IMPROVEMENT OF SEED YIELD IN FIELD BEANS,
Phaseolus vulgaris L., BY USING MORPHOLOGICAL COMPONENTS OF YIELD AS SELECTION CRITERIA

By

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DECLARATION

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

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Date 15/4/88

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Abstract

This study was carried out with the objective of identifying the important quantitative predictors of yield and to assess the utility of such predictors in improving seed yield of two Kenyan bean accessions, PAS/001 and PAS/002.

To assess the components of variation in the two populations, 45 plants from each population were randomly chosen. The seeds from these plants were used to develop 45 lines from which data were taken. The lines were planted out on a randomized complete block design with two replications during the short rains of 1986 and long rains of 1987 at the Field Station of the Department of Crop Science, University of Nairobi. Variation analysis was conducted for the total number of effective primary branches, the total number of effective pods per plant, the average number effective pods per branch, the number of seeds per pod, the weight of twenty seeds, the total seed yield per plant, the average pod length, the number of effective podding nodes and the number of days to flowering.

In the population PAS/001 significant variation among the lines was observed for the number of effective pods per plant, the number of effective pods per branch, the weight of twenty seeds, the average pod length and the number of effective podding nodes. The contribution of seasonal differences on phenotypic variation was significant for all the traits studied except the average pod length. The variation due to line-season interaction was significant for all characters except the number of seeds per pod and the weight of twenty seeds. Similarly, the variance component analysis for the PAS/002 population revealed significant variation among the lines for the number of effective pods per plant, the number of effective pods per branch, the weight of twenty seeds, the total seed yield per plant, the average pod length, the

number of effective podding nodes, and the number of days to flowering. Variation due to seasonal differences was important for the number of effective branches per plant, the number of effective pods per plant, the number of seeds per pod, the number of effective podding nodes per plant and the number of days to flowering. The variation due to the interaction between the lines and seasons was significant for the weight of twenty seeds only.

Phenotypic correlations analyses revealed the number of effective pods per plant and the average pod length as the morphological characteristics with the highest correlation to yield in PAS/001. Similarly, the number of effective pods per plant and the number of effective podding nodes were shown to be traits most closely associated with the total seed yield in PAS/002. The multiple linear regression analysis confirmed the number of effective pods per plant to be an important determinant of yield in the two populations. The contribution of the average pod length to the total seed yield per plant was significant for PAS/001 only.

The populations arising from the various cycles of selection were subjected to a comparative performance trial in a three-replicate completely randomized block design at the Department of Crop Science Field Station and at the National Dryland Farming Research Station, Katumani during the long rains of 1987. Selection for increased number of effective pods, the total seed yield per plant and the average pod length in PAS/001 lead to no significant direct response. However, the use of these traits as selection criteria lead to significant indirect responses in the number of effective podding nodes. Improving seed yield in PAS/001 by using the number of effective pods per plant as the selection criterion was 42 per cent more efficient in improving seed yield during the second cycle of selection than

than was selection for yield per se. In PAS/002, the use of the number of effective pods per plant and the number of effective podding nodes per plant also lead to significant responses in seed yield. The number of effective pods per plant was 9 per cent more efficient in improving seed yield of PAS/002 during the first cycle of selection and 4 per cent more efficient during the second cycle of selection. The number of effective podding nodes per plant was the most efficient approach for yield improvement in this population. It was inferior to selection for yield per se during the first cycle of selection. However, its efficiency improved tremendously during the second cycle of selection in which it was observed to be 16 per cent more efficient in improving yield than was selection for yield per se.

1. INTRODUCTION

The developing nations depend largely on vegetable proteins to meet their protein requirements. Most of these protein requirements are supplied by grain legumes. Several inherent advantages make the grain legumes the most suitable crops for alleviating human malnutrition. They can grow vigorously under a range of environments and on poor soils without supplemental nitrogen. They provide nonprocessed, easily storable and transportable protein that is rich in lysine, tryptophane and methionine. They are also simple to prepare and can be eaten in several forms such as tender green shoots, green leaves, unripe whole pods and mature seeds.

In Kenya, the most commonly grown legumes are field beans (*Phaseolus vulgaris L*.), pigeon peas (*Cajanus cajan*) , cowpeas (*Vigna unguiculata*), green grams (*Vigna radiata*), and field peas (*Pisum sativum*). Of these, field beans are the most widely cultivated. The crop has been grown in Kenya for nearly 300 years (Mukunya and Keya, 1975). It is grown in most parts of the country where there is adequate rain. The total acreage covered by the crop annually is approximately 1,000,000 hectares, most of which is found in Central and Eastern Provinces. As a food crop in Kenya, it ranks second to maize.

Several cultivars of beans, mostly land races, are grown in Kenya. The naming of these cultivars depend on the location where they are grown. The most common ones include

Tongmire, a Luo name referring to Rosecoco; Wairimu , a Kikuyu name referring to Red Haricot; and Kibuu, a Kikuyu name referring to Mwezi Moja. Others include Gituru, Kathiga, and Mwitemania, referring to Canadian Wonder, Rosecoco and Pinto respectively.

Within any given cultivar or land race, variations occur for seed size, seed shape and seed colour (Rheenen, 1979). However, it is not clear as to whether variations exist for other traits like yield and yield components.

No intensive research on beans was known in Kenya until 1973 when the National Grain Legume Project was initiated at the National Horticultural Research Station, Thika for the improvement of grain legumes. The Grain Legume Project (GLP) has since then released a number of improved varieties. These include GLP2 (Rosecoco), a variety well adapted to the high rainfall areas; GLP-24 (Canadian Wonder), a variety well adapted to the medium rainfall areas; GLP-1004 (Mwezi Moja), a variety which performs well in dry areas; and GLP-X.92 (Mwitemania or Pinto) , a variety with wide adaptation to all ecological zones. Others include GLP-X 585 (Red Haricot) and GLP-X.1127 (a) (New Mwezi Moja) which are respectively adapted to high rainfall areas and to all ecological zones. The yield potential of these varieties are as shown in Appendix I.

There is evidence which indicate that yield improvement in the Kenyan field bean varieties is still possible. For example, comparing the pure stand performance and performance under mixed cropping, the former is almost always double the latter. This disparity in yield may be because the Kenyan bean varieties have not been bred to behave as what Allard and Adams (1969) referred to as good neighbours or good competitors. In a mixed stand, a bean variety which is a good neighbour would consistently enhance the performance of the other crop without relative reduction in its own performance. A good competitor would consistently perform relatively better in a mixed stand than in a pure stand. Since most of the beans grown in Kenya are under intercropping, breeding to improve the yield performance of dry beans under intercropping still remains to be done. Furthermore, the yield of beans in Kenya is known to be lower than the yield of beans in other countries. For example, the 1979 average dry bean yield in Kenya was 624 kg/ha as compared to 776 kg/ha for Uganda, 861 kg/ha for Tanzania, 2005 kg/ha for Libya, 2034 kg/ha for Egypt and 4860 kg/ha for Morocco (Londono et al., 1983 and FAO, 1985). However, it is important to note that there has been a steady improvement in the yield of Kenyan beans due to the improved disease resistance and better agronomic practices.

Compared to the cereal crops, breeding of grain legumes for improved yields has seen no decisive break-throughs. The grain legumes continue to give lower yields than the cereal crops (Jain, 1975). This observation seems to suggest that the grain legumes such as beans have lower genetic potentials for yield than the cereal crops. However, the available evidences indicates that the grain legumes have as high or higher genetic potentials for yield than the cereal crops (Jain, 1975). The low yields prevailing in the grain legumes may be due to the stress conditions in which these crops have evolved (Jain, 1975). The stress conditions might have led to the development of morphological and physiological survival strategies that are associated with lower yields. Alternatively, it is possible that these crops have not been subjected to enough intensive selection for increased yields.

Increased yields in cereal crops such as maize and rice have been achieved through restructuring of the plant architecture. On the other hand little work has been done to restructure the morphology of the bean plant so as to attain a more efficient plant type. The failure to develop more efficient plant types in beans is probably due to the lack of knowledge about the ideotypes that a breeder should look for (Ramanujam, 1975; Adams, 1973 and Evans, 1973). A thorough knowledge of those plant characteristics that affect yield (yield components) and how they interact to affect yield is necessary. In the cereal crops, the yield components have been defined as the number of heads per plant, the number of grains per ear, seed weight and the average per cent dry matter in the grain (Engeldow and Wadham, 1923). In the field beans (*Vicia faba* L.), Rowlands (1955) defined the number of pods per plant, the number of seeds per pod and seed size as the primary yield components. These primary components are further influenced by a number of secondary components including the first flowering node, the first podding node, the number of nodes, plant height and the number of branches (Kambal, 1969) .

