CHAPTER 5
GENERAL DISCUSSIONS

This study was carried out by planting six generations of azuki bean crosses which included P1, P2, F1, F2, BC1 and BC2 generations. Four parents of azuki bean were crossed in all possible combinations without reciprocals to develop off-spring generations, involving Kamuidainagon (K), Hondawase (H), Akatsukidainagon (A) and Erimo (E). The experiments were conducted on the three highland areas which are different in altitudes, namely, Inthanon Royal Project Research Station (1,300 m above sea level, ASL), Khunpae Royal Project Development Center (1,200 m ASL) and Pangda Royal Agricultural Station (700 m ASL). Parental lines and their off-spring generations were grown for two consecutive growing seasons during August to December in 2005 and 2006 in a field in a randomized block design with four replicates. Genetic control for yield and yield components in crop were studied as the following topics: (1) number of gene control, (2) combining ability, (3) generation mean analysis, (4) heterosis, (5) generation variance analysis, (6) heritability and (7) genetic gains and response to selection. Discussions for each studied topic are as follow:

5.1 Number of gene control

Results of study indicated that numbers of gene control were different among the studied traits of azuki bean. Most of traits such as number of seeds per pod, 100-grain weight, plant height and so on, were quantitatively controlled by a number of gene pairs. For example, there were 20.45-28.68 gene pairs for controlling 100-seed weight while number of seeds per pod was controlled by 6.46-22.72 gene pairs. Results also clearly indicated that genetic variations were largely influenced by environmental factors for estimating numbers of gene control for seed yield and yield components of azuki bean. It was found that numbers of gene control for individual trait varied from location to location and from year to year. So that improving of seed yield and yield components of azuki bean which are quantitatively gene-controlled and are influenced largely by environmental factors, breeders should realize that superior homozygous lines could be obtained slower than traits which are controlled by only a few genes. Probably, more
generations are needed to select and wait until every gene loci reach full homozygosity (Falconer, 1989). However, selection might be more effective if gene actions as well as heritability of selected traits are involved in making decision of selection.

5.2 Combining ability

Combining ability is one method which is widely used for estimating gene action for controlling of individual trait. The combining ability effect also indicate the performance of parents as a good general combiner or good specific combining ability of the traits in the crosses. Results of combining study indicated that both yield and yield components of azuki bean were controlled by additive and non-additive gene effects (Tables 4 and 5). However, magnitude of gene effects was different among the traits such as for 100-grain weight, additive gene effect was more important than non-additive gene effect. In contrast, for seed yield per plant and number of pods per plant, non-additive gene effects were greater than additive gene effect (Tables 4 and 5).

Results of study also clearly indicated that there was interaction between specific combining ability with locations (s.c.a x L) of seed yield per plant, indicating that non-additive gene effect responded greatly to environmental change. In order to select this trait with more effectiveness, breeder should select carefully, together with using suitable sites. In addition, combining ability is also useful for crop improvement either for self- or cross-pollinated crops which are different in genetic components and objective to develop better varieties or populations. In self-pollinated crops, combining ability gives informations for breeding method and selection criteria to obtain superior inbred line while specific combining ability gives useful informations for selecting good inbred parents to formulate the superior cross in hybrid varieties.

5.3 Generation mean analysis

Generation mean analysis is one of the methods which is widely used for estimating different types of gene action. These generation means involved additive, dominance and epistatic gene actions which can be estimated from population means and variances of the basic generations, including P1, P2, F1, F2, BC1 and BC2. All of these gene actions are useful informations for improving crop varieties. For example, if additive gene effect is more important than dominance gene effect for controlling any kind of traits, such as 100-seed weight, basic selection methods such as pedigree, single-
seed descent or bulk methods can be used with high efficiency. But for seed yield per plant which non-additive gene effect (both dominance and epistasis) has much greater effect than additive gene effect, successful breeding methods will be those that accumulate the genes to form a specific genotype, interacting in a favorable manner. A possible breeding programme is to do a bi-parental or multiparental mating, followed by delaying selection until desirable genotypes are observed. These breeding strategies are useful for exploitation of both fixable and non-fixable types of gene and were recommended by many breeders (Hayman, 1958; Allard, 1960; Falconer, 1989; Kearsey and Pooni, 1996). This study also further demonstrated that the inheritance of seed yield per plant of azuki bean is quite affected by environmental factors, suggesting that an appropriate choice of the environments should be considered for improving on this trait. However, in some specific case which additive x dominance gene effect is identified for controlling any kind of traits, transgressive segregation is expected to occur in F2 or later generations. This acquired segregation is desired for improving trait of self-pollinated crops.

Results of generation mean analysis also showed that all of gene actions were influenced by locations and years, suggesting that optimum environments on the highland areas should be selected for improving yield and yield components of azuki bean in order to allow any kind of gene action to be fully expressed.

5.4 Heterosis

Hybrid vigor or heterosis is defined as an F1 hybrid exhibits higher or better performances over their mid-parents (H) or better-parents (Hb). This vigor resulted from expression of heterozygous genes which may express in either additive or non-additive gene action. Results of heterosis estimation of individual trait indicated that both H and Hb values were different among crosses, locations and years. Yield components which gave moderately high H and Hb values included plant height which gave H and Hb values ranging from -13.50 to 42.38 and -15.64 to 37.81 percent, respectively. Seed yield per plant and number of pods per plant gave rather high values for both H and Hb, ranging from 2.21 to 151.58 and 7.39 to 109.66 percent for H; from -0.28 to 118.39 and -11.16 to 86.52 percent for Hb, respectively.

