical mixtures and cross-pollination with inferior varieties and

(4) selection for one or few characters without regard to other important characters in the genetic complex.

The amount of cross-pollination in sorghum and its various types has been reported to vary widely (Hays et al., 1955). For example outcrossing rate ranging from 0.6 to 50 per cent has been found to occur between adjacent rows by several workers, (Hogg and Ahlgren, 1943; Garber and Atwood, 1945). Crossing of 10 to 20 per cent are quite common. In a study on outcrossing rate in Sudan grass by Garber and Atwood (1945) alternated rows of red and tan pigmented strains were seeded 30.48 cm to 76.2 cm apart. Natural crossing was determined by the proportion of red segregates from tan (recessive) plants. Percentages of natural crossing in three successive seasons (1941 - 1943) were 76.4, 18.4 and 34.4 respectively indicating that natural crossing varied with seasons. Possible explanations for this kind of variation could be due to

(1) demographic changes in the pollinator insects

(2) variations in wind velocities and

(3) changes in day length hence variations in photoperiodic responses in the

different varieties in that study.

Cross-pollination in sorghum, as in cotton, undoubtedly serves to create new genetic combinations and thus provide the material for effective selection by farmers and breeders. Heterosis has been reported in sorghum (Conner and Karper,1927; Lanzany and Bajal, 1986). There exists marked heterosis in sorghum for leaf size, chlorophyll development, and grain yield. Maturity in sorghum is also markedly delayed due to heterosis. The latter is important in breeding program for which earliness and high grain yield are to be considered simultaneously.

2.1.2. Significance of mating system studies in crops

Mating system studies are useful in crop plants improvement and genetic studies. The development of different mating designs has fueled the improvement programs of different crop plants. Hybrid development, backcross, topcross, polycross, diallel and partial diallel designs, North Carolina designs I, II and III, reciprocal selection designs and other intermating designs, and inbred line development all point at the available mating designs which have been developed for crop plants improvement (Fehr and Harley, 1980). Selecting the kind of mating design in crop plant improvement and genetic studies depends upon

(1) predominate type of pollination (self or cross pollinating)

(2) type of crossing used (artificial or natural)

(3) type of pollen dissemination (wind or insect)

(4) unique features, such as cytoplasmic or genetic male sterility,

(5) purpose of the project (breeding or genetic) and

(6) size of population required.

All the plant breeding programmes have a set of stated or implied objectives. To accomplish the objectives there is a need to understand the mating system to be adopted for the crop to be improved. Depending on the mating system adopted, the breeding objectives, can be achieved in a short or after a long period Welsh (1981).

The improvement of a crop can be achieved in a number of ways depending on the plant species, the environment, and the program goals. There is need to have a knowledge of the method by which the plant species under improvement will be reproduced and finally channel the genetically improved crop to the growers. Most common methods for which improvement on a crop can take are pure line, hybrid, synthetic and composite and asexual reproduction. The method to use will depend on the mating system.

Estimation of outcrossing has also been done for purpose of comparing the breeding system of closely related plant species. Vasek and Harding (1976), reported the outcrossing estimates from three populations of Clarkia exilis and one population of C. unguiculata . The latter species has an outcrossing rate of essentially 100%, an estimate in accord with expectation based on its long styled, protandrous flowers. Clarkia exilis gave a lower outcrossing rate compatible with its short styled, synandrogynous flower structure. Accordingly, there exists both intra and inter specific variation in the population genetic structure.

The continued development of new crop cultivars with superior and specific agronomic characteristics demand programs for seed increase which insure the retention of genetic purity and prevention of outcrossing. For proper design of such programs the knowldge of mating system is indispensable.

For the purpose of comparing breeding system of plant species, mating system studies are inevitable. Also the same studies permit an evaluation of

inbreeding in the plant species and an evaluation of selection by comparing gametic with sporophytic gene frequencies (Vasek and Harding, 1976).

2.1.2.1 Genetic structure of populations as related to mating system

The genetic structure of natural populations is usually dynamic and very complex given that populations are not constant, mating patterns change, conditions for mutation, migration and selection also do change. The genetic structure of the plant populations differ with respect to mating system, whether they are self or cross pollinating. Populations in self-fertilized species tend to become highly homozygous. For a simple diallelic locus, the amount of heterozygosity at one locus in any generation can be expressed by the formula $(1/2)^n$ where n is the number of segregating generations under selfing without selection or any other mechanism which imposes genetic change in the population. Under multiloci system, the formula $[(2^n - 1)/2^n]^n$ can be used to estimate the proportion of homozygous genotypes in each segregating generation (Welsh , 1981). The term n is the number of segregating generations, and m is the number of loci involved. Inbreeding due to selfing results into a genetically dimorphic population with respect to the genotypes produced. The dominant and recessive alleles are fixed into the homozygous dominant and homozygous recessive genotypes respectively. This polarization of the population into two distinct genotypes is usually due to continued inbreeding by selfing and elimination of heterozygotes. A part from genotypic frequencies, there would be no change in the allelic frequencies under selfing if other mechanisms leading to changes in the population are non-operational.

Cross-fertilized population dynamics are expressed in the Hardy-Weinberg law which states that allelic and genotypic frequencies are maintained in equilibrium after one round of random mating if the following conditions are

satisfied:

(1) completely random mating,

(2) no differential selection,

(3) no unidirectional mutation rates,

(4) no migration of alleles,

(5) large number of individuals in the population and

(6) diploid composition (Hardy, 1908).

Hay-Weinberg principle can generally be applied to many cross-fertilized species (Welsh, 1981). In a cross-fertilized species a large number of heterozygotes are maintained and a recessive allele can remain hidden in the heterozygotes. The proportion of heterozygosity can be estimated by the formula $c = k(k-1)/2$ where c is the different forms of combinations that can be achieved from k alleles under a multiallelic system (Hedrick, 1983). As k increases, c will have a corresponding upward trend. This increase in heterozygosity eventually terminates at a maximum when allelic frequencies are equal (i.e. $p = q_i = r_i = s_i = t_i = \ldots\ldots\ldots = z_i = 1/k$ for a multiallelic locus system in which p,q,r,s,t, ...,z are the respective allelic frequencies for k alleles).

From the genetic standpoint artificial self-pollination in a normally cross-pollinated crop leads to the production of homozygous lines. In many crops, notably maize (Zea mays), there is a rapid reduction in vigor when self-pollination is practiced (Hayes, et al. 1955). Use of male sterility has been deployed in the recent past enabling breeders to avoid laborious task of detasseling of maize in the production of hybrid maize varieties. Heterosis has received considerable attention because of its marked effect on yield improvement. This increased productivity on crossing different strains of corn was first noted in the nineteenth century and was then developed

according to systematic genetic procedures by East and Jones (1919), Jones (1917, 1922), and Shull (1952). Cytoplasmic male sterility has also been used to produce hybrid varieties of onions (Allium cepa), carrots (Daucus carota) and sugar beet (Beta vulgaris) that are presently used in commercial plantings (Strickberger, 1985).

2.1.3 Mating system studies in grain amaranths

Walton (1968) estimated nearly 20 percent outcrossing in the grain amaranths without giving any experimental details. Kauffman (1979), on the other hand, reported an experimetal design involving a plant with red flowers placed in the centre of a plot of plants with green flowers and concluded that "outcrossing was minimal" although his data seem to suggest as high as 40 - 60 per cent outcrossing . Simmonds (1979) listed grain amaranths as an outbred-inbred crop, i.e. in the habitually outbreeding (or often cross-pollinated) class, which includes sorghum and cotton. Pal (1972), judging from the description of floral morphology including monoecy, protogyny, insect visits concluded that rather wide variation in the rates of natural outcrossing of grain amaranths occurs among genotypes and geographical regions. This wide variability in natural outcrossing rates limits general application of already established estimates of rate of outcrossing in grain amaranths to extensive different environmental conditions.

Jain, et al (1982) estimated outcrossing rate in several collections of grain amaranths using three sets of data . The first involved a red-green seedling color locus (R,r). The progenies of recessive mothers (rr) grown at the University of California, Davis, gave a wide range of values (mean rate of outcrossing was 31 per cent, standard error was 25 per cent).
The families of plants collected at four sites in India gave estimate of 3.5 to 14 per cent outcrossing at locus R/r. Using two allozyme loci, progenies

of individual plants collected from fields in India and South America gave estimates of 3 to 25 per cent outcrossing rate, with significant interpopulation variation. This level of variation in breeding systems of grain amaranths calls for special interest in further studies of its ecological and morphological components, and in relation to the effects of domestication, on the breeding structure of different populations. For some individual plants, Jain et al (1982) found outcrossing rate estimate of more than 100 per cent and this, they said could be due to

(1) a large standard error of estimation (unlikely since the standard error for each individual plant estimate were low as progeny sizes were nearly 100);

(2) gametic selection favouring allele R or self-incompatibility involving some rr mothers;

(3) selection favouring heterozygotes prior to stage of seedling census.

It is not clear, without further genetic analyses, whether (2) or (3) might be important factors influencing the estimates of outcrossing rate. The wide range of outcrossing rate estimates obtained by Jain, et al (1982) justifies Simmonds' (1979) categorization of grain amaranths as often outbred. No single value of outcrossing rate would seem to characterize grain amaranth (Hauptli and Jain, 1985). The outcrossing rate in grain amaranths is not yet properly established as has been done for other crops. Breeding system of this crop appears to be very complex, and under strong environmental influence, as seen by a large difference in the range of outcrossing rates between successive generations. Also outcrossing rates across species are not well documented. More detailed and numerous sets of such estimates would be useful. Moreover, different populations with known amounts of outbreeding, history of cultivation and levels of genetic variation would be useful to study for the potential role of heterosis in their improvement by choosing alternative breeding procedures.

The knowledge of the genetic inheritance of morphological traits is essential for identification of genetic markers necessary for mating system studies, the improvement of the crop and may provide information on the genome organisation in the crop. Kauffman (1979) noted that to properly conduct outcrossing rate trials in grain amaranth there is need to have varieties that are true-breeding for red and green pigmentation. Kulakow et al (1985) studied the genetics of grain amaranths and reported the control of seed color by two loci in A. hypochondriacus and A. caudatus giving a 12:3:1 segregation ratio for black-yellow-plale and black-brown-pale colour classes, respectively. Three loci are described for pigments on plant parts: red seedling color was inherited as a single gene dominant; orange versus red mature plant color was controlled by a diallelic locus; and betacyanin distribution to the stem, leaves, and inflorescence was inherited as a single gene dominant. Gudu (personal com.) studied the inheritance of some morphological traits in grain amaranths and reported that seedling colour, inflorescence colour, seed coat colour and oval leaf mark segregated to a 3:1 genetic ratio and therefore each was controlled by a single gene. The purple leaf mark segregation in F2 gave 9:7 genetic ratio and hence may be controlled by two dominant complementary epistatic genes. The knowledge of genetic inheritance of morphological traits is essential for identification of genetic markers necessary for the improvement of the crop and may provide information on the genome organisation in the crop.

2.1.3.1 Gene flow in grain amaranths as a result of outcrossing

The knowledge of the breeding system of grain amaranth species is essential to determine appropriate breeding strategies, optimal genetic structure of improved varieties and isolation requirements for seed production (Jain, et al 1984). Studies on the role of heterosis in cultivated populations will suggest whether to treat grain amaranth as an inbred or outbred crop. Hauptli and Jain (1985) reported that landrace populations of grain amaranth from Central and South America, exhibited very low levels of heterozygosity despite outcrossing rates ranging from 0.10 to 0.50. In contrast, Indian landraces seemed to have significantly higher amounts of genetic variation, higher outcrossing rates, and overall a larger role of heterotic selection (Hauptli and Jain, 1985).

Kulakow et al (1985) studied genetics of grain amaranths and noted that there was great homology among three different species (A. cruentus, A. hypochondriacus, and A. caudatus). This homology was attributed to the fact that the three species were related closely enough to suspect that many loci were homologous among them. Evidence from electrophoretic studies (Hauptli and Jain, 1980) and segregation patterns in the populations derived from interspecific hybrids also suggests a high degree of homology among the species. This clearly illustrates the gene flow in grain amaranths. Genetic markers have been deployed in grain amaranths and there is evidence of gene flow within and across species of the crop (Jain et al, 1982).

