HETEROSIS AND COMBINING ABILITY IN COMMON BEAN (*Phaseolus vulgaris* L.) IN KENYA.

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DECLARATION

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

Date 26.8.88

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This thesis has been submitted for examination with my approval as a University supervisor.

Date 26.8.1988

Dr. P.M. Kimani

DEDICATION

To my loving mother, Mrs. Marta N. Rushokye.

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ABSTRACT

Bean production in Eastern Africa has been relatively low compared to other major bean producers in Africa and other parts of the world mainly due to diseases, pests and use of unimproved cultivars. This study was designed to determine the nature of gene action and heterosis for yield, yield components and other plant traits in some promising bean cultivars in Kenya.

Seven dry bean (*Phaseolus vulgaris* L.) cultivars, their F_1, reciprocal and F_2 progeny, were evaluated for yield, yield components, maturity traits, branches per plant, and pigmentation of stems, cotyledons and flowers at Kabete and Thika in 1986 and 1987. The experimental design was a completely randomised block with three replications at each location. General and specific combining ability were determined by Griffing's (1956a) Method 3, Model I.

Morphological abnormalities such as seed cracking and crinkling, 'tetrad' trifoliolates and hybrid dwarfism were observed in F_1 plants. The occurrence of these abnormalities was found to be limited to specific crosses involving small- and

large- or medium-seeded parents. Dwarfness was controlled by two complementary dominant genes. The inheritance of cotyledon and stem pigmentation followed a simple monohybrid pattern with purple dominant to green. Flower colour was also found to be simply inherited with purple dominant to white, except in crosses involving L226-10 and other white flowered parents, in which flower colour was controlled by two complementary dominant genes.

Yield heterosis of the F_1 over the highparent ranged between 8-44% and 13-24% at Kabete and Thika, respectively. Twelve hybrids flowered and eighteen matured earlier than their better parents. Among the parental cultivars, GLP-X.92 was the best combiner for yield and yield components, except 100-seed weight. In addition, GLP-X.92, GLP-2 and GLP-288 were found to impart earliness to their progeny.

General combining ability was more important than specific combining ability for branches per plant, maturity traits, yield per plant, 100-seed weight, pods per plant, seeds per pod and seeds per plant in both F_1 and F_2. All traits studied except seeds per pod were found to be strongly influenced by the environment. Reciprocal effects were generally not important.

CHAPTER ONE

INTRODUCTION

Dry beans (*Phaseolus vulgaris* L.) are an important food legume crop and provide an essential part of the daily diet for millions of people especially in Latin America, Central and Eastern Africa, the Middle East and Asia (Schwartz *et al.*, 1982). A substantial part of the population in these countries are low or medium income families who are not able to obtain or afford the relatively expensive animal protein sources (Roberts, 1970; Smartt, 1976). Therefore, beans offer a cheaper source of proteins since they contain 20-28% protein (Leakey, 1970; Laing *et al.*, 1984).

Bean production in Eastern Africa is mainly by subsistence farmers in the wetter bimodal rainfall areas and highlands between 1200 and 2400 meters above sea level (Acland, 1971; Leakey and Simbwa-Buunya, 1972). Yields in Kenya are generally low (375 kg/ha intercropped and 750 kg/ha monocropped) compared to other principal bean producers in Eastern Africa (Londano *et al.*, 1980; Njuguna *et al.*, 1980), and Latin America (Sanders and Schwartz, 1980).

Among other factors, diseases, pests and use of unimproved cultivars have contributed to this low productivity.

Although work on improvement of bean 'cultivars' available to farmers in Kenya has been going on since early 1970's more work needs to be done especially on genetic improvement of bean. Bean improvement programmes were initiated at the University of Nairobi and at the National Horticultural Research Station (N.H.R.S.), Thika, in the early 1970's. Prior to this, most work on bean improvement had been concentrated in Uganda and Tanzania (Leakey, 1970).

In order to enhance genetic variability on which improvement could be based, over 6,000 local and exotic bean lines were collected at the Department of Crop Science, University of Nairobi. Most improvement work both at the N.H.R.S. and the University of Nairobi has been centered on screening this germplasm for disease resistance, yielding ability and adaptation, and agronomic practices such as biological nitrogen fixation and intercropping with maize (Leakey, 1970; Mukunya, 1974; Mukunya and Keya, 1975; Njuguna et al., 1980; Keya et al., 1981; Stoetzer and Omunyin, 1983; Muigai, 1983; Smit et al., 1983; Mwangi, 1986). After extensive testing

over bean growing districts of Kenya, the Grain Legume Project (GLP) at the N.H.R.S. released six bean varieties to the farmers (Van Rheenen et al., 1984).

A mutation breeding programme was initiated at the Department of Crop Science, University of Nairobi in 1979 with the objective of developing resistance to the important diseases of food beans (Phaseolus vulgaris L.), cowpea [Vigna unguiculata L. (Walp.)] and pigeonpea (Cajanus cajan L. Millsp.) (Onim, 1983). Only advanced generation lines derived from radiation treated bean cultivar Canadian Wonder have been evaluated for their yield performance and response to rhizobium inoculation. The results of the inoculation showed increased grain yield and seed weight but delayed duration to maturity of the mutant lines (Kimani, 1988).

Despite the fact that a certain level of improvement has been reached with regard to bean (Phaseolus vulgaris L.) cultivars in Kenya, plant breeders must look for new sources of hereditary components to make further advances. Little work has been done to determine the components of genetic variance for various traits in Phaseolus vulgaris L. in Kenya. Hardly any work has been done on the inheritance of quantitative characters in common bean

in Kenya and Eastern Africa in general. Such knowledge would be important to bean breeders in evaluating the relative importance of genes contributing to complex economic traits like yield and yield components. In view of this, the objectives of this study were to:

1. Determine the nature of gene action governing yield, yield components and other plant traits in common bean.

2. Evaluate heterotic response in some promising bean cultivars in Kenya.

CHAPTER TWO

LITERATURE REVIEW

2:1 Combining Ability and the Use of Diallel Analysis

The term "general combining ability" (GCA) is used to designate the average performance of a line in hybrid combinations, while "specific combining ability" (SCA) is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved (Sprague and Tatum, 1942). Sprague and Tatum (1942) developed the concept of general and specific combining ability and used this method for evaluating the relative importance of genes contributing to yield in single crosses of maize.

A diallel cross is a set of all possible matings between genotypes which may be defined as individuals, clones and homozygous lines (Hayman, 1954). The diallel cross method is a technique widely used to investigate general properties and evaluate the performance of parents and crosses in plant breeding programmes. Jinks (1954) used the

diallel cross method to investigate reciprocal differences, heterosis, genotype X environment interaction and modes of gene action for height, flowering time and leaf length for crosses involving inbred lines of Nicotiana rustica.

Using crosses of Nicotiana rustica, Hayman (1954) developed a diallel cross mathematical model that permits the measurement of additive and dominance properties of homozygous parental lines. He also considered the effects of complications such as genic interactions. Hayman's approach was used by Johnson and Aksel (1959) to analyse the inheritance of yield and yield parameters in barley. Aksel and Johnson (1963) further illustrated its use in estimates of genetic components and inheritance of kernels per head in barley.

Another approach of diallel analysis introduced and discussed by Kempthorne (1956), Griffing (1956a, b), and Kempthorne and Curnow (1961) used the diallel cross technique to estimate genetic variances and the combining abilities of the parental cultivars and their crosses. Gardner and Eberhart (1966) presented a model for the estimation of genetic effects from a diallel cross using a fixed set of random-mating maize varieties. He suggested the use of this model

in planning, analysing and interpreting results of experiments involving either a fixed set of random-mating varieties or a fixed set of homozygous lines as parents.

When a diallel crossing system is used in genetic studies, the additive and non-additive components of the parent genotypic variance are estimated as GCA and SCA effects and/or variances, respectively. Griffing (1956a) partitioned the population genotypic variance by taking dual epistacy into consideration. He defined GCA and SCA effects and variances and their relationship to additive and non-additive genetic effects and variances as follows:-

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_I$$

However, $2\,\sigma^2_{g.c.a.} = \sigma^2_A + 1/4\ \sigma^2_I$

and $\sigma^2_{s.c.a.} = \sigma^2_D + (\text{residual } \sigma^2_I)$

Therefore $\sigma^2_G = 2\,\sigma^2_{g.c.a.} + \sigma^2_{s.c.a.}$

where, σ^2_G = population genotypic variance

σ^2_A = Additive genetic variance

σ^2_D = Dominance variance

σ^2_I = Total epistatic variance

$\sigma^2_{g.c.a.}$ = General combining ability variance

$\sigma^2_{s.c.a.}$ = Specific combining ability variance.

The dominance (σ^2_D) and epistatic (σ^2_I) variance comprise the non-additive (σ^2_{NA}) genetic variance.

The models and theories on diallel analysis cited above show that this technique is an important tool in the investigation of mechanisms of gene action in inheritance of various traits. It is particularly useful in genetic studies of quantitative characters which have complex modes of inheritance. The significance of combining abilities is that they provide an empirical summary of complex observations and a reasonable basis for forecasting the performance of yet untested crosses, but still make no genetical assumptions (Simmonds, 1979). In view of this, the diallel analysis was employed in this study in order to investigate the genetics of inheritance of yield and yield components and other quantitative traits in beans (Phaseolus vulgaris L.) in Kenya.

2:2 Heterosis

Heterosis in plants has usually been identified with hybrid vigor as a major component (Allard, 1960). Allard (1960) regarded hybrid vigor or heterosis as the converse of the deterioration that accompanies inbreeding. He described heterosis as the manifestation of greater vigor in height, leaf area, growth, dry matter accumulation and higher yield in the F_1 hybrid in comparison with its inbred parents. Since all the beneficial effects of crossing are manifested in F_1 hybrids, hybrid vigor has always been emphasized more than inbreeding depression (Allard, 1960).

Suresh and Renu (1975) related heterosis and hybrid vigor in a mechanism and product theory. They stated that hybrid vigor is the phenotypic expression of heterosis which is a genetic phenomenon. However, Williams (1959) included inbreeding depression, hybrid stability or homeostasis, general and specific combining ability and hybrid vigor in its broadest sense as the components of heterosis. Many theories have been put forward to explain the cause of heterosis. These include the dominance hypothesis, overdominance, physiological stimulus, complementation

at cellular and subcellular level, balanced metabolism, hormonal and other factors (Allard, 1960; Suresh and Renu, 1975). Despite the many theories put forward to explain heterosis, present-day concepts of heterosis have no clear cut unifying hypothesis. This has led to the absence of a direct relationship between gene and complex phenotypic expressions seldom recognised in interpretation of quantitative characters (Williams, 1959; Allard, 1960; Suresh and Renu, 1975).

2:2:1. Heterosis in Phaseolus vulgaris L.

The list of crops in which heterosis has led to economic gains is ever increasing (Wittwer, 1974; quoted by Suresh and Renu, 1975). Wittwer (1974) listed field beans (Phaseolus vulgaris L.) among the "future" food crops to be investigated for commercial hybrid varieties. Literature available suggests that little effort has been made in looking for heterosis in beans and establishing commercial hybrids. It could be argued that the negative correlation coefficients among yield components, the very low heritability estimates and large genotype X environment interactions reported for the same traits in P. vulgaris (Adams, 1967; Coyne, 1968; Bennet et al., 1977) might have discouraged workers from developing hybrid beans.

Most reports on heterosis in beans have been centered on grain yield and plant architecture. Coyne (1965) reported heterosis for plant height and its components (internode length and number) in two common bean variety crosses. He explained heterosis for plant height as a result of the multiplicative interaction on the phenotypic level of the components of the trait. In F_1, F_2 and backross generations of a field bean cross 'GN 1140 X PI 165078, Coyne (1968) reported heterosis for number of seeds per pod. He reported low heritability estimates for all the traits studied indicating that selection would not be effective for seed yield or for any of the yield components.

The results of a cross between Iranian and American bean (Phaseolus vulgaris L.) cultivars made by Sarafi (1978) showed that heritability for yield components in F_2 and F_3 populations was high enough to be useful for selection based on pods per plant instead of yield per se. Large and significant heterosis values in common bean were reported by Fooland and Bassiri (1983) for yield (40 - 105%), numbers of seeds and pods per plant (32 - 103%), numbers of seeds per pod (13 - 28%) and number of days from planting to flowering (-11 to -21%). In a study of relationships among yield and yield

components in dry bean, Nienhuis and Singh (1986) observed yield heterosis above the high parent in 20 of the 36 crosses at Palmira and in 4 of the 36 crosses at Popayan.

2:3. Inheritance and Relationships among Yield, Yield components and Architectural Traits.

In recent years techniques involving diallel crosses have been used in problems concerning quantitative inheritance. In soybean, Anand and Torrie (1963) reported low heritability estimates for pods per plant and seeds per pod. They found no correlation between seed weight and seed yield. They further indicated that phenotypically, the number of pods per plant and seeds per pod were more closely related to seed yield than seed weight.

Seven varieties of snap bean (Phaseolus vulgaris L.) and their F_2 progeny were evaluated in a diallel experiment by Dickson (1967). He found additive genetic variance was predominant for number of seeds per plant, number of seeds in the best five pods, length of pod, number of pods per plant and days to flowering but not for plant height and width.

Duarte and Adams (1972) using a path coefficient

analysis showed that leaf number and leaf size have highly significant effects on yield of beans through direct influences upon number of pods per plant and seed size. They showed that leaf number was strongly correlated with pod number and that leaf size was highly correlated with seed size. They suggested a physiological relationship between architectural traits and yield in an effort to find alternatives to yield components as indirect selection criteria. This has led to descriptions of plant ideotypes expected to maximise yield through enhanced adaptation to specific cropping systems and/or environments (Denis and Adams,1978; Nienhuis and Singh, 1986).

In an effort to explain yield heterosis, Suresh and Renu (1975) suggested that there was need to understand the physiological analysis of yield of a given crop. This, they suggested, is important because it can lead to directed efforts in search of yield at the varietal level. If the components leading to yield heterosis could be identified, it would become possible to select varieties with the desired trait (Suresh and Renu, 1975). Denis and Adams (1978) suggested that the development of higher yielding bean cultivars must be based upon relatively large plants bearing numerous nodes, leaves and

reproductive structures, and with an architectural display of phytomeric units which facilitate more uniform interception throughout the canopy.

