CHAPTER 2
LITERATURE REVIEWS

2.1 Number of gene control

Quantitative characters are generally controlled by polygenes or multiple genes on which the Mendelian ratios cannot be exhibited by their quantitative differences. Thus, methods of Mendelian analysis are inappropriate for identifying the number of gene control and their actions (Falconer, 1989).

The genetical analysis of quantitative traits cannot follow the standard procedure used to analyse major gene traits such as looking for a one-gene (3:1 or 1:2:1) or two-gene (15:1 or 9:3:3:1) phenotypic ratios in an F2. Because it is not possible to follow the segregation of the separate and underlying polygenes, therefore, it is necessary to look at the degree of similarity or difference among related individuals and families by using various statistics such as means, variances, covariances, regressions and correlations.

The number of gene control of quantitative characters are important for varietal improvement. It is difficult to examine the number of gene pairs for controlling quantitative traits by standard procedure. The number of gene pair control was estimated by these formulas, such as, Barton (1951), using the mean of parents and F1 and variance of F1 and F2; Sinnot *et al*. (1953), using mean of parents and variance of F1 and F2; Mather and Jinks (1982) used estimate of population mean and genetic effects; Falconer (1989), estimated by using variance in a segregating F2 and variance within and between groups; Wright (1968) and Kast (1983), using the means and variances of six basic generation (P1, P2, F1, F2, BC1 and BC2). Poehlman and Sleper (1995) proposed the procedure to examine the number of gene pairs to control quantitative traits by using mean values of parents and variances of F1 and F2.

The number of gene pair control of quantitative characters had been studied and reported in many crops. Chaitieng *et al*. (2003) reported that the resistance to

powdery mildew in mungbean was controlled by a single dominant gene. Jacobs and Broers (1989) reported that the number of effective factors controlling on latency period of wheat leaf rust in spring wheat was estimated as one or two for Akabozu, three or more for Westphal 12A, and two or three for BH 1146 variety. In this crop, Snijders (1990) reported that the number of segregating genes governing to head blight disease caused by *Fusarium culmorum* was between one to six genes, and Danon and Eyal (1990) studied in wheat and found that the resistance to *Septoria tritici* could be controlled by a small number of genes. In maize, Landi *et al*. (1990) concluded that the minimum number of genes involved in the control of chlorsulfuron response was estimated to be four for shoot height and five for shoot weight. Unay *et al*. (2004) found that the number of genes which controlled yield in maize was approximately 4 genes, and k value was 3.929.

2.2 Gene and gene actions

Fasoulas (1973) pointed out that the expression of genes resulted from both allelic and non-allelic interaction. Allelic gene action may express in terms of dominance, codominance, semidominance and recessive; but non-allelic gene action will express as epistasis, co-epistasis, semi-epistasis and hypostasis. The behavior of gene expression of any genotype or character will involve any one of the following actions (1) additive gene action, (2) dominance gene action and (3) non-allelic gene action or epistasis. In living diploid species, if trait is controlled by a single gene (A, a), three genotypes, AA, Aa and aa will be expressed and each of genotype will show genotypic value which deviate from the center between AA and aa genotype which can be observed in the following figure:
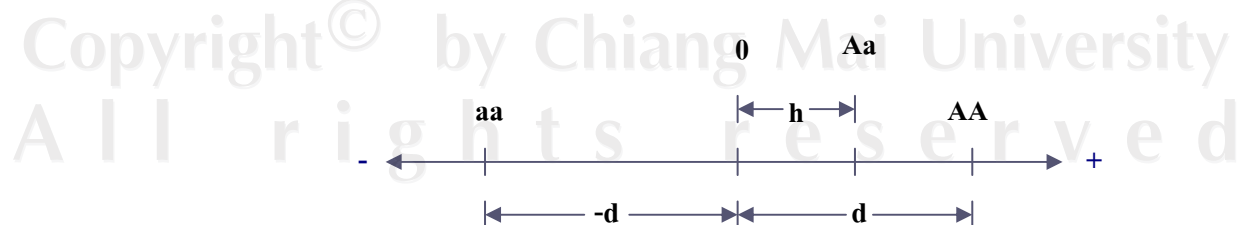
[d] = Behavior of additive gene action, genetic variation is fixed.