Apart from being influenced by the component traits, yield is also highly influenced by the environment. This makes it an unreliable selection criterion in breeding programmes focussed on yield improvement. An alternative approach to yield prediction is to examine the various yield components and give attention to those having greatest influence on yield. The components are known to be less sensitive to environmental changes, easier to observe and measure and have higher heritabilities (Frankel, 1947; Rasmusson and Cannel, 1970; Wallace, 1973 and Bravo et al., 1980).
The decision regarding the component traits to use as selection criteria in yield improvement programmes depends on the magnitude of their genetic variance, heritability estimates and their genotypic correlations with yield (Falconer, 1981). The question as to whether to use direct or indirect selection also depends on which of the two is more efficient in achieving the basic objective. This can be judged by comparing the rate of genetic progress in improving the genetic merit of the basic trait under the two selection programmes (Searle, 1965 and Falconer, 1981). Most of the studies on indirect selection have however ignored this kind of comparison.

Though information on the interaction of the yield components and their relative influence on yield is necessary for designing selection experiments, few of such studies have been reported for the Kenyan bean cultivars. Given the role played by the field beans in Kenya and the urgent need for increasing its yield, such studies are necessary. Therefore, the present study was undertaken with the following objectives:

1. To study the quantitative variations for a number of traits in two bean accessions from Kenya.
2. To identify the most useful quantitative predictors for bean yield.
3. To investigate the possibility of using indirect selection for improving yield of field beans.

2. LITERATURE REVIEW

2.1 Yield and its components

The success of selection in a breeding programme is partly dependent on the penetrance and expressivity of the gene or genes controlling the character under selection. The character under selection may be controlled by either the major genes or the minor genes, hence referred to as qualitative or quantitative characters respectively. The qualitative characters show discontinuous variation and are easily recognized. On the other hand, the quantitative characters show continuous variation and are strongly influenced by the environment (Frankel, 1947). Therefore, selection for the quantitative characters not only depend on the presence and magnitude of genetic variations, but also on the degree to which the environmental factors render the genetic variations unrecognizable. Yield is a typical quantitative character. Because of the nature of its inheritance, yield has been referred to as having a complex heredity (Frankel, 1947 and Wallace, 1973). It is believed to be directly or indirectly influenced by a number of morphological traits, often referred to as yield components.

The attempt to resolve yield into its components was first undertaken by Engledow and Wadham (1923). They partitioned cereal yield into what they referred to as the "governing factors of yield", namely, the number of heads per plant, the average number of grains per ear, the average weight of a single grain and the average per cent dry matter in the grain. Grafius (1956) described yield in oats as a geometric construct, a parallelepiped with the edges being panicles per unit area, kernels per panicle and kernel weight. Whitehouse (1953) described the yield of wheat plant as the product of mean kernel weight, kernels per spikelet, spikelets per ear and ears per plant. In field beans, the primary components of yield were described by Rowlands (1955) as the number of pods per plant, the number of seeds per pod and seed size. In addition to the primary components, a number of secondary components are believed to influence bean yield by acting through the primary components. The secondary components were described by Kambal (1969) as the first flowering node, the first podding node, the number of nodes per plant, plant height and the number of branches.

2.2 Plant architecture and yield

The yield components have been used in developing plant architectures which are efficient in utilizing the environmental resources. This has involved morphological changes leading to the development of varieties that are efficient in utilizing the environmental resources and partitioning of the photosynthates. In wheat and rice the development of plants with reduced culm length, high tillering ability, lack of sensitivity to day-length and responsiveness to nitrogen without reduction in straw: grain ratio led to increased yields (Adams, 1973). In maize, the replacement of single-eared plants with the multiple-eared plants has led to increased grain yields (Adams, 1973). It has also been suggested that plant modifications which lead to the development of plant ideotypes have the potential of increasing yields of grain legumes (Adams, 1973 and Ramanujam, 1975). A plant ideotype in grain legumes has been described as having a high number of pods, a high number of seeds per pod and large seeds (Adams, 1973). An increase in the number of pods can be achieved by increasing the number of bunches per plant and pods per bunch (Ramanujam, 1975). Alternatively, the number of pods can be increased by selecting for large inflorescences combined with better pod set. Selection for large inflorescences with high pod set will lead to improved performance because pod set and pod number are known to be under the influence of additive genes (Dickson, 1967 and Hicks and Pedelton, 1969). Jain (1975) and Adams et al. (1978) have pointed out the importance of harvest index as a selection criterion for the improvement of yield in grain legumes.

2.3 Yield, yield components and their interrelationships

In addition to the investigations on the nature of plant ideotypes required for improved yields, studies have been undertaken to understand the nature of the relationships among the yield components and how the components relate to yield. For example, in upland cotton (Gossypium hirsutum L.) Miller and Rawlings (1967) reported positive correlations between lint percent and lint yields. The other characters like boll weight, fibre length, fibre strength, fibre elongation and fibre fineness had negative correlations to lint yield. In all cases, the magnitudes of correlation coefficients declined as selection progressed.

Acikgoz and Tekeli (1980) analysed the association patterns between seed yield and various yield components in thirteen cultivars of smooth broomgrass (Bromus ineris Leys) and observed wide variations among and within cultivars for seed yield and the yield components. Path-coefficient analysis showed that seeds per panicle and seed weight had the strongest direct effect on seed yield. In tomatoes Cuartero and Cubero (1982) showed that fruits per cluster and early harvesting had the highest phenotypic correlation to yield. They noted that as long as the environmental correlations were lower than the genotypic correlations the phenotypic correlation coefficient was a good index of the genotypic correlations.

Other correlation studies have been conducted by Chandhanamutta and Frey (1973) in oats, Rasmusson and Cannel (1970), Puri et al. (1982) and Ayiecho and Onim (1983) in barley and Ayiecho (1985) in grain amaranths. The work done by Ayiecho (1985) involved the association studies and direct and indirect selection for yield improvement in grain amaranths. Using step-wise regression analysis he identified plant height, head weight, threshing percent and yield:height ratio as the best yield predictors in two grain amaranth populations. The yield : height ratio was the most consistent selection criterion for yield improvement.

Among the correlation studies which have been done on grain legumes are those of Ramseur et al.(1984) and Bravo et al.(1980) in soybeans, Brian and Stoffela (1985) in cowpeas, Tikka et al. (1976) in Phaseolus aconitifolius, Adams (1967), Kambal (1969) and Duarte and Adams (1972) in field beans. In the study by Kambal (1969), pod number and seed weight were negatively correlated in the Egyptian field bean varieties. The number of pods was observed to be higher in one local line than in the improved varieties. The high pod number in the local line was attributed to the ability of the line to produce more pods per stem rather than the ability to produce more stems per plant. The correlation studies revealed the number of pods per plant as the character most closely associated with grain yield in the three populations studied ($r = 0.984$) followed by the number of seeds ($r = 0.877$). This was confirmed by path analysis. In addition to the usual yield components, Duarte and Adams (1972) extended their studies to include more aspects of plant morphology, namely, leaf number and leaf size. These characters were expected to have influences on the number of pods per plant, the number of seeds per pod and seed weight. They summarized their findings as follows:

1. The number of pods per plant exerted a preponderant effect upon seed yield in every set of family studied.
2. The number of leaves per plant was highly associated with the number of pods per plant and leaf size was highly associated with seed size.

A review of several association studies carried out by various workers on a number of food legumes has been done by Sinha (1975). From his review the following conclusions were made:

i) The number of pods per plant correlates most strongly with seed yield. Seeds per pod and seed size are also positively correlated with seed yield.

ii) Plant height and the number of branches often have no significant correlation with yield.

iii) The number of pods per plant, the number of seeds per pod and seed size are usually negatively correlated among themselves.

He pointed out that when deciding on the importance of a character for the purpose of breeding, the question relating to the stability of the character over the environments must be answered.

The use of yield components as selection criteria for yield improvement was pointed out by Frankel (1947). He noted that once the limit to direct selection for yield has been attained, further advancement in yield can only be attained indirectly through the yield components. The advantages of yield components over yield per se lie on their higher heritabilities, efficiency and ease of observation (Searle , 1965; Kambal, 1969 and Brian and Stoffela, 1985). The yield components have been used as selection criteria in a number of crops including oats (Frey, 1967 and Chandhanamutta and Frey, 1973), wheat (Sidwell et al., 1976 and Allexander et al. 1984), grain amaranths (Ayiecho, 1985) and soybeans (Hartwig and Collins, 1962 and Bravo et al., 1980). Chandhanamutta and Frey (1973) carried out selection for panicle weight in oats and reported an average direct response of 7.5 percent per cycle for panicle weight and an indirect response of 5.6 percent per cycle for grain yield. Eighty percent of the response in seed yield was attributed to the increased number of seeds per panicle and twenty percent to the increase in seed weight. In wheat, Sidwell et al., (1976) used correlations and path co-efficient analysis to show that kernel weight was the most effective selection criterion for grain yield improvement. Allexander et al.(1984) also reported improvement in wheat yield when selection was done for wheat kernel weight. And in soybeans, Bravo et al. (1980) used pod width to improve seed weight. Selection for pod width was shown to be more efficient in improving seed weight than was selection using yield itself.