The methods of pollen transfer are varied in grain amaranths. It is generally considered that pollen is wind-borne in wild types (Jain et al, 1984). These workers further observed that pollen of grain amaranth is sticky

and heavy, a characteristic which probably reduces pollen movement. Bees have been reported to visit grain amaranths, in Texas and California (Jain et al, 1984).

Intraspecific and interspecific crosses have been attempted between several populations of each of the cultivated grain amaranth species (Pal and Khoshoo, 1974; Kulakow and Jain, unpub. data). In the study by Pal and Khoshoo (1974) success of hybridization varied depending on the popualtions used. A history of prior natural hybridization may explain relaxed crossing barriers between certain specific populations. Appendix I summarizes the range of results for each type of cross under Davis, California, conditions as obtained by Jain et al (1984). A study of the inheritance of a reproductive isolation barrier between certain A. hypochondriacus and A. caudatus populations has shown that few genes control the presence of the barrier. Using appropriate populations it should be possible to transfer genes among all the four cultivated taxa.

The extent of reproductive isolation and genetic differentiation between cultivated and weedy amaranth species is of interest in determining the feasibility of wide gene transfers in plant breeding and the likelihood of incorporation of desirable weedy germplasm into cultivated species.

2.1.3.2. Mating system as related to the genetic structure of grain amaranth population

Jain et al (1980) using field observations on population structure, habitat diversity, morphological variations for plant form, pigmentation of various plant parts, and the occurrence of "weedy" characteristics reported a great deal of variation among and within populations. In order to evaluate the crop for its improvement potential, the genetic variation in existing germplasm must be characterized for its kind, amount and geographic

distribution.

Hauptli and Jain (1984a) studied genetic structure of landrace populations of the S. America grain amaranths and observed that most of the landraces were mixtures of highly homozygous genotypes. In their study four simply inherited pigmentation traits and 18 other morphological traits were studied in six landrace populations. The populations varied for the amount of polymorphism for marker loci, and exhibited little heterozygosity. Furthermore, the analysis of variance for the quantitative traits showed significant interpopulation differences for each of the observed characters. The high levels of variations for quantitative traits established by Hauptli and Jain (1984a) conformed well with the allozyme variation pattern for esterase (Hauptli, and Jain,1978; Jain, et al, 1980). Gudu and Gupta (1988a) characterised grain amaranth varieties using an electrophoretic approach showing intra- and inter-specific variations. Earlier, other identification methods had been deployed which also illustrated intra-and inter-specific variations within grain amaranths (Kowal, 1954; Grant, 1959; Pai-Chi Huang, 1980). Kulakow (1987) found significant selection gains and gave estimates of heritability in the range of .35 to .66 for anthesis time and 0.08 to 0.19 for leaf length. This suggested a large additive term in the total genetic variance to grant wide variation that exsists within grain amaranth species. Thus both allozyme and morphological markers have shown amaranth landrace populations to have large amount of variation. Breeding system parameters are therefore, largely unkown for the various specific regions (Hauptli,and Jain, 1984b).

Grain amaranth species have a mixed mating system with capability of controlling pollinations both genetically and mechanically, making provision for the utilization of plant breeding methods that combine features of classical selfed and outcrossed sytems. The mating system thus further

influences the genetic system of the crop as 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, labour and other management costs (Kulakow and Jain, in preparation).

The knowledge of genetic structure of populations in a crop species is essential in designing strategies of optimum sampling, evaluation and utilization of genetic resources. An understanding of the patterns of genetic variation among and within landrace populations can elucidate the importance of various factors of microevolution. Biometrical studies describing population similarities, heterozygosity levels, breeding system and morphological data provide evidence for the importance of heterosis, changes in breeding structure and the role of interpopulation gene flow through seed exchanges or hybridization (Vaidya and Jain, 1985).

Also, information on the breeding system and the extent of genetic variation in a new crop species is essential for the formulation of an effective breeding method to achieve maximum genetic gain (Vaidya and Jain, 1985). Vaidya and Jain (1985) further stated that their observations from variety trials suggested ubiquitous polymorphism for inflorescence colour and large phenotypic variances in numerous agronomic traits within the strains developed at Rodale.

2.1.4. Some methods used in outcrossing studies

Several biometrical methods have been devised to estimate outcrossing rate in plants. All the methods devised involve the counting of proportions of different genotypes among the progeny of individual plants (Brown and Allard, 1970), or of pooled individuals in a population (Jain, 1978). These methods

are generally population measures. One must assume pollen pool frequencies in each of the maternal genotypes to be homogenous and the relative success of outpollinations also to be identical in the progeny (cf. Harovitz and Harding, 1972, Harding and Tucker, 1964;). Such experiments, using a single morphological locus could not be appropriate if the locus might somehow involve selection or pollinator preference. More recently, methods have been devised which estimate outrcrossing rate utilizing information from more than one locus simultaneously (Ritland and Jain, 1981).

It is important to distinguish between outcrossing and naturual crossing which are usually confused (Masatoshi and Katsumi, 1958). The degree of outcrossing is defined as the proportion of ovules fertilized by the pollen of foreign individuals irrespective of the genotypes, while that of natural crossing is the proportion of hybrids produced by the crossing of different genotypes in an open pollination.

In any of outcrossing studies, the first important step is to choose a good genetic marker locus with clear phenotypic classes and regular Mendelian segregation. Simultaneous use of several marker loci provides further generalization about the breeding system of a species. Likewise, estimates from population grown under different environments provide evidence of variation in estimates as noted by many researchers (Frankel and Galun,1977). Planting designs (alternate rows, concentric circles, e.t.c.) are useful in studies of "contamination" through outcrosses as related to the spacing of isolation plots. In addition to morphological traits such as colour and leaf pubescence, use of electrophoretic assays of protein variation in population provides many useful genetic markers for getting the estimates of outcrossing rate (Jain, 1979). Using gene markers to establish outcrossing rate, several alternative methods have been developed over the years (Vasek, 1968; Jain, 1979). Some of these methods are outlined below.

2.1.4.1 Equilibrium method: (Vasek, 1968)

The method is based on frequencies according to Wright's equilibrium as follows.

D		H		R		
p^2 +	pqF	+	2pq - 2pqF	+	q^2 + pqF	= 1

Where F = inbreeding coefficient

p = dominant gene frequency

q = recessive gene frequency

The outcrossing frequency, t, relates to F such that, at equilibrium and in the absence of selection, t = (1-F)/(1+F) and F = (1-t)/(1+t) [Mastoshi and Katsumi, 1958). By this method the observed zygotic frequencies, D, H and R are determined by counting phenotypes in the population and then by progeny-testing the dominant phenotypes to determine the proportion of the homozygotes to the heterozygotes. Two of the expected frequencies of the equilibrium are set equal to the observed frequencies and

H = 2pq - 2pqF ..... (1')

R = q2 + 2pqF ..... (2')

The two equations are simultaneously solved for F and p. The solutions are p = D + (1/2)H and F = [(4 x D x R) - H^2]/(2D + H)(H + 2R). This method assumes that the population is in equilibrium and there is no selection, and that cross-fertilization is at random with respect to the several genotypes.

2.1.4.2 Allard method (Vasek, 1968).

In this method, the expected frequency of the dominants in progenies of the wild recessive is a function of the dominant gene frequency (p) in the pollen pool and the frequency of cross fertilization (t) (cf. Jain, 1979). Setting the observed frequency (DR) equal to the expected frequency (tp) gives

DR = tp ..... (3')

The dominant gene frequency is estimated from the zygotic proportions, as in the equilibrium method, subsitituted for p, and the equation is solved for t. Despite its simplicity and directness, the method suffers from major assumption of the gene frequency in the pollen pool being the same as in the zygotes that produced the pollen grains. In addition, the resulting outcrossing estimate is assumed to apply equally to all the genotypes in the population.

2.1.4.3 Fye and Bailey (1951) method.

The method utilizes the progenies from naturally pollinated recessive and naturally pollinated heterozygotes. The frequency of dominants in the progenies of wild recessive is the same estimator (DR) used in the Allard Method. The second estimator is the frequency of recessives observed in the progenies of wild heterozygotes (RH). The latter is expected in the frequency of (1/4)(1-t)+(1/2)/(tq) (Vasek, 1968) or (Ht-2tp)/4. Setting the observed frequency equal to the expected frequency gives RH = (1+t-2tp)/4.....(4'). Equations (3') and (4') are solved simultaneously for estimates of t and p. The major assumption is that the recessive and heterozygote genotypes have the same outcrossing frequency. The estimator RH is an unreliable estimator due to exceedingly large error of estimation (Vasek, 1968).

2.1.4.4 Double-Recessive method (Vasek, 1968)

In the populations where two markers are available, an estimate of dominant gene frequencies in the outcrossing fraction of the pollen pool may be obtained for each marker and utilized to solve equation (3') for an estimate of t. In the progenies of the double recessive genotype the proportion of the dominant genotype for one marker among the dominant genotype for the other marker provides a direct estimate for p in the outcrossing fraction of the pollen pool. This method assumes that the frequency of the dominant for one marker among dominant for the second marker is the same as the frequency of dominants for the first marker among recessive for the second marker. In other words, independent association of the two markers is assumed.

2.1.4.5 Combination methods (Vasek, 1968)

This approach involves the utilization of two or more of the four methods mentioned above given that each method describes the expected frequency for independent observed set of data. Any two equations may be used to solve for t and p simultaneously. Four estimates of t and p may be obtained from the simultaneous solution of the following pairs of equations: (1') and (3'), (1') and (4') and (2') and (4'). Since all the expectations are expressed in terms convertible to the two unknown components t and p, other estimates of t may be obtained by estimating p, substituting, and solving all the equations for t. This also compounds the assumptions for the individual methods.

2.1.4.6 Prout's digenic outcrossing model (Vasek, 1968).

Professor Timothy Prout, suggested a model for estimating outcrossing which involves estimating outcrossing rates separately for each phenotype. Thus the parameters to estimate are t_1, t_2, t_3, t_4, A_1, A_2, A_3 and A_4 where

the t's are the outcrossing rates corresponding to each phenotype and the A's are the frequencies for each genotype used for a given population. This allows excess of degree of freedom which should permit a X^2 test for goodness of fit.

2.1.4.7 Allelic frequency of known pollen pool (Jain, 1979):

2.1.4.7.1 Marker locus with no dominance (Jain, 1979)

Assuming diallelic locus with three genotypic classes (AA, Aa and aa) which are phenotypically distinct a polymorphic population can be censused to obtain the estimates of the three genotypic proportions (D,H,R) in a sample of n individuals. For sufficiently large n, the variance of estimated D,H,R are given by the multinomial expectations and are D(1-D)/n, H(1-H)/n and R(1-R)/n respectively .....(1").

Allelic frequencies are estimated by:

$p = D + (1/2)H$, and $q = 1 - p = R + (1/2)H$ .....(2")

variance of their estimates are also given by

$p(1 - p)/2n$ and $q(1 - q)/2n$ respectively .....(3")

If s and t are relative proportion of selfing and outcrossing respectively then the expected heterozygote frequencies are pt and qt respectively, i.e. H = pt (Aa among aa) and H =qt (Aa among AA). If aa and AA outcross at different rates, say t_1 and t_2 , then

$$H_1 = a/(a+b) \qquad H_2 = c/(c+d)$$

$$\hat{t}_1 = H_1/p \qquad \hat{t}_2 = H_2/p$$

$$\hat{\sigma}_t^2 = \hat{t}_1 (1-p)/(a+b)p(1-q) \qquad \hat{\sigma}_t^2 = \hat{t}_2 (1-q)/(c+d)q(1-p)$$

.....(4")

here a and b are numbers of Aa and aa among progeny tested aa individuals, and

c and d are numbers of Aa and AA among progeny tested AA individuals.