[h] = Behavior of dominance gene action, genetic variation is not fixed or unfixable heritable variation.

In addition, levels of dominance gene action of each trait can be explained in terms of relationship between [h] and [d] as follows:-

[h] = [d]	is defined as complete dominance
[h] > [d]	is defined as over dominance
[h] < [d] ; [h] ≠ 0	is defined as partial dominance
[h] = 0	is defined as no dominance

Mather and Jinks (1982) illustrated by reference to an F2 in which generation for all the types of interaction show characteristic segregation ratios. The standard F2 segregation is grouped into four phenotype classes with frequencies 9:3:3:1, the classical complementary genes with 9:7, the classical duplicate genes with 15:1, the complementary interaction becomes the classical recessive epistasis with 9:3:4 and the duplicate relation becomes the classical dominant epistasis with 12:3:1 ratio. Indeed, any interaction of two genes can be achieved by imposing appropriate conditions.

The study of gene action in azuki bean under highland growing conditions in Thailand had been reported by Kunkaew *et al.*(2006; 2007a; 2007b) which indicated that there were the importance of both additive and non-additive gene effects for number of branches per plant, seed size and seed yield per plant.

The works of gene action in other crops were reported such as Paschal and Wilcox (1975) who reported in soybean that mean square for g.c.a. was significant for yield, indicating the importance of additive genetic variance, and this trait showed year x g.c.a. interaction was significant but year x s.c.a. not significant, indicating s.c.a. was more stable than g.c.a. for yield in this crop. Malhotra and Singh (1990) reported in chickpea that cold tolerance was governed by both additive and non-additive gene effects with the preponderance of additive gene effects. Sarawat *et al.* (1994) reported in pea (*Pisum sativum* L.) that both additive and non-additive gene effects were important in the expression of grain yield, total dry matter, harvest index, and so on. Lange *et al.* (1995) reported in wheat that dominance effects were generally much higher than the additive effects, especially for plant regeneration.

2.2.1 Combining ability

Combining ability is the relative capacity of an individual to transmit a desirable characteristic to its progeny (Hayes and Immer, 1942).

The concept and application of combining ability was first employed by corn breeders. It was widely used to test the potential performance of inbred lines. The tested inbred lines were either saved or discarded, based on the mean of their respective crosses. Much time and effort was required in making and testing potential parental combinations when the number of lines became large. Jenkins and Bruson (1932) proposed a more efficient method of testing inbred lines. This method was to cross the selected inbred lines with a commercial variety, then compared the performance of the progeny of such crosses. Using this method, they suggested that it is possible to eliminate 50 % of the lines without danger of losing any superior materials. Since then, the inbred-variety method has been used extensively in corn breeding programs.

Sprague and Tatum (1942) defined combining ability in terms of general and specific combining ability, general combining ability is the average performance of a line in hybrid combination, and as such, general combining ability is recognized as primarily a measure of additive gene action. Specific combining ability describes those instances in which certain hybrid combinations do relatively better or worse than would be expected, based on the averaged performance of the lines involved. It is regarded as an estimation of the effects of non-additive gene action.

A diallel crossing system, proposed by Griffing (1956), is meant one in which a set of p inbred lines is chosen and crosses among these lines are made. This procedure gives rise to a maximum of p^2 combinations. Data from such combinations can be most conveniently set out in a p x p table in which Xii represents the mean value for the ith inbred, Xij the mean value for the F1 resulting from crossing the ith and jth inbreds, and Xji represents its reciprocal. Thus, the p^2 combinations can be divided into three groups: (1) the p parental lines themselves, (2) one set of 1/2 p(p-1) F1's and (3) the set of 1/2 p(p-1) reciprocal F1's. The study of combining ability by diallel crossing method had been used by most of scientists, such as Hayman (1954), Griffing (1956) and Gardner and Eberhart (1966).

