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GENETIC RELATIONSHIPS BETWEEN PLANT ARCHITECTURE,

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GENETIC RELATIONSHIPS BETWEEN PLANT ARCHITECTURE, SEED SIZE AND ALLOZYMES IN COMMON BEAN (*PHASEOLUS VULGARIS* L.)

By

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ABSTRACT

GENETIC RELATIONSHIPS BETWEEN PLANT ARCHITECTURE, SEED SIZE AND ALLOZYMES IN COMMON BEAN (*PHASEOLUS VULGARIS* L.)

By

Mary Elizabeth Malburg

Genetic relationships between upright plant architecture, seed size, and a diaphorase (DIA) allozyme variant were investigated in F_2 populations derived from crosses between navy bean (20 g/100 seeds) and pinto bean (40 g/100 seeds) *Phaseolus vulgaris* lines differing for type I, II and III growth habit and DIA genotype. Upright plant architecture, a highly heritable trait, segregated independent of seed size. The results provide evidence that, due to yield component compensation, the pinto ideotype differs from the navy architype for such pod traits as number of pods per plant or number of seeds per pod.

The *Diap-2*^{105} allele was present in 71% of pinto, navy, and great northern genotypes with type II plant architecture. The allele, however, was not linked to the architectural complex or the architectural traits investigated. Due to random drift, the *Diap-2*^{105} allele may be maintained in upright genotypes without being associated with a locus or linked loci governing upright plant architecture.

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GENERAL INTRODUCTION

Traditionally, breeding for enhanced yield potential emphasizes the selection of yield per se, or the incorporation of genes conferring resistance to diseases and/or insects (Mock and Pearce, 1975). Ideotype breeding differs from traditional breeding in that goals are described for specific morphological traits, resulting in a defined model plant (Rasmusson, 1987). The model plants, or 'ideotypes', are expected to perform in a predictable manner within a defined environment. Donald (1968) proposed that genetic advances for yield could be made when selecting for yield-enhancing morphological traits where the phenotypic goal for each trait is predetermined.

While Donald's ideotype emphasized the selection of modified morphological traits, Blixt and Vose (1984) noted that morphological phenotypes are the result of a biochemical or physiological message expressed in the phenotype. They contended that the genotype should be considered in defining an ideotype because allelic interactions within the genotype and interactions between alleles and the environment produce the resulting phenotype. Rasmusson (1987) expanded the ideotype definition even further to include physiological, biochemical, anatomical and phenological traits. He assumed that such traits can be genetically manipulated and assembled into one genotype to enhance yield.

Ideotypes, designed for yield enhancement, have been defined for many crops including rice (Jennings, 1964), barley (Rasmusson, 1987), wheat (Donald, 1968), peas (Snoad, 1985), corn (Mock and Pearce, 1975) and dry beans (Adams, 1973). Adams' (1973) original ideotype was later modified and described as an 'architype' (Adams, 1982) because of the emphasis placed on specific architectural characteristics of the plant. The proposed architype featured a moderate number of basal branches, upper internodes longer and more numerous than basal internodes, thick hypocotyl, tall stature, narrow profile, high values of first-order yield components (pod number, seed weight, and seeds per pod), leaf area index near four at flowering, and an indeterminant type II growth habit.

The three main dry bean plant habits grown in North America are types I, II, and III. Type I beans are determinate whereas, type II and type III beans are indeterminate. Beans with type III growth habit have relatively weak and semi-prostrate branches and concentrated pod load in the basal portion of the plant. Unlike type III growth habit, both the main stem and branches are strong and upright in type II beans (Singh, 1982).

Kelly et al. (1987) reported that type II upright growth habit provided greater yield stability in Michigan than either type I or type III growth habits. The erect growth habit of type II beans was also shown to decrease the severity of white mold (*Sclerotinia sclerotiorum*) through disease avoidance (Blad et al., 1978). The microclimate beneath the canopy of the type II plants was dryer, warmer, and less favorable for white mold development than the microclimate beneath the canopy of prostrate materials.

The success of ideotype breeding in the small-seeded (20 g/100 seeds) navy bean market class (Kelly et al., 1984) prompted the architectural improvement of the prostrate, type III, medium-seeded (40 g/100 seeds) pinto bean market class. The low frequency of genotypes possessing medium seed size in combination with type II growth habit, suggests a genetic barrier limiting recombination of the two traits. Within the 16,799 accessions catalogued at the CIAT (Centro Internacional de Agricultura Tropical; Cali, Colombia) germplasm bank, only 0.5% possess erect, type II architecture in combination with medium seed size (Kelly and Adams, 1987). In artificial crosses, genetic recombination between the architectural traits of the navy and black bean gene pools and the desired seed size, shape, and color of the pinto bean gene pool was also limited.