Nienhuis and Singh (1986) carried out a study to identify the principle types of gene action involved in the inheritance of yield, yield components (pods per plant, seeds per pod, 100-seed weight) and architectural traits in common bean. In contrast to previous reports (Dickson, 1967; Chung and Stevenson, 1973; Fooland and Bassiri, 1983), they found GCA values larger and more important than SCA values for yield, yield components and plant height in both F_1 and F_2 analyses. They further reported a general lack of differences between F_1 hybrids and their reciprocals. This is in contrast with results of Fooland and Bassiri (1983) who found significant reciprocal effects for seed yield and number of seeds per plant. On correlations, Nienhuis and Singh (1986) found moderate to large positive phenotypic and genotypic correlations between all architectural traits studied (except branches per plant) and yield.

Yield components could be most effective in breeding for yield if they were positively correlated phenotypically and physiologically with each other, or at least unrelated. Unfortunately, most of the

studies reported indicate negative correlations among most of these characters. The phenomenon of component compensation, low heritabilities and large genotype X environment interactions are thought to be the major causes of failure to use yield components as indirect selection criteria in common bean (Anand and Torrie, 1963; Adams, 1967; Coyne, 1968; Emping et al., 1970; Sarafi, 1978). There exists negative genetic relationships among yield components especially in stressful environments which promote within plant competition for metabolites (Adams, 1967). Adams (1967) believed these negative correlations to be developmental rather than genetic per se and postulated that they were caused by genetically independent components.

2:4. Hybrid Dwarfism in the Genus Phaseolus

Only four species (2n=2x= 22) of the genus Phaseolus are prominent as cultivated food crops and include P. vulgaris L. P. coccineus L., P. acutifolius Gray var. latifolius Freem., and P. lunatus L. var. lunatus (Bliss, 1980). Successful interspecific crosses have been obtained using various methods of hybridisation (Honma, 1955, 1956; Honma and Heeckt, 1959; Coyne, 1964; Smartt, 1970; Braak and Kooistra, 1975). However, some combina-

tions produced dwarf and misshapen plants with various amounts of sterility and self-incompatibility (Smartt, 1970).

Dwarfism in F_1 hybrids within Phaseolus vulgaris L. has been observed in over 100 crosses at the Centro International de Agricultura Tropical (CIAT), Cali, Colombia (Shree and Gutierrez, 1984). In field conditions at Palmira, Shree and Gutierrez (1984) reported dwarf F_1 hybrids characterised by reduced and stunted growth of leaves and stem. In some crosses, all such plants died within the first few weeks after germination while in others they survived to maturity, flowered and produced 1 to 3 small pods. Previous studies on hybrid dwarfism (also refered to as 'crippled' or 'sub-lethal' development) in Phaseolus vulgaris L. suggest that dwarf hybrids were from crosses betweeen small-seeded and medium - or large - seeded parents (Davis and Frazier, 1964; Coyne, 1965; York and Dickson, 1975; Van Rheenen, 1979; Shii et al., 1980, 1981).

Shii et al., (1980, 1981) reported that the abnormal development of the F_1 hybrids was inherited through two complimentary dominant genes which were named DL_1 and DL_2. Evidence was provided that the severity of expression of the crippled character and

lethality were dependent upon allelic dosages of DL_1 and DL_2. The allelic dosages of DL_1 in the root and DL_2 in the shoot were reported to determine the severity of the character expression.

Since the DL system affects a wide range of developmental events, Shii et al., (1980) hypothesized that DL_1 and DL_2 may be related to the regulation of certain key processes of normal development, such as hormone biosynthesis or metabolism. Through hydroponic studies using F_1 plants heterozygous for DL_1 and DL_2, Shii et al. , (1981) revealed that the primary abnormal developmental event associated with the appearance of mutant phenotypes was restricted to root growth. The direct effect of exogenously supplied cytokinin in overcoming the abnormal growth of the roots led these workers to further postulate that the mutations affect hormonal metabolism.

Apparent differences in the adaptiveness and yielding ability of small and large seeded beans led Shree and Gutierrez (1984) to postulate that the mutant genes DL_1 and DL_2 have played a key role in the evolution of bean types of different seed sizes.

They suggested the use of a 'bridge' line in order to combine desirable genes from two incompatible parental lines.

CHAPTER THREE

MATERIALS AND METHODS

3:1 Parental Material

Seven dry bean (*Phaseolus vulgaris* L.) cultivars were selected for this study on the basis of their varying characteristics (Table 1). Four of these are from an extensive testing programme (Grain Legume Project) of dry bean varieties for local consumption at the National Horticultural Research Station (N.H.R.S.), Thika. They include the Rose coco type (GLP-2 and GLP-288), Mwitemania or Pinto bean (GLP-x.92) and Canadian Wonder (GLP-24). Apart from GLP-288, the other three have been released to farmers after extensive national yield trials, each recommended for parts of Kenya it is most suited to (Van Rheenen *et al.*, 1984). NB 123 is a small-seeded black bean indigenous in Kenya, and is resistant to all common races of bean anthracnose (Mwangi, 1986), halo blight and rust (Mukunya and Keya, 1978) in Kenya.

The white, small-seeded cultivar, L226-10, is one of the two breeding lines of navy beans (*Phaseolus vulgaris* L.) which were developed and

released cooperatively by ARS-USDA and the agricultural experiment station of Michigan State University and the University of Puerto Rico. It has an upright architecture and combines high levels of disease resistance (Rust, Bean common mosaic virus, and several root rot diseases) and high yield potential (Freytag et al., 1985). It is resistant to angular leaf spot (Isariopsis griseoli Sacc.) and bean rust (Uromyces appendiculatus) under field conditions at Kabete (Buruchara, 1987. Personal communication). The seventh cultivar, M535, is one of the advanced generation (M_9) lines derived from radiation treated bean cultivar Canadian Wonder. Earlier generations have been evaluated for resistance to common bean diseases like anthracnose (Colletotrichum lindemuthianum), angular leaf spot (Isariopsis griseoli Sacc.) and rust (Uromyces appendiculatus) in Kenya, and an 11% increase in grain yield in M_5 and M_6 generations has been reported (Kimani, 1988). M535 will be referred to as 535 throughout the text.

3:1:1 Preliminary data collection

In a preliminary trial, parental cultivars were grown at the Field Station, Kabete, during the short rains (October - December) 1986. The purpose of this

trial was to get more information regarding yield and other plant characteristics of the parental material before the main experiments were set out. A randomised complete block design with three replications was used. Every replication had seven plots. Each plot consisted of eight rows, 3m long and 50 cm apart. Plants were spaced 10cm apart within the row.

Diammonium phosphate (18%N, 21-23%P) fertilizer was applied at a rate of 100kg per hectare. Bean plants were sprayed with Rogor L40 (40% W/V Dimethoate) at a rate of 30 ml in 18 lt. of water every two weeks to control whitefly, beanfly and bean aphids. Supplemental irrigation was done due to irregularity and low amounts of rainfall. The field was kept weed-free by hand weeding throughout the growing season.

Table I shows the parental traits for which data was collected. Cotyledon colour was noted from emergence until just before the cotyledons withered. Stem colour was observed right from emergence (hypocotyl colour) until plant maturity. Flowering date was recorded when half of the total number of plants in each row had at least one opened flower. Flower colour and growth habit were also recorded.

Table 1: Bean (*Phaseolus vulgaris* L.) parental material and some of their characteristics.

Parent	Growth habit*	Days to 50% flower	Days to mature	Grain yield (kg/ha)	Seed size gm/100	Seeds per pod	Seed colour	Flower colour	Stem colour	Cotyledon Colour
GLP-2	TYPE I (a)	49	91	1,828	52	5	Variegated pink on cream	White	Green	Green
GLP-2[illegible]	TYPE I (a)	47	96	1,201	43	4	Variegated Brown	Pink	Green	Green with pink tint
GLP-x.92	TYPE III(a)	48	92	1,472	39	4	Variegated grey on cream	White	Green	Green with pink tint
GLP-24	TYPE II (a)	52	100	1,662	34	5	Maroon	Pinkish White	Green	Green
535 (M_9)	TYPE II (a)	54	98	1,732	49	6	Maroon	Pink	Green	Green
L226-10 (No. 52)	TYPE I (a)	56	104	1,907	18	7	White	White	Green	Green
NB123	TYPE IV (a)	52	97	1,722	20	6	Black	Purple	Purple	Purple

* Adapted from Shree P. Singh (1982) Ia=Determinate: IIa=Indeterminate erect: IIIa=Inditerminate, Semi-prostate: IVa= Indeterminate prostate, and viny.

* >40g = Large-seeded

30-40g = Medium-seeded

<30g = Small-seeded

Duration to maturity was recorded as days from sowing until pod maturity (90% of the pods on each plant were brown, and seeds loosely attached within the pod). Number of seeds per pod and 100-seed weight were recorded on 20 randomly selected plants per plot. Bulk weight of dry seed per replication was recorded and from this yield per hectare was computed.

3:2 Diallel Crosses

3:2:1 Soil preparation and plant management in the glasshouse

Crossing was carried out under glasshouse conditions at the Field Station, Faculty of Agriculture, Kabete for a period of four months (September-December 1986). Plastic pots of 8" diameter were filled with unsterilised soil mixture made from top forest soil, sand and farmyard manure in a ratio of 2:1:1 by volume, respectively. Diammonium phosphate (18%N, 21-23%P) fertilizer was added at a rate of 20g per debe (20 litre tin) of soil mixture (Okiror, 1981). One week before planting, the glasshouses were thoroughly washed with pressurised water and fumingated with Dithane M45

(50g in 20l water) and Rogor L40 (50ml in 20l water) to kill any floating fungal spores, mites and whitefly respectively.

Seeds were dressed with Aldrin (40% WP) at a rate of 10g/1kg seed before planting for protection against beanfly. Three seeds were planted per pot and later thinned to two plants per pot. Watering was regularly done to avoid moisture stress which is detrimental to bean plant growth (Laing, et al., 1984). Water splashing on the plants and benches during watering was avoided to reduce possible spread of pathogens.

Spraying of the plants with a mixture of Rogor L40 and Dithane M45 (30cc in 20l water and 30g in 20l water, respectively) at 2-week intervals kept the plants free of any fungal infection and kept mite populations low. All the plants were staked for support owing to the greenhouse conditions which enhanced viny growth even for the non-climbers. In addition, the glasshouse floor was thoroughly wetted to keep humidity high throughout the crossing period. High relative humidity reduces the desiccation of flowers after emasculation and is conducive to good seed set (Bliss, 1980).

3:2:2 Preparation of the female flower

Buds which were plump, showing colour and would open the following day were chosen as the female parent (Plate 1b). Using a fine-tipped forceps, the standard petal was opened by inserting the point of the forceps into the suture and pushing from side to side (Plate 2). The wings were carefully removed with the forceps to expose the coiled keel (Plate 3). A small incision was made near the base of the keel with the point of the forceps and the upper half of the keel was grasped and carefuly peeled up and back to expose the anthers and the stigma (Plate 4).

Using a X10 magnifying lens, the anthers were examined to find out whether they had dehisced and shed pollen. In the event of the latter having taken place, the bud was rejected because self-pollination most probably had taken place. If anthers had not shed pollen, the 10 stamens were removed carefully together with the other half of the keel so as not to rupture the anther sacs and cause self-pollination (Plate 5). Because all stamens could seldom be removed altogether, it was helpful to count those held by the forceps at each attempt and to dispose of the anthers until all 10 were accounted for.

Plate 1:

(a) Immature bud; not ready for emasculation

(b) Mature, plump bud ready for emasculation

Plate 2: Opening of the standard petal to start emasculation process

Plate 3: Wings removed, exposing the coiled keel

Plate 4: Upper half of the keel is peeled up and back

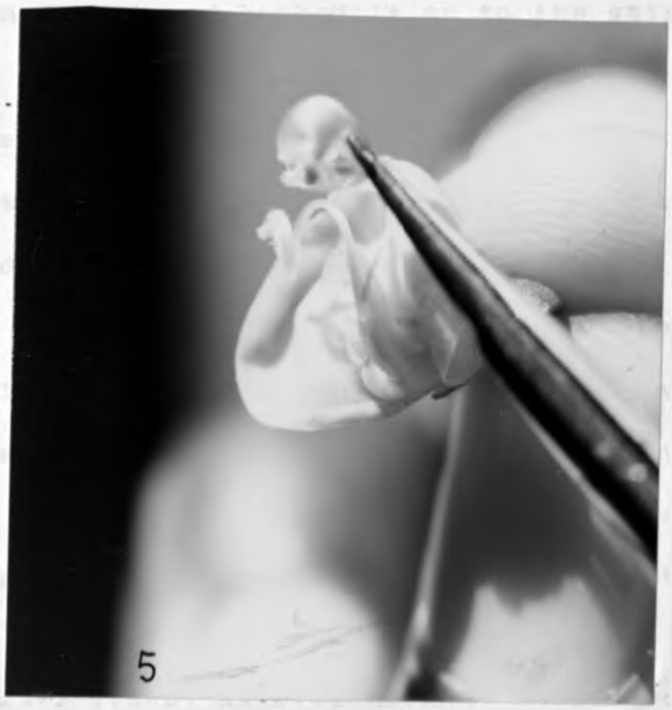

Plate 5: Stamens and lower half of the keel removed to complete the emasculation process

3:2:3 Pollination

Immediately after emasculation, pollination was done using a slight modification of the hooking method of Buishand (1956). Flowers which were used as pollen source were those which had freshly opened that morning (Plate 6). They were picked, placed on a petri-dish and used immediately for pollination. The wings were removed using a forceps (Plate 7), and half of the coiled keel was removed by peeling up and back (Plate 8 and 9).

In his hooking method, Buishand (1956) pulled the stigma bearing loosely attached pollen out of the opened keel and hooked it on to the stigma of the female flower (Plate 14). In this study, after half of the keel was peeled off, the remaining half with all its contents (stigma, anthers, loose pollen) was grasped and removed near its base, then carefully hooked on to the stigma of the female flower (Plates 10,11,12,13). This modification proved very successful and ensured complete contact between pollen and female stigma. It also ensured larger amounts of pollen getting in contact with the female stigma than in Buishand's (1956) method. Unlike in Buishand's (1956) hooking method, pollination process

Plate 6: Freshly opened flowers to be used as pollen source

Plate 7: Wings removed

Plate 8: An incision is made along the middle of the keel

Plate 9: Top half of the keel is snipped off at the base, pulled up and back to expose pollinated stigma, anthers and loose pollen

Plate 10: Lower half of the keel is grasped at the base and snipped off together with its contents

Plate 11: Transfer of pollen-ladden half-keel and stigma to stigma of the female emasculated flower

Plate 12: Hooking process

Plate 13: Hooking process is completed. Tight contact between the two stigmas has been accomplished

Plate 14: Buishad's (1956) hooking process. Note the loose attachment between the stigmas

Plate 15: Standard petal pulled back to close the bud and complete the pollination process

Plate 16: Persistent hooked-on male contents (indicated by the arrow) on a successful pod, 3 - 4 days after crossing

was easier, took less time, and the problem of the male stigma dropping off was not encountered since the hooking was more tight (compare plates 13 and 14). After hooking, the standard petal was carefully closed, enclosing the female stigma with the hooked-on male contents (Plate 15). This hooking method modification ensured persistance of the hooked-on male contents up to the time when the pod was almost 3cm long (Plate 16).

