GENETIC AND MULTIVARIATE STATISTICAL EVALUATION OF A PHENOTYPIC RECURRENT SELECTION PROGRAM FOR RECOMBINING ERECT ARCHITECTURE AND LARGE SEED SIZE IN PHASEOLUS VULGARIS L.

By

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DEDICATION

To Theresa, my beloved wife,
and our kids - Parry and Kwasi.

ACKNOWLEDGEMENT

I came to the Michigan State University because of Prof. M.W. Adams. His paper on "Plant architecture and yield breeding" formed the basis of the research proposal I submitted in partial fulfilment of the requirements of the fellowship which funded my studies. Naturally, MSU was my first choice of American universities at which to study. Even though Prof. Adams was 'no show' at the meeting of IAEA-contracted scientists in Seoul, South Korea, in 1983, for which his paper had been circulated for our consideration, I am very glad I showed up at MSU. I have thoroughly enjoyed the opportunities and challenges the research offered me and wish to express my sincere and heartfelt gratitude to Prof. Adams, my major adviser, for having me learn at his feet.

The members of my committee deserve special mention, too. Dr. Jim Kelly made the research practically possible. Most of the materials for the recurrent selection were supplied by him. In addition, Jim assisted in planting the experiment and guided the selection in the field. Thank you very much, Jim. I liked statistics before coming to MSU but I am leaving here loving it. This is largely due to the effective teaching of Dr. C.E Cress who made the subject enjoyable. I also appreciate his help during the data analysis. Dr. Tom Islieb, in addition to making himself available for consultation on statistics and genetics, loaned me his complete set of SAS statistical and graphics manuals. These made my computing tasks a lot easier and I am most gratefull to him. A successful ideotype breeding program has its foundation on sound physiological-genetic knowledge. Dr. James Hanover of the Department of Forestry increased my understanding of the area and helped me appreciate the ideotype concept much better and for that I am deeply thankfull.

The critical review of the draft of this dissertation by the members of my advisory committee, and especially by my major advisor, Prof. Adams, is very deeply appreciated.

The assistance of the technical staff, namely, Mary Lauver and Jerry Taylor, is hereby acknowledged with much thanks. The general support of my colleagues in the bean fraternity cannot be overlooked. I hope we have made friends and established life-long ties for future research cooperation.

The work in Guatamala was made possible through the cooperation of Dr. Wallace of Cornell University and Dr. Masaya of ICTA in Guatamala who planted the experiment and assisted in the data collection. The hospitality of especially Dr Masaya and Mr. Fernando Aldano and all the staff of the bean group at ICTA extended to me during my stay in Guatamala is deeply appreciated.

I am greatly indebted to the University of Cape Coast in Ghana, my employer, for granting me study leave with pay for the duration of my program. The program was made possible principally through funding provided by the Fulbright Hayes Foundation and supplemented by the Margoes Foundation, both of the USA. The research in Guatamala was made possible with travel grants from the Candice Thoman Foundation chaneled through MSU. I thank these distinguished educational funding bodies for the invaluable contribution to international education. The generous financial assistance provided by the Sage Foundation towards the preparation of this dissertation is hereby acknowledged with much thanks.

Finally, and most importantly, I thank God for the great things He has done !

ABSTRACT

GENETIC AND MULTIVARIATE STATISTICAL EVALUATION OF A PHENOTYPIC RECURRENT SELECTION PROGRAM FOR RECOMBINING ERECT ARCHITECTURE AND LARGE SEED SIZE IN *PHASEOLUS VULGARIS* L.

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Genetic and multivariate procedures were employed to evaluate populations from five cycles of phenotypic recurrent selection in a dry bean ideotype breeding program. The populations derived from crosses between representatives of two distinct germplasm pools, namely, the indeterminate, small-seeded, narrow-profiled, erect architectural pool, and the indeterminate, decumbent, large-seeded pinto pool, both from the Meso-American center of domestication. The populations were grown at Michigan State University, East Lansing and at Chimaltenango, Guatemala.

Differences in traits at the two locations were due to scale. Multiple regression, corroborated by other multivariate procedures, selected hypocotyl diameter, plant height, branch angle, pods on the main stem and pods in the middle third of the plant as the most effective indicators of bean plant architecture. Genetic consequences due to divergence between the two germplasm pools were manifest in the lack of desirable recombinations and poor yield in the early cycles. The principal sources of divergence were seed size and number of seeds per pod. Architectural traits were recovered *in toto* in the original cycle while seed weight was accumulated gradually. Principal factor analysis was used to summarize architectural traits into a height (elongation) factor, a structural (skeletal) factor and a distribution (number) of reproductive parts factor. Compensatory relationships were encountered among yield and architectural components. Phenotypic recurrent selection was ultimately effective in recombining erect architecture and large seed size.

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CHAPTER ONE

INTRODUCTION

The plant breeder is in the business of nudging nature toward his or her specific breeding objectives, manipulating the genetic text of his or her plants to varying degrees depending on the special objectives, with the ultimate goal of optimizing economic production.

Before the breeder sets out to develop a crop cultivar certain considerations must be understood, of which physiological-genetic, environmental and cultural are paramount. The former has to do with the biological machinery of the plant which is fueled by the meteorological, abiotic and biotic environmental components, for harnessing by the farmer within cultural limits. The biological machinery may be made to work more efficiently through genetic manipulation based on sound physiological principles, for optimal exploitation of the environment, the uncertainties of the latter notwithstanding. Agriculture and culture are bedfellows and thus crop cultivars must be amenable to particular cultural practices.

Sometimes, the breeder may encounter a situation in which a combination of plant attributes and environmental

factors will "nick" and translate into optimal economic yield. This is the basis of the concept of ideotype breeding, the development of a "designer cultivar" for a specific cultural and environmental milieu.

Such a breeding program has been embarked upon at the Michigan State University and has successfully produced commercial navy and black bean cultivars for mechanized farming under favourable conditions in the "Thumb" region of Michigan (Adams, 1982; Kelly et al, 1984). In achieving this goal, the architecture of the navy bean was transformed from a low-growing, branching, determinate bush, into a sturdy, erect form. Induced mutagenesis played a significant role in producing basic germplasm for the subsequent development of the new cultivars (Adams, 1982). The success in navy and black beans prompted the application of the ideotype concept to the breeding of the pinto class of beans for upright architecture in order to facilitate direct combine harvesting. A phenotypic recurrent selection program was designed to achieve recombination between the erect plant architecture of the navy bean and the larger seed size and pattern of the pinto bean (Kelly and Adams, 1987). This breeding program was initiated without the benefit of some basic genetic information. The program quickly encountered some problems of genetic origin. The genetic recombination between the two gene pools did not

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occur as freely as was expected. Nonetheless, it appeared to have succeeded although several cycles of selection were required. Certain traits distinguish a plant with desirable architecture from plants with less desirable architecture. These traits include hypocotyl diameter, height, branch angle, number of branches, pod distribution and many more. When selecting plants on a phenotypic basis it is necessary to know which traits are effective predictors of the desired objective and how they are inherited. A knowledge of the associations among the characters along with their genetic control will help in adopting effective and efficient breeding procedures. The literature is deficient in such information as it pertains to dry beans.

When quantitative traits such as those defining plant architecture are considered, numerous relationships, both favorable and adverse, are bound to be encountered. Studying the traits independently may not reveal the true nature of interrelated effects and there is the need, therefore, to consider them together. The latter objective is accomplished by the elegant procedures of multivariate data analysis.

In view of the foregoing, the research herein reported, using materials from the Michigan State University pinto bean breeding program, sought to bridge the information gap by investigating the following:

1. Follow, through successive cycles of recurrent selection, the changes in frequency and metric value of plant traits as recombination coupled with selection occurred.
2. Determine the statistical associations among morphological traits .
3. Study the changes in the pattern of association of traits under selection.
4. Determine the stability of the traits in various environments.
5. Identify the pattern of recovery of plant architecture and the cycle in which recombination between the two diverse gene pools took place.
6. To identify the traits which are good indicators of bean plant architecture.
7. To determine whether evidence exists for linkage between plant architecture and seed size (or any association that could be attributed to genetic linkage).
8. To determine the genetic control of the plant traits under consideration.

To this end, simple correlation and multivariate statistical procedures, namely, principal component analysis, principal factor analysis, canonical correlation, canonical discriminant analysis, Mahalanobis' D^2 analysis, and multiple regression were employed to evaluate selections from five cycles of phenotypic recurrent selection planted at two locations. Some information was also obtained from a second experiment comprising a 2 x 3 factorial cross among representative parents from the gene pools.

CHAPTER TWO

LITERATURE REVIEW

2.1 BOTANY AND EVOLUTION OF THE BEAN CROP AND THEIR IMPLICATONS IN THE BREEDING OF THE CROP.

Dry bean (*Phaseolus vulgaris* L.) has papilionaceous, hermaphroditic and cleistogamous flowers which are self-fertilizing (Singh and Gutierrez, 1984). This relatively closed breeding system suggests that the crop may be prone to genetic vulnerability and that breeders should make an effort to broaden the genetic base of cultivars to guard against adverse consequences. Singh and Gutierrez (1984) observed in Latin America, the primary center of bean diversity, that small-seeded bean types are predominant in the relatively warmer lowlands of Central America, Mexico and over most of Brazil and Venezuela. This region is also called the Meso-American region, Brazil and Venezuela not included. The medium and large-seeded bean forms, they observed, abound in the moderately cooler environments of Mexico, Colombia, Equador and Peru. This region is also termed the Andean region, Mexico not included.

In addition to this geographical distribution of dry bean forms, genetically controlled incompatibility has been found to occur in crosses between the two groups by various workers, including Davis and Frazier (1964) and Coyne (1965). Singh and Gutierrez (1984) proposed a two complementary dominant gene (DL_1 , DL_2) system of control for this apparent incompatiblity. The small-seeded bean group carries the DL_1 allele while the medium- and large-seeded group carries the complementary DL_2 allele, and in concert produce dysgenic effects called dwarf lethals.

Gepts (1984) has further shown that two centers of domestication of dry beans exist which can be differentiated electrophoretically on the basis of a major seed storage protein (phaseolin) type. The Mexican center of origin is characterized by a Sanilac (S-type) gel banding pattern while the Andean group possesses a Tendergreen (T-type) banding in gel electrophoresis. Incompatibility in hybridization occurred when the parents in a cross exhibited the opposite phaseolin protein types described (Gepts, 1984).

Singh and Gutierrez (1984) suggested that this genetic situation in dry beans may have had significant evolutionary implications through the imposition of restricting genetic barriers to inter-group hybridization. They further suggested that should it become necessary to use parents from the two gene pools in a breeding program the problem may be circumvented by using a suitable parent as a bridge between the two pools. Kelly and Adams (1987) also suggested that parents, to the extent possible, be selected from within the same center of domestication to minimize hindrance to genetic recombination.

The germplasm utilised in the present study is characterised by the S-type phaseolin marker and derives from the Central American-Mexican center of origin, according to Kelly and Adams (1987).

2.2 IDEOTYPE BREEDING: THE CONCEPT AND ITS APPLICATION WITH SPECIAL REFERENCE TO DRY BEAN.

Ideotype breeding may be viewed as the science of custom designing of crops.

Donald (1968) was credited with the origin of the concept of breeding plants with model characteristics (ideotype) known to influence photosynthesis, growth and economic production. As Mock and Pearce (1975) further elaborated, ideotype breeding involves defining a crop production environment, designing a plant model from morphological and physiological traits known to influence performance in that environment, and combining the traits in one plant type. On the subject of ideotype breeding Adams (1982) added that the strategy has to do with the number, size, shape, structure, arrangement and display of particular plant parts. The ideal plant architecture, he further stated, has no value on its own in terms of economic yield unless such a structure translates into accentuated physiological responses and eventually into productive superiority. In other words, a crop ideotype should maximize both biomass and partition.

In embarking upon the ideotype concept the breeder, as Adams (1982) pointed out, implicitly operates on the premise that an agronomic situation is identifiable which will especially favor the genetic model characteristics and confer upon the "designer cultivar" superior fitness. In this respect, ideotype breeding should aim at the improvement of yield potential and stability of a crop (Adams, 1973). A crop ideotype will exploit efficiently the environmental resources (Donald, 1968).

Concepts such as this are not without their detractors. . Coyne (1980), questioning the ideotype concept, stated that information on the relative merits and contribution of many of the morphological (architectural) and physiological genetic yield components is inadequate to contribute to the design of a model plant with superior yielding ability. Such objections notwithstanding, the ideotype strategy has been successfully employed to improve many crops, including wheat (Donald, 1968), rice (Jennings, 1964), maize (Mock and Pearce 1975), barley (Donald, 1979) and dry bean

(Adams, 1973, 1982; Kelly _et al_, 1984).

2.2.1 Anatomy of a bean ideotype

Adams (1973), in designing a bean ideotype for mechanized agriculture in favourable environments in the midwest region of the USA, enunciated certain plant morphological attributes. These were later revised (Adams, 1982) as follows:

1. Tall, with main stem nodes numbering 12-15.
2. Moderate number of basal branches, 3-5.
3. Indeterminate growth, large overall plant size, but not with extended vine growth.
4. Upper internodes longer and more numerous than basal internodes.
5. Thick stem diameter.
6. Narrow plant profile.
7. High values of first-order yield components in keeping with commercial class requirement.
8. Leaf area index near four at flowering time.

Some of the architectural attributes may be seen in Figure 1. This ideal plant design has subsequently been referred to as an "architype" (Adams, 1982). Singh (1982) described three distinct plant habits in beans as type I (bush), type

Figure 1. Comaparison of the representative parents of the germplasm used: Midnight (left) represents the architecture pool while UI 114 (right) represents the pinto pool.

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II (indeterminate, erect) and type III (indeterminate, prostrate). The type II plant habit has shown superior yielding stability across diverse locations, in dry beans (Kelly et al, 1987) and in soybeans (Beaver and Johnson, 1982).

2.3 MULTIVARIATE STATISTICS IN CROP BREEDING

Multivariate analysis is the branch of statistics concerned with analyzing multiple measurements that have been made on one or several samples of individuals (Cooley and Lohnes, 1971). The variates are inter-dependent among themselves so that we cannot split off one or more from the others and consider it by itself (Kendall, 1957). However, handling data with multicolinearity can be unwieldy and some meaningful summarization is required.

Multivariate techniques have been classified by Cooley and Lohnes (1971) as presented in Figure 2a. Kendall (1957) further summed up the models in the figure as follows:

A. Interdependence models - represented by models in quadrat Q1 (principal component, factor analysis).

B. Dependence models - represented by models in quadrats Q2, Q3, and Q4 (include multivariate analysis of variance, classification functions, discriminant function, multiple correlation, canonical correlation). These models may be

		POPULATION	
		ONE POPULATION	TWO OR MORE POPULATITIONS
VARIABLES	ONE SET	Principal component Factor analysis Q1	Multivariate analysis of variance Discriminant functions Classification functions Q2
	TWO OR MORE SETS	Q3 Polynomial fit Multiple correlation Canonical correlation Multiple partial correlation	Q4 Multivariate covariance

Figure 2a. Classification of multivariate procedures (Cooley and Lohnes, 1971).

summed under the general regression theory and differ from the other set of models in the sense that the researcher may specify predictor variables as well as criteria variables.

Various multivariate procedures have been used independently or along with others to effectively summarize and interprete data in plant breeding and genetics. Those used in this study will be briefly reviewed.

2.3.1 Factor analysis

A variable is explained to the extent that its variance can be attributed to an identifiable source (Geer, 1971). Factor analysis may be use to find ways of identifying fundamental and meaningful dimensions of a multivariate domain Cooley and Lohnes, 1971).

Factor analysis is a decision-making model for extracting subsets of covarying variables (Guertin and Bailey, 1970). This method entails reformulating a set of natural or observed inter-correlated variables into a new set (usually fewer in number) of independent variables such that the latter set has certain desired properties specified by the analyst (Stopher and Meyburg, 1971).

Factor analysis is frequently accomplished by first performing a principal component analysis (PCA) and using the resulting principal factors as a set of reference axes for determining the simplest structure of factors (Cooley and Lohnes, 1971). Factors are hypothetical constructs (Harman, 1976). In Figure 2b, the factor analysis model (b) assumes that a set of observed variables x can be interpreted as dependent on a set of unobserved variables f (de Geer, 1971). The f variables are called factors and according to Guertin and Bailey (1970) are of three types:

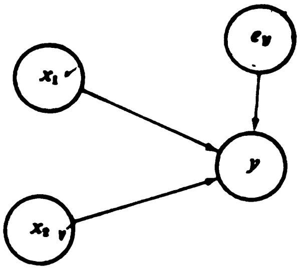
a. General - shows all variables have sizeable loadings on this factor.

b. Group - this factor has 2, 3 or few variables with sizeable loadings.

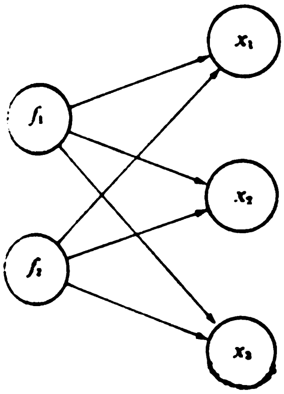
c. Specific - one variable only gets loaded on this factor alone.

From the factor patterns names may be assigned to each factor. Naming a factor is merely a mnemonic convenience (Guertin and Bailey, 1970). The factor analysis should be conceptually interpretable, that is, the components or factors should be named sensibly such as to convey information to both the analyst and audience (Stopher and Meyburg, 1971).

There is no test of significance of factor loadings so the selection of level of 'cut off' is arbitrary. Guertin and Bailey, 1970) suggest that factors be cut off only until 95% of the complete principal axes variance is accounted for except with variables of 50 or more.



Multiple correlation.



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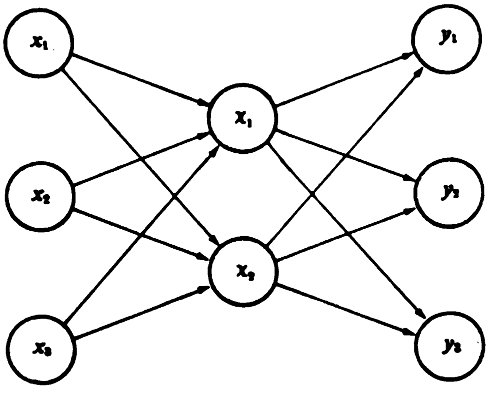

Canonical correlation.

Figure 2b. Diagramatic presentations of various multivariate procedures (Geer, de 1971).

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Bramel et al (1984), while observing the scanty reports on the use of principal factor analysis (PFA) in plant research, used the procedure to identify plant characters associated with seed yield (and, hence, have some predictive powers for yield) in three stem termination types of soybeans. The authors also reported that by using PFA they reduced the number of variables from 25 to eight. Further, they suggested that grouping of traits into concepts and then selecting traits for developing prediction equations from within the grouping would result in equations that have measurements of different biological functions instead of repeated measurements of characters related to the same func-tion in the plant. The last procedure has the effect of reducing bias due to multicolinearity (Bramel et al, 1984). Rao and Paroda (1982) used the centroid method of factor analysis to analyse the pattern of diversity in 40 genotypes of cluster bean (Cyamopsis tetragoloba (L.) Taub) based on nine characters. They observed changes in factor loadings from one environment to another but none-the-less found that the compositions of the variables in the factors remained the same. The coefficients of the residual matrix were negligible after the first three factors had been extracted, the three accounting for 98.88% of the original variance.

Walton (1971) used the maximum likelihood method of

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estimating communalities in a factor analysis of wheat characters to determine predictors for yield selection. He cautioned that information from factor analysis be taken to relate, in detail, to the range in genetic variability test-ed.

In dry beans, Denis and Adams (1978) used image covariance matrix procedure to extract eigenroots and eigenvectors in PFA to search for and identify patterns of morphological characteristics in a set of bean cultivars which are related to yield. A total of 22 morphological characters and 16 cultivars were used. Only factor loadings of values above 0.72 were used in identifying and naming a conceptual factor. Three principal factors were retained and named weight (or size), number, and plant architectural factors, respectively. The plant architectural factor was loaded by variables including number of long internodes, average long internode length and total number of internodes. Linear correlations among loading coefficients in principal factors from data at two locations were highly significant and mostly positive.

2.3.2 Principal component analysis

The PCA is a common ordination numeric technique which reduces the dimensions of multivariate data by removing intercorrelations among the traits under study and thereby enables multidimensional relationships to be plotted on 2 or 3 principal axes (Harman, 1976). PCA is the same as the PFA analysis except the factors are not rotated. If the only objective of a factor analysis is to provide a reduction in the number of variables to be used for prediction or description, the PCA is appropriate (Guertin and Bailey, 1970).

The number of factors extracted from a PCA is usually equal to the number of variables employed in the intercorrelations. Each principal component is a linear combination of the original variables. The first principal component (PC1) has the largest variance of any unit-length linear combination of the observed variables (Rao, 1964).

Akoroda (1983) used PCA to identify the principal characters which account for the major variation among yellow yams (<u>Dioscorea cayenensis</u> Lam). Data based on 20 accessions and 49 characters were analysed. The first three factors accounted for only 56.14% of the original variance and these were used to construct a three dimensional ordination of the accessions. Using the magnitude of eigenvalues of the first three principal axes, he was able to select six characters for a metroglyph from which he identified clusters of accessions similar to what was observed from the PCA analysis.

Adams (1977) used a modification of the PCA (Adams and Wiersma, 1978) to estimate distances among dry bean cultivars to serve as an index of genetic homogeneity for the crop in various regions of the USA.

PCA was used in a more conventional way by Ghaderi et al (1984) to reveal quality traits of navy and pinto beans. Loadings of 15 quality traits in 12 principal components were examined. The results indicated that quality traits, namely, dry characters, soaking characters and cooking characters were independent, having loaded in separate axes. This prompted the authors to suggest a tandem selection procedure to be followed by construction of selection indices for a breeding a program.

2.3.3 Discriminant analysis and Mahalanobis' D^2 analysis

This is a dimension-reduction techinique related to principal component analysis and canonical correlation (SAS, 1985).

According to Spoher and Meyburg (1971), discriminant analysis has two assumptions:

1. A population is made up of two subpopulations
2. It is possible to find a linear function of certain measures and attributes of the population that will allow an

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observer to discriminate between the two subpopulations. They further pointed out that the procedures are not designed for seeking population groupings (as is the case in cluster analysis) because the population has already been grouped (for example into cycles as in the present study).

The solution is nothing but a principal component solution applied after transformation to spherical variance (that is, the error variance is normalized to identical value in all directions) according to de Geer (1971).

Mahalanobis' D^2 statistic is often a part of the discriminant analysis procedure and is used in order to indicate the biological distance between separated groups. Lee and Kaltsikes (1973) used D^2 estimates to discern divergence among durum wheat (*Triticum turgidum* L.) cultivars, while Ghaderi *et al* (1984) used it to estimate the genetic distance between parents in dry beans (*Phaseolus vulgaris* L.) beans (*Vicia faba* L.) as an indicator of the of the in- herent capacity of their hybrids for superior performance. To achieve the latter, the relationships between D^2 estimates for eight cultivars and heterosis for various traits in their F_2 progenies were studied.

Vairavan *et al* (1973) used the canonical discriminant analysis along with D^2 estimates to study the nature of divergence in rice (*Oryza sativa* L.) germplasm. Just as with PCA, the first two canonical variables extracted represent, geometrically, the axes along which the separation of the groupings is greatest (Walters and Evans, 1978). When the first canonical variables account for most of the total variation (about 90% or more) the grouping based on the first two vectors would amply serve this purpose (Vairavan _et al_, (1973). In dry beans, Walters and Evans (1978) used canonical variate analysis to evaluate beans from various countries, using eight characters. Plotting the first two canonical variates, they found it to be a reasonable reflection of the 'distance' between samples from the eight countries studied. Ghaderi _et al_ (1984) used a canonical discriminant function to indicate the effects of location on quality traits. The same cultivar grown in two locations was distinctly separated along the canonical discriminant function on a location basis. Ramagosa _et al_ (1986) used canonical discriminant analysis to classify sugarbeet (_Beta vulgaris_ L.). plants within environments.

Multivariate analyses are sometimes used to support each other. Narayan and Macefield (1976) used canonical factor and D^2 analyses to evaluate 5477 chickpea (_Cicer arietinum_ L.) lines on the basis of eight characters related to firness and yield, for adaptive responses and genetic divergence. Plant type was found to be the most important character affecting genetic divergence between geographical groups. Ghaderi _et al_ (1982), in studying environmental response patterns in commercial classes of common bean, used canonical analysis to support evidence from a cluster analysis. The first two canonical variates in the study accounted for 88.8% of the total variation. Navy and pinto bean classes fell into distinct groups with a significant D^2 estimate of 8.20 between them.

2.3.4 Multiple regression analysis

This is a model-developing procedure which allows the researcher to specify a dependent variable as well as a set of predictor variables (Figure 3). From the latter, variables which best indicate the former may be identified. There are four general procedures available for model-fitting:

a. Forward selection:- The procedure begins with a zero-variable model and includes independent variables as their calculated F statistic satisfies the specified minimum significance level. Once selected, a variable cannot be dropped.

b. Backward elimination:- This is the reverse of the forward process. An all-variable model is started with and systematically reduced through elimination of variables whose F-statistic fails to satisfy a specified level of significance, which was 0.10 in this study.

c. Stepwise:- This variation of the forward procedure does not guarantee a place for a variable in a model once selected. A variable may be ejected from a model at any time when, upon evaluation, it fails to produce an F-statistic which is significant at a specified level due to the inclusion of new variables.

d. Maximum R^2:- This technique produces a series of models which eventually includes all variables in the model. The first, a one-variable model, will include the variable which produces the highest R^2 (coefficient of determination) and follows with a two variable model, the latter adding on the variable which produces the greatest increase in R^2. The difference between this procedure and stepwise is that in the former, all switches are evaluated before any switch is made, while in the latter the 'worst' variable may be removed without considering what adding the 'best' remaining variable might accomplish (SAS,1985).

These stepwise model selection methods were conducted on a PRS cycle basis including architectural traits only. Variables selected by each procedure were further evaluated on the basis of the magnitude and significance of their F-statistic. Those retained were compared among the four iterations and pooled together to produce a list of architype-influencing variables for each cycle. The five lists were compared and summarized on the basis of frequency of occurrence in the cycles to determine which variables were important in all cycles and thus are major indicators of bean plant architecture.

Multiple regression analysis may suffer from bias due to multicolinearity and thus preceding it with factor analysis to group traits and then selecting from the groupings for prediction equations may be advisable (Bramel *et al*, 1984). Walton (1971) used factor analysis and multiple stepwise regression in the suggested complementary way to determine dependence relationship between yield, its components and other morphological structures in wheat.

Lee and Kaltsikes (1973) also employed stepwise regres sion and factor analysis to identify potent indicators of yield in F_1 and F_2 diallel populations of durum wheat (*Triticum turgidum* L.).

2.3.5 Canonical correlation analysis

This analysis is a generalisation of the multiple correlation procedure (de Geer, 1971). The technique was developed by Hotelling (1936) to analyse the relations between two sets of variables drawn from the same subjects. An assumption is made that there are unobserved variables dependent on a known set of variables x, and determining another known set, y. The intermediating unobserved variables are used to canalize the influence of set x on set y (de Geer, 1971). Model c in Figure 3 illustrates this last point. A comparision of models b and c shows that factor analysi hidden in canonical analysis (de Geer, 1971) and may be used along with factor analysis (Cooley and Lohnes, 1971).

2.4 Recombination analysis

Anderson (1939) first proposed the concept of the recombination spindle and presented a model for it. He proposed that in the absence of restriction to free recombination among traits, all possible recombinants, according to the genic differences between parents for the traits, should, theoretically, be attained in the F_2 such that the vortices of a correlation cube (a hyperspace) are occupied. In reality, however, there are usually restrictions to free recombination, as enunciated elsewhere in this dissertation, whose effects reduce the number of recombinants such that the cube is only partially filled, in an ellipsoidal fashion (a spindle shape), as shown in Figure 4. It must be pointed out that in any genetic system, extreme recombinants occur less frequently than the others and hence the density of the recombinants will be decreased at the margins of the ellipsoid as compared to its center.

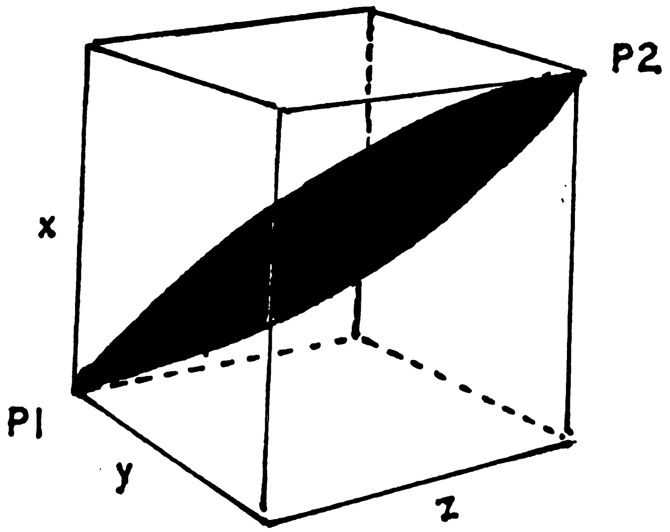

Figure 3. Model for recombination spindle analysis using raw trait scores. P_1 and P_2 = parents; x, y, and z = traits in which parents exhibit the most contrasts.

2.5 GENETIC BASIS FOR RECURRENT SELECTION AND ITS IMPLICATIONS IN THE BREEDING OF SELF-POLLINATED CROPS.

Recurrent selection is a cyclic breeding procedure of which phenotypic recurrent selection (PRS) is one and perhaps the simplest of the types. As a breeding procedure it has two main purposes (Briggs and Knowles, 1967) which are:

1. to increase the frequency of superior genes in the population, and
2. to increase the chances for genetic recombination to occur.

Each cycle comprises two general steps:

1. evaluation and selection of parents, and
2. intermating of selected parents .

Intermating in each cycle coupled with selection enables the purposes of recurrent selection to be achieved. In PRS, evaluation is solely visual (or on a phenotypic basis without progeny testing) and hence is especially useful for traits of high heritability (Briggs and Knowles, 1967). Significant handicap in employing PRS (and for that matter all types of recurrent selection) is the difficulty of obtaining a sufficient number of successful crosses (Khadr and Frey, 1965).

Recurrent selection has been successfully used to improve quantitative characters in self-pollinated crops

(Miller and Fehr, 1979; Kenworthy and Brim, 1979; Sullivan and Bliss, 1983). VandeLogt et al (1984) observed that numerous agronomic traits in crop plants are influenced by genes segregating at many loci, causing the variation in segregating generations to be continuous or quantitative in nature. It would be useful adjunct information to know the degree of linkage and nature of the gene action involved in these traits.

The breeding method adopted will be influenced by the presence or absence and type of linkage (Croissant et al, 1971). If coupling relationships predominate for a particular character, the existing combinations are usually desired. Hansen (1959) observed that if parents are elite, significant linkages would be in coupling phase. A breeding method such as the backcross will keep favorable gene blocks intact. A preponderance of additive genetic variance and coupling phase linkage suggests a different breeding approach from a preponderance of dominance variance with repulsion phase linkage (VanderLogt et al, 1984). New genic recombinations will be required when repulsion phase linkage predominates. Presumably, blocks of favorable alleles are present in the two sets of parents in the last situation (Hansen, 1959).

The need for intermating in breeding programs for self-pollinating crops has been quite widely discussed.

Jensen (1970) stated that the lack of intermating beyond the initial cross, as is the case in systems for breeding self-pollinated crops such as mass selection, pedigree and single seed descent, limits the recombination options to those that are residual in isolated lines of descent following meiosis of the hybrid plant.

Intermating has been shown to break up linkage groups. Miller and Rawlings (1967) reported dissipation of initial linkage disequilibrium upon intermating two divergent inbred lines of cotton. Generalizing, Hanson (1959) concluded from a theoretical study of breaking of initial linkage blocks that at least four cycles of intermating will be required to accomplish substantial breakup of linkage blocks in self-pollinated crops.

As to the generation in which intermating should start, Hanson (1959) favored an early generation, F_2, while Pederson (1974) cautioned that from a two-locus theory study, intermating in the F_2 will be effective only if close linkages are predominantly in the repulsion phase of a multi-locus character. Such intermating will result in increase in the relative frequency of desirable homozygotes after repeated self-fertilization.

Kelly and Adams (1987) acknowledged the disadvantage of intermating in the S_2 without selfing by stating that desired characters are not necessarily fixed by then so that S_2 parents may not serve efficiently as genetic donors. On the other hand, they found the procedure to quicken the breeding program by enabling them, with the help of a winter nursery, to obtain one cycle per year, in addition to increasing the chance of genetic recombination between heterozygous parents.

The actual selection process may be done visually or with the aid of a selection index, the latter being very laborious. Kelly and Adams (1987) suggested that when the desired traits are easily recognizable, selecting on a phenotypic basis has the advantage of allowing the breeder to evaluate large populations, thereby increasing the chance of finding desired recombinant types.

2.6 PHENOTYPIC RECURRENT SELECTION (PRS) IN IDEOTYPE BREEDING OF PINTO BEANS AT THE MICHIGAN STATE UNIVERSITY (MSU).

The above breeding program is the subject of evaluation in this dissertation. The details of the program, whose objective was to recombine the large seed size of the pinto bean with the desirable erect plant architecture of the navy/black, have been presented in a paper by Kelly and Adams (1987). A summary of the materials and methods, as well as results, is presented herein to provide a basis for discussion.

Table 1 summarizes this program. The base population (C_0) was established by making 124 genetically different crosses between nine pinto parents, 16 architypes and six intermediate types. Forty four percent of these crosses were either three or four-way crosses.

Table 1. Number of various genetic materials utilized in the PRS program at MSU.

Year	1980-1981	1981-1982	1982-1983	1983-1984	1984-1985
Cycle	C_0	C_1	C_2	C_3	C_4
Parents	27	133	169	108	109
Crosses	124	267	136	344	600
S_1 populations	55	351	399	bulk	bulk
S_1 individuals #	13	277	338	94	57
S_1 selections	271	1,272	524	1,064	402

#: figure shown x1000 = number of individuals planted
C_n: where C = cycle and n = stage of recurrent selection.

By using a winter nursery, one cycle of recurrent selection was obtained per year. Selection was done in the S_1 generation and the progeny from the selected individuals (S_2) crossed (large-seed selections with architypes) to generate the next cycle.

To maintain adequate variability for traits from the two sources of germplasm, less desirable recombinants (good architecture with smaller than desired seed size and desirable seed size with poor architecture) were chosen as parents. Plant selections were evaluated on the basis of maturity (early, medium, late), plant habit (type I, II, III), architecture (compressed, architype, ragged), height (short, medium, tall), pod number, and location of pods. The selection criteria were modified to include seed shape and disease resistance (rust) after C_3.

The results at the end of each recurrent selection cycle are presented below, where C_n designates the cycle and the stage of recurrent selection and S_n the level of selfing.

C_0S_1:

- No favourable recombinants found; plants showed predominantly parental characteristics.
- Compromise selection made for certain architectural

types with smaller seeds and likewise for pinto, to maintain the desired seed type in the population.

- Seed size range for small-seeded selections was 22-25 gm/100 seeds.

C_1S_1:

- Progress made for highly heritable traits such as color of seed testa and architype.
- Recombinants with good architype rating and small pinto-like seeds were found.
- Seed size range was 23-25 gm/100 seeds.

C_2S_1:

- Architypes still had small seeds (30gm/100 seeds).
- Suggested, based on the size of the population and the low frequency of desired recombinants, that a tight linkage would exist between genes for architype and small seed characteristics.
- Considered advancing the selections through more recurrent cycles since seed size is controlled by additive genes (Coyne, 1968) and also, according to Motto _et al_, (1978) is accounted for by at least 10 factors.

C_3S_1:

- Selected 1064 recombinants with good architecture and large seed size (29-53gm/100 seeds) out of a population of 94,000 individuals. The pinto parents averaged 38gm/100seeds. - Further identified 280 individuals with good architype and superior seed size.

Reflecting on this breeding program, Kelly and Adams (1987) observed that progress of recovery of the architype trait was not characterised by gradualism (or partial step-by-step recovery) but rather, the complex traits comprising architype were recovered in-toto.

2.7 ASPECTS OF THE QUANTITATIVE GENETICS OF ARCHITECTURAL TRAITS WITH SPECIAL REFERENCE TO BEANS.

Adams (1982) remarked that little is known about the degree to which architectural traits in bean may be associated as linked effects in inheritance. Harmsen (1983) reported a very significant and positive correlation between hypocotyl diameter and yield in beans. Internode length on the main stem was not significantly associated with bean yield. She also observed significant heterosis in the F_1 for nodes on the main stem, pods on the main stem and plant height. Pod number was highly determined architecturally by number of nodes (or leaves) according to Adams (1982). He also reported that the main stem number of nodes correlated highly with plant height. By including some tropical cultivars the number of main stem nodes correlated negatively and significantly with number of effective (fruit-bearing) branches.

Ghaderi and Adams (1981) reported high broad-sense heritability for plant height (80%), pod length (97%), number of branches (75%), hypocotyl diameter (84%), number of seeds per pod(74%), main stem nodes below 15cm (81%) in dry beans. Narrow-sense heritability of 75% was reported for seed weight in cowpea (<u>Vigna</u> <u>unguiculata</u> L.) by Drabo <u>et</u> <u>al</u> (1984).

Using generation means analysis, Ghaderi and Adams (1981) reported, preliminarily, that plant height and hypocotyl diameter were affected by both additive and dominant gene action. The results were not the same for all crosses. Dominance effects were present in number of nodes below 15cm while pod length and number of nodes above 15cm exhibited additive effects. Croissant and Torrie (1971) presented evidence for repulsion phase linkage between height and yield and dominance effects for height and seed weight in soybean.

Dickson (1967), working with snap beans, found additive gene control of seed number per pod while Drabo <u>et</u> <u>al</u>

(1984) reported that seed weight in cowpea was predominantly under additive gene control but with significant dominance and additive x additive epistasis. Seed weight in cowpea was inherited quantitatively, small seed size being partially dominant to large seed size (Aryeetey and Laing, 1973; Drabo *et al*, 1984). Aryeetey and Laing (1973) reported also that seed size in cowpea was controlled by 10 pairs of genes. This conclusion was reached on the basis of an estimate of the number of effective factors (K) proposed by Mather (1973).

CHAPTER THREE

GENERAL MATERIALS AND METHODS

3.1 SOURCES OF GERMPLASM

Two experiments were conducted utilizing germplasm drawn from two diverse gene pools whose charateristics were described by Kelly and Adams (1987) and are herein summarized as follows:

A. Architecural germplasm source:

- Small-seeded navy and black architectural types which range between 18 - 22 gm/100 seed.
- Type II classified indeterminate plant habit.
- A dominant main stem with an upright branching pattern.
- 2 - 3 branches angled acutely upwards.
- Tall (50 - 55 cm) and producing nodes vertically rather than laterally.
- Pods not set predominantly in the lower nodes but

distributed throughout the plant canopy and sufficiently high off the ground to facilitate direct harvesting.

- Thick hypocotyl.
- Thick tap root.
- 6 to 8 seeds per normal pod.

B: Pinto germplasm source:

- Large-seeded pinto cultivars averaging 40 gm/100 seeds.
- Type I or III plant habit.
- Flatter seed shape.
- Pinto seed color: variegated dark brown on light tan seed color.

In addition to genetic materials from these two germplasm pools, other lines or cultivars with characteristics not strictly allied with either source were incorporated. These included a small-seeded, single-stem, indeterminate line (791583) from Cornell University and a breeding line, A 35.

In 1980, a phenotypic recurrent selection (PRS) breeding program was started at MSU with the objective of developing a large-seeded erect pinto bean utilising materials from the two germplasm pools described above. Table 1 (adapted from Kelly and Adams, 1987) summarizes the breeding program.

I joined this program at the cycle three (C_3) stage. The original cycle (C_0) was reconstituted using 16 and nine parents from the achitectural and pinto source populations, respetively. Remnant sed lots for each succssive cycle were obtained from storage. The first three cycles (C_0 to C_2) contained predominantly architectural types since desirable recombinants with large seed and the preferred architecture were not found in these cycles. To maintain the desirable pinto seed size in the population, plants with mediocre architecture but large seed size were also selected and advanced in these cycles. Selection pressure and target traits were changed from one cycle to another according to the progress made towards attaining the breeding goal.

3.2 EXPERIMENT I

This experiment was conducted at two locations whose geographic and meteorological characteristics are presented in Table 2. A second location in Guatemala was excluded from the analysis because of very poor plant stand in the field.

Table 2. Location and weather information for the two sites at which research was conducted.

Location	East Lansing (Michigan, USA)	Chimaltenango (Guatemala, CA)
Longitude	84^{o} 36'W	90^{o} 48'W
Latitude	42^{o} 47'N	14^{o} 38'N
Elevation	255 m asl	1793 m asl
Temperature #	19.44^{o} C	19.10^{o} C
Precipitation #	243.59 mm	232.60 mm

: monthly average during growing season

In this experiment, selections from five cycles were evaluated in the field. The first four cycles were produced as described by Kelly and Adams (1987). The original cycle, C_0, was reconstituted in the 1983/84 growing season in East Lansing because original remnant seed of that cycle was not available. The appropriate parent materials were planted in pots in the green house in October of 1983 followed by intermating between the two sets of germplasm in a factorial design. The F_1 seeds were planted in the greenhouse in 1984 to produce S_1 seed from field planting.

All the S_1 phenotypic selections were threshed individually and kept in separate seed envelopes. One hundred envelopes were randomly selected from each cycle and four sets (replications) of single seed bulks created. The bulks were field planted in separate rows at a spacing of 20cm within rows and 50cm between rows. The rows were completely randomized and planting was done by a tractor drawn seed planter. There were four rows (replications) of each cycle, consisting of 100 selections randomized within each row and bodered on both ends by a standard variety. Each parent had only two rows. In effect, each plant was considered as a plot. The experiment in East Lansing was planted in summer of 1985 and harvested in fall, 1985. The Chimaltenango experiment was planted in May, 1986 and harvested in August 1986. For practical reasons, the Guatemala study comprised 50 S_1 lines randomly selected from the 100 planted at East Lansing.

At maturity, the plants were pulled up and tied in bundles of about 10 plants each and hung on wires in a field laboratory until the time for data collection. All the listed traits were measured on each individual plant. A total of 1900 plants were measured at East Lansing and 800 at Chimaltenango. These included parents from each of the two gene pools.