Four Griffing's experimental methods for diallel analysis were; (1) parents, one set of F1's are included and reciprocal F1's are included (all p^2 combinations), (2) parents and one set of F1's are included but reciprocal F1's are not (1/2 p(p+1) combinations), (3) one set of F1's and reciprocal are included but not the parents (p(p-1) combinations) and (4) one set of F1's but neither parents nor reciprocal F1's is included (1/2 p(p-1) combinations). Each method has two models for experimental materials. In model I, the experimental material is to be regarded as the population about which inferences are to be made. The objectives are to compare combining abilities of the parents when the parents themselves are used as testers, and to identify the higher yielding combinations. In model II, the assumption is that we are dealing with random samples from some parent population, and the inferences are not to be made about the individual lines in the sample but about the parameters in the parent population. Diallel mating designs are an important tool in breeding programs to obtain information on inheritance. The DIALLEL-SAS program has been developed recently by Zhang and Kang (1997) to analyse diallel-cross data and has been extensively used in crops such as maize (*Zea may* L.), wheat (*Triticum aestivum* L.), rapeseed (*Brassica napus* L.) and so on (Zhang and Kang, 2005).

Combining ability in azuki bean crosses was studied by Kunkaew *et al*. (2006; 2007a) which indicated that some yield components such as number of pods per plant and 100-seed weight were polygenetically controlled and the additive genetic effects were important to the inheritance of these traits and the expression of additive genes was influenced greatly by environments. In soybean, Kunta *et al*. (1997) revealed that SCA mean square was highly significant for seed yield which indicated that non-additive gene effect was involved in the expression of this trait, both GCA and SCA were stable in performance over environments for seed yield. These similar results were reported in this crop by Cho and Scott (2000) who found that significant g.c.a. was caused mainly by additive effects, even though non-additive effects may also be involved. Large positive g.c.a. values indicated effective transmission of genes for seed vigor from parents to their offspring. Significant positive g.c.a. effects were found for seed weight in all large-seeded parents, but nearly all small-seeded parents showed significant negative g.c.a. effects for seed weight. These results indicated that genes associated with seed weight in large-seeded parents combined positively in

these crosses because it was easier to fix these genes due to the additive nature. Both g.c.a. and s.c.a. were significant for seed weight of F2, and g.c.a. was positive for large and negative for small-seeded parents. It is possible that additive x additive variability might have contributed to seed weight of F2 by small-seeded parents.

Layrisse *et al*. (1980) reported in peanut that additive genetic effects were more important than non-additive effects for seed yield, seed size, protein and oil content, and so on, and revealed that a Spanish line and a Valencia-like intermediate line from the Guarani region had the highest g.c.a. effects for fruit yield, seed yield and meat content and transmitted consistently their characteristics to their F2 progeny.

Ranalli *et al*. (1989) revealed that additive genetic components were important for characters such as day to flowering, plant height, nodes and pods per plant in pea. As a consequence, an appropriate selection method such as a pedigree method was recommended for handling the segregating generations.

Combining ability analysis has been used by most plant breeders for evaluating parents or inbred lines in producing superior progenies or F1 hybrid cross in many crops, such as, in chili pepper, Marin and Lippert (1975) reported that the g.c.a. sum of squares which contributed to total variance greatly exceeded that of s.c.a. for endocarp, seed, stem, placenta and exocarp. Additive gene action, therefore, is predominant in the expression of variability for component percentages in dry chili fruits within this population. Lack of significant heterosis in hybrids further supports the role of additive gene action. The g.c.a. x year interaction is not strong, as in this case, and the performance of a parent agreed with its g.c.a. value. The predominance of g.c.a. over s.c.a. values were recorded for all characteristics evaluated in this chili pepper study, suggesting that a recurrent selection program incorporating germplasm from at least four parental entries selected on the basis of g.c.a. peformance is a logical approach to population improvement.