Heterogeneity of values of t can be tested as follows: If $t_1, t_2 \ldots\ldots\ldots t_k$ are estimated from samples of size $n_1, n_2 \ldots\ldots\ldots\ldots n_k$ with standard errors of $s_1, s_2 \ldots\ldots\ldots\ldots\ldots s_k$ respectively the test statistic for heterogeneity is

$$X^2 = \sum_{f=1}^{K} (\hat{t}_f - \bar{t})^2 / S_f^2$$

where

$$\bar{t} = \sum_f (\hat{t}_f / s_f^2)\ (1/s_f^2)$$

f = sample of size $n_1, n_2 \ldots n_n$

S = sample variance

The heterogeneity X^2 has (k-1) degrees of freedom. Heterogeneity among t_f values would suggest non-random outcrossing. Causes for non-random outcrossing may be preferential or assortative mating, non-random pollen dispersal and the unequal pollen production.

2.1.4.7.2 Use of Dominance/Recessive Planting Arrangements (Jain, 1979).

This involves planting genotypes AA and aa in alternate row in 1:1 ratio or some other ratios. If plant densities within rows are the same, pollen pool allelic frequency (p) is one-half with the alternate row design, or, one-third if pollen donor line (AA) is planted with a row of (aa) on each side. Dividing the frequency of the hybrids i.e. Aa by p adjusts for intragenotypic pollinations. Estimators of t and S^2 are the same as given by equation [4"].

This method does not correctly describe the consequences of outcrosses in a polymorphic population.

2.1.4.7.3 Use of a marker locus with dominance (Jain, 1979).

If an allele A is dominant, it is necessary to grow progenies of AA and Aa to determine the frequency of the dominant allele (A). The method has been used for composite cross pollinations in barley (Jain and Allard, 1960). The frequencies D and H are estimated from a large number of dominant class per generation. These estimates of D, H and R are then used to estimate p; the rest of the procedure is identical to that described above in equation (3") and (4").

The variance of the estimate as given by Allard and Workman (1963) is:

$$\hat{\sigma}_t^2 \approx (1/p)^2 \left[H(1-H)/N_1 \right) + (H/P^2)^2 (P(1-P)/N_2 \right] \quad \ldots\ldots\ldots\ldots\ldots\ldots (5")$$

where N_1 = Number of progenies

N_2 = Average size of progeny used for estimate of p and

H = proportion of heterozygotes.

2.1.4.8 Natural populations in equiliburium (Jain, 1979).

A population with a polymorphic diallelic locus, mixed selfing and random mating, and no selection, migration or mutation changes (i.e. analog of Hardy-Weinberg population) would have equilibrium genotypic composition of

$D = p^2 + pqF$, $H = 2pq(1-F)$, $R = q^2 + pqF$, where $F = (1-t)/(1+t)$

(cf. Vasek Equilibrium method).

$\hat{F} = 1 - (H/2pq)$ and is an estimate of fixation index.

$\sigma_{\hat{F}}^2 = [1/2q(q-1)]\, \sigma_{\hat{w}}^2 + [H(1-2q^2)]/2q\,(1-q)^2)\, \sigma_q^2$

where $\hat{t} = (1-\hat{F})/(1+\hat{F})$;

$$\hat{\sigma}_t^2 = (1+\hat{t})\hat{t}[(1-\hat{t}).(1+3\hat{t})]/(4pqN)+[4\hat{t}(3\hat{t}-1)]pq \quad \ldots\ldots\ldots\ldots\ldots (6")$$

2.1.4.9 Simultaneous estimation of p and t by a bulk method (Jain,1979).

The most recommended method is one which involves simultaneous estimation of both p and t. The bulks of A- and aa classes can be used to estimate the proportion of outcrosses. Considering a diallelic locus with dominance and seed harvested from the dominant and recessive classes as separate bulks say, with n_1 and n_2 individuals, respectively, a bulk seed lot could be scored for dominant (A-) and recessive (aa) classes so that $(D + H) = n_1/(n_1+n_2)$ and $R = n_2/(n_1+n_2)$. The two samples can then be grown to score the dominant genotypes appearing among the progeny of recessives and vice versa. The expectations are:

Parent Progeny class	observed no.	Probability (π_t)
recessive ------->dominant	a	Rpt
recessive ------->recessive	b	R(1 - pt)
dominant -------->recessive	c	1/4H(1-t+2tq)
dominant -------->dominant	d	(D+H)-1/4(1-t+2tq)

where t = proportion of random outcrossing, $p = D + (1/2)H$ is the frequency of allele A and $q = 1-p$ is the frequency of allele a, ($a + b = n_1$, $c + d = n_2$). The three unknowns t, D and H (since $R = 1-D-H$) can be estimated simultaneously by the maximum likelihood method using interative solutions. The scoring method employing $\frac{1}{\pi_t}\frac{\partial \pi_t}{\partial t}$ is useful for maximum likelihood equations that cannot be solved analytically. The trial values of t, D and H are given by the expressions $D = 1-R$, $t = a/RD$ and H from the positive solution of the quadratic $H^2(a-(1/2)R) + H(R-R^2-a'+2a'R+2c'R) - 4c'R(1-R) = 0$.

where $a' = a/n$, $b' = b/n$ and $c' = c/n$, $d' = d/n$ and $n_1 + n_2 = n$.

2.1.4.10 Simultaneous estimation of p and t by use of progeny data (Jain, 1979). Given a diallelic locus with no dominance the maternal genotype frequencies (D,H and R) can be scored at the time of seed harvest. Maternal gene frequency $p = D + (1/2)H$, and fixation index, $F = (4DR - H^2)/4pq$, can be scored, also to be scored is r plants per family for f families, then

$$\hat{\sigma}_{\hat{p}}^2 = \hat{p}\hat{q}(1+\hat{F})/2f$$

and

$$\hat{\sigma}_{\hat{p}}^2 = [(1-2\hat{F})(1-\hat{F})^2/f + \hat{F}(1-\hat{F})(2-\hat{F})/2\hat{p}\hat{q}f]$$

2.1.4.11 Measures based on autofertility test and inbreeding depression (Jain, 1979)

Autofertility is not a direct measure but certainly a useful and simple one to measure in outbreeders and is possibly correlated with natural rates of selfing.

2.1.4.12 Components of quantitative genetic variation (Jain, 1979).

An estimator of the rate of outcrossing can be developed based on an estimator of F as follows: If b equals to the parent - progeny regression coefficient, $h^2 = b/2r_{x,y}$ where $r_{x,y}$ = coefficienct of genetic relation between relatives x and y (say, parent x and y). For a random mating population, $r_{x,y} = 1/4$, for F_2 and F_3 (of a biparental cross) $r_{x,y} = 3/4$, and in general $r_{x,y} = (1+Fx)/2$. Now $F_x = (1-t)/(1+t)$ (at equilibrium, assuming no selection and other factors which alter the genotypic gene frequencies), so that $r_{x,y} = 1/(1+t)$.

Three main points emerge from this survey of various methods of estimating natural outcrossing rates:

(a) Various genetic and experimental design features are similar in that phenotypic and genotypic frequency data in any method are obtained from a parent and its progeny.

(b) Estimation procedures vary with locus, size of progenies, and resources available but generally they are simple conceptually and numerically, and may be extensively used by breeders.

(c) The use of several methods in the same materials might not always lead to concordant estimates.

2.1.5.0. Gene flow in other crops as a result of outcrossing

Outcrossing studies have been conducted in several other crops. Jain, et al., (1979) found out that outcrossing rate in highly inbreeding species, such as barley, may not be a simple parameter. At the genotype level, there is evidence of a strong interaction of the awnless allele in pollen pool with the recipient female genotype. When the outcrossing rates were examined in terms of individual loci, linear allelic differences in the propensity to outcross were present at both loci. Similar results were reported by Harding and Tucker (1964) in lima bean; the recessive allele at seed coat color locus (s/s) outcrossed nearly two times the rate of dominant allele. Outcrossing estimates have been obtained for three populations of Clarkia exilis and one population of C. unguiculata. The latter species has an outcrossing frequency of essentially 100%, an estimate in accord with expectations based on its long styled, protandrous flowers (Vasek and Harding, 1976).

The amount of outcrossing on three short stature male steriles of rice (Oryza sativa L.) was studied when planted in alternate rows with pollinators

constituted of a mixture of tall cultivars. Seed set was very poor in the male sterile lines hence giving very poor result of the estimated outcrossing (Azzini and Rutger, 1982).

Berry, et al (1970) observed at least 13 percent crossing in Vernonia anthelmintica (L.) using alternate row planting technique for white (recessive) and violet - flowered plants (dominant) and eventually scoring for the heterogeniety in the white - flowered progeny. Using similar approach Copeland and Hardling (1970) estimated outcrossing in ryegrasses (Lolium spp.) as determined by flourescence tests.

Breese (1959) reported success in manipulating outcrossing rate through selection for heterostathmy (a quantitative form of heterostyly) in Nicotiana rustica. Although delay in anther dehiscence time was more effective than actual heterostathmy in increasing outcrossing rates, the two traits were strongly associated, and a significant response to selection was reported in the breeding system.

Holden and Bond (1960) observed response to high and low outcrossing selection in field beans (Vicia faba). Knudsen and Poulesen (1981) further analyzed the progress in its breeding programs directed toward shift to autogamy, with emphasis on inbreeding depression to be overcome during early generations. The evloution of tomato cultivars from their self-incompatible wild relatives with "pin" type stigma-anther relationships to the highly selfed "thrum" flower structure suggests a complex and gradual evolutionary genetic change (Rick, 1950; Rick et al; 1977).

Inheritance of breeding system characteristics of many legumes have been reported to be polygenic and intermediate in outcrossing expression (Harding and Tucker, 1964; Green et al, 1980). Drayer (1959) and Holden and Bond (1960) reported a situation of field beans which is similar to grain amaranth where homozygotes which produce less pollen, were more dependant on tripping

and crosspollination for seed production than heterozygotes, which produce abundant pollen.

2.2 Yield prediction studies

Yield improvement is the ultimate goal in virtually every plant breeding program. The yield trait reflects the performance of all the plant components and is considered as the final result of many other traits (Welsh, 1981). Improved yield can generally be attributed to:

(1) an inherent physiological production capacity that operates on energy, nutrients, water and other artificial and natural factors required for crop plant performance and

(2) protection against environmental hazards.

Not all genotypes have iso-inherent physiological capacity to yield. In rice for example, the introduction of semi-dwarf genes reduced plant height and improved the plants capacity to use the natural resources at its disposal more efficiently (Welsh, 1981). Some of the increase in yield potential was due to the stiff straw characteristics of the semi-dwarf that allowed it to stand erect and maximize use of very high irrigation and fertilizer levels. However, some other genetic contributions leading to more numbers of grains per panicle did increase yield.

Reduction of environmental hazards such as diseases and insect pests, drought, winter injury, high salinity levels in the soil or irrigation water will be reflected in yield improvement. These represent separate breeding objectives which are always addressed in different breeding programs.

The heritability of yield is normally low because of the large number of genes involved and the high level of environmental interaction. This makes breeding for high yields very difficult to achieve because of the many genes

involved and the high proportion of environmental component in the phenotypic variance. Despite all the difficulties associated with yield, improvement in this trait has been achieved both by breeding and genetic techniques in most species (Welsh, 1981). Some of the most dramatic yield improvements on record have been realized in controlled environments with few limitations imposed on the plant. "The Green Revolution" varieties of wheat and rice are good examples (Ishizuka, 1969). Ishizuka (1969) further reported yield improvement on rice and attributed the rapid rate of improvement to a combination of the factors outlined herebelow:

(a) New varieties developed by scientific and systematic breeding
(b) Improvement in cultivation techniques
(c) Chemical fertilizers, especially nitrogen
(d) Fungicides, insecticides and herbicides
(e) Soil improvement through ameliorative practices.

Yield analysis studies have been performed in several cereals like maize, sorghum, rice, wheat, barley and grain amaranths. In these crops studies have been focused on the analysis of yield in terms of its components or related traits like plant height, biomass yield, harvest index, threshing percentage, head weight, days to flowering, plant height, seed weight, seed number per head, head size, tiller number, and plant weight, (Hadley et al., 1965; Graham and Lessman 1966; Singh and Stoskopf, 1971; Yap and Harvey, 1972; Eckebil et al., 1977; Ayiecho and Onim, 1983; Hauptli and Jain, 1985; Ayiecho Jain, 1989; Ivara and Ayiecho, 1989).