Using a recurrent selection breeding scheme, Kelly and Adams (1987) combined erect plant architecture with medium seed size to develop a pinto bean ideotype. However, erect plants with medium seed size were not recovered until cycle three (C_3) of recurrent selection. Previous selections based on desired architecture had small seed size, whereas selections based on medium seed size were architecturally undesirable. The difficulty of combining erect architecture with medium seed size was attributed to a genetic barrier caused by a negative linkage between the two traits.

Acquaah (1987) investigated plants originating from five distinct cycles of a phenotypic recurrent selection breeding scheme developed by Kelly and Adams (1987). Parental correlation analysis indicated a highly significant, negative correlation between architecture rating and seed weight. The negative association was weakened after one cycle of intermating and presumably broken in C_3 when medium-seeded, upright plants were recovered. Using factor analysis, he also confirmed that architectural traits and seed size traits represent two divergent gene pools. In the analysis, architectural traits had positive loadings, and seed size traits were negatively loaded, providing further evidence for a negative linkage. Acquaah (1987) concluded that phenotypic recurrent selection was effective in recombining plant architecture and medium seed size in the pinto bean ideotype.

In the recurrent selection breeding scheme, medium seed size was gradually recovered over cycles (Acquaah, 1987). Erect plant architecture, on the other hand, was established in early cycles and stabilized in C_3. The complex of traits governing plant architecture was recovered almost as a unit. Furthermore, plant architecture, although a quantitative trait, can be scored qualitatively for selection and that score is stable across environments.

Acquaah et al. (1991) used stepwise multiple regression to determine traits significantly contributing to plant architecture. Hypocotyl diameter, plant height, branch angle, and pods on the main stem (especially in the mid section) most frequently contributed to architecture rating. The traits were moderately heritable (Acquaah et al., 1989), therefore, erect type II growth habit can be achieved when selection is based on the architectural traits.

Based on growth habit, morphological characteristics, and regions of adaptation, Singh (1989) identified six gene pools within the Middle American center of domestication (Mesoamerican) and four gene pools within the South American center of domestication (Andean). The Andean snap or stringless bean has two additional groups of variation. Singh et al. (1991a) further defined six races composed of one or more of the previously determined gene pools. Multivariate statistical analysis based on morphological, agronomic, and molecular data, determined three races within each of two major gene pools: Middle American (Mesoamerican) and Andean South American. The Middle American gene pool consists of races Mesoamerica, Durango, and Jalisco. Races Chile, Nueva Granada, and Peru compose the Andean South American center of domestication (Singh et al., 1991a).

One subgroup of race Mesoamerica within the Mesoamerican gene pool is characterized by indeterminate, erect, type II landraces (Singh et al., 1991a) identified previously by Adams (1973) as sources for improved plant architecture. The same landraces also cluster on the basis of a common diaphorase (DIA) allele, *Diap-2*^{105}. (Locus and allele designation is as described by Koenig and Gepts, 1989.) This group corresponds to cluster E of Singh et al. (1991b).

Sprecher (1988b) surveyed advanced, architecturally erect bean lines for DIA and found a high frequency of the 'Unique' banding pattern or zymotype among ideotypes. In *P. vulgaris*, Weeden (1984) reports three distinct zymotypes for DIA, a tetrameric enzyme coded by two tightly linked loci (Sprecher, 1988a). Sprecher (1988a) determined the presence of seven alleles, including two nulls, at the two DIA loci, *Diap-1* and *Diap-2*. *Diap-1* displays four alleles and *Diap-2*, three alleles. The five banded pattern visualized in genotypes homozygous at both loci results from the formation of two intra-locus homotetramers and three inter-locus heterotetramers (Harris and Hopkinson, 1976; Pasteur et al., 1988). The Unique zymotype associated with type II architecture is produced by the DIA genotype *Diap-1*^{95}/*Diap-2*^{105}.