Young and Virmani (1990) reported in rice that cytoplasmic effects on g.c.a. is important for proper assessment of different parents in hybrid rice breeding programs, and found that A4 (IR54752A) and A8 (IR22107-113-3-3A) parents showed consistently positive, but not always significant, cytoplasmic effect on g.c.a. for yield in all six environments. Cytoplasm appeared to have less influence on s.c.a. effects for yield. Also it appears that cytoplasmic effects on s.c.a. are not strong as on g.c.a.

Barten *et al*. (1993) revealed that the blossom-end scar index (BSI) in tomato, showed significant g.c.a. and s.c.a. effect in both environments, and revealed that estimated variance components for g.c.a. and s.c.a. effects indicated that BSI inherited mainly additively in both environments. Variation among the interaction of g.c.a. effects with environments was highly significant, whereas s.c.a. x environment interaction were insignificant.

Simon (1995) reported in onions that parents with low pyruvate and solid levels had highly significant negative g.c.a. effects whereas those with high levels had highly significant positive g.c.a. effects, so g.c.a effect is important to the overall analysis of variance.

Kang *et al*. (1999) reported in maize that the g.c.a. effect and year x g.c.a. interaction effect for rind puncture resistance were significant for second internode but not for the third internode, and s.c.a. effects were not significant for either internode. Rind puncture resistance would be a relatively easy trait to improve, using germplasm developed from the seven inbred lines evaluated in this study because g.c.a. was of primary importance and because of the absence of otherwise complicating s.c.a. effects and year x s.c.a. effects. However, breeders would need to measure rind puncture resistance in more than one environment to make environment-dependent estimation more precise.

Mwanga *et al*. (2002) reported in potato that g.c.a. effects were more important than s.c.a. effects for resistance to sweetpotato virus disease (SPVD). Resistant parents exhibited high g.c.a., indicating that additive gene effects were predominant in the inheritance of resistance to SPVD and recovery.

2.2.2 Generation mean analysis

Gene action of each quantitative trait can be evaluated by generation mean analysis. Several models have been developed for analysis of generation mean, such as, Anderson and Kempthorne (1954), Hayman (1958), Van der Veen (1959), Gamble (1962) and Gardner and Eberhart (1966). Procedures used to estimate mean and variance of quantitative traits were proposed by using six basic generations which included parents (P1 and P2), F1, F2 and first two backcrosses (BC1 and BC2). Additive (d), dominance (h), and epistatic interaction (i, additive x additive; j, additive

x dominance; and l, dominance x dominance) are parameters of gene actions. Some important crops had been reported on genetic effects of genes for controlling quantitative traits. Chaitieng *et al.* (2003) reported in mungbean that both additive and dominant gene effects were observed similarly in magnitude and were responsible for the inheritance of powdery mildew resistance whereas epistatic interaction was not found in any of the crosses. Jogloy *et al.* (1999) studied in peanut crosses and found that additive gene action was important for disease score of rust, late leafspot and lesion number per 100 cm^2 of leaf area of rust. Generation mean analyses were reported in other crops, such as, in wheat, Mullaney *et al.* (1982) reported that additive gene action was of major importance in the inheritance of lesions per cm^2 and percent necrotic leaf area in wheat. Epistatic gene effects were significant in one or more tests for both characters affected. The inconsistency of gene effect estimates over the three tests was in part due to low precision, but also illustrated the sensitivity of the host-pathogen interaction to small changes in environmental conditions. Jacobs and Broers (1989) reported in this crop and revealed that additive component appeared to be the most important factor, the dominance component was less important, and found that additive x additive, additive x dominance and dominance x dominance components were of minor importance for latency period of wheat leaf rust in spring wheat. And in this crop, Snijders (1990) reported that the joint-scaling test showed that the additive-dominance model fitted for most crosses and found that significant additive gene effects occurred more frequently and were larger than dominance effects, indicating that additive effects predominantly determined the differences in resistance to Fusarium head blight within F2 populations, and was in agreement with the finding that general combining ability effects were much more important than specific combining ability effects. Therefore, selecting for resistance on a single-plant basis in a segregating population could be successful if sufficient genetic variation was available.