Ayiecho and Jain (1989) carried out studies on yield prediction for a population of A. cruentus and A. hypochondriacus based on the correlation coefficients and multiple stepwise regression. Ayiecho and Jain (1989) reported that the best seed yield predictors were plant height, head weight,

threshing percentage and yield: height ratio. Path-coefficient analyses indicated that most of the predictors affected seed yield through yield: head ratio. Head weight was also an important indirect path for some predictors. Earlier, Hauptli and Jain (1984a) reported that days to flowering was negatively correlated with yield while plant height and head length were positively correlated. Hauptli and Jain (1984a) further reported the potential of the correlations in developing early flowering and high yielding cultivars. Breeding strategies for improving grain yields via increased leaf area may be implemented either by increasing the area of each individual leaf or leaf bearing nodes. Hauptli and Jain (1978) found that the allocation of biomass to seed production was positively correlated with the seed yields in the grain amaranth cultivars. Therefore, to develop the highest harvest index there is need to consider flowering time, optimal and cardinal temperatures, best planting densities, and response to edaphic conditions. Sauer (1976), and Pal and Khoshoo (1974) concluded that despite some polemic about natural species barriers, it would be extremely valuable to hybridize many amaranth species for recombining their desirable characteristics of plant type, flowering requirements, seed output, differing yield components and physiological adaptations.

CHAPTER 3

MATERIALS AND METHODS

3.1. Materials

The following grain amaranth populations with red and green seedling pigmentation given in Table 1 were used in the study.

Table 1: Grain amaranth populations used in the study

Population	Species	Pigmentation	Days to flowering	Country of origin
1024	*Amaranthus hypochondriacus*	Red	60	Mexico
1008	*A. hypochondriacus*	Green	50	Taiwan
434	*A. cruentus*	Red	65	Mexico
1034	*A. cruentus*	Green	60	Dahomey

The grain amaranth populations were obtained from the Kenyan Grain Amaranth Project Germplasm Stock, University of Nairobi. The populations with the red marker were comprised of red plants only while those with green marker were comprised of green pigmented plants only. The red pigmentation gene was treated as dominant to the green pigmentation gene as reported in studies by Kulakow *et al* (1985).

3.2 Methods

3.2.1 Experimental design:

Four sets of experiments running simultaneously were conducted to determine outcrossing rates in the grain amaranths using the above mentioned populations. The experiments were conducted at Kabete Campus of the University of Nairobi, and the National Horticultural Research Station, Thika, during the long rains and short rains of 1988. Two experiments were designed to determine the intraspecific outcrossing rates while the other two were used to determine interspecific outcrossing rate as described below.

3.2.1.1 Intraspecific outcrossing rate experiments

(i) Experiment A: This was to estimate the outcrossing rates within *A. hypochondriacus* using population 1008 as the resessive marker gene parent and population 1024 as the dominant marker gene parent.

(ii) Experiment B: This was to estimate the outcrossing rates within *A. cruentus* using population 1034 as the recessive marker gene parent and population 434 as the dominant gene parent.

3.2.1.2 Interspecific outcrossing rate experiments.

(i) Experiment C: This was to estimate the outcrossing rates between *A. hypochondriacus* and *A. cruentus* using population 434 (*A. cruentus*) as the dominant marker gene parent and population 1008 (*A. hypochondriacus*) as recessive marker gene parent.

(ii) Experiment D: This was to estimate the outcrossing rates between *A. hypochondriacus* and *A. cruentus* using population 1024 (*A. hypochondriacus*) as the dominant marker gene parent and population 1034 (*A. cruentus*) as recessive marker gene parent.

In each experiment a two-replicate alternate row method where the dominant red pigmentation parent was planted in the centre with the recessive

green pigmentation parent on either side was used. This gives a pollen pool with the ratio of 1 dominant allele : 2 recessive allele assuming homozygosity within the two populations. The spacing within the row was 2.5 cm and between the row was 30 cm in a plot of 10 m by 0.6 m. The Katumani Composite maize variety was planted on either side of each plot as guard rows.

In each experiment, the two replicates were separated by a stretch of 20m of maize crop. On the other hand the isolation distance between any two different experiments was at least 100m with a maize field separating them. A similar isolation distance of 100 m was maintained with any other grain amaranth field or a field which had a grain amaranth crop the previous season. Rogueing of any off-types in the experimental field or any grain amaranth plants within the 100 m isolation distance was done.

To synchronize flowering dates of the populations used, planting was done at different dates. The late maturing populations were planted early in each experimental plot while the early maturing populations were planted at a later date as indicated in Table 2 below.

Table 2: Differences in days of planting to synchronize flowering dates in each experiment.

Experiment	Populations used	Differences in planting dates (days)
D	1034	
	1024	0
C	1008	
	434	15
A	1008	
	1024	10
B	1034	
	434	5

In each experiment seeds were harvested from the 100 individual green parents from each of the green pigmented parents. The harvested seeds were then grown in the greenhouse and the number of seedlings with red pigmentation among their progenies obtained. The outcrossing rate was estimated from the proportion of seedlings with red pigmentation scored among the progenies of the recessive parents.

3.2.2. Gene Frequency in the Dominant Pollinator Populations

Heterogeneity levels were scored in the dominant pollinators in order to ascertain the proportions of the red pigmentation (R) and the green pigmentation (r) alleles. This was done by selfing a sample of 150 plants from each of the two populations with dominant markers in the greenhouse. The selfed seed was planted out in the green house to determine the number of segregating families. The information thus obtained was used to estimate the frequency of the R and r alleles in the pollen pools in the outcrossing experiments.

3.2.3 Data collection on quantitative traits:

Individual plant data were taken from 100 random plants per population in each experiment per season for the number of days to flowering, the number of days to maturity , plant height, the sun dried head weight of mature plants, head length and seed yield.

3.2.4 Statistical Analyses:

3.2.4.1 Outcrossing rates:

The frequencies p and q of the dominant R and recessive r alleles respectively in the dominant marker populations were determined as

$p = (2N_3 + N_2)/2N_1$

$q = N_2 / 2N_1$

Where

N_1 = No. of progeny tested red plants (150 plants)

N_2 = No. of progeny tested red plants showing segregation

N_3 = No. of progeny tested red plants not showing segregation

The frequencies of the dominant and recessive alleles in the pollen pool in the respective outcrossing experimental plots were determined as

$\bar{p} = 1/2[(2N_3 + N_2)/2N_1 + 0] = 1/2P$

$\bar{q} = 1/2[(N_2/2N_1) + 1] = 1-(1/2)p$

Where

$\bar{p}$ = the proportion of R allele in the pollen pool

$\bar{q}$ = the proportion of r allele in the pollen pool

The outcrossing rate was estimated for each experiment according to the method described by Jain (1979) as follows:

$H = a/(a+b)$

$t = H/p$

$\hat{\sigma}_t^2 = t(1-p)/(a+b)p(1-q)$

$\hat{\sigma}_t = SE = \sqrt{\hat{\sigma}_t^2}$

Where:

H = the proportion of the heterozygotes (Rr) scored in the progeny tested recessive (rr) plants

a = the number of heterozygotes (Rr) genotypes i.e. red pigmented plants, among the progenies of the progeny-tested (rr) plants (Green pigmented)

b = the number of green (rr genotypes) among the progenies of the progeny-tested rr plants

$\hat{t}$ = estimate of outcrossing rate

$\hat{\sigma}_{\hat{t}}^2$ = the estimated variance of the estimate of outcrossing rate estimate.

$\hat{\sigma}_{\hat{t}}$ = the estimated standard error (SE) of the outcrossing rate estimate.

3.2.4.2 Yield prediction

The data collected on quantitative traits given above, were used to conduct phenoptypic correlation and multiple regression analyses as described by Neter and Wasserman (1976), Snedecor and Cochran (1980) and Steel and Torrie (1981). The correlation coefficients and multiple regression coefficients were subjected to statistical tests at P = 0.05.

CHAPTER 4

RESULTS

4.0 Determination of gene frequency in the dominant pollinator populations and pollen pool gene frequencies.

The two populations, 1024 and 434 had a fairly high frequencies for the dominant red pigmentation gene (Table 3). The high value for p showed that the two populations had many of the genotypes of the constitution dominant homozygotes (RR) as compared to the dominant heterozygotes (Rr). The recessive gene frequency estimates of 0.26 and 0.30 in populations 1024 and 434 respectively suggest high level of heterozygosity in the two populations. These results, therefore, indicate heterogeneity within the two populations.

The proportions of the dominant marker genes in the pollen pool of 0.37 and 0.35 for populations 1024 and 434 respectively were fairly low (Table 4). This is basically due to the high heterogeneity within the two populations as suggested by the data in Table 3 and the fact that unlike the recessive marker gene which is contributed by the dominant and recessive marker parents for the pollen pool, the dominant marker pollen is solely contributed by the dominant marker parent . The proportions of the recessive marker genes in the pollen pools were 0.63 and 0.65 in the outcrossing experiments where the two populations 1024 and 434 were used as dominant pollinators respectively (Table 4).

Table 3: The estimates of gene frequencies in the dominant pollinator populations.

Population	Gene Frequency	
	p(for red pigment)	q (for green pigment)
1024	0.74	0.26
434	0.70	0.30

Table 4: Estimates of pollen pool gene frequencies.

Dominant Pollinator Population	Recessive Pollinator Population		Pollen Pool Gene Frequency	
	Intraspecific Outcrossing	Interspecific Outcrossing	- •	- •
1024	1008	1034	0.37	0.63
434	1034	1008	0.35	0.65

Same source of experimental material was used for each experiment per season per site.

4.1 OUTCROSSING RATES

4.1.1 Intraspecific outcrossing rates within A. hypochondriacus(population 1024 and 1008).

The outcrossing rate estimates over two sites (Kabete and Thika) and two seasons (April,1988 and October, 1988) involving two populations of A. hypochondriacus, population 1024 and population 1008 are given in Tables 5 The data from Kabete indicated significant difference between the mean outcrossing for April 1988 (2.11%) and the mean for October 1988 (2.80%) seasonal intraspecific outcrossing rate varaition for the species. The mean outcrossing rate over the two seasons was 2.46% with a range of 0 to 10 per cent outcrossing rate for the individual plants. There was no significant difference between the seasonal outcrossing rate means at Thika . The outcrossing rate estimates for individual plants ranged between 1 to 32 per cent outcrossing. The mean over the two seasons was 18.33% . In this study the species showed wide locational intraspecific outcrossing rate variations. Both seasons (April,1988 and October, 1988) offered sufficiently large locational intraspecific outcrossing rate variation between the two sites (Kabete and Thika). Outcrossing rate estimates at Thika were higher than the estimates from Kabete in both seasons. The overall mean estimates for the two sites over the two seasons was 10.39%. This result suggest that the species is often outbred like for the sorghum and cotton. The very low estimates of outcrossing under Kabete condition suggest that other than the locational factors, other environmental components influencing the pollinator behaviour could be useful in understanding the reported estimates.

4.1.2 Intraspecific outcrossing rate within A. cruentus: (population 434 and 1034) .

The outcrossing rate estimates over two sites (Kabete and Thika) and two seasons(April,1988 and October,1988) for A. cruentus are given in Table 5. Both locational and seasonal intraspecific outcrossing rate differences for A. cruentus were significant. At Kabete outcrossing rate estimates ranged from 1.50 to 23.0 per cent and 0.5 to 14.0 per cent for April,1988 and October,1988 seasons respectively. Thika outcrossing estimates ranged from 3.10 to 25.0 per cent and 2.0 to 21.45 per cent for April,1988 and October,1988 seasons respectively. The Kabete and Thika intraspecific outcrossing rate estimates varied significantly with a range of 0.5 to 25 per cent. The locational and seasonal intraspecific outcrossing rate variation indicates that the environment variation may be an important factor in influencing outbreeding of the species.

The intraspecific outcrossing rate estimates for A. cruentus under Kabete conditions were quite high as compared to the estimates of A. hypochondriacus under the same site (Table 5). The Thika estimates for A. hypochondriacus were higher as compared to A. cruentus for both April and October seasons. These results suggest that the two species in this study differ in intraspecific outcrossing rate and the locational and seasonal differences seems to influence both the species differently.