2.4 Mass selection for yield and yield-related characters in self fertilizing species

Mass selection had been extensively used by plant breeders because it permitted a rapid and inexpensive propagation of a large number of plants. However, it was later thought to be ineffective for characters with low heritabilities and therefore became less attractive as a means of improving crop plants. For example, by the 1920's, plant breeders shifted from mass selection to other crop improvement methods such as pedigree selection (Matzinger and Wernsman, 1968). Recently there has been a renewed interest in mass selection following the development of a stratified mass selection technique by Gardner (1961). This technique makes it possible to carry out mass selection successfully for characters with low heritabilities like yield. The technique has been successfully applied to improve crop yields directly or indirectly in a number of studies (Gardner, 1961 and Ayiecho, 1985).

Mass selection can be applied to both self-fertilizing and cross-fertilizing species (Romero and Frey, 1966 and Frey, 1967). In self-fertilizing species, progress from mass selection is limited due to lack or little opportunities for genetic recombination in successive generations. It has however been applied with some success in various self-fertilizing crops (Romero and Frey, 1966; Frey, 1967 and Chandhanamutta and Frey, 1973). The method is more important where the character is under additive gene control (Gardner, 1961). Due to the nature of gene action involved, progress from mass selection should be expected for various components of yield in beans. Dickson (1967) reported a preponderance of additive gene variance for the number of seeds per plant, seeds per pod, pod length, number of pods per plant and days to flowering.

In light of the foregoing literature, it is evident that the breakthroughs in yield improvements which have been achieved in various crops resulted mainly from the restructuring of plant architectures, thereby obtaining more efficient plant types. Similar restructuring of plant type in field beans have been limited due to scarce knowledge about the architectural traits which associate most closely with yield, and are able to improve the efficiency with which bean yield can be selected. To this end, further association studies between yield and its components and the efficiency of such components as selection criteria are necessary for the Kenyan bean populations.

3. MATERIALS AND METHODS

The materials for this study were obtained as a result of a germplasm acquisition expedition organised by the University of Nairobi. One population consisted of a mixture of Mwezi Moja variety (hereafter referred to as PAS/002) acquired from a small scale farmer in Machakos district of Eastern Province. It consisted of seeds of various sizes and shapes. The second population , a small dark-grey seeded land race, was obtained from Kisumu district of Nyanza province where it is locally known as Okwodo. The population is referred here as PAS/001.

The two populations were subjected to phenotypic variation analysis during the short rains of 1986 and long rains of 1987. Direct and indirect selection for yield were initiated on the two populations during the long rains of 1986 as described below.

3.1 Genetic variation analysis

To assess the variation in each population for the number of effective pods per plant, the number of effective primary branches per plant, the average number of effective pods per branch, the average number of seeds per pod, twenty-seed weight, seed yield per plant, the average pod length, the average number of effective podding nodes and days to flowering, 45 lines from each population were planted in a two-replicate completely randomized block design during the short rains of 1986 and long rains of 1987 at the Field Station of the Department of Crop

Science, University of Nairobi. The 45 lines were developed by randomly chosing 45 plants from each population during the long rains of 1986. The progenies of each of the 45 plants were treated as a line and planted in a two-replicate completely randomized block design during the short rains of 1986 and the long rains of 1987. In each replicate, every line was represented by a row of ten plants. The between and within row spacing were 50 cm and 10 cm respectively. Data were recorded on four middle plants in each row. Each plant was scored for the following plant attributes:

1. The number of effective primary branches
2. The total number of effective pods
3. The average number of effective pods per primary branch
4. The average number of seeds per pod
5. Twenty seed weight
6. The total seed yield
7. Average pod length
8. The number of effective podding nodes
9. The number of days to flowering.

An effective pod is defined here as a pod with at least one mature seed. An effective primary branch is defined as a primary branch with at least one effective pod. The average number of effective pods per primary branch was estimated from the knowledge of the total number of effective primary branches and the total number of effective pods.

3.2 Direct and indirect mass selection

Mass selection experiments were initiated on the two populations during the long rains of 1986 at the Field Station of the University of Nairobi. This involved planting 1050 plants from each population in a 7m by 7m plot. The between and within row spacings were 50 cm and 10 cm respectively. Leaving out a one metre wide perimeter around each plot, the plots were subdivided into 15 sub-plots, each three rows by one metre in size. This was to simulate the gridding system of Gardner (1961). Data were recorded on plants from ten randomly chosen sub-plots. Each plant in the ten sub-plots was scored for the above traits. The data obtained was used to compute the phenotypic correlation and multiple regression coefficients for identifying the two best yield predictors in each population. The identified predictors were used as the indirect selection criteria for yield improvement. For example, in the PAS/001 population, the number of pods per plant and the average pod length emerged as the best selection criteria. In PAS/002, the number of pods per plant and the number of podding nodes were identified and consequently used as the selection criteria. Both populations were subjected to a first and second cycle of direct and indirect mass selection for yield, with a 10% selection pressure.

3.3 Comparative evaluation

For each population, the following six selections and the original control population (CO) were subjected to a comparative performance trial in a three-replicate completely randomized block design at the Department of Crop Science Field Station and at the National Dryland Farming Research Station, Katumani during the long rains of 1987.

1. The population arising from the first cycle of selection for the total

number of effective pods per plant (CP1)

2. The population arising from the second cycle of selection for the total number of effective pods per plant (CP2)
3. The population arising from the first cycle of selection for total seed yield per plant (CY1)
4. The population arising from the second cycle of selection for total seed yield per plant (CY2)
5. The population arising from first cycle of selection for average pod length (CL1) in the case of PAS/001; or the population arising from the first cycle of selection for the number of podding nodes (CN1) in the case of PAS/002.
6. The population arising from the second cycle of selection for the average pod length (CL2) in the case of PAS/001; or the number of podding nodes (CN2) in the case of PAS/002.

Each entry was planted in a 3 row by 1 metre sub-plot in each replicate. In each entry, data was taken for each fo the above traits on 5 middle plants from the middle row so as to avoid any effect of the between-entry competition.

3.4 Statistical analysis

Genotypic variation analysis was carried out on the two populations using the random effect model of the analysis of variance outlined by Zar (1984) as follows:

Table 1: Form of analysis of variance for deriving of the genotypic variance for the PAS/001 and PAS/002 populations.

Source of variation	df	MS	EMS
Replications in seasons	y(r - 1)		
Seasons	y - 1	M_4	$\sigma^2 e + r\sigma^2 gy + rg\sigma^2 y$
Lines	g - 1	M_3	$\sigma^2 e + r\sigma^2 gy + ry\sigma^2 g$
Season-line interaction	(y-1)(g-1)	M_2	$\sigma^2 e + r\sigma^2 gy$
Error	y(r-1)(g-1)	M_1	$\sigma^2 e$

y, r and g represent the number of seasons, replications per season and lines respectively.

$\sigma^2 e$, $\sigma^2 gy$, $\sigma^2 y$ and $\sigma^2 g$ are the variance components due to the error, interaction between lines and seasons, seasons and the lines respectively.

Using the results of the above analysis, various quantitative parameters were estimated according to Searles (1965) and Falconer (1981) as follows:

Predicted genetic gain:

$R = ih^2\sigma\bar{P}$

Where:

i is the intensity of selection

h^2 is the heretability estimate

$\sigma\bar{P}$ is the phenotypic standard deviation obtained from the above analysis of variance as follows:

$$\sigma\bar{P} = \left[\sigma^2 g + \frac{\sigma^2 gy}{y} + \frac{\sigma^2 e}{ry}\right]^{\frac{1}{2}}$$

Where:

$\sigma^2 g$ is the estimate of genotypic variance component obtained from the analysis of variance as follows:

$$\sigma^2 g = \frac{M_3 - M_2}{ry}$$

$\sigma^2 gy$ is the estimate of the variance component due to the interaction between the lines and the seasons and is equal to: $\frac{M_2 - M_1}{r}$

$\sigma^2 e$ is the estimate of the variance component due to error and equals M_1.

The heritability estimate:

$$h^2 = \frac{\sigma^2 g}{\sigma^2 \bar{P}}$$

Being a self-fertilizing species, it was expected that individual bean plants were homozygous at most loci controlling the various characters. Consequently, it was further assumed that the genetic component of variation was mainly due to additive and additive x additive gene action. This assumption follows the knowledge that dominance is manifested only when there is heterozygosity at given loci. Therefore, dominance variance was considered negligible. Based on these assumptions, the genetic variance components estimated as above ($\sigma^2 g$) were considered to be the variance due to additive and additive x additive gene action.

The realized heritability estimate from mass selection:

$$h^2_{ms} = \frac{\text{\% Realized mass selection gain}}{\text{\% Mass selection differential}}$$

The efficiency of indirect selection relative to direct selection calculated as the ratio of the expected means:

$$RSE = \frac{CRx}{Rx}$$

where: CRx is the correlated response of X when selection was applied for another character Y.