Diaphorase is a widely distributed flavoprotein (Dixon and Webb, 1979) involved in the pyruvate dehydrogenase complex and the 2-oxoglutarate dehydrogenase complex (Webb, 1984). The enzyme is reported as Enzyme Commission (EC) 1.6.4.3

(Brown et al., 1978; Kiang and Gorman, 1983; Taggart et al., 1990), EC 1.6.99.3 (Brown, 1983; Pedersen and Simonsen, 1987),and EC 1.8.1.4 (Westphal and Wricke, 1989). Enzyme Commission 1.6.4.3 was later reclassified as EC 1.8.1.4 (Webb, 1984). All enzymes catalyze oxidoreduction reactions but differ as to their respective acceptor compounds (Webb, 1984). Diaphorase may have evolutionary significance because of the close association between the *Diap-2*^{105} allele and type II growth habit in beans.

The *Diap-2*^{105} allele is found only in cultivated erect plants with type II growth habit. Singh et al. (1991b) assayed a total of 227 landraces representing a geographical distribution from Mexico to Argentina and Chile. Variability for nine polymorphic loci provided information on gene flow, from wild to cultivated *P. vulgaris*. In wild *P. vulgaris* materials, four alleles, *Diap-1*^{102}, *Diap-1*^{100}, *Diap-1*^{96}, and *Diap-1*^{95}, are present at the *Diap-1* locus, whereas cultivated materials display only two alleles, *Diap-1*^{100} and *Diap-1*^{95}. At the *Diap-2* locus however, wild materials possess fewer alleles than do the cultivars. Alleles *Diap-2*^{100} and *Diap-2*^{105} are present at the *Diap-2* locus in the cultivated *P. vulgaris*. Wild materials possess the *Diap-2*^{100} allele but lack the *Diap-2*^{105} allele (Singh et al., 1991b). Allozyme analysis of 83 wild *P. vulgaris* accessions representing a region from Mesoamerica to Argentina also lack the *Diap-2*^{105} allele (Koenig and Gepts, 1989). The *Diap-2*^{105} allele was not present in the sampled wild materials and may be the result of a mutation during or shortly after the domestication of type II genotypes (Singh et al., 1991b).

Plant domestication is an evolutionary process whereby wild plants are changed genetically by human selection, usually rendering them less fit for survival in the wild (Pickersgill, 1986). The genetic variability of the domesticated populations is due, in part, to the number of individuals involved in the formation of the domesticated population (Ladizinsky, 1985). Populations domesticated from a small sample of wild materials represent a limited fraction of the variability present in the wild population (Pickersgill, 1986). This phenomenon of reduced variability is also known as 'founder effect'. Founder effect refers to the establishment of a new population by a small number of individuals representing only a portion of the total variability (Mayr, 1942). The genetic composition of a population is limited to the alleles introduced by the founders (Schwaegerle and Schaal, 1979).

The significance of founder effect on reduced variability depends not only upon the number of founding individuals but also upon: 1.) the rate of gene exchange between the wild and the cultivated populations and 2.) the appearance of mutations during or after the founding event (Ladizinsky, 1985). Restricted gene exchange either by geographical isolation or reproductive isolation is a crucial requirement of speciation (Mayr, 1942). In common bean, self-pollination decreases the chance of hybridization between cultivated materials and their wild relatives and allows the founder plants to establish separate populations (Ladizinsky, 1985). Although founder effect typically results in reduced variability, the appearance of mutations during speciation may produce novel variability in the crop plant. Introduction of crop plants to new environments allows for the selection of the mutations and the establishment of geographic races (Ladizinsky, 1985).

In the first chapter of this thesis, the genetic relationship between erect plant architecture and seed size is investigated. In addition, the heritability of the architectural complex is examined. The objective of the second chapter is to determine the genetic relationship between erect plant architecture and the *Diap-2*^{105} allele.

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CHAPTER ONE

INTERRELATIONSHIP OF PLANT ARCHITECTURE AND YIELD COMPONENTS IN THE PINTO BEAN IDEOTYPE

ABSTRACT

Linkage relationships between architectural traits, plant architecture, and seed size were analyzed in F_2 populations derived from crosses between type I, II, and III *Phaseolus vulgaris* lines from small-seeded (20 g/100 seeds) and medium-seeded (40 g/100 seeds) common bean lines. The architectural trait branch angle was the most significant contributor to plant architecture. Upright plant architecture was estimated to be moderately high to highly heritable (h^2 = 0.60-0.85). Seed size and upright plant architecture were not linked. However, a negative linkage would appear to exist if selection for a medium-seeded pinto ideotype were based visually on the pod traits of the navy ideotype. Our results provide evidence that, due to yield component compensation, the pinto ideotype differs from the navy architype for such pod traits as number of pods per plant or number of seeds per pod.