Emasculation and pollination were done at the same time, during early morning hours (before 11.30 a.m.) to avoid afternoon heat which would cause rapid dessication of the freshly pollinated stigma (Bliss, 1980). All subsequent flowers and selfed pods were removed regularly to avoid competition between crossed and selfed pods (Buishand, 1956; Bliss, 1980). The two plants in each pot served both as female parent and pollen source for crosses in all possible combinations to obtain a complete set of 42 F_1's. At least five crosses were made per plant. After crossing, a tag labelled with the pedigree of the cross was tied loosely on the flower stalk. At maturity, the pods were harvested, together with their identification tags, into separate paper bags . They were further sun-dried and hand threshed. The

dry seed was kept in separate envelops which were stapled and on which the pedigree of the cross was labelled.

3:3 F_1 Yield Performance Trial

3:3:1 Locations

This study was conducted at two locations, Field Station, Kabete (Nairobi District) and at the National Horticultural Research Station (N.H.R.S.), Thika (Muranga District). Both locations are in the bean growing districts in Kenya but have variation in soils and moisture availability.

Kabete is on ~~altitude~~ latitude 1° 14' 20"S, longitude 36° 45'E and an altitude of 1,820 metres above sea level. On the average, Kabete receives about 1,046 mm of rainfall per annum with mean temperatures of 23.4° (max.) and 12.6°C (min.). The soils are deep, friable clay type resistant to erosion (Keya and Mukunya, 1979).

Thika is on latitude 01° 01'S, longitude 37° 04'E and an altitude of 1,600 metres above sea level. The station receives an average rainfall of 1,018 mm per annum with mean temperatures 26°C and 13.3°C

(maximum and minimum respectively). The soils are very deep, well-drained, dusky-red to dark reddish-brown, friable clay with moderate fertility (Jaetzold and Schmidt, 1983).

3:3:2 Field layout and management

In the long rains of 1987 (April - July), parents, F_1's and reciprocals were grown at the two locations in order to evaluate their performance.

The experimental design was a randomised complete block with three replications. The 21 plots per block were each made up of a single 3-m row of each of the two parents of a cross, their F_1 and reciprocal. Each plot was boarded on either side with a row containing a mixture of the two parents of the cross. Between row spacing was 45cm while within row spacing was 15cm. An effective plant stand of 148,148 plants per hectare was established.

Diammonium phosphate (18%N, 21-23% P) fertilizer was applied at a rate of 100kg per hectare (or 1kg per 100-m planting furrow) at planting time. Furadan was applied to the planting furrow at a rate of 2g per meter furrow to control seedling insects like cutworms. Before planting, seeds were dressed

with Aldrin 40% WP (10g per kg seed) for protection against the beanfly. At both locations, the plants were sprayed with Benlate (1kg in 1,000 litres water per hactare or 20g in 20 litres water) and Rogor L40 (30cc in 18 litres water) starting 14 days after planting to control fungal diseases and insect pests, respectively. Spraying with the same chemicals was repeated just before flowering, at full bloom and pod-filling period. The fields were kept weed free by hand weeding throughout the growing season. This necessitated weeding four times at Kabete and three times at Thika. Supplemental irrigation was done at Thika due to irregularity of the rains.

3:3:3 Data collection

The number of days from planting to flowering (50% of the plants in each row with at least one open flower) were recorded on row basis. At physiological maturity (90% of the pods on a plant yellow-brown, seeds loose within the pod), data on number of primary branches per plant and pods per plant were recorded on five randomly selected plants per row. Pods from each of the five plants were harvested into separate bags. The individual plant samples were sun-dried, seeds per pod was recorded on single plant basis and the samples were hand threshed. Seed

number per plant and seed yield per plant were then recorded. 100-seed weight was recorded on replication basis. Mean values per plot on the basis of the five plants were then computed.

3:4 F_2 Populations

Of the 42 F_1's grown at Kabete and Thika during the long rains 1987, only 35 crosses yielded F_2 seed. Bulk F_2 seeds from each of the $35F_1$ crosses were evaluated at the Field Station, Kabete. A randomised complete block design with two replications was used. Each block had 35 plots. A plot consisted of five rows, each 5-m long and was boardered on either side by a row of the two parents of the cross. Inter-row spacing was 45cm and plants were 15cm apart within the row. Field management and data collection was as for F_1 yield trial (Sec. 3:3). With the remaining F_1 seed, another F_1 yield trial, similar to the one described in section 3:3, was set up alongside F_2 trial at Kabete during the short rains 1987. The purpose of this trial was to compare F_1 and F_2 populations grown together for the various parameters that were measured.

3:5 Inheritance of Cotyledon and Stem Colour

Data was recorded on the following crosses (and their reciprocals):- NB123xL226-10, NB123xGLP-2 and NB123xGLP-X.92. Cotyledon colour was observed on parent, F_1 and F_2 plants right from seedling emergence up to when the cotyledons were starting to wither. In F_2, the number of plants with purple cotyledon colour were counted and so were the number of plants with green cotyledon colour. Ratios of purple: green were then computed from the actual numbers of plants counted.

Stem colour was recorded on the same plants as cotyledon colour. Stem colour was observed from seedling emergence until pod maturation. Counting of plants with purple and green stems was done at 10 day intervals during this observation period. Segregation ratios (purple:green) were then computed from the actual numbers of plants counted in F_2.

3:6 Inheritance of Flower Colour

Two different flower colours, white and purple were the basis for choice of parents. Accordingly, crosses involving GLP-2 (white) GLP-X-.92 (white),

L226-10 (white) and NB123 (purple) were used for this study. Data were recorded on the four parents, their F_1 reciprocal and F_2 progenies. At flowering time, number of plants with white and purple flowers were counted. F_2 segregation ratios were then computed from actual number of plants counted.

3:7 Hybrid Dwarfism

Dwarf plants were observed from the time their leaves showed chlorosis. Height of dwarf plants was measured at 20 day intervals using a ruler, on 10 randomly selected plants per row. Height per plant was taken as a mean value in centimetres of the ten plants. In both F_1 and F_2 populations, the number of dwarf plants were counted at weekly intervals until plant maturity. In addition, the number of normal plants in F_2 populations were counted and segregation ratios were then computed from actual number of dwarf and normal plants counted.

3:8 Data Analysis

3:8:1 Diallel analysis

Data from parental, F_1 and F_2 populations were first subjected to analysis of variance to test the

significance of genotypic differences. In these analyses, plot mean values for each character per replication were used. Mean separation was carried out using multiple comparisons (Steel and Torrie, 1980) for the purpose of comparing parental performance at Kabete and Thika. This was done only when genotypic differences were detected according to the formula:-

$$lsd = t_{\alpha/2}\sqrt{2EMS/r}$$

where:-

lsd = least significant difference

EMS = error mean square

r = sample size

$t_{\alpha/2}$ = tabulated t value for an α level test against two sided alternatives, using error degrees of freedom.

Data from each location was subjected to analysis of variance separately, then a combined analysis of variance of F_1 data from both locations was performed to determine the magnitude of genotype X environment interaction.

After analysis of variance, the data from F_1 and F_2 generations were analysed separately according to Griffing's (1956a) combining ability analysis using

Method 3 (one set of F_1's and reciprocals only) and Model I (fixed). For the purpose of combining ability analyses, data for all characteristics was re-arranged into replication means from plot mean values. The statistical model for combining ability analysis in Method 3, Model I is:-

$$X_{ij} = u+g_i+g_j+s_{ij}+r_{ij}+\frac{1}{bc}\sum_{k}\sum_{l} e_{ijkl}$$

$$i,j = 1,\ldots\ldots,\ p,$$

$$k = 1,\ldots\ldots,\ b,$$

$$l = 1,\ldots\ldots,\ c$$

Where:-

p = genotypes

b = blocks

c = individuals for each of the pb plots

and,

X_{ij} = the mean of the ixjth genotype over k and l

u = population mean

g_i = general combining ability (GCA) of the ith parent

g_j = GCA effect of the jth parent

s_{ij} = specific combining ability (SCA) effect for the cross between the ith and jth parents such that $s_{ij} = s_{ji}$

r_{ij} = reciprocal genotypic effect such that $r_{ij} = -r_{ji}$

e_{ijkl} = environmental effect peculiar to the ijklth observation.

The following restrictions are imposed on the combining ability effects:-

1. $\Sigma g_i = 0$

2. $\sum_{i \neq j} s_{ij} = 0$ (for each j)

The combining ability effects were tested by comparing with a standard/critical value (S.V.) calculated as follows:-

$$S.V. = S.E \times t = \sqrt{\text{variance}} \times t \text{ (tabulated)}$$

where S.E. = standard error

Each comparison was a two-tailed test, with error degrees of freedom. Variances of combining ability effects were calculated according to Griffing's (1956a) experimental method 3, model I; and all calculations followed a worked example by Singh and Chaudhary (1977).

3:8:2 Testing Mendelian ratios

A chi-square goodness-of-fit test was employed to predict whether the observed ratios from actual number of plants counted for cotyledon, stem and flower color, and number of dwarf and normal plants, followed the theoretical expectations (George, 1982). In all cases, the formula employed was as follows:

$$\text{Chi-square} = \sum \frac{(O - E)^2}{E}$$

where:-

O = Observed numbers

E = expected numbers

The calculated chi-square value was then compared to the tabulated chi-square value based on the chi-square distribution with k-1 degrees of freedom. k is the number of pairs of comparisons and in these analyses k was 2 in all cases.

3:8:3 Heterosis

Heterosis for all characters studied was expressed as percent F_1 heterosis over the mid-parent value (Walton, 1971) and as percent F_1 heterosis over the better or high parent value (Shull, 1952; Allard, 1960; Suresh and Renu, 1975). The formulas used were as follows:-

1) Heterosis over mid-parent

$$H = \frac{\overline{F_1} - \overline{MP}}{\overline{MP}} \times 100$$

2) Heterosis over high parent

$$H = \frac{\overline{F_1} - \overline{HP}}{\overline{HP}} \times 100$$

Where:-

H is heterosis,

$\overline{MP}$ is mid-parental value (mean) = P1+P2;
P stands for 'parent',

$\overline{HP}$ is high parental value (mean),

$\overline{F_1}$ is hybrid value (mean) of the cross between any two parents for the particular trait

The significance of heterosis values was tested using comparison of sample means; meaningufly paired observations as described by Steel and Torrie (1980).

CHAPTER FOUR

RESULTS

4:1 Success Rate in Crossing

A total of 2,139 pollinations were done among the seven parents (Appendix 1). Of these, 1,799 were successful, giving an overall 84.1 percent of successful crosses with each pod containing 4-7 seeds. This percentage is relatively high compared to the average of 30-40% reported by Buishand (1956). It is, however, comparable to the 70-80% recorded at Max Plank Institute at Voldagen (Buishand, 1956).

4:2 Morphological Deformities in F_1 and F_2 Populations of *Phaseolus vulgaris* L.

Hybrids with abnormal development were obtained when particular parental genotypes of *Phaseolus vulgaris* L. were crossed. All the F_1 and reciprocal plants in crosses between NB123 and GLP-288, GLP-24 and 535 showed abnormal development. The same was true for crosses between GLP-288, GLP-24 and 535 with L226-10. In addition, the crosses NB123x535 and NB123xGLP-288 (and reciprocals) yielded deformed F_1 seeds.

4:2:1 Symptoms

4:2:1:1 Seed deformities

Some F_1 seeds resulting from the cross 535 (M_9) xNB123 and the reciprocal cross were cracked at one end causing a wedge-like opening with the seed coat pulled back (Plate 17a). In all cases, seeds were cracked on opposite end to embryo end and therefore such seeds germinated perfectly well. Seed cracking was observed in 27% of the total number of seeds per plant in this cross.

The cross GLP-288xNB123 and its reciprocal yielded misshapen seeds (Plate 17b). About 19% of the total number of seeds per plant had irregular shapes with crinkled centres. However, in this cross the seeds were not cracked. No F_2 seeds were recovered from both crosses because seedlings dried before maturity.

4:2:1:2 "Tetrad" trifoliolate leaves

Hybrid plants from the cross L226-10xGLP-2 showed vigorous growth and development. However, it was observed in all the three replications at both Thika and Kabete that 20% of the plants in a row had

the first trifoliolate leaf bearing four leaflets (Plate 18). In some cases, the middle leaflet was much larger and broader compared to the other two, with a wide notch at the tip (Plate 19). The subsequent trifoliolate leaves on such a plant produced the normal three leaflets. None of this 'tetrad' trifoliolate was observed on either parents of the cross and this condition was not observed on F_2 plants of this cross or any other crosses.

4:2:1:3 Hybrid Dwarfism

The F1 seeds from crosses involving both L226-10 and NB123 germinated almost 100 percent. Healthy seedlings emerged and initially grew normally. The first two foliage leaves unfolded. At this point, hybrid plants from crosses involving GLP-288, GLP-24, 535 and having NB123 as one of the parents, apparently ceased to grow. The first trifoliolate leaves emerged but failed to unfold. The first two foliage leaves became chlorotic and somehow crinky and brittle. In plants where the first pair of trifoliolates unfolded, they did not expand to the normal sizes. They too became chlorotic. Slowly they became necrotic (Plate 20b) and fell off leaving a leafless plant (Plate 20c).

Plate 17: (a) The female parent 535 (M-9) and its F_1 with NB123. showing cracked seeds

(b) The female parent GLP-228 and its F_1 with NB123 showing misshapen seeds

Plate 18: Hybrid plant from the cross L226-10 x GLP-2 bearing a "tetrad" trifoliolate leaf

Plate 19: Hybrid plant from the cross L226-10 x GLP-2 bearing notched middle leaflet

The tap-root degenerated together with the secondary roots that were beginning to form (Plate 20b and c). The plants attempted to initiate adventitious roots along the stem just above the soil surface. The adventious roots looked fleshy in the morning, but on a hot day withered by evening time. The tap-root dried up and this drying continued up the stem until eventually by 20-25 days after sowing the whole plant was dead. All F_1 plants having NB123 as one of the parents died without producing seed, except 2 plants from the cross GLP-288xNB123 (female x male) which produced 1 pod per plant each with one seed per pod, at Kabete.