3.3 EXPERIMENT II

This experiment was conducted at East Lansing beginning in the Fall of 1983. Two cultivars (Olathe and UI 114) representing the pinto gene pool, and two varieties and a line (C-20, Midnight and X80149) representing the architecture gene pool, were planted in the greenhouse and intermated in a factorial design. Sixteen F_1 seeds of each of the six crosses were planted in the field in the summer of 1984. In the fall of 1984, 80 F_2 seeds (five seeds per F_1) were planted in the greenhouse to generate materials for planting F_3 families in the following season.

The final planting of this experiment in the field was made in the summer of 1983 at East Lansing, Michigan. Each set of six crosses comprised four sets of each parent, 16 F_2 populations and 80 F_3 families, giving a total of 104 entries per combination. The planting was done in a 25 x 25 simple lattice design. Each plot consisted of a single row of five plants spaced 20 cm apart in the row and 50cm between rows. There were a total of 625 rows per replication including one filler row. At maturity, the three inner plants in each row were uprooted and handled as described for Experiment I.

3.4 DATA COLLECTION

The same kinds of data were collected for both experiments at both locations except for a few additional data at Chimaltenango. Only post-harvest data were taken, as follows:

1. Plant height - Distance between the soil level and the top of the central axis excluding the vine.
2. Architype rating - A scale of 1 - 5 was employed based on an intuitively composed index. A rating of 1 was least representative, while a rating of 5 was most representative of the type which has been described previously as 'architype'.
3. Number of branches per plant - A count of primary branches.
4. Branch angle - Angles were drawn on a board with the help of a protractor. Placing the central axis of a plant on the 90° line and the node with the branch to be measured on the 90° - 0° intersection, the inclination of the branch to the central axis was determined. The larger the value, the wider the plant profile.
5. Hypocotyl length- Measured as the distance between the soil level and the lowest branch position on the main stem.
6. Hypocotyl diameter- Determined by placing the portion

just below the cotyledonary node against a ruler.

7. Lowest pod height- Distance from soil level to the point of pod attachment of the lowest pedicel.

8. Pod distribution - Each plant was divided into three equal sections based on height and the pods in each section, namely, upper, middle and lower, were counted and recorded.

9. Number of pods on the main stem - Total number of pods after branches had been removed.

10. Node distribution on the central axis- The central axis was divided as in (8) and the nodes in each section counted

11. Length of internodes on the central axis - The average length of internodes in each of the three sections in (10) was determined.

12. Pod width - Six pods (two from each section) were picked and measured across a seed locule in the mid-section of each pod and averaged.

13. Pod length - The distance between the point of attachment to the pedicel and the base of the beak was measured for each pod and averaged over the six pods used in 12.

14. Number of seeds per pod - The number of seeds in each of the six pods used for the pod dimension measurements were counted and averaged.

15. 100-seed weight - 50 seeds were randomly selected and weighed after equilibrating to 10% moisture content, and

expressed as 100-seed weight.

16. Plant yield - Total seed weight per plant at 10% moisture.

17. Maturity - The average days to physiological maturity averaged over all plants in the group. (Taken at Guatemala only).

A list of abbreviated names for the variables described above which are used in this dissertation is presented below:

1. HEIGHT - plant height (cm)
2. ARCHITYPE - architype rating
3. NBRANCH - number of branches
4. ANGLE - branch angle
5. HYPOLEN - hypocotyl length (cm)
6. HYPODIAM - hypocotyl diameter (mm)
7. LOWPODHT - lowest pod height (cm)
8. Pod distribution:
    a. PODSUP - number of pods in the upper third of the plant
    b. PODSMID - number of pods in the middle third of the plant
    c. PODSLOW - number of pods in the lower third of the plant

9. PODSMAIN - number of pods on the central (main) axis

10. Node distribution:
    a. NODESUP - number of nodes in upper third of plant
    b. NODESMID - number of nodes in middle third of plant
    c. NODESLOW - number of node in lower third of plant

11. Internode length (cm):
    a. INTNODUP - internode length in upper third of plant
    b. INTNODMID - internode length in middle third of plant
    c. INTNODLOW - internode length in lower third of plant

3.5 STATISTICAL METHODOLOGIES

The Statistical Analysis System (SAS) package installed on the MSU IBM 3090 180 VM mainframe computer was used for most of the analysis. In addition, the MSTAT statistical package developed at MSU in collaboration with the University of Norway was used for data management prior to the mainframe work as well as for basic statistical analysis.

3.5.1 Multiple linear regression

The SAS (1985) STEPWISE procedure was used. With the architype rating taken as the dependent variable and all architectural traits as independent variables, the objective of this analysis was to determine which of the independent variables (x's) have predictive value for plant architecture (y).

A model was developed for each cycle separately as well as for parents and F_3 populations. Traits that were included in a model were ranked according to the magnitude of the partial F estimate. The frequency of inclusion of a variable in a model in the five cycles was computed.

3.5.2. Principal Factor Analysis (PFA)

The PFA technique of SAS (1985) was used. Prior communalities (the amount of variance of a test shared with all others in a common-factor space) were estimated using squared multiple correlations of each variable with all other variables. Factors were extracted by the method of principal components using the mineigen criterion; all factors with eigenvalues of 1.0 or less were eliminated. The principal factors are called eigenvectors and an eigenvalue or latent root is the sum of squared factor loadings.

The retained factors were then submitted to orthogonal rotation about their origin by the varimax method. The process has the effect of increasing the magnitude of the large variable loadings while diminishing the size of the small ones. Factors extracted later contain a higher proportion of error (Guertin and Bailey, 1970).

The factor scores were standardized to unit variance. The rotated pattern (table showing linear composition of variables in terms of factors in the form of regression equations), factor structure (table of correlations between variables and factors), variance explained by each factor, and, the original and calculated communalities, were obtained for each cycle. The analysis was performed using all the selected variables together in one run and separately for two subsets of variables classified as architecture and seed-pod traits.

3.5.3 Canonical Correlation Analysis (CCA).

Mathematically, the canonical correlation technique finds a linear compound of the x-variable set that has the maximum correlation with a linear compound of the y-variable set (de Geer, 1971). This linear combination is called a canonical variable.

The SAS (1985) procedure CANCORR was used to perform that analysis. After identifying the first canonical variable, the procedure continues by finding a second set of canonical variables, uncorrelated with the first pair, that produces the second highest correlation, and so on. Canonical correlation may be conceived of as a stepwise procedure (Cooley and Lohnes, 1971). The canonical correlation coefficients were standardized and a canonical redundancy analysis performed to examine how well the original variables are predicted from the calculated canonical variables. The analysis was performed on each cycle independently using data from Experiment I only, and architectural traits and seed-pod traits as the two sets of variables.

3.5.4 Principal Component Analysis (PCA).

Each principal component is a linear combination of the original variables. The SAS (1985) PRINCOMP for PCA was used to compute principal components from a correlation matrix. A covariance matrix is not standardized and hence not invariant under scaling (de Geer, 1971). The analysis produces the eigenvalues of the correlation matrix (the discriminating power of the axes), the difference between successive eigenvalues, the proportion of variance explained by each eigenvalue, as well as the cummulative proportion of variance explained, for interpreting the data.

3.5.5 Canonical Discriminant Analysis (CDA).

Given a classification variable, cycles, and quantitative variables (architectural traits and seed-pod traits) the SAS (1985) CANDISC routine derives canonical variables (linear combinations of quantitative variables) that summarize between-class variation in much the same way that principal components summarize total variation. Variation between the classification variable is maximized with respect to the variation within it. The canonical variables are derived in the same way as described for canonical correlation.

The classification variable in this study was cycles. Three sets of variables were analysed, the first for seed-pod traits, the second for architectural traits and the third for a combination of the two. Aplot of the first two canonical variables was made in each case. Wilks' lambda test was performed to test the significance of the discriminating power of the measurement battery for the grouping criterion.

3.5.6 Mahalanobis' D^2.

In this study, the SAS (1985) MAH option was specified in the CANDISC procedure to obtain the generalized distances among the various grouping criteria. The steps involved according to Narayan and Macefield (1976) are:

a. Uncorrelated linear combinations (y's) were obtained by pivotal condensation of the common dispersion matrix of correlated variables (x's).

b. The mean values for all the traits specified were transformed into the mean values of a set of uncorrelated linear combinations (y's).

c. The D^2 between the ith and jth populations for k characters was calculated as

$$D^2{}_{ij} = \sum_{t\ 1} (Y_{it} - Y_{jt})^2$$

3.5.7 Other statistical procedures used.

a. Simple correlations:

Simple correlations among all traits were estimated by the Pearson procedure using the SAS (1985) CORR procedure.

b. Frequency analysis:

The MSTAT statistical package was used to obtain frequency classes for all traits on a cycle basis. For each trait, the frequencies were plotted using the Plotit graphics package and the cubic spline procedure to obtain smooth curves.

c. Mean separation:

Trait means were computed on a cycle basis and compared using the Duncans multiple range test (DMRT) as test criterion.

3.6 RECOMBINATION SPINDLE ANALYSIS.

In this study, a modification of the model proposed by Anderson (1939) was used. Data from Experiment II were submitted to a PCA, analysing parents, F_2's and F_3's separately. The first PC has the largest variance of any unit-length linear combination of the observed variables, according to Rao (1964). With PC 1 as a regression line, the variance contributed by the remaining PCs may be taken to represent deviations from the regression line. Plotting the

PC scores in multi-spacial configuration such that the vortices are occupied by parents displaying contrasting traits and the PC 1 as the principal axis or the regression line from which the other PC's project at right angles, their lengths being proportional to their contribution to variance, an ellipsoid is produced. Since the length of each PC in a hyperspace is equivalent to its eigenvalue, each successive PC axis is shorter than the preceeding one. If the first two PC's account for most of the variation, a two-dimensional plot would suffice, otherwise, a three dimensional model should be considered. The bulge of this ellipsoid indicates the extent of recombination that ocurred in the population after intermating.

A similar analysis was performed on data from Experiment I.

3.7 QUANTITATIVE GENETIC ANALYSIS

Data from Experiment II were used in this analysis to obtain information on gene action and heritability. The data were first submitted to analysis of variance and then the variance due to the mean was partitioned into the contributions by the contrasts below which were tested by the t-test to indicate the significance of gene action, as follows:

a. Test of dominance:

$$F_2 \text{ vs } \frac{1}{2}(P_1 + P_2)$$

b. Test of epistasis:

$$F_3 \text{ vs } \frac{1}{2}(F_2 + MP)$$

where P_1 = navy parent

P_2 = pinto parent

MP = mid-parent

c. Broad sense heritability (H)

$$H = ((VF_2 - \frac{1}{2}(VP_1 + VP_2)) / (VF_2) = V_g/V_p$$

Where VF_2, VP_1 and VP_2 = variance of F_2, P_1 and P_2, respectively, and V_g and V_p = genotypic and phenotypic variance, respectively (Knowles and Briggs, 1967).

CHAPTER FOUR

STABILITY OF BEAN TRAITS

4.1 Introduction

The observed phenotype for a trait is produced from an interaction between the genotype and the environment in which the trait is evaluated. Traits, to varying extents, are environmentally labile and may be expressed to varying degrees in different environments. Cultivar testing programs evaluate materials at a number of locations and for several years within the same location to determine the stability of the cultivar and its performance for desired traits.

An ideotype breeding program is, by definition, organised for a specified environmental and cultural situation. However, for a specified objective such as architecture development, there may be certain fundamental and salient features of the design which would be applicable to a wide variety of situations. These features would have to be stable in different environments to be useful in this suggested manner.

The purpose of this study was to determine if changes in the magnitude of expression of traits in different environments was due to scale (expression of a trait consistently lower or higher at one location) or rank (expression of a trait inconsistent - higher and lower values crisscrossing environments).

4.2 Materials and methods

Data from Experiment II were utilized in this study. Representative parents from the two germplasm pools were compared within each location. These parents were:

N1 = X80149	P1 = Olathe
N2 = Midnight	P2 = UI 114
N3 = C-20	P3 = Ouray

where N and P represent navy/black and pinto, respectively. Only Midnight and UI 114 were tested in East Lansing.

Owing to the large difference between locations, genotype x environment interaction was not considered a useful estimate. The five recurrent cycles were also compared on the basis of average expression of each trait. In addition, the trend of change in the expression of traits were compared for the means of cycles at the two locations.

The Duncan's multiple range was the test statistic employed to discriminate among trait means in this study.

4.3 Results and discussion

4.3.1 Comparison of the locations

The two locations, East Lansing in Michigan and Chimaltenango in Guatemala, differed mainly in latitude and elevation, the former being at a higher latitude while the latter was at a higher altitude (Table 2). East Lansing, located in the temperate midwestern USA, experienced humid and warm conditions during the growing season. The day length in this region was longer than in Guatemala during the period in question. Chimaltenango is located in the tropics. Despite the big difference in elevation of over 1000m, the difference in average temperature during the growing season was only very slight (less than one degree). The average precipitation differed only slightly. For both meteorological variables, higher values were recorded at East Lansing. The means of these variables do not indicate that the two environments were dissimilar. Any difference observed in this study may be due to differences in the diurnal temperatures as well as the conditions at critical stages in the plant growth, including emergence, early growth and flowering. Day length differences would induce maturity differences, the plants in East Lansing being delayed in maturity, and, with prolonged growing season, growing to larger sizes.

4.3.2 Comparison of the parents at two locations

Trends in response of bean plant characters to different environments were similar in nearly all cases. Cultivars in the navy class were generally taller than those from the pinto class at the Chimaltenango location (Appendix A, Table 1). The two classes were of similar height at East Lansing. Plants at the East Lansing location were generally taller than those at Chimaltenango. Cooler temperatures at Chimaltenango may have slowed down plant growth resulting in shorter plants, while plants at East Lansing displayed a more vigorous growth. The shorter day length also contributed to the shortness of plants by causing plants to mature early. Architype rating was higher for the navy group than for the pinto group at both locations (Appendix A, Table 1). Further, the rating was higher at East Lansing for the navy group but lower for pinto as compared to the scores at Chimaltenango. The difference is due largely to height effects. Tallness is one attribute of good architecture and it affects other traits such as lowest pod height and pod distribution in the plant profile which were all considered in the rating of architecture. Shorter plants tended to have pods bunched together and set lower on the plant and, thus, appeared less architecturally desirable.

Plants branched considerably more at the East Lansing location than at Chimaltenango (Appendix A, Table 2). This is attributable to more vigorous plant growth at the former than at the latter location. The navy group, generally, had more branches than the pintos at Chimaltenango. With regard to hypocotyl length (measured as lowest branch height) there was variability in the groups even though, considering the locations together, it appears the pinto group tended to branch nearer to the ground than the navy (Appendix A, Table 2).

Parents from the architectural germplasm source had larger hypocotyls (hypodiam) and set their pods higher above the ground (lowpodht) than the pinto parents (Appendix A, Table 3). The larger value for lowpodht at Chimaltenango than at East Lansing may be due to the fact that with more vigorous growth at the latter location, the plants got more viny and pulled branches farther down so that pods were nearer the ground.

The navy cultivar had a narrower plant profile than the pinto cultivar at East Lansing, whereas P2 had a profile narrower than all the navy varieties in Chimaltenango (Appendix A, Table 4). The pintos, it should be recalled, had fewer branches at that location and this may have contributed to the narrower plant profile than the navy parents. The long vines of the pintos caused them to produce fewer nodes in the upper third of the plant (Append-ix A, Table 4). Shorter internodes and hence more nodes increases the erectness of a plant and may account for why parents from the architectural group had more nodes (Appendix A, Table 5).

The trends in pod distribution were similar at the two locations. The architectural varieties bore more of their pods in the upper two-thirds of the plant while the pintos bore most of their pods in the lower two-thirds of the plant (Appendix A, Tables 6 and 7). It appears the pintos yielded poorly at Chimaltenango. Their pods set poorly as indicated by podslow in Appendix A, Tables 6 and 7. Generally, the navy group set more pods on the main stem (podsmain) as indicated by the results in Appendix A, Table 7.

Internode lengths were generally longer throughout the plant in the pinto group than the navy group (Appendix A, Tables 8 and 9). Some navy parents had long internodes, especially in the upper and middle parts of the plant.

Parents from the pinto group, generally, had wider and longer pods but fewer seeds per pod than the parents from the navy group (Appendix A, Tables 9 and 10). The pintos also had higher seed weight (seedwt) and matured earlier than the navy parents (Appendix A, Tables 10 and 11). The late maturity is attributable to increased number of pods in the upper third of the architectural types.

4.3.3 Changes in magnitude of expression of traits under recurrent selection.

Trends in the behavior of bean plant characters across cycles of recurrent selection were very similar at the two locations. On the basis of the patterns of change, the traits were assigned to four general groups as described bellow. Where the trends were not similar for the two locations, the East Lansing trend, which was based on a much larger sample, was chosen to represent the group.

a. Traits which decreased in magnitude of expression before subsequently increasing.

Traits in this group generally decreased in magnitude of expression from C_0 before eventually increasing in value in the advanced cycles. They included nodesup, totpods, intnodup, intnodmid, intnodlow, yield and height (Figures 4 to 10). These traits may be further reduced to two, namely, yield and height, since the others are components of these. Totpods is a component of yield while internode measurements reflect plant height. Yield decreased in the early cycles before increasing in the later ones because there was a lack of substantial recombination between large seed size and architecture in C_0, with the result that plants selected for good architecture had small seeds. Further, the high-yielding pinto group was characterised by pods predominantly set in the lower third of the plant and since this was one of the traits selected against, the early cycles were poor-yielding. In the advanced cycles, as delibrate efforts were made to increase seedwt and number of pods in the top two-thirds of the plant, yield began to increase.

This trend may also be explained with reference to the thoughts of Mather (1973) alluded to earlier, who hypothesized the existence of functionally-integrated or 'relationally-balanced ' gene blocks. The lack of substantial

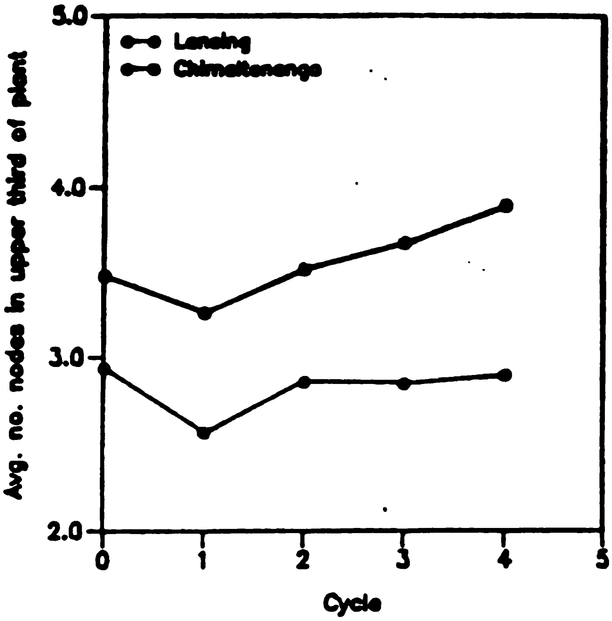

Figure 4. Average number of nodes in the upper third of plants in different cycles and at two locations.

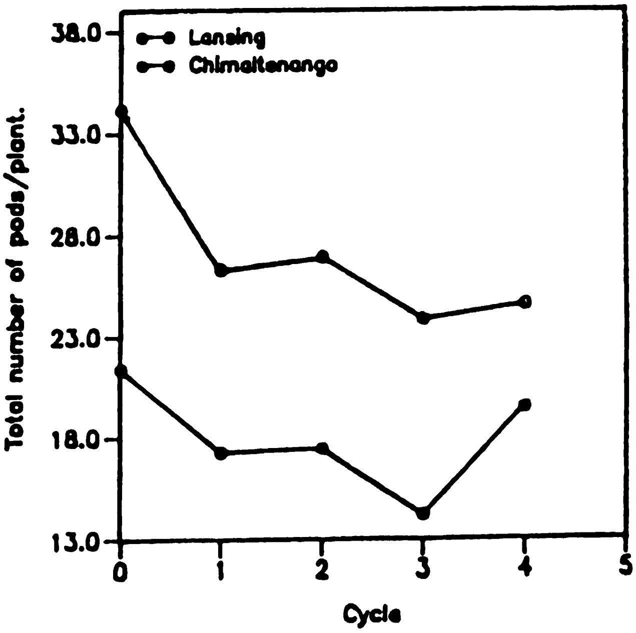

Figure 5. Total number of pods per plant in different cycles and at two locations.

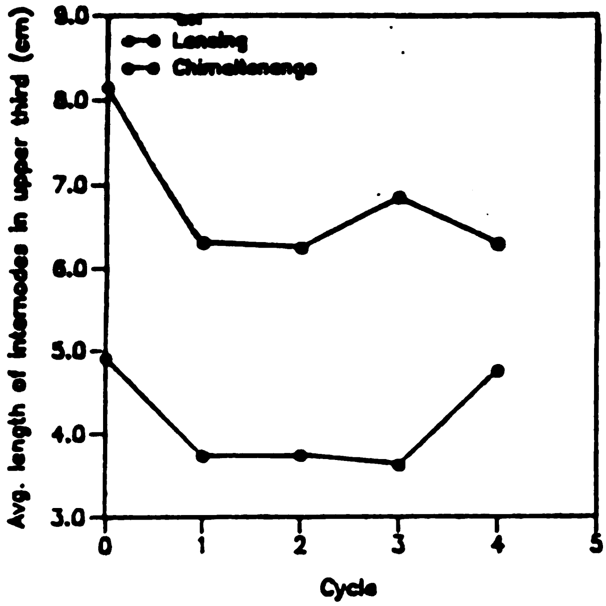

Figure 6. Average length of internodes in the upper third of plants in different cycles and at two locations.

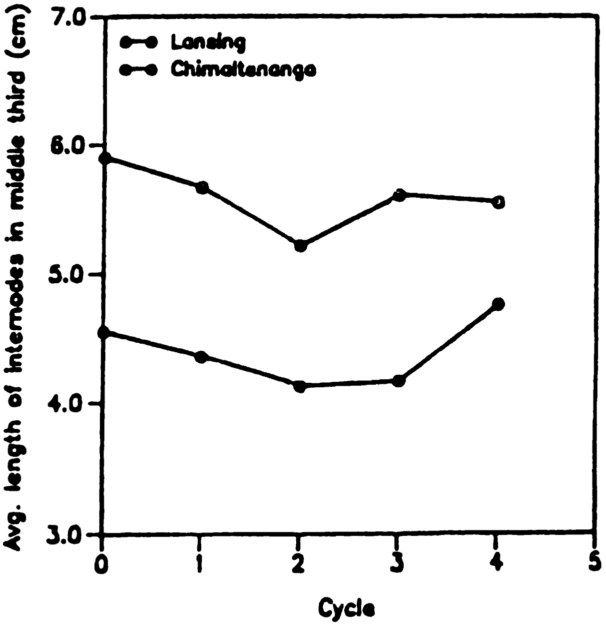

Figure 7. Average length of internodes in the middle third of plants in different cycles and at two locations.

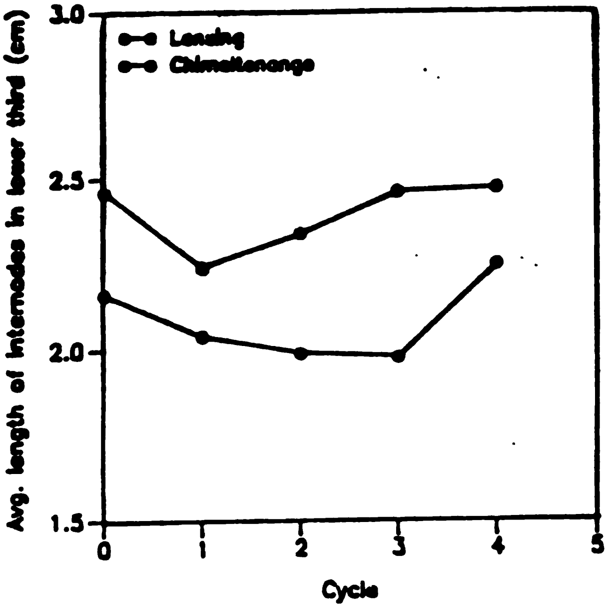

Figure 8. Average length of internodes in the lower third of plants in different cycles and at two locations.

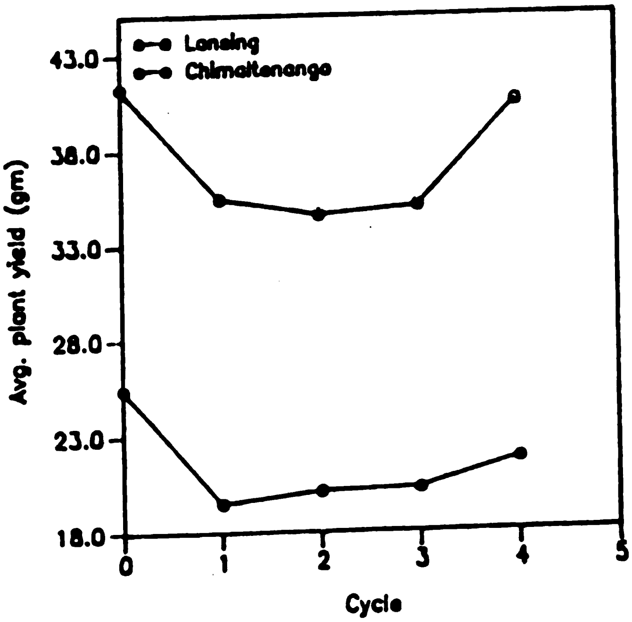

Figure 9. Average yield of plants in different cycles and at two locations.

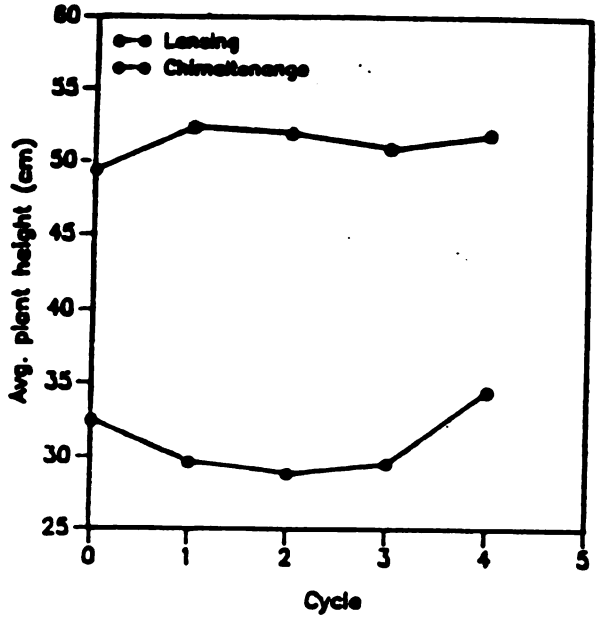

Figure 10. Average plant height in different cycles and at two locations.

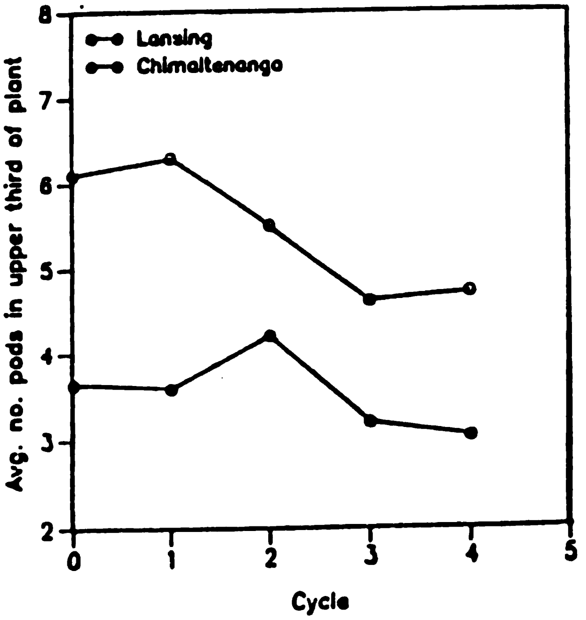

Figure 11. Average number of pods in the upper third of plants in different cycles and at two locations.

recombination in the early cycles may in fact be due to what Kelly and Adams described as " a 'linkage-freeze' upon free and random recombination for effects regulated by genes in the integrated linkage segments". An effect of recurrent selection is to concentrate desirable genes in a population. With time, the adaptive gene complexes were regrouped in some of the advanced cycle selections, restoring them to peak functional status. At that stage, plant yield started to increase.

b. Traits which increased in magnitude of expression from the original cycle before subsequently decreasing.

Traits in this group included podsup, lowpodht, branch angle and nodesmid (Figures 11 to 14). This trend is attributable to the fact that a selection objective was to displace pods in the lower third of the plant to the upper parts while maintaining a narrow plant profile. As seedwt increased and the pods became longer, wider and heavier, the plants assumed the branch angle characteristic of the pinto parents, thereby decreasing lowpodht as well as branch angle.

The number of pods in the upper-third of the plant (podsup) had to decrease in the advanced cycles because

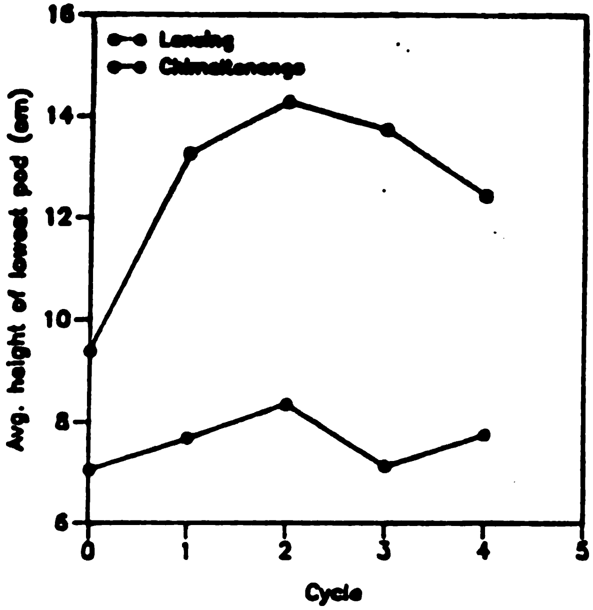

Figure 12. Average height of lowest pod of plants in different cycles and at two locations.

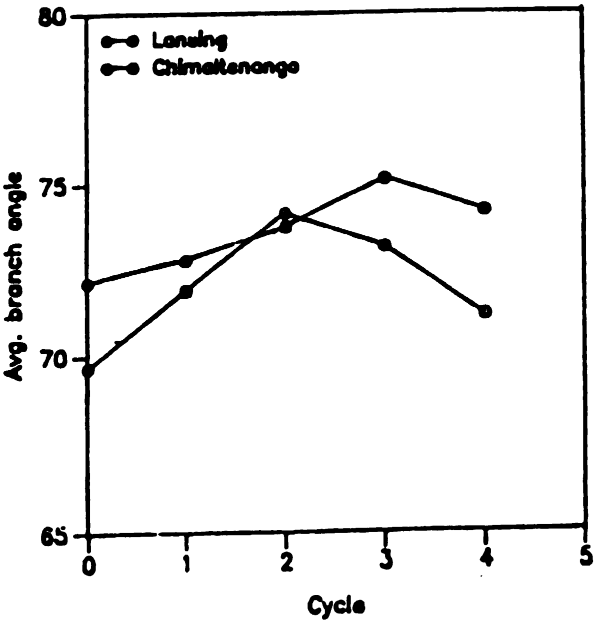

Figure 13. Average branch angle of plants in different cycles and at two locations.

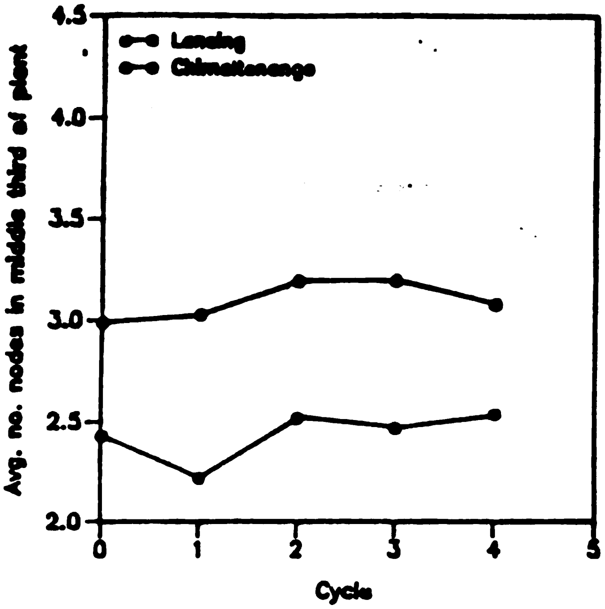

Figure 14. Average number of nodes in the middle third of plants in different cycles and at two locations.

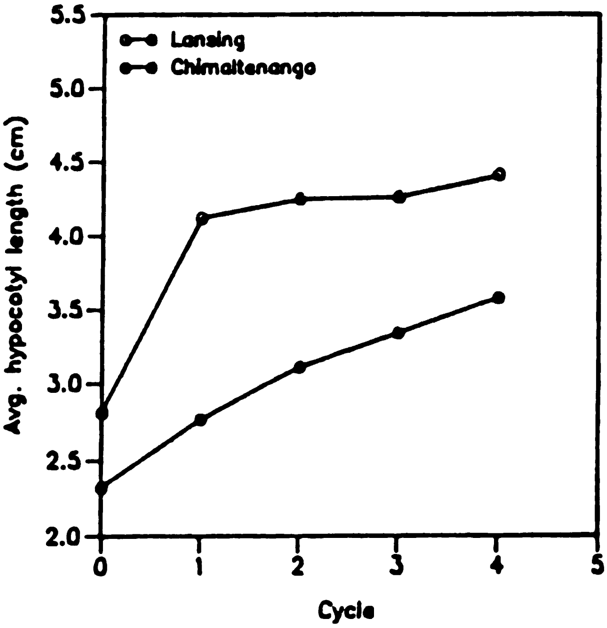

Figure 15. Average hypocotyl length of plants in different cycles and at two locations.

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with more pods in that region, maturity time was delayed. Late maturing plants were not selected or were discarded during evaluation in the field laboratory, after harvesting.

c. Traits which increased in magnitude from the original cycle to the advanced cycles.

These traits, generally, showed a progressive increase in mean value from C_0 to C_4 and included hypolen, podlen, podwidth, seedwt, architype, nodeslow and hypodiam (Figures 15 to 21). Architecture and large seedwt (size) were the principal selection objectives in the breeding program. The multiple regression analysis indicated hypodiam as one of the principal indicators of plant architecture. It was not surprising, therefore, that architype rating, hypodiam and seedwt showed a trend of general increase from C_0 to C_4.

Seed size was estimated as 100-seedwt. In addition to size, the shape that was desired was flatish and not-kidney-like. The drop in C_2 may be a result of discarding large seeds which did not meet other qualities. From C_2 onwards, the curves show a steady increase in seedwt (Figure 18).

Pod length had to increase progressively to accommodate the increase in seedwt. With longer pods, plant branches needed to be set well above the ground so that the

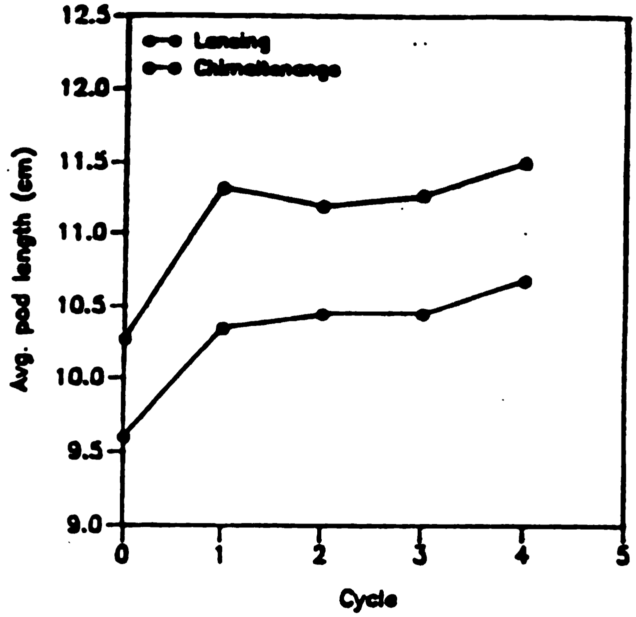

Figure 16. Average pod length of plants in different cycles and at two locations.

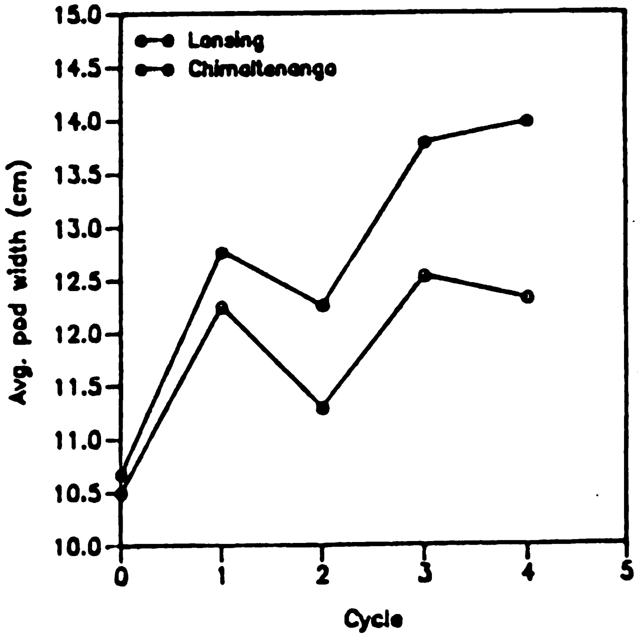

Figure 17. Average pod width of plants in different cycles and at two locations.

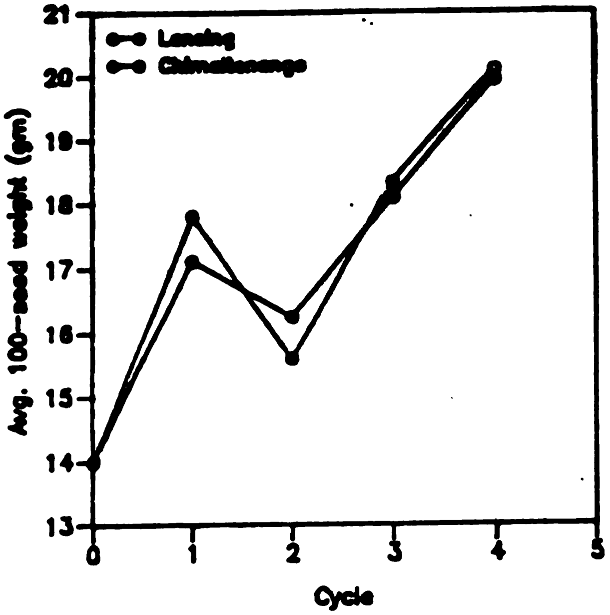

Figure 18. Average 100-seed weight of plants in different cycles and at two locations.

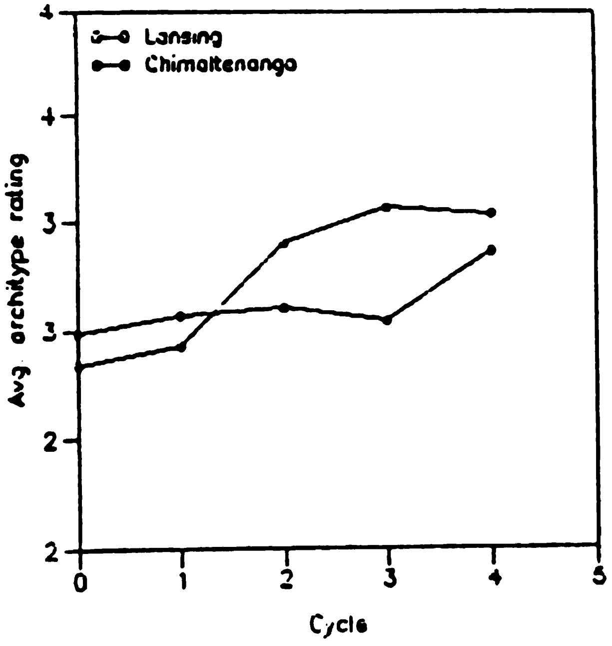

Figure 19. Average architype rating of plants in different cycles at two locations.

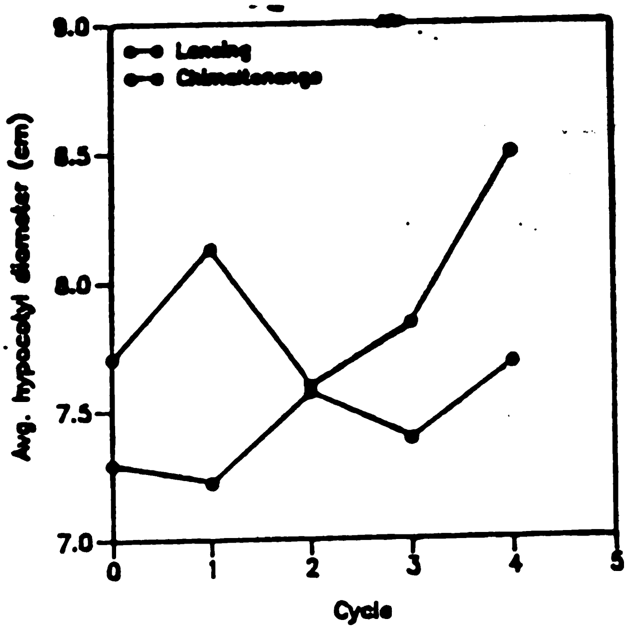

Figure 20. Average hypocotyl diameter of plants in different cycles and at two locations.

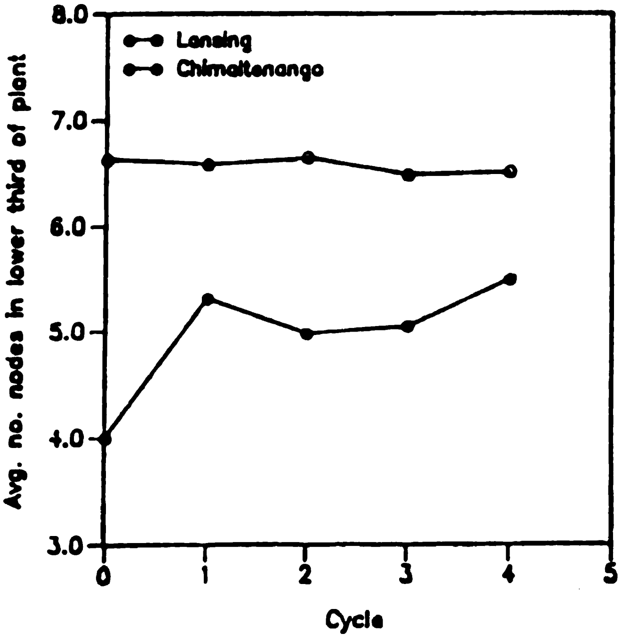

Figure21. Average number of nodes in the lower third of plants in different cycles and at two locations.