Rx is the direct response to selection for character X.

The comparative performance trials were subjected to the mixed effects model of the analysis of variance as outlined by Zar (1984) as given below. The effects due to seasons were treated as random effects.

Table 2: Form of analysis of variance for deriving the variance among the generation means for PAS/001 and PAS/002 populations

Source of variation	df	MS	EMS
Replications	l(r-1)		
Locations	(1-1)	M_4	$\sigma^2 e + r\sigma^2 gl + rg\sigma^2 l$
Selections	g-1	M_3	$\sigma^2 e + r\sigma^2 gl + rl \frac{\Sigma T_i^2}{(g-1)}$
Location-selection interaction	(1-1)(g-)	M_2	$\sigma^2 e + r\sigma^2 gl$
Error	1(g-l)(r-1)	M_1	$\sigma^2 e$

where g, l and r represent the number of selections, the number of locations and the number of replications per location respectively.

$\sigma^2 e$, $\sigma^2 gl$, $\sigma^2 l$ and ΣT_i^2 are the variance components due to error, the location-selection interaction, locations and selections respectively.

Duncan's multiple range test was used to compare the means of the selection groups. Simple phenotypic correlations and multiple linear regression analysis were carried out in a BBC Computer with the aid of the INSTAT package.

4. RESULTS

4.1 Quantitative variation

4.1.1 Quantitative variation in PAS/001

The variation analysis results for PAS/001 are given in Tables 1 and 2. Significant variation among the lines was observed for the number of effective pods per plant, the number of effective pods per branch, the weight of twenty seeds and the average pod length. The other plant characters studied did not have any significant variation among the lines. The variation due to the seasonal differences was significant for all the characters except the average pod length. Apart from the number of seeds per pod and the weight of twenty seeds, all the characters studied had significant variation due to line-season interaction effects. The components of variation, heritability estimates and expected selection gains from mass selection for PAS/001 population are presented in Table 3. From the heritability estimates, no exploitable variation was detected for the number of effective branches. The other characters studied had heritability values varying from 0.20 for the number of effective podding nodes per plant to 0.92 for the average pod length.

4.1.2 Quantitative variation in PAS/002

The means, standard errors and coefficients of variation based on individual plants are given in Table 1 for PAS/002. The geno-

Table 3 The means standard errors and coefficients of variations based on plot means for the original population

Traits	PAS/001			PAS/002		
	Mean	S.E.	C.V. %	Mean	S.E.	C.V. %
The number of effective branches per plant	4.399	0.1306	11.43	4.185	0.2356	18.77
The number of effective pods per plant	30.317	1.3737	18.32	16.975	0.7530	22.78
The number of effective pods per branch	6.834	0.2930	16.70	4.106	0.2850	20.75
The number of seeds per pod	5.268	0.0655	13.99	3.772	0.0570	10.09
The weight of twenty seeds (gm)	4.338	0.0252	7.15	9.607	0.1270	6.02
The total seed yield per plant (gm)	32.523	1.8225	20.09	30.907	1.2750	26.67
The average pod length (cm)	9.614	0.0897	3.42	10.679	0.0782	5.86
The number of effective podding nodes per plant	16.267	0.6300	17.29	12.354	0.4359	20.38
The number of days to flowering	43.199	0.0242	2.03	32.087	0.1486	3.32

Table 4 The analysis of variance for PAS/001 original population

Trait	df	Mean Squares			
		Season 1	Line 29	Line-Season 29	Error 58
The number of effective branches per plant		92.331**	0.346	0.570**	0.253
The number of effective pods per plant		2231.719**	150.510*	70.921**	30.839
The number of effective pods per branch		23.302**	4.851*	2.311*	1.303
The number of seeds per pod		7.257**	0.656	0.456	0.544
The weight of twenty seeds		1.398**	0.315**	0.117	0.096
The total seed yield per plant		2136.755**	129.617	90.528**	42.685
The average pod length		0.464	2.546**	0.192*	0.108
The number of effective podding nodes per plant		207.533**	21.311**	17.140**	7.909
The number of days to flowering		51385.7**	2.050	1.322*	0.767

* - Significant at P = 0.05

** - Significant at P = 0.01

Table 5 The components of variation, heritability estimates and expected selection gains for PAS/001

Trait	$\sigma^2 p$	$\sigma^2 G$	h^2	Expected % gains
The number of effective branches per plant	0.1425	0	0.00	0.00
The number of effective pods per plant	37.6275	19.89725	0.53	18.87
The number of effective pods per branch	1.21275	0.635	0.52	14.74
The number of seeds per pod	0.186	0.05	0.27	3.89
The weight of twenty seeds	0.07875	0.0495	0.63	7.17
The total seeds yield per plant	32.4043	9.7723	0.30	9.23
The average pod length	0.6365	0.5885	0.92	13.42
The number of effective podding nodes per plant	5.3278	1.0428	0.20	4.99
The number of days to flowering	0.5125	0.182	0.36	1.05

typic variation among the lines was significant for all the traits studied except the number of effective branches per plant and the number of seeds per pod (Table 4). The variation due to the seasonal differences was significant for the number of effective branches per plant, the number of effective pods per plant, the number of seeds per pod, the number of effective podding nodes per plant and the number of days to flowering. With the exception of the weight of twenty seeds, the line-season interaction effects were not significant for the characters studied. The heritability estimates in Table 5 indicated that the existence of exploitable genetic variation was present for all the characters.

4.2 Direct response to selection

4.2.1 Direct response to selection in PAS/001

The means for the selections and the control population for various traits are given in Table 6. The analysis of variance among the selections (Table 7) revealed significant differences for the number of effective podding nodes only. The selections also differed with respect to their performance in the two locations for the number of effective pods per plant, the number of effective pods per branch, the number of seeds per pod, the total seed yield per plant, the average pod length and the number of days to flowering. The realized heritability

Table 6 The analysis of variance for PAS/002 original population

Trait	df	Mean Squares			
		Season	Line	Line x season	Error
		1	34	34	68
		M_3	M_4	M_2	M_1
The number of effective branches per plant		33.467**	0.691	0.549	0.617
The number of effective pods per plant		441.656**	28.976*	13.122	14.954
The number of effective pods per branch		0.577	1.303**	0.522	0.72
The number of seeds per pod		10.109**	0.314	0.207	0.145
The weight of twenty seeds		1.345	4.743**	0.990**	0.334
Total seed yield per plant		5292.444	151.541*	70.886	67.926
The average pod length		1.434	4.142**	0.423	0.392
The number of effective podding nodes per plant		93.514**	10.687**	4.019	6.338
The number of days to flowering		604.366**	12.559**	0.897	1.138

* - Significant at P= 0.05

** - Significant at P= 0.01

Table 7 Heritability, expected selection gains and components of variation for PAS/002

Trait	$\sigma^2 p$	$\sigma^2 G$	h^2	Expected % gains
The number of effective branches per plant	0.18975	0.0355	0.19	3.58
The number of effective pods per plant	7.701	3.9635	0.51	14.67
The number of effective pods per branch	0.37525	0.19525	0.52	13.64
The number of seeds per pod	0.78425	0.026675	0.34	4.51
The weight of twenty seeds	1.1858	0.9383	0.79	15.72
The total seed yield per plant	37.8853	20.1638	0.53	18.54
The average pod length	0.96205	0.9298	0.97	15.64
The number of effective podding nodes per plant	3.2515	1.667	0.51	13.52
The number of days to flowering	3.2013	2.9168	0.91	8.91

Table 8 The plant means based on plot means for the selection evaluation experiments

	PAS/001							PAS/002						
	CO	CP_1	CP_2	CY_1	CY_2	CL_1	CL_2	CO	CP_1	CP_2	CY_1	CY_2	CN_1	CN_2
The number of effective branches per plant	3.50	3.567	3.967	3.775	3.733	3.900	4.100	3.10	3.633	3.258	3.208	3.608	3.467	3.583
The number of effective pods per plant	18.217	22.267	28.033	23.042	23.367	24.400	20.967	8.633	11.000	11.000	10.067	11.067	10.617	13.117
The number of effective pods per branch	5.292	6.323	7.050	6.123	6.258	6.435	5.035	2.775	3.122	3.137	2.988	3.055	3.100	3.570
The number of seeds per pod	4.647	4.595	4.292	4.772	4.533	4.270	4.918	2.847	3.167	3.000	3.052	3.147	3.047	3.418
The weight of twenty seeds	4.287	4.455	4.757	4.484	4.590	4.418	4.577	-	-	-	-	-	-	-
The total seed yield per plant	17.550	21.703	25.877	23.160	23.412	22.258	22.452	12.270	19.172	19.505	17.45	18.682	16.443	21.707
The average pod length	9.398	8.867	8.602	9.055	9.893	9.398	9.995	8.947	10.068	10.060	10.247	9.690	9.978	10.508
The number of effective podding nodes per plant	10.922	14.217	17.533	14.467	14.800	13.783	13.100	6.842	9.200	8.692	8.367	8.667	7.933	10.167
The number of days to flowering	42.467	42.217	42.533	42.267	42.167	42.433	42.733	33.117	34.067	34.692	33.758	32.633	34.933	34.850