The F_1 plants having L226-10 as one of their parents survived longer than hybrids of NB123. They were in two classes; those which survived up to pod and seed maturation and those which did not. The latter group passed through the same trend of degeneration and death like those of NB123 but leaf chlorosis commenced 9-12 days after the first foliage leaves unfolded. Such plants managed to produce one pair of trifoliate leaves which unfolded but did not expand to the normal leaflet sizes. Both the primary and trifoliate leaves stayed green longer than in NB123 hybrids but eventually became chlorotic and plants died 31-40 days after sowing.

Plate 20: Developmental differences between a parental normal plant (a) and its F_1 progeny in the cross L226-10 x GLP-228. Note the necrotic primaries (b), the leafless plant after total defoliaton (c) and the severely reduced root system of the hybrids (b and c). The three plants were all about 35 days old.

The hybrids which survived up to pod formation were not normal either. They were stunted (8-25 cm tall) and had greenish-yellow leaves. They produced up to four pairs of trifoliate leaves, yielded 1-4 'mini-pods' per plant with 1-4 seeds per pod. Their root system was poorly developed though not as severely as in the two cases mentioned above. No adventitious roots were formed by such plants. They flowered (27-30 days) and matured (10-13 days) later than the normal F_1 plants involving the same parents. It was noticed that stunted plants which got partially or wholly covered by the canopy of the normal parental plants (next row in the plot arrangement: Plate 21) had dark green leaves compared to the plants which were always exposed. The severely restricted growth of the hybrids with abnormal development contrasted sharply with the rapid and normal development of the parental plants in the field (Plate 21). There was no reciprocal cross difference in the expression of these abnormal phenotypes.

Among F_2 populations, normal and dwarf plants were recovered. Some of the dwarf seedlings behaved like F_1's which died within the first month after sowing, while others survived to produce pods and seeds. Those in the latter category produced more

Plate 21: The cross L226-10 (52) x GLP-228 (228) (and the reciprocal) in the field. Note the leaf chlolosis of the F_1's (middle rows) and their size as compared to the parents (52 and 228)

than six pairs of trifoliate leaves and leaf chlorosis did not result into defoliation. The frequency of distributions of F_2 progeny, classified into normal and dwarf plants is presented in Table 2. Since the calculated chi-square values are much smaller than the critical value (0.05 probability for 1 degree of freedom = 3.84), the data supports the hypothesis of a 9:7 (Dwarf:Normal) segregation for hybrid dwarfism in the three crosses.

4:3 Inheritance of Cotyledon and Stem Colour

Among the parents used in this study, only NB123 has purple stem and cotyledon colour (Table 1). The other three parents all have green cotyledons and stems. NB123 was the common parent in all the six crosses. The resulting F_1 and reciprocal hybrids all had purple cotyledons and stems. It was observed that all plants with purple cotyledon colour also had purple stems. This was observed on parent, F_1, reciprocal and F_2 plants. For this reason, the same plants were analysed for cotyledon and stem colour in F_2 (Table 3).

Table 2: Segregation for dwarf and normal plants in F_2 populations of *Phaseolus vulgaris* L.

Cross	Number of plants		Calculated χ^2	Expected ratio
	Dwarf	Normal		
GLP-288xL226-10	59	46	0.15×10^{-3} NS*	9:7
535 x L226-10	68	48	0.13 NS	9:7
GLP-24 x L226-10	66	50	0.02 NS	9:7

*NS - Non-significant compared to chi-square value of 3.84 ($P<0.05$; df=1).

A change in stem colour was observed on F_1 and F_2 plants at the three-trifoliate-leaf stage. The main stem became less purple in intensity giving way to green. The secondary branches that were produced were, however, purple in colour. At pod-filling stage, it was observed that only the secondary branches exposed to sunlight were purple. Furthermore, a given section or length of a secondary branch could posess dual colouration: being purple on the side exposed to sunlight but totally green on the shaded side. Towards maturity when most leaves had been shed, the main stems gained the purple colouration but it didn't last long as it turned to brown as the plants dried up. There was no noticeable change in colour of green stems until maturity when they turned brown and dried. Cotyledon colour (green or purple) did not change with time.

The frequency of distribution of individuals in each F_2 cross populations (Table 3) for stem/cotyledon colour was not significantly different from the ratio of 3:1 (purple: green).

Table 3: Segregation for stem and cotyledon colour in F_2 and reciprocal populations of *Phaseolus vulgaris* L.

Cross	Number of plants		Calculated χ^2		Expected Ratio
	Purple	Green			
1) NB123xL226-10	205	70	0.030	NS*	3:1
L226-10xNB123	222	81	0.485	NS	3:1
2) NB123 x GLP-2	226	82	0.433	NS	3:1
GLP-2 x NB123	195	74	0.904	NS	3:1
3) GLP-x.92 x NB123	228	79	0.086	NS	3:1
NB123 x GLP-x.92	232	81	0.129	NS	3:1

*NS - Non-significant compared to chi-square value of 3.84 ($P<0.05$, df=1).

4:4 Inheritance of Flower Colour:

All the parents used in this study have white flowers except NB 123 which bears purple flowers (Table 1). F_1 plants from the ten crosses presented in Table 4 all had purple flowers. Unexpectedly, crosses of L226-10 with GLP-2 and GLP-X.92 resulted into F_1 plants bearing purple flowers although none of the three parents bears purple flowers. It was observed that these same F_1 and reciprocal hybrids had purple cotyledons and stems and segregated for purple and green stem and cotyledon colour in F_2 (data not presented).

The data presented in Table 4 can be grouped into two classes. In the first class, NB123 is the common parent while in the second class L226-10 is the common parent. Analysis of the goodness of fit of the F_2 population in the first class showed that they did not segregate significantly from the expected ratio of 3:1 (Purple:White). In the second class, the frequency distribution of individual crosses was not significantly different from the theoretical 9:7 (Purple:White) ratio. All the crosses showed no reciprocal differences for inheritance of flower colour.

Table 4: Segregation for flower colour in F_2 and reciprocal populations of *Phaseolus vulgaris* L.

Cross	Number of plants Purple	White	Calculated Chi-square value		Expected Ratio
1) L226-10 x NB123	173	68	1.329	NS*	3:1
NB123 x L226-10	169	63	0.162	NS	3:1
2) GLP-2 x NB123	136	41	0.318	NS	3:1
NB123 x GLP-2	170	57	1.75×10^{-3}	NS	3:1
3) GLP-x.92 x NB123	162	55	0.014	NS	3:1
NB123 x GLP-x.92	161	58	0.257	NS	3:1
4) GLP-2 x L226-10	93	60	0.437	NS	9:7
L226-10 x GLP-2	89	59	0.908	NS	9:7
5) GLP-92xL226-10	120	107	1.058	NS	9:7
L226-10xGLP-92	118	97	0.163	NS	9:7

*NS - Non-significant compared to chi-square value of 3.84 (P.0.05. df=1).

4:5 Heterosis

Owing to death before maturity of many of the hybrids involving L226-10 and NB123, results on parental, F_1 and F_2 generations discussed are of a 5x5 complete diallel crossing system instead of a 7x7 complete diallel crossing system. Mean values of parental lines and F_1 heterosis above midparent and highparent values are presented in Tables 5, 6 and 7 respectively.

4:5:1 Number of primary branches per plant:

At Kabete, most parents were significantly different from each other for this trait except GLP-24 and GLP-288, GLP-X.92 and 535 while at Thika, 40% of the parents showed no significant difference (Table 5). Among the parents, GLP-X.92 had the highest number of primary branches per plant at both locations, and had the same value with GLP-24 at Thika. All parents had more primary branches per plant when planted at Kabete than at Thika.

Table 5: Mean values of different characteristics for five parental bean lines grown at two locations in 1987 (long rains).

	Primary branches per plant		Pods per plant		Seeds per pod		Seeds per plant (g)		Seed yield per plant (g)		100-seed weight(g)		Days to 50% flowering		Days to physiological maturity	
Parent	K*	T*	K	T	K	T	K	T	K	T	K	T	K	T	K	T
GLP-2	5.00	3.60	16.90	9.27	5.60	3.73	70.33	24.67	49.23	12.33	69.87	49.63	39.0	37.0	92.0	82.0
GLP-24	4.50	4.07	29.47	26.07	5.67	4.67	135.67	103.87	56.98	33.24	41.83	32.22	48.3	44.0	102.3	88.3
GLP-288	4.73	4.00	22.80	22.13	4.73	4.27	82.33	78.87	51.87	39.43	62.81	49.89	37.0	33.0	97.7	86.0
GLP-x.92	6.20	4.07	43.13	21.80	5.40	4.33	157.93	65.07	86.86	32.53	55.46	49.50	36.3	33.7	99.3	86.0
535	5.17	3.53	29.20	14.73	6.13	4.07	139.60	57.07	78.17	21.12	55.64	36.93	49.7	41.0	107.3	90.3
Overall parental mean	5.10	3.90	28.30	18.80	5.51	4.21	117.17	69.91	64.62	27.73	57.12	43.59	42.06	37.7	99.7	86.5
lsd	0.23	0.29	3.66	4.13	0.12	0.28	17.27	16.53	9.7	5.38	0.29	1.89	0.96	0.70	1.05	0.51

* K=Kabete; T=Thika

Table 6: Percent F_1 heterosis above midparent (MP) and highparent (HP) in 20 bean crosses for primary branches and maturity traits.

Cross	Primary branches per plant				Days to 50% flowering				Days to physiological maturity			
	$\overline{MP}$		$\overline{HP}$		$\overline{MP}$		$\overline{HP}$		$\overline{MP}$		$\overline{HP}$	
	K	T	K	T	K	T	K	T	K	T	K	T
GLP-2xGLP-24	7.87*	0.91	1.40	-4.91	14.55*	-6.99	3.52	-14.32**	4.17**	2.17*	-1.08	-1.47
Reciprocal	2.13	6.91	-4.00*	0.74	9.97**	0.49	-0.62	-7.49**	2.21**	0.65	-2.93**	-2.94*
LP-2xGLP-288	11.00*	1.84	8.00**	-3.25	0.00	9.43**	-2.56	3.51	0.47	-2.38*	-2.46**	-4.65**
Reciprocal	2.77	10.53**	0.00	5.00	-7.89*	-2.00	-10.26**	-7.30*	-1.21	0.00	-4.09**	-2.35*
GLP-2xGLP-x.92	3.57	-7.95	-6.45**	-13.27**	-2.52	-0.14	-5.90*	-4.59	2.14**	6.31**	-1.61	3.84**
Reciprocal	1.25	6.13	-6.55**	0.00	-4.38	1.84	-7.69**	-2.70	2.77**	1.19	-1.01	-1.16
GLP-2x535	0.88	45.86**	-0.77	44.44**	-3.04	5.13	-15.48**	0.00	4.97**	-0.99	-2.52**	-5.54**
Reciprocal	0.88	40.25**	-0.77	38.89**	8.91**	7.69*	-2.82	2.44	4.06**	1.80*	-3.36**	-2.88*
GLP-24xGLP-288	-2.37	-2.60	-3.13	-3.44	11.84**	4.68	-1.24	-8.41**	0.30	8.20**	-1.96**	6.80**
Reciprocal	-0.95	-2.60	-1.27	-3.44	12.54**	4.68	-0.62	-8.44**	2.00	7.06**	-0.29	5.66**
GLP-24xGLP-x.92	-4.34	4.91	-18.23**	4.91	-13.24**	-9.91**	-24.0**	-20.14**	-2.48**	3.27**	-3.91**	2.93*
Reciprocal	-26.42**	4.91	-37.10**	4.91	-10.17**	-10.68**	-21.33**	-21.14	-1.09*	2.12*	-2.54**	0.79
GLP-24x535	4.50	3.42	-3.29	-3.44	-0.61	-13.65**	-2.01	-16.59**	3.05**	6.05**	0.65	4.87**
Reciprocal	-2.40	-7.90	-9.67**	-14.01**	2.04	-14.58**	0.60	-17.50**	4.96**	4.93**	2.52**	3.77**

.../66

Table 6 contd.

GLP-288xGLP-x.92	-4.85	-2.60	-16.13**	-3.44	0.14	10.04**	-0.81	11.21**	1.22*	1.51	0.40	1.51
Reciprocal	1.19	0.87	-10.81**	0.00	0.14	7.95*	-0.81	9.09**	2.54**	0.00	1.71**	0.00
GLP-288x535	-3.03	9.70*	-7.16**	3.25	3.81	10.81**	-9.46**	0.00	2.44**	1.30	-2.10**	-1.11
Reciprocal	-3.03	18.73**	-7.16**	11.75**	8.42**	2.70	-5.43*	-7.32*	2.44**	-0.96	-2.10**	-3.32**
GLP-x.92x535	10.30*	43.95**	1.13	34.40**	-11.63**	-0.13	-23.50**	-9.02**	-3.87**	-0.17	-7.46**	-2.55*
Reciprocal	-6.24	19.21**	-14.03**	11.30**	-19.30**	7.9	-30.20**	-1.71	-2.52**	-2.44**	-6.15**	-4.76**

*K = Kabete; T = Thika

*, ** = Significance of differences between F_1 and midparent or F_1 and high parent means compared to S_D at 0.05 and 0.01 probability levels, respectively.

TABLE 7: Percent F_1 heterosis above midparent (MP) and highparent (HP) for yield and yield components in 20 bean crosses.