Table 5: Estimates of intraspecific outcrossing rates in two grain amaranths.

		SITE			
		Mean percent outcrossing rate + percent standard error			
EXPERIMENT	SEASON	KABETE	THIKA	Mean	t_1
A *A. hypochondriacus*	April, 1988	2.11 ± 0.03	17.05 ± 13.37	9.58 ± 6.7	11.15**
1024 Vs 1008	October, 1988	2.80 ± 1.29	19.6 ± 15.25	11.2 ± 8.27	10.98**
	Mean	2.46 ± 0.66	18.33 ± 14.31	10.39 ± 7.49	
	t_2	5.31**	1.26		
B *A. cruentus*	April, 1988	10.90 ± 5.80	13.11 ± 7.17	12.01 ± 6.49	2.40*
434 Vs 1034	October, 1988	8.95 ± 1.54	10.7 ± 5.02	9.83 ± 3.28	3.30**
	Mean	9.93 ± 3.67	11.91 ± 6.10	10.92 ± 4.88	
	t_2	5.42**	2.74**		

* = significant at P= 0.05

** = significant at P= 0.01

t_1 = t values for paired comparision for the site means

t_2 = t values for paired comparision for the seasonal means

4.1.3 Interspecific outcrossing rates between A. hypochodnriacus(population 1024) and A. cruentus: (population 1034).

The interspecific outcrossing rate estimates over two sites (Kabete and Thika) and two seasons (April,1988 and October,1988) between A. hypochondriacus and A. cruentus using A. hypochondriacus (1024) as the dominant marker gene pollinator are given in Table 6. There was marked locational and seasonal interspecific outcrossing rate variation. The individual plant data from Kabete ranged from 0 to 3.10 per cent and from 0 to 3.40 per cent for April and October seasons respectively. Thika displayed a range of 0 to 4.32 per cent and 0 to 1.2 per cent for April and October seasons respectively. These are very low values compared to the values of the intraspecific outcrossing rate estimates. The fairly low interspecific outcrossing rate between the two species suggests that gene flow between the two species may be restricted.

April season had mean outcrossing rates higher for both sites (Kabete and Thika) as compared to the October values. This result suggests that seasonal variation may be an important factor in influencing interspecific outcrossing rates between the two species. October estimates for Thika were nearly zero (0.08 per cent). This suggests that despite seasonal and locational variation, outbreeding between the two species seems to be restricted.

Table 6: Estimates of interspecific outcrossing rates in two grain amaranths.

EXPERIMENT	SEASON	Mean percent outcrossing rate ± percent standard error SITE: KABETE	SITE: THIKA	Mean	t_1
C	April, 1988	1.36 ± 0.15	2.26 ± 0.2	1.81 ± 0.18	36.00**
A. hypochondriacus (1024) Vs	October, 1988	1.16 ± 0.16	0.08 ± 0.01	0.62 ± 0.09	54.00**
A. cruentus (1034)	Mean	1.26 ± 0.16	1.17 ± 0.11	1.22 ± 0.13	
	t_2	10.00**	72.67**		
D	April, 1988	9.96 ± 3.42	12.22 ± 8.34	11.09 ± 5.88	2.51*
A. cruentus (434) Vs A. hypochondriacus (1008)	October, 1988	2.04 ± 1.04	1.82 ± 0.51	1.93 ± 0.78	1.83
	Mean	6.00 ± 2.23	7.02 ± 4.43	6.51 ± 3.33	
	t_2	22.00**	12.38**		

* = significant at P= 0.05
** = significant at P= 0.01
t_1 = t values for paired comparision for the site means
t_2 = t values for paired comparision for the seasonal mean

4.1.4 Interspecific outcrossing rates between A. hypochondriacus(population 1008) and A. cruentus:(population 434).

Interspecific outcrossing rate estimates over two sites (Kabete and Thika) and two seasons (April,1988 and October,1988) between A. hypochondriacus and A. cruentus using A. cruentus (434) as the dominanat marker gene pollinator are given in Table 6 above. The data at both sites showed significant differences between the two seasons. The Kabate data had outcrossing rate estimates with a range of 0 to 15.02 per cent and 0 to 4.51 per cent for April and October seasons respectively. Similarly Thika data showed a range of 0 to 16.31 per cent and 0 to 3.92 for April and October seasons respectively. For both sites the interspecific outcrossing rate estimates were relatively higher as compared to the interspecific outcrossing rate estimates in which A. hypochondriacus (1024) was the dominant marker parent and A. cruentus (1034) the recessive marker parent. In these estimates, the dominant pollinator parent was A. cruentus (434) giving a higher gene flow as compared to the case when A. hypochondriacus was used as the dominant pollinator parent in 4.1.3 above.

There was a significant locational interspecific outcrossing rate variation for April,1988 with a range of 0 to 16.31 per cent outcrossing. The October, 1988 data showed considerably low interspecific outcrossing rate estimates coupled with insignificant locational difference. For both locational and seasonal outcrossing estimates, there were higher rates of outcrossing when A. cruentus (434) was used as the dominanat pollinator parent.

4.2 YIELD PREDICTION

4.2.1 Multiple regression and multiple correlatioin on yield related traits in population 1008: (*A. hypochondriacus*)

Individual plant data from 100 randomly selected plants per season per site were subjected to multiple regression and multiple correlation analysis for days to flowering, the number of days to maturity, plant height at maturity, head length, sun dried head weight of mature plants, and seed yield per plant. The mean values for these traits are presented in Table 7. There was no differnce between all the six traits for the Kabete, April and October means. A part from plant height and head weight there was no difference between the locational means of the other traits for the April season. October means showed difference between seed yield per plant and plant height for Kabete and Thika means while the other four traits never offered any difference between the means. The Thika, April and October data suggested differences between the seasonal means for plant height, head length and head weight . Seed yield per plant, days to flowering and days to maturity were not different with respect to their seasonal means for Thika. In the multiple regression seed yield per plant was used as the dependant variable . The regression coefficients and multiple correlation coefficients for the above traits over two seasons and two sites are given in Tables 8 (regression coefficients) and Tables 9 and 10 (for correlation coefficients) repectively.

Both the regression coefficients and correlation coefficients indicated high correlation of head length , head weight to seed yield per plant at Kabete for the April,1988 season. The seasonal and locational variation seem to display an important role in influencing the relationships between the above yield related traits. The Thika, April,1988 data did not have any trait

Table 7: Mean values (x_i), standard error(S.E) and least significant difference(LSD) for six quantitative traits in population 1008

	Season: April, 1988		Season: October, 1988					
	Kabete	Thika	Kabete	Thika				$LSD_{0.05}$
Trait	$x_1 \pm$ S.E	$x_3 \pm$ S.E	$x_2 \pm$ S.E	$x_4 \pm$ S.E	x_1 vs x_2	x_1 vs x_3	x_2 vs x_4	x_3 vs x_4
Seed yield per plant (gm)	10.67 ± 6.75	14.48 ± 3.43	10.54 ± 0.11	11.49 ± 0.21	13.40	15.04	0.47[N]	6.83
Plant height(cm)	80.25 ± 0.81	75.09 ± 1.01	77.84 ± 1.44	82.56 ± 1.53	3.28	2.57[N]	4.48[S]	3.64[S]
Head length(cm)	44.78 ± 0.84	42.57 ± 1.08	44.57 ± 1.50	47.40 ± 1.50	3.42	2.72	4.21	3.67[N]
Head weight(gm)	34.55 ± 0.73	32.86 ± 0.31	36.72 ± 0.96	36.78 ± 0.95	2.40	1.58[N]	2.68	1.99[S]
Days to flowering	66.78 ± 3.72	64.09 ± 2.17	67.61 ± 3.03	69.39 ± 2.32	9.55	8.57	7.58	6.31
Days to maturity	97.73 ± 2.12	95.27 ± 1.15	103.76 ± 1.98	96.2 ± 1.38	11.82	4.79	4.80[S]	3.57

Table 8: Regression coefficients for yield related traits in population 1008

	Season: April,1988						Season: October,1988					
	Kabete			Thika			Kabete			Thika		
Trait	c	t	S.E	c	t	S.E	c	t	S.E	c	t	S.E
Plant height (cm)	-1.679	1.421	0.012	-1.436	1.179	0.223	-1.758	0.200 *	0.810	1.136	0.553	0.051
Head length (cm)	3.322	2.835*	0.175	1.369	1.258	0.091	-1.018	1.072	0.491	1.047	4.853*	0.162
Head weight (gm)	5.694	6.873*	0.287	2.334	1.291	0.019	0.114	12.210*	0.050	0.195	23.570*	0.090
Days to flowering	-3.585	0.348	0.105	9.034	0.154	0.879	3.036	8.554*	0.552	-3.225	5.996*	0.374
Days to maturity	3.854	0.449	0.588	2.184	0.317	0.981	-2.717	7.286*	0.046	2.427	5.489*	0.481

S.E= Standard error for the estimate (c).
c= Coefficient of regression for the variable.
t= t statistic.
* = Significant, P = 0.05
Seed yield per plant is dependable variable in this analysis.

Table 9: Phenotypic correlations for population 1008 at Thika

		1	2	3	4	5	6
Seed yield per plant(gm)	1		0.23	0.26	0.26	0.19**	0.19**
Plant height (cm)	2	0.71		0.96	0.79	0.50	0.47
Head length (cm)	3	0.74	0.98		0.78	0.46	0.44
Head weight (gm)	4	0.96	0.68	0.72		0.30	0.28
Days to flowering	5	0.29	0.55	0.52	0.27		0.94
Days to maturity	6	0.27	0.52	0.49	0.25	0.95	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

Table 10: Phenotypic Correlations For 1008 Population at Kabete.

		1	2	3	4	5	6
Seed yield per plant (gm)	1		0.61	0.69	0.78	0.10^{NS}	0.12^{NS}
Plant height (cm)	2	0.66		0.90	0.70	0.24	0.25
Head length (cm)	3	0.69	0.93		0.73	0.19^{NS}	0.21
Head weight (gm)	4	0.90	0.78	0.82		0.09^{NS}	0.10^{NS}
Days to flowering	5	0.19^{NS}	0.54	0.53	0.27		0.91
Days to maturity	6	0.19^{NS}	0.54	0.53	0.27	0.98	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

with regression coefficient significantly different from zero whereas there was significant positive correlation between seed yield per plant and plant height, head length and head weight except for the days to flowering and days to maturity. The Thika, October, 1988 data indicated significant positive correlation of seed yield per plant to plant height, head length, head weight, days to flowering and days to maturity. Under this situation, plant height, head length, head weight, days to flowering and days to maturity may be useful traits for improvement work on seed yield. There seems to be very strong correlation between seed yield per plant to these quantitative traits (plant height, head length and head weight) given that fairly high correlation was also true for the traits at Kabete in April, 1988 and October,1988 data as for the Thika data. Consequently the three traits, plant height, head length and head weight are useful yield predictors in this study for population 1008. Plant height was significantly positively correlated to head length, head weight, days to flowering and days to maturity.

4.2.2 Multiple regression and multiple correlation on yield related traits in 1024 population (A. hypochondriacus).

Like population 1008, population 1024, both of which belong to A. hypochondriacus, did not show differences with regard to the seasonal means for Kabete data (Table 11). Locational means for the April data showed that days to maturity did not show differences. All the other five traits were different. Locational means for October data showed that only head weight and days to maturity showed differences between the two sites whereas all the other traits did not show any differences. Seasonal means for Thika showed that head weight did not vary with seasons whereas all the other four traits were varied with seasons.