- Readings not taken because of low number of seeds

Key to Table 6

CO - The control population

CP_1 - The first cycle selection for the number of effective pods

CP_2 - The second cycle selection for the number of effective pods

CY_1 - The first cycle selection for the total seed yield

CY_2 - The second cycle selection for the total seed yield

CL_1 - The first cycle selection for the average pod length

CL_2 - The second cycle selection for the average pod length

CN_1 - The first cycle selection for the number of effective podding nodes

CN_2 - The second cycle selection for the number of effective podding nodes

Table 9. The analysis of variance for selection evaluation for PAS/001 and PAS/002 populations

	Mean squares for PAS/001				Mean squares for PAS/002			
	Locations	Selections	Location-selection	Error	Locations	Selections	Locations - selection	Error
Trait df	1	6	6	23[1]	1	6	6	24
The number of effective branches per plant	0.017	0.277	0.133	0.287	32.682**	0.282	0.867	0.483
The number of effective pods per plant	2318.457**	54.911	15.249**	15.327	572.393**	10.732	2.985	4.289
The number of effective pods per branch	165.093**	2.807	1.802	1.001	3.480*	0.356	0.168	0.151
The number of seeds per pod	5.117**	0.337	0.425	0.165	10.360**	0.187	0.187	0.116
The weight of twenty seeds	1.861	0.134	0.041	0.066	-	-	-	-
The total seed yield per plant	2235.155**	37.697	23.491	16.669	3006.007**	53.240*	11.849	23.305
The average pod length	4.005**	1.249	0.320	0.206	68.992**	1.498	0.753	0.322
The number of effective podding nodes per plant	644.527	23.626*	3.537	5.088	286.004**	6.402	1.756	3.144
The number of days to flowering	6.482**	0.240	0.253	0.375	34.020*	4.783	5.270	2.864

1 - The error degrees of freedom was adjusted for missing plot

* - Significant at $p = 0.05$

** - Significant at $p = 0.01$

estimates from the first cycle of selection for the number of effective pods per plant and the average pod length (Table 8) were lower than the respective heritability values given in Table 3. The realized heritability value for the total seed yield per plant was close to the predicted value. The realized heritability estimates from first and second cycles of selection for the number of effective pods per plant were almost equal. The average pod length did not respond to the first cycle of selection (Table 8 and Figure 1). However, it had a response of 7.65 percent and a realized heritability 0.49 during the second cycle of selection. The realized heritability for the total seed yield per plant showed a remarkable decrease during the second cycle of selection. Duncan's multiple range test (Figure 2) separated the means of the number of effective podding nodes for the various selection entries into four groups with the entry for the second cycle of selection for high number of effective pods per plant having the highest mean and the control population having the lowest mean. Though the heritability estimate was high for the number of effective pods per plant ($h^2 = 0.53$) and the variation among the lines significant ($P = 0.05$) in the original population, no significant response to selection was observed for the total seed yield per plant and the average pod length. The average direct response of 26.94 percent

Table 10 The realized selection gains and realized heritabilities for PAS/001 and PAS/002

Trait	Realized % gains		Realized heritabilities	
	Cycle 1	Cycle 2	Cycle 1	Cycle 2
PAS/001				
The number of effective pods per plant	22.23	25.89	0.25	0.28
The total seed yield per plant	31.97	1.09	0.31	0.01
The average pod length	0.00	7.65	0.00	0.49
PAS/002				
The number of effective pods per plant	27.42	0.00	0.35	0.00
The total seed yield per plant	42.22	7.06	0.52	0.14
The number of effective podding nodes per plant	15.95	28.16	0.23	0.42

Figure 1 Cummulative direct response to selection in PAS/001

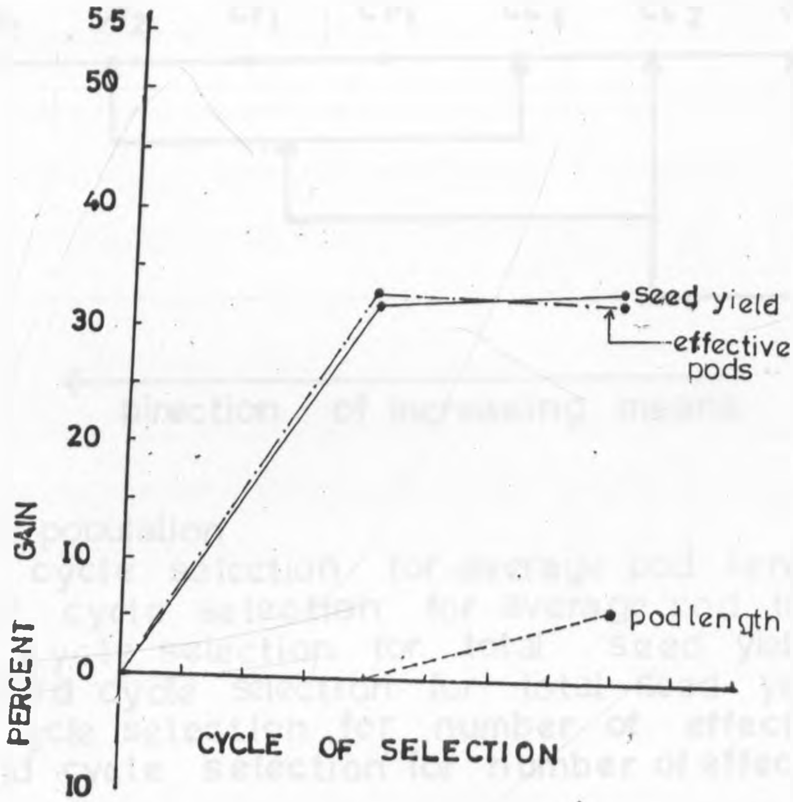
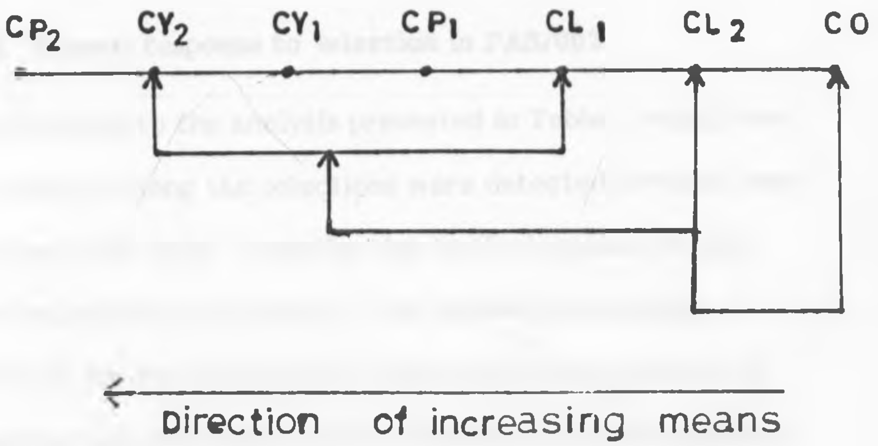


Figure 2 Duncan's multiple range test for the number of effective podding nodes among the PAS/001 selections



CO- control population
CL1-first cycle selection for average pod length
CL2-second cycle selection for average pod length
CY1- first cycle selection for total seed yield
CY2- second cycle selection for total seed yield
CP1-first cycle selection for number of effective pods
CP2- second cycle selection for number of effective pods

per cycle for the number of effective pods per plant, 16.70 percent per cycle for the total seed yield per plant and 3.18 percent per cycle for average pod length (Table 9) were all insignificant.