Cross	Pods per plant				Seeds per pod				Seeds per plant				Seed yield per plant(g)				100-seed weight(g)			
	$\overline{MP}$		$\overline{HP}$		$\overline{MP}$		$\overline{HP}$		$\overline{MP}$		$\overline{HP}$		$\overline{MP}$		$\overline{HP}$		$\overline{MP}$		$\overline{HP}$	
	K	T	K	T	K	T	K	T	K	T	K	T	K	T	K	T	K	T	K	T
GLP-2x-GLP-24	7.27	-27.96**	-15.60**	-51.17**	-1.66	31.67**	-2.47	16.42**	1.10	-38.12**	-23.25**	-61.71**	23.55**	-16.50	15.15**	-14.13**	13.11**	10.40**	-9.59**	-8.97**
Reciprocal	20.77**	-21.90**	-5.00	-47.07**	-1.66	30.95**	-2.47	17.77**	15.68**	-37.92**	-12.19**	-61.59**	45.82**	-17.62	35.99**	-43.53**	15.54**	18.00**	-7.84**	2.70
GLP-2x-GLP-288	-10.98*	1.08	-22.50**	-28.29**	0.66	3.25	-7.14**	-3.28	-7.77	-0.91	-14.49**	-34.96**	6.27	11.01	3.57	-27.14	18.04**	13.51**	12.06**	13.44**
Reciprocal	-10.68*	18.47*	-22.2**	-15.95*	-7.07**	13.25**	-14.29**	6.09	-8.65	27.67**	-15.30**	-18.04	4.85	58.58**	2.18	4.08	14.34**	24.39**	8.56**	24.31**
GLP-2xGLP-x.92	22.61**	18.44*	-14.70**	-15.60*	-12.73**	17.37**	-14.29**	9.24*	16.30**	38.02**	-15.96**	-4.83	22.89**	29.78**	-3.73	-10.51	1.01	-4.23*	-9.40**	-4.35*
Reciprocal	12.38**	80.09**	-21.80**	14.08	-11.45**	17.37**	-13.04**	9.24*	0.12	87.65**	-27.65**	29.40**	7.47*	87.70*	-15.81**	29.42**	1.60	1.34	-8.87**	1.21
GLP-2x535	24.08**	40.83**	-2.10	14.73	-12.53**	28.21**	-16.31**	22.85**	6.89	38.00**	-19.63**	-1.17	25.05**	68.43**	1.19	33.38**	13.89**	11.51**	2.29	-2.78
Reciprocal	14.23**	130.00**	-9.80**	87.37**	-9.12**	64.10**	-13.05**	57.25**	-2.63	168.68**	-26.79**	92.40**	15.51**	231.60**	-5.87	182.59**	15.37**	9.08**	3.62*	-4.88*
GLP-24xGLP-288	34.42**	-13.69*	19.2**	-20.21**	-1.84	0.00	-9.46**	-4.28	29.79**	-15.51*	4.28	-25.68**	50.76**	-15.01*	44.00**	-21.68*	11.66**	-3.14	-8.99**	-20.17**
Reciprocal	12.22**	1.54	-0.48	-8.14	3.85*	1.34	-6.78*	-2.30	-1.47	-6.87	-20.80**	-19.83**	17.76**	10.00	12.48*	1.37	18.83**	17.62**	-2.85	-3.08
GLP-24xGLP-x.92	17.71**	4.45	-0.90	-4.10	-7.32**	22.89**	-9.52**	18.42**	-2.68	4.81	-9.54**	-14.77*	7.27*	24.04**	-11.18**	22.71*	18.78**	13.71**	-2.81	-6.14**
Reciprocal	2.20	25.34**	-14.00**	15.07*	-7.86**	22.89**	-10.05**	18.42**	-13.56**	24.07**	-19.65**	0.90	-8.48	48.80**	-22.57**	45.04**	7.92**	12.21**	-5.34*	-7.37**
GLP-24x535	42.73**	-8.52	42.10**	-28.85**	-3.90*	9.84**	-7.84**	2.78	23.17**	-12.50	21.44**	-32.22**	32.98**	-1.58	14.34**	-19.52*	7.99**	9.59**	-5.41**	2.80
Reciprocal	27.94**	7.84	27.40**	-15.61*	-9.66**	7.55*	-13.05**	0.64	15.91**	1.81	14.29**	-21.12**	25.12**	5.52	8.16*	-13.72	9.72**	1.88	-3.98*	-4.80
GLP-288xGLP-x.92	33.70**	20.19**	2.20	19.30**	-6.61**	8.80*	-12.41**	7.85*	19.6**	17.65*	-9.03**	7.35	18.06**	8.25	-5.72	-1.22	-4.88*	-7.85**	-8.62**	-8.83**

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Reciprocal	34.70**	33.26**	2.9	32.26**	-5.23**	5.35	-11.11**	4.82	12.38**	32.28**	-14.52**	20.70**	14.8**	24.35**	-8.32*	13.47*	-0.47	-4.67*	-6.29**	-4.85*
GLP-288x535	20.30**	9.22	7.1	-9.04	-5.52**	24.70**	-16.31**	21.78**	-0.33	19.32**	-20.80**	2.83	15.67**	17.85*	-3.79	-9.51	15.10**	3.74	8.53**	-9.58**
Reciprocal	29.20**	34.56**	15.10**	12.07	-5.52**	34.29**	-16.31**	31.15**	10.42**	37.71**	-12.23**	18.68**	24.38**	42.23**	3.45	9.21	12.06**	6.83*	5.67**	-6.88**
GLP-x.92x535	13.8**	66.44**	-4.8	39.45**	-21.42**	28.57**	-26.10**	24.71**	-13.24**	52.94**	-18.27**	43.54**	-9.28**	42.74**	-13.83**	17.71*	4.08*	-4.50	3.86*	-16.83**
Reciprocal	20.00**	39.45**	0.8	16.83*	-18.99**	28.90**	-23.82**	23.09**	3.07	38.09**	-2.91	29.60**	9.64**	38.42**	4.16	14.14*	8.07**	2.44	5.90**	-10.57**

*K = Kabete; T= Thika

*, ** = Significance of differences between F_1 and midparent or F_1 and highparent means compared to S_D at 0.05 and 0.01 probability levels, respectively.

Heterosis above the midparent for this trait was observed in 9 of the 20 crosses and above the highparent in 6 of the 20 crosses (Table 6). Highest values of heterosis above the high parent were shown by the hybrid GLP-2 x 535 and its reciprocal hybrid at Thika.

4:5:2 Maturity traits

The parental lines showed significant differences in their flowering and maturity dates at both locations except at Thika where GLP-288 and GLP-x.92 matured at the same time. These two cultivars flowered earliest but GLP-2 was the earliest to mature, taking 82 and 92 days at Thika and Kabete, respectively. Cultivar 535 was the latest to mature (90.3 and 107.3 days at Thika and Kabete, respectively), giving a range of 8 and 15 days between earliest and latest maturing cultivar at Thika and Kabete, respectively. On the average, parents flowered 4 days and matured 13 days earlier when grown at Thika than at Kabete.

Regardless of location, 11 hybrids flowered earlier and five hybrids matured earlier than both parents. All these hybrids had GLP-2, GLP-288 or GLP-x.92 as one of their parents. Crosses involving

the late maturing cultivars i.e. GLP-24 and 535 tended to have significant positive heterosis values for days to 50% flowering and physiological maturity. This indicated that the two parents imparted lateness to their progeny.

4:5:3 Number of pods per plant

There were significant differences in number of pods per plant among the parents. GLP-x.92 had the highest number of pods per plant at Kabete while GLP-24 performed best for the same trait at Thika (Table 5). Despite better performance of parents at Kabete than at Thika for this trait, a good number of thin, crooked pods were observed on both parent and F_1 plants grown at Kabete. No disease symptoms were observed on such plants or their pods.

Table 7 shows that an average of 9 out of 20 hybrids exceeded the highparent while 18 out of 20 hybrids exceeded the midparent means for pods per plant. Useful heterosis above the high parent ranged between 15-87%. It is noteworthy that the largest heterosis values were attained whenever cultivars 535

and GLP-x.92 were involved in the cross. Most of the crosses involving GLP-2 exhibited highly significant negative heterosis values indicating that they performed poorer than the midparent.

4:5:4 Number of seeds per pod

Overall parental performance was once more greater at Kabete than at Thika, averaging 4 and 6 seeds per pod at Thika and Kabete, respectively. Cultivar 535 had the highest number of seeds per pod at Kabete but did not do as well at Thika where GLP-24 performed best (Table 5). There was significant difference among the parents for this trait at both locations.

Table 7 shows that almost all the crosses exhibited significant heterosis above midparent and highparent means at Thika while at Kabete the same crosses had negative heterosis values for seeds per pod. This indicated that the environment affected expression of heterosis for seeds per pod. The magnitude of F_1 heterosis above both midparent and highparent tended to be greater in crosses between cultivar 535 and other groups other than Canadian Wonder and was highest in the cross 535 x GLP-2.

4:5:5 Number of seeds per plant

Seed number per plant was higher at Kabete than Thika for all parents. Three of the five parents, GLP-2, GLP-x.92 and 535 yielded more than twice the number of seeds per plant when grown at Kabete than at Thika. GLP-24 and GLP-x.92 were the best yielders, having an average of 120 and 112 seeds per plant, respectively.

The highest magnitude of F_1 heterosis for seeds per plant above both midparent (168.7%) and highparent (92.4%) was shown by the hybrid 535 x GLP-2. When 535 was used as the male parent, the magnitude of heterosis was much smaller than when it was used as the female parent. This was true for the hybrids 535 x GLP-2, 535 x GLP-288 and 535 x GLPx.92. Generally, most hybrids again performed poorly at Kabete as compared to Thika.

4:5:6 Seed yield per plant

Significant differences were observed among parents for this trait at both locations although some parents like GLP-2 and GLP-288 did not differ significantly from each other. GLP-x.92 has the highest seed yield per plant while GLP-2 had the

lowest. The poor performance of GLP-2 could be attributed to its very low numbers of pods per plant, seeds per pod and seeds per plant as compared to other parents (Table 5).

Regardless of location, most crosses did not differ significantly in seed yield from the midparent mean. The hybrid 535xGLP-2 excelled in performance and yielded more than 200% and 160% above midparent and highparent means, respectively. The cross between the highest yielding parents, GLP-x.92 x 535 (and the reciprocal cross) did not show useful heterosis above the highparent mean. Heterosis variation in magnitude at the two locations was again evident for seed yield per plant as for other traits above.

4:5:7 100-seed weight

Unlike for other trais, GLP-2 exhibited the highest 100-seed weight (60g), followed by GLP-288 (56g). The lowest value for 100-seed weight at both locations was shown by GLP-24 (41.83g and 32.22g at Kabete and Thika, respectively). Overall parental mean seed weight was 47g higher at Kabete than at Thika for this trait.

Significant heterosis above the midparent mean was observed at both locations in 11 of the 20 crosses. The cross (and reciprocal cross) between cultivars with the heaviest seeds (GLP-2 and GLP-288) was the only one that exhibited highly significant heterosis above the highparent value at both locations. Negative heterosis values at either or both locations was observed in crosses between GLP-2 and GLP-288 with the other three parents indicating that such hybrids performed poorer than the midparent.

4:6 Combining Ability

General combining ability (GCA), specific combining ability (SCA) and reciprocal mean squares from diallel analyses of F_1 and F_2 generations are presented in Table 8 and 9, respectively. The results of the analyses of variance over locations are shown in Table 10. Estimates of GCA, SCA and reciprocal effects are presented in Tables 11, 12 and 13 respectively.

4:6:1 Number of primary branches per plant

GCA mean squares for this trait were highly significant at both locations while SCA mean squares were significant only at Thika. Reciprocal mean squares were not significant at both locations. The magnitude of GCA mean squares were one to four times larger than SCA mean squares for primary branches per plant (Table 8). No mean squares were calculated for this trait in F_2 generation because of lack of significance of genotypic differences for this trait in the analysis of variance. The results presented in Table 9 show highly significant differences between locations for primary branches per plant. The GCA x location interaction was highly significant for this trait, and so was the SCA x location interaction.

TABLE 8: SCA, SCA and reciprocal mean squares of F_1 bean hybrids grown at Kabete and Thika in 1967 (Long rains).

Source	d.f.	Number of Primary Branches per plant		Number of pods per plant		Number of seeds per pod		Number of seeds per plant		Seed yield per plant(g)		Number of 100-seed weight (g)		Number of days to 50% flowering		days to physiological maturity	
		K*	T*	K	T	K	T	K	T	K	T	K	T	K	T	K	T
GCA	4	0.72**	0.53**	271.64**	69.61**	0.34**	0.49**	2259.41**	919.54**	237.49**	130.11**	256.30**	115.07**	130.16**	9.98**	55.24**	39.26**
SCA	5	0.18	0.40**	27.61	24.47	0.03	0.53**	467.55**	295.78	111.78	102.89**	14.97**	22.06**	19.97**	10.04**	14.60**	11.53**
Reciprocal	10	0.14	0.09	5.98	13.32	0.03	0.12**	149.40	217.67	50.84	64.79	1.36	7.03	3.00**	2.66**	0.99	2.13
Error	38	0.13	0.08	11.84	11.55	0.04	0.04	132.74	166.29	48.60	35.13	1.25	5.80	0.91	0.72	0.57	1.38
GCA:SCA ratio		4.00	1.33	9.84	2.87	11.33	0.92	4.83	3.11	2.12	1.26	17.12	5.22	6.52	0.99	3.78	3.41

*K = Kabete; T= Thika

*, ** = Significant at 0.05 and 0.01 probability levels, respectively.

TABLE 9: GCA, SCA and reciprocal mean squares for F_2 generation of five P. vulgaris lines grown at Kabete in 1987 (short rains).

Source	d.f	Number of pods per plant	Number of seeds per pod	Number of seeds per plant (g)	Seed yield per plant	100-seed weight(g)	Number of days to 50% flowering	Number of days to physiological maturity
GCA	4	148.991**	0.295**	134.633**	177.767**	142.320**	45.867**	103.30**
SCA	5	5.641	0.025	91.472	88.735**	15.230	2.917	13.893*
Reciprocal	10	1.534	0.015	45.106	77.180**	11.969	3.250	28.123**
Error	19	4.547	0.03	58.506	15.387	8.653	2.253	5.044

*, ** = Significant at 0.05 and 0.01 probability levels, respectively.

TABLE 10: Mean squares for general and specific combining ability of 20 F_1 and reciprocal bean crosses grown at two locations in 1987 (long rains).

Source	d.f	Number of primary branches per plant	Number of pods per plant	Number of seeds per pod	Number of seeds per plant	Seed yield per plant (g)	100-seed weight(g)	Number of days to 50% flowering	Number of days to physiological maturity
Locations(L)	1	2.59**	435.67**	0.002	7034.33**	5234.60**	673.29**	59.22**	554.2**
Rep./L	4	-	-	-	-	-	-	-	-
Crosses(C)	19	-	-	-	-	-	-	-	-
GCA	4	1.03**	317.90**	0.49	2616.11**	246.11**	321.88**	96.31**	79.55**
SCA	5	0.21	17.57	0.30	301.67**	69.59	34.83	22.50	19.93
Reciprocal	10	0.18	4.51	0.078	96.67	30.56	4.99	2.33	0.81
C x L	19	-	-	-	-	-	-	-	-
GCA x L	4	4.76**	801.27**	0.34	12872.92**	9282.98**	1577.75**	147.47**	984.92**
SCA x L	5	1.58**	227.45**	0.53	3725.67**	2338.98**	391.11	66.27	239.87**
Pooled error	76	0.25	25.50	0.33	61.32	65.68	43.34	12.89	9.47

*,** = Significant at 0.05 and 0.01 probability levels, respectively.