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pods set on them would not touch the ground. The hypolen (height of the lowest branch) thus progressively increased in value.

The closeness of curves for architype rating and especially seedwt indicated that these traits were relatively more environmentally stable. Reports of heritability estimates for seedwt have frequently indicated high values but no reports are available for architype rating. The manner in which architecture was recovered in this breeding program seems to suggest that, complex as this trait may appear to be, it may have a simple mode of inheritance. The genes controlling architecture would have to be tightly linked to be inherited en bloc. Selecting for architecture and seed size in a breeding program will be effective, a proposition which is consistent with the outcome of the breeding program being evaluated.

d. Traits which decreased in magnitude from the original cycles to the advanced cycles.

Traits in this group behave oppositely of those in the previous group. These traits, generally, decreased in magnitude of mean value from C_0 to C_4 (Figures 22 to 26). The decrease was not systematic and trends were more erratic than those of the other traits. They comprised predominantly numeric traits and included podsmid, seednum, podslow,

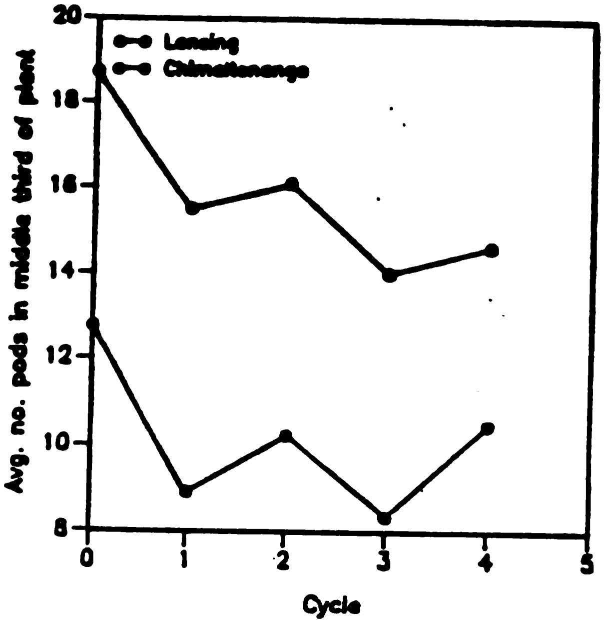

Figure 22. Average number of pods in the middle third of plants in different cycles and at two locations.

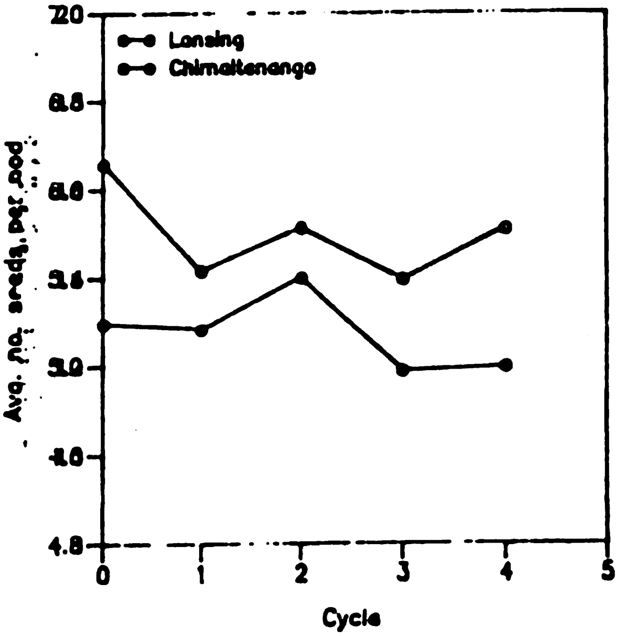

Figure 23. Average number of seeds per pod of plants in different cycles and at two locations.

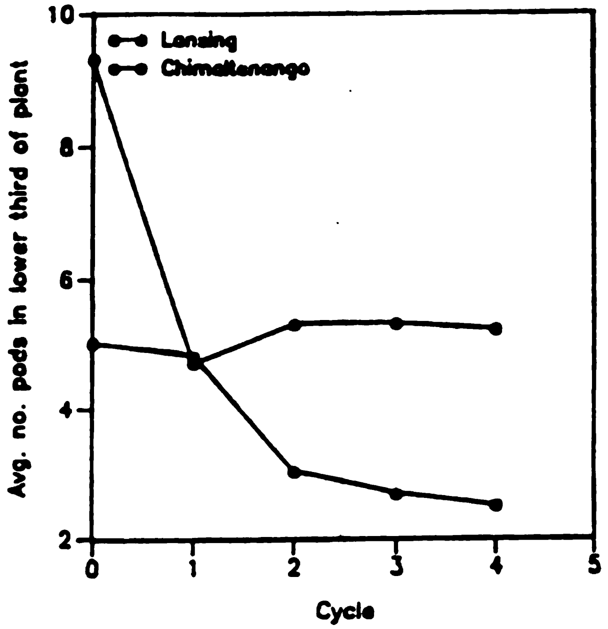

Figure 24. Average number of pods in the lower third of plants in different cycles and at two locations.

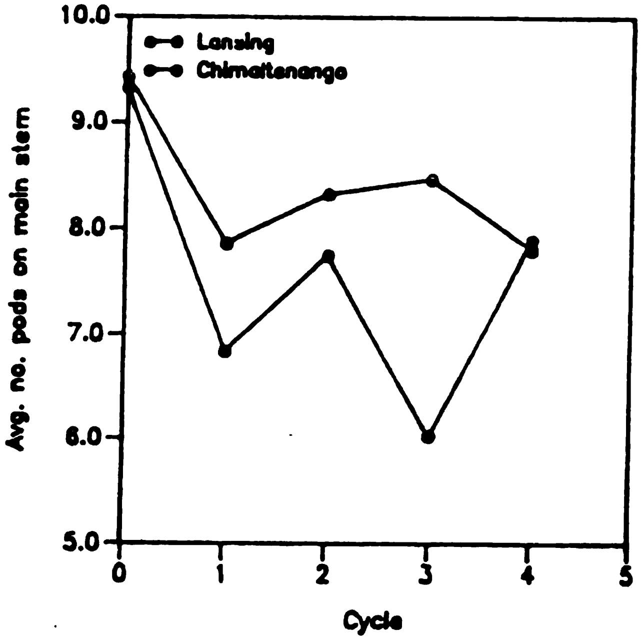

Figure 25. Average number of pods on the main stem of plants in different cycles and at two locations.

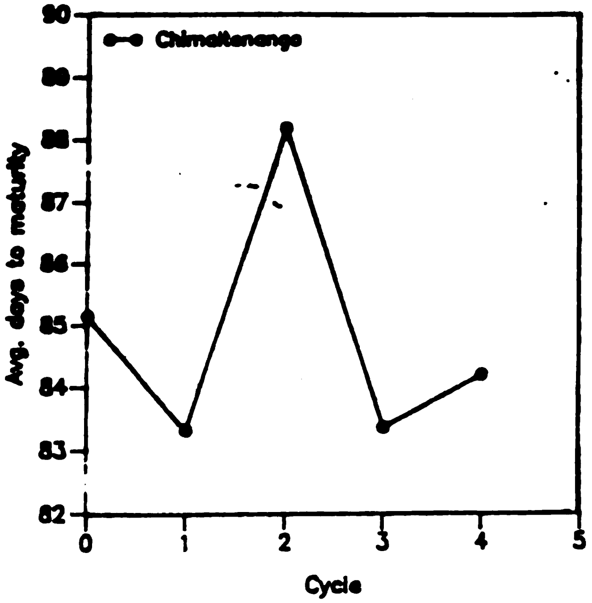

Figure 26. Average number of days to maturity of plants in different cycles.

podsmain and maturity. The number of pods in the lower-third of the plant (podslow) was about the only trait in this group which showed a steady, less erratic decrease. This trait was readily observed in the field and could be selected for on a phenotypic basis without counting. Except for C_3 in Chimaltenango , podsmain also showed a steady pattern. Unlike podslow, podsmain was not directly selected for from C_0 to C_4 since it could be effectively scored only after the branches had been removed from the stem, as was done during data collection in this study. This notwithstanding, podsmain appears to have responded well to selection probably because of close association with one or more of the other traits which were directly selected for in the field by Kelly and Adams (1987). Considering especially the curve for East Lansing, podsmain appears to have stabilized around 8 pods, after the initial drop between C_0 and C_1. A few pods may have been lost when the plant height was reduced due to selecting against vinyness of the central axis and for increased hypolen (higher first branch). It may also have been due to the reorganization of plant parts which moved some pods from the main stem to the branches.

Number of pods in the middle-third (podsmid) was also easy to observe and in fact, was one of the traits directly selected for in the field. Its pattern was very similar to that for the total pods per plant (totpods). Except for a sharp drop from C_0 to C_0, podsmid appeared to fluctuate around a line parallel to the x-axis (Figure 22).

Maturity, which was scored only in Chimaltenango, showed a curve similar to podsup at that location (Figures 11 and 26). This indicated that as pods in the upper-third of the plant increased, plant maturity was delayed. Late-maturing plants were selected against, causing a decrease in maturity time in the next cycle. The fluctuations would have had some effect on the pod distribution in the plant profile, especially those in the upper two-thirds, and might have contributed to the fluctuations observed in trends for these traits.

At this juncture, a general statement may be made to explain, partly, some of the erratic trends observed in this study. As was mentioned earlier, this practical breeding program being evaluated was not meant to supply data for theoretical purposes. Selection pressure was not uniformly exerted from one cycle to another, changing as the breeders assessment of progress in a previous cycle dictated. It is not expected that for even the desirable traits which were directly selected for, that progress would be smooth and gradual since emphasis most realistically shifted from one cycles to another. Traits in which progress was made early may have received less attention in the advanced cycles, with the results that they actually retrogressed or were surpassed by others temporarily, until they were seriously reconsidered later.

4.3.4 Comparison of means for traits from various cycles

The means of especially C_0 and C_4 were of interest. On the basis of comparison between these two cycles, two classes of traits were identified as follows:

a. C_4 mean greater than C_0 mean.

This class included height, architype rating, hypolen, hypodiam, lowpodht, branch angle, nodesup, nodesmid, nodeslow, podlen, podwidth and seedwt. (Appendix A, Tables 12 to 19). The principal architectural traits, namely, height, hypodiam, branch angle and seedwt were included in this class. These traits were also included in those proposed by Adams (1982) as the desired traits for a bean ideotype. This indicates the success of the breeding program. The phenotypic recurrent selection strategy employed was effective in breaking any associations which might have existed in the parental classes of beans and was also effective in reorganising the variability into a new desired genetic combination. Figure 27 compares the representative

Figure 27. Comparison of representative parents from the two germplasm pools utilized in the phenotypic recurrent selection program at MSU and a recombinant selection from cycle three. Midnight (left) represents the atchitecture pool and UI 114 (right) represents the pinto pool. The selection is in the center.

parents from the two germplasm pools used in the breeding program with a selection from an advanced cycle. The selection carries genes for the desired excellent architecture of the navy/black and the seed-pod size of the pinto.

b. C_4 mean smaller than C_0 mean.

This group comprised nbranch, podsmain, seednum, yield intnodup, intnodmid, maturity, totpods, and the pod distribution traits (podsup, podsmid, podslow). The plant selections were spaced-planted in the experiment and this favoured the pinto traits whose frequency and thus genetic contribution was greatest in the C_0. A denser population, similar to that used for planting commercial navy will make up for the descrepancy in performance and cause the type II pinto to improve in yield.

The original type III pinto parents were earlier than the type II navy parents (Appendix A, Table 11). By selecting against late maturity, the semi-determinate type II pintos became relatively earlier-maturing than the semi-determinate type II parents and the selections from the original cycle (Appendix A, Table 23). The new pinto material had a seednum average of 5.77 which was between the average for the parents at the East Lansing location (Appendix A, Tables 10 and 18). The same trend was true for the Chimaltenango location. This indicates that high seed number was sacrificed for increased seed size. There may be a physiological genetic limitation on the number of seeds per pod. It is also possible that while pod length increased, seed size also increased and with a negative developmental dependancy between seedwt and seednum, the two could not be increased simultaneously.

4.3.5 Comparison of trait means at the two locations.

Because of the vast distance between the two locations used in this study, genotype x environment interaction was not considered a useful estimation and hence was not extracted in the analysis of variance. Except in the case of branch angle (Figure 12), podwidth (Figure 17) and hypocotyl diameter (Figure 20), all other trait; means from the East Lansing data were larger in all cycles than those from Chimaltenango. The effect of environment (location) on these traits thus appears to have been predominantly one of scale and not rank. Any traits identified as significant indicators of plant architecture may be effectively selected irrespective of the environment. The need to design a cultivar for specific situations (ideotype) may be inferred from the results since nearly all traits were expressed to different extents at the two locations, the expression being greater at East Lansing where the plants were originally selected, and lower at Chimaltenango. Branch angle means were greater in Chimaltenango because the plants were shorter, smaller and more compact, Even though the pods were wider, the seedwt means were not larger than means from East Lansing (Figure 18).

CHAPTER FIVE

CHANGES IN FREQUENCY AND METRIC VALUE OF TRAITS UNDER RECURRENT SELECTION

5.1 Introduction

Recurrent selection has the effect of breaking linkages and coupled with selection is able to change associations among characters and increase the frequency of desired genes in the population. It is expected that the modal class frequency of traits would shift from one cycle to another if steady selection pressure is exerted on these target traits. Further, the advanced cycles would have narrower ranges of variation under this condition. In the absence of recombination between the two gene pools under consideration, tendencies to bimodality in the frequency curves may occur.

The objective of this analysis was to study the changes in the modal class frequency of traits under recurrent selection. The results may shed some light on the actions of the breeders and the patterns of progress that was made from one cycle to another.

5.2 Materials and methods

Data from Experiment II were used. The frequencies of plant selections in various classes were obtained as percentages of the total number of selections included, for each trait. The frequencies were plotted against the class means using the cubic spline procedure of the Plotit graphics package.

5.3 Results and discussion

The curves showed fairly normal distribution with slight skewing in some cases. Occasionally, some curves in the early cycles tended to show bimodal distribution. The highest peaks for high-valued traits were usually recorded by the advanced cycles. The trends in selected traits are presented below.

5.3.1 Architectural traits

a. Architype rating:

The frequency curves separated into two distinct groups, the early cycles (C_0 and C_1) in one and the rest in the the other (Figure 28). The early cycle group had a

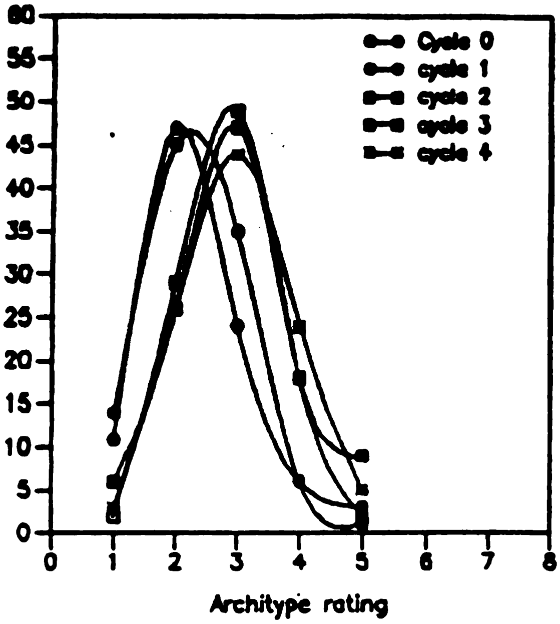

Figure 28. Frequency of architype rating in five recurrent selection cylces.

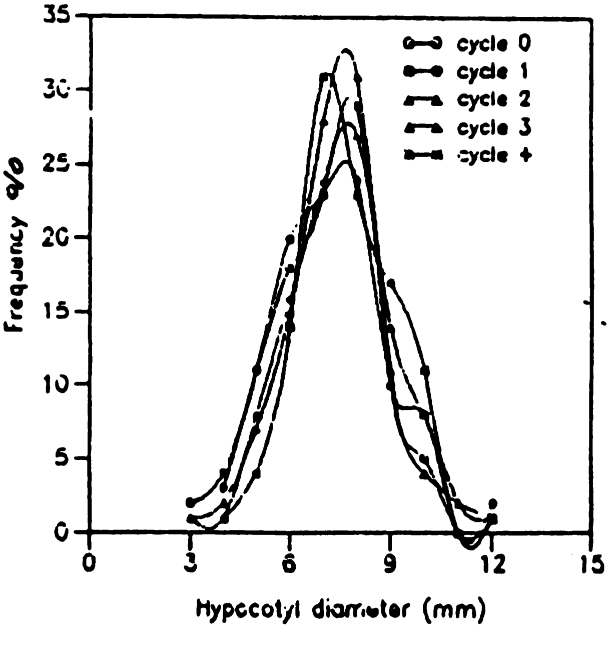

Figure 29. Frequency of branch angle in five recurrent selection cycles

modal class which peaked around a rating of 2 while the advanced cycles peaked around an architype rating of 3. The modal class frequencies for the advanced cycles shifted very slightly, staying around 45%. The ranges for all cycles were the same except that the advanced cycle group had the lowest frequencies (less than 5%) for the lowest rating and the highest frequencies (up to 10%) for the highest architype rating. The converse was true for the early cycle group.

The frequency pattern suggests that architecture did not change gradually from one cylce to another but rather was established in the early cycles. However, it was not until C_3 that architecture stabilized. Some major modifications appear to have been made between C_0 and C_2. Failure by Kelly and Adams (1987) to observe desired recombinants in the early cycles caused them, in fact, to advance some compromise plants to maintain adequate variability for seed and plant architecture. Stronger selection pressure was possible in the later cycles and was probably responsible for the quantum leap from a modal class frequency of about 2 in the C_0 to 3 in the later cycles.

b. Hypodiam

The modal classes for C_0 to C_4 bunched together between 7 and 8mm (Figure 29). It appeared the class frequencies for C_3 and C_4 lagged slightly behind those for C_0 and C_2. The modal class frequencies for C_3 and C_4 were 30% while the rest had lower values. The range was similar for all cycles.

From Figure 20, it is seen that the increase in hypocotyl diameter from C_0 to C_4 was not systematic. This may be due to the effect of varying selection pressure on the trait from one cycle to another. Besides, hypocotyl diameter was not given priority attention in the field selection as were traits such as seedwt, maturity, plant habit, general architecture and height, which were the characters evaluated on S_1 plant selections by Kelly and Adams (1987) for choosing individuals to be used as parents in subsequent cycles.

c. Branch angle:

The frequency pattern was similar for C_0 to C_3 (Figure 30). The modal class for these was around 75^o and the frequency in that class around 40%. The curve for C_0 was distinctly separated from the rest with a modal class peaking around 65^o. It was also evident that the C_4 modal class was lower than those for C_1 to C_3 (Figure 30). The range was widest for C_0 and C_4 and spanned 50^o (38^o to 88^o).

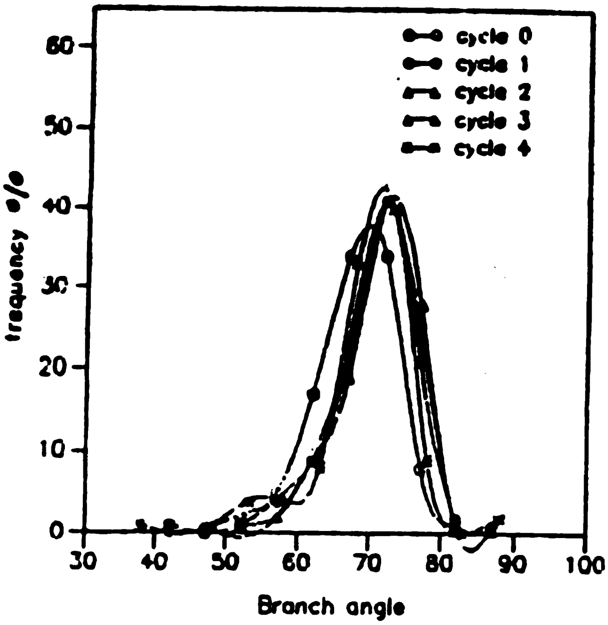

Figure 30. Frequency of branch angle in five cycles of recurrent selection

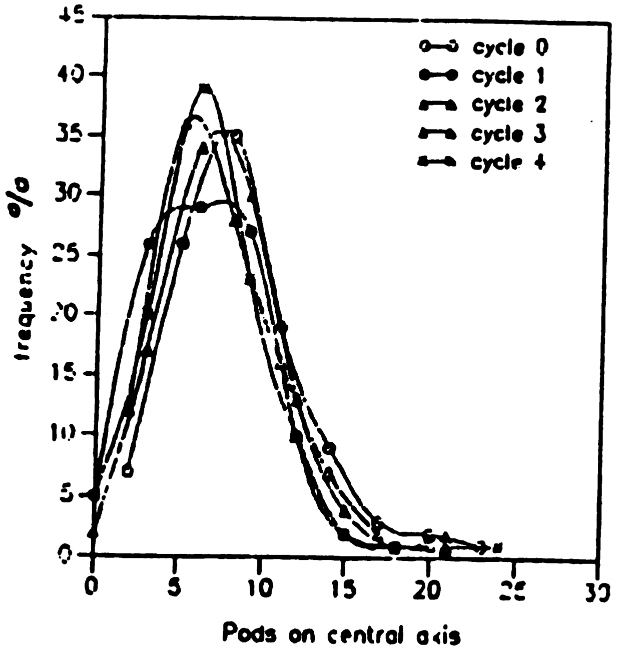

Figure 31. Frequency of pods on central axis of plants in five recurrent selection cycles.

The distinct separation of the C_0 from the rest indicates that, just as occurred in architecture, the desired branch angle was recovered after the first cycle. The subsequent cycles did not undergo major changes until C_4 whose curve lags behind those of C_2 and C_3. This lag may be due to wider branch angles in C_4, probably the result of the fact that at this stage, pinto seeds and pods were associated with a navy architecture. Wider branch angle is a characteristic of the pinto germplasm.

d. Podsmain:

The curves showed a general skewing to the right (Figure 31). The modal classes for the advanced cycles peaked around a lower mean podsmain (six pods) than, and generally lagged behind those for the early cycles, which peaked around eight pods. Except for C_1, the frequencies for the modal classes were between 35% and 40%.

Pods on the main stem generally decreased from the original cycle to the advanced ones (Appendix A, Table 17) and so did the total number of pods (Appendix A, Table 20). The latter event influenced the former. As selection gains are made for larger pods and seeds, it is expected that there will be slightly fewer pods per plant (Adams, 1967).

e. Height:

Cycle 1 showed a bimodal tendency, peaking around 35cm and 50cm (Figure 32). Cycle 0 peaked around 45cm with a modal class frequency of 30% while the other cycles peaked around 50cm, the frequency being highest for C_4 (40%) and the same for the ramaining cycles (about 32%).

Plant height was one of the criteria used for selecting parents with which to initiate subsequent cycles. It appears height was improved in three steps; it was increased from C_0 to C_1 and therafter stabilized (with minor fluctuations) around a mean for the next two cycles. Height was then increased in C_4 with more of the population being taller.

f. Podslow:

The curves for this trait were the most skewed of all (Figure 33). The modal class peak frequencies were lowest for the advanced cycles (20% to 30%) and highest in the earlier cycles (31 to 39). Cycle 0 had the widest range of about 1 to 35 pods while C_4 had the shortest range of between 1 and 16 pods. The other cycles ranged between 1 and 25 pods.

It is clear that pods in the lower-third of the plant were effectively selected against in the breeding program,

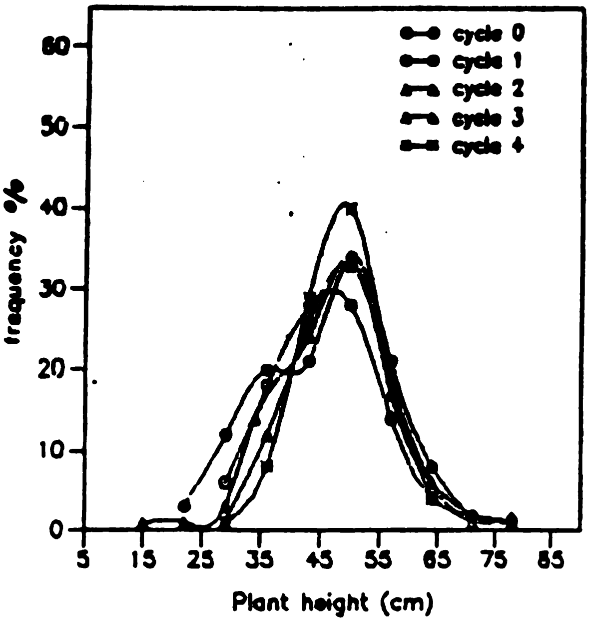

Figure 32, Frequency of plant height in five cycles of recurrent slection

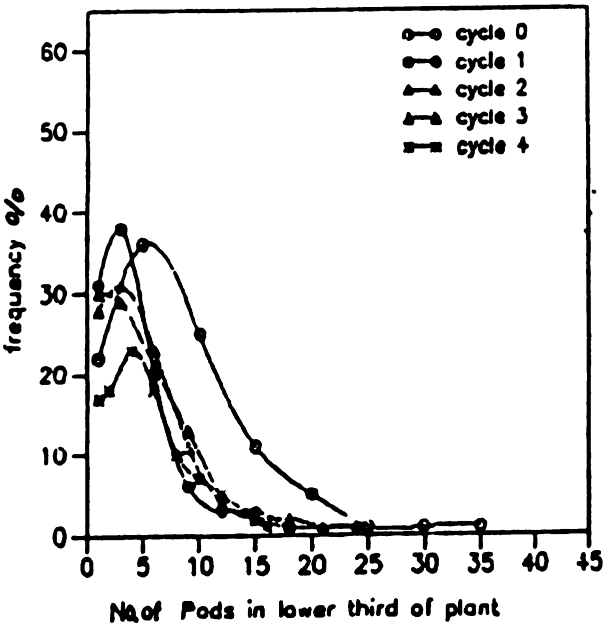

Figure 33, Frequency of pods in the lower third of plants in five recurrent selection cycles.

reducing progressively from C_0 to C_4. This trait was easy to observe and to select against. A breeding objective was to select plants with good pod distribution in the plant profile as against the tendency of pinto varieties to concentrate most of their pods in the lower region.

5.3.2 Seed and pod traits

a. Podwidth:

The curve for C_1 showed a slight bimodality, with C_0 and C_2 peaking around the lower mode at about 11mm, while the advanced cycles peaked around the higher mode at about 13mm (Figure 34). The class ranges were different. Cycle 0 ranged between 8 to 14mm, C_1 from 8 to 16mm, C_2 from 9 to 15mm, C_3 from 9 to 19mm, and C_4 from 10 to 16mm.

Pod width had to increase to accommodate the increase in seed size (seedwt) as the cycles advanced. Cycle 0 had some very large pods but these were not filled with large seeds. This observation may have also been caused by the fact that compromise plants were advanced, as mentioned earlier, to maintain the desired variablity in the program.

b. Podlen:

Pod length in cycle 0 ranged from 1 to 13cm while C_4

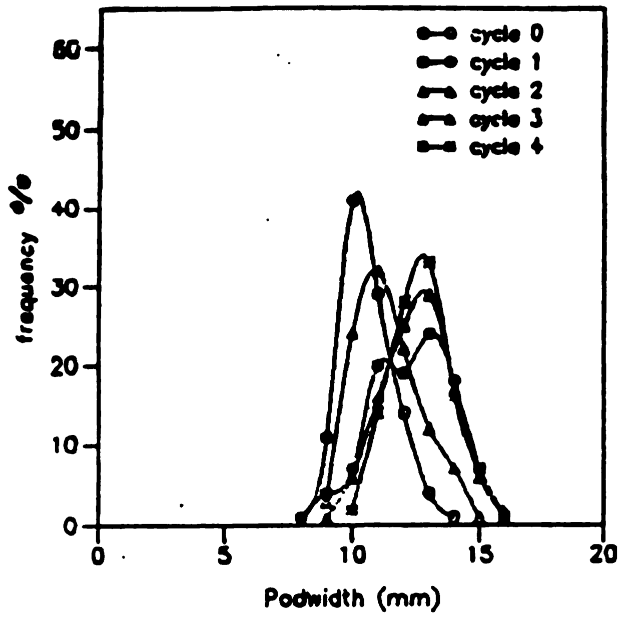

Figure 34. Frequency of pod width in five cycles of recurrent selection

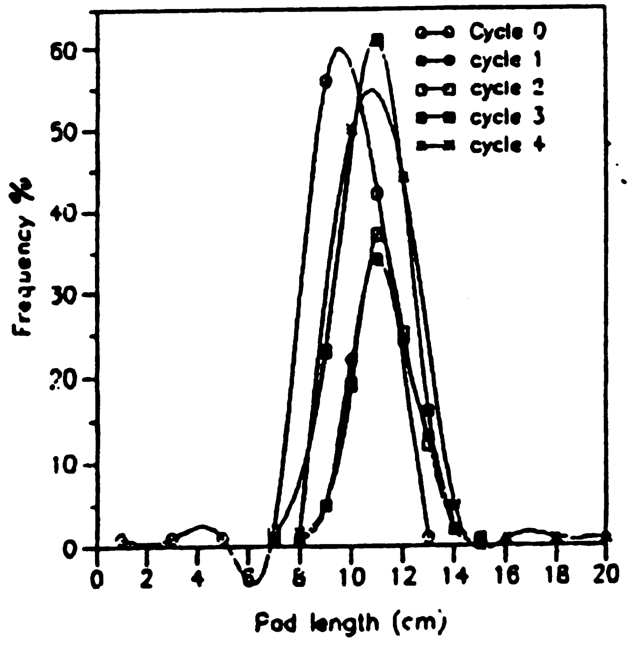

Figure 35. Frequency of pod length in five recurrent selection cycles

ranged from 8 to 20cm (Figure 35). The extremes of the ranges, however, occurred at very low frequencies of about 1%. The modal classes for cycles C_1 to C_4 peaked around 11cm but differed in the frequency, C_1 and C_2 being around 35% while C_3 and C_4 were around 55% and 60%, respectively. The C_0 modal class peaked around 9cm.

This seem to indicate that a pod length of about 11cm was about ideal since the mode of the curve did not shift toward longer pods but instead the population, as the cycles advanced, moved, numerically, toward this 'ideal' length that was achieved already in the C_1. The same is true of pod width (Figure 34).

c. Seednum:

The frequency curves showed very slight shifts in modal classes (Figure 36). The modal class frequencies were higher (about 55%) for the early cycles (except C_1) than for the advanced cycles (about 50). The modal class peak values were similar for C_0 and C_4, being at about six seeds per pod. With the exception of C_1 (in which seednum of above eight was recorded as a very low frequency) all cycles recorded a maximum of 8 seeds per pod, the maximum being at a very low frequency of about 1% or 2%.

Tables 10 and 22 (Appendix A) show that the average

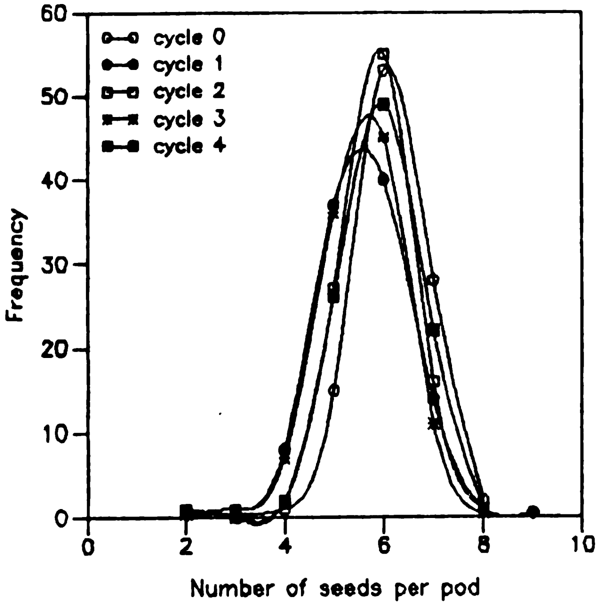

Figure 36. Frequency of number of seeds per pod in five recurrent cycles.

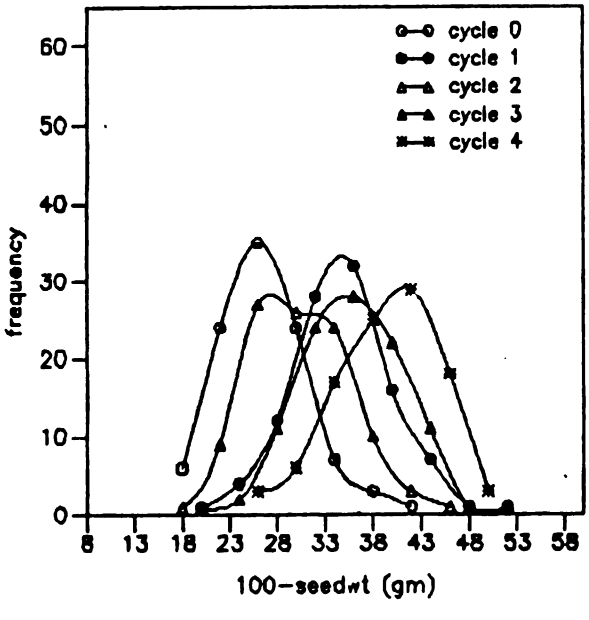

Figure37. Frequency of 100-seedwt in five cycles of recurrent slection

seed number per pod for C_4 was between the parental averages. It suggests that increase in seedwt was attained at the expense of seed number per pod. Since seednum of above eight was rarely found, it appears dry beans may not be able to optimally support more than eight seeds per pod. There may be a physiological genetic limitation on this trait. However, it may only reflect the fact that neither of the initial gene pools carried genes for high seednum.

d. Seedwt:

This trait showed the most separation among the frequency curves from the various cycles (Figure 37). The parental gene pools showed more variation for this trait than for many others such as number of seeds per pod. The curves showed greater ranges. The C_4 modal class peaked around 43gm while C_0 peaked around 25gm. C_0 ranged between 18 and 43gm while C_4 ranged between 25 and 50gm. There was approximately 8gm of change in modal value between successive cycles, the change being slightly greater from C_0 to C_1.

Unlike pod dimensions (length and width) in which there was basically one shift from early to advanced cycles, seedwt showed successive shifts at remarkably fairly even intervals. This suggests that seedwt (seed size) was recovered by a gradual step-by-step process, as observed by Kelly and Adams (1987). The seedwt mean for the parent check (UI 114) was 36.07gm which was attained, for most of the selections, first in the C_3 (Figure 37). Though the curve indicates that this seed weight was attained much earlier, it must be pointed out that the desired combination of large seed size and erect architecture was not achieved before C_3. Further, as mentioned previously, compromise plants were advanced in the early cycles, hence accounting for the presence of large seed in these cycles. Stringent selection pressure may account for the set back in progress in C_2 as shown in Figure 37. Considering the fact that C_2 showed a tendency to bimodality, it would have been expected that the preceding cycles would have shown a similar pattern and perhaps to a greater degree. From Table 1, it appears to be a problem with numbers. Cycle 0 (which was recreated) and C_1 had large initial S_1 populations (more than 1000) to select from as compared to about 500 for C_2. The curves for the first two cycles showed fairly normal distribution, due perhaps to a large size and range of materials to select from for planting the experiments. One would also have expected the C_4 and possibly C_3 to have relatively smaller ranges than the previous cycles. As explained earlier, there were differences in selection pressure applied from one cycle to another. With 1064 S_1

to choose from (Table 1), the C_3 had a wider range than the C_4. The lower value of the range for the C_4, however, is distinctly higher than the rest. It appears stringent selection was not applied in the C_4, the breeders having just observed the desired recombinants in the previous cycle. The selections retained included some small-seeded plants causing this wide range.

CHAPTER SIX

IDENTIFICATION OF INDICATORS OF ERECT PLANT ARCHITECTURE OF BEANS

6.1 Introduction

Breeders frequently depend on target traits as indicators of complex traits in a breeding program. When handling large numbers of plants in a segregating population, the advantage of the ability to select for or against a few traits to achieve the desired breeding objective cannot be over-emphasized. These target traits should not only be easy to evaluate but should also be heritable in order to ensure rapid progress, especially when selecting on a phenotypic basis.

In designing an optimum architecture for beans, Adams (1982) enumerated certain desirable attributes of such a plant structure, which have been presented elsewhere in this dissertation. These traits are not equally important and, besides, cannot all be practically considered in a large breeding program.

The purpose of this study is to identify traits which are effective indicators of erect bean plant architecture and their relative importance to enable recomendations to be made for target traits in a breeding program for such and objective. Selection is practised in a segregating population and thus this study was designed to find out if the same traits would be identified as important indicators of erect plant architecture in different segregating populations.

6.2 Materials and methods

Data from both Experiments (I and II) were used in this study. Using plant architype rating as dependent variable and all other architectural traits as independent variables, the data were submitted to the stepwise multiple regression analysis. Each cross, and cycle, as well as the parents, were analysed separately. The traits included in a model were ranked in each analysis on the basis of the magnitude of the partial F values. The frequency of selection of a trait as significant by a test of the F value was recorded in each of the five cycles and also in each cross. This served as a basis for determining relative importance of traits. Only traits which were significant at the .05 level or higher were included in a model. The R^2 was obtained for each model.

6.3 Results and discussion

6.3.1 Magnitude of R^2

The magnitude of R^2, the proportion of variance in the dependent variable explained by variations in the independent variables, indicates the goodness of fit of the regression model. The greater the value, the better the fit.

The magnitude of the estimates of this statistic was low for the models obtained for various cycles at East Lansing. The estimates ranged from 7.70% to 28.66%. Each model contained different number of significant variables. The values were higher at Chimaltenango, ranging from 46.06% to 69.83% (Appendix B, Tables 1 to 5). The estimate for the parents was 80.25% (Table 3). The six F_3 families produced low to moderate estimates of R^2 ranging from 25.72% to 58.35% (Appendix B, Tables 6 to 8).

The data seem to suggest a difference in R^2 estimates for the parents (pure lines), as compared with the crosses and cycles which were all segregating populations. The low estimates may be due to the fact that architype, the independent variable, was scored as a qualitative trait instead of the quantitative trait that it is. The battery of measurements were unable to explain, adequately, the variance in this subjective estimate. This difference may also have been caused by the inability to distinguish precisely between the wide range of variability in the segregating populations during the scoring process. While parental extremes may have been readily identified and scored appropriately, the numerous intermediates in the cycles and cross populations may frequently have been given the middle score on the scale, leading to a 'blurring' of classification and consequently to lower values of R^2.

6.3.2 Frequency of including a trait in a model

The model selection procedure identified traits which were similar but not identical from one cycle to another, at a location (Appendix B, Tables 1 to 5). Some traits were selected more frequently than others. Podsmain, hypodiam and branch angle were selected most frequently in cycles in East Lansing while height, podsmid, hypodiam, nodeslow and intnodup were the most frequently selected traits in cycles in Chimaltenango (Table 3).

In the parents, three variables were retained on the basis of the significance of the F value. These were hypodiam, podsmain and podslow (Table 4).

In the crosses, hypodiam, branch angle and podsup were the most frequently selected traits (Table 3).

Table 3. Frequency of selection of a trait by the stepwise multiple regression procedures with architype as dependent variable.

Trait	Frequency Cycles (East Lansing)	Cycles (Chimaltenango)	F_3 families
Hypodiam	4	3	5
Angle	3	2	6
Height	3	5	2
Podsmain	5	0	2
Podsmid	2	4	1
Nodeslow	1	3	2
Podsup	1	1	3
Intnodlow	2	2	1
Intnodup	2	3	0
Nbranch	2	1	1
Nodesmid	2	0	2
Intnodmid	1	1	1
Lowpodht	0	1	2
Nodesup	2	0	0
Hypolen	1	0	0

Table 4. Architectural traits selected in the parent population by the stepwise multiple regression procedure with architype as the dependent variable.

Trait	Partial R^2	prob. > F
Hypodiam	41.91	***
Podsmain	22.19	***
Podslow	16.15	***
Model ^{2}	80.25%	

*** : significant at .001 level.

The plants at Chimaltenango were shorter and more erect than those at East Lansing. This might have contributed to height being of importance and selected in all cycles at the former location. The decrease in height caused more pods to be located in the lower parts of the plant. This may also account for the fact that fewer pods were found on the main stem as compared with plants at East Lansing. Based upon the frequency results in Table 3, the selected traits were grouped into two classes as follows:

Class A: traits which were selected more frequently, namely, hypodiam, angle, height, podsmain and podsmid, in this approximate order of importance as indicators of erect plant architecture.

Class B: traits which were selected less frequently, namely, nodeslow, podsup, intnodlow, intnodup, nbranch, nodesmid, intnodmid, podslow and nodesup, in this approximate order of importance.

Reassembling of genes into new combinations notwithstanding, the traits in class A appear to be basic features around which changes and reorganizations took place.

The list produced from the analysis of parents should not be misconstrued to indicate the array of desirable traits. They represent the list that best characterises architecture as it ranges from one extreme (type II) to the other (type III, standard pinto).

It may be concluded from the above evidence that the principal indicators of plant architecture in dry beans are high values of hypocotyl diameter, plant height, and the number of pods on the main stem and in the middle of the plant, and low values of branch angle. A pinto architype, in summary, would be tall, have a large hypocotyl, a narrow plant profile and many pods on the main stem. In addition, it would have fewer number of basal branches, and good pod distribution in the plant profile. The internodes in the top region should preferably be shorter than those in the standard pinto parents to eliminate the tendency to vininess.

These traits are in agreement with those proposed by

Adams (1982). They are also easy to observe and evaluate phenotypically except podsmain which can be readily evaluated only after the branches have been removed.