Quisenberry (1975) reported in cotton that joint-scaling test showed all characters (plant height, main stem internode length, fruiting branch internode length, node of the first fruiting branch) adequately fit an additive-dominance model and that the estimates of m, (d) and (h) were not biased to any significant extent by effects which were not attributable either to the additive or dominance action of the genes.

For all characters, the estimates of (d) were significantly different from zero, and the estimates of (h) were not significantly different from zero. Therefore, we concluded that dominance genetic effects were not a major factor in the inheritance of any of the characters and that the expression of each character was caused primarily by additive genetic effects.

Landi *et al*. (1990) reported on chlorsulfuron (CS) tolerance, shoot height and shoot weight in maize that the differential behaviour of the generations was adequately explained by the simple genetic model which does not consider the among-loci interaction as indicated by the non-significant chi-square values of Cavalli's joint-scaling test. Nor were the [h] estimates significant, indicating that either dominance effects are not appreciable or they offset one another. In this context, it is noteworthy that in our previous research, crosses among tolerant (T) and susceptible (S) lines had intermediate responses to CS, i.e., between T x T and S x S crosses.

Scott and Jones (1990) reported in tomato that for seed germination trait, the additive effects were considerably smaller than dominance effects without correction for censoring, but they were nearly equal after correction. The dominant maternal effect increased after correction for censoring, reflecting the increased means of T3 and T3 x PI120256.

Rajamony *et al*. (1990) reported in muskmelon that susceptibility was found to be partially dominant over medium resistance and the latter was dominant over resistance for cucumber green-mottle mosaic virus (CGMMV). This resulted in the duplicate epistasis nature of most of the interacting crosses. The resistance happened to be a highly-recessive character and on backcrossing with the commercial but susceptible recurrent parent, the progeny showed increased susceptibility to the virus. In view of this finding, it would not be advisable to undertake backcrossing programme.

Ramsay *et al*. (2001) reported in swedes that additive genetical variation was found for resistance to powdery mildew, neck length, growth cracks, sugar content and hardness while non-additive variation was less important. There was evidence of additive x dominance and dominance x dominance epistasis for mildew additive x additive epistasis for neck length and hardness.

2.3 Heterosis

Heterosis or hybrid vigor was described by Shull (1952) who proposed this word as the unusual vigor of the F1, resulting from hybridization of two inbred lines of maize. The general term of heterosis is the fitness lost on inbreeding tends to be restored on crossing (Falconer, 1989). Briggs and Knowles (1967) defined as a manifestation of heterozygosity, expressed as increasing of vigor, size, fruitfulness, and resistance to diseases, insects or climatic extremes. In addition, Mather and Jinks (1982) defined heterosis as the amount by which the mean of an F1 family exceeds its better parent.

Moll and Stuber (1974) and Banga (1998) explained the heterotic performance which were affected from three types of gene action; partial to complete dominance, over dominance and epistasis. These types of gene action gave three kinds of heterosis: relative heterosis (deviation of hybrid from mid-parent value), heterobeltiosis (superiority of the hybrid over the better parent of the cross) and standard heterosis (superiority of the hybrid over the commercial check variety).

Heterosis was reported in azuki bean by Kunkaew *et al.* (2006) who revealed that F1 hybrids exhibited both negative and positive heterotic effects on seed yield per plant over their mid- and better-parents which, averaged over the two test sites, were -0.6 to 31.8 % and -10.7 to 20.5 %, respectively. The different climatic conditions between the test sites evidently influenced the patterns of heterotic expression. The works of heterotic effect were reported in many important crops such as, in mungbean, Xin *et al.* (2003) found that the hybrid yield with maximum heterosis was close to 10 % in the cross CM5 x K7 but this heterotic value was not economically feasible to produce commercial hybrid seed. In soybean, Kunta *et al.* (1997) reported that heterotic for seed yield when averaged over crosses, high-parent heterosis was 18.7 % in year one and was 16.8 % in year two, as well, heterosis level expressed differently among hybrids, indicating that a large number of crosses may need to be evaluated in order to identify superior combinations. Paschal and Wilcox (1975) reported average high-parent heterosis for yield on soybean was 8 % and revealed that twelve F1 of thirty hybrids showed significant mid-parent heterosis for this trait when averaged over two years. Some crosses showed marked differences in percentage of heterosis from one year to the other. Moll *et al*. (1978) studied yield in maize and