TABLE 11: Estimates of general combining ability (GCA) effects of five bean lines grown at two locations in 1987 (Long rains).

	Primary branches per plant		Pods per plant		Seeds per pod		Seeds per plant		Seed yield per plant (g)		100-seed weight (g)		Days to 50% flowering maturity		Days to physiological	
Parents	K*	T*	K	T	K	T	K	T	K	T	K	T	K	T	K	T
GLP-2	0.23	0.05	-9.39**	-4.98**	0.05	0.04	-26.98**	18.28**	-7.22**	-3.99	8.64**	5.61**	-0.31	-0.36	-2.55**	-3.33**
GLP-24	-0.52**	-0.35**	1.08	-1.79	0.32**	0.04	14.05**	-5.56	0.82	-5.55*	-6.83**	-4.06**	5.04**	-0.24	1.61**	3.62**
GLP-288	-0.15	-0.17	-2.82*	0.29	-0.07	-0.45**	-14.31	2.23	-10.43**	2.82	3.86**	3.18**	-0.46	0.29	-1.19**	-0.41
GLP-x.92	0.36**	0.04	8.87**	5.20**	-0.34**	0.02	15.19**	12.98**	4.16	5.54**	-5.82**	-0.43	-7.23**	-1.98**	-2.40**	-0.89*
535	0.08	0.44**	2.26	1.12	0.04	0.68**	12.05**	8.63	7.67**	1.19	0.10	-4.30**	2.97**	1.57*	4.53**	1.01*

*, ** = Significantly different from the standard value (S.V) at P = 0.05 and 0.01 levels, respectively.

*K = Kabete; T = Thika

TABLE 12: Estimates of specific combining ability (SCA) effects in 10 crosses of bean based on the mean performance of F_1 hybrids grown at two locations.

Cross	Primary branches plant		Pods per plant		Seeds per pod		Seeds per plant		Seed yield per plant(g)		100-seed weight (g)		Days to 50% flowering		Days to physiological maturity	
	K*	T*	K	T	K	T	K	T	K	T	K	T	K	T	K	T
GLP-2xGLP-24	0.15	0.10	0.99	-2.29	-0.02	0.40**	1.23	-13.72*	2.54	-7.55*	-0.58	-1.20	2.17**	1.19*	0.05	-2.19**
GLP-2xGLP-288	0.04	-0.03	-3.85*	-0.40	-0.07	-0.30**	-11.98**	-2.60	-4.37	-0.04	1.96**	3.89**	-4.83**	-2.24**	-2.90**	-1.51*
GLP-2xGLP-x.92	0.07	-0.49**	2.03	-0.91	0.04	-0.37**	11.95*	0.97	6.05	-1.70	-1.95**	0.91	1.78**	-0.63	1.82**	3.13**
GLP-2x535	0.26	0.42**	0.83	3.78*	0.05	-0.06	-1.21	15.35*	0.79	8.86**	0.57	0.03	0.88	1.68**	1.03**	0.58**
GLP-24xGLP-288	0.09	0.26	0.21	1.82	-0.10.	-0.14	1.37	6.17	7.30*	2.39	0.11	-1.58	1.17*	-2.36**	-0.42	2.34**
GLP-24XGLP-x.92	-0.43*	0.23	-3.79*	1.77	0.06	0.43**	-17.69**	11.85	-8.16*	8.75**	3.26**	4.26**	-2.57**	-0.83	-1.35**	-1.49*
GLP-24x 535	0.19	-0.57**	2.60	1.12	0.06	-1.02	-14.37*	-4.30	3.33	-3.69	-2.80**	2.05	-0.77	-2.73**	1.72**	1.33*
GLP-288xGLP-x.92	0.80	-0.06	4.42*	0.03	0.09	-0.58**	15.12*	-2.67	11.65**	-2.28	-2.80**	-2.64*	2.28**	0.14	2.80**	-2.19**
GLP-228x 535	-0.21	-0.17	-0.77	-1.27	0.07	0.12	-4.51	-0.91	5.43	-0.40	0.73	0.33	1.38**	-0.26	0.52	-0.54
GLP-x.92x535	0.28	0.32*	-2.66	-0.71	-0.19*	-0.38**	-9.38	-10.14	-4.54	-4.77	1.50*	1.11	-1.50**	1.31**	-3.27**	-1.36*

*, ** = Significantly different from the standard value (S.V.) at P=0.05 and 0.01 levels, respectively.

*K = Kabete; T = Thika.

TABLE 13: Estimates of reciprocal effects in 10 crosses of bean based on the mean performance of F_1 hybrids grown at two locations.

Cross	Number of primary branches per plant		Number of pods per plant		Number of seeds per pod		Number of seeds per plant		Seed yield per plant(g)		100-seed weight (g)		Number of days to 50% flowering		Number of days to physiological maturity	
	K	T	K	T	K	T	K	T	K	T	K	T	K	T	K	T
GLP-2xGLP-24	0.14	-0.12	-1.57	-0.54	0.10	0.02	-7.5	-0.07	-5.92	-0.1	-0.68	-1.56	1.00	-1.50*	0.95	0.65
GLP-2xGLP-288	0.20	-0.17	-0.03	-1.37	0.20	-0.20	0.34	-7.45	0.36	-6.16	1.23	-2.70	1.50*	2.00**	0.80	-1.00
GLP-2xGLP-x.92	0.70	-0.27	1.54	-3.24	-0.04	0.00	9.23	-11.14	5.25	-6.50	-0.19	-1.38	0.35	-0.35	-0.30	2.15
GLP-2x 535	0.00	0.10	1.14	-5.35*	-0.10	-0.70**	5.0	-26.70**	3.04	-13.65**	-0.47	0.53	-2.65**	-0.50	0.46	-1.20
GLP-24xGLP-288	-0.17	0.00	2.9	-1.84	-0.17	-0.03	17.04**	-3.04	8.98	-4.55	-1.3	-4.25*	-0.15	0.00	-0.85	0.50
GLP-24x GLP-x.92	0.59*	0.17	2.82	-2.50	0.02	0.00	7.99	-8.14	4.95	-3.71	0.69	0.31	-0.69	0.15	-0.70	0.50
GLP-24x535	0.17	0.22	2.17	-1.47	0.17	0.05	5.0	-5.77	2.65	-0.97	-0.42	1.33	-0.65	0.20	-1.00	0.50
GLP-288xGLP-x.92	-0.17	-0.07	-0.17	-1.44	-0.04	0.07	4.34	-5.27	1.13	-2.90	-1.05	-0.79	0.00	0.35	-0.65	0.65
GLP-288x535	0.00	-0.17	-1.17	-2.34	0.00	-0.20	-5.97	-8.25	-2.83	-3.69	0.9	-0.87	-1.00	1.50*	0.00	1.00
GLP-x.92x535	0.47	0.47*	-1.17	2.47	-0.07	0.04	-12.13	4.54	-7.91	0.58	0.57	-1.50	1.65**	-1.50*	-0.70	1.00

*, ** = Significantly different from the standard value (S.V) at P=0.05 and 0.01 levels, respectively.

K = Kabete; T = Thika.

Of the five parents, GLP-x.92 and 535 had highly significant positive GCA effects and were the best general combiners for primary branches per plant. GLP-24 was the poorest general combiner with highly significant negative GCA effects at both locations. Positive estimates of SCA effects at both locations were found in 3 of the 10 crosses. The best specific combiner was GLP-2 x 535 (S_{ij} = 0.42) and GLP-2 x GLP-x.92 was the poorest (S_{ij} = -0.48) when grown at Thika. The crosses between the two Canadian Wonder cultivars and Pinto showed significant reciprocal effects for this trait.

4:6:2 Number of pods per plant

Highly significant GCA mean squares were observed for pods per plant at both locations in F_1 generation (Table 8). SCA and reciprocal mean squares were not significant for this trait. A similar trend was observed in F_2 analysis for the same trait (Table 9). Locational differences were significant ($P<0.01$) for pods per plant as shown in Table 10. GCA x location and SCA x location interactions were highly significant and larger in magnitude than GCA and SCA mean squares, respectively, and GCA was more important than SCA mean squares.

Highly significant positive GCA effects were shown for pods per plant by GLP-x.92 while GLP-2 showed highly significant negative GCA effects (Table 11). The data presented in Table 12 indicates that four of the ten crosses exhibited positive SCA effects at both locations. Significant positive SCA effects were shown by the crosses GLP-2x535 and GLP-288xGLP-x.92 at Thika and Kabete, respectively. Reciprocal effects for pods per plant were not significant.

4:6:3 Number of seeds per pod

GCA mean squares for seeds per pod followed a trend similar to that for primary branches per plant and pods per plant in both F_1 and F_2 generations (Tables 8 and 9). At Thika, SCA mean squares were highly significant and reciprocal mean squares were significant ($P<0.05$). Despite the high significance of SCA mean squares at Thika, the GCA:SCA ratio at Kabete was much greater than unity (11.33) indicating that the magnitude of GCA mean squares were larger than SCA mean squares for this trait. In F_2, SCA and reciprocal mean squares were not significant for seeds per pod. No significant difference was

detected between locations for this trait (Table 10). There also were no significant differences for the GCA x location and SCA x location interactions.

Only the two parents belonging to the Canadian Wonder group (GLP-24 and 535) had highly significant GCA effects for seeds per pod. Highly significant negative GCA effects for this trait were shown by GLP-x.92 and GLP-288 (Table 11). At Kabete, there was a general lack of significance of SCA effects for seeds per pod, but at Thika both highly significant positive and negative SCA effects were shown by the hybrids. Apart from the cross GLP-2x535 which exhibited highly significant negative reciprocal effect, the rest of the crosses showed no reciprocal effects for this trait.

4:6:4 Number of seeds per plant

In the F_1 generation, both GCA and SCA mean squares were highly significant, but the latter at one location only. However, the GCA:SCA ratio was greater than unity at both locations indicating the larger magnitude of GCA mean squares as compared to SCA mean squares. There were no significant reciprocal mean squares at either location in F_1, and at Kabete in F_2. SCA mean squares in F_2 were not

significant but GCA mean squares were highly significant in the same generation for seeds per plant. There were highly significant differences between locations for this trait and both GCA x location and SCA x location interactions were highly significant. GCA x location interaction was about five times larger in magnitude than GCA mean square while SCA x location interaction was more than ten times greater in magnitude than SCA mean square (Table 10).

Again GLP-x.92 was the best general combiner for this trait, with highly significant GCA effects at both locations (Table 11). All the parents had a positive value for GCA effects at one or both locations. Negative and highly significant GCA effects were detected for GLP-288 and GLP-2 at Kabete and almost all their progeny posessed negative SCA effects for seeds per pod at one of the two locations (Table 12). As for number of seeds per pod, the cross GLP-2x535 showed highly significant negative reciprocal effects for seeds per plant.

4:6:5 Seed yield per plant

As reported for the four traits above, GCA mean squares were more important than SCA mean squares for

seed weight per plant in F_1 generation. However, unlike in other traits, both SCA and reciprocal mean squares were highly significant in F_2 generation. Locations were highly significant for this trait and so were the GCA interactions with locations.

GCA estimates (Table 11) were large and positive for GLP-x.92 and 535 indicating that these parents were the best combiners for this trait. The poor general combining ability of GLP-2 is again apparent for seed weight per plant at both locations. Nevertheless, GLP-2 combined well with 535 giving one of the best specific combiners (S_{ij} = 8.86). GLP-288 combined well with GLP-24 and GLP-x.92, while the crosses GLP-x.92 x 535 and GLP-2 x GLP-288 were the poorest specific combiners. Apart from the cross GLP-2 x 535 with highly significant negative reciprocal effects, the other crosses showed no significant reciprocal effects for seed weight per plant.

4:6:6 100-seed weight

From diallel analyses of F_1 generation, both GCA and SCA mean squares were highly significant for 100-seed weight. However, the GCA:SCA ratio was significantly greater than unity indicating the

superiority of GCA over SCA mean squares for seed weight. The importance of GCA was further confirmed in F_2 analyses (Table 9). There was no reciprocal significance in both F_1 and F_2 for this trait. There were highly significant differences for 100-seed weight between the two locations. The GCA x location and SCA x location interactions were highly significant and larger in magnitude than GCA and SCA mean squares, respectively.

The best general combiner for 100-seed weight was GLP-2 and the poorest was GLP-24 at both locations. Highly significant positive GCA effects were also shown by GLP-288. The cross combining the two best general combiners, GLP-2 x GLP-288 showed highly significant positive SCA estimates at both locations (Table 12). GLP-x.92 showed very poor general combining ability for 100-seed weight but its combination with GLP-24, another poor combiner, yielded the best specific combining cross (Table 12). There was a general absence of reciprocal effects for 100-seed weight.

4:6:7 Maturity traits

These two traits showed highly significant GCA and SCA mean squares in F_1 generation. However, SCA mean squares were not significant for days to 50% flowering in F_2. In addition, reciprocal mean squares were not significant for days to physiological maturity in F_1 and for days to 50% flowering in F_2, but the former trait showed highly significant reciprocal mean squares in F_2. The GCA:SCA ratio in F_1 generation indicated that GCA mean squares were of larger magnitude than SCA mean squares for the two traits. Significant differences between locations and maturity traits were observed. Also, GCA x location and SCA x location interactions for the two traits were highly significant.

Apart from 535, the other four parents had negative GCA estimates for days to 50% flowering. Both cultivars of the Canadian Wonder group showed highly significant positive GCA estimates for days to physiological maturity. The Rosecoco and Pinto beans showed negative GCA estimates for the two traits. The Pinto bean, GLP-x.92, combined well with GLP-24 and 535, but not so well with the Rosecoco beans, GLP-288 and GLP-2 (Table 12). Poor specific combining ability was shown by GLP-2 x GLP-24 and

GLP-2 x 535, both crosses with highly significant positive estimates of SCA for both traits. Reciprocal effects were significant in five of the ten crosses for days to 50% flowering and in only one cross for days to physiological maturity (Table 13).

CHAPTER FIVE

DISCUSSION

5:1 Success Rate in Crossing

The high percentage (84.1%) of successful pollinations achieved in this study could be explained as a result of the use of the modification of the hooking method of Buishand (1956). With this modification, more amounts of pollen remain in contact with the stigma of the female flower. This allows for fertilization of more ovules resulting in a high number of hybrid seeds per pod. Secondly, the high percentage could be due to the fact that environmental conditions necessary for successful pollinations (Buishand, 1956; Bliss, 1980) were strictly provided during the crossing period.