When heterosis estimation and gene action analysis were considered together, it was found that most of azuki bean traits were controlled by both additive and non-
additive gene effects (Tables 4 and 5). In addition, non-additive gene effect including dominance and epistasis were involved in controlling among the studied traits. Plant height which showed higher in heterotic effect because of additive, dominance and additive x dominance gene effects were important in controlling this trait (Tables 8 and 10). For 100-seed weight, heterotic effect was also high since both additive and additive x dominance gene effects also play significant role for controlling this trait as well. Hans et al. (1979) reported that 100-seed weight of azuki bean was controlled by partial dominance and vigor of F1 hybrids, resulted from non-additive gene effects. These similar results were reported by Kunkaew et al. (2006; 2007a) in azuki bean, in mungbean by Xin et al. (2003) and in soybean by Paschal and Wilcox (1975) and Kunta et al. (1997).

5.5 Generation variance analysis

Results obtained from generation variance analysis for identifying the magnitude of genotypic variation of yield and yield components of azuki bean are presented in Tables 42 to 48. Results of study indicated that additive variance ($V_A$), dominance variance ($V_D$) and environmental variance ($V_E$) of every trait were different from location to location and from year to year (Tables 42 to 48). $V_A$, $V_D$ and $V_E$ of number of nodes per plant, number of branches per plant, number of seeds per pod and 100-seed weight were low compared with plant height, number of pods per plant and seed yield per plant which were rather high (Tables 42 to 48). These genetic component variances will be useful for estimating heritability values of traits which will be described in subsequent topic.

5.6 Heritability

Results of heritability study are presented in Tables 49 to 55. There are two kinds of heritability, broad-sense heritability ($h^2_b$) and narrow-sense heritability ($h^2_n$). $H^2_b$ is the ratio of total genetic variation to the total phenotypic variation, while $h^2_n$ measures the proportion of the variation which is due to additive effect of genes to the total phenotypic variation. Results of this study revealed that both $h^2_b$ and $h^2_n$ varied among traits. $H^2_b$ and $h^2_n$ of seed yield per plant when averaged from crosses, locations, and years were 47.49 percent and 40.27 percent, respectively. Heritabilities of yield components such as, $h^2_b$ for number of pods per plant, number of seeds per pod and 100-seed weight were 48.48,
45.57 and 47.75 percent and for $h^2_n$ were 37.87, 40.16 and 43.89 percent, respectively. It was found that both $h^2_b$ and $h^2_n$ values for seed yield per plant were quite low which might probably be due to high value of environmental variance involving in the gene expression of this trait (Table 48). In addition, $h^2_n$ was low since dominance gene effect was greater than additive gene effect (Tables 4, 5, 32 and 34). For 100-seed weight, it was found that additive gene effect was greater than non-additive gene effect, resulting in high values of $h^2_b$ and $h^2_n$ obtained (Tables 4, 5, 28 and 30). Results of heritability estimate revealed that both $h^2_b$ and $h^2_n$ varied from location to location and year to year because each trait was influenced greatly by environmental factors. These environmental effects were large if traits were quantitatively controlled by many genes and environmental factors were quite strong. These similar results were reported in mungbean, bean (Phaseolus vulgaris), chickpea, tomato, and oat (Chaitieng et al., 2003; Ranalli et al., 1991; Scott and Jones, 1990; Foolad et al., 2002; Long et al., 2006; Malhotra and Singh, 1990). In order to obtain true heritability values of any trait in azuki bean, experiments should be conducted in suitable environmental conditions, as well, selection of trait should be made in optimum environments in order to allow genes to express as much as possible as suggested by Ranalli et al. (1991); Waldia et al. (1993); Unay et al. (2004) and Long et al. (2006).

5.7 Genetic gains and response to selection

Genetic gains of each trait could be calculated by using the data obtained from 5 percent of top five values of each trait in F2 population, $h^2_n$ and its standard deviation ($\sigma_p$). Results of study indicated that average genetic gains of each trait of azuki bean in 2005 growing season ranged from 8.5 to 43.9 percent and from 13.3 to 38.4 percent in 2006 growing season. Seed yield per plant gave highest genetic gains since this trait had higher values of $h^2_n$ and standard deviation ($\sigma_p$) than the other yield components. However, genetic gains of seed yield per plant varied from location to location and from year to year. So that, selection for increasing high seed yield per plant in azuki bean crop, optimum environments should be selected.

Response of selection of 100-seed weight revealed that observed value and expected value of 100-seed weight were not significantly different since additive gene effect for controlling this trait was greater than non-additive gene effect (Tables 4, 5, 28 and 30). So, this 100-seed weight could be selected effectively by using basic selection
methods such as pedigree, single-seed descent or bulk selection in order to improve larger seed size. For seed yield per plant, it was indicated that observed value differed significantly from expected value since non-additive gene effect played more important role in controlling this trait than additive gene effect. In order to increase seed yield per plant of azuki bean, it was recommended that an appropriate selection method should be used for this trait. Selection made in later generations would be more effective than early-generation selection in order to allow every gene loci reach high homozygosity. As well, intense selection in early generations will not be effective either, since dominance gene effect play more important role in controlling this trait than additive gene effect. Otherwise, more chance of heterozygous genotypes might be selected than homozygous genotypes.