CHAPTER SEVEN

PHENOTYPIC CHARACTER ASSOCIATION AND THE EFFECTS OF RECURRENT SELECTION ON ASSOCIATION IN BEANS

7.1 Introduction

Phenotypic correlations incorporate contributions from both genetic and environmental sources. The basic nature of genetic correlation is complex and may be due to pleiotropy, linkage disequilibrium and change in gene frequencies upon selection (Rutledge et al, 1973). Two measurable traits are likely to be correlated if they share at least a proportion of the genes that are involved in their expression (Ecochard and Ravelomanatsoc, 1982).

Four forces are capable of altering the initial character association in the parents. These are:

a. selection

b. recombination and reassortment

c. effects of environment (genotype x environment interaction), and

d. sampling error.

It must be borne in mind that in the various cycles, the selections were made in the C_nS_1 genetic state (where n is a cycle) and hence, essentially, should be considered as members of segregating populations.

A segregating population provides new variablity arising from the breakup, partially or fully, of some of the associations which Mather (1973) described as adaptive complexes or functionally-integrated gene blocks, that existed in the parents and that had been maintained over long periods of selfing with selection. The phenotypic expressions in parents would be against a background of interdependence or multicolinearity while in a segregating population, it would be in an environment of relative independence, which will allow greater freedom of expression of relationships. The latter scenario would reduce the incidence of spurious correlations and eliminate weak ones.

The correlations from this study are of much wider application since the populations involved exhibit great diversity, involving different classes of _Phaseolus vulgaris_ L. Recurrent selection has the effect of breaking linkages and promoting recombination and reassortment of genes. Coupled with selection, recurrent selection would change gene frequencies which should show up as changes in the correlation matrix from one cycle to another.

Sometimes, it may be desirable to determine if there are relationships between two sets of data, for example, architectural traits and seed-pod traits in this study, collected on the same subjects, such that components of one group could be an effective predictor of the components of the other. Such predictions are made through abstract unobserved variables called canonical variables. To be able to predict another, it is implicit that the traits have some strong associations which may be extrapolated to suggest sharing of some genes in common, as in a factor analysis.

7.2 Materials and methods

Data from the two experiments were used. Simple linear correlations on a phenotypic basis were calculated for the parents, F_3 families and all the cycles, separately, for the two locations. All the six F_3 families were lumped together for the analysis.

The trends with regard to magnitude, significance and sign of the coefficients were examined for pairs of traits for all cycles.

For canonical correlation analysis, the two sets of data were architectural and seed-pod traits. In addition to obtaining a canonical correlation matrix, a redundancy analysis was performed to determine the amount of variance of each data set explained by its own canonical variables, as well as the variance of a set explained by the canonical variables of the opposite data set.

7.3 Results and discussion

7.3.1 Comparison of correlation at the two locations.

The coefficients of correlation among traits in East Lansing and Chimaltenango were generally low to moderate in magnitude. The highest coefficient (r = .943) in Chimaltenango was produced by the association between seednum and seedwt (Table 6d). Component compensation as described by Adams (1967) has clearly been violated. In East Lansing, the correlation between yield and podsmid produced the highest coefficient of r = .725 (Table 5b). Trends of the sign of association from C_0 to C_4 were generally similar at both locations for pairs of traits. However, certain statistically significant associations showed opposite signs at the two locations. These included the correlations of architype vs height and intnodup vs architype (Table 5a) and, seedwt vs seednum and seedwt vs podsup (Table 5d), which were all negative at East Lansing but positive in some cycles at Chimaltenango (Tables 6a and 6d). Similarly, branch angle vs architype (Table 5a), podwidth vs seedwt (Table 5c) and podlen vs seedwt (Table 5e) were positively correlated in East Lansing but negatively associated in Chimaltenango (Tables 5a, c, and e). These reversals in

Table 5a. Phenotypic character association (r) among bean traits at East Lansing.

	Cycle	Height	Architype	Hypodiam	Angle	Podsmid
Architype	C0	.095*				
	C1	-.118**				
	C2	.031				
	C3	-.088				
	C4	-.248***				
Hypodiam	C0	.177	.092*			
	C1	.253***	.271***			
	C2	.367***	.198***			
	C3	.307***	.241***			
	C4	.181**	.327***			
Angle	C0	-.078	-.064	-.094*		
	C1	-.173***	.139**	-.266***		
	C2	.048	.030	-.053		
	C3	-.073	.146**	-.142**		
	C4	-.123**	.178***	-.183**		
Podsmid	C0	.369***	.143***	.224***	-.210***	
	C1	.465***	.242***	.465***	-.286***	
	C2	.284***	.197***	.474***	-.025	
	C3	.176***	.299***	.398***	-.239***	
	C4	.171***	.177***	.314***	-.111*	
Podsmain	C0	.055	.214***	.008	.001	.208***
	C1	.101*	.254***	.110*	-.005	.219***
	C2	.126**	.156***	.162***	-.019	.224***
	C3	.074	.213***	.146**	-.022	.240***
	C4	.027	.145**	.102*	.101*	.216***
Intnodup	C0	.473***	-.061	.104*	.014	.231***
	C1	.304***	-.140**	.031	-.035	.231***
	C2	.276***	-.194***	.202**	-.045	.101*
	C3	.422***	-.137**	.140**	.016	-.023
	C4	.145*	.014	.044	-.036	-.044
Nodesup	C0	.056	-.064	.099*	-.097*	.096*
	C1	.333***	-.163**	.158**	-.035	.111
	C2	.217***	.005	.262***	.018	.177***
	C3	.153**	.029	.184***	.029	.086
	C4	.156**	-.044	.090	-.100*	.045

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 5b. Phenotypic character association (r) among bean traits at East Lansing.

	Cycle	Height	Architype	Hypodiam	Angle	Podsmid
Seedwt	C0	.100*	-.032	-.016	-.017	-.005
	C1	.063	-.041	-.043	.016	-.045
	C2	.094*	-.021	-.005	.031	-.044
	C3	.095*	-.062	.003	-.029	-.029
	C4	.062	-.001	-.066	-.013	-.058
Podwidth	C0	-.009	.034	.009	-.089	-.111
	C1	.202***	.014	.036	-.141**	.106*
	C2	.113*	-.094*	-.003	-.004	-.134**
	C3	.113*	-.120	.081	-.004	-.103*
	C4	.083	-.039	.023	-.073	-.044
Podlen	C0	.098*	-.032	.105*	-.219***	.084
	C1	.085	-.002	.083	-.005	.072
	C2	.130**	.073	.221***	-.069	.094
	C3	.227***	.013	.237***	-.133**	.141**
	C4	.165**	.064	.214***	-.179**	.280***
Seednum	C0	.091	.044	.023	-.040	.083
	C1	.211***	.147**	.254***	.016	.238***
	C2	.119**	.138**	.296***	-.056	.225***
	C3	.228***	.045	.152**	-.166***	.076
	C4	.141**	.127**	.275***	-.249***	.233***
Yield	C0	.455***	.146**	.244***	-.363***	.581***
	C1	.415***	.214***	.431***	-.380***	.725***
	C2	.327***	.195***	.447***	-.067	.458***
	C3	.340***	.198***	.409***	-.368***	.648***
	C4	.308***	.117*	.403***	-.211**	.593***
Podslow	C0	.403***	-.034	-.272***	-.105*	.287***
	C1	.384***	-.140**	.105*	-.284***	.314***
	C2	.297***	-.014	.217***	-.093	.054
	C3	.344***	-.120**	.134**	-.161**	.081
	C4	.192**	-.097	.091	-.147**	-.003
Podsup	C0	.229***	.109*	.194***	-.183***	.279***
	C1	.086	.241***	.365***	-.079	.222***
	C2	.015	.180***	.283***	-.045	.102*
	C3	-.037	.220***	.333***	-.172***	.252**
	C4	.084	.163**	.259***	-.040	.163**

***, **, * : Significant at .001, .01, and .05 levels, respectively.

Table 5c. Phenotypic character association (r) among bean traits at East Lansing.

	Cycle	Podmain	Intnodup	Nodesup	Seedwt	Podwidth
Intnodup	C0	-.009				
	C1	-.111*				
	C2	.097*				
	C3	-.051				
	C4	-.122*				
Nodesup	C0	.107*	-.039			
	C1	.066	-.069			
	C2	.041	.107*			
	C3	-.046	.044			
	C4	.072	.178**			
Seedwt	C0	-.118**	.083*	-.014		
	C1	.033	.088*	.081		
	C2	-.138**	-.028	-.001		
	C3	-.078	.078	.094		
	C4	-.257***	.229***	.097		
Podwidth	C0	-.138**	-.130**	.075	.100*	
	C1	.104*	-.011	.201***	.331***	
	C2	-.068	.132**	.043	.437***	
	C3	-.020	.091	-.017	.291***	
	C4	.034	.076	.040	.251***	
Podlen	C0	-.138**	.091*	.075	.052	.367***
	C1	.005	.046	.107*	-.009	-.020
	C2	-.120**	-.005	.044	.153**	.197***
	C3	-.003	.019	.003	.104*	.229***
	C4	.028	-.069	.108*	.151*	.075

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 5d. Phenotypic character association (r) among bean traits at East Lansing.

	Cycle	Podsmain	Intnodup	Nodesup	Seedwt	Podwidth
Seednum	C0	-.071	.046	-.059	-.036	-.039
	C1	.115*	.115*	.026	-.264***	-.102*
	C2	-.011	.049	.110*	-.246***	-.113*
	C3	-.152**	.155**	.066	-.047	-.059
	C4	-.223***	-.022	.092	-.063	-.150*
Yield	C0	.173***	.285***	.175***	.128**	-.071
	C1	.257***	-.029	.146**	.095*	.216***
	C2	.196***	.007	.140**	.125**	.026
	C3	.152**	.071	.137**	.248**	.053
	C4	.097	-.089	.111*	.206**	.033
Podslow	C0	.153**	.293***	.088	.056	-.125**
	C1	.133**	-.013	-.069	.002	.138**
	C2	.298***	.183***	.052	.031	.108*
	C3	.129**	.181***	.037	.075	.134**
	C4	.157**	-.082	-.025	.003	.047
Podsup	C0	.182***	.082	-.012	-.074	-.227***
	C1	.213***	-.082	-.069	-.104*	-.034
	C2	.147**	-.140**	.107*	-.094*	-.170***
	C3	.129**	-.113*	.131**	-.173***	-.092
	C4	.169**	-.091	.028	-.159**	-.062

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 5e. Phenotypic character association (r) among traits at East Lansing.

	Cycle	Podlen	Seednum	Yield	Podlow	Podsup
Seednum	C0	.116**				
	C1	.147**				
	C2	.625***				
	C3	.636***				
	C4	.151**				
Yield	C0	.184***	.085			
	C1	.035	.361***			
	C2	.120**	.149**			
	C3	.338***	.358***			
	C4	.458***	.437***			
Podslow	C0	.018	.015	.492***		
	C1	-.016	.081	.415***		
	C2	-.067	-.012	.320***		
	C3	-.041	-.054	.357***		
	C4	.066	-.127*	.306***		
Podsup	C0	-.035	.072	.366***	.053	
	C1	-.026	.122**	.345***	.419***	
	C2	-.077	.083	.141**	-.168***	
	C3	.143**	.049	.280***	-.139**	
	C4	.077	.244***	.334***	-.010	

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 6a. Phenotypic character association (r) among bean traits at Chimaltenango.

	Cycle	Height	Architype	Hypodiam	Angle	Podsmid
Architype	C0	.567***				
	C1	.452***				
	C2	.633***				
	C3	.566***				
	C4	.537***				
Hypodiam	C0	.387***	.330***			
	C1	.200*	.264**			
	C2	.240**	.334***			
	C3	.523***	.647***			
	C4	.301**	.059			
Angle	C0	.174	-.022	.014		
	C1	-.267**	-.186*	.009		
	C2	-.169	-.351***	-.199*		
	C3	-.190*	-.081	-.104		
	C4	-.120	-.178	-.150		
Podsmid	C0	.084	.006	.0288	-.220*	
	C1	.218*	.539***	.353***	-.286**	
	C2	.252**	.516***	.162	-.310**	
	C3	.263**	.397***	.265**	-.085	
	C4	.034	.255**	.199*	-.261*	
Podsmain	C0	.157	.150	-.164	.119	.335***
	C1	.328**	.366***	-.201*	-.288**	.525***
	C2	.266***	.365***	.172	-.264**	.564***
	C3	.251**	.354***	.248**	-.116	.433***
	C4	.397***	.305**	.176	-.069	.405***
Intnodup	C0	.078	-.095	.205*	-.062	.014
	C1	.528***	.273**	.104	-.134	.209*
	C2	.410***	.206*	.119	.122	.130
	C3	.674***	.225*	.233**	-.036	.092
	C4	.629***	.049	.288**	-.044	.015
Nodesup	C0	-.053	.051	.012	-.065	.130
	C1	.352***	.258**	.085	-.120	.290**
	C2	.237**	.206*	.126	.053	.271**
	C3	.486***	.198*	.223*	.063	.067
	C4	.200*	.296**	-.038	-.083	.001

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 6b. Phenotypic character association (r) among bean traits at Chimaltenango.

	Cycle	Height	Architype	Hypodiam	Angle	Podsmid
Seedwt	C0	-.028	-.193*	.165	.152	-.380***
	C1	.106	.072	-.017	.135	-.005
	C2	-.235**	-.125	.159	.103	-.146
	C3	-.074	-.081	-.191	-.036	-.116
	C4	-.234**	-.217*	-.360**	.152	-.360***
Podwidth	C0	.088	.187*	.044	-.175	-.180*
	C1	.090	.007	.122	.010	.060
	C2	.251**	.116	-.047	-.204	.146
	C3	-.027	-.061	.006	.038	-.145
	C4	.241**	-.044	.077	.007	-.088
Podlen	C0	.167	.187**	-.051	-.101	.272**
	C1	-.004	.002	-.077	-.297**	.046
	C2	-.140	.013	.134	-.020	.067
	C3	.090	.218*	.129	.060	.176*
	C4	.161	.202*	.167	-.042	.208*
Seednum	C0	-.014	-.128	.175	.114	-.339***
	C1	.101	.056	-.048	.122	-.001
	C2	-.322**	-.153	.121	.136	-.126
	C3	-.055	.042	.099	.118	.126
	C4	.118	.044	.234**	-.014	-.044
Yield	C0	.128	.170	.069	.093	.048
	C1	.172	.319**	.083	-.015	.208*
	C2	.030	.093	.127	-.198*	.260**
	C3	-.055	.087	.036	-.045	-.055
	C4	.101	.101	-.140	-.153	.088
Podslow	C0	.069	.024	.028	.003	.086
	C1	.437**	.393**	.146	-.170	.369**
	C2	.164	.015	.003	.103	.130
	C3	.561***	.453***	.347***	-.088	.296**
	C4	.629***	.320**	.024	-.115	-.220*
Podsup	C0	-.169	-.089	-.022	-.193*	.160
	C1	-.021	.098	-.173	.097	-.198*
	C2	-.040	-.009	.047	-.184	.104
	C3	-.142	.153	.136	-.009	-.055
	C4	-.116	.123	.054	-.424***	.278*

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 6c. Phenotypic character association (r) among bean traits at Chimaltenango.

	Cycle	Podsmain	Intnodup	Nodesup	Seedwt	Podwidth
Intnodup	C0	.035				
	C1	.346***				
	C2	.234**				
	C3	.235**				
	C4	.162*				
Nodesup	C0	.334***	-.099			
	C1	.274**	.206			
	C2	.357***	.104			
	C3	.248**	.460***			
	C4	.089	-.074			
Seedwt	C0	-.295**	-.054	-.017		
	C1	-.280**	.027	.157		
	C2	-.158	-.086	-.130		
	C3	-.002	.002	.157		
	C4	-.529***	-.119	.036		
Podwidth	C0	-.091	-.142	-.058	-.006	
	C1	.053	.118	-.118	-.359***	
	C2	-.043	.123	.172	-.410***	
	C3	-.309***	-.019	-.056	-.174	
	C4	.107	.322**	-.079	.156	
Podlen	C0	.284**	-.059	-.004	-.741***	.219**
	C1	.286**	-.008	-.113	-.861***	-.075
	C2	-.158	-.075	-.142	.449***	-.075
	C3	.071	.124	-.040	-.147	.229**
	C4	.237*	.117	-.277**	-.039	.433***

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 6d. Phenotypic character association (r) among bean traits at Chimaltenango.

	Cycle	Podsmain	Intnodup	Nodesup	Seedwt	Podwidth
Seednum	C0	-.305**	-.118	-.017	.028	.028
	C1	-.268**	.016	.170	.943***	-.376***
	C2	-.121	-.109	-.221*	.836***	-.528***
	C3	-.045	-.027	-.326***	-.079	.178*
	C4	.219*	.138	-.189	-.244**	.164
Yield	C0	.134	.062	-.200*	.075	-.068
	C1	.064	.037	.267**	.410***	.047
	C2	.052	.121	-.204	-.039	.026
	C3	-.125	-.092	-.134	.110	.057
	C4	.085	.158	.004	.045	.126
Podslow	C0	.073	.369***	-.261**	.018	.011
	C1	.417***	.512***	.302***	.105	.092
	C2	.298**	.528***	.038	-.021	-.062
	C3	.430***	.240**	.269**	.140	-.195*
	C4	.331**	.325**	.049	-.221	.166
Podsup	C0	-.033	-.116	.137	.249**	-.053
	C1	.070	-.080	.165	.254**	-.326**
	C2	.288**	-.172	.260**	.006	-.076
	C3	.212*	-.077	.028	.097	-.045
	C4	.080	-.053	.024	-.213	-.152

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 6e. Phenotypic character association (r) among bean traits at Chimaltenango.

	Cycle	Podlen	Seednum	Yield	Podslow
Seednum	C0	-.647***			
	C1	-.825***			
	C2	.555***			
	C3	-.147			
	C4	.114			
Yield	C0	-.118	.040		
	C1	-.306***	.393***		
	C2	-.119	-.076		
	C3	.071	.110		
	C4	.067	.077		
Podslow	C0	-.067	-.015	.078	
	C1	-.057	.109	.141	
	C2	.114	.056	-.027	
	C3	-.161	-.129	-.063	
	C4	.054	.149	.242*	
Podsup	C0	-.204*	.252**	-.024	-.024
	C1	-.220*	.222**	.113	-.088
	C2	.022	-.072	-.023	-.130
	C3	.231**	.041	.163	-.069
	C4	-.016	.008	.188	-.233*

***, **, * : significant at .001, .01, and .05 levels, respectively.

sign are attributable to genotype x environment interaction.

Stress and differences in environments have been known to change phenotypic correlations (Grafius, 1964; Adams, 1967). Falconer (1952) suggested that a trait measured in two environments should not be considered as one but two traits associated by genetic correlation. Differences in plant density could be a reason for the observations only for the fact that the plants at Chimaltenango were smaller in size and, thus, even though the spacings between plants at the two locations were identical, competition among plants was different at the two locations. It is probable that sampling error played a role since the number of selections at Chimaltenango was half that at East Lansing.

Plants at Chimaltenango were observed to be more erect, shorter and of compact, narrow profile. This may have contributed to the observed association in architype vs height and architype vs intnodup. It is expected that larger seeds would require wider pods while longer pods would be needed for more seeds per pod. The unexpected negative associations between seednum vs podlen and podwidth vs seedwt, and the positive association between seednum vs seedwt at Chimaltenango may be due to the problems of adaptation. Large pods did not necessarily mean large seeds and long pods failed to fill properly. In Figure 17, podwidth in Chimaltenango was larger in all cycles than at East Lansing but in Figure 18, the reverse was true for seedwt.

It is evident from the correlations that negative associations disappeared or became statistically non-significant in the advanced cycles (Tables 6a, c and e). The early cycles had a high proportion of the pinto genes from the pinto group that were actively retained.

7.3.2 Patterns of association at two locations

a. None or only occasional significant associations at both locations.

Traits in this category of associations included intnodup vs angle and podwith vs nodesup (Table 5a) and podwidth vs architype, podwidth vs nodesup and podwidth vs angle (Table 5b). Others were podwidth vs nodesup, podlen vs nodesup, intnodup vs angle and seedwt vs nodesup (Table 5c). Seedwt correlated significantly with very few of the architectural traits. It correlated significantly and negatively with only podsmain at both locations (Table 5c) and with podsmid at Chimaltenango (Table 6c). These two traits have earlier been identified as key traits in plant architecture. At East Lansing, seedwt correlated negatively with podsup (Table 5d) but the association was positive in the early cycles at Chimaltenango (Table 6d).

Low correlation coefficients for pairs of traits indicate that selection for them could be carried out independently without the undesirable effects of negative correlations (Ghaderi *et al*, 1984). Most of the correlations in this group involved seed-pod traits with architectural traits. With the observed *in toto* recovery of architecture in the early cycles, the trait might be controlled by a block of genes which are tightly linked and inherited *en bloc*. Several rounds of intermating were necessary to break this linkage allowing recombination to occur in the region.

Stated in another way, this could be a situation of 'linkage freeze' on free and random recombination for effects regulated by genes in the gene blocks, alluded to by Kelly and Adams (1987), as a consequence of intermating between divergent germplasm pools.

Looking at the parent correlation analysis, it is seen that seedwt and architype rating were highly significantly ($r = -.646$ ***) and negatively correlated (Appendix C, Table 1). This correlation, however, is almost completely dissipated to a paltry yet statistically significant ($r = -.089$*) value in the F_3 (Appendix C, Table 2). This suggests an association which was weakened after only one round of intermating. Seedwt and architype were negatively correlated in all cycles but this association was not significant at East Lansing (Table 5b). At Chimaltenango, the association was significant only in the C_0 and C_4 (Table 6b).

Crossing elite parents, as was the case in this study, would represent a situation in which seed size and extreme architecture genes would be in repulsion phase association. This being the case, recurrent selection would be an effective method for assembling architecture and large seed size in one genotype. The report by Kelly and Adams (1987) underscores the last statement.

b. No association in C_0 but significant association in later cycles.

There were many associations which were non-significant in the C_0 but became very significant in some or all subsequent cycles, at both locations. These included angle vs height, angle vs architype, podsmain vs height, podsmain vs hypodiam and intnodup vs architype (Table 5a). Others were seednum vs height, seednum vs architype, seednum vs hypodiam (Table 5b), and, seednum vs seedwt, seednum vs podwidth, seednum vs nodesup and seednum vs intnodup (Table 5d).

Many such associations were between seednum and architectural traits. The hoped-for effect of recurrent selection is to increase the frequency of desired alleles in a population. Changes in gene frequencies for two or more traits in a multiple trait selection program is, as stated by Rutledge et al, (1973), a source of genetic correlation. Recombination and reassortment can organize genes into new genetic matrices and introduce new kinds of association.

c. Associations remaining strong and/or getting 'stronger' from one cycle to another.

These associations were predominantly positive and occurred among architectural traits. The traits were ones that have been selected from the multiple regression analysis be principal indicators of bean plant architecture. With selection progressively biased towards these traits, their gene frequencies in the population would have increased and contributed to stronger genetic correlations. Some of these associations were architype vs height, hypodiam vs height, podsmid vs architype, hypodiam vs architype and hypodiam vs podsmid (Table 6).

d. Associations getting 'weaker' from one cycle to another.

Two examples may be cited from this analysis. These are nodesup vs height (Table 5a) and intnodup vs podsmid (Table 6 a). Both were non-significant in the parents (Appendix C, Table 1) but were significant in the F_3 families (Appendix C, Table 2). This suggests that these were new associations brought about by intermating with selection. By selecting for shorter internodes and more nodes, the erectness of the plant became more pronounced and well defined, as the vininess of the central axis was curtailed. However, as selection proceeded for taller plants, the internodes in the upper region of the plant got longer and hence fewer nodes and pods were recorded for that region. With longer internodes, fewer nodes were recorded in the mid-section thus weakening the association.

e. Significant associations changing in sign from one cycle to another.

These associations were found at Chimaltenango and occurred among seed-pod traits, involving seednum vs other traits. The sign change took place in or after C_2. From C_3, the sign for the significant associations were the same at the two locations. Seednum vs seedwt was expected to be a negative correlation while seednum vs podlen was expected to be positive since, for the same situation, pods with larger seeds would have fewer seeds per pod while longer pods had more seeds. This was not the case in the early cycles at Chiamltenango (Tables 6d and e). This observation is attributable to genotype x environment interaction.

f. Associations between yield and its components and among components.

Correlations between yield and its components were positive in all cycles but not significant in every cycle at Chimaltenango. Podsmid produced the highest coefficients among the pod distribution traits (Tables 5a and 6a). Seednum and seedwt contributed significantly to yield at Chimaltenango in C_2 only, but at East Lansing, their contributions were significant in all cycles except in C_0. The signs of the correlations among yield components have been summarized in Table 7. Seednum correlated positively with podsup and podsmid but negatively with podslow and seedwt. These could be residual relationships from the parents. Seedwt correlated negatively with podsup and podsmid but positively with podslow, the last two being statistically non-significant. This relationship reflects the structural

Table 7. Sign of correlations among grain yield components in the PRS cycles.

	Seednum	Seedwt	Podsup	Podsmid	Podslow
Seedwt	- (-)				
Podsup	+ (-)	- (-)			
Podsmid	+ (+)	- (-)	+ (+)		
Podslow	- (+)	+ (-)	- (+)	+ (+)	

Sign of associations in parents are in brackets

organisation in the pinto seed and plant type where pods are predominantly set in the lower third of the plant and are large-seeded. Pods in the upper parts of the plant tend to have smaller seeds.

The parental correlations indicated that increasing the number of pods in any region decreased the seedwt (Table 7). Pods in the lower region of the plant had more seeds per pod than those in the upper parts but the correlations in some cycles for seednum vs podsup were positive while seednum vs podslow were negative, suggesting that new correlations were established. By deploying pods to the upper regions, the negative correlation between podsup vs seednum in the parents changed to positive while the positive correlation between podslow vs seednum changed to negative in C_4.

The observation that podsmid produced the highest coefficient among the pod distribution traits and the fact that it was extracted as one of the principal indicators of architecture in the regression analysis suggests that when breeding for high-yielding architypes, plants with more pods in the middle should be a selection criterion.

The problem of adaptation is encountered again. Seednum and seedwt contributed significantly to yield in C_2 at Chimaltenango. With respect to associations among yield components and especially to the East Lansing data since the Chimaltenango data had problems with adaptation, it is seen that, frequently, the associations were negative. This agrees with the observation by Adams (1967) of negative correlations among yield components of the field bean. The correlations were attributed to developmental rather than genetic sources. The primary yield components were postulated by Adams to show an interdependence which enables them to compensate for each other in the face of stress in the environment, such that the optimal geometric configuration of the yield construct is attained. In this study, numbers, sizes and positions of plant parts were reorganized from one cycle to another and attempts were made through intermating to break up associations. It appears these developmental associations are not easily broken up. It is noteworthy that seednum correlated negatively with seedwt, but with two of the pod distribution traits (podsup and podmid), the associations were positive. Seednum correlated negatively with podslow, the third pod distribution trait. Seedwt also correlated negatively with podsup and podsmid but positively with podslow. When a plant has a high podslow value, it resembles a standard pinto and would be likely to carry also the large seed of the pinto, leading to low seednum as in the pinto. Pods in the lower third of the plant have heavier seeds. But as pods are deployed to the upper parts of the plant where seeds are smaller, yield loss is compensated for by an increase in pod and seed numbers.

g. Negative associations among architectural traits

It is noteworthy that significant negative associations were found predominantly in associations involving branch angle and all three pod distribution traits (Table 5a and b). This suggested that there is a limit to the emphasis that should be placed on selection for plant profile. When plants get too narrow, plant yield will be drastically reduced through reduction in pod numbers throughout the plant profile. Narrow branch angle may impose competition for space by the pods in the plant profile. Selection for moderate branch angle (60^{o} to 70^{o}) may be recommended. On the other hand, since yield is more a population than individual phenomenon, yield could be increased by planting plants with narrow profile at higher densities.

Plant height was negatively correlated with architype rating and branch angle. The non-architypes tended to be prostrate. With intermating and recombination, the prostrate nature was reduced so that plants became more erect and tall but with long vines. Selecting against long vines reduced the plant and improved lodging resistance. As vine lengths were reduced the plants became relatively shorter but had narrower profiles due to more acute branch angles.

h. Negative associations between seed-pod traits and architectural traits.

The associations in this group included podwidth vs podsup, seedwt vs podsmain, podwidth vs podsmid, podwidth vs podsmain, seednum vs angle, and podlen vs angle. However, these associations were non-significant in all cycles.

7.3.3 Canonical correlation analysis

None of the canonical correlations observed at Chimaltenango was significant, except for C_3. At East Lansing, three significant correlations were observed in all the cycles, except C_0 in which only two were significant (Appendix D, Table 1). This indicates that there were two to three independent dimensions of the architectural traits set which were significantly related to corresponding dimensions of the seed-pod traits.

Loadings of opposite signs were frequently encountered in the standardized canonical coefficients matrix with some reversal in sign in the canonical structure (correlation between the original variables in a set and their canonical variables).

In the redundancy analysis in this study, the variance of the architectural traits explained by their canonical variables ranged from 9.70% to 25.53%. over the cycles at East Lansing. The variance explained by the opposite set of variables (seed-pod traits) ranged from a mere 2.41% to 5.84%. On the other hand, the variance of the seed-pod traits explained by their own canonical variables ranged from 75.04% to 81.99% over the five cycles. This suggests a stronger within-pool relationship for the seed-pod traits than for the architectural traits. However, the variance of the seed-pod traits explained by the architectural traits was still low, being 8.42% to 18.15%, over the cycles. An example of the analysis is presented in Appendix D, Tables 2a and b. Since the results were non-significant it would serve no useful purpose to present the voluminous data on these variates.

From the squared multiple correlation matrix, it was observed that the canonical variables had very small loadings (Appendix D, Tables 3 and 4).

It was clear from the redundancy analysis that relationships between the two data sets which characterised the two germplasm pools were weak. This will prevent any reliable conclusions from being made from the analysis. The squared multiple correlation matrix indicates further that none of the canonical variables had loadings large enough to be considered to have predictive power for any other variables.

It would not be possible to make reliable predictions between gene pools about architecture on the basis of seed-pod data, and vice versa.

CHAPTER EIGHT

ANALYSIS OF RECOMBINATION AMONG BEAN TRAITS

8.1 Introduction

Kelly and Adams (1987) were unable to find recombinants for large seed size and erect plant architecture in the early cycles of recurrent selection. They attributed this to a linkage probably in the repulsion phase. By analysing the recombination patterns in various cycles, it may be possible to identify the cycle in which recombination for the above-mentioned traits first occurred. This would indicate the stage at which the postulated linkage was broken. The analysis would also be able to identify traits which are involved in recombination in each cycle.

Anderson (1939) proposed a procedure by which the extent of recombination among three selected traits could be demonstrated using raw data. This procedure limits the study of recombination in this fashion to three traits. The use of principal component analysis would allow more traits to be considered, as will be considered in the following presentation.

8.2 Materials and methods

In this study, data from the F_2 and F_3 populations as well as five recurrent cycles were independently submitted to principal component analysis usisng the SAS (1985) PRINCOMP routine. From the factor patterns, traits were followed through consecutive cycles to find out the changes in the magnitude and sign of their loadings from PC1 to later PCs and from one cycle to another, where applicable. Notice was taken of whether or not a trait was loaded with large values in one or several PCs.

The proportions of variance due especially to the first three PCs were compared among the various populations. The contribution by PC2 was converted to a length relative to the length of PC1 which was proportional to the variance it contributed.

The extent of recombination was diagramatically represented as a spindle in a multidimensional space as proposed by Anderson (1939) except that the elipsoid was drawn with straight sides due to difficulty of judging perspective correctly.

8.3 Results and discussion

8.3.1. Recombination F_2 and F_3 populations.

The first PC accounted for only 17.01% of the total variance and it required five and six PCs to account for 55% of the total variance in the F_2 and F_3, respectively (Appendix E, Tables 1 and 2). PC1 showed loadings of opposite sign but the trend, with regard to sign of loading, was similar to PC1 in the parents. Changes in sign were observed in hypolen, angle, podwidth and podlen (Appendix E, Table 1). Seedwt was the only variable with high negative loading. The contribution from internodes and number of branches decreased. The loadings on PC2 and later PCs frequently varied in sign and magnitude from those in the parents. The proportion of contribution by PC1 and PC2 in the F_2 were similar (17.01% and 15.60%) while in the F_3 the ratio was approximately 2:1 in favour of PC1, as was the case in the parents (Table 8). The almost 50% reduction in the contribution to variance by PC1 from the parents to the segregating populations may be explained by the observation that traits such as height, hypodiam and podsmid, whose loadings were among the highest and confined to PC1 in the parental population, resolved into several PCs in the segregating populations. That is, they loaded significantly in more than one, usually successive, PCs (Table 9 and Appendix E, Table 1). This is attributable to recombination from intermating whose effect is breaking up of associations and assorting genes to establish new relationships. This caused the contribution to variability to

Table 8. Contributions to variance by the first three principal components in parents, F_2 and F_3.

	PC1	PC2	PC3	Cumulative
Parents	38.24$^+$	16.97	10.23	65.45
F_2	17.01	15.60	9.55	42.17
F_3	18.20	10.25	8.27	36.42

+, expressed as percentage of total variance

Table 9. Loadings in the first six most important principal components in the parents.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.3367	.0010	.0618	.1569	.0736	.1406
Nbranch	.2068	.2191	-.1270	-.1000	-.0101	.5949
Hypolen	-.1886	.2343	.4038	.0134	.0681	.0167
Hypodiam	.3019	.0426	.0565	-.1975	-.2740	.1168
Angle	.1458	.2502	.4211	.0498	.0969	-.1476
Podsup	.2513	.1951	-.1281	-.3943	.1340	.1077
Podsmid	.3219	.1255	-.0121	-.2128	-.0335	.1370
Podslow	.2208	-.3086	.0332	.0790	-.0356	.1960
Nodesup	.1027	-.3243	-.1233	-.4380	.2265	-.2011
Nodesmid	.0511	-.2783	.3956	.0463	-.3575	.2237
Nodeslow	.2618	-.1725	.0618	.1122	.4219	.2053
Lowpodht	.1161	.4403	-.0791	.1085	-.0844	-.1448
Podsmain	.1544	-.0192	.4425	.2718	.2595	.0659
Powidth	-.2357	.0331	.0178	.0370	-.2783	.3486
Podlen	-.2711	-.0809	-.2085	.0054	.1187	.3136
Seednum	.1237	-.4050	-.0192	.1135	.0830	-.1004
Seedwt	-.2891	.0806	-.1389	.2264	.1795	.3001
Intnodup	.1945	-.0787	-.3366	.5157	.0413	-.0156
Intnodmid	.2279	.2900	-.2245	.2530	.0659	-.1621
Intnodlow	.2077	-.0918	-.1173	.1694	-.5625	-.1301
PROPORTION	38.24^{+}	16.97	10.23	6.49	5.97	4.92
CUMULATIVE	38.24	55.21	65.45	71.95	77.92	82.85

+, expressed as percentage of the total variance be distributed thinly over several more effective sources of variation.

The F_3 required more PCs to account for the same amount of variation because during the selfing of the F_2 the residual heterozygosity from the F_2 provided material for further recombination.

Seed-pod traits were significantly positively loaded in PC2 through PC5 in the F_2 populations. In the F_3 families, their effects were non-significant as indicated by the lack of significant loading in the first six PCs. The tendency to be loaded significantly in more than one PC suggests that genes for these traits were involved in the recombination and reassortment processes. Number of branches and branch angle as well as the internode length in the upper and lower thirds of the plant were traits which, hitherto, contributed significantly to variance by virtue of their being loaded in the PC1 in the parents, but failed to be significantly loaded in the PC1 in the F_2. This may suggest that these traits may have undergone reorganisation through recombination. Further, the reversal of sign for the pod dimension traits indicates that new associations between the two germplasm pools, even though weak, were begining to form. However, this did not include seedwt which maintained its negative sign throughout (Table 9 and Appendix E, Table 1).

9.3.2 Recombination in cycles.

The contributions to variance by various PCs were similar from one cycle to another. The first six PCs accounted for a total of less than 60% of the total variance in each cycle (Tables 10 to 14). Height, hypodiam and podsmid were consistently highly positively loaded in all cycles. Branch angle was also consistently negatively loaded.

The results reinforce previous ones and compels the conclusion that, indeed, height, hypocotyl diameter and pods in the middle part of the plant are the most important predictors of bean plant architecture. Branch angle was positively associated with PC1 in the parents but after intermating in the F_2, it remained negative throughout the cycles. In effect, this change in relationship between architecture and branch angle came about when changes in pod dimensions of the architype were initiated by recombination. It would be recalled from the correlation analysis that significant negative correlations among the architectural traits were found predominantly in those involving branch angle and pod distribution traits (podsup, podsmid, podslow). For the new pinto architype to maintain its large pods, the branch angle would have to be smaller in value than in the parent navy architype. The branch angle for the

Table 10. Loadings in the first six most important principal components in C_0.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.3891	.0920	.2480	-.0253	.3683	-.0035
Nbranch	.3021	.1752	-.1396	.1000	-.4094	-.1273
Hypolen	-.1998	.1850	.2365	.2661	.4268	-.2533
Hypodiam	.1608	.1485	-.0267	.2109	-.1033	.4720
Lowpodht	-.1466	.1064	.2782	.3512	.0313	.3229
Angle	-.1139	-.3621	.1044	-.2523	.0608	.1384
Podsup	.1834	-.0321	-.1073	.5191	.1730	.0110
Podsmid	.3597	.0891	-.1406	.2409	-.0818	.0105
Podslow	.3680	-.0167	-.1093	-.2408	.0252	-.1979
Nodesup	.1067	.1840	-.3098	-.2295	.0452	.3781
Nodesmid	.0285	.3984	-.1482	-.1920	.3791	.0285
Nodeslow	.3483	.0330	-.1050	-.1031	.1696	-.1654
Podsmain	.1050	-.1928	-.3315	.1062	.3126	.1043
Intnodup	.3133	-.1418	.3759	-.0403	.0167	.0346
Intnodmid	.2462	-.3399	.2819	-.0223	-.2177	.0910
Intnodlow	.1872	-.0096	.3823	-.1185	.1829	.3181
Podlen	.0603	.4198	.1960	-.0009	-.2928	.0090
Podwidth	-.1071	.4383	.1634	-.1918	-.1015	.0998
Seednum	.0603	.0617	.1513	.2252	-.1011	-.4245
Seedwt	.0362	.1176	.1913	-.2933	.0450	-.2254
PROPORTION	16.94[+]	9.59	8.31	7.53	6.42	5.44
CUMULATIVE	16.94	26.53	34.85	42.37	48.79	54.24

+, expressed as a percentage of the total variance

Table 11. Loadings on the first six most important principal components in C_1.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.3825	.0930	.2296	.0415	-.0443	.1322
Nbranch	.1306	.3666	-.1243	-.1232	-.1096	-.3842
Hypolen	.0661	-.1017	-.3290	.3146	-.1638	.4128
Hypodiam	.2899	.2658	-.0809	.1357	.1400	-.1882
Lowpodht	-.0007	.1599	.0353	.5360	.3656	.0293
Angle	-.2111	-.1251	.1041	.0571	.3362	-.1346
Podsup	.1028	.3041	-.2838	.2408	.0307	-.2616
Podsmid	.3444	.2369	-.1177	.0577	-.1052	-.0716
Podslow	.2636	-.0392	-.0227	-.3370	-.4387	.0557
Nodesup	.3002	-.3223	.0715	-.0701	.2094	-.0192
Nodesmid	.3712	-.2811	-.0746	-.0095	.1929	-.0894
Nodeslow	.3411	.0159	.1781	-.1930	.1172	-.0906
Podsmain	.1237	-.0165	-.2124	.1920	-.1261	.0978
Intnodup	.0197	.2791	.4876	.0253	-.0823	.1987
Intnodmid	-.1833	.3974	.3293	.0723	-.1797	.1082
Intnodlow	.2473	-.0947	.3722	.1321	.1942	-.0077
Podlen	.0728	.0543	.0935	-.1349	.1758	.3335
Podwidth	.1424	-.2347	.0605	.4176	-.3804	.1160
Seednum	.1541	.2569	-.1391	-.0884	.2042	.4997
Seedwt	.0239	-.1788	.3251	.3117	-.2887	-.2851
PROPORTION	18.38^{+}	11.12	9.62	7.24	6.92	5.75
CUMULATIVE	18.38	29.50	39.13	46.37	53.20	59.04

+, expressed as a percentage of the total variance

Table 12. Loadings in the first six most important principal components in C_2.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.3487	.2559	.1640	-.0011	.1021	.0673
Nbranch	.3152	-.1537	-.1785	-.0135	-.4185	.0229
Hypolen	-.1255	.3553	-.0569	-.0360	.3630	-.0379
Hypodiam	.4393	-.025	-.0408	.0520	-.0734	-.0379
Lowpodht	-.0029	.1710	-.2050	.2119	-.1759	.2908
Angle	-.0356	.1056	-.0440	-.0804	-.00049	.3597
Podsup	.1309	-.2384	-.2480	-.0431	-.1156	-.0625
Podsmid	.3620	-.0688	-.1057	-.0916	-.0496	-.0256
Podslow	.1930	.1105	.3727	-.1517	.0514	-.3024
Nodesup	.2435	.1668	-.1007	-.0706	.0912	.3074
Nodesmid	.2268	.3531	-.2359	-.2506	.1836	.1486
Nodeslow	.3536	.0493	.1239	-.1429	-.1741	.0244
Podsmain	.1428	-.0874	.2292	-.2828	.2488	-.2658
Intnodup	.1854	.0144	.4558	.1250	.0161	.1762
Intnodmid	-.0014	-.2721	.4485	.3073	-.1360	.1405
Intnodlow	.0605	.0136	.1817	.2304	.2082	.5245
Podlen	.1643	.0364	-.2110	.5583	.1926	-.2703
Podwidth	-.0339	.4588	.1551	.2785	-.0791	-.1997
Seednum	.2450	-.2173	-.1900	.3888	.3812	-.1228
Seedwt	-.0309	.4164	.0099	.1978	-.4925	-.1819
PROPORTION	15.79^+	9.92	9.36	8.65	6.19	5.92
CUMULATIVE	15.79	25.71	35.08	43.73	49.94	55.85

+, expressed as a percentage of the total variance

Table 13. Loadings in the first six most important principal components in C_3.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.3698	.2678	.1094	.1570	.0131	-.1924
Nbranch	.2719	-.3546	-.1706	-.1150	-.1983	.0708
Hypolen	-.1708	.1097	.4405	.1047	.0793	-.0044
Hypodiam	.4005	-.0883	-.0258	-.0058	.1147	.1832
Lowpodht	.0757	-.0437	.0925	-.1702	.1180	.1933
Angle	-.1492	.1699	-.2465	-.0704	-.1445	-.0774
Podsup	.1833	-.3294	-.0993	-.1885	.2142	.1935
Podsmid	.3145	-.3030	-.0219	.1406	.0899	.0237
Podslow	.1704	.1440	.0124	.4942	.1418	.0189
Nodesup	.1859	-.0110	-.0795	.0246	-.3729	-.0062
Nodesmid	.1878	-.1004	.2816	.3237	-.2584	.3227
Nodeslow	.3382	.0085	-.1971	.0958	-.3237	.0703
Podsmain	.0802	-.0612	-.0685	.3633	.5788	.0786
Intnodup	.2340	.3967	-.1858	-.0481	-.0048	-.1250
Intnodmid	.1239	.3808	-.3204	-.2633	.1529	.1850
Intnodlow	.1863	.3455	-.0856	-.0743	.1808	-.2381
Podlen	.2400	.0286	.4448	-.3382	.1390	.0617
Podwidth	.0422	.2335	.2347	.0688	-.0717	.5914
Seednum	.2310	.0239	.3446	-.4031	.0257	-.2957
Seedwt	.0384	.1970	.1966	.1096	-.3240	.4237
PROPORTION	15.49$^+$	11.83	8.80	8.33	6.49	6.22
CUMULATIVE	15.49	27.33	36.14	44.46	50.96	57.18

+, expressed as a percentage of total variance

Table 14. Loadings in the first six most important principal components in C_4.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.2545	.0335	.2977	.0735	.3003	-.1868
Nbranch	.2599	-.2063	-.1495	.0259	-.4171	-.1619
Hypolen	-.1825	-.0743	.0641	.3247	.4441	-.2448
Hypodiam	.3753	-.0486	-.0691	-.1134	.0215	.0267
Lowpodht	-.0356	.1054	-.3282	.3822	.1482	.1511
Angle	-.2364	.0840	-.0174	-.1434	.0709	.4722
Podsup	.2147	-.0083	-.2686	-.1876	.2682	.0441
Podsmid	.3675	-.0824	-.0723	-.1576	.0063	.0700
Podslow	.0973	-.2259	.4020	-.2946	-.1093	-.2594
Nodesup	.1529	.0986	.1927	.1291	.3097	.0982
Nodesmid	.0178	-.3559	.3263	.1826	.1122	-.1108
Nodeslow	.3215	.0506	.1495	.0071	-.0993	.1642
Podsmain	.0585	.0833	.0894	-.5204	.3528	.1469
Intnodup	.1101	.4927	.1919	.0356	-.0770	-.1407
Intnodmid	.1258	.4974	-.1603	-.0980	-.1299	-.2044
Intnodlow	.1182	.4415	.1881	.1031	.0862	-.1507
Podlen	.3548	-.1486	.0404	.1872	.0849	.2717
Podwidth	-.0339	.0788	.2893	.0411	-.0129	.4893
Seednum	.3807	-.0504	-.2534	.2880	.0921	.0023
Seedwt	.0307	.1017	.3336	.3159	-.3717	.2566
PROPORTION	13.74$^+$	11.70	9.48	8.86	6.46	6.09
CUMULATIVE	13.74	25.45	34.93	43.80	50.26	56.35

+, expressed as a percentage of the total variance

navy check parent was 23.33^{o} while it was 28.84^{o} in the C_4 (Appendix A, Tables 4 and 15).