INTRODUCTION

Ideotype breeding in dry beans (*Phaseolus vulgaris*) has been used successfully to improve plant architecture and yield stability (Kelly et al., 1984; Kelly et al., 1987). The dry bean ideotype, or 'architype' (Adams, 1982), emphasizes a moderate number of basal branches, thick hypocotyl, tall stature, narrow profile, and indeterminant type II growth habit (Adams, 1973). Singh (1982) defined three dry bean growth habits, type I, determinant upright; type II, indeterminate upright; and type III, indeterminate prostrate. Type II upright growth habit provides greater yield stability (Kelly et al., 1987) and can reduce the incidence of disease (Blad et al., 1978). Acquaah et al. (1991) identified hypocotyl diameter, plant height, branch angle, and pods on the main stem, especially in the midsection, as substantial contributors to upright plant architecture.

Architectural improvement based on the architype concept was successful in the small-seeded (20 g/100 seeds) navy bean market class (Kelly et al., 1984) which motivated the architectural improvement of the medium-seeded (40 g/100 seeds) pinto bean market class. Pinto beans differ from the navy architype in having prostrate, indeterminant type III growth habit while producing 70% of the pods at the basal nodes (Kelly and Adams, 1987). The majority of pods are in contact with the soil surface. Architectural improvement was limited in the pinto class by negative linkages between seed size and upright plant architecture (Kelly and Adams, 1987; Acquaah, 1987).

Kelly and Adams (1987) used a phenotypic recurrent selection breeding scheme to combine the architectural characteristics of the small-seeded navy architype with the seed size, shape and color of the prostrate type III pinto bean. The complex of traits interacting to produce the architype were recovered almost as a unit. However, the frequency of recovery was low in the initial cycles of recurrent selection. In the initial cycles, the architectural selections had small seed size (20-25 g/100 seeds) whereas selections based on large seed size (>30 g/100 seeds) were architecturally undesirable. Characteristics such as seed color and mottling recombined freely in the first segregating generations, but architecture and seed size did not show evidence of recombination until cycle 3 (C_3). When the seed size traits of the pinto bean class were combined with the architectural traits of the navy architype, the resulting pinto ideotype had larger but fewer pods than the navy architype (Acquaah et al., 1991).

This investigation was conducted to (1) determine the genetic relationship between the complex traits of seed size and upright plant architecture and (2) to define a pinto bean ideotype for the humid midwestern United States.

MATERIALS AND METHODS

The genetic relationship between seed size and upright plant architecture

Plant materials

A partial diallel was created with six dry bean lines representing small (20 g/100 seeds) and medium (40 g/100 seeds) seed-size classes and types I, II, and III growth habits (Table 1.1). The small-seeded navy bean parental lines were Seafarer, N84004 and Michelite, whereas Ouray, P89405, and UI-114 were the medium-seeded pinto bean parents. N84004 and P89405 are MSU breeding lines developed as sources of upright, type II plant architecture in navy and pinto bean germplasm. Crosses were made between seed sizes but within growth habits (three crosses), between growth habits but within seed sizes (six crosses), and between both seed sizes and growth habits (six crosses) for a total of 15 crosses.

Approximately 320 seeds per F_2 population were planted at a 20 cm spacing within rows and a 51 cm spacing between rows in East Lansing, Michigan, 1990. Where emergence was poor, a type I kidney bean, Isabella, was hand planted two weeks later to ensure uniform interplant competition. Parental lines were included as checks on each side of the F_2 populations.

F_1 plants from the six crosses segregating for both seed size and plant type were backcrossed to each parent to provide narrow-sense heritability estimates. The six crosses

Table 1.1. Characteristics of small-seeded (20 g/100 seeds) navy and medium-seeded (40 g/100 seeds) pinto bean lines used as parents.

Bean Line	Commercial Class	Seed Size	Growth Habit	Architecture Rating
UI-114	Pinto	Medium	III	1 (prostrate)
Michelite	Navy	Small	III	2
Seafarer	Navy	Small	I	4
Ouray	Pinto	Medium	I	5
P89405	Pinto	Medium	II	8
N84004	Navy	Small	II	9 (upright)

included: Seafarer x P89405, Seafarer x UI-114, N84004 x Ouray, N84004 x UI-114, Michelite x Ouray, and Michelite x P89405.

Agronomic evaluation

At maturity, approximately 210 plants per F_2 population, 30 plants per parental genotype and 35 F_1 plants per backcross were individually rated for plant architecture on a scale from 1 to 9. A rating of 1 depicts prostrate growth habit, whereas a rating of 9 represents the upright navy architype. Ratings 2 through 8 were scored according to the degree of deviation from the two extremes.