Table 11: Mean values (x_i), standard error(S.E) and least significant difference(LSD) for six quantitative traits in population 1024

	Season: April, 1988		Season: October, 1988					
	Kabete	Thika	Kabete	Thika				
Trait	$x_1 \pm$ S.E	$x_2 \pm$ S.E	$x_3 \pm$ S.E	$x_4 \pm$ S.E	x_1 vs x_2	x_1 vs x_3	x_2 vs x_4	x_3 vs x_4
					$LSD_{0.05}$			
Seed yield per plant (gm)	17.16 ± 0.72	10.45 ± 2.89	17.26 ± 2.05	17.21 ± 0.75	4.32	6.11*	4.34	6.12*
Plant height(cm)	95.46 ± 2.66	74.48 ± 1.52	87.80 ± 9.39	103.19 ± 4.99	19.39	6.09*	21.13	10.38*
Head length(cm)	66.76 ± 2.73	42.20 ± 1.87	67.20 ± 8.84	58.14 ± 2.90	25.89	6.57*	18.48	6.86*
Head weight(gm)	47.64 ± 4.00	34.60 ± 0.77	54.56 ± 5.52	33.12 ± 2.36	13.54	8.09*	11.93*	4.93
Days to flowering	70.46 ± 0.88	65.96 ± 1.45	72.50 ± 3.53	73.19 ± 1.01	2.57	3.37*	7.29	3.51*
Days to maturity	102.16 ± 0.97	99.76 ± 1.28	106.05 ± 3.23	113.00 ± 0.98	6.70	3.19	2.74*	3.20*

Regression and correlation coefficients are given in Table 12 and Tables 13 and 14 respectively. The regression coefficient for plant height was significantly different from zero for the Thika, October,1988 data (Table 12). There were on the other hand, significant positive correlation between plant height and seed yield per plant, head length, days to flowering and days to maturity for the Thika, October data (Table 13). Plant height did not show significant correlation to head weight and days to flowering at Thika, April, season. The Kabete data showed strong correlation between plant height and the five other traits (Table 14).

The regression coefficient for head length was significantly different from zero for the Kabete April,1988 data whereas there was lack of significant difference from zero for the rest of the data on the head length at Kabete October and Thika, April and October . The correlation coefficients for head length indicated high significance correlation to seed yield per plant, plant height, days to flowering and days to maturity at Kabete (Table 14). The Thika, April,1988 data showed insignificant correlationship between head length and days to flowering whereas there were significant correlation coefficients between head length and the five other traits (Table 13).

Head weight seems to be strongly related to the seed yield per plant in 1024 population given that for all the data analysed over the two sites and two seasons, there was significant difference between the regression coefficient from zero. This is definitely a useful relationship for seed yield improvement given that the heavier the head weight the higher the plant yield as also confirmed by the significant positive correlation between the two traits over the period of study. Selection and breeding program to exploit

Table 12: Regression coefficients for yield related traits in population 1024

	Season: April, 1988						Season: October, 1988					
	Kabete			Thika			Kabete			Thika		
Trait	c	t	S.E	c	t	S.E	c	t	S.E	c	t	S.E
Plant height (cm)	-1.569	0.710	0.211	-3.971	0.537	0.567	-0.139	1.344	0.101	2.841	2.512*	0.131
Head length (cm)	0.114	4.408*	0.070	-9.729	1.337	0.679	5.364	0.566	0.473	2.085	1.137	0.831
Head weight (gm)	0.117	10.029*	0.062	0.096	6.225*	0.005	0.135	5.338*	0.140	0.265	10.935*	0.040
Days to flowering	-2.319	1.291	0.273	0.040	1.894	0.003	5.169	2.497*	0.021	0.333	1.293	0.032
Days to maturity	-1.572	9.601*	0.160	-2.112	0.855	0.420	0.297	1.155	0.050	-0.399	1.518	0.063

S.E= Standard error for the estimate (c).
c= Coefficient of regression for the variable.
t= t statistic.
* = Significant, P = 0.05
Seed yield per plant is dependable variable in this analysis.

Table 13: Phenotypic correlations for population 1024 at Thika.

		1	2	3	4	5	6
Seed yield per plant(gm)	1		-0.00**	0.21	0.79	0.52	0.38
Plant height (cm)	2	0.56		0.44	0.13**	0.18**	0.23
Head length (cm)	3	0.59	0.21		0.57	-0.13**	-0.22
Head weight (gm)	4	0.96	0.47	0.57		0.17**	0.05**
Days to flowering	5	0.29	0.57	0.27	0.27		0.95
Days to maturity	6	0.26	0.55	0.24	0.25	0.99	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

Table 14: Phenotypic correlations for population 1024 at Kabete.

		1	2	3	4	5	6
Seed yield per plant(gm)	1		0.61	0.83	0.92	0.33	0.33
Plant height (cm)	2	0.85		0.82	0.50	0.48	0.49
Head length (cm)	3	0.88	0.98		0.70	0.46	0.47
Head weight (gm)	4	0.95	0.82	0.87		0.27	0.28
Days to flowering	5	0.61	0.85	0.79	0.49		0.98
Days to maturity	6	0.63	0.87	0.80	0.51	0.98	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

higher plant yield through heavier head weight may therefore be very practical under the experimental locations for this study and areas with similar environmental conditions.

Days to flowering and days to maturity did not offer any significant regression coefficient except for days to flowering and days to maturity for the Kabete ,October,1988 and Kabete, April,1988 respectively. There was significant correlationship between seed yield per plant and days to flowering and days to maturity for both sites over the two seasons.

There seems to be seasonal effect on the correlation of yield related traits (Table 13). The Thika, April 1988 data gave many insignificant correlations for the six traits whereas the Thika October,1988 data greatly contrasted.

4.2.3 Multiple regression and multiple correlation on yield related traits in population 1034, (A. cruentus)

Regression and correlation coefficients are given in Table 16 and Tables 17 and 18 respectively.

Least significant difference comparisons for the means of the six traits of population 1034 (Table 15) showed that a part from head weight, the other traits were different for Kabete, April and October seasons means. On the other hand only plant height showed difference for the Thika, April and October seasonal means. The April, locational means showed that only seed yield per plant did not differ whereas all the other five traits had their means different. For the October, locational means, seed yield per plant, plant height and head length were different with head weight, days to flowering and days to maturity not showing difference.

Table 16: Regression coefficients for yield related traits in population 1034

Trait	Season: April, 1988						Season: October, 1988					
	Kabete			Thika			Kabete			Thika		
	c	t	S.E	c	t	S.E	c	t	S.E	c	t	S.E
Plant height (cm)	5.775	1.140	0.891	-9.151	0.279	0.998	-1.488	1.401	0.011	1.648	1.223	0.351
Head length (cm)	2.608	0.235	0.112	-1.375	2.404*	0.712	-4.063	3.989*	0.705	-1.052	1.012	0.010
Head weight (gm)	0.102	4.039*	0.251	0.119	14.062*	0.007	0.189	24.301*	0.084	0.247	23.613*	0.041
Days to flowering	8.869	0.891	0.992	0.890	1.321	0.756	1.890	0.100	0.128	-4.800	0.341	0.143
Days to maturity	-8.217	0.770	0.973	0.014	0.315	0.003	6.780	0.525	0.131	4.491	0.333	0.141

S.E= Standard error for the estimate (c).
c= Coefficient of regression for the variable.
t= t statistic.
* = Significant, P = 0.05
Seed yield per plant is dependable variable in this analysis.

Table 15: Mean values (x_i), standard error(S.E) and least significant difference(LSD) for six quantitative traits in population 1034

	Season: April, 1988		Season: October, 1988					
	Kabete	Thika	Kabete	Thika				LSD$_{0.05}$
Trait	$x_1 \pm$ S.E	$x_3 \pm$ S.E	$x_2 \pm$ S.E	$x_4 \pm$ S.E	x_1 vs x_3	x_1 vs x_2	x_3 vs x_4	x_2 vs x_4
Seed yield per plant (gm)	10.25 ± 0.11	10.29 ± 1.42	14.52 ± 0.62	17.02 ± 0.59	1.25*	2.83	1.70*	3.32*
Plant height(cm)	91.18 ± 1.94	85.39 ± 1.84	122.60 ± 2.64	96.19 ± 2.17	6.51*	5.31*	6.79*	11.37
Head length(cm)	45.98 ± 1.97	40.25 ± 1.40	85.28 ± 3.48	54.07 ± 1.99	7.95*	4.80*	7.96*	4.83*
Head weight(gm)	38.27 ± 0.78	33.18 ± 0.70	41.61 ± 3.84	43.68 ± 2.20	7.79	1.54*	8.79	7.49*
Days to flowering	70.46 ± 0.88	65.96 ± 1.45	72.50 ± 3.53	73.19 ± 1.01	2.57	3.37*	7.29	3.51*
Days to maturity	104.46 ± 1.14	98.25 ± 1.18	108.31 ± 1.23	113.30 ± 2.54	3.33*	3.26*	5.61	5.56*

For both the sites and the two seasons there was no significant regression coefficient for plant height whereas there was a significant positive correlationship between plant height and seed yield per plant, head length, head weight, days to flowering and days to maturity. Head length showed significant regression coefficient for the Thika, April,1988 and the Kabete, October,1988 data where both coefficients were negative of c= -1.375 and c= -4.063 respectively (Table 16).

There was significant positive correlation between head length and the other five traits over the two sites and two seasons. This is particularly interesting given the positive relationship of plant height to seed yield and subsequent positive relationship of plant height to head lenght. A combination of plant height and head length therefore can be useful for the imporvement of yield on 1034 under the study locations.

Head weight showed significant positive regeression coefficients over the two sites and two seasons for this populations. Also there was significant positive correlation between head weight and the five other traits except for the days to flowering and days to maturity for the April data under Thika conditions and days to maturity under Kabete conditions for the October 1988 data. Head weight was strongly correlated to seed yield per plant (tables 17 and 18) with correlation coefficients ranging between (r= 0.77 to r=0.96) over the two sites and two seasons. This is a useful observation particularly where the recovarable grain ralative to head size is not considered for the seed yield improvement.

Days to flowering and days to maturity showed insignificant regression coefficients over the two sites and seasons. There was weak correlation between days to flowering and seed yield per plant and similarly for days to

Table 16: Regression coefficients for yield related traits in population 1034

Trait	Season: April, 1988						Season: October, 1988					
	Kabete			Thika			Kabete			Thika		
	c	t	S.E	c	t	S.E	c	t	S.E	c	t	S.E
Plant height (cm)	5.775	1.140	0.891	-9.151	0.279	0.998	-1.488	1.401	0.011	1.648	1.223	0.351
Head length (cm)	2.608	0.235	0.112	-1.375	2.404*	0.712	-4.063	3.989*	0.705	-1.052	1.012	0.010
Head weight (gm)	0.102	4.039*	0.251	0.119	14.062*	0.007	0.189	24.301*	0.084	0.247	23.613*	0.041
Days to flowering	8.869	0.891	0.992	0.890	1.321	0.756	1.890	0.100	0.128	-4.800	0.341	0.143
Days to maturity	-8.217	0.770	0.973	0.014	0.315	0.003	6.780	0.525	0.131	4.491	0.333	0.141

S.E= Standard error for the estimate (c).
c= Coefficient of regression for the variable.
t= t statistic.
* = Significant, P = 0.05
Seed yield per plant is dependable variable in this analysis.

Table 17: Phenotypic correlations for population 1034 at Thika.

		1	2	3	4	5	6
Seed yield per plant (gm)	1		0.36	0.64	0.90	0.10**	0.10**
Plant height (cm)	2	0.65		0.78	0.51	0.55	0.45
Head length (cm)	3	0.45	0.58		0.81	0.36	0.29
Head weight (gm)	4	0.96	0.65	0.45		0.15**	0.13**
Days to flowering	5	0.23	0.60	0.37	0.21		0.91
Days to maturity	6	0.23	0.59	0.36	0.21	0.97	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

Table 18: Phenotypic correlations for population 1034 at Kabete.

		1	2	3	4	5	6
Seed yield per plant(gm)	1		0.50	0.74	0.77	0.19**	0.18**
Plant height (cm)	2	0.49		0.72	0.63	0.47	0.46
Head length (cm)	3	0.71	0.74		0.95	0.28	0.31
Head weight (gm)	4	0.95	0.60	0.83		0.21	0.22
Days to flowering	5	0.13**	0.49	0.24	0.17		0.90
Days to maturity	6	0.16**	0.51	0.29	0.19**	0.81	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

maturity to seed yield per plant for the Thika and Kabete October data and insignificant correlation between the traits for April 1988 data over the two sites. Days to flowering and days to maturity are particularly not very useful predictors of seed yield for the improvement on seed yield for population 1034 under both Thika and Kabete conditions. Plant height and head length are therefore most important yield predictors for 1034 under the Thika and Kabete conditions in this particular study.