Seedwt loaded positively in PC1 in all cycles except C_2, the magnitude of the loading being negligible each time. However, the magnitude of seedwt loadings was quite large and positive in the PC2 in all cycles, and, along with podwidth was the most important variable in PC2 in C_2 (Table 12).

It is noteworthy that while pod traits, namely, podlen and podwidth, on the whole were mostly positive in all the cycles and generally were loaded with increasing magnitude of the coefficients from C_0 to C_4, seedwt only maintained nonsignificant positive loadings on the PC1s. This suggests that when recombining architecture and seedwt, new relationships created in the recombinants were stronger between the pod dimension traits and architectural traits than between archtectural traits and seedwt. Podwidth and seedwt were usually loaded with identical sign in the PCs and the two were positively correlated. This may indicate that the association of seedwt and architecture in the pinto architype may be via podwidth.

Seednum loaded positively and of significant magnitude along with the architectural traits in PC1 in all cycles except C_0. This confirms that this trait is more of an architectural attribute than it is a seed-pod trait. Seednum depends on the number of racemes which in turn depends on the number of nodes, the latter being an architectural trait. With this relationship, it is not surprising that seednum loaded in the PC1 along with architectural traits. The ratio of proportion of contributions to total variance by the first two PCs indicate a relationship of approximately 2:1 in favour of PC1, from C_0 to C_2, as was the case in the F_3. Thereafter, the two contributions were similar. The value would indicate a greater amount of recombination after C_2. As was reported earlier, the pod traits loaded with increasing magnitude for the coefficients on the PC1 as cycles advanced. Kelly and Adams (1987) failed to recover recombinants in the early cycles. The reason could be that recombinants in the early cycles involved mainly architectural traits. Significant recombination between seed-pod traits occurred in the C_3, the cycle in which Kelly and Adams first observed satisfactory recombinants, and beyond.

The fact that the primary architectural traits were significantly loaded in PC1 in all cycles suggests that the basic structure for architecture was recovered in C_0 and maintained as such, with minor modifications, as seed-pod traits were added. The failure to recover satisfactory recombinants in the early cycles should not be misconstrued to mean a lack of recombination at all between seedwt and architecture. Figure 37 indicates that while architecture may have been recovered *in toto* in C_0, seedwt changed gradually. It has been suggested earlier in this discussion that pod dimensions recombined with architecture in the early cycles.

8.3.3 Recombination spindle

In Figures 38 and 39, the shaded portions indicate, proportionally, the fraction of the multi-dimensional space which represents realized recombination. Complete recombination would be a rectangle represented by ACBD. AB represents PC1 and is equal in length to CD. Partial recombination would produce a parallelogram defined by AcBd. PC2 is drawn along CD. It is difficult to present the 'spindle' in three dimensions but by being consistent in presentation, the diagrams would reflect the differences in the data.

By setting a length for AB, the length of cd can be obtained. The proportional lengths of the various genetic populations are presented in Table 15. The F_2 population has the highest value for the length of the PC2 axis while the parents have the smallest. The area AcBd for the F_3 was nearly a rectangle (Figure 38). F_2 is the genetically most variable population in a cross. Maximum recombination takes place in this generation. With one round of selfing (F_3) the length of PC2 dropped to near that of the parents. Populations become progressively homozygous with selfing, reducing

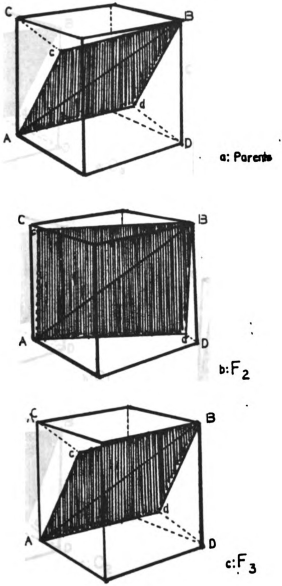

Figure 38. Recombination analysis in F_2 amd F_3 generations of bean crosses, using principal components.

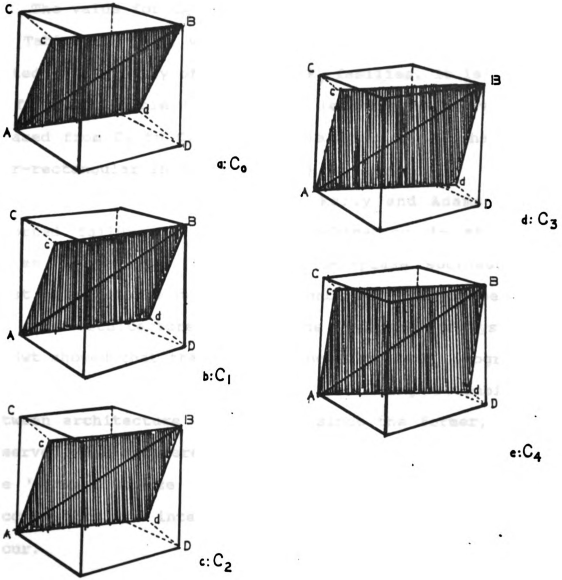

Figure 39. Recombination analysis in five phenotypic recurrent cycles using principal components.

the residual variability available at meiosis for recombination.

The value for C_0 was almost identical to that for the F_3 (Table 15). This was not surprising since the C_0 consisted essentially of groups of F_3 families. It is observed from this table that the PC2 length progressively increased from C_0 to C_4. The parallelogram in C_0 changed to near-rectangular in C_4 (Figure 39)

It would be recalled that Kelly and Adams (1987) reported failure to observe recombination in the early cycles between the two diverse germplasm sources. They first selected the desirable recombinant (large seed size and good architecture) in C_3. The frequency analysis for seedwt showed that there was a generally steady progress in seedwt increase from C_0 to C_4 indicating recombination between architecture and seedwt, since the former, it was observed, was recovered in the C_0. As the cycles advanced, the 'linkage freeze' suggested by Kelly and Adams (1987) succumbed to the intermating and allowed recombination to occur.

Table 15. Length of PC2 axis in various bean populations.

Population	Length of PC2
Parents	3.55
F_2	7.33
F_3	4.55
Cycles	
C_0	4.52
C_1	4.84
C_2	5.03
C_3	6.11
C_4	6.81

CHAPTER NINE

IDENTIFICATION OF FUNDAMENTAL AND FUNCTIONAL RELATIONSHIPS IN BEAN TRAITS

9.1 Introduction

In a breeding program, a breeder may target one or several traits for selecting. To be able to handle a large number of plants in a segregating population, the breeder needs to know a few traits are effective indicators of his objectives. Some traits which are fundamentally related to others in that they influence the same general function and may be under the same kind of genetic control. Using traits which are functionally related as target traits may tantamount to unecessary duplication and waste of time and resources in a breeding program. The breeder may be better of chosing traits from different functional groups to offer him a broader and more effective basis for selecting towards his breeding objectives.

This study was conducted to identify such functional groups among all the bean traits scored.

9.2 Materials and methods

Data from Experiment I were used in this study. The traits measured were separated into two classes, seed-pod traits (four traits) and architectural traits (15 traits), to reflect the two diverse sources of germplasm employed. This allowed three sets of analysis to be made, two for the classes independently and one for the classes combined. This would offer an opportunity to examine both inter- and intra-class relationships.

In factor analysis, the choice of traits to include has a direct bearing on the outcome. In this study, traits which were considered response variables in that they were products of other traits, or derived traits which were calculated from other data, were excluded. For example, yield is a product of seedwt x seednum; height is a function of internode number and their lengths; total number of pods was derived from podsup, podsmid and podslow. By so doing, a chance was given for the analysis to reconstruct these and other concepts without bias and in the process supply information on possible genetic relationships.

Variables whose loadings were positive and of large magnitude in the factors were also highly correlated with each other as indicated by the correlation analysis. Similarly, variables with high negative loadings were found to be negatively correlated with those with high positive loadings in the same factor.

In factor analysis, it is desirable eventually to associate a factor with a concept (biological in this case). The traits which showed high negative loading coefficients were found to be 'anti-concept', that is, they worked to suppress the expression of the identified biological concepts. The first two factors accounted for most of the variance but their contribution was not of large enough magnitude in the cycles such that a plot of these factors would serve any useful purposes.

9.3 Results and discussion

9.3.1 Relationships among the seed-pod traits

The factor patterns at the two locations were similar, as confirmed by the positive correlations among factor loadings in the various cycles at the two locations (Appendix F, Table 1). Two principal factors (PF) were extracted in each cycle. The traits with the highest loadings were essentially the same in each cycle at both locations except in C_0 where seedwt had the highest loading at Chimaltenango while seednum loaded most significantly in East Lansing in PF2. In C_1, the traits switched between factors at the two locations; podlen and seednum loaded in PF2 at East Lansing but in PF1 at Chimaltenango (Tables 17 and 22).

In C_0, podlen and podwidth were associated in one factor from the seed traits. However, starting from C_1, seednum and podlen were associated in one factor while podwidth and seedwt were associated in another.

It should be noted that the association between seednum and seedwt was inverse in the same factor and further, that in C_0, these were the highest-loading in PF2 at both locations. This was not the case in subsequent cycles. C_0 was an unselected population. The negative association in the same factor suggests a relationship in which the two traits may be governed by two sets of genes which are inversely related. The two sets of genes were contributed by different elite parents, seednum being associated with architectural gene pool while seedwt is a pinto trait. The inverse relationship, depicting a developmental compensatory relationship, may exist in the repulsion phase because of the sources of the genes. Table 26 offers an alibi to this suspected repulsion phase linkage in the parents. The two factors extracted were highly loaded by seedwt in the PF1 and seednum in PF2. In PF1, the two traits were inversely related. There, obviously, was no dissociation in this linkage and hence no opportunity for recombination in this region, in C_0. As the cycles advanced, the linkage was

Table 16. Loadings on the first two most important principal factors in C_0 for seed-pod traits in East Lansing.

Trait	PF1	PF2
Podlen	.8246	.1463
Podwidth	.7863	-.2149
Seednum	.1989	.8158
Seedwt	.2477	-.5750
PROPORTION	35.04^{+}	26.54
CUMULATIVE	36.04	61.58

+, expressed as a percentage of the total variance

Table 17. Loadings on the first two most imporant principal factors in C_1 for seed-pod traits in East Lansing.

Trait	PF1	PF2
Seedwt	.8084	-.1259
Podwidth	.7610	.0580
Podlen	.1591	.8555
Seednum	-.3919	.6235
PROPORTION	37.36^{+}	26.41
CUMULATIVE	37.36	63.78

+, expressed as a percentage of the total variance

Table 18. Loadings of the first two most important principal factors in C_2 for seed-pod traits in East Lansing.

Trait	PF1	PF2
Seednum	.9023	-.2561
Podlen	.8987	.2548
Seedwt	-.0753	.8523
Podwidth	.0731	.8297
PROPORTION	40.83$^+$	38.63
CUMULATIVE	40.83	79.46

+, expressed as a percentage of the total variance

Table 19. Loadings of the first two most important principal factors in C_3 for seed-pod traits in Lansing.

Trait	PF1	PF2
Seednum	.9115	-.1424
Podlen	.8946	.2204
Podwidth	.0810	.8118
Seedwt	-.0245	.7845
PROPORTION	41.93$^+$	32.61
CUMULATIVE	41.93	74.55

+, expressed as a percentage of the total variance

Table 20. Loadings of the first two most important principal factors in C_4 for seed-pod traits in East Lansing.

Trait	PF1	PF2
Seednum	.8890	-.1916
Podlen	.8867	.1967
Podwidth	-.0842	.7868
Seedwt	.0874	.7818
PROPORTION	39.79^+	32.64
CUMULATIVE	39.79	72.43

+, expressed as a percentage of total variance

Table 21. Loadings of the first two most important principal factors in C_0 for seed-pod traits in Chimaltenango.

Traits	PF1	PF2
Podlen	.8593	.0030
Podwidth	.7210	.0621
Seedwt	.1637	.9119
Seednum	.5943	-.6125
PROPORTION	42.40	28.83
CUMULATIVE	42.40	71.23

+, expressed as a percentage of the total variance

Table 22. Loadings of the first two most important principal factors in C_1 for seed-pod traits in Chimaltenango.

Trait	PF1	PF2
Podlen	.8010	.1513
Seednum	.6914	-.2256
Podwidth	.1790	.8441
Seedwt	-.2872	.5435
PROPORTION	31.10	26.80
CUMULATIVE	31.10	57.90

+, expressed as a percentage of the total variance

Table 23. Loadings of the first two most important principal factors in C_2 for seed-pod traits in Chimaltenango.

Trait	PF1	PF2
Podlen	.8601	.2458
Seednum	.8455	-.2205
Podwidth	.2884	.7230
Seedwt	-.2401	.7076
PROPORTION	40.11	28.10
CUMULATIVE	40.11	68.21

+, expressed as a percentage of the total variance

Table 24. Loadings on the first two most important principal factors in C_3 for seed-pod traits in Chimaltenango.

Trait	PF1	PF2
Seednum	.8721	.1632
Podlen	.7612	-.3378
Seedwt	.1032	.8896
Podwidth	.3719	-.5130
PROPORTION	41.20	28.75
CUMULATIVE	41.20	69.95

+, expressed as a percentage of the total variance

Table 25. Loadings of the first two most important principal factors in C_4 for seed-pod traits in Chimaltenango.

Traits	PF1	PF2
Podlen	.8309	.0554
Seednum	.6958	.5505
Podwidth	.5680	-.2808
Seedwt	-.3227	.8353
PROPORTION	35.68 +	26.32
CUMULATIVE	35.68	62.00

+, expressed as a percentage of the total variance

Table 26. Loadings of the first two principal factors in the parents for seed-pod traits.

Trait	PF1	PF2
Podlen	.8406	-.0912
Seedwt	.7649	-.4795
Seednum	-.0996	.6316
Podwidth	.4379	-.4729
PROPORTION	90.42+	9.10
CUMULATIVE	90.42	99.52

+, expressed as a percentage of the total variance

broken, the negative coefficient dwindling in magnitude (Tables 16 to 19). In effect, it was not possible to recover large-seeded pods with many seeds (recombinants) in the early cycles until after C_2, which is in consonance with the report by Kelly and Adams (1987) who first encountered desirable recombinants in C_3.

Chronologically, seedwt and seednum were independently extracted in different factors, in the parents, but they came together in C_0 in an antagonistic relationship, and had to separate under the pressure of intermating with selection, starting from C_1. In the last separation, it appears a truce, so to speak, had been achieved to permit limited exchange of genes across the genetic borders of the two sets of seed genes. To accommodate this recombination which was to permit seeds in a pod to be numerous while getting larger, pod dimension traits had to reorganize. In the parents and C_0, they were associated together in PF1, but subsequently, seedwt and podwidth were associated in one factor while seednum and podlen were associated in another (Tables 16 to 20). This new arrangement is logical; large seeds need large pods while many seeds need longer pods for accommodation.

The only notable descrepancy in these trends arose in C_3 in Chimaltenango, where podwidth and seedwt were, unexpectedly, inversely related in PF2 (Table 24). It would be recalled from an earlier discussion and especially from Figure 17, that podwidth at Chimaltenango was one of three traits which were consistently larger in value in all cycles than those at East Lansing. Seedwt, however, did not follow this aberrant pattern (Figure 18). This means the correspondence between seedwt and podwidth at the two locations had to be inverse. Large pods at Chimaltenango did not necessarily carry heavier seeds. This might have been a problem with genotype x environment interaction. It is customary, in factor analysis, to attempt the task of assigning of meaningful concepts which reflect a functional relationship of traits significantly loaded in a factor. Tables 2a to f (Appendix F) summarize the concepts for seed-pod traits in the cycles and parents. It is very clear in the tables that there are a set of genes which control seed number. Looking at Figure 36, it would be difficult to exceed a certain maximum seed number for beans without adverse consequences. In the C_0, we can identify a pod dimension factor (PF1) in addition to seed number in PF2. Generalizing from the other cycles, two concepts may be proposed for bean seed-pod traits:

i. Size factor: Comprising seedwt and podwidth, this factor is concerned with genes which promote seed size, and therefore pod size.

ii. Number factor: This consists of pod length and seed number, and suggests that these traits are under the same genic regulation, and responsible for defining seed number and pod length jointly.

The pod dimension factor identified in C_0 was a transient genetic system in the process of recombining two diverse gene pools, since the C_4 concepts compare with the parental concept.

9.3.2 Relationships among the architectural traits

Linear correlations among loading coefficients at the two locations indicated high significance for the first three factors in all cycles (Appendix F, Tables 3 to 7). Correlations in C_3 especially were low.

Factor loadings of above .50 were underlined for use in obtaining a name for each factor but emphasis was placed on higher loading coefficients in the factor patterns.

Six factors were retained in each cycle in the East Lansing data while five or six were retained in the Chimaltenango analysis. The retained factors together accounted for between 68.93% and 71.35% of the total variance in Chimaltenango, the first two factors accounting for between 34.96% and 46.05% of the total variance (Tables 27 to 31). In East Lansing, the six retained factors accounted for a total of between 62.09% and 68.84% of the total variation while the first two factors accounted for 30.18% to 34.92%

Table 27. Loadings of the first six most important principal factors in C_0 in Chimaltenango for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Intnodmid	.8805	-.0851	.0332	-.0973	.1008	.2092
Intnodlow	.8578	.1978	.0194	.1608	.0394	-.1103
Intnodup	.7311	-.2006	.1810	-.2255	-.1130	-.0415
Nodeslow	.5564	-.5125	.0429	.2265	-.2787	.3507
Nodesup	.0573	.7713	-.2465	-.0126	-.1572	.0219
Nodesmid	.0502	.6145	.1892	.3199	-.0856	.1452
Podslow	.4027	-.6489	.0981	.0743	-.1085	.2170
Hypodiam	.2541	-.0168	.8351	.0027	.0569	-.0913
Nbranch	-.0093	-.1170	.7738	.0269	-.0430	.0119
Podsmid	.0488	.0222	.0164	.8332	-.0406	.1184
Podsup	-.1246	.0497	-.0076	.7324	.1008	-.2369
Hypolen	.0729	-.1062	-.1780	.0870	.8788	-.0766
Lowpodht	-.1094	-.0065	.4644	-.0503	.6843	.1044
Angle	.0126	-.2020	.0327	-.1751	.1211	.7599
Podsmain	.0893	.3914	-.1489	.1390	-.2035	.6856
PROPORTION	21.18^{+}	13.78	11.15	8.87	8.47	7.86
CUMULATIVE	21.18	34.96	46.11	54.97	63.45	71.31

+, expressed as a percentage of the total variance

Table 28. Loadings of the first five most important principal factors in C_1 in Chimaltenango for architectural traits.

	PF1	PF2	PF3	PF4	PF5
Intnodup	.8693	.0956	-.0082	-.1524	-.1070
Intnodmid	.8449	.1083	.0077	.2814	.1991
Intnodlow	.8289	.0110	.2038	-.0908	.1237
Podslow	.6507	.4694	.0939	-.2533	-.0938
Nodeslow	.5858	.4646	.1250	-.2527	.0733
Podsmid	.2006	.6567	.4952	-.0215	.1620
Podsmain	.3531	.6441	.2119	.2226	-.1465
Nodesup	.3898	.4746	.2367	.3251	-.0639
Angle	.0599	-.7872	.1290	.1356	-.1450
Hypodiam	-.0697	-.0594	.8758	-.1102	-.0499
Nbranch	.1802	.1774	.7557	-.0418	-.0876
Nodesmid	.3664	.2878	.4672	-.3297	-.1778
Podsup	-.1725	-.0280	-.2207	.8863	-.0054
Lowpodht	.1671	.0859	-.0201	.3088	.7943
Hypolen	-.0401	.0209	-.1177	-.2417	.7759
PROPORTION	32.98^+	13.08	9.47	8.67	7.15
CUMULATIVE	32.98	46.06	55.53	64.20	71.35

+, expressed as a percentage of the total variance

Table 29. Loadings of the first five most important principal factors in C_2 in Chimaltenango for architectural traits.

	PF1	PF2	PF3	PF4	PF5
Intnodmid	.7426	-.1828	.2759	-.1176	-.2452
Intnodlow	.6913	.3165	-.0377	-.3752	.0549
Podslow	.6879	.0772	.0170	.2719	.3396
Intnodup	.6854	.0093	-.1523	.2063	.1157
Nodeslow	.6581	-.3365	.3250	.1356	-.0909
Podsmain	.4779	.1362	.4679	.3857	-.3448
Hypolen	.0553	.8430	-.0062	-.0891	-.0764
Nodesmid	-.0450	.8309	-.0216	.2546	-.0004
Hypodiam	.0884	.0332	.6389	.1375	.4039
Podsmid	.3953	.0053	.5778	.3095	-.1326
Angle	.0977	.0311	-.7956	.2079	.0393
Nodesup	.1291	.2127	.0797	.7847	.0632
Lowpodht	-.0828	.4956	.1369	-.6179	-.1446
Nbranch	-.0213	-.0512	.0852	.1140	.8792
Podsup	-.2938	.3672	.3033	.3837	-.5046
PROPORTION	22.87[+]	15.22	11.43	10.95	8.46
CUMULATIVE	22.87	38.09	49.51	60.47	68.93

+, expressed as a percentage of the total variance

Table 30. Loading of the first five most important principal factors in C_3 in Chimaltenanago for architectural traits.

	PF1	PF2	PF3	PF4	PF5
Intnodup	.8408	-.0611	.0971	.0775	.0590
Intnodlow	.8360	.1386	-.1936	.0123	-.1596
Intnodmid	.8237	.1340	-.2363	-.1778	.1387
Nodesup	.6898	.1203	.2460	.0098	.1092
Nodeslow	.6081	.4852	.1535	.0396	.1408
Podsmid	.0006	.7370	.0623	-.0882	.0504
Podsmain	.3263	.7023	-.0049	-.3652	-.1326
Podslow	.3754	.6753	-.1510	.2611	-.1015
Nodesmid	-.2321	.4105	.1166	.0862	.3976
Angle	-.1070	-.1732	.8671	.0954	.0086
Nbranch	.1409	.2435	.8010	-.0268	.0963
Hypolen	-.0985	.0740	.1379	.7784	.2801
Podsup	-.1235	.1774	.0583	-.7382	.3122
Lowpodht	.1649	-.1439	.0574	.0342	.8442
Hypodiam	.4434	.4123	-.0254	-.2501	.5127
PROPORTION	28.58$^+$	12.72	11.43	8.71	7.50
CUMULATIVE	28.58	41.30	52.73	61.44	68.94

+, expressed as a percentage of the total variance

Table 31. Loadings of the first five principal factors in C_4 in Chimaltenango for architectural traits.

	PF1	PF2	PF3	PF4	PF5
Podslow	.8366	.1200	.2902	.0382	-.2566
Nodeslow	.8283	.2057	-.2318	.1288	.0543
Nodesup	.6188	-.1178	-.1272	-.1473	.2525
Intnodmid	.0730	.9081	-.0648	-.1137	.0602
Intnodup	.1953	.8977	.1826	-.0330	.0567
Hypolen	.3306	-.5280	.2487	-.1880	.0387
Angle	-.2944	-.0891	.7244	-.1123	-.1772
Intnodlow	.2467	.3424	.6992	.0954	.3041
Podsup	-.0430	.1296	-.6832	.1975	.4436
Lowpodht	-.0798	-.0116	.1197	.8099	.2026
Nbranch	.0773	-.2442	-.3162	.7337	.1208
Hypodiam	.1043	.3536	-.1734	.5880	-.0203
Podsmid	-.0251	.0069	-.1592	.3200	.8488
Podsmain	.5359	.1905	.0592	.0021	.6148
Nodesmid	-.0372	-.1685	.1331	-.0804	.0298
PROPORTION	21.31^+	17.31	13.09	10.31	8.60
CUMULATIVE	21.31	38.61	51.70	62.01	70.60

+, expressed as a percentage of the total variance

of the variance, over the five cycles (Tables 32 to 36).

In Chimaltenango, internode length measurements were consistently the highest loading variables in PF1 in all cycles except C_4 in which they dominated PF2. In East Lansing, intnodup, intnodmid and intnodlow were frequently loaded together in one factor. They became progressively more important as the cycles advanced, moving from PF3 in C_0 to PF1 in C_4 (Tables 32 to 36). In East Lansing, PF1 was frequently loaded by node and pod distribution variables along with traits such as hypocotyl diameter and number of branches. Factors were found sometimes to resolve into others in the sense that traits could be highly loaded in more than one factor, or related measurements such as podsup, podsmid and podslow could be loaded in different factors.

PF2 and PF3 were significantly loaded by more than one trait at both locations. In other words, these factors were frequently competitively loaded by more than one trait. In East Lansing, PF4 to PF6 were frequently independently loaded by variables such as podsmain and branch angle. The relative importance of traits and the composition of factors on the basis of the magnitude of loading coefficients was variable from one cycle to another at both locations, especially, between PF2 and PF4.

Table 32. Loadings of the first six most important principal factors in C_0 in East Lansing for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Podsmid	.6773	.2451	.1380	-.0785	.2036	.1331
Nbranch	.6772	.3253	-.0106	-.0846	.2135	-.3741
Podsup	.5770	-.1683	.0414	-.1317	.0360	.4620
Angle	-.6106	.0173	.0548	-.3029	.1420	.0322
Podslow	.2478	.6996	.3125	.0766	.0248	-.0258
Nodeslow	.3001	.5814	.1963	.0675	-.0148	.1634
Lowpodht	.1167	.6653	.1490	.0274	-.0906	-.1049
Intnodlow	-.0706	-.0812	.7930	.1493	.1446	-.0427
Intnodup	.1538	.2004	.7215	-.2421	-.0778	-.0083
Nodesmid	.0636	.1004	.0512	.8195	.0314	-.0857
Intnodmid	.0300	.2067	.5058	-.6034	.0515	.0335
Hypodiam	.3429	-.2661	.1443	.0209	.6325	.0652
Nodesup	-.0658	.2333	-.0191	.4024	.5532	.2091
Hypolen	.0379	-.4427	-.0041	.2713	-.6358	.1913
Podsmain	.0161	.2304	-.0547	-.0539	.0505	.8305
PROPORTION	19.50+	11.41	9.69	8.36	7.13	6.88
CUMULATIVE	19.50	30.91	40.60	48.96	56.09	62.09

+, expressed as a percentage of the total variance

Table 33. Loadings of the first six most important principal factors in C_1 in East Lansing for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Nodesmid	.7482	.1258	-.1023	-.0518	.1606	.0028
Nodesup	.7428	-.0569	-.2769	-.0983	-.0371	.0273
Intnodlow	.7261	-.0474	.3202	.1450	.0251	.0386
Nodeslow	.6305	.2958	.0941	-.2295	-.1001	-.0257
Nbranch	-.1517	.7599	-.0122	-.1389	-.0549	-.2735
Hypodiam	.3271	.6805	.0787	.1333	.0742	.1044
Podsmid	.2676	.6581	.0417	-.1269	.2665	.1331
Podsup	-.1640	.6503	-.0992	.1936	-..0381	.3650
Intnodup	.1200	.0001	.8317	.0142	-.0236	-.0899
Intnodmid	-.3827	.0435	.7775	.0650	-.1162	.0122
Lowpodht	.0698	.1533	.1128	.8082	.1460	-.0282
Podslow	.2318	.1565	.0288	-.7419	.2391	.0902
Hypolen	-.0928	-.0772	-.2580	.1578	.7678	.2091
Angle	-.0977	-.3056	-.1185	.2883	-.6556	.1990
Podsmain	.0493	.0913	-.0601	-.1207	.0515	.9026
PROPORTION	20.75^{+}	13.67	11.35	9.41	6.88	6.79
CUMULATIVE	20.75	34.42	45.71	55.18	62.06	68.84

+, expressed as a percentage of the total variance

Table 34. Loadings of the first six most important principal factors in C_2 in East Lansing for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Nbranch	.7759	.02276	-.0813	-.2279	-.0790	-.1160
Hypodiam	.7166	.1484	.0250	.2707	.2259	-.0529
Podsmid	.6279	.1759	-.0220	.2397	.0375	.0478
Nodeslow	.5809	.1215	.4078	.0900	-.1283	.2010
Hypolen	-.4893	.3845	-.1190	.2567	.0986	.0918
Nodesmid	.1776	.8233	.0938	.0138	.0806	.0096
Nodesup	.3044	.4680	.1319	-.0247	.3139	.0447
Intnodmid	.0520	-.7637	.2215	.0709	.3554	.0220
Podslow	.1143	.0807	.6162	.3527	-.1024	-.2276
Intnodup	.1879	-.2172	.6160	.0791	.3540	.0545
Podsup	.3911	-.1200	-.6455	.3386	.0285	-.1043
Podsmain	.0680	-.0338	.1028	.8770	-.0615	.0173
Intnodlow	-.0448	-.0578	.0825	.0039	.7899	-.1121
Lowpodht	.0059	.1566	-.3144	-.1786	.4384	.2214
Angle	-.0331	.0104	-.0215	.0094	-.0333	.9254
PROPORTION	17.98^+	12.41	9.65	8.61	7.28	6.77
CUMULATIVE	17.98	30.39	40.03	48.64	55.92	62.69

+, expressed as a percentage of the total variance

Table 35. Loadings of the first six most important principal factors in C_3 in East Lansing for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Nbranch	.8027	-.1241	.0737	-.1541	.0411	-.1636
Podsmid	.5820	-.1106	.2291	.3110	.0964	-.2642
Nodeslow	.5501	.3055	.3740	-.0798	-.1879	.0351
Podsup	.5156	-.1533	-.1054	.1427	.4969	-.0612
Hypodiam	.4665	.2884	.3064	.2473	.3714	-.1726
Hypolen	-.6558	-.1355	.1801	-.0465	.1341	-.2819
Intnodup	.0411	.8160	.0589	-.0717	-.1604	-.1023
Intnodmid	.0781	.7946	-.3719	-.0721	.0502	.0660
Intnodlow	-.1423	.6328	.1476	.2008	.1856	.2198
Nodesmid	-.0180	-.1380	.8018	.0431	-.0379	-.1781
Nodesup	.2191	.1084	.5419	-.0620	.1383	.3942
Podsmain	.0295	-.0508	-.0586	.9237	.0269	.0412
Podslow	.0071	.2377	.2257	.4951	.4670	-.3008
Lowpodht	-.0684	.0663	.0608	-.0359	.7391	-.0749
Angle	-.1171	.0382	-.0561	-.0109	-.0980	.8229
PROPORTION	17.98^+	13.93	10.09	8.27	7.77	6.91
CUMULATIVE	17.98	31.91	42.00	50.27	58.04	64.95

+, expressed as a percentage of the total variance

Table 36. Loadings of the first six most important principal factors in C_4 in East Lansing for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Intnodup	.8270	.0815	.0215	-.0803	.0092	.1202
Intnodmid	.7691	.0807	-.1332	.1420	-.0022	-.3609
Intnodlow	.7546	-.0018	-.0046	-.0558	-.0092	.2319
Nodeslow	.1503	.7750	-.0088	-.1251	.0161	.2098
Podsmid	-.0762	.6185	.0113	.3433	-.1393	.0408
Hypolen	-.1309	-.5598	-.1992	-.0942	-.1022	.4689
Podslow	-.1164	.1159	.8124	-.1094	-.1458	.0710
Lowpodht	-.0110	.0445	-.8307	-.0477	-.0179	.1127
Podsup	-.0762	.0513	-.0897	.7574	-.0988	-.0094
Podsmain	.0964	.1107	.3924	.5417	.4454	.1543
Hypodiam	.0215	.3902	.0475	.4582	-.3897	.1003
Angle	-.1284	.1170	-.1603	-.0892	.7834	-.1627
Nbranch	-.1833	.3960	-.0310	.0298	-.6480	-.2065
Nodesup	.1982	.1223	-.0401	.1313	.0213	.7050
Nodesmid	-.4247	.1692	.1923	-.4333	-.1029	.4799
PROPORTION	15.67$^+$	14.50	10.36	9.55	7.90	7.22
CUMULATIVE	15.67	30.18	40.54	50.09	57.99	65.21

+, expressesd a percentage of the total variance

The populations under consideration in this study are segregating populations. Identifying individual factors by concepts on a cycle basis alone may not be a useful excercise since recommendations for selection would not be made on that basis but general for a breeding program. A more useful and worthwhile approach would be:

i. Identify associations within factors: This would help in recognizing the traits which are likely to be defining or influencing the same biological function. Further, it would also help in the recommendation of one or two traits which are easy to evaluate, from the group, for use in selection in a breeding program.

ii. Observe the relative ranking with regard to PFs: Those which are frequently loaded in the first two to four PFs may be considered more important indicators of what the traits represent (architecture in this case).

iii. Compare the outcome with results from the regression analysis for the purpose of corroboration of evidence.

In Table 37, PF1 for the parents is loaded by branch number and pod distribution traits just as PF1 in C_0 in East Lansing (Table 32). It may be noted that in C_0 branch angle was loaded in PF1 by a coefficient of similar magnitude, except that it had a negative sign. Since most pods are borne on the branches, the more of the latter, the more of the former. But the number and how they are distributed in the profile depends on the branch angle.

For the same number of pods, wider angles would cause more pods to be located in the lower region of the plant. Path coefficient analysis by Duarte and Adams (1972) in dry beans suggested that the number of pods per plant may be influenced through the number of nodes and the number of leaves in this sequence. Included in the PF1 in the parents is hypocotyl diameter. It influences the number of branches via plant height. It may not have many genes in common with pods and number of branches. PF2 in the parents was principally a nodes factor (Table 37). The moderate loading coefficient of podslow was not unexpected since Adams (1982) suggested that nodes influence the number of pods via the number of racemes, which must form only at an axillary position (which means leaves and nodes). Internode length measurements dominated PF3 and since plant height, in part, is a fucntion of internode length, this PF may be called a height factor. PF5 and PF6 are branch angle and pods on the main stem factors, respectively. For selection purposes, number of branches, number of nodes in the upper-third of the plant, branch angle, and the number of pods on the main stem would be recommended from this analysis. These were among traits identified previously as substantive indicators of architecture.

In the cycles, the internode measurements loaded together in the same factor in each cycle and at both locations. This suggests that the three traits are strongly associated and any attempt to change the length in one region would be accompanied by changes in the other two. This particular association was stronger at Chimaltenango, where the three internode lengths dominated PF1 from C_0 to C_3 and in PF2 in C_4. The low contribution of factors to total variance in the cycles as compared to the parents indicates the amount of change due to recombination with selection that took place. To follow cycle-to-cycle changes, concepts were assigned to factors after examining the analysis and observing specific patterns of association and their possible roles in plant architecture. The concepts are as follows:

a. Height (elongation) factor: This factor comprised traits which promoted stem elongation, the sum total of which indicated plant height. The traits from the factor pattern were intnodup, intnodmid and intnodlow (internode length measurements) which were most of the time associated with the same factor.

b: Structural (skeletal) factor: Traits in this factor are those responsible for the framework of the plant and may be further partitioned into:

i. Sturdiness factor: Comprising hypodiam and hypolen, these traits are anti-lodging and ensure the erectness of the plant.

ii. Profile factor: This is made up of branch angle and number of branches, traits which define the plant profile.

c. Distribution (number) of reproductive parts factor: These traits are concerned with the number of units or reproductive components within the plant frame. The traits are podsup, podsmid, podslow, podsmain nodesup, nodesmid, nodeslow and lowpodht.

Tables 8 to 12 (Appendix F) present the factor patterns in the concepts for various cycles and locations. The height factor was consistently the most important factor in Chimaltenango in all cycles. Height at East Lansing became progressively more important from its third position in C_0 to first in C_4. This indicates that height is one of the reliable indicators of architecture. The structural factor also became progressively more important from its fifth position in C_0 to first in C_3. The most important structural traits in the cycles were hypocotyl diameter and number of branches. Together with height, these three traits were clearly the most important determinants of plant architecture in dry beans. This evidence corroborates that from the multiple regression analysis. Further, it supports the suggestion by other researchers, including Bramel _et al_ (1984), that preceding, for example, a multiple regression analysis with a PFA will enable summarization of the data for selecting traits for inclusion in the prediction equation while eliminating bias due to multicolinearity.

With minor exceptions in C_1 and C_3 in Chimaltenango, and C_4 in East Lansing, all five biological concepts described above were found in each cycle at both locations. The order of extraction of these concepts was not, however, the same in each cycle, indicating that different traits were important in different cycles, and this was due to changes in selection pressure and targets from one cycle to another.

9.3.3 Relationships among all traits combined.

For the parents, the first five PFs accounted for 81.09% of the total variance. Combining all traits in one analysis produced only one significant change. PF2 was loaded by seed-pod traits, shifting the loadings in Table 37 (architectural traits only) one PF later. PF2 may be described as a seed-pod factor. PC1 remained the same at the top as when only architectural traits were considered. All architectural traits, except nodesmid, were positively loaded while all seed-pod traits had negative loadings. The reverse was true in PF2, except for podslow (Table 38). In each case, the exceptions had negligible coefficients. This, once again, confirms that there were genes from two divergent pools in the breeding program. These sets of genes were 'anti-each-other' (or antagonistic).

Table 37. Loadings of the first six most important principal factors in parents for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Podsmid	.8758	.2059	.1063	.0193	.1434	.0267
Nbranch	.8274	-.2353	.1622	.0285	-.0389	.1166
Podsmid	.8196	.2017	.1365	.3280	.2892	.1968
Hypodiam	.6620	.1063	.0280	.4969	.2555	.1305
Nodesup	.0631	.9178	.0274	.0584	-.1160	-.0039
Intnodup	.1087	.0514	.9103	.2300	-.0732	.1395
Intnodmid	.4137	-.0978	.5830	.1565	.4759	-.0003
Hypolen	-.2198	-.4577	-.5177	-.3009	.1846	.1953
Intnodlow	.1755	.0148	.2653	.8424	-.0035	.0133
Podslow	.1221	.4721	.1721	.5422	-.0697	.4609
Angle	.1940	-.1105	-.1026	-.0312	.8651	.2923
Lowpodht	.3978	-.4012	.1504	.0875	.4924	-.1009
Podsmain	.0976	-.0637	.0119	.0630	.1765	.7604
Nodeslow	.3064	.4342	.3779	-.0056	.1540	.5840
Nodes	-.0734	.0648	-.0552	.1720	.0358	.1938
PROPORTION	40.18$^+$	21.10	13.46	8.60	7.18	5.00
CUMULATIVE	40.18	61.28	74.73	83.33	90.52	95.52

+, expressed as a percentage of the total variance

Table 38. Loadings of the first six most important principal factors in the parents for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Nbranch	.8855	-.0171	-.2127	.1261	.0378	-.0120
Podsup	.8334	-.2286	.2231	.1263	.0004	.1100
Podsmid	.7781	-.3397	.1778	.1426	.2791	.2647
Hypodiam	.6096	-.5145	.0185	-.0006	.4109	.1843
Podlen	-.2493	.7634	-.0765	-.2203	-.1257	-.2834
Seedwt	-.3084	.7281	-.2145	-.0216	-.2530	-.1394
Nodesup	.0194	-.1474	.9420	-.0076	.0437	-.1181
Intnodup	.1101	-.0734	.0256	.9075	.2138	-.0985
Intnodmid	.3757	-.2544	-.1043	.6012	.1183	.3954
Intnodlow	.1246	-.2622	-.0128	.2272	.8480	-.0528
Podslow	.1814	.0432	.4425	.1788	.5882	.0667
Angle	.1544	-.2419	-.1149	-.0657	-.0417	.8884
Seednum	-.1030	-.1138	.2054	.1725	.0997	-.1543
Nodeslow	.3290	-.0396	.3833	.3716	-.0082	.2540
Nodesmid	-.0712	-.1627	.0327	-.0671	.1466	.0694
Lowpodht	.3552	-.1888	-.3758	.1741	.0602	.3994
Podsmain	.0711	-.1787	-.0363	.0273	.0589	.1631
Podwidth	-.2417	.2378	-.1089	-.1166	-.1667	-.0922
Hypolen	-.1967	.1266	-.3782	-.3985	-.2654	.1482
PROPORTION	38.11[+]	18.77	11.11	6.86	6.23	5.10
CUMULATIVE	38.11	56.89	68.00	74.86	81.09	86.19

+, expressed as a percentage of the total variance

The correlations among the factor loadings from the two locations were generally significant and positive (Appendix F, Tables 13 to 17). Between six and eight factors were extracted from the data at both locations. The factors retained in Chimaltenango accounted for 68.82 to 80.17% of the total variance, the first two accounting for 29.19% to 38.47% (Appendix F, Tables 18 to 22). In East Lansing, the retained factors accounted for 59.02% to 72.04% of variance while the first two contributed between 25.29% and 28.67%, over the cycles (Appendix F, Tables 23 to 27).