concluded that heterosis was increased after reciprocal recurrent selection and decreased slightly after full-sib family selection. In this crop, Unay *et al*. (2004) revealed that the mid-parent heterosis values for yield ranged from 46.11 % to 573.12 %. Generally, high heterosis values showed parallelism with the mean dominance effect of the heterozygote locus (h^2) parameter, indicating the mean dominance effects of the heterozygote locus. Heterosis has been widely studied and reported in other crops, such as tobacco in which Legg *et al*. (1970) reported that the average heterosis values over three years were small but significant for yield, day to flower and plant height. Sarawat *et al*. (1994) reported in pea on the positive heterosis levels over the mid-parent and better parent for number of pods per plant and suggested that dominant or over-dominant genes controlled the expression of this character. The lack of heterosis for seed weight may be attributed to the presence of genes with oppositional dominance or no dominance. Hundred-seed weight was the least heterotic of the yield components and no hybrid had significantly larger seeds than the high parent of the cross. Negative heterosis for days to onset of flowering has usually been considered desirable, as this would cause the hybrids to mature earlier than their parents, thereby increasing their productivity per day and per unit area. Most of the F1 hybrids started flowering earlier than the mid-parent except F1 hybrids from crosses between different subspecies, but no cross was earlier than the earliest parent. Thus, genes controlling this trait would be partially dominant for earliness of flowering. In addition, they reported that the levels of heterosis for pods per plant, total dry matter and grain yield were higher in poor-yielding conditions than in high-yielding conditions. The significance of the heterosis x environment interaction for yield and other traits has confirmed that in order to get valid heterosis estimates for each breeding programme, it is important to evaluate hybrids and parents in environments corresponding to the target area.

    In rice, Young and Virmani (1990) revealed that heterosis for days to flowering, plant height and grain yield was also affected by cytoplasm. However, manifestation of cytoplasmic effects was higher for heterosis for days to flower than in heterosis for yield and plant height. Dwivedi *et al*. (1998) reported in this crop that trends of magnitude of heterosis for grain yield were indica x japonica > indica x indica > japonica x japonica hybrids. Estimates of standard heterosis (%) for grain

yield at environment E1 (optimum sowing and high fertility) were more favorable for higher heterosis expression than E2 (both optimum sowing and fertility) and E3 (late sowing and high fertility) environments. Hybrids were identified in specific environments for direct exploitation in hybrid breeding. Therefore, testing of promising hybrids across locations in the irrigated ecosystem in larger plots would help establish their real potential and adaptability.

2.4 Generation variance and Heritability

The genetic variance is the second-degree statistics and was estimated for six populations: P1, P2, F1, F2 and two backcrosses, BC1 and BC2. Keaesey and Pooni (1996) explained that segregating generation variances are expected in terms of VA which is the additive genetic component of variance, VD is the dominance or non-additive genetic component of variance, VAD is the covariance and its sign will depend on the direction of dominance, and VE is the environmental variation within families and is calculated for non-segregation generation variances. Each genetic component of variances was evaluated from six basic generation variances. Many important crops had been reported in genetic variances, such as in rice, Ram *et al.* (1989) reported for 100-seed weight that the estimates of components of genetic variation was negative and considered equal to zero, indicating the importance of additive and epistatic genetic variance for controlling this trait.

Kasrawi and Amr (1990) revealed, in tomato, that genotypic variances were significant for color, juice yield, titratable acidity (TA) and pH in population I and specific gravity of the fruits in population II. The results suggested that major variations for these traits were due to genetic effect.