It should be noted that the number of pollinations made per plant apparently had no effect on pod and seed set. Accordingly, bud abscission and seed abortions were not encountered despite the number of pollinations made per plant. This is in contrast to Buishand's (1956) report that the fewer the number of pollinations made per plant, the higher the success rate. There was a strong correlation ($r = 0.67$) between number of pollinations and

successful pods per cross (Appendix 1). As many as 12 pollinations per plant were made in some cases and all the pods grew to maturity. This was possible on the first 'flush' of flowers in all cultivars. Crosses made on 'late' flowers resulted in abscission of 6-8 days old pods. Therefore, cultivars of beans (Phaseolus vulgaris L.) compatible for hybridisation purposes should be able to produce many 'ripe' buds (and therefore, flowers) within the first 3-4 days after flowering commences. If all the first buds are used for crossing using the modified hooking method, there are high chances of getting successful pollinations with the desirable number of seeds per pod.

5:2 Morpholodical deformities in P. vulgaris L.

5:2:1 Seed deformities

All seeds from all crosses were dried and stored under similar conditions, so the environmental conditions may not account for seed cracking in one cross and not in others. The F_1 plants from these two crosses had very small primary leaves

and dried up soon after germination. These symptoms were observed in Phaseolus vulgaris L. by Shii et al., (1980) and such seedlings were classified as lethal.

According to the genetic hypothesis for the occurrence of abnormal plant types in Phaseolus vulgaris L., the three cultivars NB123, 535 and GLP-288 most probably are carriers of the 'dosage dependent lethal' (DL) genes responsible for abnormal development of F_1 hybrids in Phaseolus vulgaris L. (Shii et al., 1980, 1981). Since the DL system affects a wide range of developmental events (Shii et al., 1980), the appearance of these deformed seeds could be due to the genetic incompatibility caused by the presence of DL genes in NB123, 535 and GLP-288. Formation of abnormal seeds by a large proportion of recombinants from normal crosses of non-carrier ($dl_1dl_1dl_2dl_2$) genotypes of small and medium or large seed types has been reported (Shree and Gutierrez, 1984). Since NB123 is small seeded, and 535 and GLP-288 large-seeded, this could further explain deformities of their F_1 seeds as due to a certain degree of incompatibility correlated with differences in parental seed sizes.

5:2:2 "Tetrad" trifoliolate leaves in *Phaseolus vulgaris* L.

The four leaflets could have resulted from the splitting of the middle leaflet into two as indicated by the notched middle leaflet in some cases. The four leaflets were not smaller than the leaflets on subsequent trifoliolate leaves on the same plant. The absence of this character in either of the parents and in F_2 progeny suggests that it could be a physiological expression of seedling hybrid vigor by increased leaf area.

This suggestion concurs with the report by Suresh *et al.*, (1975) that heterozygosity provides some physiological stimulus that results in the enlarged size, vigor and higher yield of hybrids. The increased leaflet number without reduction in leaf size is a manifestation of heterosis in leaf area which is strongly correlated with pod number and seed size (Duarte and Adams, 1963, 1972). Since increased leaflet number is strongly correlated with pod number (Duarte and Adams, 1972) this could have an increased effect on grain yield. In contrast to this, the cross L226-10 x GLP-2 showed negative heterosis over both the midparent and highparent

means for yield and yield components (Appendix 2). Further research on correlation of this 'tetrad' character with grain yield is, however, necessary because the percentage (20%) of plants bearing this trait was quite low and the number of such 'tetrad' trifoliolates per plant was very low.

5:2:3 Hybrid dwarfism

The symptoms characterising dwarf F_1 plants in this study are similar to those previously reported (Davis and Frazier, 1964; Coyne, 1965; York and Dickson, 1975; Van Rheenen, 1979; Shii et al., 1980, 1981; Shree and Gutierrez, 1984). Since the occurrence of abnormal F_1's was limited to specific parental combinations grown at both Thika and Kabete, it was suspected that the abnormal development was of a genetic nature rather than pathological or nutritional. The contrasting development of parents and F_1 plants and the distinct segregation of phenotypic classes in F_2 progeny populations confirmed that the dwarf phenotypes were of a genetic origin.

The number of plants within each phenotypic class in F_2 progeny did not differ significantly from the expected 9:7 (dwarf:normal) ratio suggesting that

the dwarf phenotypes are inherited through the combination of two complementary dominant genes. Coyne (1965) suggested that the 'crippled' character was determined by two complementary recessive genes and proposed symbols cr_1, cr_2 and cr_3 to represent the complementary genes in G.N. Nebraska #1, Yellow Eye PI 209806 and Dark Red Kidney varieties respectively. However, previous workers have reported the inheritance of hybrid dwarfism in Phaseolus vulgaris L. to be through two complementary, dominant genes (York and Dickson, 1975; Van Rheenen, 1979; Shii et al., 1980, 1981). The absence of reciprocal cross differences for hybrid dwarfism in this study suggests that the genetic differences between phenotypic expressions are likely due to nuclear genes and not cytoplasmic factors. In contrast, Davis and Frazier (1964) reported presence of maternal effects in the F_2 crosses involving both WST and 2466 varieties.

When crossing was restricted to parents with similar seed sizes, all F_1 hybrids followed normal growth and development. Dwarfism of the F_1 hybrids occurred only when a small-seeded parent was crossed with either a medium- or large-seeded type. This suggests that genetic incompatibility is strongly associated with genes that determine seed size in

Phaseolus vulgaris L. The same observation was made by Shree and Gutierrez (1984) studying the geographical distribution of the DL_1 and DL_2 genes causing hybrid dwarfism in Phaseolus vulgaris L.

Considering the proposed genetic hypothesis for the occurrence of abnormal plant types (Shii et al., 1980) and with the knowledge that all the parents involved in crosses which yielded dwarf F_1 hybrids are homozygous lines, the small-seeded lines (NB123 and L226-10) possess the genotype $DL_1DL_1dl_2dl_2$ with the DL_1 gene responsible for suppressed root growth and development. Similarly, the medium-and large-seeded lines (GLP-288, GLP-24, 535) possess the genotype $dl_1dl_1DL_2DL_2$ with the DL_2 gene responsible for reduced growth and development of the stem parts. Consequently, the F_1's were of the heterozygous genotype $DL_1dl_1DL_2dl_2$ and hence were phenotypically abnormal under field conditions.

The different degrees of lethality expressed by F_1's from different crosses may be due to the influence of the environment on the expression of some of these abnormalities and the allelic dosages of DL_1 (in the root) and DL_2 (in the shoot) (Shii et al., 1980, 1981). That GLP-2 and GLP-x.92 (large-and medium-seeded respectively) produced normal F_1

hybrids with L226-10 and NB123 suggests that they are non-carriers of the DL genes and so their genotypes are $dl_1dl_1dl_2dl_2$. Consequently, their F_1 hybrids with L226-10 and NB123 are of the genotype $DL_1dl_1dl_2dl_2$ and are phenotypically normal under field conditions. It should, however, be emphasized here that the findings reported above are not entirely conclusive because of lack of supportive backcross progeny ratios.

5:3 Inheritance of Cotyledon, Stem and Flower Colour

It was observed that a bean plant with purple cotyledons also had hypocotyl, stem, peduncles and flowers coloured purple while the one with green cotyledons had the rest of the above mentioned parts coloured green (except flowers which were either white or tinted pink). Hybrids derived from purple x green coloured parents were easily identified at seedling emergence because they all had purple coloured hypocotyls and cotyledons. Hybrids from both parents with green cotyledons and hypocotyl were confirmed as true hybrids (not selfs) at later stages of plant growth and at harvest time because the hybrids were generally taller with broader leaves and had seed coat colours markedly different from either of their parents.

The observations made about hypocotyl, cotyledon, stem and flower colour suggest that there could be an association between pigmentation of the various parts of the bean plant. Pompeu (1963) showed that there is a perfect correlation between the flower colour and the pigmentation of the cotyledon in Phaseolus vulgaris L. The genetic association between production and distribution of colour pigments has been reported in the potato, Solanum tuberosum (Howard, 1969) and in the cowpea, Vigna unguiculata L. (Fery, 1985). Anthocyanins are responsible for the pink, red, blue and purple pigmentations of sprouts, stems, tubers and flowers in the potato (Howard, 1969). Fery (1985) also reported that anthocyanins are responsible for all the colour in the flower petals, seed pods, peduncles, petioles, stems and leaves of the cowpea. It could be possible that the same type of pigment is responsible for colour in hypocotyl, cotyledon, stem and flower of the common bean. The change in stem colour from purple to green with shading could imply that the purple pigment is chemically unstable, either under direct sunlight or relatively high temperature and changes to a stable pigment responsible for green colour under reduced light

intensity or low temperature (when shaded). However, additional research work in this field is needed in order to substantiate these suggestions.

The data presented in Table 3 suggest that the inheritance of cotyledon and stem colour follow a simple monhybrid pattern (3 purple:1 green) with purple dominant to green. The crosses studied showed no significant reciprocal differences for stem and cotyledon colour, indicating the absence of maternal effects. These results are in agreement with the report by Bliss (1980) that purple stippling of the cotyledons of germinating seeds is dominant to green cotyledons and that purple hypocotyl is dominant to green hypocotyl in Phaseolus vulgaris L. Shii et al., (1980) also found the purple hypocotyl and flower colour in Phaseolus vulgaris L. to be a simple dominant trait. The genetic control of green versus white cotyledon in Lima bean (Phaseolus lunatus L.) was found to be due to a single gene pair where recessive individuals (gg) bear green cotyledons and dominant individuals (GG) bear white cotyledons (Magruder and Wester, 1941).

The genetic control of purple versus white flower colour in crosses involving NB123 seems to be

due to a single gene pair, with purple dominant to white. This monohybrid inheritance of flower colour has been reported previously in Phaseolus vulgaris L. (Honma and Heeckt, 1959; Bliss, 1980; Shii et al., 1980). Flower colour has been used to identify F_1 hybrids in Phaseolus vulgaris L. (Antunes et al., 1973; Fooland and Bassiri, 1983) and in flax (Comstock, 1965). Kolhe (1970) found that purple flower colour in cowpeas was conditioned by a dominant gene for which he proposed the symbol Pf.

The purple flower hybrids from white flower parents could be explained by assuming complimentation of two independent loci controlling flower colour. Assuming that purple colour is the wild (dominant) phenotype and white is recessive, the genotypes of the two parents can be symbolized as $a^1a^1b^+b^+$ x $a^+a^+b^1b^1$. All F_1's are therefore of the genotype $a^1a^+b^1b^+$. At each locus, there is one wild type allele (a^+ and b^+), therefore, the offspring (F_1) must be of dominant phenotype (purple). The deviation from the 3:1 (purple:white) expected ratio in F_2 to the 9:7 ratio confirms that flower colour in crosses involving L226-10 is conditioned by two complementary dominant genes. However, it is not clear whether these nonallelic loci controlling

flower colour are correlated with the genes for dwarfism present in L226-10. From these results it seems that the mode of inheritance of flower colour varies with genotypes.

The results presented and discussed on the inheritance of cotyledon, stem and flower colour in the present study are not conclusive since no backcross or F_3 progeny ratios were used to confirm the observed F_2 segregation ratios. However, one can postulate that purple pigmentation of cotyledons, stems and flowers in Phaseolus vulgaris L. varieties under the present study can be used as a genetic marker. More work is needed to establish the correlation between hypocotyl, cotyledon, stem and flower pigmentation, and their correlation with important quantitative traits such as yield and earliness in Phaseolus vulgaris L. in Kenya. Such information would be vital for bean breeders in identifying higher yielding and early maturing hybrids at seedling stage thus allowing most effort to be concentrated on the best material.

5:4 Heterosis

Among the parents, the Pinto type GLP-x.92 excelled in performance, having the highest number of primary branches per plant, pods per plant, seeds per plant and seed yield per plant. Irrespective of location, it was one of the earliest to flower and mature. The Canadian Wonder types, GLP-24 and 535 had the lowest seed weight, were the latest to flower and mature, but had the highest seed number per pod and were second to GLP-x.92 in number of pods per plant. The Rosecoco types performed poorly for all characters except 100-seed weight but were the earliest to flower and mature.

In all characters except 100-seed weight, heterosis was greater in crosses between groups than within groups. This observation is in agreement with reports by Fooland and Bassiri (1983) and Nienhuis and Singh (1986) in common bean. The existence of useful heterosis above the highparent in some hybrids for pods per plant, seeds per pod, seed yield per plant and 100-seed weight is encouraging as it indicates that gene combinations exist which can result in enhanced yield performance in common bean cultivars in Kenya. The superiority of some F_1 hybrids for yield and yield components suggest that

if an economical method of producing F_1 seed could be found, commercial production of hybrid beans should be advantageous. Unfortunately, most of the cross-pollinating mechanisms that have been tried in common bean have met with limited success. Nagata and Basset (1985) obtained outcrossing rates of 5 to 47% using a dwarf outcrossing mutant in common bean, but the level of outcrossing was severely lowered in the field by environmental conditions like drought and rain. The use of both genic and cytoplasmic male sterility to enforce cross-pollination in bean has met with limited success (Agbo and Wood, 1977; Basset and Shuh, 1982).

There was a substantial decrease in number of days to flowering and to physiological maturity of the F_1 progeny relative to the parents as was indicated by negative heterosis values for these two traits. GLP-x.92, GLP-2 and GLP-288 tended to transmit earliness to their progeny and so could be favourable parents for use in breeding programmes where variety earliness is the major objective. GLP-24 and 535 would not be suitable parents in such a programme due to their tendency to impart lateness to their progeny.

The marked poor performance of parents for all traits at Thika as compared to Kabete could be attributed to the lower and poorly distributed rainfall received at Thika (425.0 mm) than at Kabete (544 mm) during the growing season (Appendix 3 and 4). At Thika, the rainfall was unevenly distributed, leaving dry spells of more than seven days, especially at early seedling stage and around bloom. In addition, the particular field where the beans grew had been extensively cultivated in previous seasons causing the soil to be very light with patches of hard pans. Consequently, its water-holding capacity was very low.

Phaseolus vulgaris L. is considered to be a crop with poor tolerance to severe water deficits especially during seedling stage, before flowering and during pod filling. At CIAT, prolonged water stress before flowering restricts canopy development and this in turn limits yield in P. vulgaris L. (Laing et al., 1984). Since photosynthetic surface area and fruiting nodes are prerequisites for pod production, Silbernagel (1986) noted that early seedling vigor is essential to realisation of maximum yield potential in snap beans.