4.2.4 Multiple regression and multiple correlation on yield related traits in population 434 (A. cruentus).

Least significant different for the means of the six quantitative traits of population 434 were assessed (Table 19). The Kabete, seasonal means offered no difference for any of the six traits. Thika, seasonal means showed that seed yield per plant and days to maturity were the only traits which showed difference. Seed yield per plant differed for the two sites for the April season. Plant height and head length showed differences for the two sites for the October seasons.

Regression and correlation coefficients are given in Table 20 and Tables 21 and 22 respectively. Plant height showed no significant regression coefficients over the two sites and the two seasons. There was a strong correlation between the plant height and head length for the Thika and Kabete April, 1988 data with correlation coefficients of r= 0.94 and r= 0.84 for Thika and Kabete respectively (Tables 17 and 18 repectively).

Head length did not offer significant regression coefficient over the two sites and two seasons. The correlation coefficients between head length and the five other traits were significant over the two sites and the two seasons. This result conforms to the other five traits for the variety 1034 which also

Table 19: Mean values (x_i), standard error(S.E) and least significant difference(LSD) for six quantitative traits in population 434

	Season: April, 1988		Season: October, 1988					
	Kabete	Thika	Kabete	Thika				LSD$_{0.05}$
Trait	$x_1 \pm$ S.E	$x_2 \pm$ S.E	$x_3 \pm$ S.E	$x_4 \pm$ S.E	x_1 vs x_2	x_1 vs x_3	x_2 vs x_4	x_3 vs
Seed yield per plant (gm)	16.60 ± 1.40	11.63 ± 0.35	14.78 ± 1.04	19.11 ± 2.81	3.47	2.87*	6.14	5.82*
Plant height(cm)	118.32 ± 7.81	119.80 ± 3.74	142.26 ± 4.56	118.65 ± 3.13	17.97	17.20	10.99*	9.69
Head length(cm)	49.68 ± 4.23	44.13 ± 2.02	54.44 ± 3.70	45.15 ± 2.71	11.17	9.31	9.11*	6.72
Head weight(gm)	50.47 ± 3.63	54.33 ± 3.23	57.53 ± 2.46	59.87 ± 3.83	8.71	9.65	9.04	9.95
Days to flowering	65.58 ± 1.13	67.87 ± 1.93	70.23 ± 1.45	69.25 ± 2.04	1.30*	4.44	5.01	5.61
Days to maturity	108.47 ± 1.20	109.53 ± 2.71	124.71 ± 3.17	120.75 ± 1.95	6.73*	5.89	7.39	6.63*

Table 20: Regression coefficients for yield related traits in population 434

	Season: April, 1988						Season: October, 1988					
	Kabete			Thika			Kabete			Thika		
Trait	c	t	S.E	c	t	S.E	c	t	S.E	c	t	S.E
Plant height (cm)	5.930	1.919	0.907	-1.641	1.798	0.125	-1.881	1.445	0.302	1.858	0.847	0.123
Head length (cm)	-6.674	1.180	0.657	-6.838	0.308	0.224	1.864	0.521	0.612	-7.461	1.191	0.989
Head weight (gm)	0.356	5.169*	0.008	0.133	3.235*	0.003	0.187	7.334*	0.009	0.400	13.753*	0.067
Days to flowering	-0.175	0.543	0.002	4.701	0.394	0.115	0.293	0.313	0.138	-2.051	7.138*	0.287
Days to maturity	-6.238	2.167*	0.888	-1.608	0.115	0.014	-0.709	0.304	0.330	2.883	9.922*	0.291

S.E= Standard error for the estimate (c).
c= Coefficient of regression for the variable.
t= t statistic.
* = Significant, P = 0.05
Seed yield per plant is dependable variable in this analysis.

Table 21: Phenotypic correlations for population 434 at Thika.

		1	2	3	4	5	6
Seed yield per plant(gm)	1		0.59	0.94	0.96	0.40	0.38
Plant height (cm)	2	0.65		0.55	0.73	0.61	0.56
Head length (cm)	3	0.92	0.83		0.94	0.46	0.42
Head weight (gm)	4	1.00	0.65	0.93		0.44	0.41
Days to flowering	5	0.33	0.79	0.57	0.33		0.97
Days to maturity	6	0.31	0.77	0.55	0.32	0.99	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

Table 22: Phenotypic correlations for population 434 at Kabete.

		1	2	3	4	5	6
Seed yield per plant (gm)	1		0.83	0.81	0.95	0.44	0.44
Plant height (cm)	2	0.66		0.83	0.84	0.72	0.70
Head length (cm)	3	0.95	0.71		0.89	0.58	0.53
Head weight (gm)	4	0.98	0.71	0.97		0.49	0.49
Days to flowering	5	0.17**	0.56	0.27	0.19**		0.95
Days to maturity	6	0.16**	0.54	0.26	0.19**	1.00	

Upper half are April, 1988 correlations while the lower half are the October, 1988 correlations.

NS = not significant, P = 0.05

belongs to the same species as for 434. It follows therefore that the head length and plant height are good yield predictors for the two varieties and may also be useful predictors for other varieties within the species.

Head weight is the only trait which showed significance regression coefficient over the two sites and two seasons. There was a very strong correlation between the head weight and the seed yield per plant. This is a very useful observation as regards the seed yield improvement on the species. The correlation between the head weight and plant height was significant for all the data over the two sites and two seasons. This observation further gives insight into the stategy for the breeding program for exploitation of the yield through plant height and head weight. Also there was significant correlation between head weight and head length and could be exploitable by use of appropriate selection and mating design to improve the yield.

A part from the Kabete April,1988 data, days to flowering and days to maturity were significantly correlated to the seed yield per plant (Tables 17 and 18). There was significant regression coefficient for the Thika, October 1988 data of c= -2.051 for the days to flowering. Days to maturity registered significant regression coefficient for Kabete, April 1988 and Thika, October 1988 data. The two traits, days to flowering and days to maturity did not offer very strong correlations to the seed yield for this variety.

For the six quantitative traits assessed for the yield prediction, plant height, head length and head weight offered very strong indication of the levels of the seed yield per plant. Improvement on seed yield per plant can be a good indicator of the yield improvement on a variety subsequently plant length, head length and head weight are useful yield predictors in this study for this population 434.

CHAPTER 5

DISCUSSION:

5.1: Outcrossing rate in grain amaranths:

The high level of heterogeneity within populations 1024 (*A. hypochondriacus*) and 434 (*A. cruentus*) means that without further inbreeding and selection, the two populations cannot be used as pure lines. Other genetic marker traits could be utilized to confirm heterogeneity in populations with similar pigmentation. The conventional methods used to distinguish various cultivars in the genus *Amaranthus* are largely based on morphological a longside physiological characterization. A combination of morphological, physiological, cytological and chemical charaterization can enhance determination of the variability more accurately in the grain amaranth varieties (Xu,1987 and Gudu and Gupta, 1988a). The range of variation as related to the gene frequencies in each population has not been properly established. Without restricted breeding, the gene frequencies in grain amaranth populations will continue to show wide allelic frequency variation. The heterogeneity in the dominant mother populations (Table 3) is probably contributed by natural intraspecific and interspecific hybridization and introgression between different taxa (Sauer, 1950; Grant, 1959 and Edema and Fakorede, 1978).

The genus *Amaranthus* from the four populations(1008,1024 for *A. hypochondriacus* and 1034 and 434 for *A. cruentus*) used in this study presented a wide intraspecific and interspecific outcrossing rate variation. This confirms wide dispersion between outcrossing rate estimates in grain amaranth reported by Jain *et al* (1982). The breeding system of this crop

calls for development of a specific breeding system package for each ecogeographical condition if the desired results in the crop improvement are to be achieved.

Outcrossing rate involving population 1024 and 1008 probably requires more elaborate search for it would be interesting to establish further variation for intraspecific outcrossing rate in A. hypochondriacus. Lack of significant difference in the seasonal outcrossing rate estimates at Thika implied that seasonal variation might not be an important factor in influencing the intraspecific outcrossing rate in the species at this location. Also more such experiments on outcrossing rate estimates under the Thika environment using more genetic markers and more dominant pollinator populations for the species can be very useful in studying the breeding system of this species.

The fact that there was locational and seasonal intraspecific outcrossing rate variation in the species indicate that genotype x environment interaction may be an important factor in the outbreeding of this particular species. Seasonal and locational variation would lead to differential outcrossing rate of various genotypes. It has been reported by Jain (1969) that genetic differences in selfing probabilities lead to the fixation of alleles with higher probabilities of selfing. However, Jain and Marshall (1968) noted that differential response of such alleles to variations in environmental conditions would counteract their fixation by favouring different allels in various environment. Such a season dependent or locational dependent regulation of outcrossing rate differ from the supposition that occassional outbursts of outcrossing provides new recombinants sporadically in the breeding populations(Stebbins, 1957). The estimates on intraspecific outcrossing rate (Table 5) showed that the outbreeding of the species A.

cruentus may be greatly environment dependant other than being attributed to largely the flower architecture. Environmental factors such as pollinator insects and geographic conditions could have greatly influenced the outcrossing rate estimates. Environmental differences have also been shown to influence outcrossing rates significantly in monoecious crops by Frankel and Galun, (1977); Moran and Brown, (1980) and Freeman et al.(1981).

In species that are not obligate outcrossers or obligate self pollinators, the frequency of cross-fertilization may vary between 0 and 100 per cent. Rough estimates of the cross-fertilization frequency may be deducted from observations of pollinator behaviour and from knowledge of the flower structure . Protandry and long, exerted styles obviously promote outcrossing and proximity of receptive stigmas to mature anthers promotes self-pollination (Vasek, 1968). Monoecy, protogyny, insect visit have also been reported to be responsible for wide variations in natural outcrossing rates in the grain amaranths among genotypes and geograhical regions (Jain et al. 1982). In the present study visual observation on the pollinator behaviour particularly, the bees , was done without taking any data on their population density during the study. It was visually noted that Thika had a higher number of population of bees. The high population of bees must have directly contributed to the higher rates of outcrossing observed in this site. The experimental plots at Thika were mostly surrounded by , among other things , many ornamental plants, a large plantation of the pineaple and many fruit trees. These features would be expected to have high insect populations. Unlike Thika, Kabete experimental plots were mostly surrounded by maize plantations. The fact that there were seasonal and locational outcrossing rate variations for both the two species strongly suggest that genotype-environment interaction is an important factor in influencing outcrossing rate in grain amaranths. The seasonal and locational variation seemed to have played a large role in influencing the

pollinator insect behaviour which consequently influenced the estimates of outcrossing rates greatly. There was great genetic variation in outcrossing rates in the genus Amaranthus as showed by the two species (A. hypochondriacus and A. cruentus) in this study. This confirms report by Hauptli and Jain (1985). The breeding system in the amaranth can be represented by the outcrossing rate parameters as suggested in this study and the sex ratio with glomerules as reported by (Hauptli and Jain, 1985 and NBRI, 1987). Such a genetic component of the variation in the breeding system has significant implication in the evolution of amaranth species and landrace under domestication. The knowledge of the pollination biology is thus essential to an understanding of the evolutionary process in plants. For crop plants, estimates of outcrossing as compared to selfing rate are of primary interest since the choice of a breeding method and it's necessary modifications depend in large part on the biology and mating system of the crop.

A. cruentus and A. caudatus are not reproductively isolated "biological species" and for most purposes they are pooled together in a crop development breeding program (Jain et al.,1982). This, therefore, implies that an attempt to describe the breeding system of A. cruentus could easily be extended to cover A. caudatus. In this study, the breeding system of A. cruentus has been described using intraspecific and interspecific outcrossing rates. There seems to be a higher propensity in the intraspecific outbreeding for the A. cruentus compared to A. hypochondriacus on the basis of Kabete data (Table 5) despite the fact that the overall mean intraspecific outcrossing for each species oscillated around 10 per cent.

Very low values of interspecific outcrossing rates were observed for both the species in this study. Also believed to be important factors influencing the observed estimates of interspecific outcrossing rates were 1) genotypic

weedy amaranths species is of interest in determining the feasibilty of wide gene transfers in plant breeding. Jain et al. (1984) indicated the presence of linked character complexes differentiating the crop (A. cruentus) and weed (A. retroflexus).