In wheat, Woodend and Glass (1993) reported that variance estimates tended to be associated with large errors, and in some instances, estimates of narrow sense heritability could not be obtained due to negative estimates of additive variance. Practical considerations and their results indicated that selection for improved potassium uptake and utilization is more likely to be effective if practised among families rather than among single plants. Lange *et al.* (1995) reported in this crop that the estimates of phenotypic and environmental variances were very similar for embryogenesis among the different crosses, but not for plant regeneration. Genetic

variance estimates and heritability in the broad sense had very distinct values among the crosses for both traits. Pacheco *et al*. (1995) reported that the decomposition of the phenotypic variance showed high values to environmental variance. Concerning flag leaf lamine area, in most cases, larger values for genetic variance were revealed in crosses between genotypes with more differentiated areas. The genetic variance of the flag leaf lamine area duration showed similar behaviour as presented by the flag leaf lamine area. However, in the cross between the genotype Frontana and BR23, with similar green duration of the flag leaf lamine area, the existence of high genetic variance was verified. On the other hand, the cross between the genotypes Frontana and BR34, with different green duration, did not present genetic variance. For most crosses, the environmental variances had high values, indicating that the green duration of the flag leaf lamine area was strongly affected by the environment. The reducing values of genetic variance were easier to observe through the analysis of low values of heritability.

In alfalfa, González-García *et al*. (2000) revealed that the magnitude of the dominance genetic variance compared to the additive genetic variance estimates, and the average degree of dominance for male and females, indicated a large contribution of non-additive genetic effects for erect glandular trichome density.

Ünay *et al*. (2004) reported in maize that genotypic environmental variation (E) and additive genetic variance (D), were not different from zero. The parameter D, which may also include a portion of the additive x additive epistatic variances as well as additive genetic variance itself, was non-significant for grain yield. Dominance variance (H_1) and corrected dominance variance (H_2) were significantly different from zero. It may thus be concluded that grain yield is under control of the dominance gene effect.

Heritability is one of the most useful statistics in genetical analysis. The heritability is generally defined as the ratio of genetic variance to phenotypic variance. An equivalent meaning of the heritability is the regression of breeding value on phenotypic value (Falconer, 1989). In addition, Kearsey and Pooni (1996) defined as the proportion of genetic variance to the total phenotypic variance of a population, in the present case an F2 population, that is attributable to the effects of genes and is represented by the symbol h^2.

Two types of heritability are used. The first is based on the ratio of total genetic variation to the total phenotypic variation and is called the broad-sense heritability, h^2_b. The second type of heritability is more important because it provides a measure of the breeding value of a proportion of the variation which is due to the additive effects of genes in a specific population, this type is called narrow-sense heritability, h^2_n. Heritability is a useful value in plant improvement program since breeders can estimate the quantitative traits that they are interested to improve as how much could be genetically inherited. Heritability values of yield and yield components of many crops had been reported, such as in mungbean, Chaitieng *et al.* (2003) revealed that broad-sense heritability for resistance to powdery mildew, calculated from variance components of all crosses and environments, varied from 0.71 to 0.89. However, the low narrow-sense heritability indicated that in improving this character, conventional procedures such as pedigree breeding would not be effective. Alternatively, the backcross method is recommended to develop powdery mildew resistant lines.

Ranalli *et al.* (1991) reported in bean (*Phaseolus vulgaris*) that broad-sense heritability for seed yield per plant character in eighty-nine selection lines was 61.03 percent.

Malhotra and Singh (1990) found that the estimate of narrow-sense heritability for cold tolerance in chickpea was 87.94 percent. In this crop, Waldia *et al.* (1993) revealed that for root length, heritability in broad sense ranged from 51.5 to 77.0 percent in different crosses. This heritability value is fairly good for the transfer of character from one generation to the next generations.