The combined analysis for the cycles, similar to the parents, yielded little significant changes. The seed-pod traits were loaded together in nearly identical manner to that obtained in the seed-pod traits PFA (Appendix F, Tables 16 to 20). In C_0, pod dimension traits were loaded in PF6; in C_1, seedwt and seednum were loaded with inverse signs in PF6 with, podwidth loaded in PF5. By C_2, the pairing had changed to the expected podlen + seednum and podwidth + seedwt in PF3 and PF4, respectively (Appendix F, Table 25). This pattern was maintained up to C_4 by which stage seednum and podlen were loaded in PF2 with seedwt loaded fairly highly in PF1. It would be recalled that architype was shown to have been recoverd *in toto*. This means that emphasis was placed on incorporating seed-pod traits into architecture as the cycles advanced, confirming the earlier suspicion that target traits as well as selection pressure changed from one cycle to another. This may be the reason for the seed-pod traits becoming gradually more important from PF6 in C_0 to PF2 in C_4. There were occasions in which the loadings of seed-pod traits were associated with fairly large loadings from architectural traits (Appendix F, Table 27). Some of such associations involved podwidth with either hypocotyl traits or number of branches. But this rare observations may indicate that seed-pod trait genes are quite unique from architectural trait genes.

There may be a direct association between seed size and architectural traits. In fact, where architectural traits loaded significantly and positively, seed-pod traits were weakly to moderately negatively loaded. Parents showed highly significant negative correlations between seedwt and architype rating, height, hypocotyl diameter and pods in the middle-third of the plant. Thus, as expected, intermating reduced the strength of associations. To obtain a tall, large-seeded plant, the negative association between seedwt and height must be broken. The negative association did not appear to be developmental but rather genetic, having dissipated after the initial rounds of intermating as was evident in the East Lansing results.

The combined data may be summarized as was done for the previous categories by combining the concepts. The seed-pod traits were called 'economic traits'. Height again showed up as one of the most important concepts, the economic factor appearing in PF3 (Appendix F, Tables 28 to 32). Except for height, the other concepts were frequently loaded in more than one factor in each cycle.

CHAPTER TEN

GENETIC DIVERGENCE AMONG PARENTS AND CYCLES OF RECURRENT SELECTION OF BEAN

10.1 Introduction

The germplasm utilized in the phenotypic recurrent selection by Kelly and Adams (1987) was obtained from two sources which displayed certain readily descernible contrasts in morphology, especially in seed size and gross plant architecture. Workers, including Singh and Gutierrez (1984), have reported that genetically controlled hindrance to hybridization exists in some crosses between the large- and small-seeded classes. Kelly and Adams (1987) did not report any widespread dysgenic events in their program to indicate prevalence of this problem.

This study was designed to find out how divergent the parents from the two germplasm pools were and also to identify the traits which are principal sources of divergence. By studying the divergence from one cycle to another, it would be possible to determine if significant genetic shifts were made, and between which cycles most changes were effected. This should shed some light on the patterns of recovery of traits in the above-mentioned breeding program.

10.2 Materials and methods

Two and three representative parents from the pinto germplasm pool and architectural pool, respectively, were investigated in this study, in addition to 100 selections fro each of the five recurrent cycles. Principal component analysis was performed on the parents to determine traits which were responsible for most of the variance. The procedure may also identify fundamental relationships among the traits which may indicate the divergence between the two sources of germplasm utilized in the breeding program by Kelly and Adams (1987).

Mahalanobis' D^2 distances among the five parents were calculated independent of the distances among the five cycles. In each case, the biological distances were estimated on the basis of architectural traits and seed-pod traits, separately.

In addition to a D^2 analysis, the populations were submitted to canonical discriminant analysis, using the two sets of traits separately and then together as measurement batteries. By calculating the standardized canonical coefficients for each set of traits, it was possible to obtain an indication of traits in each set which were responsible for most of the divergence among populations. The first two canonical variates were plotted in addition to constellations of the cycles on the basis of the D^2 analysis.

10.3 Results and discussion

10.3.1 Divergence among parents

The first six principal components (PC) accounted for 82.85% of the total variance, PC1 alone accounting for 38.24% (Table 9). Loadings of opposite sign were encountered in PC1; all architectural traits had positive loadings (except hypolen), while all seed-pod traits were negatively loaded (except seednum). The highest positive loadings were given by height, hypodiam and podsmid, while the highest negative loadings were produced by podwidth, podlen and seedwt.

Height, hypocotyl diameter and pods in the middle of the plant, it would be recalled, were among traits identified as the principal indicators of architecture in the multiple regression analysis. These traits hence may be considered the most representative of the architectural germplasm pool. The highest negatively loaded traits were all seed-pod traits and, similarly, may be taken to be representative of the large seed (pinto) germplasm pool. It is significant to note that seednum (number of seeds per pod), even though biologically and technically a seed-pod trait, was the only positively loaded trait of the group. This is because high seed number is actually an attribute of architecture. In fact, in PC6 which was dominated by high positive loadings from seed-pod traits, seednum, this time, was the only trait with a negative loading coefficient (Table 9). Unlike traits such as nbranch and hypolen which contributed significantly and positively to variance in more than one PC, these architectural traits mentioned above contributed to variance only in PC1, the most important PC. This may further indicate the primary role of these traits in bean plant architecture.

The opposite signs of the loading coefficients shown by the two groups of traits suggest negative association between them; traits which promote architecture are anti-seedwt. It may be said, also, that the architectural traits promote seed number and seed number is 'anti' seedwt. Further, the fact that the loadings of the most important principal component, PC1, could be grouped clearly into two "sub-factors" according to sign and attributed to biological concepts, namely, architecture and seed-pod traits, which reflect the nature of the parental gene pools, would indicate the existence of two functionally distinct gene groups.

To achieve recombination between the two groups, the negative association had to be broken. This was achieved by the phenotypic recurrent selection in this study as evidenced by the change in association, the initial negative correlation in the parents (r = -.646 ***) dissipating to r = -.096 * in the F_3 generation and being non-significant in the cycles.

The internode measurements (intnodup, intnodmid, intnodlow) frequently were loaded alike as in PC1, PC3, PC4, and PC6 (Table 9). The other important architectural traits such as nbranch, angle, podsmain and podslow were all extracted with significant loadings in the first three PC's. These results confirm the findings of the regression analysis that these traits have causative influences on bean plant architecture.

The representative samples from the two germplasm pools differed significantly in terms of architectural traits, according to the D^2 estimates. The results further show that there were similarities in cultivars within the architectural pool for these traits (Table 39). Seed-pod traits produced very highly significant differences between the two pools (Table 40). The Wilk's lambda test of the discriminating power of the measurement battery for

Table 39. Mahalanobis' D^2 distances between parents on the basis of architectural traits.

	Olathe	UI 114	X80149	Midnight	C-20
UI 114	2.91				
X80149	2.92	2.69			
Midnight	5.29*	5.65*	4.21		
C-20	7.14*	7.50**	6.34*	3.38	

**, *: significant at .01 and .05 levels, respectively.

Table 40. Mahalanobis' D^2 distances between parents on the basis of seed-pod traits.

	Olathe	UI 114	X80149	Midnight	C-20
UI 114	1.83				
X80149	4.51**	5.16***			
Midnight	5.52***	6.20***	1.25		
C-20	6.23***	7.18***	2.49	1.57	

***, **, significant at .001, .01 levels respectively.

Table 41. Standardized canonical coefficient for seed-pod traits in parents.

	CAN1	CAN2	CAN3
Podwidth	.4221	.2721	-.3550
Podlen	-.4517	.4062	-1.6198
Seednum	.3124	1.1875	.6183
Seedwt	3.2689	-.0515	1.7075
PROPORTION	93.39	.0604	.0050
CUMULATIVE	93.39	99.43	100.00

the grouping criterion was significant at the .0001 level. The first two canonical variates accounted for 99.43% of the total variance, indicates that the first vector is the predominant axis of variation. Traits loaded on this axis are the most important sources of variation. Using the absolute magnitude of the coefficients, the relative importance of traits in the primary axis can be obtained. Seedwt, clearly, is the most important source of divergence in the two germplasm pools. Vector 2 indicates seednum to be the next most important source of divergence. These results suggest that the parent germplasm sources differed in seedwt, especially, and seednum. Seednum has been shown to be more of an architectural attribute than seed-pod. It appears the parents did not differ architecturally as drastically as in seed size and pod characteristics. Morphologically, all plants from the two pools looked alike in the early growth, standing erect until later stages of growth when the pinto group became viny and assumed a decumbent growth form. From Appendix A, Tables 1 to 11, it is evident that clearcut differences between the pools were observed in very few traits including height, podsmid and intnodlow. Seedwt ratio for the two germplasm pools was about 2:1 in favour of the pinto group. Such a dramatic difference was not found, generally, among the architectural traits. In the plot of the first two canonical variates, the navy group clustered to the left while the pinto group clustered to the right (Figure 40).

8.3.2 Divergence among cycles

a. Architectural traits as measurement battery.

The first and second canonical variables accounted for 96.63% of total variance at East Lansing and 84.88% at Chimaltenango (Tables 42 and 43). Wilk's lambda test was significant at the .01 level. A plot of the first two canonical variates shows that there is an overlap, but both C_0 and C_1 separate out fairly clearly; C_2 clusters out to the right portion though it is rather dispersed as a group. C_3 and C_4 are most similar, being located at the periphery of the general cluster (Figure 41).

This indicates that the architectural traits were recovered in the early cycle of selection, recovered _in toto_ as Kelly and Adams (1987) observed. The later cycles only fine-tuned the architectural traits complex to accommodate the seed-pod traits introduced from the pinto group. The D^2 estimates of biological distances between cycles when architectural traits alone were used as the basis for estimating distance indicated that the distance between C_3 and C_4 was not significant at East Lansing. This further

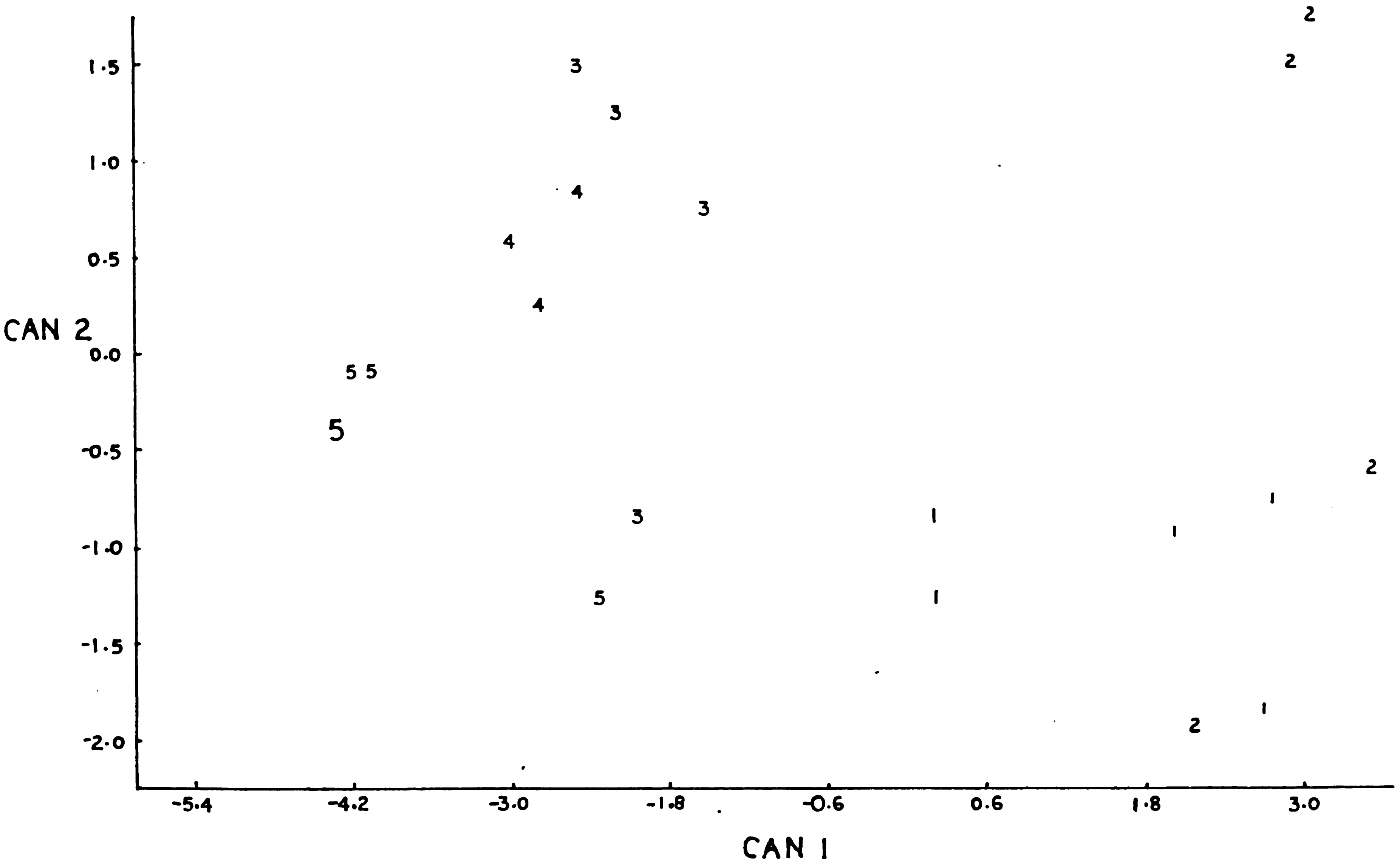

Figure 40. Plot of the first two canonical discriminant functions in parents using seed and pod traits for grouping. Numbers 1 and 2 = Pinto; 3, 4, and 5 = Navy /Black.

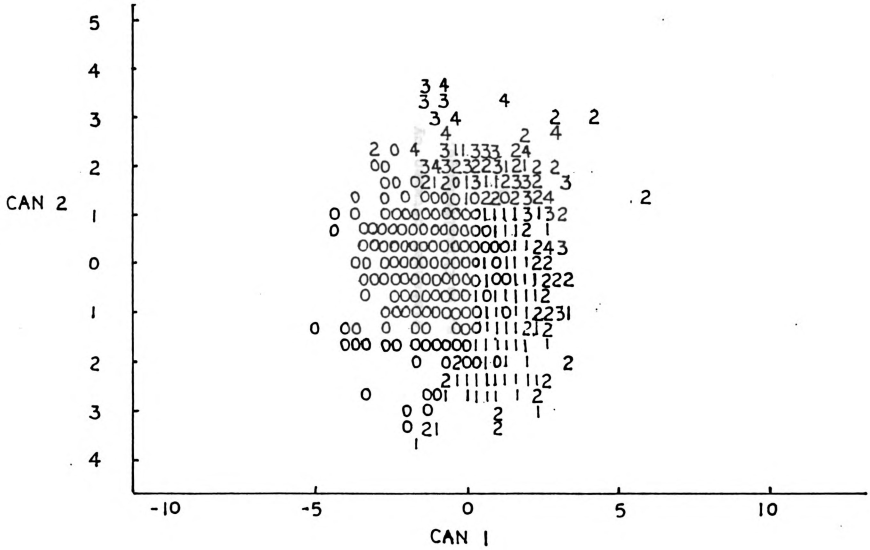

Figure 41. Plot of the first two canonical discriminant functions using architectural traits for grouping. Numbers in the plot indicate various cycles.

Table 42. Mahalanobis' D^2 distances between cycles on the basis of architectural traits, in East Lansing.

	C_0	C_1	C_2	C_3	C_4
C_1	2.26***				
C_2	2.01*	.87***			
C_3	2.04*	.72***	.48***		
C_4	2.06*	.83***	.54*	.36	

***, *, significant at 0.001, and .05, levels respectively; C = cycle.

Table 43. Mahalanobis' D^2 distances between cycles on the basis of architectural traits, in Chimaltenango.

	C_0	C_1	C_2	C_3	C_4
C_1	1.36***				
C_2	1.34***	1.22*			
C_3	1.32*	1.47**	1.65***		
C_4	1.34*	1.52**	1.68**	1.21	

***, **, *, significant at .001, .01, .05 levels, respectively; C = cycle.

indicates that the major changes in architectural traits were made in earlier cycles.

On the basis of the absolute magnitude of the coefficients of the canonical vectors, characters of high influence in differentiating between cycles include hypolen, podslow, height, intnodup, podsmid, nbranches and branch angle in East Lansing, and podsmid, hypolen, hypodiam, nodeslow, and intnodup, in that order of decreasing magnitude of the size of the coefficients, at Chimaltenango (Tables 44 and 45). These traits have previously been identified as effective indicators of plant architecture. The changes in sign observed between canonical variables for nearly all traits indicates, according to Narayan and Macefield (1976), a balancing effect for intermediate optima under diverse influences of natural and human selection.

b. Seed-pod traits as battery of measurements

Four seed and pod traits, namely, podwidth, podlen, seednum and seedwt, comprised the measurement battery used for the grouping criterion (cycles). The first two canonical variates accounted for 99.84% and 99.29% of the total variance at East Lansing and Chimaltenango, respectively (Tables 46 and 47). Wilk's lambda test was significant at the .0001 level. Figure 42 shows a plot of the first two canonical

Table 44. Standardized canonical coefficients for architectural traits at East Lansing.

	Canonical variable		
Trait	CAN1	CAN2	CAN3
Height	.5401	-.5075	-.3600
Nbranch	.2231	-.4675	.1920
Hypolen	.6285	.3086	-.0913
Hypodiam	.1480	.2452	-.1191
Lowpodht	.0855	.0932	.3371
Angle	.2145	.0601	.6113
Podsup	-.1907	-.3535	-.0391
Podsmid	-.3629	.0811	-.2142
Podslow	-.5965	.2322	.0708
Nodesup	.0440	.4678	-.4128
Nodesmid	.0124	.0662	.6227
Nodeslow	.1281	-.0266	.0692
Podsmain	-.0185	.0411	.4047
Intnodup	-.4646	.2080	.1968
Intnodmid	.1966	.0413	.1389
Intnodlow	-.1101	.4032	.0373
PROPORTION	78.09 +	18.53	.0337
CUMULATIVE	78.09	96.63	100.00

+, expressed as a percentage of the total variance

Table 45. Standardized canonical coefficients for architectural traits at Chimaltenango.

	Canonical variable		
Trait	CAN1	CAN2	CAN3
Nbranch	.1800	-.0922	-.2299
Hypolen	-.5005	-.2981	.1749
Hypodiam	-.4010	.5759	.3000
Lowpodht	.0534	.3242	-.0247
Angle	-.0733	-.0042	.3791
Nodesup	-.0868	-.4131	.2173
Nodesmid	.0040	-.0545	.3853
Nodeslow	-.3893	-.0353	-.0413
Podsup	-.0983	.0774	-.2668
Podsmid	.6352	-.3893	.0043
Podslow	.2587	.7642	-.2800
Podsmain	.5102	.0966	.0395
Intnodup	.3625	-.4705	-.1029
Intnodmid	-.1130	.3145	.2378
Intnodlow	-.0515	.2478	.2537
Height	.1593	-.3239	.3390
PROPORTION	62.66 +	22.22	15.12
CUMULATIVE	62.66	84.88	100.00

+, expressed as a percentage of the total variance

Table 46. Standardized canonical coefficients for seed-pod traits at East Lansing.

	Canonical variable		
Trait	CAN1	CAN2	CAN3
Podlen	.2072	-.0875	.9504
Podwidth	.8635	-.5490	-.4855
Seednum	-.1397	.6105	-.3073
Seedwt	.5781	.8763	.0943
PROPORTION	97.22 +	.0262	.0016
CUMULATIVE	97.22	99.84	100.00

+, expressed as a percentage of the total variance

Table 47. Standardized canonical coefficients for seed-pod traits at Chimaltenango.

	Canonical variable		
Trait	CAN1	CAN2	CAN3
Podwidth	1.0037	-.5514	-.2728
Podlen	.2205	-.4001	.7186
Seednum	-.2082	.4983	.6212
Seedwt	.7567	1.0191	.0423
PROPORTION	91.78 +	.0750	.0071
CUMULATIVE	91.78	99.29	100.00

+, expressed as a percentage of the total variance

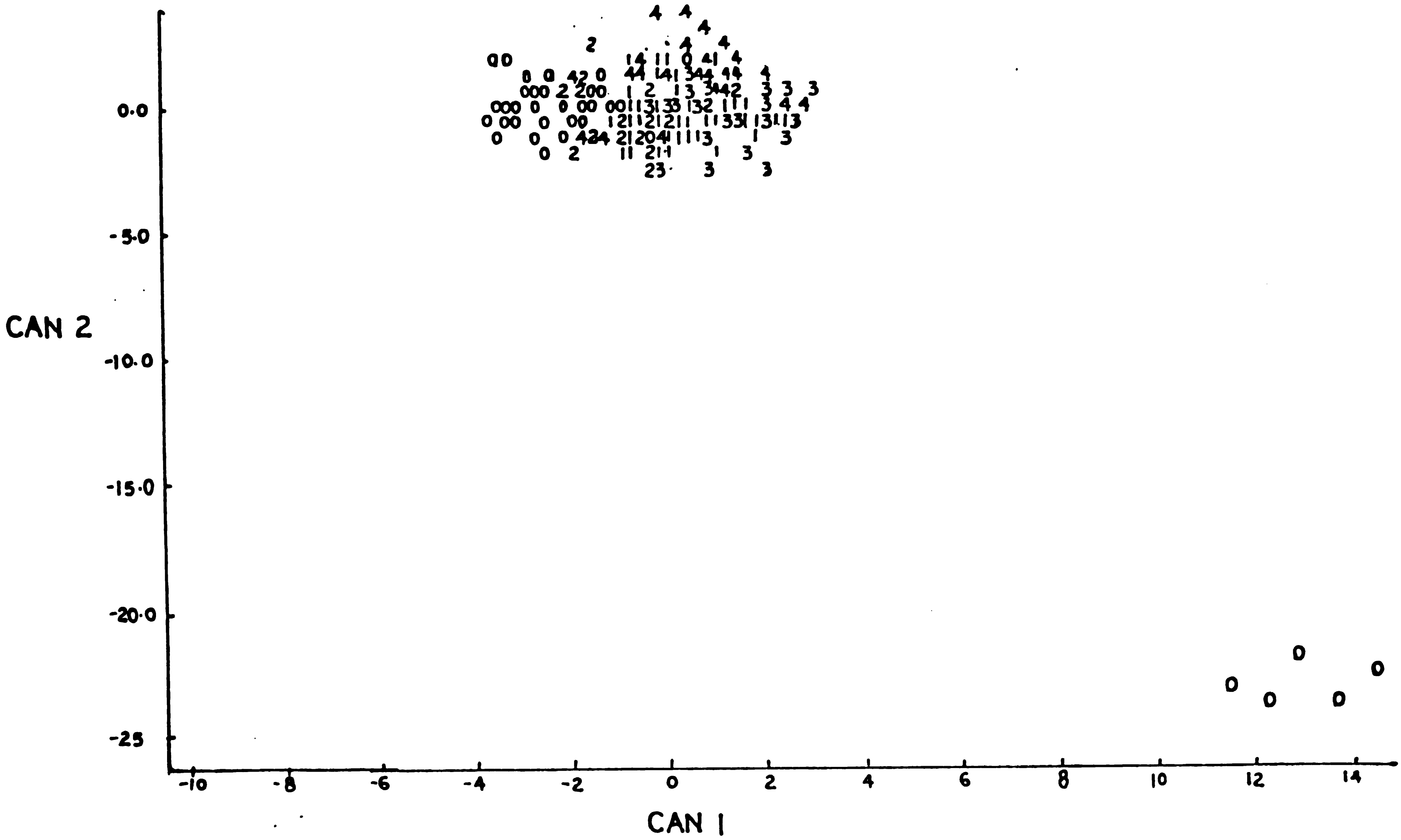

Figure 42. Plot of the first two canonical discriminant functions using seed and pod traits for grouping. Numbers in the plot represent various cycles.

variates. While separation was not as clear as for the architectural traits, the C_0 group was again separated very clearly from the others. Another distant cluster of only C_0 was observed. C_1, C_3 and C_4 overlapped but each could be seen as a reasonably homogeneous group. C_2 appeared to be swamped by the dispersion from the other groups.

No independent secondary cluster of C_0 was observed when architectural traits were used. This may be because architectural traits recombined between the groups in the C_0, as has already been said, while seedwt failed to recombine in the early cycles, leaving the two distinct size classes virtually intact, and hence the dual clustering. The two clusters represent the two seedwt classes (large and small). The C_0 was an unselected population and this may have contributed to the separation in C_0.

The spread of the plot is much narrower than in the case of architectural traits. This may indicate restricted variability. The overlap in the clustering may be due to the fact that selection was not stringent for the traits; some compromise plants were advanced deliberately to keep the genes of the parents in the pool.

The standardized canonical coefficients in Tables 46 and 47 indicate that podwidth and seedwt are the main traits responsible for diversity in the two germplasm groups, on the basis of seed-pod traits. The D^2 analysis suggests that steady progress was made in seed-pod traits from one cycle to another as the measures of biological distance among cycles were significant (Tables 48 to 50).

c. Architectural and seed-pod traits combined as measurement battery.

Better separation among the cycles was produced when all traits were considered in one analysis. Two clusters were still observed from C_0 (Figure 43). C_1 and C_2 overlapped the most with C_3 just starting to break free from the cluster. This is interpreted to mean that recombination occurred mainly among the architectural traits as has been discussed before. The D^2 analysis showed significant differences among the cycles, suggesting that significant genetic rearrangement occurred to produce variability which was effectively selected in making for progress from one cycle to another (Tables 51 and 52).

The standardized coefficients showed that height, nbranch, podsmid, podslow and intnodup had high coefficients in the first canonical variable at both locations for the architectural traits, with hypodiam and branch angle of high magnitude at one location (Appendix G, Tables 1 and 2). These traits, along with seedwt and podwidth,

Table 48. Mahalanobis' D^2 distances between cycles on the basis of seedwt in East Lansing.

	C_0	C_1	C_2	C_3	C_4
C_1	.96***				
C_2	.99***	.14*			
C_3	1.09***	.13*	.23**		
C_4	1.54***	.58***	.44***	.40**	

***, *, significant at .001, and .05 levels, respectively; C = cycle.

Table 49. Mahalanobis' D^2 distances between cycles on the basis of seed-pod traits, in Chimaltenango.

	C_0	C_0	C_1	C_3	C_4
C_1	2.30***				
C_2	2.52***	1.21***			
C_3	3.24***	1.01***	.98**		
C_4	2.92***	1.15***	.96**	.90**	

***, **, significant at .001, and .01, levels, respectively; C = cycle.

Table 50. Mahalanobis' D^2 distances between cycles on the basis of seed-pod traits, in East Lansing.

	C_0	C_1	C_2	C_3	C_4
C_1	.85***				
C_2	.64***	.35***			
C_3	.58***	.34***	.21*		
C_4	.57**	.35***	.24	.04	

***, **, *, significant at .001, .01, .05 levels, respectively; C = cycle.

Table 51. Mahalanobis' D^2 distances between cycles on the basis of architectural and seed-pod traits, in East Lansing.

	C_0	C_0	C_1	C_3	C_4
C_1	2.50***				
C_2	2.36*	.91***			
C_3	2.33*	.74***	.51***		
C_4	2.36*	.86***	.57*	.37	

***, **, *, significant at .001, .01, .05 levels, respectively; C = cycle.

Table 52. Mahalanobis' D^2 distances between cycles on the basis of architectural and seed-pod traits, in Chimaltenango.

	C_0	C_1	C_2	C_3	C_4
C_1	2.50***				
C_2	2.75***	1.01***			
C_3	3.45***	1.11***	1.50***		
C_4	3.06***	1.42***	1.43***	1.75***	

***, significant at .001 level; C = cycle.

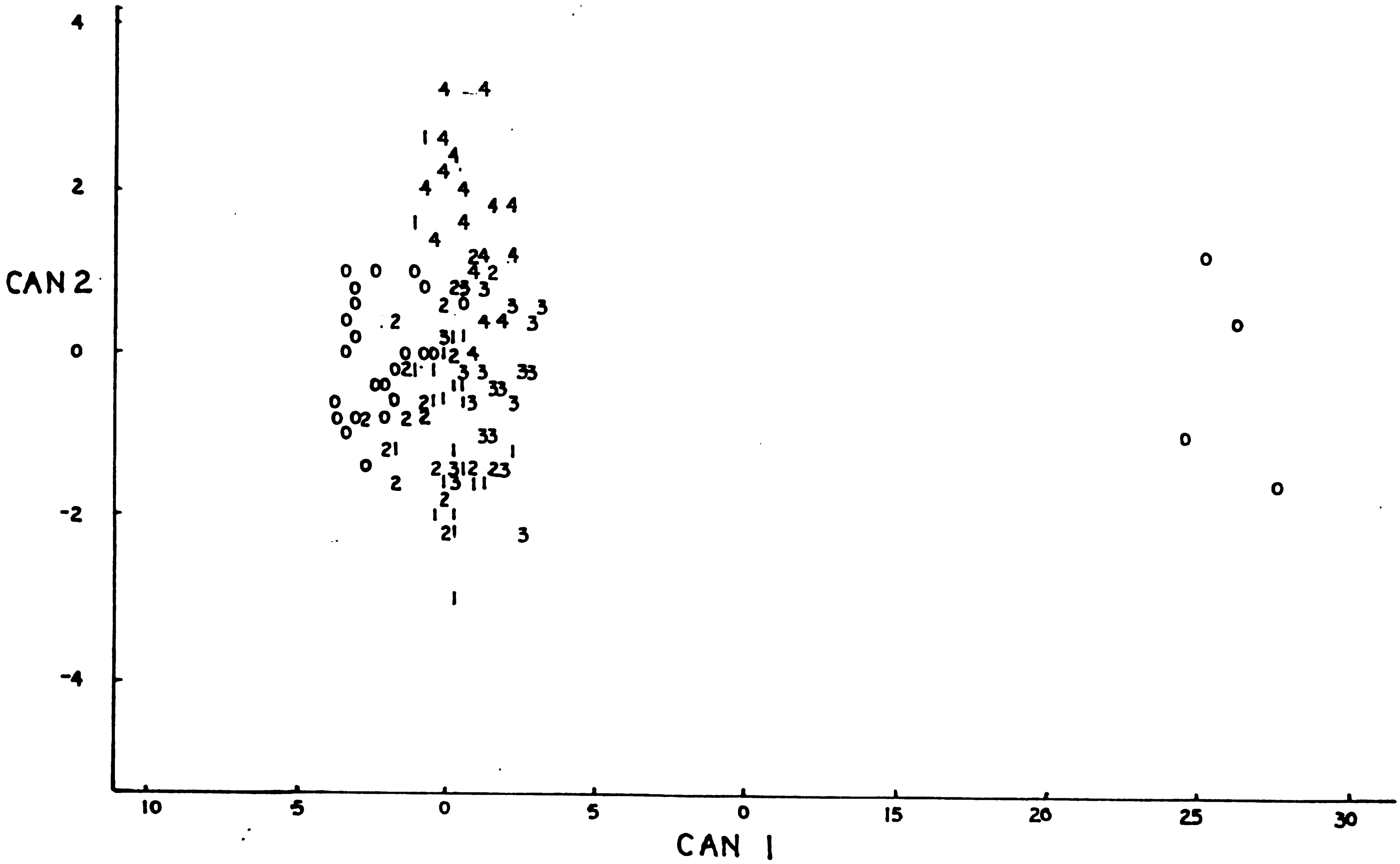

Figure 43. Plot of the first two canonical discriminant functions using all traits for grouping. Numbers in the plot indicate various cycles.

constitute the characters for primary differentiation between the two sources of germplasm. Branch angle and the number of pods on the main stem were the only traits which maintained their original sign in all three canonical vectors. Using the explanation offered by Narayan and Macefield (1976), it may be concluded that while most traits under recombination with selection and diverse environments were balancing for an intermediate optimum, podsmain and branch angle changed to accommodate changes in other traits and did not stabilize.

CHAPTER ELEVEN

HERITABILITY AND GENETIC CONTROL OF BEAN TRAITS

11.1 Introduction

A single major gene whose expression is subject to environmental variations would produce continuous variation. Heritability estimates are properties of the crop, environment and, generally, specific to the experiment. Estimates obtained from data taken from several locations would be more reliable than from a single location.

The presence of additive genetic variation will make systematic improvements in a trait possible through a cyclical breeding strategy. The presence of inter-locus interaction would complicate matters, requiring that the appropriate loci be assembled together for expression of traits.

Multiple regression analysis would identify good indicators of a desirable plant architecture which may be recommended to breeders for selecting in a breeding program. It is necessary, however, to know how heritable these traits are, especially, in a phenotypic recurrent selection program. Such information would influence the recommendations for various selection strategies.

11.2 Materials and methods

Data from experiment II were used in this analysis. The data were first submitted to analysis of variance and then the variance was partitioned into the contributions by the contrasts as presented below which were tested by the t-test to indicate the significance of some gene action, as follows:

a. Test of dominance

$$F_2 \text{ vs } \frac{1}{2}(P_1 + P_2)$$

b. Test of epistasis

$$F_3 \text{ vs } \frac{1}{2}(F_2 + MP)$$

where P_1 = navy parent

P_2 = pinto parent

MP = mid-parent

c. Broad sense heritability (H)

$$H = ((VF_2 - \frac{1}{2}(VP_1 + VP_2)) / (VF_2) = V_g/V_p$$

Where VF_2, VP_1 and VP_2 = variance of F_2, P_1 and P_2, respectively, and V_g and V_p = genotypic and phenotypic variance, respectively (Knowles and Briggs, 1967).

The following crosses were made:

Cross 1 = Olathe x X80149
Cross 2 = UI 114 x X80149
Cross 3 = Olathe x Midnight
Cross 4 = Olathe x C-20
Cross 5 = UI 114 x C-20
Cross 6 = C-20 x Midnight

In this study, data from only one environment were available. With only two replicates, the estimates of error may not have been very good.

11.3 Results and discussion

The parents used in the crosses differed significantly in height, podsup, podsmid, podslow, branch angle and seedwt, in nearly all crosses (Appendix H, Tables 1 to 6).

11.3.1 Tests of dominance and epistasis

No significant deviations from the mid-parents by the F_2 mean were observed in any cross for any trait in this study. Similarly, the test of epistasis failed to yield significant differences (Appendix H, Tables 1 to 6).

11.3.2 Broad-sense heritability.

The estimates were generally low to moderate in magnitude for most traits.

a. Architectural traits

Broad-sense heritability estimates for nbranch ranged from 42% to 57%, while those for branch angle ranged between 51% and 65%. For podslow, the estimates were between 40% and 64% while nodesup estimates were between 46% and 58%. On the whole, estimates for the architectural traits were lower in magnitude than those for the seed-pod traits (Table 54). The broad-sense heritability estimates for podsmid were above 70% in two crosses and above 50% in two others. The length of the hypocotyl (hypolen) had estimates of between 13% and 20% in three crosses and 56% to 68% in the others.

Since not all crosses were made between parents that were genetically widely different for all traits, some traits would show low heritability because of low genetic variances.

b. Seed-pod traits.

Broad-sense heritability estimates were generally of moderate to high magnitude and more stable in all crosses than was the case for the architectural traits. Seednum was the least heritable among the seed-pod traits with estimates between 23% and 56%, while seedwt showed consistently high heritability over crosses with a range of 53% to 88% (Table 54). Podwidth was also highly heritable, and so was podlen, except for two estimates of less than 50% in the case of the latter trait.

Table 54. Broad-sense heritability estimate for bean traits in six crosses.

Trait	Cross 1	Cross 2	Cross 3	Cross 4	Cross 5	Cross 6
Height	45.06	38.58	-	8.50	43.53	37.95
Architype	51.70	-	9.89	-	-	-
Nbranch	-	56.64	41.88	-	-	56.55
Hypolen	55.60	68.22	12.97	65.69	14.73	19.80
Hypodiam	38.12	33.36	-	-	32.10	31.13
Angle	55.24	64.64	-	-	50.72	51.41
Podsup	80.30	57.39	-	-	19.10	4.89
Podsmid	85.26	54.54	30.94	25.10	72.78	50.01
Podslow	61.75	54.59	40.30	63.75	49.66	-
Nodesup	45.65	-	48.58	58.38	-	55.75
Nodesmid	31.86	-	29.44	45.70	-	-
Nodeslow	36.24	64.56	-	30.99	-	25.79
Lowpodht	88.88	31.36	1.56	-	26.22	9.36
Podsmain	60.63	18.46	9.70	-	-	79.67
Podwidth	81.06	65.06	87.61	-	72.32	38.96
Podlen	67.43	31.82	84.09	44.00	85.52	65.02
Seednum	29.66	-	55.60	22.95	45.69	-
Seedwt	76.94	87.51	62.46	74.39	52.61	69.37

The data suggest at best that some of the important architectural traits and seedwt are under the influence of additive gene action. The heritabilities of the seed and pod traits were generally higher than those of the architectural traits. The success of the phenotypic recurrent selection program is testimony to the fact that the traits selected for improvement were at least moderately heritable. With the exception of hypodiam, the substantive indicators of architecture produced moderate range of heritability estimates over all crosses.

CHAPTER TWELVE

GENERAL DISCUSSION

The results herein presented and discussed derive from the analysis of data collected from a practical breeding program. The program was not initiated to satisfy an academic quest but was motivated by commercial needs. It would be of interest to discover some of the genetic consequences of breeders' decisions and actions while pursuing a practical breeding program.

This dissertation does not consider physiological traits directly as none were measured due to time constraints and size of study. The importance of physiological information in ideotype breeding is respectfully acknowledged but it is my contention that physiological responses should, ultimately, find expression in the structural and physical realm. Morphological (metrical) traits are readily measurable and differences are more easily descernible, making them prefered in field selection, especially when handling large numbers of plant materials. Any physiological inference made in this dissertation will, therefore, not be illegitimate.

Measurements were made on the single plant basis and utilized as such in the analysis (as in correlation) or averaged over a number of selections in a class (a cycle). Some traits, notably yield, are more of a population than an individual phenomenon and care should be taken in drawing inferences from the results.

Hybridization followed by recombination and reassortment under self-fertilization has the effect of reorganizing genes in a new genetic matrix. Self-fertilizing crop species possess a mechanism for delimiting their genetic pool. The long-term effect of this is the evolution of certain adaptive complexes which are ideosyncratic to species and are functionally-integrated, as hypothesized by Mather (1973). Clausen and Hiesey (1960) remarked that the finely balanced genetic equilibrium that makes it possible for an organism to live and adjust to its environment are so complex that many generations are required to reassemble them after they have been broken down through hybridization. The extent of this reorganisation will depend, in part, on the opportunities a breeding program offers for recombination. Resistance to recombination will not depend only on the strength of linkage within the adaptive complex but, in part, it would be influenced by the degree of divergence between parents. In this study, the parents were drawn from two diverse gene pools and submitted to a cyclic breeding strategy which offered repeated opportunities for breakup of initial linkage blocks. Some of the above-mentioned events were envisaged in this study and the results have elucidated some consequences of divergence and intermating on the breeding program, which was the subject of this dissertation.

The breeder, according to Grafius (1964), differs from the geneticist in the complexity of the problems which confront him/her, the former having to handle more genes, more characters, more environments and more individuals. This study was not an exception to this distinction. The natural recourse to handling super matrices is to resort to the use of multivariate statistics for data summarization for easier interpretation. Since there is no one all-inclusive approach in performing statistical analysis, the data was summarized from different perspectives with the hope that their results will corroborate each other, leading to more reliable conclusions. The characters under consideration in this dissertation were grouped into meaningful classes and analysed on such a basis, independently as well as together. This permited the study of effects and trends of effects with little confounding.

It is an inescapable fact that certain complex traits are better handled as such rather than by way of their components. But as Grafius (1964) observed, the sequential nature of development of traits should persuade breeders to consider components in breeding. Conventional wisdom would, however, caution against the amount of time and labor required in data collection in component breeding. Architecture, a very complex trait, was, admittedly, subectively scored in this study. Each individual rating could be satisfied by several, if not many, permutations and combinations of the morphological traits which were considered. Even though the list does not exhaust all morphological traits which could possibly affect plant architecture, earlier work by other researchers suggest that the range considered in this study was adequate. It was desired to identify from these results and assign component status to traits to guide breeders in plant architecture breeding, especially as it pertains to beans.

It is common knowledge that of the components of genotype x environment interaction, genetype x years is the most variable and perharps the most important to practical breeding since it is largely unpredictable. This latter situation offers a challenge to the breeder to develop cultivars which are versatile and resilient. In this study, however, time limitation did not permit this bio-physical relationship to be ascertained. It is not unreasonable to expect plants to behave differently in a tropical environment from a temperate one. On the other hand, it was desirable to find out if the differences are due to scale or rank.