4.2.2 Direct response to selection in PAS/002

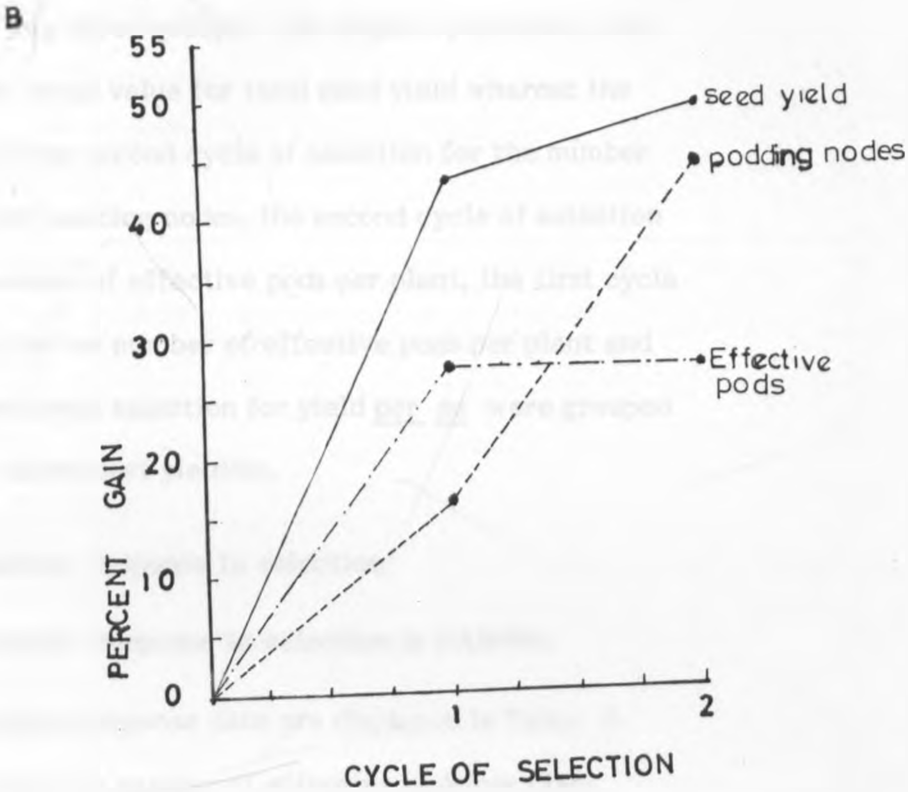
According to the analysis presented in Table 7, significant differences among the selections were detected for total seed yield per plant only. Variation due to the location effects were important for all traits. The realized heritability estimates for the first cycle of selection for the number of effective pods per plant and the number of effective podding nodes per plant (Table 8) were lower than the respective heritability estimates presented in Table 5. However, the realized heritability estimate from the first cycle of selection for the total seed yield per plant was very close to the heritability estimate from the original population. The realized gains from the first cycle of selection for the number of effective pods per plant and the total seed yield per plant were both higher than their expected values (Tables 5, 8 and Figure 3). On the other hand, the realized gains from the first cycle of selection for the number of effective podding nodes per plant was almost equal to its expected value . The average percent gains of 12.60 forthe number of effective pods per plant and 24.30 for the number of effective podding nodes per plant

Table 11 The average percent gains per cycle of selection for PAS/001 and PAS/002

	Selection Criteria					
	PAS/001			PAS/002		
Trait	The number of effective pods per plant	The total seed yield per plant	The average pod length	The number of effective pods per plant	The total seed yield per plant	The number of effective podding nodes
The number of effective branches per plant	6.67	3.33	8.57	2.55	8.19	7.79
The number of effective pods per plant	26.94	14.14	7.55	12.60	14.10	25.97
The number of effective pods per branch	16.61	9.12	-2.43	6.93	5.44	14.79
The number of seeds per pod	-3.82	-1.23	2.92	2.69	5.27	10.03
The weight of twenty seeds	5.48	3.53	3.38	*	*	*
The total seed yield per plant	23.73	16.70	13.97	29.48	26.13	38.46
The average pod length	-4.23	-2.69	3.18	6.22	4.15	8.72
The number of effective podding nodes per plant	30.26	17.75	9.98	13.52	13.34	24.30
The number of days to flowering	0.10	-0.35	0.31	2.29	-0.73	2.62

* The average percent gain for 20 - seed weight in PAS/002 could not be obtained because of poor seed set at the Katumani site.

Figure 3 Cummulative direct selection respone in PAS/002



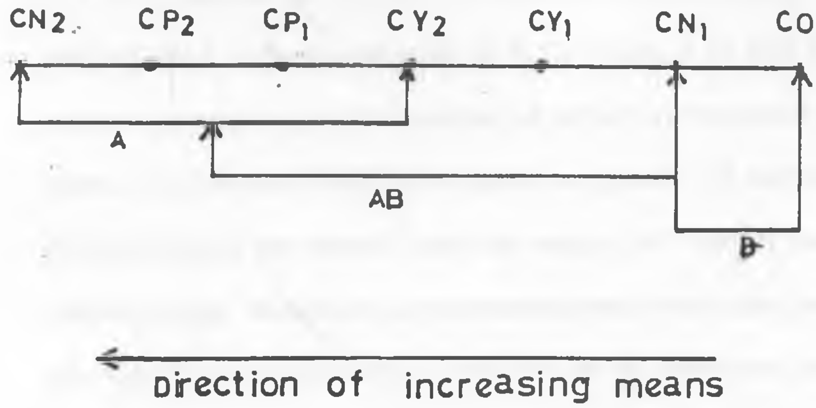
were both insignificant. Duncan's multiple range test (Figure 4) separated the means for the total seed yield per plant into three groups. The original population had the lowest mean value for total seed yield whereas the entries for the second cycle of selection for the number of effective podding nodes, the second cycle of selection for the number of effective pods per plant, the first cycle selection for the number of effective pods per plant and the second cycle selection for yield *per se* were grouped together as the best yielders.

4.3 Indirect response to selection

4.3.1 Indirect response to selection in PAS/001

Correlated response data are displayed in Table 9. Selection for the number of effective pods per plant led to no significant response in any of the traits except the number of effective podding nodes per plant which had an average response of 30.26 percent per cycle. Correlated response for yield under this selection regime was higher than direct response for yield *per se*. An average response of 16.70 percent per cycle was achieved under direct selection for yield as compared to the average correlated response of 23.73 percent when the number of effective pods per plant was used as the selection criterion (Table 9). These responses however were not

Figure 4 Duncan's multiple range test for the total seed yield among the PAS/002 selections



CO - control population
CP1 - First cycle selection for the number of effective pods
CP2 - Second cycle selection for the number of effective pods
CY1 - First cycle selection for total seed yield
CY2 - second cycle selection for total seed yield
CN1 - First cycle selection for effective podding nodes
CN2 - Second cycle selection for effective podding nodes

significant. Selection for yield *per se* effected a significant increase in the number of effective podding nodes per plant of 17.75 percent per cycle. This was accompanied by insignificant average response of 3.33, 14.14, 9.12 and 3.53 percent per cycle for the number of effective branches per plant, the number of effective pods per plant, the number of effective pods per branch and the weight of twenty seeds respectively. Selection for increased seed yield also led to non-significant reductions in the number of seeds per pod, the average pod length and the number of days to flowering. Selection for pod length led to the lowest average gains in most of the characters measured as compared to the other two selection criteria. A non-significant reduction in the number of effective pods per branch was observed when pod length was used as a selection criterion.

4.3.2 Indirect response to selection in PAS/002

From the analysis of variance in Table 7, only the total seed yield showed significant differences among the selections, suggesting significant response to selection. Selection for the number of effective pods led to an average significant correlated response in yield of 29.48 percent per cycle

(Table9) .. This response was slightly higher than the average direct response in yield of 26.12 percent per cycle, thus making this selection approach slightly more efficient in improving yield than the direct selection for yield (Table 10). Correlated response in the other traits when the number of effective pods per plant was used as the selection criterion were all insignificant. When total seed yield was used as a selection criterion, insignificant correlated responses of 8.19, 14.10, 5.44, 5.27, 4.15, 13.34 and - 0.73 percent per cycle were realized for the number of effective branches, the number of effective pods per plant, the number of effective pods per branch, the number of seeds per pod, the weight of twenty seeds, the average pod length, the number of effective podding nodes per plant and the number of days to flowering respectively. Selection for the number of effective podding nodes led to a significant average correlated response of 38.46 percent for the total seed yield. The other correlated responses to selection for higher number of effective podding nodes were not significant. The efficiency of this character as a yield predictor increased with increasing cycles of selection. (Table 10).

Table 12 . The realized selection efficiencies for PAS/001 and PAS/002*

Trait	Cycle 1	Cycle 2
PAS/001		
The number of effective pods per plant	0.74	1.42
The average pod length	0.84	0.84
PAS/002		
The number of effective pods per plant	1.09	1.04
The number of effective podding nodes per plant	0.94	1.16

* Efficiencies calculated relative to the efficiency of direct selection for yield *per se* .

4.4 Phenotypic correlation and multiple linear regression analysis

The phenotypic correlation coefficients for the original populations are presented in Table 11. The multiple linear regression results for the two populations are also presented in Table 12.

4.4.1 Correlation and multiple linear regression analyses in PAS/001

All the characters studied were found to be significantly correlated to yield, with correlation coefficients ranging from -0.27 for the number of days to flowering to 0.852 for the number of effective pods per plant (Table 11). The latter trait had the strongest association with yield followed by the average pod length (r = 0.825). The association between the number of effective pods per plant and the other plant traits were significant and positive with the exception of the number of seeds per pod (r = 0.081), the number of effective podding nodes per plant (r = 0.075) and the number of days to flowering (r = -0.301). The average pod length showed significant correlations with all the traits except the number of effective podding nodes. With the exception of the number of days to flowering, the correlation among the other plant traits were mainly positive. Days to flowering showed significant negative association to all the traits except the number of effective pods per branch, the number of seeds per pod, and the number of effective podding nodes per plant.