Male sterility has been reported in A. hypochondriacus variety Jumla (Gudu and Gupta, 1988b) it would be useful to ascertain if the male sterility is wide spread in this species. Male sterility has potential application in plant breeding both in facilitating genetic recombination and in the production of commercial hybrid seeds. The presence of male sterility in grain amaranth may be very useful in eliminating the laborious process of emasculation particularly if the male sterlity is transferable to other grain amaranth varieties. For very low outcrossing rate estimates, it is possible that the breeding system for the species might have shifted toward a greater selfing rate between the advanced cultivar populations. Also, a mixed stand of short plant pollinators and taller mother plants under wind pollen transfer sytem could be contributed to the low outcrossing rates. Amaranth has been reported to be dependant on both wind (Simmond, 1979) and honeybee (Singh, unpub.) pollen vectors.Differences in population structure may easily have contributed to a large proportion of the outcrossing rate variation at both intraspecific and interspecific levels. Using the breeding system as represe-nted by the outcrossing rates it is possible to understand and appreciate the evolutionary history and breeding systems development of a crop species. The population genetic analyses of mating system are also indispensable in analy-sing the evolutionary process in polymorphic mating systems. The breeding system in grain amaranth is very complex and probably depend upon interactions between numerous morphological and functional characteristics of plants and their environment (Hauptli and Jain, 1985). The interactions seems to be true given the locational and seasonal outcrossing rate variability as recorded in

this study (Table 5 and 6). Jain and Marshal (1968) reported genotype x environment interaction for the variations in outcrossing rate as relates to genetic variation in selfing populations using barley. Jain et al (1982) observed a large dispersion between outcrossing estimates obtained from populations of A. cruentus. Differences in density and structure of the populations could explain the wide dispersion Jain et al (1982). In the present study locational, seasonal and population structural differences seems to explain the variation in the outcrossing rate estimates. Such large variance among populations for any measure of breeding system are not uncommon unless major genes for heterostly, male sterility or cleistogamy are present (Hauptli and Jain, 1985). In the present study the range of outcrossing rates conforms to Simmonds' (1979) categorization of grain amaranth as an outbred-inbred crop, or often cross-pollinated class as for sorghum and cotton. Under very strong environmental influence it would be expected that grain amaranths can exhibit wider variations in the outcrossing tendency. It is not yet clear as to what factors are very important in influencing the outcrossing rate in grain amaranth . Hauptli and Jain (1985) used the estimates of outcrossing rate variation among individuals and their response to mass selection to describe the breeding system of the grain amaranth population. Harding and Tucker (1964) and Green et al (1980) reported inheritance of breeding system characteristics of many legumes to be polygenic and intermidiate in outcrossing expression. Drayer (1959) Holden and Bond (1960) described field beans to be similar as for the case of grain amaranth in their breeding system as reported by Hauptli and Jain (1985).

Plant breeders have identified the importance of breeding system variables in designing optimal procedures for recombination, selection and cultivar development . Quantitative studies on natural selfing and outcrossing rates are of necessity for at least three reasons: (a) new breeding procedures

that emphasize recurrent cycles of recombination, and therefore, manipulation of breeding system (Grindle and Frohberg, 1966; Kehr, 1973); (b) population genetic research in relation to the theory of population structure and dynamics under mixed selfing and random mating (Allard et al, 1968; Jain, 1978) and (c) domestication of many new crop plants with a greater awareness of population studies on genetic resource Berry et al,(1970,1975). Studies on barley (Hordeum vulgare L.), lima bean (Phaseolus linatus L.), wild oats (Avena fatua L.), all assumed to be predominantly selfing species, have shown that low outcrossing rates from 1 to 10 per cent could play a significant role in the genetic structure of their populations (Harding and Tucker, 1964; Jain and Allard, 1960; Jain , 1976). The presnt study, using the intraspecific and interspecific outcrossing rate variation suggested existence of genetic structural variation, within the two species (A. hypochondriacus and A. cruentus). The role of breeding system in the genetic structure of a species that enables it to meet the conflicting requirements of long term flexibility and immediate fitness was examined by Mather (1943), Stebbins (1957), Grant (1958) and Allard et al (1968).

The intraspecific outcrossing rate for the grain amaranth on the basis of this study averaged 10.65 per cent indicating a high proportion of the inbreeding tendency. Furthermore, because of enviromental effects , the study suggests that locational improvement programmes could better exploit organized introductions, mass selection, pure line selection, hybridization, backcross breeding and other methods for breeding self-pollinated crops like sorghum and cotton. Ayiecho (1985) reported use of mass selection and S1 selection method for amaranth yield prediction. Mass selection and S1 selection may be useful breeding methods for the grain amaranths as regards the finding in the present study. Breeding system parameter for grain amaranth collections or landraces

are largely unknown despite the fact that New world populations exhibit predominantly selfing tendency coupled with low heterozygosity (Hauptli and Jain, 1984a). Populations of grain amaranths are distinct and vary in their levels of polymorphism consequently useful in crop imporvement and development programs. Vaidya and Jain (1985) determined response to mass selection for plant height and grain yield in grain amaranths. The results of Vaidya and Jain (1985) indicated genetic variability within the amaranth landrace populations. This further suggests the potential for grain amaranth populations improvement. As grain amaranth breeding programs are established it will be desirable to know which breeding methods and selection criteria will give the greatest short term gains in seed yield. In the long term, it will also be important to know what conditions will provide the most efficient and sustained response to selection. As a mixed mating crop, a wide range of breeding methods are feasible. Pedigree systems that lead to the development of pure lines and the population improvement schemes that maintain selections in variable bulk populations can also be exploited for grain amaranths. The mixed mating system of grain amaranth requires good understanding of the natural outcrossing rates to determine the amount of isolation and pollen control needed to achieve a particular breeding system. This would be useful in achieving breeding system that would vary from self-pollination in the development of pure lines to high outcrossing in the development of random mating populations. The most economical breeding method for grain amaranths would be expected to exploit natuaral pollination without having to rely on controlled selfing of panicles or enforced cross-pollination.

5.2: Yield prediction in grain amaranths.

Mean values of the six quantitative traits investigated in this study indicated variation when subjected to least significant difference test ($LSD_{0.05}$) for fairly a good number of the cases tested. The variation that exists within a population over seasons in an area is particularly useful if exploited for selection response with subsequent selection gain. The mean seed yield per plant for the dominant pollinator populations 1024 (A. hypochondriacus) and 434 (A. cruentus) were mostly higher compared to the two populations 1008 (A. hypochondriacus) and 1034 (A. cruentus) for the Thika, April season. This observation is believed to have been due to more vigorous vegetative phase exibited by populations 1024 and 434. Mean seed yield per plant for population 434 was fairly high compared to seed yield for population 1034. Population 434 was visually observed to have brown seed whereas population 1034 had black seed without taking any data and seed yield per plant seems to be correlated to seed colour. Earlier Olufolaji et al (1988) reported that black seeded cultivars of grain amaranths are poor seed yielders compared to the white seeded cultivars.

Multiple regression and multiple correlation analyses indicated that the best predictor variable for seed yield per plant in all the four populations were constantly plant height and head weight. Earlier, plant height had been reported to be one of the best amaranth grain yield predictors (Hauptli and Jain, 1984a; Ayiecho, 1985). Graham and Lessman (1966) noted that differences between yield of short and tall plants were due to differences in micro-environment around the plants. Hauptli and Jain (1980) reported that taller plants yielded higher than shorter ones. Ayiecho (1985) reported positive

correlation of plant height to seed yield in two populations of grain amaranths (A. cruentus and A. hypochondriacus). It would be undesirable to achieve higher grain yield by increasing plant height due to lodging tendency as large losses in seed yield may occur due to lodging.

Head weight offered good prediction levels for seed yield for all the populations considered in the present study. Ayiecho (1985) reported head weight as a useful predictor for seed yield in grain amaranth. Head weight seems to be closely related to the other traits (plant height, head length, days to flowering and days to maturity) also investigated in this study. Head weight, therefore, may be a useful variable seed yield parameter for yield prediction in grain amaranth particularly for A. hypochondriacus (1008 and 1024) and A. cruentus (1034 and 434). Days to flowering and days to maturity were closely related for the four populations but mostly insignificantly correlated to seed yield per plant. These traits were not useful predictors of yield in the four populations of grain amaranth. For marginal areas, early flowering varieties of grain amaranths would be ideal to exploit fully the early periods of good rainfall in these areas. Ayiecho (1985) described grain amaranth as a potential health food and cash crop on marginal lands. On the other hand late flowering varieties of grain amaranths would be most profitable in the high rainfall areas.

Combination of dwarfism and heavier head weights might be a very useful avenue to enhancing higher yields in grain amaranths. Dwarfing genes have been reported in grain amaranth (Ayiecho 1985; Kulakow,1987) which can be utilized in a breeding programme tuned to improving seed yield coupled with reduction of lodging losses. For a more comprehensive yield prediction, there would be need to investigate on the genotype x environment interaction in order to assess the stability of the available grain amaranth populations over

different eco-geographical zones. This would help identify suitable population for the different locations with an aim of higher seed yield per plant for those specific areas.

Seed yield per plant seems to be closely related and correlated to plant height, head length, head weight, days to flowering and days to maturity under Kabete conditions (Table 14). This information is particularly useful for the improvement on yield on the variety under the Kabete conditions. The increased yield arising from bigger plants probably was due to improved source-sink relationships as a result of increased foliage and vegetative parts which were able to support the higher seed yield. An investigation on the genotypic correlationship of these six quatitative traits would be useful to determine the extent of the phenotypic correlations reported in the present study. While traits like leaf length, node number, plant height, days to flowering, seed yield: height ratio, head weight , threshing percentage and harvest index had been shown as important seed yield predictors (Hauptli et al, 1985 and Ayiecho, 1985) the present study has tried to bring days to maturity into the picture. Days to maturity seems to be useful in amaranth breeding as the trait showed fairly high variations over the seasons at both sites and over the locations for both seasons.

Seed yield per plant showed very high correlation to plant height, head lenght and head weight whereas correlation coefficients between seed yield per plant to days of flowering and days to maturity were mostly small or not significant for population 1008 (A. hypochondriacus). This relationship suggests that plant height, head length and head weight could be useful yield predictor variable for the population under the two sites. On the other hand population 1024 (A. hypochondriacus) contrasted despite the fact that head

weight and head length remained highly correlated to seed yield for the Thika, October data (Table 13). The quantitative traits correlationship variation for the two populations 1008 and 1024 of A. hypochondriacus suggest intraspecific genetic variation which may be useful for crop improvement programme. Phenotypically and morphologically, the two populations differ and consequently difference in the quatitative traits performance would be expected. Table 14, showed that head length and head weight were very good yield predictors for seed yield alongside the significant regression coeffient for particularly head weight. The present study suggest that head length and head weight may be useful yield predictor variables for population 1024 under the two sites. Like population 1008 (A. hypochondriacus) population 1034 (A. cruentus) showed strong correlation between seed yield per plant to plant height, head length and head weight. Head weight particularly was very closely correlated to seed yield per plant as observed for both cases of the multiple regression coefficients and the multiple correlation coefficients (Tables 16 ,17 and 18). Head weight was particularly useful yield predictor variable for the population 1034 in the present study.

Head weight showed quite strong relationship to seed yield for population 434 (A. cruentus). Therefore, like population 1034(A. cruentus), head weight seems to be good yield predictor variable for population 434. Despite little variations, the present study recorded head weight as the best yield predictor variable for the four populations used in the study.

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Appendix I: Crossability within and between cultivated *Amaranthus* species

	A. cruentus	*A. hypochondriacus*	*A. caudatus*	*A. edulis*
A. cruentus	HF			
A. hypondandriacus	MF, I	HF		
A. caudatus	d, I	LF, abn	MF, LF	
A. edulis	X	LF	MF	HF

HF = high fertility

MF = moderate fertility

LF = low fertility

d = died at seedling

abn = abnormal growth

X = failed

Source: Jain *et al* (1984).