In tomato, Scott and Jones (1990) reported that heritability estimates, based on sample variances, were altered by correction for right-censoring. Broad-sense heritability was estimated to be 58 percent without correction for censoring and 42 percent after correction for censoring. Narrow-sense heritability was 59 percent without correcting variances for censoring and 28 percent after correction. Narrow-sense heritability of 59 percent holds promise that improvement in the trait can be achieved by selection. However, the estimate of 28 percent heritability suggests that selection holds little promise for rapid improvement and may explain the lack of progress in developing improved cultivars with this trait. Foolad *et al.* (2002) reported

in this crop that the estimates of narrow-sense heritability for early blight resistance, computed as the correlation coefficients between F3 progeny means and F2 individual plant values, ranged from 0.65 to 0.71, indicating that early blight resistance of resistant breeding lines was heritable.

Humphreys and Mather (1996) revealed that narrow-sense heritability estimates for β-glucan content in oat were between 0.27 and 0.45. In this crop, Long *et al*. (2006) found that the high line-mean heritability for grain yield (0.67) and 100-seed weight (0.94) measured suggested that both traits should respond well to selection on the basis of line means among C_0 and C_1 populations.

2.5 Genetic Advance from Selection (genetic gains)

Genetic advance from selection analysis is one of the procedures that has been widely used for predicting the progress of selection of particular quantitative traits in the advance generations. Most of the important crops had been evaluated and reported on these genetic gains. In wheat, Whan *et al*. (1982) revealed that improvement in yield through selection was obtained when the response was measured at the same site and in the same year as the selection. Selecting the best 10% of F2 to F4 derived lines gave F5 derived lines that outyielded from random selection by 5-53%. Johnson *et al*. (1983) studied in oat and found that direct and indirect selection for increasing grain yield could be carried out on a population of oats. In bean (*Phaseolus vulgaris*), Ranalli *et al*. (1991) reported that the realized gain in seed yield which could be reached after one cycle of selection (C1) was 6.5 g, about 20% over the base population (C0). The expected gain from selection based on the superior 5% plants in C2 families was 25.5% and approached the realized gain. In alfafa, Tecle *et al*. (2006) concluded that selection for neutral detergent-soluble fiber (NDSF) concentration and indirectly for crude protein (CP), total cell wall (CW) concentration and composition, and in vitro dry matter digestibility (IVDMD) of alfafa forage was successful. Hof *et al*. (1999) studied the responses to mass selection of oil content in *Dimorphotheca pluvialis* and revealed that the average gain in oil content per selection cycle varied from 5% to 12%. Oboh and Fakorede (1990) reported in oil palm, the results showed that early yield, usually are the second and third years of production, single or in combination with one or two traits, could be used to select for oil palm genotypes that

would be high-yielding at mature plants. This implies that a breeding cycle of 7 to 8 years would be sufficient for efficient selection for higher productivity in the oil palm.

In onion, Hamilton *et al*. (1999) reported that greater genetic gain for thrips resistance in onion can be achieved by selection on a family basis rather than using single plant selection. Wall *et al*. (1996) found that the responses to selection in onion may be varied between populations. Selection was made by using the pyruvic acid technique which gave more effectiveness in lowering the pungency of the offspring in population.

In sunflower, Fick (1975) showed actual gain in F3 from simulated selection for high oil content in the F2 generation which was in good agreement with that predicted from the regression estimate. Roumen (1996) studied in rice and reported that selection for improving partial resistance to leaf blast is possible as early as the F2. The efficiency of selection was probably much higher if replicated tests could be made, and better results were therefore expected if selection among F3 lines were carried out. Malhotra and Singh (1990) studied cold tolerance in chickpea and revealed that narrow-sense heritability of this trait was 87.9 %. Results of study indicated that selection for cold tolerance in early generation should be more effective.

Wilcox *et al*. (1975) stated that predicted response to selection was close to observed gains, when the most resistant 10 % of the plants in each generation were evaluated in the next generations. This study was conducted in soybean.

In pure line breeding, selection starts in segregating generation, the effectiveness of selection depends on the relation of additive to epistatic variance. If epistatic variance is important, then the number of F2 families has to be reduced and the number of F3 families and F4 families must be increased. The same selection is true if the nongenetic variance is increased (Weber, 1982). Genetic advance estimates were low due to lack of additive variance (Martíne and Foster, 1998).