Table 13 Phenotypic correlations for PAS/001 (upper half) and PAS/002 (lower half), 1986

Trait	1	2	3	4	5	6	7	8	9
1. The number of effective branches per plant	-	0.615*	-0.073	0.135	0.089	0.548**	0.596**	0.092	-0.315**
2. The number of effective pods per plant	0.518**		0.457**	0.081	0.160*	0.852**	0.917**	0.075	-0.301**
3. The number of effective pods per branch	0.339**	0.432**		-0.130	0.068	0.377**	0.380**	-0.008	0.004
4. The number of seeds per pod	0.228**	-0.015	-0.098		0.154	0.328**	0.162*	0.503**	0.073
5. The weight of twenty seeds	0.318**	0.208*	0.017	0.114		0.348**	0.192*	0.297**	-0.195*
6. The total seed yield per plant	0.534**	0.802**	0.337**	0.179*	0.317**		0.825**	0.289**	-0.270**
7. The average pod length	0.120	0.218**	0.176*	-0.085	0.030	0.154		0.113	-0.252**
8. The number of effective podding nodes per plant	0.506**	0.836**	0.325**	-0.008	0.240**	0.779**	-0.130		-0.020
9. The number of days to flowering	0.003	0.045	-0.030	0.046	-0.126	-0.015	-0.127	0.123	-

* - Significant at P = 0.05

** - Significant at P = 0.01

Table 14 The multiple linear regression analysis results for PAS/001 and PAS/002, 1986

Trait	PAS/001			PAS/002		
	Estimate	SE	t	Estimate	SE	t
The number of effective branches per plant	0.047587	0.43912	0.11	0.57533	0.39991	1.44
The number of effective pods per plant	0.64379	0.12138	5.30**	0.46019	0.18276	2.52*
The number of effective pods per branch	0.17881	0.23232	0.77	0.56722	0.46579	1.22
The number of seeds per pod	2.8853	0.58458	4.94**	2.1168	0.57304	3.69**
The weight of twenty seeds	-0.02679	2.2145	-0.01	-0.71558	0.43478	-1.65
The average pod length	0.8309	0.5035	1.65	3.33600	1.0452	3.19**
The number of effective podding nodes per plant	0.15441	0.21907	0.70	7.1552	0.23805	3.01**
The number of days to flowering	-0.1013	0.28637	-0.35	0.24113	0.18166	1.33
	Overal F	=	71.813	Overal F	=	49.947
	R - squared	=	0.8370	R - Squared	=	0.7823

* - Significant at P= 0.05

** - Significant at P= 0.01

The multiple linear regression analysis identified the number of effective pods per plant and the number of seeds per pod as the traits having the greatest significant contribution to the yield of PAS/001 (Table 12). Hence, the analysis confirmed the importance of the number of effective pods per plant as a yield predictor in support of the correlation coefficient analysis. The contribution of the average pod length was small and insignificant. Therefore multiple linear regression analysis did not detect the average pod length as a useful predictor for seed yield. However, the results from the phenotypic correlation analysis suggested that the average pod length is a useful trait for yield prediction.

4.4.2 Correlation and multiple linear regression analyses in PAS/002

The phenotypic correlation results showed that the total seed yield per plant was significantly associated with all the characters except the average pod length and the number of days to flowering (Table 11). The number of effective pods per plant and the number of effective podding nodes per plant showed the strongest association to yield (r = 0.802 and r = .779 respectively) and were therefore identified as the best predictors of seed yield in this population. These two traits are also positively correlated to each other (r = 0.836).

The number of effective pods per plant had strong association with all the traits except the number of seeds per pod and days to flowering. Apart from the number of seeds per pod , the average pod length, and the number of days to flowering, the number of effective podding nodes had significant positive correlations to all the traits studied. The association among the other plant characters were generally positive with the exception of the number of days to flowering which had weak negative associations with the number of effective pods per branch ($r = -0.030$) the weight of twenty seeds ($r = -0.126$), the total seed yield per plant ($r = -0.015$) and the average pod length ($r = -0.127$).

According to the multiple linear regression analysis (Table 12), the number of effective pods per plant, the number of seeds per pod, the average pod length and the number of effective podding nodes had significant contribution to the total seed yield of PAS/002. The average pod length had the highest coefficient ($b = 3.336$) followed by the number of seeds per pod ($b = 2.1168$). This analysis confirmed the usefulness of the number of effective pods per plant and the number of effective podding nodes as seed yield predictors.

5. DISCUSSION

5.1 Quantitative variation and response to selection

5.1.1 Quantitative variation and response to selection in PAS/001

From the variation analysis (Table 2) and the heritability estimates (Table 3), only a minor progress of 9.23 percent was expected from direct selection for seed yield in the population. This was because no significant genetic variation was detected in the original population for this character. Hence, the insignificant average selection response of 16.70 percent was observed (Table 9) could have been due to the environmental influence. Alternatively, this response could have risen from undetected genetic variation in the original population. Yield, however, could be improved indirectly through its three basic components, namely, the number of effective pods per plant, the number of seeds per pod and the weight of twenty seeds. These three components are known to combine multiplicatively towards the manifestation of bean plant yield (Rowlands, 1955). Two of these components, namely, the number of effective pods per plant and the weight of twenty seeds had significant variation in the original PAS/001 population. The two components also had heritability values which were higher than that of the total seed yield in this population. (Table 3).

The question as to whether these characters could be effective only when combined into an index or whether they could successfully be used individually as selection criteria for yield improvement could not be clearly answered from the variation analysis data alone. The data from the phenotypic correlation and the multiple linear regression analyses (Tables 11 and 12) suggested that seed yield could be improved by using some of the individual components traits as selection criteria. The number of effective pods per plant and the average pod length had the highest positive correlation to yield. The estimates of the regression coefficients were also significant for the number of seeds per pod (b = 2.8853) and the number of effective pods per plant (b = 0.64379) only. Therefore, based on the variation, phenotypic correlation and multiple linear regression analyses, the number of effective pods per plant and the average pod length were identified as the best yield predictors in PAS/001.

The direct response to selection for the number of effective pods per plant in the population PAS/001 was not significant. The first cycle selection response of 22.23 percent was close to the predicted value of 18.87 percent. The realized heritability of 0.25 was however lower than the estimated value of 0.53. Such deviations from the expected values may arise as a result of random genetic drift, sampling errors in estimating the generation means, differences in selection differential and environmental influence (Falconer, 1981). Falconer (1981) noted that these factors may give rise to erratic fluctuations in selection responses. The effect of random drift could have influenced the observed responses considering that the sample selected as parents for the successive cycles of selection constituted only ten percent of the total population, that is, thirty plants selected out of three hundred plants. It was also noted that the character showed a very high variance due to the season and the line-season interaction effects. These environmental influences could have also led to the observed responses.

Selection for the average pod length led to no direct response in the first generation and only to a small direct response of 7.65 percent during the second cycle. These realised responses were much lower than the predicted value of 13.42 percent (Table 3). Five hypotheses may be used to explain these observations. Firstly, it is possible that the response pattern of this character is a reflection of the behaviour of the trait under genetically mixed population. It is known that certain plants will express higher levels of a given trait when they are subjected to intergenotypic competition (Allard and Adams, 1969). It is expected that selection pressure effected a reduction in the magnitude of genetic variability within the population and thereby reduced the effect of competition. The uniformity so achieved could have removed the "positive" effect of the competition thus leading to the observed reduced performance after the first cycle of selection. Considering the non-significant responses as the absence of response, an explanation in terms of optimal gene combination can be offered. Adams and Grafius (1971) have pointed out that strong linkages between genes may promote an optional balance among components for a specific environment. It can be visualized that when such an association occurs, the plant will be reacting in a manner that will counteract any forces that may lead to a shift away from the optimal balance, thereby leading to no response in the affected trait. Falconer (1952) , Falconer and Latyszewski (1952), Comstock and Moll (1963), Allard and Bradshaw (1964) and Daday et al. (1973) have discussed the influence of stress environments on the expected response to selection and on the changes in relative ranking of varieties. It is noted that the selection programme for this work was carried out at the Field Station of the University of Nairobi, a site which had fairly favourable rainfall and temperature conditions for bean growth. The performance trials were carried out at the same site and also at the National Dryland Farming Research Station, Katumani. The latter site is considered to be highly unfavourable for bean growth and productivity because of low rainfall (Appendix 2). Thus a possibility exists that the absence of response to selection recorded for this character could have been, in part, due to the choice of environments. Falconer (1952) reported situations where stress conditions led to the reversion of relative ranking of selections and as well on reversion of heritability estimates. Nienhuis and Singh(1985) also indicated that selection for bean plant ideotypes with enhanced expression of certain architectural traits can result in limited adaptation and reduced yield potential in some environments.