Day temperatures at Thika rose as high as 26.8°C at around flowering time while at Kabete it ranged between 23° and 24.4°C during bloom (Appendix 3 and 4). These high temperatures could account for the lower number of pods per plant, seeds per pod, seeds per plant and seed weight per plant at Thika as compared to Kabete. Leakey (1970) reported that in the hotter parts of northern Uganda, many dry bean (P. vulgaris L.) varieties set very few pods even though flowering was quite satisfactory. In Canada, Ormrod et al., (1967) observed that high day temperatures resulted in failure of fruit set in P. vulgaris L. According to Farlow et al.,(1979), high day time temperatures (>35°C) reduce pollen production and/or viability in P. vulgaris L.

Probably, the higher temperature at Thika as compared to Kabete can also explain why the cultivars flowered and matured earlier at the former location than the latter. It has been reported that the effect of increasing temperature on completely day-neutral cultivars of P. vulgaris L. is to decrease the number of days to flowering (Laing et al., 1984).

The appearance of misshapen (crooked) pods on plants grown at Kabete could be due to the low minimum temperature (10.6°C) recorded at this

location. Farlow (1981) observed that the rate of failure of female reproductive organs was progressively higher as temperatures were reduced from 21°C to 10°C and this resulted in fewer pods per plant, seeds per pod and more crooked pods. The various stress conditions that the crop experienced at both locations led to lower performance than expected of all the cultivars. When environmental stress affecting final yield occurs during the development of a bean plant, the yield component that is formed first in the productive phase, pods per plant, generally shows the greatest stress response, followed by seeds per pod and weight per seed (Adams, 1967). It was not surprising that yield for some cultivars like Canadian Wonder was markedly lower than expected.

Heterosis variation in both magnitude and sign in relation to locations indicated genotype by location interaction. This is in agreement with observations made by Nienhuis and Singh (1986) that significant heterosis x location interactions existed for yield, pods per m^2, seeds per pod, seed weight and some architectural traits in common bean. It also shows that tests of potential parents for the expression of heterosis should be conducted over a number of locations (and seasons) whenever possible.

Genetic diversity alone will not guarantee the expression of heterosis if environmental conditions are not suitable (Walton, 1971).

5:5 Combining ability

The magnitude of general combining ability or specific combining ability mean squares is indicative of the relative importance of additive or non-additive gene effects in the inheritance of a trait. In this study, the ratio of GCA:SCA mean squares was greater than unity indicating that the magnitude of GCA mean squares was larger than SCA mean squares for all the traits studied. This suggests that, although SCA mean squares were significant for some traits, a large part of the total genetic variability associated with the eight traits was a result of additive gene action. The predominance of additive gene action in the expression of these traits was further confirmed by the results of the analyses in the F_2 generation.

These results are in contrast with some previous reports of diallel analysis in bean in which SCA mean squares were generally found to be larger than those of GCA for yield, yield components and some architectural traits (Dickson, 1967; Chung and Stevenson, 1973; Fooland and Bassiri, 1983).

However, they are in agreement with the findings of Leffel and Hanson (1961) in soybean, Kronstad and Foote (1964) and Brown et al.,(1966) in wheat, and of Nienhuis and Singh (1986) in common bean.

Highly significant GCA x location interactions for all traits except seeds per pod indicate that the GCA effects associated with parents were not consistent over locations. Such variation could be a result of locational effects such as temperature, moisture regimes and soil conditions. These factors also could explain the failure of non-additive gene action to be consistently expressed over locations as substantiated by the highly significant SCA x location interactions for all traits except number of seeds per pod.

The larger magnitude of GCA x location compared to GCA mean squares, and SCA x location compared to SCA mean squares suggests that the interaction effects were of relatively major importance for all traits except seeds per pod. This suggestion is in contrast to that of Nienhuis and Singh (1986) and implies that yield and yield components (except seeds per pod), flowering and maturity duration, and branches per plant in common bean are strongly influenced by environmental conditions. The failure

of non-additive gene action to be consistently expressed over locations is a handicap to hybrid bean production because though it may be economically feasible, the significant interactions with locations would suggest that the F_1 hybrid bean may not manifest broad adaptation.

GLP-x.92 exhibited highly significant positive estimates of GCA effect for seed yield per plant, seeds per plant, pods per plant and primary branches per plant, and should therefore contribute positive, additive effects for these traits to its progeny. The same cultivar showed highly significant negative estimates of GCA effects for days to 50% flowering and to physiological maturity indicating that its crosses have the greatest possibility of producing early maturing progeny.

The Rosecoco beans, GLP-2 and GLP-288 tended to show significant negative GCA effects for all yield components except 100-seed weight, and so have a poor chance of being selected based on other yield components since only those parental lines showing positive GCA effects for yield are normally selected. However, their good hybrid combination (GLP-2 x GLP-288) with the highest positive SCA estimate in both locations for 100-seed weight suggests that the two

cultivars contribute favourable additive effects for seed size to their progeny. Moreover, the crosses involving the two cultivars had significant negative SCA estimates for days to 50% flowering and maturity indicating their ability to transmit earliness to their progeny. On this basis, GLP-2 and GLP-288 might be quite useful in a hybrid bean programme for increased seed size and earliness.

GCA and SCA effects showed that the Canadian Wonder cultivars GLP-24 and 535, were the best overall parents in terms of GCA for seeds per pod, but were the poorest as far as earliness was concerned. The positive significant SCA effects for the hybrid GLP-24 x GLP-x.92 for 100-seed weight, seed yield per plant and seeds per pod indicates that the mean of that hybrid was greater than expected, based on the mean performance of the lines involved. This further suggest that a poor general combiner for some trait can be quite useful in specific hybrid combination for that same trait with another poor general combiner or with a good one. Therefore, caution should be excercised during selection based on general combining ability of parental lines.

All traits studied showed no significant reciprocal effects except days to 50% flowering in F_1, and seed weight per plant and days to physiological maturity in F_2 generation. This general lack of reciprocal effects indicates the possible absence of maternal effects. Other workers have reported similar observations in common bean. Fooland and Bassiri (1983) reported total absence of reciprocal effects for 100-seed weight in common bean. In diallel analyses for yield, yield components and architectural traits in dry bean, Nienhuis and Singh (1986) reported a general absence of reciprocal effects for all traits studied.

It is encouraging to note that the genetic variation for yield and yield components in the common bean population used in this study was mainly due to additive gene action which is fixable and hence easily exploitable. The exploitation of additive gene effects could be achieved by selecting superior segregants in the early generation and/or by single plant selection. The value of predictions based on early generation performance and the exploitation of additive gene effects was discussed in barley by Smith and Lambert (1968), and in common bean by Hamblin and Evans (1976).

The significance of both GCA and SCA mean squares for same traits under the present study suggested that both additive and non-additive gene effects were responsible for the manifestation of variability for these traits. In a situation where both gene effects are important, an improvement could be made by selecting superior segregates in early generations followed by more intensive selection in advanced generations, hence exploiting additive gene effects.

Predictions involving a character controlled largely by an additive system would be expected to be more reliable than predictions involving characters controlled by non-additive systems (Smith and Lambert, 1968). On this basis, it would appear from the present study that predictions for yield based on yield components could be reliable since additive genes were found to be important for yield and yield components. The estimation of cross yields could therefore be made using early generation bulks and parental yields.

GLP-x.92 which was the best general combiner for all yield components except 100-seed weight, and the Rosecoco types which combined well for 100-seed weight and earliness appear to be the most promising

parental cultivars for future breeding work. The superior crosses, GLP-2xGLP-288 and GLP-24xGLP-x.92 (for 100-seed weight); GLP-2x535 and GLP-288xGLP-x.92 (for pods per plant); GLP-2xGLP-24 and GLP-24xGLP-x.92 (for seeds per pod) and GLP-228xGLP-x.92, GLP-2x535, GLP-24xGLP-x.92 (for yield per plant) could be used in further selection programmes to improve yield in common bean cultivars in Kenya.

5:6 CONCLUSIONS

(1) The occurrence of abnormal F_1's in crosses of Phaseolus vulgaris L. was found to be limited to specific crosses involving small-and large- or medium-seeded parents. The morphological abnormalities observed in F_1 included seed cracking and crinkling, four leaflets on the first 'trifoliolate' leaf (or 'tetrad' trifoliolates), and dwarf or stunted F_1 plants. The appearance of deformed seeds could be due to genetic incompatibility correlated with differences in parental seed sizes. The occurrence of 'tetrad' trifoliolates could probably be a physiological expression of seedling hybrid vigor by increased leaf area. Hybrid dwarfism was found to be conditioned by two complementary dominant genes.

(2) The data presented in this study suggest that the inheritance of cotyledon and stem colour follow a simple monohybrid pattern with purple dominant to green. Hybrid bean plants can, therefore, be easily identified at seedling emergence using cotyledon and stem or hypocotyl pigmentation as genetic markers.

(3) From this study, it appears that flower colour is not always simply inherited and therefore should be used with caution as a genetic marker. The mode of inheritance varied with genotypes.

(4) Yield heterosis above the highparent was observed in 14 of the 20 crosses, and heterosis above the high-parent for 100-seed weight, pods/plant, seeds/pod and seeds/plant was observed in 7, 10, 13 and 8 crosses, respectively. Regardless of location, 16 crosses flowered earlier and 12 crosses matured earlier than their better parents. This heterosis may be sufficiently large to stimulate interest in the feasibility of commercial production of hybrid bean seed. The modified hooking method for pollinations in bean presented in this study could be utilised, but there is need to study more and economical large-scale methods of producing bean hybrid seed.

(5) The data presented in this study indicated that both additive and non-additive gene effects were responsible for the manifestation of variability in all traits studied except pods per plant. It was also clear that although non-additive gene effects were important for some traits, the predominance of additive gene action was obvious for pods/plant, seeds/

pod, seeds/plant, 100-seed weight, branches/plant and days to physiological maturity.

The general lack of differences between reciprocal F_1 hybrids suggested that extranuclear inheritance was relatively unimportant in relation to yield components, flowering and maturity duration and branches per plant. The occurrence of significant mean squares for SCA x location interactions for all traits except seeds per pod reflected the failure of non-additive gene action to be consistently expressed over locations. All traits studied except seeds per pod were found to be strongly influenced by the environment.

(6) Among the parental cultivars , GLP-x.92 appeared to be the most promising for use in breeding for yield and yield components since it had large GCA estimates for these traits. In addition, GLP-x.92, GLP-2 and GLP-288 could be used in selections to increase seed weight and reduce duration of flowering and maturity in bean cultivars in Kenya. The estimation of SCA effects identified nine crosses with significant positive SCA values for 100-seed weight, pods per plant, seeds per pod and yield per plant. The nine crosses could therefore, be used in further selection programmes to improve yield in common bean.

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APPENDIX 1

Results of Pollinations for a 7x7 complete diallel system in common bean (Sept. - Dec. 1986):

Cross	No. of pollinations	No. of pods harvested	% of successful pollinations
GLP-2xGLP-24	47	24	51.1
xGLP-288	52	45	86.5
xGLP-x.92	48	36	75.0
xL226-10	32	24	75.0
xNB123	46	32	69.6
x535	52	45	86.5
GLP-24xGLP-2	53	51	92.2
xGLP-288	56	56	100.0
xGLP-x.92	52	46	88.5
xL226-10	53	53	100
xNB123	68	68	100
x535	62	59	95.2
GLP-288xGLP-2	44	28	63.6
xGLP-24	48	43	89.6
xGLP-x.92	43	42	97.7
xL226-10	35	33	94.3
xNB123	42	22	52.4
x535	52	49	94.2
GLP-x.92xGLP-2	46	46	100
xGLP-24	54	47	87
xGLP-288	54	46	85.2
xL226-10	42	26	61.9
xNB123	79	74	93.7
x535	51	50	98
L226-10xGLP-2	35	29	82.9
xGLP-24	45	37	82.2
xGLP-288	44	35	79.6
xGLP-x.92	40	34	85
xNB123	48	35	72.9
x535	55	33	60
NB123xGLP-2	51	29	56.9
xGLP-24	59	49	83.1
xGLP-288	45	38	84.4
xGLP-x.92	58	56	96.6
xL226-10	25	10	40
x535	56	50	89.3
535xGLP-2	68	64	94.1
xGLP-24	53	41	77.4
xGLP-288	61	52	85.3
xGLP-x.92	57	48	84.2
xL226-10	69	60	86.9
xNB123	59	54	91.5
Totals	2,139	1,799	84.1

$r = 0.67$, $P<0.05$

APPENDIX 2

Percent heterosis above the midparent ($\overline{MP}$) and highparent ($\overline{HP}$) for yield and yield components in the cross L226-10 x GLP-2 grown at Kabete (K) and Thika (T), 1987 (long rains).

	Parental mean				% Heterosis			
	GLP-2		L226-10		$\overline{MP}$		$\overline{HP}$	
Yield Traits	K	T	K	T	K	T	K	T
Pods per plant	16.9	9.3	78.8	38.9	-2.7	1.7	-55.8	-37.0
Seeds per pod	5.6	3.7	7.6	6.7	-10.6	11.5	-22.4	-13.4
Seeds per plant	70.33	24.7	476.3	190.2	-31.6	2.1	-60.7	-44.6
Yield per plant	49.23	12.3	104.6	34.2	-5.3	-32.0	-30.4	-7.6
100-seed weight	69.9	49.6	21.9	17.8	-15.3	-55.5	-44.3	-39.5

APPENDIX 3

Rainfall (mm) and Mean Atmospheric Temperature during the growing seasons 1986/87 at Kabete.

Year	Month	Total Rainfall	Mean Atmospheric Temperature Max. (°C)	Min. (°C)
1986	October	40.4	25.1	13.1
"	November	202.0	21.8	13.5
"	December	91.5	22.8	12.5
1987	January	79.5	23.8	12.7
"	February	95.5	25.4	12.5
"	March	15.4	26.8	10.5
"	April	278.9	24.4	14.3
"	May	145.0	23.1	13.7
"	June	95.1	21.7	10.6
"	July	9.4	21.2	11.6
"	August	12.5	21.6	11.5
"	September	17.4	26.8	13.8
	Total	1,082.6	-	-
	Mean	-	23.7	12.5

APPENDIX 4

Rainfall (mm) and Mean Atmosphere Temperature during the growing season (1987) at Thika.

Year	Month	Total Rainfall (mm)	Mean Atmosphere Temperature (°C)	
			Max.	Min.
1987	January	5.7	26.2	13.4
"	February	3.6	28.1	13.1
"	March	6.3	29.8	13.8
"	April	159.9	25.3	15.0
"	May	102.5	26.8	20.4
"	June	137.5	23.6	14.0
"	July	18.6	23.5	12.6
"	August	33.9	23.8	12.9
"	September	NIL	27.3	13.7
	Total	468.0	-	-
	Mean	-	26.0	14.3