The breeder is especially interested in heritable variation and more so if he/she is selecting on a phenotypic basis, as was the case in this study. A knowledge of the genetic regime which governs the traits will illumine our understanding of the behaviour of traits during the breeding program. Results from one location and one experiment only are available for this genetic study, denying us information on other useful sources of variation. The results will be considered preliminary but none-the-less useful for present purposes.

Ideotype breeding has a four-pronged approach:

a. the crop - consideration must be given to the physiological and genetical idiosyncracies of the crop such as the heritability of traits, gene action, linkages and optimal leaf area, among others;
b. the environment - the design must be able to efficiently exploit the enviromental resources for optimal productivity while coping with hazardous situations such as excess moisture at harvesting time;
c. the farmer - the changes in the gross morphology should suit the cultural practices of the farmer.
d. the consumer - the farmer will grow only what he will have a market for.

In designing a crop ideotype, it is desirable to know the relative importance of components and their genetics.

In this study, the preponderance of the evidence indicates that hypocotyl diameter, plant height, branch angle and the number of pods in the middle of the plant are the most substantive indicators of bean plant architecture. Traits selected by the multiple regression analysis and confirmed by other procedures such as principal factor and component analyses were in concordance with those which Adams (1982) proposed. This remarkable consistency furnishes tenuous evidence for the above conclusion. These salient features of the bean architecture are easy to score phenotypically and will facilitate breeding programs in which they are the selection objectives.

Erectness appears to be the most fundamental feature of plant architecture and this is primarily dependent upon the hypocotyl diameter. But the breeder should not be oblivious of the fact that a very thick hypocotyl diameter may pose a serious practical problem to both mechanized and manual harvesting. Thick hypocotyls may be difficult to uproot by hand or cut by the knives of a combine harvester.

Still on the subject of components, Nienhaus and Singh (1985) observed that general enhancement of architectural traits would increase yield but selection for increased expression of certain architectural traits may result in compensation for those by a decrease in other traits, since the architectural traits are interrelated. Yield component compensation first reported by Adams (1967) in beans was confirmed by the correlation results in this study. As the number of pods increased, the seed weight decreased. Further, as the plant profile got narrower, the number of pods and consequently plant yield decreased. In view of the aforementioned, it would be imperative to conduct agronomic studies to determine optimal density for planting the new pinto ideotype. Branch angle appears to control pod distribution in the plant profile since most of the pods are borne on branches.

The theoretical advantage of recurrent selection with intermating over the conventional breeding methods in self-pollinating crops include the accumulation of alleles affecting a selected trait(s) and maintenance of genetic variability for non-correlated and unselected traits (Frederickson and Kronstad, 1985). The results of the frequency analysis showed these effects to be true by their generally normal distribution for nearly all traits. Genes for large seedwt and pinto shape were progressively accumulated with recurrent selection. Selection on a phenotypic basis calls for a keen "breeders' eye" for good progress to be made in a breeding program.

Multivariate procedures such as PCA and PFA are not technically statistical procedures since they give no basis for making decisions about hypothesis. PCA is tied more closely to the original variables they interpret than the PFA. This weakness not withstanding, the multivariate procedures employed in this study contributed in no small way to elucidating the underlying interrelationships within and between the two germplasm pools involved. Cumulatively very powerful evidence accrued from PFA, PCA and canonical discriminant analyses to indicate the existence of significant divergence between the two pools. This divergence manifests itself in the genetic consequences of lack of recombination and low plant yield in the early cycles of recurrent selection. The parents used in this breeding program differed in a wide array of characters manifest principally in their seed and pod traits and also in several aspects of their architectural traits. Crop varieties differ extensively in the physiological processes which determine yield. Genotypes possessing the physiological complementation and balance needed for high yield may not have been assembled in the early cycles due probably to 'linkage freeze' suggested by Kelly and Adams (1987), leading to poor yield in the early cycles. Mather (1973) described inbreeders as possessing internal balance in their haploid set. Outcrossing plants on the other hand have relational balance because at fertilization the haploid sets are genetically dissimilar. Hybridization between two divergent gene pools in self-pollinated crops imposes a situation in which chromosomes which are relationally unbalanced and not co-adapted are brought together as observed by Dobzhansky (1948) in Drosophila psuedoobscura. Such a hybrid population would be predisposed to subpar performance and would need some adjustments. As Mather (1973) pointed out, this adjustment or balance should be for optimal rather than maximum expression of traits.

The presence of linkage was not directly tested in this study but the results furnish appreciable circumstantial evidence to indicate a strong association among architectural traits and the possible existence of a tight linkage block. Strong evidence came from the PCA and the frequency analyses. There was evidence to associate the seed and pod traits with the pinto germplasm pool and the architectural traits with the navy and blacks. This would suggest a repulsion phase linkage between the two sets of genes from the elite parents at fertilization.

The broad genetic base of the populations involved in the study would make the results applicable to a broad spectrum of classes in the Phaseolus vulgaris L. species. Since changes in the traits at the two locations were due mainly to scale, the selected components of the bean plant architecture will serve as uncommonly reliable selection indices in different locations for similar breeding program.

The PFA showed that the architectural traits and the seed-pod traits loaded independently in the factors, suggesting that the two sets of traits may be under separate genetic systems of control. The nagative correlation between architecture and large seed size will prevent a tandem selection strategy to be used for such a breeding program. The recurrent selection procedure was most appropriate since it offered repeated chances for breaking up linkages. The correlations encountered were both genetic and developmental in origin, the latter serving as a caution for breeders to beware of compensatory relationships among yield and architectural components.

Though architectural traits have been highlighted in this dissertation, and so because of the objectives of the breeding program evaluated, ideotype may incoporate other traits, morphological as well as biochemical, phenological and other physiological traits. Consumer preference may dictate the consideration of certain traits such quality.

CHAPTER THIRTEEN

SUMMARY AND CONCLUSIONS

The plant breeder does not always have the good fortune and luxury of meeting his/her germplasm needs from a common gene pool which would permit a smooth journey through generations without genetic barriers. Sometimes, and not infrequently, a need arises which dictates the incorporation of germplasm from close or even distant relatives, a step which is not without genetic consequences, albeit minuscule.

In addition to knowing the environment and the farmer's needs, a knowledge of the components of plant architecture, with regard to their relative importance and genetics, will not only aid in an effective design of a crop ideotype but will be useful in determining the breeding strategy to adopt to achieve the desired objectives.

This dissertation evaluated a phenotypic recurrent selection breeding program aimed at recombining the desirable type II erect architecture of the navy and tropical small-seeded black beans with the large-seededness of type III pinto beans. Five recurrent selection cycles were evaluated at two locations, namely, East Lansing in Michigan, in the USA, and Chimaltenango in Guatemala, in Central America. With the exception of days to maturity, only post-harvest data were collected.

Various genetic, statistical and multivariate procedures were employed to analyse the data to understand, among other things, a) the statistical association among bean traits and their patterns of change under recurrent selection, b) the stability of traits in different environments, c) the realtive importance of components of bean plant architecture and their genetic control, and d) the relationship between plant architecture and seed size.

Empirical evidence accrued warrants the following conclusions:

1. Architecture, as complex as it may be, can be scored qualitatively for effective selection. This score was found to be stable over environments since the components of architecture changed only in scale and not in rank from one environment to another.

2. Optimum bean plant architecture was defined principally by height, hypocotyl diameter, branch angle and the number of pods in the middle third of the plant, the last trait being a proxy trait for the less readily scorable but effective indicator of plant architecture, the number of pods on the main stem. A good architype would have high

values of all these traits, except branch angle in which a small value is prefered.

3. Compensatory relationships existed among the bean traits studied. These may be developmental in origin since they were infrangible under repeated intermating. Caution must be excercised when components of architecture are targeted for selective improvement.

4. Optimum plant architecture was recovered _in toto_ in the original cycle of selection and appeared to have been inherited _en bloc_, suggesting a tight linkage of the major genes controlling this quantitative trait.

5. The architectural traits were effectively associated with the parents from the small-seeded architectural germplasm pool while the seed and pod tratis, with the exception of seednum (number of seeds per pod), were entirely associated with the large-seeded pinto germplasm pool. This provided circumstantial evidence for linkage in the repulsion phase between plant architecture and large seed size.

6. Mating between the two diverse germplasm pools encountered significant barriers to free recombination between architecture and large seed size in the early cycles. Seed size was gradually accumulated as opposed to the _in toto_ recovery of the architectural traits. The remarkably fairly

regular amounts of increase in seed size from one cycle to another may indicate the additive nature of genetic control of seed size in beans.

7. There was evidence of a possible physiological-genetic upper limit to expression of traits such as seed number per pod, this ceiling being eight in this case.

8. The architecture and the large seed-pod genes appeared to be under the control of relatively independent genetic systems, being loaded mostly independently in the principal factor analysis.

9. The principal architectural and seed-pod traits, in the preliminary investigation, were low to moderately highly heritable, on the basis of broad-sense estimates from single row plots at one location.

10. Architectural and seed-pod traits changed in scale from one environment to another.

11. The principal sources of divergence between the two sources of germplasm were seed weight and number of seeds per pod.

12. Phenotypic recurrent selection was effective in recombining erect plant architecture and large seed size into a new pinto ideotype.

13. It was possible to demonstrate the extent of recombination by using principal component analysis. This procedure is superior to that proposed by Andersen (1939) since the fomer allows the researcher to study recombination involving more traits than the limit of three imposed by the latter.

LITERATURE CITED

1. Adams, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean,*Phaseolus vulgaris*. Crop Sci. 7:505 - 510.

2. Adams, M.W. 1973. Plant arhcitecture and physiological efficiency in the field bean, pp. 266 - 278. *In*: Potentials of field beans and other food legumes in Latin America. Series Seminars No. 2E. Cali, Colombia (Centro Internacional de agricultura Tropical).

3. Adams, M.W. 1977. An estimation of homogeneity in crop plants with special reference to genetic vulnerability in the dry bean, *Phaseolus vulgaris L.*. Euphytica 20:665 -679.

4. Adams, M.W. 1982. Plant architecture and yield breeding. Iowa State Journal of Research. Vol 56, No. 3:225 - 254.

5. Adams, M.W. and J.V. Wiersma. 1971 . An adaptation of principal components analysis to an assessment of genetic distance. Research Report, Technical Information. Mich. Agric. Expt. Stn.

6. Akoroda, M.O. 1983. Principal components analysis and metroglyph of variation among Nigerian yellow yams. Euphytica 32:565 - 573.

7. Anderson, E. 1939. Recombination in specie crosses.*In* Architecture of germplasm. John Wiley, New York and London. pp 669 - 697.

8. Aryeetey, A.M. and E. Laing. 1973. Inheritance of yield components and their correlation with yield in cowpea (*Vigna unguiculata* L. Walp). Euphytica 22:386 - 392.

9. Beaver, J.S. and R.R. Johnson. 1981. Yield stability of determinate soybeans adapted to the Northern United States. Crop Sci. 21:449 - 454.

10. Bos, I. 1977. More arguments against intermating F_2 plants of a self-fertilizing crop. Euphytica 26: 33 - 46.

11. Bramel, P.I., P.N. Hinz, and D.E. Green. 1984. Use of principal factor analysis in the study of three stem termination types of soybean. Euphytica 33: 387 - 400.

12. Briggs, F.N. and P.F. Knowles. 1967. Introduction to plant breeding. Rheinhold Publishing Corporation.

13. Clausen J. and Wm. M. Heisey. 1960. The balance between coherence and variation in evolution. Proc. Nat. Aca. Sci. 46: 494 - 506.

14. Compton W.A. 1968. Selection in self-pollinated crops without extensive crossing. Crop Sci. 8:773.

15. Cooley, W.W. and P.R. Lohnes. 1971. Multivariate data analysis. John Wiley and Sons, Inc.

16. Coyne, D.P. 1968. Correlation, heritability and selection of yield components in field beans, Phaseolus vulgaris L. Proc. Am. Soc. Hort. Sci. 93:388 - 396.

17. Coyne, D.P. 1965. A genetic study of 'crippled' morphology resembling virus symptoms in Phaseolus vulgaris L. J. Heredity 56:162 - 176.

18. Coyne, D.P. 1980. Modification of plant architecture and crop yield by breeding. Hort. Science 15:244 - 247.

19. Croissant, G.L. and J.H. Torrie. 1971. Evidence of non-additive effects and linkage in two hybrid populations of soybeans. Crop Sci. 11:675 - 677.

20. Davis, D.W. and J.H. Frazier. 1964. The evidence of three abnormalities in F2 progeny of crosses between true bushes and Blue Lake derived bush snap beans. Ann. Rept. Bean. Impr. Coop. 7:14 - 16.

21. Denis, J.C. and M.W. Adams. 1978. A factor analysis of plant variables related to yield in dry beans. I. Morphological traits. Crop Sci. 18:74 - 78.

22. Dobzhansky, T.H. (1948). Genetics of natural populations XVIII. Experiments of chromosomes of Drosophila psuedobscura from different geographic regions. Genetics 33:588 - 602.

23. Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17:385 - 403.

24. Donald, C.M. 1979. A barley breeding programme based on an ideotype. J. Agric. Sci. Camb. 93:261 - 269.

25. Drabo, I., R. Redden, J.B. Smithson and V.D. Aggarwal. 1984. Inheritance of seed size in cowpea (Vigna unguiculata L. Walp). Euphytica 33:929 - 934.

26. Duarte, R.A. and M.W. Adams. 1972. A path coefficient analysis of some yield component interrelations in field bean (Phaseolus vulgaris (L.). Crop Sci. 12:579 - 582.

27. Ecochard, E. and Y. Ravelomanantsoa. 1982. Genetic correlations derived from full-sib relationship in soybean (Glycine max L. Merr.). Theor. Appl. Genet. 63:9 - 15.

28. Fredrickson, L.J. and W.E. Kronstad. 1985. A comparison of intermating and selfing following selection for heading date in two diverse winter wheat crosses. Crop Sci. 25:555 - 560.

29. Green, Van de. 1971. Introduction to multivariate analysis for the social sciences. W.H. Freeman and Co. San Fransisco.

30. Gepts, P. 1984. Nutritional and evolutionary implications of phaseolin seed protein variability in common bean (Phaseolus vulgaris L.). Theol. Appl. Genet. 63:17 - 22.

31. Ghaderi, A. and M.W. Adams. 1981. Preliminary studies on the inheritance of structural components of plant architecture. Ann. Rept. Bean. Impr. Coop. 22:31 - 35.

32. Ghaderi, A., M.W. Adams and A.W. Saettler. 1982. Environmental response patterns in commercial classes of common bean (Phaseolus vulgaris L.). Theor. Apppl. Genet. 63:17 - 22.

33. Ghaderi, A., G.L. Hosfield, M.W. Adams and M.A. Ubersax. 1984. Variability in culinary quality, component interrelationships, and breeding implications in navy and pinto beans. J. Amer. Soc. Hort. Sci. 109:85 - 90.

34. Ghaderi, A., M.W. Adams and A.M. Nassib. 1984. Relationship between genetic distance and heterosis for yield and morphological traits in dry edible bean and faba bean. Crop Sci. 24:37 - 42.

35. Gouk, H.P., J.C. Wynne and H.T. Stalker. 1986. Recurrent selection within a population from an interspecific peanut cross. Crop Sci. 26:249 - 253.

36. Grafius, J.E. 1964. A geometry for plant breeding. Crop Sci. 7:505 - 510.

37. Guertin, W.H., and J.P. Bailey, Jr. 1970. Introduction to modern factor analysis. Edward Brothers, Inc. Ann Abor Michigan.

38. Hanson, W.D. 1959. The breakup of initial linkage blocks under selected mating system. Genetics 44: 857 - 863.

39. Harman, H.H. 1976. Modern factor analysis. 3rd ed. University of Chicago Press. Chicago.

40. Harmsen, R.H. 1983. Genetics and developmental inter-relationships of architectural traits in beans (Phaseolus vulgaris L.) with emphasis on branching. MSc. disseration. Michigan State University, East Lansing, Michigan.

41. Hull, F.H. 1945. Recurrent selection for specific combining ability in corn. J. Am. Soc. Agron. 37:134 - 145.

42. Jenkins, M.T. 1940. The segregation of genes affecting yield of grain in maize. J. Am. Soc. Agron. 32: 55 - 63.

43. Jennings, P.R. 1964. Plant type as a rice breeding objective. Crop Sci. 4:13 - 15.

44. Jensen, N.F. 1971. A diallel selective mating system for cereal breeding. Crop Sci. 10:629 - 635.

45. Johnson, E.C., K. S. Fisher, G.O. Edmeades and A.F.E. Palmer. 1986. Recurrent selection for reduced plant height in lowland tropical maize. Crop Sci. 26:253 - 260.

46. Kelly, J.D., M.W. Adams, A.W. Saettler, G.L. Hosfield and A, Ghaderi. 1984. Registration of C-20 navy bean. Crop Sci. 24:822.

47. Kelly, J.D. and M.W. Adams. 1987. Phenotypic recurrent selection in ideotype breeding of pinto beans. Euphytica 36:69 - 80.

48. Kendall, M.G. 1965. A course in multivariate analysis. Charles Griffin and Co. London.

49. Kenworthy, W.J and C.A Brim. 1979. Recurrent selection in soybeans. I. Seed yield. Crop Sci. 19:315 - 318.

50. Khadr, F.H. and K. J. Frey. 1965. Effectiveness of recurrent selection in oat (Avena sativa L.) breeding. Crop Sci. 5:349 - 353.

51. Kwon, S.H. and J.H. Torrie. 1964. Visual discrimination for yield in two soybean populations. Crop Sci. 4:196 - 198.

52. Lee, J. and P.J. Kaltsikes. 1973. Multivariate statistical analysis of grain yield and agronomic characters in Durum wheat. Theor. Appl. Genet. 43: 213 - 221.

53. Lee, J. and P.J. Kaltsikes. 1973. The application of Mahalanobis's generalized distance to measure genetic divergence in Durum wheat. Euphytica 22: 124 - 131.

54. Mather, K. (Ed). 1973. Genetic structure of populations Chapman and Hall Publ. London. 197 pp.

55. Meredith, Jr W.R. and R.R. Bridge. 1971. Breakup of linkage blocks in cotton, Gossypium hirsutum L. Crop Sci. 11:695 - 698.

56. Miller, P.A and J.O. Rawlings. 1967. Breakup of initial linkage blocks through intermating in a cotton breeding population. Crop Sci. 7:199 - 204

57. Miller, J.E. and W.R. Fehr. 1979. Direct and indirect recurrent selection for protein in soybeans. Crop Sci. 19:101 - 106.

58. Mock, J.J. and R.B. Pearce. 1975. An ideotype of maize. Euphytica 24:613 - 623.

59. Narayan, R.K.S. and A.J. Macefield. Adaptive responses and genetic divergence in a world germplasm collection of chick pea (Cicer arietum L.). Theor. Appl. Genet. 47:179 - 187.

60. Nienhius, J. and S.P. Singh. 1985. Effects of location and plant density on yield and structural traits in dry beans. Crop Sci. 25:579 - 584.

61. Pederson, D.G. 1974. Arguments against intermating before selection in a self-fertilizing species. Theor. Appl. Genet. 45:157 - 162.

62. Romagosa, I., R.J. Hecker, T. Tsuchiya and J.M. Lasa. 1986. Primary trisomics in sugarbeet. I. Isolation and morphological characterization. Crop Sci. 26: 243 - 249.

63. Rao, C.R. 1973. Linear statistical inference. Sankya A 26:329 - 358.

64. Rao, G.V.S. and R.S. Paroda. 1982. Factor analysis in cluster bean (Cyamopsis tetragonoloba (L.) Taub). Thoer. Appl. Genet. 62:173 - 276.

65. Rutledge,J.J., E.J. Eisen and J.E. Legates (1973). An experimental evaluation of genetic correlation. Genetics 75:709 - 726.

66. Statistical Analysis System (SAS). 1985. SAS Institute Inc. Box 8000, Cary NC 27511-8000.

67. Singh, S.P. 1982. A key for identification of different growth habits of Phaseolus vulgaris L. Ann. Rept. Bean Impr. Coop.(New York). 25:92 - 94.

68. Singh, S.P. and J.A. Gutierrez. 1984. Geographical distribution of the DL_1 and DL_2 genes causing hybrid dwarfism in Phaseolus vulgaris L., their association with seed size, and their significance to breeding. Euphytica 33:337 - 345.

69. Stophert, P.R. and A.H. Meyburg. 1971. Survey sampling and multivariate analysis for social scientists and engineers. Lexington Books, D.C. Heath and Co. Lexington, Mass. Toronto.

70. Sullivan, J.G. and F.A. Bliss. 1983. Recurrent mass selection for increased seed yield and protein percentage in the common bean (Phaseolus vulgaris L.). J. Amer. Soc. Hort. Sci. 108:42 - 46.

71. Vairavan, S., E.A. Siddiq, V. Arunachalam and M.S. Swaminathan. 1973. A study on the nature of genetic divergence in rice from Assam and North East Himalayas. Theor. Appl. Genet. 43:213 - 221.

72. Van de Logt, M.B., M.A. Brinkman and R.A. Forsberg. 1984. Variance components and linkage effects for quantitatively inherited traits in two barley crosses. Crop Sci. 24:322 - 327.

73. Walters, D.E. and A.M. Evans. 1978. The use of multivariate statistical techniques in the evaluation of bean characteristics. Ann. Rept. Bean Impr. Coop. 21:63 - 66.

74. Walton, P.D. 1971. The use of factor analysis in determining characters for yield selection in wheat. Euphytica 20:416 - 421.

75. Walton, P.D. Factor analysis of yield in spring wheat (*Triticum aestivum* L.). Crop Sci. 12:731 - 733.

Appendix A

Trait means for parents and five recurrent selection cycles at two locations.

Table 1. Means of traits measured on parents at two locations

Trait	Height (cm)			Architype	
Location	Chimatenango	East Lansing		Chimalenango	East Lansing
Parent			Parent		
N3	32.67a		N2	3.33a	5.00
N1	31.67a		N3	3.00ab	
N2	30.33ab	42.00a	N1	2.67bc	
P1	28.33b		P1	2.33c	
P3	25.67c		P3	2.33c	
P2	19.00d	42.67a	P2	1.67d	1.33b
SE	.78	1.37		.14	.24

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT. N = navy, P = pinto.

Table 2. Means of traits measured on parents at two locations

Traits	Nbranch			Hypolen (cm)	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
N2	4.67a	5.33a	P2	3.67a	2.22a
N3	4.33a		N1	2.83b	
N1	3.67b		N3	2.83b	
P3	3.33b		P1	2.67c	
P2	2.67c	6.00a	P3	2.00c	
P1	2.33c		N2	2.00c	3.33a
SE	.12	.75		.13	.67

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT. N = navy, P = pinto.

Table 3. Means of traits measured on parents at two locations

Trait	Hypodiam (mm)			Lowpodht (cm)	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
N2	10.33a	9.67a	N1	11.00a	
N1	9.67a		N2	9.00b	13.00a
N3	8.33b		P2	8.33bc	3.33b
P3	7.00c		P1	7.33bc	
P1	6.67c		N3	6.67cd	
P2	6.33c	5.67b	P3	5.33d	
SE	.23	.67		.59	1.43

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT. N = navy, P = pinto.

Table 4. Means of traits measured on parents at two locations

Trait	Angle			Nodesup	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
P2	18.00a	40.00a	N3	3.33a	
P3	42.33b		P3	3.00ab	
N1	25.67bc		N1	2.67bc	
P1	27.17bc		P1	2.67bc	
N3	28.67c		N2	2.67bc	3.33b
N2	35.67d	23.33b	P2	2.33c	2.00a
SE	1.15	6.24		.14	.24

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT. N = navy, P = pinto.

Table 5. Means of traits measured on parents at two locations

Trait	Nodesmid			Nodeslow	
Location	Chimalt- enango	East Lansing		Chimalt- enango	East Lansing
Parent			Parent		
N1	2.67a		N3	6.67a	
P3	2.33b		N1	6.00a	
N2	2.33ab	3.33a	N2	5.00b	6.33a
P2	2.00bc	2.67a	P2	5.00b	6.33a
N3	2.00bc		P1	4.67b	
P1	1.67c		P3	4.67b	
SE	.10	.33		.30	.33

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT.
N = navy, P= pinto.

Table 6. Means of traits measured on parents at two locations

Trait	Podsup			Podsmid	
Location	Chimalt- enango	East Lansing		Chimalt- enango	East Lansing
Parent			Parent		
N1	4.00a		N2	13.67a	20.00a
N2	3.67a	7.00a	N1	13.00ab	
P1	3.00ab		N3	9.67bc	
P2	3.00ab	1.67b	P3	8.00c	
N3	1.67bc		P2	6.67c	7.00b
P3	1.33c		P1	6.33c	
SE	.46	1.55		1.23	2.08

Means in the same column and followed by identical letter(s) are not significantly different at the .05 levelby DMRT. N = navy, P = pinto.

Table 7. Means of traits measured on parents at two locations

Traits	Podslow			Podsmain	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
P3	5.67a		N1	9.00a	
N3	6.67a		N3	8.67ab	
N1	2.33b		P2	7.67abc	4.00b
N2	2.33b	4.00b	N2	7.00cd	13.67a
P1	2.00b		P1	6.00cd	
P2	1.67b	9.67a	P3	5.33d	
SE	.46	1.03		.57	.05

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT. N = navy, P = pinto.

Table 8. Means of traits measured on parents at two location

Trait	Intnodup (cm)			Intnodmid (cm)	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
N3	5.83a		P1	5.27a	
P3	4.37b		N3	5.20a	
P1	4.33b		P3	4.07b	
N1	3.20c		N2	3.67bc	3.00a
P2	2.67cd		P2	3.20cd	3.67a
N2	2.50d		N1	2.83d	
SE	.21			.17	.62

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT. N = navy, P = pinto.

Table 9. Means of traits measured on parents at two locations.

Trait	Intnodlow (cm)			Podwidth (mm)	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
P1	2.60a		P2	12.00a	14.33a
P2	2.20b	2.33a	P1	10.67b	
P3	2.00b		P3	10.67b	
N3	1.97b		N1	9.67c	
N2	1.80bc	1.67b	N2	9.17d	10.33b
N1	1.47c		N3	8.83e	
SE	.12	.33		.09	.24

Means in the same column and followed by identical letter(s) are not significanlty different at the .05 level by DMRT. N = navy, P = pinto.

Table 10. Means of traits measured on parents at two locations.

Trait	Podlen (cm)			Seednum	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
P3	14.33a		N3	6.33a	
P1	12.00b		P1	5.67b	
N2	10.00c	9.67a	N1	5.67b	
N3	10.00c		N2	5.67b	7.00a
P2	9.33d	10.83a	P3	5.33bc	
N1	8.17		P2	5.00c	6.67b
SE	.15	.44		.19	.47

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level by DMRT.

Table 11. Means of traits measured on parents at two locations.

Trait	Seedwt (gm)			Maturity (days)	
Location	Chimaltenango	East Lansing		Chimaltenango	East Lansing
Parent			Parent		
P3	40.33a	36.07a	P1	81.6	
P1	37.00b		P2	78.6	
P2	32.67c		P3	77.0	
N1	20.67d		N1	114.5	
N3	19.33de		N2	99.3	
N2	17.33e	20.40b	N3	111.3	
SE	.69	.84		.52	

Means in the same column and followed by identical letter(s) are not significantly different at the .05 level. N = navy, P = pinto.

Table 12. Means of bean traits in various cycles and at two locations.

Trait	Height (cm)		Architype	
Location	East Lansing	Chimaltenango	East Lansing	Chimaltenango
Cycle				
0	**49.42d**	**32.47b**	**2.34d**	**2.49c**
1	**52.31a**	**29.65c**	**2.43c**	**2.57bc**
2	**51.92ab**	**28.87a**	**2.90b**	**2.60b**
3	**50.90c**	**29.57c**	**3.06a**	**2.54c**
4	**51.84b**	**34.48d**	**3.03a**	**2.86a**
SE	.101	.068	.008	.010

Means followed by identical letters are not significantly different at the .01 level by the DMRT

Table 13. Means of bean traits in various cycles and at two locations.

Trait	Nbranch		Hypolen(cm)	
Location	East Lansing	Chimaltenango	East Lansing	Chimaltenango
Cycle				
0	**4.45a**	**3.77a**	**2.81d**	**2.32c**
1	**4.50a**	**3.65b**	**4.12c**	**2.79b**
2	**4.47a**	**3.57bc**	**4.25b**	**3.11a**
3	**3.87b**	**3.51c**	**4.26b**	**3.34a**
4	**3.86b**	**3.44a**	**4.41a**	**3.58b**
SE	.017	.014	.025	.042

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 14. Means of bean traits in various cycles and at two locations.

Traits	Hypodiam (mm)		Lowpodht (cm)	
Location	East lansing	Chimaltenango	East Lansing	Chimaltenango
Cycle				
0	7.29d	7.70d	9.39e	7.06c
1	7.22d	8.13b	13.28c	7.69b
2	7.57b	7.60e	14.29a	8.35a
3	7.39c	7.84c	13.74b	7.13c
4	7.68a	8.50a	12.42d	7.75b
SE	.021	.014	.070	.050

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 15. Means of bean traits in various cycles and at two locations.

Traits	**Angle**		**Nodesup**	
Location	**East Lansing**	**Chimaltenango**	**East Lansing**	**Chimaltenango**
Cycle				
0	69.67e	72.14e	3.48c	2.94a
1	71.91c	72.79d	3.26d	2.57c
2	74.15a	73.76c	3.52c	2.86b
3	73.17b	75.16a	3.67b	2.85b
4	71.16d	74.20b	3.89a	2.90ab
SE	**.110**	**.031**	**.013**	**.010**

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 16. Means of bean traits in various cycles and at two locations.

Traits	Nodesmaid		Nodeslow	
Location	East	Chimaltenango	East	Chimaltenango
Cycle				
0	2.99d	2.43c	6.63ab	4.00b
1	3.03c	2.22d	6.58b	5.32a
2	6.20a	2.52ab	6.65a	4.98a
3	3.20a	2.47bc	6.48c	5.05a
4	3.08b	2.54a	6.51c	5.50a
SE	.005	.010	.012	.010

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 17. Means of bean traits in various cylcles and at two locations.

Traits	Podsmain		Podlen (cm)	
Location	East Lansing	Chimaltenango	East Lansing	Chimaltenango
Cycle				
0	9.43a	9.32a	10.27e	9.60d
1	7.86d	6.84c	11.32b	10.35c
2	8.33c	7.75b	11.19d	10.45b
3	8.47b	6.02d	11.27c	10.45b
4	7.80d	7.90b	11.50a	10.68a
SE	.030	.034	.007	.010

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 18. Means of bean traits in various cycles and at two locations.

Traits	**Podwidth (mm)**		**Seednum**	
Location	**Lansing**	**Chimaltenango**	**East**	**Chimaltenango**
Cycle				
0	10.50e	10.67e	6.14a	5.24b
1	12.24c	12.77c	5.54c	5.21b
2	11.28d	12.26d	5.78b	5.50a
3	12.53a	13.79b	5.49d	4.97c
4	12.32b	13.98a	5.77b	4.99c
SE	**.015**	**.010**	**.030**	**.010**

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 19. Means of bean traits in various cycles and at two locations.

Traits	**100-seedwt (gm)**		**Yield (gm)**	
Location	**East Lansing**	**Chimaltenango**	**East Lansing**	**Chimaltenango**
Cycle				
0	13.98e	14.01e	41.26a	25.39a
1	17.80c	17.11c	35.40c	19.52c
2	15.58d	16.25d	34.55d	20.13cd
3	18.34b	18.10b	35.01cd	20.26c
4	20.10a	19.95a	40.50b	21.76b
SE	**.021**	**.014**	**.163**	**.106**

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 20. Means of bean traits in various cycles and at two locations.

Trait	**Totpods**		**Podsup**	
Location	**East Lansing**	**Chimaltenango**	**East Lansing**	**Chimaltenango**
Cycle				
0	34.10a	21.40a	6.1	3.64b
1	26.31c	17.30c	6.3	3.59b
2	26.92b	17.46c	5.5	4.20a
3	23.86e	14.21d	4.6	3.19c
4	24.58d	19.50b	4.7	3.03d
SE	.100	.098	.194	.014

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 21. Means of bean traits in various cycles and at two locations.

Trait	**Podsmid**		**Podslow**	
Location	**East**	**Chimaltenango**	**East**	**Chimaltenango**
Cycle				
0	18.70	12.75a	9.3	5.01ab
1	15.5	8.91d	4.7	4.80b
2	16.1	10.23c	5.3	3.03c
3	14.0	8.34e	5.3	2.68c
4	14.6	10.48b	5.2	2.49c
SE	.345	.020	.220	.102

Means followed by identical means are not significantly different at the .01 level by the DMRT.

Table 22. Means of bean traits in various cycles and two locations.

Trait	**Intnodup (cm)**		**Intnodmid (cm)**	
Location	**East Lansing**	**Chimalt-enango**	**East Lansing**	**Chimalt-enango**
Cycle				
0	8.14a	4.90a	5.90a	4.55b
1	6.30c	3.73c	5.67b	4.36c
2	6.24c	3.74c	5.22c	4.13d
3	6.84b	3.62d	5.61b	4.17d
4	6.28c	4.75b	5.55b	4.76a
SE	.035	.010	.029	.014

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Table 23. Means of bean traits in various cycles and at two locations.

Traits	**Intnodlow (cm)**		**Maturity (days)**	
Location	**East Lansing**	**Chimalt-enango**	**East Lansing**	**Chimalt-enango**
Cycle				
0	2.46a	2.16b		85.14b
1	2.24c	2.04c		83.32d
2	2.34b	1.99d		88.19a
3	2.46a	1.89d		83.36d
4	2.47a	2.25a		84.19c
SE	.008	.031		.097

Means followed by identical letters are not significantly different at the .01 level by the DMRT.

Appendix B

Traits selected by the tepwise multiple linear regression procedure in parents, six crosses, and five recurrent selection cycles.

Table 1. Architectural traits selected from C_0 by different stepwise multiple regression procedures with architype as dependent variable.

	Location			
	East Lansing		Chimaltenango	
	Trait	prob. > F	Trait	prob. > F
	Podsmain	***	Height	***
	Height	***	Intnodlow	**
	Intnodup	**	Intnodup	**
	Nodesup	*	Hypodiam	**
	Hypodiam	*	Podsmid	**
	Angle	*	Angle	*
	Intnodlow	+	Nodeslow	+
	Nbranch	+	Podsmain	+
R^2 :	11.12% - 12.51%		46.06% - 47.35%	

***, **, *, + : significant at .001, .01, .05, and .10 level, respectively.

Table 2. Architectural traits selected in C_1 by four different stepwise multiple regression procedures from data from two locations, with architype as dependent variable.

	Location			
	East Lansing		Chimaltenango	
	Trait	prob. > F	Trait	prob. > F
	Hypodiam	***	Podsmid	***
	Angle	***	Height	***
	Podsmid	***	Nodeslow	***
	Podsmain	***	Lowpodht	***
	Hypolen	**	Podslow	**
	Height	**	Podsup	*
	Nodesup	**	Intnodmid	+
	Podslow	**	Nbranch	+
	Intnodlow	**	Hypodiam	+
	Nodeslow	+	Nodesup	+
R^2:	31.45% - 33.72%		57.04% - 58.43%	

***, **, *, +: significant at .001, .01, .05,and .10 level respectively.

Table 3. Architectural traits selected in C_2 by four different multiple regression procedures from data from two locations, with architype as dependent variable.

Location			
East Lansing		Chimaltenango	
Trait	prob. > F	Trait	prob. > F
Intnodup	***	Height	***
Intnodmid	***	Podsmid	***
Nodesmid	***	Hypodiam	*
Hypodiam	***	Podslow	*
Podsup	***	Angle	*
Podmain	*	Intnodmid	+
Podslow	*	Lowpodht	+
Intnodlow	+	Podsup	+
R^2 : 16.73% - 17.40%		58.08% - 61.42%	

***, **, *, + : significant at .001, .01, .05, .10 level, respectively.

Table 4. Architectural traits selected in C_3 by four different stepwise multiple regression procedures from data from two locations, with architype as dependent variable.

Location			
East Lansing		Chimaltenango	
Trait	prob. > F	Trait	prob. > F
Angle	***	Nbranch	***
Podmain	***	Nodesmid	***
Nbranch	***	Intnodup	**
Hypodiam	***	Height	**
Podsup	***	Hypodiam	**
Nodesmid	**	Podsup	**
Hypolen	**	Intnodmid	*
Intnodup	*	Intnodlow	*
		Podsmid	*
R^2 : 28.40% - 29.01%		72.87% - 72.98%	

***, **, * : significant at .001, .01, .05 levels, respectively.

Table 5. Architectural traits selected in C_4 by the stepwise multiple regression procedure for data from two locations, with architype as dependent variable.

Location			
East Lansing		Chimaltenango	
Trait	prob. > F	Trait	prob. > F
Hypodiam	***	Height	***
Height	***	Podsmid	**
Angle	***	Intnodup	**
Nbranch	***	Hypodiam	*
Podmain	*	Podsup	+
Intnodmid	+	Lowpodht	+
R^2 : 29.66% - 30.58%		48.24% - 55.98%	

***, **, *, + : significant at .001, .01, .05, .10 levels, respectively.

Table 6. Architectural traits selected in two crosses by the stepwise multiple regression procedure, with architype as dependent variable.

Cross 1		Cross 2	
Trait	prob. > F	Trait	prob. > F
Hypodiam	***	Angle	***
Nbranch	**	Hypodiam	***
Angle	**	Intnodmid	*
Height	*	Podsmain	*
Nodesmid	*	Intnodlow	+
Podsup	*		
Nodeslow	*		
Intnodlow	*		
R^2			

***, **, *, + : significant at .001, .01, .05, and .10 levels, respectively.

Table 7. Architectural traits selected in two crosses by the stepwise multiple regresssion procedure with architype as dependent variable.

Cross			
3		4	
Trait	prob. > F	Trait	prob. > F
Hypodiam	***	Podsmain	***
Angle	***	Angle	***
Nodesup	*	Hypodiam	***
Lowpodht	*	Podslow	***
Intnodup	+	Nodesmid	**
Hypolen	+	Lowpodht	**
		Podsmid	*
		Intnodlow	*
R^2			

***, **, *, + : significant at .001, .01, .05, and .10 levels respectively.

Table 8. Architectural traits selected in two crosses by the stepwise multiple regression procedure with architype as dependent variable.

Cross			
5		6	
Trait	prob. > F	Trait	prob. > F
Podsmid	***	Hypodiam	***
Podsup	**	Angle	***
Intnodmid	**	Height	**
Lowpodht	*	Nodeslow	**
Angle	*	Podsup	**
Nodesmid	*	Hypolen	*
Hypodiam	+	Podslow	*
Nodesup	+	Intnodlow	+
R^2 :			

***, **, *, + : significant at .001, .01, .05, and .10 levels, respectively.

Appendix C

Phenotypic character associations among bean traits in parents and F_3 families.

Table 1a. Phenotypic character association (r) among bean traits in the parents.

	Height	Architype	Nbranch	Hypolen	Hypodiam	Angle
Architype	.543**					
Nbranch	.530**	.390*				
Hypolen	-.395*	-.020	-.295			
Hypodiam	.757***	.647***	.578**	-.342		
Angle	.445*	.528**	.166	.247	.351	
Podsup	.547**	.420*	.677***	-.236	.592**	.262
Podsmid	.822***	.619***	.659***	-.331	.829***	.409*
Podslow	.655***	.083	.108	-.444*	.476**	.042
Nodesup	.174	-.052	-.179	-.513**	.138	-.198
Nodesmid	.156	.066	-.088	-.051	.180	.145
Nodeslow	.769***	.331	.353	-.462*	.478***	.294
Lowpodht	.271	.470*	.399*	.117	.310	.473**
Podsmain	.495**	.600***	.177	.169	.217	.411*
Podwidth	-.508**	-.463*	-.255	.330	-.433*	-.225
Podlen	-.678***	-.705***	-.289	.237	-.623***	-.523**
Seednum	.312	.029	-.145	-.490**	.220	-.204
Seedwt	-.655***	-.646***	-.260	.388*	-.775***	-.337
Intnodup	.569**	.052	.238	-.564**	.220	-.134
Intnodlow	.459**	.232	.203	-.468**	.552**	-.013

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 1b. Phenotypic character association (r) among bean traits in the parents.

	Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
Podsmid	.840***					
Podslow	.191	.469*				
Nodesup	.239	.229	.4727**			
Nodesmid	-.185	.023	.347	.097		
Nodeslow	.370*	.508**	.630***	.412*	.216	
Lowpodht	.441*	.449*	-.256	-.416*	-.410*	-.045
Podsmain	.091	.292	.341	-.038	.275	.481
Podwidth	-.502**	-.488**	-.315	-.216	.112	-.502**
Podlen	-.479**	-.635***	-.236	-.145	-.214	-.389*
Seednum	-.076	.107	.539***	.368	.382	.511**
Seedwt	-.515**	-.664***	-.436*	-.373*	-.308	-.465*
Intnodup	.212	.309	.386	.082	-.030	.486**
Intnodlow	.198	.437*	.556**	.093	.210	.149

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 1c. Phenotypic character association (r) among bean traits in the parents.

	Lowpodht	Podmain	Podwidth	Podlen	Seednum	Seedwt	Int'up
Podsmain	.015						
Podwidth	-.133	-.377*					
Podlen	-.291	-.484**	.432*				
Seednum	-.377	.138	-.380*	-.082			
Seedwt	-.173	-.314	.569**	.756***	-.429*		
Intnodup	.165	.100	-.303	-.292	.357	-.230	
Intnodlow	.148	.132	-.360	-.404*	.206	-.491**	.442*

***, **, * :significant at .001, .01, and .05 levels, respectively.

Table 2a. Phenotypic character association (r) among bean traits in the F_3 families.

	Height	Architype	Nbranch	Hypolen	Hypodiam	Angle
Architype	-.020					
Nbranch	.199***	-.063				
Hypolen	.066	.025	-.112**			
Hypodiam	.427***	.211***	.354***	-.037		
Angle	-.102*	.278***	-.204***	.060	-.228***	
Podsup	.207***	.001	.256***	-.016	.312***	-.082
Podsmid	.470***	.077	.463***	-.019	.517***	-.289***
Podslow	.465***	-.041	.308***	-.149***	.321***	-.173***
Nodesup	.103*	-.019	-.038	-.066	.101*	-.002
Nodesmid	.206***	.001	.028	.134**	.145***	-.001
Nodeslow	.482***	.070	.157***	-.155***	.303***	-.108**
Lowpodht	.105*	.083	-.021	.211***	.073	.018
Podsmain	.138**	.219***	-.108**	-.098*	.160***	-.016
Podwidth	.045	-.227***	-.095*	-.023	-.065	-.143***
Podlen	.017	.068	.078	-.057	.150***	-.027
Seednum	.155***	.150***	-.009	.102*	.247***	-.035
Seedsize	.004	-.089*	.045	-.038	-.027	-.148***
Intnodup	.437***	-.096*	.131**	-.049	.073	-.095*
Intnodlow	.336***	.012	-.046	.025	.191***	-.085

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 2b. Phenotypic character association (r) among bean tratis in F_3 families.

	Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
Podsmid	.370***					
Podslow	-.006	.297***				
Nodesup	.060	.029	.001			
Nodeslow	.060	.169***	.029	.250***		
Lowpodht	.192***	.304***	.496***	.157***	.146***	
Podsmain	.146***	.021	-.314***	-.012	.125**	-.135**
Podwidth	.171***	.192***	.250***	.080	.051	.245***
Podlen	-.071	-.038	.037	.023	.030	.059
Seednum	.032	.020	.180***	.052	-.097*	.065
Seedwt	.116**	.163***	.023	.059	.156***	.112**
Intnodup	.056	.180***	.356***	-.051	-.175***	.292***G2
Intnodlow	.092*	.162***	.105*	.096*	-.020	.047

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 2c. Phenotypic character association (r) among bean traits in F_3 families.

	Lowpodht	Podsmain	Podwidth	Podlen	Seednum	Seedwt	Int'up
Podsmain	-.081						
Podwidth	-.008	-.015					
Podlen	-.029	-.034	-.005				
Seednum	.139	.038	-.011	.083*			
Seedwt	-.106*	-.094*	.033	-.021	-.211***		
Intnodup	-.069	.092*	.015	.077	-.074	.074	
Intnodlow	.116**	.123**	.022	.057	.008	-.026	.301***

***, **, * : significant at .001, .01, and .05 levels, respectively.

Appendix D

Canonical correlations between architectural traits and seed-pod traits in five phenotypic recurrent selection cycles

Table 1. Canonical correlation between architectural traits and seed-pod traits in various selection cycles in East Lansing.

	Cycle				
Canonical variable	C_0	C_1	C_2	C_3	C_4
1	.409***	.497***	.428***	.426***	.622***
2	.311*	.319***	.352***	.380***	.455***
3	.213	.290*	.283**	.317**	.358*
4	.157	.186	.217	.169	.319

***, **, *, significant at .001, .01, and .05 levels, respectively.

Table 2a. Canonical redundancy analysis.

Standardized variance of the seed-pod traits explained by:

a. Their own canonical variables		b. the architype variables	
Proportion	Cumulative	Proportion	Cumulative
.2204	.2204	.0545	.0545
.1940	.4144	.0198	.0743
.3309	.7453	.0280	.1023
.2547	1.0000	.0088	.1111

Table 2b. Canonical redundancy analysis.

Standardized variance of the architype traits explained by:

a. Their own canonical variables		b. the seed-pod variables	
Proportion	Cumulative	Proportion	Cumulative
.1173	.1173	.0290	.0290
.0934	.2108	.0095	.0385
.0872	.2980	.0074	.0459
.0433	.3413	.0015	.0474

Table 3. Squared multiple correlations between the architecture variables and the canonical variables of the seed-pod traits.

	Canonical variable			
Trait	1	2	3	4
Height	.085	.100	.101	.101
Architype	.012	.015	.023	.023
Nbranch	.001	.004	.019	.022
Hypolen	.069	.096	.097	.100
Hypodiam	.038	.056	.067	.071
Lowpodht	.007	.008	.013	.019
Angle	.059	.060	.062	.062
Podsup	.004	.004	.022	.022
Podsmid	.060	.068	.073	.076
Podslow	.028	.029	.029	.029
Nodesup	.028	.029	.052	.054
Nodesmid	.046	.046	.051	.051
Nodeslow	.006	.030	.030	.032
Podsmain	.024	.027	.027	.027
Intnodup	.001	.020	.020	.021
Intnodmid	.013	.028	.028	.028
Intnodlow	.004	.029	.060	.060

Table 4. Squared multiple correlations between the seed-pod traits and the canonical variables of the architure traits.

	Canonical variable			
Trait	1	2	3	4
Podlen	.000	.022	.030	.054
Podwidth	.131	.137	.170	.170
Seednum	.086	.109	.143	.144
Seedwt	.000	.028	.064	.074

Appendix E

Principal component analysis of F_2 populations and F_3 families of beans.

Table 1. Loadings on the first six most important principal components in the F_2populations.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.4038	.2202	-.1162	-.1011	-.0745	.0654
Nbranch	.0277	.1219	.0542	.5691	.0142	.3270
Hypolen	.2034	-.1211	.0494	.2407	-.3484	-.1611
Hypolen	.3289	.0483	.0459	.1986	.2021	.1236
Angle	-.0280	-.2266	.0717	-.0927	-.0956	.3871
Podsup	.3127	-.0890	.2815	-.0012	-.1674	.1726
Podsmid	.3039	.2055	.1238	.0532	.3304	-.2066
Podslow	.0423	.3336	-.2124	-.1536	.4075	.1759
Nodesup	.1920	-.3295	.0915	-.1093	.3793	-.0795
Nodesmid	.2315	-.3159	-.1838	-.1459	-.0192	.0021
Nodeslow	.2890	.1675	-.2001	.1386	-.0527	.4444
Lowpodht	.3367	-.1108	.1428	.2318	-.2812	-.2272
Podsmain	.2712	-.0397	.1368	-.2016	.2124	.1794
Podwidth	.0187	.0530	.2678	.3595	.3105	-.3592
Podlen	.0486	.2611	-.5035	.1449	-.1333	-.2079
Seednum	.2048	-.1063	-.5220	-.0042	.0026	-.2512
Seedwt	-.2170	.2039	.0224	.2311	-.0869	.1728
Intnodup	.0133	.4088	.2114	-.2436	-.1151	-.0595
Intnodmid	.0644	.3944	.2513	-.1803	-.1511	-.1935
Intnodlow	.1914	.0987	.0808	-.3013	-.3003	.0112
PROPORTION	17.01+	15.60	9.55	7.29	6.68	5.78
CUMULATIVE	17.01	32.68	42.17	49.45	56.14	61.93

+, expressed as a percentage of total variance

Table 2. Loadings of the first six most important principal components in the F_3 families.

	PC1	PC2	PC3	PC4	PC5	PC6
Height	.3956	.0413	.1212	.1882	.1848	.2411
Nbranch	.2505	.0571	-.1554	-.5195	.0185	.0526
Hypolen	-.0691	.2084	.2994	.0372	.2802	.4521
Hypodiam	.3531	.2059	.0171	-.1598	-.0451	-.0589
Angle	-.1802	.0419	.0732	.2671	-.3571	.3210
Podsup	.2171	.2050	.1658	-.2054	-.2358	-.2968
Podsmid	.3743	.1776	.0078	-.2267	.0146	-.0617
Podslow	.3408	-.1479	-.3292	.1155	-.0148	.2810
Nodesup	.0727	.1578	-.0644	.3422	.0797	-.4370
Nodesmid	.0659	.4553	-.1095	.2463	.2771	.0065
Nodeslow	.3282	.0357	-.2609	.2619	-.0286	.1054
Lowpodht	-.0219	.2567	.4829	-.0839	.1520	-.0235
Podsmain	.1690	.0119	-.0567	.3520	-.3309	-.2490
Podswidth	.0062	-.0702	-.0450	.1903	.4016	-.2120
Podlen	.0873	-.0621	-.0460	-.0792	-.2149	.1366
Seednum	.1021	.3293	.1267	.0741	-.1519	.1625
Seedwt	-.0046	-.1915	-.2137	-.1154	.4897	-.0784
Intnodup	.2697	-.3794	.1603	.1022	.0604	.2299
Intnodmid	.1931	-.4304	.3664	-.0278	-.0566	-.1477
Intnodlow	.2015	-.1708	.4281	.1982	.0855	-.1466
PROPORTION	18.20	10.25	8.27	7.21	6.28	5.54
CUMULATIVE	18.20	28.45	36.72	43.94	50.22	55.76

+, expressed as a percentage of total variance

Appendix F

Principal factor analysis: Biological concepts associated with factors, correlations between factors at two locations and the factor loadings on the basis of all traits for various cycles.

Table 1. Correlation between principal factors extracted from data from the two locations.

Cycle	PF1 x PF1	PF2 x PF2
0	0.830 *	0.957 *
1	0.998 ***	0.883 *
2	0.858 *	0.664
3	0.914 *	0.158
4	0.608	0.102

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*, ***, significant at 0.05 and 0.001 levels respectively.

Table 2a. Biological concepts associated with principal factors extracted from parents for seed-pod traits.

Factor	Concept
1	Size (Pod length Seedwt)
2	Number (Seed number)

Table 2b. Biological concepts associated with principal factors in C_0 at two locations for seed-pod traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Pod dimension (Length/ width)	Pod dimension (Length/ width)
2	Number (Seed number)	Number (Seed number)

Table 2c. Biological concepts associated with principal factors in C_1 at two locations for seed-pod traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Number (Pod length Seed number)	Size (Seedwt Pod width)
2	Size (Pod width Seedwt)	Number (Pod length Seed number)

Table 2d. Biological concepts associated with principal factors in C_2 at two locations for seed-pod traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Number (Pod length Seed number)	Number (Seed number Pod length)
2	Size (Pod width Seedwt)	Size (Seedwt Pod width

Table 2e. Biological concepts associated with principal factors in C_3 at two locations for seed-pod traits.

	Location	
	Chimaltenango	Lansing
Factor	Concept	Concept
1	Number (Seed number Pod length)	Number (Seed number Pod length)
2	Size (Seed size Pod width)	Size (Pod width Seed size)

Table 2f. Biological concepts associated with principal factors in C_4 at two locations for seed-pod traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Number (Seed number Pod length)	Number (Seed number Pod length)
2	Size (Pod width Seedwt)	Size (Pod width Seedwt)

Table 3. Correlations among factor loadings in C_0 at two locations for architectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
PF1	.450*					
PF2		.830***				
PF3			.634**			
PF4				.068		
PF5					.610**	
PF6						.534*

***, **, *, significant at .001, .01, and .05 level, respectively.

Table 4. Correlations among factor loadings in C_1 at two locations for architectural traits.

	PF1	PF2	PF3	PF4	PF5
PF1	.776***				
PF2		.711***			
PF3			.545*		
PF4				.360	
PF5					-.501*

***, *, significant at .001, and .05 levels, respectively.

Table 5. Correlations among factor loadings in C_2 at two locations for architectural traits.

	PF1	PF2	PF3	PF4	PF5
PF1	.506*				
PF2		-.286			
PF3			.649**		
PF4				.476*	
PF5					.093

**, * , significant at .01, and .05 levels, respectively.

Table 6. Correlations among factor loadings in C_3 at two locations for architectural traits.

	PF1	PF2	PF3	PF4	PF5
PF1	.159				
PF2		.601**			
PF3			.646**		
PF4				.337	
PF5					.356

**, significant at .01 level.

Table 7. Correlations among factor loadings in C_4 at two locations for arhitectural traits.

	PF1	PF2	PF3	PF4	PF5	PF6
PF1	.840***					
PF2		.730***				
PF3			.084			
PF4				.543*		
PF5					-.037	
PF6						.163

***, *, significant at .001 and .05 levels,respectively.

Table 8. Biological concepts associated with principal factors in C_0 at two locations for architectural traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Height	Distribution (Pods) Structural (nbranch)
2	Distribution (Nodes)	Distribution (Pods)
3	Structural (Sturdiness /profile)	Height
4	Distribution (Pods)	Distribution (Nodes)
5	Structural (Sturdiness)	Structural (Sturdiness)
6	Structural (Profile)	Distribution (Pods)

Table 9. Biological concepts associated with principal factors in C_1 at two locations for architectural traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Height	Distribution (Nodes)
2	Distribution (Pods)	Structural (Profile)
3	Structural (Sturdiness / profile)	Height
4	Distribution (Pods)	Distribution (Pods)
5	Distribution (Pods)/ Structural (Sturdiness)	Structural (Sturdiness)
6		Distribution (Podsmain)

Table 10. Biological concepts associated with principal factors in C_2 at two locations for architectural traits.

	Locations	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Height	Structural (Profile /sturdiness)
2	Structural (Sturdiness) Distribution (Nodes)	Distribution (Nodes)
3	Structural (Sturdiness) Distribution (Pods)	Height Distribution (Pods)
4	Distribution (Nodes)	Distribution (Pods)
5	Structural (Profile)	Height
6		Structural (Profile)

Table 11. Biological concepts associated with principal factors in C_2 at two locations for architectural traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Height	Structural (Profile)
2	Distribution (Pods)	Height
3	Structural (Profile)	Distribution (Nodes)
4	Structural (Sturdiness)	Distribution (Pods)
5	Distribution (Pods)	Distribution (Pods)
6		Structural (Profile)

Table 12. Biological concepts associated with principal factors in C_4 at two locations for architectural traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Distribution (Pods/nodes)	Height
2	Height	Distribution(Nodes/pods)
3	Structural (Profile)	Distribution (Pods)
4	Structural (Sturdiness /profile)	Distribution (Pods)
5	Distribution (Pods)	Structural (Profile)
6	Distribution (Nodes)	Distribution (Nodes)

Table 13. Correlations among principal factors extracted at the two locations in C_0 for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6	PF7
PF1	.822***						
PF2		.247					
PF3			.543**				
PF4				.745***			
PF5					.668***		
PF6						.498*	
PF7							.114

***, **, *, significant at .001, .01, and .05 level, respectively.

Table 14. Correlations among principal factors extracted at two locations in C_1 for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
PF1	.611**					
PF2		.610**				
PF3			.340			
PF4				-.287		
PF5					-.150	
PF6						-.098

**, significant at .01 level.

Table 15. Correlations among principal factors extracted at two locations in C_2 for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6	PF7
PF1	.604**						
PF2		.801***					
PF3			.723***				
PF4				.385			
PF5					.352		
PF6						.327	
PF7							.383

***, **, significant at .001, and .01 levels, respectively.

Table 16. Correlations among principal components extracted at two locations in C_3 for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6	PF7
PF1	.666***						
PF2		.301					
PF3			.554**				
PF4				.144			
PF5					.044		
PF6						.497*	
PF7							.299

***, **, * : significant at .001, .01, and .05 levels, respectively.

Table 17. Correlations among principal factors at two locations in C_4 for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6	PF7
PF1	.677***						
PF2		.346					
PF3			-.195				
PF4				-.048			
PF5					-.463*		
PF6						.674***	
PF7							.590**

***, **, * : significant at .001, .01 and .05 levels, respectively.

Table 18. Loadings of the first six most important principal factors in C_0 in Chimaltenango for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Intnodup	.8753	.0140	-.1306	.0426	-.1195	.1281
Intnodlow	.8221	.2462	.1917	.0718	.0787	.0101
Intnodup	.7067	-.1502	-.2841	.2160	-.2346	-.1210
Nodeslow	.6562	-.3664	.0397	.0012	.2557	-.2382
Nodesup	-.0497	.7787	-.0890	-.2076	-.0605	-.1519
Nodesmid	.0587	.6649	.0801	.1023	.3106	.0293
Podslow	.5043	-.5251	-.0631	.0160	.1280	-.0270
Podlen	-.0086	-.0445	.8836	.0747	-.0987	-.1732
Seednum	-.3022	-.0154	.6483	.0296	.1354	.2185
Podwidth	.0581	.0766	.6117	-.0808	-.1464	.1585
Hypodiam	.2504	-.0134	.0146	.8317	.0020	.0913
Nbranch	.0004	-.1160	.0449	.7855	.0520	-.0621
Podsmid	.0810	.0746	-.0801	.0024	.8423	-.0171
Podsup	-.1556	.0455	-.0020	.0421	.6880	.0447
Hypolen	.0683	-.1371	.0451	-.1880	.0564	.8473
Lowpodht	-.1303	-.0129	-.0899	.4280	-.0283	.7207
Angle	.0972	-.1279	.0591	.0254	-.1415	.0859
Podsmain	.1202	.5087	-.0422	-.1857	.1522	-.1820
Seedwt	-.0950	.0451	-.0099	.0978	-.1885	.0100
PROPORTION	17.73$^+$	11.45	9.61	8.68	7.46	7.14
CUMULATIVE	17.73	29.19	38.80	47.48	54.94	62.07

+, expressed as a percentage of the total variance

Table 19. Loadings of the first six principal factors in C_1 in Chimaltenango for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Intnodmid	.8697	.0111	.0255	-.2815	.1263	.1430
Intnodup	.8624	.0111	-.0292	.2085	-.0609	-.0716
Intnodlow	.8193	.1405	-.0525	.1140	.0681	.1010
Podslow	.6878	.2579	.2621	.2618	-.0627	-.2208
Nodeslow	.6278	.2909	.2477	.2137	.1107	-.2393
Nodesup	.4604	.3525	.3252	-.2752	-.2236	.1891
Hypodiam	-.0916	.7761	-.2845	.1212	-.0462	.0996
Nbranch	.1678	.7241	.0045	.1847	-.0058	.1505
Podsmid	.2804	.6993	.3601	-.0651	.1040	-.1888
Nodesmid	.3654	.5479	.0710	.3365	-.0726	-.0431
Podsmain	.4380	.4586	.3014	-.2850	-.1942	-.2640
Podlen	.0576	-.1818	.8456	.0816	.0231	-.0123
Angle	-.0447	-.1824	-.7564	.0050	-.0466	-.0116
Podwidth	.0707	.0546	.0423	.7971	-.0178	.1340
Podsup	-.1421	-.2230	.0060	-.7461	-.0223	.1664
Hypolen	-.0218	-.1059	.1295	.0403	.7178	-.2033
Lowpodht	.1916	-.0842	.3229	-.2845	.6582	.1817
Seednum	.0274	-.1404	.3299	-.1100	-.6496	-.0568
Seedwt	-.0202	.0822	.0148	-.0055	-.0491	.9115
PROPORTION	26.42+	12.05	8.71	8.33	7.31	6.00
CUMULATIVE	26.42	38.47	47.18	55.51	62.82	68.82

+, expressed as a percentage of the total variance

Table 20. Loadings of the first six most important principal factors in C_2 in Chimaltenango for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Podslow	.7666	.0779	.0473	.3085	.2011	-.0133
Intnodup	.7502	.0391	.0588	-.0656	.1323	.0293
Nodeslow	.5893	.4567	-.3111	-.0499	.0516	-.2351
Intnodlow	.5784	.1990	.2195	-.0833	-.3892	.2084
Podsmain	.2472	.7672	.1916	-.0716	.2391	-.1920
Podsmid	.1561	.7614	.0180	.2572	.2001	.0545
Intnodmid	.5394	.5592	-.1865	-.0086	-.2156	-.0543
Angle	.2483	-.6159	.0930	-.0678	.3249	-.1783
Nodesmid	-.0024	-.0129	.8502	.0766	.1121	.0038
Hypolen	.0715	-.0260	.8139	.1149	-.2492	-.0517
Podsup	-.4191	.3545	.4621	.0851	.2048	-.3544
Seednum	.0885	.1093	.0417	.8820	.0234	-.0624
Podlen	-.0681	.0386	.1974	.7584	-.1613	.2586
Nodesup	.1187	.2732	.3587	-.1294	.7040	.1589
Lowpodht	-.1156	-.0068	.3810	.0228	-.7091	-.0809
Podwidth	-.0869	.0854	.0274	-.0195	-.0047	.8657
Nbranch	.1396	-.1717	-.1353	.2633	.2487	.6941
Seedwt	-.0369	-.1346	.0618	-.1811	.0342	.0219
Hypodiam	.1904	.2968	-.0252	.2928	.0354	.0824
PROPORTION	18.42$^+$	12.70	10.43	9.49	8.50	6.32
CUMULATIVE	18.42	31.17	41.60	51.09	59.59	65.91

+, expressed as a percentage of the total variance

Table 21. Loadings of the first six most important principal factors in C_3 in Chimaltenango for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Intnodmid	.8390	.1858	.1265	-.2463	-.0301	-.0458
Intnodup	.8379	.0062	.0032	.1175	.0409	.0351
Intnodlow	.7908	.2289	-.0864	-.1664	-.0161	-.2466
Nodesup	.7379	-.0017	-.1133	.2182	-.1488	.2551
Podsmid	-.0614	.7672	.1098	.0490	-.1824	-.0227
Nodeslow	.5270	.6626	-.0021	.1877	.0168	.0487
Podslow	.3207	.6210	-.4340	-.1419	-.0682	.0808
Hypodiam	.4657	.5123	.3449	-.0067	.0053	.0212
Podlen	.0382	.0072	.7959	-.0049	.1222	-.1628
Podsup	-.0251	.0162	.5842	-.0400	-.4585	.1959
Angle	-.1285	.1297	-.0152	.8947	.0347	.0171
Nbranch	.1392	.2268	.0637	.7622	.0359	-.0546
Podwidth	.0516	-.2011	.2513	-.0153	.7816	-.1209
Hypolen	-.0815	.0963	-.3087	.1368	.6576	.4284
Podsmain	.3213	.4963	-.1137	-.0501	-.5913	-.0497
Seedwt	-.0952	-.0037	-.1860	-.1468	-.1030	.8646
Lowpodht	.2221	.0304	.3386	.1556	.1682	.5229
Nodesmid	-.1334	.1863	.1143	.1293	.0478	.0144
Seednum	-.2257	.1980	.5655	.1757	.1844	.1545
PROPORTION	22.94[+]	11.30	10.03	9.69	7.13	5.99
CUMULATIVE	22.94	34.25	44.27	53.97	61.10	67.09

+, expressed as a percentage of the total varaince

Table 22. Loadings of the first six most important principal factors in C_4 in Chimaltenango for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Podslow	.8680	.0677	-.1250	-.0069	.2796	.0137
Nodeslow	.7839	.1568	.1748	.0957	-.2626	.1281
Nodesup	.6171	.0127	.1621	-.0773	-.2008	-.1845
Intnodup	.2153	.8974	.0508	-.0558	.1694	.1365
Intnodmid	.0644	.8884	.0511	-.1215	-.1017	.2195
Hypolen	.3515	-.5228	-.0532	-.1725	.1085	.1784
Podsmid	-.1068	.0255	.8001	.3243	-.1702	.0967
Podsmain	.4702	.1127	.7498	-.0621	.0641	.0955
Seedwt	-.1393	-.0399	-.5882	-.2599	.0066	.2177
Nbranch	.0561	-.1764	.1552	.7837	-.2343	-.1475
Lowpodht	-.0634	-.0597	.1478	.7661	.0840	.2255
Hypodiam	.0972	.3863	.0205	.5940	-.1559	.0044
Angle	-.2383	-.0939	-.1596	-.1348	.7936	-.0682
Intnodlow	.2737	.3479	.2735	.0670	.6711	.1070
Podsup	-.0929	.1380	.4597	.2221	-.5959	-.2919
Podswidth	.0935	.1595	-.1401	-.0841	-.0021	.8097
Podlen	-.0618	.1175	.2264	.2012	.0577	.7844
Seednum	.0765	.0948	-.0039	-.0216	-.1150	.1788
Nodesmid	-.0530	-.1477	.0427	-.0905	.0786	.0743
PROPORTION	19.31^+	14.81	11.53	8.85	7.78	6.78
CUMULATIVE	19.31	34.12	45.65	54.50	62.28	69.06

+, expressed as percentage of total variance

Table 23. Loadings of the first six most important factors in C_0 at East Lansing for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Podsmid	.6755	.3043	.1240	.0150	-.0659	.0176
Nbranch	.6477	.3902	-.0269	.0764	-.0452	.0517
Podsup	.5908	-.1047	.0525	-.2649	.0054	.1985
Hypodiam	.5714	-.2028	.1502	.0187	.0123	-.3317
Angle	-.4678	-.0484	.0819	-.3001	-.2747	-.2129
Podslow	.2139	.7012	.2785	-.0619	.0917	-.0306
Nodeslow	.2213	.5957	.1405	.1274	-.0465	.0037
Lowpodht	.1397	-.6840	.1074	.1259	-.0470	.0497
Intnodup	.0611	-.0861	.7522	-.0214	.1396	-.1443
Intnodmid	.1181	.2133	.7162	.0494	-.2318	.1233
Podlen	.1607	-.0006	.0580	.7881	-.0455	.0941
Podwidth	-.1622	-.1223	-.0399	.7497	.1648	-.0867
Nodesmid	.1044	.0922	-.0280	.0834	.0834	.7670
Seedwt	-.1856	.1890	.3312	.0196	.4237	.1570
Intnodmid	.0314	.1984	.5390	-.0434	-.5855	.0349
Seednum	.1639	.0735	-.0405	.1180	-.1137	.5384
Hypolen	-.1780	-.4221	-.0106	.1563	.3367	.5066
Nodesup	.1088	.2321	-.0834	.2837	.1026	-.5916
Podsmain	.0470	.1917	-.0434	-.1589	-.0915	-.1713
PROPORTION	15.71+	10.04	8.37	7.92	5.80	5.73
CUMULATIVE	15.71	25.75	34.12	42.04	47.84	53.57

+, expressed as percentage of total variance.

Table 24. Loadings of the first six most important principal factors in C_1 in East Lansing for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Nodesup	.7497	-.0801	-.2481	-.0992	.0384	.0023
Nodesmid	.7403	.1410	-.4090	-.0599	.1702	.0175
Intnodlow	.7036	-.0067	.2963	.1390	.0329	-.0926
Nodeslow	.6315	.2830	.0830	-.2173	-.1291	.0849
Nbranch	-.1147	.7216	.0269	-.1447	-.1490	-.0018
Podsmid	.2566	.6697	.0317	-.1384	.2150	.1276
Hypodiam	.3280	.6635	.0818	.1325	.0508	.1443
Podsup	-.1661	.6527	-.1243	.2036	-.0373	.0089
Intnodup	.0876	.0247	.7930	.0224	-.0191	.0357
Intnodmid	-.3963	.0524	.7574	.0734	-.1242	-.0215
Lowpodht	.0542	.1787	.0906	.8049	.1663	.0350
Podslow	.2012	.2075	-.0117	-.7444	.1962	.0099
Hypolen	-.1343	-.0245	-.2932	.1053	.7047	.1768
Podwidth	.1973	-.0724	.0524	-.0304	.6803	-.3840
Angle	-.0733	-.3524	-.1105	.3312	-.5147	-.1595
Seednum	.0837	.1862	.1206	.0308	.1527	.7372
Podlen	.2159	-.1485	.2542	-.0761	-.0846	.4270
Seedwt	.2055	-.0886	.2866	-.0032	.1390	-.6916
Podsmain	.0045	.1514	-.1296	-.1005	.1195	.0045
PROPORTION	17.04^+	11.62	9.58	7.61	7.27	5.99
CUMULATIVE	17.04	28.66	38.24	45.85	53.12	59.11

+, expressed as percentage of total variance

Table 25. Loadings in the first six most important principal factors in C_2 in East Lansing for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Nbranch	.7798	.0673	.0375	-.0339	-.1128	-.0615
Hypodiam	.6492	.1746	.2632	.0941	-.0301	.1920
Nodeslow	.6021	.1342	.0126	.0486	.3672	-.0445
Podsmid	.5714	.2058	.1671	-.0741	-.0295	.0071
Hypolen	-.5328	.3013	.0422	.2499	-.1061	-.0486
Nodesmid	.1413	.8401	-.0171	.0467	.0504	.0451
Nodesup	.2570	.5387	.0351	-.0076	.0433	.3411
Intnodmid	.0940	.7413	.0192	.0070	.1265	.4383
Podlen	.0582	-.0255	.8853	.2502	-.0911	-.0134
Seednum	.1705	.0130	.8801	-.2569	.0272	.0623
Seedwt	.0857	-.0253	-.1025	.8437	-.0586	-.1230
Podwidth	-.2123	.0583	.1116	.7685	.1727	.1124
Podslow	.1636	.0509	-.0699	.1356	.6144	.0154
Intnodup	.2020	-.1748	.0231	.0851	.5053	.4893
Lowpodht	.0429	.0871	.0395	.3249	-.4728	.2236
Podsup	.3168	-.0855	.0157	-.1133	-.6281	-.0392
Intnodlow	-.0881	.0349	.0250	-.0321	-.0789	.8303
Podsmain	.0337	-.0378	-.0781	-.1186	.1435	-.0078
Angle	-.0322	.0212	-.0505	-.0097	-.0631	-.0426
PROPORTION	15.17^{+}	10.12	9.34	9.11	6.48	6.21
CUMULATIVE	15.17	25.29	34.63	43.74	50.22	56.43

+, expressed as a percentage of total variance

Table 26. Loadings of the first six most important principal factors in C_3 in East Lansing for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Nbranch	.7985	-.1888	.1394	-.0828	-.1016	.0316
Nodesmid	.6270	.2423	-.0388	-.0153	.2083	.2594
Podsmid	.5609	-.1573	.1856	.3832	-.0969	.1954
Hypodiam	.4979	.2080	.2309	.3312	.1245	.1830
Hypolen	-.5968	-.2207	.1742	.0684	.2097	.1102
Intnodup	.1278	.7448	.1001	.0195	.1043	-.0106
Intnodmid	.1262	.7327	-.0249	-.0626	.1569	-.4402
Intnodlow	-.1568	.7290	.0923	.1250	-.1094	.1900
Seednum	.0428	.1714	.8494	-.1930	-.1448	.1022
Podlen	.0048	.0735	.8296	-.0009	.1713	.0033
Angle	-.1981	.2816	-.4211	-.2896	-.0980	.0547
Podsmain	-.0513	.0337	-.1268	.8263	-.1265	-.0305
Podslow	.0776	.1435	-.0280	.6006	.2326	.1312
Podwidth	-.0833	.0338	.0932	.0819	.7999	-.1474
Seedwt	-.0553	.0355	-.0238	-.0946	.7066	.1720
Nodesmid	.0326	-.1442	.1591	.1514	.0001	.7848
Nodesup	.2507	.1914	-.1367	-.1659	.0977	.5461
Lowpodht	-.0298	.0089	.0380	.0012	.0962	.0466
Podsup	.4627	-.1671	.1227	.1495	-.1718	-.1460
PROPORTION	14.90$^+$	11.47	9.18	8.48	6.83	6.35
CUMULATIVE	14.90	26.37	35.55	44.03	50.86	57.21

+, expressed as a percentage of the total variance

Table 27. Loadings of the first six most important principal factors in C_4 in East Lansing for all traits.

	PF1	PF2	PF3	PF4	PF5	PF6
Intnodup	.8403	-.0796	.0876	.0151	-.0281	-.0011
Intnodlow	.7772	.0467	-.0537	-.0198	.0244	.0793
Intnodmid	.6909	.0121	.1398	-.1323	.0401	-.4741
Seednum	.0353	.8060	.0737	-.2391	-.1283	.0079
Podlen	-.0889	.6995	.1443	.0167	-.0177	.20003
Hypodiam	.0310	.5078	.3647	.1256	.1358	-.0500
Podsup	-.0785	.4299	.0916	-.0810	.4086	-.2429
Angle	-.1786	-.5340	.1806	-.3547	.2843	-.0596
Nodeslow	.2076	.0709	.6982	-.0591	-.0367	.3450
Podsmid	-.0632	.3494	.5921	.0104	.1898	.0588
Nbranch	-.1767	.3006	.4299	.1468	-.4133	-.1248
Hypolen	-.0417	.0321	-.6413	-.1525	-.0346	.3768
Podslow	-.0844	-.0212	.1147	.8091	.0101	.1796
Lowpodht	.0107	.0403	-.0126	-.7872	-.1281	.0883
Podsmain	.0915	-.0782	.1548	.2466	.8005	.0322
Nodesmid	-.2978	-.0640	.0569	.1926	-.2177	.7131
Nodesup	.3156	.1824	.0137	-.0781	.2184	.5444
Podwidth	.0129	.0101	-.0692	.0774	.0550	-.0554
Seedwt	.2208	-.0435	.1150	.0355	-.5081	.1406
PROPORTION	13.89^{+}	12.31	9.51	9.22	6.59	6.19
CUMULATIVE	13.89	26.20	35.71	44.93	51.53	57.71

+, expressed as apercentage of the total variance

Table 28. Biological concepts associated with principal factors in C_0 at two locations for all traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Height	Distribution (Structural (Sturdiness)
2	Distribution (Nodes)	Distribution (Pods)
3	Economic (Pod)	Height
4	Structural (Sturdiness / profile)	Economic (Pod)
5	Distribution (Pods)	Distribution (Nodes)
6	Structural (Sturdiness)	Economic (Seed) Structural (Sturdiness)

Table 29. Biological concepts associated with principal factors in C_1 at two locations for all traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Height	Distribution (Nodes)
2	Structural (Sturdiness) /profile)	Structural (Profile)
3	Economic (Pod)	Height
4	Economic (Pod)	Distribution (Pod)
5	Structural (Sturdiness)	Structural (Sturdiness) Economic (Pod)
6	Economic (Seed)	Economic (Seed)

Table 30. Biological concepts associated with principal components in C_2 at two locations for all traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Distribution (Nodes/pods)	Structural (Profile/ sturdiness)
2	Distribution (Pods	Distribution (Pods)
3	Distributions (Nodes)	Economic (Pod / seed)
4	Economic (Pod /seed)	Economic (Seed / pod)
5	Distribution (Nodes)	Distribution (Height
6	Economic (Pod)	Heght

Table 31. Biological concepts associated with principal factors in C_3 at two locations for all traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Height	Structural(Ditribution (Nodes/pods)
2	Distribution (Pods/nodes)	Height
3	Economic (pod)	Economic (Pod /seed)
4	Structural (Profile)	Distribution (
5	Economic (Pod)	Economic (Pod / seed)
6	Economic (Seed)	Distribution (Nodes)

Table 32. Biological concepts associated with principal factors in C_4 at two locations for all traits.

	Location	
	Chimaltenango	East Lansing
Factor	Concept	Concept
1	Distribution (Pods/nodes)	Height
2	Height	Economic (Seed/pod)
3	Distribution (Pods)	Distribution (Nodes/pod)
4	Structural (Profile/ sturdiness)	Distribution (Pods)
5	Structural (Profile)	Distribution (Pods)
6	Economic (Pod)	Distribution (Nodes)

Appendix G

Canonical discriminant analysis: Standardized canonical coefficeints for all traits at two locations.

Table 1. Standardized canonical coefficients for all traits at East Lansing.

	Canonical variable		
Trait	CAN1	CAN2	CAN3
Height	.3206	-.5920	-.2949
Nbranch	.1796	-.4897	.1232
Hypolen	.4009	.1680	.0382
Hypodiam	.0999	.2114	-.0528
Lowpodht	.0603	.0614	.2960
Angle	.1853	.0101	.5274
Podsup	-.0588	-.2859	-.1217
Podsmid	-.2431	.1464	-.1936
Podslow	-.4492	.3212	.0222
Nodesup	-.0020	.4486	-.2634
Nodesmid	-.0197	.0371	.5215
Nodeslow	.1067	-.0489	.0753
Podsmain	.0002	.0508	.2815
Intnodup	-.3433	.2603	.1713
Intnodmid	.1421	.0029	.1459
Intnodlow	-.1038	.3846	.1242
Podlen	.1445	-.0317	-.0100
Podwidth	.5626	.0692	.2649
Seednum	-.1195	.1440	-.2178
Seedwt	.4464	.2385	-.5763
PROPORTION	85.06 +	11.96	.0299
CUMULATIVE	85.06	97.01	100.00

+, expressed as a percentage of the total variance

Table 2. Standardized canonical coefficients for all traits at Chimaltenango.

	Canonical variable		
Trait	CAN1	CAN2	CAN3
Nbranch	-.2597	-.0768	-.3381
Hypolen	.1262	-.0942	-.5173
Hypodiam	.1299	-.0256	.5736
Lowpodht	-.0436	.2015	.1627
Angle	.0854	.3845	.3035
Nodesup	.0760	.1621	-.2907
Nodesmid	.0471	.0555	-.0883
Nodeslow	.2586	-.1043	.1168
Podsup	-.0219	-.2938	.4695
Podsmid	-.2029	.0142	.0580
Podslow	-.2757	.2133	.6865
Podsmain	.0902	.5293	.2647
Intnodup	-.2641	-.1685	-.1475
Intnodmid	-.0077	.2359	-.2909
Intnodlow	.1858	.4306	-.0659
Podwidth	.8034	.7267	-.0896
Podlen	.3049	-.2599	.2396
Seednum	-.1867	-.2127	.0263
Seedwt	.9160	-.1802	.2796
PROPORTION	74.45 +	18.45	.0710
CUMULATIVE	74.45	92.90	100.00

+, expressed as a percentage of the total variance

Appendix H

Quantitative genetic studies: Tests of dominant and epistatic gene action in six crosses of beans.

Table 1. Test of dominance and epistasis in cross 1

Cross 1

Height	Architype	Nbranch	Hypolen	Hypodiam	Angle
2.6 * $	0 .51	0.51	0.34	1.14	0.20
6.18#	-0.02	0.32	0.22	-0.01	-0.88
0.71+	0.13	0.13	-0.17	-0.01	-0.85

Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
1.68	0.18	1.84	0.37	0.54	0.37
1.02	5.00	1.24	0.16	0.13	0.58
1.35	3.36	1.87	0.35	0.11	0.13

Lowpodht	Podsmain	Podwidth	Podlenth	Seednum	Seedwt
0.81	0.59	0.60	0.27	0.67	4.75**
0.96	0.48	0.11	0.38	0.30	1.51
-0.84	2.04	-0.30	-0.01	0.01	-0.01

$ = difference between parents
# = test of dominance; + = tes of epistasis.
*, ** = significant at .05 and .01 levels respectively.

Table 2. Test of dominance and epistasis in cross 2.

Cross 2

Height	Architype	Nbranch	Hypolen	Hypodiam	Angle
1.27	0.70	0.01	0.33	1.34	2.04**
0.31	-0.67	0.35	0.66	0.24	0.22
-0.31	-0.39	-0.13	-0.01	0.08	-0.81

Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
0.52	2.78*	0.79	0.29	0.28	0.34
-1.12	3.13	2.36	0.67	0.20	0.11
-0.12	-0.12	1.74	-0.02	0.17	0.31

Lowpodht	Podsmain	Podwidth	Podlen	Seednum	Seedwt
0.87	0.33	0.60	0.53	0.14	5.55**
-1.13	-1.13	0.88	0.27	0.23	0.13
-1.54	0.24	0.27	0.01	0.11	-0.63

= test if dominance; + = test of epistasis; $=parent
* = significant at .05, .01 level,respectively.

Table 3. Tests of dominance and epistasis in crosse 3.

Cross 3

Height	Architype	Nbranches	Hypolen	Hypodiam	Angle
8.68** $	0.80	0.40	1.73	1.73	1.80
10.87#	0.35	-0.14	-0.02	0.53	-1.77
2.58+	-0.36	-0.22	-0.02	0.67	-4.50

Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
1.38	6.67**	4.74**	0.77	0.50	1.59
0.80	5.27	3.57	0.84	0.83	1.41
0.44	4.02	4.53	0.19	0.11	0.80

Lowpodht	Podsmain	Podwidth	Podlen	Seednum	Seedwt
0.88	1.62	1.47	0.40	0.79	5.75**
0.24	1.13	-0.96	0.06	1.15	3.77
-2.07	1.43	-0.12	0.17	0.34	1.66

$ = difference between parents
# = test of dominace; + = test of epistasis.
*, ** sinificant at .05. and .01 levels, respectively.

Table 4. Test of dominance and epistasis in cross 4.

Cross 4

Height	Architype	Nbranch	Hypolen	Hypodiam	Angle
10.74**$	1.60	0.93	1.60	2.06*	6.69**
0.30#	0.26	-.16	0.29	0.30	-0.75
1.87+	-0.03	0.13	0.44	0.33	-1.59

Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
8.42**	18.64**	4.74**	0.23	0.06	0.53
-3.52	-2.09	0.23	-0.67	0.04	-0.41
-3.04	-0.83	1.16	-0.46	0.24	-0.17

Lowpodht	Podsmain	Podwidth	Podlen	Seednum	Seedwt
3.31*	1.80	1.85	1.12	0.03	7.47**
-1.19	0.40	-0.31	-0.01	-0.27	0.50
0.13	1.29	0.63	0.07	-0.03	-0.02

= test of dominance; + = test of epistasis,
$ = difference between parents
*, **, significant at .05, and .01 levels, respectively.

Table 5. Test of dominance and epistasis in cross 5.

Cross 5

Height	Architype	Nbranch	Hypolen	Hupodiam	Angle
16.06**$	0.06	0.40	0.73	1.86	4.80*
4.10#	-0.02	-0.37	0.05	-0.19	0.50
-3.73+	0.22	-0.47	-0.15	0.30	-1.68

Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
6.22**	16.68**	4.95**	0.87	0.19	1.59
-1.40	1.04	1.98	-0.03	0.01	-0.33
-0.88	-0.84	1.93	0.49	0.26	-0.32

Lowpodht	Podsmain	Podwidth	Podlen	Seednum	Seedwt
2.63*	0.98	1.85	1.85	0.50	6.77**
-0.61	-1.35	0.31	0.20	0.14	-0.94
-1.17	0.68	-0.01	0.11	0.16	-0.13

$ = difference between parents
# = test of dominance + = test of epistasis
*, **, significant at .05, .01 levels, respectively.

Table 6. Test of dominance and epistasis in cross 6

Cross 6

Height	Architype	Nbranch	Hypolen	Hypodiam	Angle
7.46**$	1.60	0.94	0.16	0.83	3.96*
-4.06#	0.33	0.63	-0.28	-0.33	2.00
-0.29+	-0.13	0.50	-0.39	0.25	-1.63

Podsup	Podsmid	Podslow	Nodesup	Nodesmid	Nodeslow
3.58**	9.77**	2.12*	0.13	0.25	0.96
-0.41	1.92	-3.02	0.36	0.05	-0.01
1.38	1.26	4.16	-0.05	-0.29	0.65

Lowpodht	Podsmain	Podwidth	Podlen	Seednum	Seedwt
0.80	2.54*	1.47	0.66	0.26	6.55
-0.17	-0.89	-0.22	0.02	-0.06	-0.55
-1.84	1.30	-0.07	1.27	-0.17	-0.56

= test of dominance; + = test of epistasis.
$ = difference between parents
*, ** significant at .05, .01 levels respectively