Ayiecho (1985), in explaining some unexpected responses in grain amaranth populations put forward his arguments in terms of small population sizes, inefficiency of identifications of superior genotypes and the masking effect of the environmental interactions as possible explanations to the observed anomalies. This was in conformity with the earlier report by Lerner (1958) who had emphasised the importance of sample size in improving the efficiency with which population parameters can be estimated. Lerner (1958) noted that the higher the number of the individuals contributing to the family mean, the closer will the mean be to the genetic merit of the family mean. Similarly, the sample size of 10 plants per line and the total of 30 lines used to estimate the population parameters of PAS/001 could have been too small for efficient estimations of such parameters.

5.1.2 Quantitative variation and response to selection in PAS/002

All the selection criteria in this population had detectable genetic variation in the base population. However, no significant direct response was registered for both the number of effective pods per plant and the number of effective podding nodes per plant. The first cycle response of 27.42 percent for the number of effective pods per plant was much higher than the predicted response of 14.67. The results of the variance component analysis for this character showed that the environmental effects had a very prominent contribution to the total phenotypic variation. The environment plays a masking effect during selection time leading to inaccuracies in identifying superior genotypes. It may also mar the expression of characters among selection groups subjected to comparative evaluation. Such observations have been reported by Frey (1964) and Johnson and Frey (1967) in oats, and Ghaderi et al. (1984) in beans. Thus, the discrepancies between the predicted and observed selection responses for the number of effective pods per plant observed in this study may be explained in terms of the environmental effects.

The total seed yield per plant was the only character for which selection led to significant direct and indirect responses. The contribution of the line-season interaction to the phenotypic variance of this character in the original population was not significant. (Table 4). This perhaps enhanced the accuracy of identifying the superior genotypes from the base population. However, the response to the first cycle selection was higher than the predicted gain.

Selection for the number of effective podding nodes led to a direct response which corresponded closely to the predicted value (15.95 percent and 13.52 percent respectively). The response was nevertheless insignificant. Furthermore, there was a big difference between predicted heritability and the realized heritability. These discrepant observations may also be explained in terms of environmental effects and small population size.

Selection for the number of effective pods in the population resulted into a population with higher mean values for the various traits studied. However, the direct and indirect responses for this trait were not significant.

Despite the high correlation among the three traits used for selection in PAS/002 and the other characters, and the presence of significant genotypic variation for most of the traits, no significant correlated response was observed for any character except the total seed yield. Whereas correlated response in the total seed yield per plant is explainable in terms of genetic variation and phenotypic correlation, the absence of correlated response for the other characters may be explained in terms of environmental effects, experimental error and small population sizes as discussed for PAS/001 population above.

5.2 Correlations, multiple linear regression and yield prediction

The majority of the correlation analyses carried out on beans have identified the number of pods per plant as the most important yield predictor. (Singh and Mehndiratta, 1970; Duarte and Adams, 1972; Adams 1972, 1973). It has also been shown that the various yield predictors do affect the yield of beans via the number of effective pods (Kambal, 1969; Duarte and Adams, 1972; Tikka *et al.*, 1976). These observations are expected since the pod is the single unit which contains the other components, namely, the number of seeds and seed weight. Therefore an improvement on the number of effective pods would be expected to reflect the combined relative effect of the number of effective pods *per se*, the number of seeds per pod and the seed weight. It is also conceivable that the number of effective pods depends on the number of nodes, the number of flowers per node and the proportion of flowers that eventually produce the pods. Using the simple linear correlation and the multiple linear regression analyses, the present study has identified the number of effective pods per plant as the best yield predictor in PAS/002 followed by the number of effective podding nodes. The number of effective podding nodes emerged as the second best yield predictor in PAS/001 after the average pod length. The character proved to be a more efficient selection approach for yield improvement than direct selection (Tables 9 and 10). This character correlated positively with most of the characters studied in the two populations. Thus, an improvement on the number of effective pods would be expected to lead to a concurrent improvement on the other important plant characters.

The number of effective podding nodes have hitherto not been given attention as a possible yield predictor in field beans.

This character was identified as a good yield predictor in PAS/002 population. Selection for this character led to an averagely better yield improvement than the other two selection criteria (Tables 9 and 10). It is speculated here that the association between a high number of podding nodes, the number of flowers that eventually produce effective pods and the number of effective pods per node could be favourable and therefore making it possible to improve on these characters concurrently.

The average pod length has also not featured as an important yield predictor in most of the studies reported. Ghaderi _et al._ (1984) identified this character as a trait least affected by the environment and hence could be a trait which contributes to the stability of seed yield across the environments. In the present study the trait was observed to have a high heritability of 0.92 in PAS/001 population. It also correlated favourably with the other important traits such as the number of effective branches per plant (r = 0.596), the number of effective pods per plant (r = 0.917), the number of seeds per pod (r = 0.162) and seed yield (r = 0.825) in PAS/001. The expected increase in yield per unit increase in pod length as indicated by multiple linear regression analysis for PAS/001 was not significant (Table 12). The character also proved to be less efficient as a selection criterion when compared to selection for yield _per se_ (Tables 9 and 10).

5.3 Concluding remarks and suggestions for further studies

One of the basic objectives of this study was to investigate the utility of the morphological components of yield in improving the yield performance of beans in Kenya. The results from this study have shown that the improvement of bean yield is possible when single morphological components are used as selection criteria. The efficiency of such predictors varied between the two populations studied. For example, the number of effective pods per plant was 42 percent more efficient in improving yield of PAS/001 than direct selection for yield *per se* in the second cycle of selection. The same yield predictor was 4 percent faster in improving yield of PAS/002 as compared to direct selection for yield in the second cycle. The number of effective podding nodes was important in PAS/002 only as revealed by the second generation selection results.

Most of the previous work on the association between bean yield and its morphological components have tended to concentrate on the primary components. The work of Bravo *et al.* (1980) is one of the few which have considered the use of secondary components in improving bean yield. In their study, Bravo *et al.* found pod width to be a more efficient selection criterion for yield improvement than yield *per se*. The present study has also emphasized the potency of secondary yield components as predictors of yield in beans by demonstrating that the number of podding nodes can be an efficient approach to yield improvement. The character was averagely more efficient than the number of effective pods per plant and yield *per se* in improving the yield of beans.

The increased efficiency in yield prediction observed for the various yield components arise mainly from the lose in efficiency of yield *per se* in detecting superior genotypes. However, yield *per se* tends to be as efficient as its components in detecting superior yielders only where there is high genetic variation hence high heritability for yielding ability in the population. To benefit from all the characters at all the levels of selection cycles, it may therefore be worthwhile to design a selection programme which combines yield and the identified yield predictors in an index. Searles (1965) and Matzinger *et al.*(1977) have pointed that index selection is superior to the single trait selection approach. Multiple trait selection approach using selection indices is therefore recommended here for further selection studies in beans.

The yield components have always been used by plant breeders when their main breeding objective is the development of plant ideoptypes, or when breeding for disease resistance and drought tolerance. It is noted here that the major bean diseases in Kenya, namely, the common bean anthracnose and the bean rust have direct bearing on pod and seed characters. Breeding programmes to develop resistance against such diseases would thus need a parameter which is independent of pods and seed yield to monitor any changes in seed yield that accompanies the incorporation of resistance genes into the breeding materials. The number of effective nodes is a character which may be used for this purpose.

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Appendix 1. Yield potential of some bean varieties released by the Grain Legume Project - Thika

Variety		Average yield (kg/ha)
GLP-2	Rosecoco	1828
GLP-24	Canadian Wonder	1662
GLP-1004	Mwezi Moja	1437
GLP-x.92	Mwitemania	1472
GLP-x.1127(a)	New Mwezi Moja	1291
GLP 585	Red Haricot	1125

Source:"Release of drybean varieties (Phaseolus vulgaris L.)." Ministry of Agriculture and Livestock Development Technical Bulletin No.3 pp 54. 1984.

Appendix 2*. The mean daily temperature, relative humidity and the total rainfall records at the University of Nairobi Field Station and the National Dryland Research Station – Katumani

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
University Field Station 1986												
Temperature in °C			19.50	18.80	17.54	15.86	15.18			19.07	17.80	17.86
Relative humidity			61.13	75.27	78.81	76.22	74.02			63.84	76.42	69.39
Rainfall in mm			62.80	237.65	255.01	29.55	5.10			40.45	204.95	91.55
University Field Station 1987												
Temperature in °C	18.22		20.22	19.41	18.40	16.74						
Relative humidity	66.76		57.34	69.70	74.60	77.3						
Rainfall in mm	79.55		9.4	285.1	145.05	95.20						
Nat. Dryland Res. Station Katumani 1987												
Temperature in °C			21.66	20.87	19.56	17.65						
Relative humidity			52.63	61.84	65.40	71.51						
Rainfall in mm			23.30	56.70	39.30	61.90						

* Data taken over the period in which the crop was in the field.

Source: Meteorological Stations – Katumani and Kabete.