In order to quantify the architectural ratings, all plants were evaluated for agronomic traits that contribute to erect plant architecture (Acquaah et al., 1991). The architectural traits included branch angle, hypocotyl diameter and plant height. Branch angle was measured as the inclination of the branch to the central axis, hypocotyl diameter was measured just above the soil surface and plant height was measured as the length of the main stem excluding the vine. Seed weight was recorded on the weight of 50 seeds.

Heritability estimates

Broad-sense heritabilities for plant architecture were calculated using the following formula:

$$H=\frac{\sigma^2_{F2} - 1/3\ (\sigma^2_{P1} + \sigma^2_{P2} + \sigma^2F_1)}{\sigma^2_{F2}} \qquad [1]$$

However, the geometric mean of the parents and the F_1 more closely estimated environmental variance and equation [2] was used to estimate broad-sense heritability for the architectural traits.

$$H=\frac{\sigma^2_{F2} - [(\sigma^2_{P1})(\sigma^2_{P2})(\sigma^2_{F1})]^{1/3}}{\sigma^2_{F2}} \qquad [2]$$

For both [1] and [2] $\sigma2_{F2}$, σ^2_{P1}, σ^2_{P2}, and σ^2_{F1} are variances of F_2, parent 1, parent 2 and F_1 generations, respectively (Fehr, 1987).

Narrow-sense heritabilities were estimated by parent-offspring regression of $F_{2:3}$ progeny means on an F_2 parent. The linear regression model proposed by Lush (1940) is:

$$Y_i = a + bX_i + e_i \qquad [3]$$

where Y_i = performance of offspring of the *i*th parent

a = mean performance of all parents evaluated

b = linear regression coefficient

X_i = performance of *i*th parent

e_i = experimental error

Narrow-sense heritability was also estimated according to the Warner backcross method (Warner, 1952). The equation used to estimate heritability is:

$$h^2 = \frac{2(\sigma^2_{F2}) - (\sigma^2_{B1} + \sigma^2_{B2})}{\sigma^2_{F2}} \qquad [4]$$

where σ^2_{F2} is the variance among F_2 plants and σ^2_{B1} and σ^2_{B2} are the variances among plants from the backcrosses of the F_1 to parent 1 and parent 2, respectively.

Realized heritability, or the ratio of response to selection differential, was estimated as the difference in mean performance of high and low F_3 progeny divided by the difference in the mean of the F_2 parents (Fehr, 1987):

$$h^2 = \frac{\bar{x}_{high,\ F3} - \bar{x}_{low,\ F3}}{\bar{x}_{high,\ F2} - \bar{x}_{low,\ F2}} \qquad [5]$$

The predicted genetic advance (G_s) due to selection for plant architecture is estimated by the population variance and the heritability of architecture (Lush, 1945).

$$G_s = i\sigma_{PH}H \qquad [6]$$

where i = selection intensity in standard deviation units

σ_{PH} = phenotypic variance

H = heritability of the quantitative trait

Directional selection for high versus low architecture rating

Four populations derived from the crosses Seafarer x P89405, N84004 x Ouray, N84004 x UI-114, and

Michelite x P89405 were selected for inclusion in a directional selection experiment. The cross N84004 x UI-114 is typical of crosses initially made by Kelly and Adams (1987) to combine the plant architecture of the navy architype with the seed size of the prostrate, type III pinto. The Michelite x P89405 cross is the reciprocal, a prostrate, type III navy crossed to the pinto ideotype. The remaining two populations, Seafarer x P89405 and N84004 x Ouray, are type I beans crossed to an ideotype.

For each population, ten F_2 plants, or approximately 5% of the plants analyzed for architectural traits, were selected for both high and low architecture ratings for a total of 20 $F_{2:3}$ families. For the N84004 x UI-114 and Michelite x P89405 families, high architecture ratings were 6 or greater and low architecture ratings were 3 or less. The Seafarer x P89405 and N84004 x Ouray populations had high architecture ratings of 7 or greater and low architecture ratings of 5 or less. The only restriction for inclusion in the study was that the F_2 plants produced 60 or more seeds.

Twenty seeds derived from a single F_2 plant were spaced planted (20 cm spacing) in a row and replicated three times in a completely randomized block design at East Lansing, Michigan, 1991. Data were collected on architecture rating and seed weight. Five plants with uniform interplant competition were randomly selected from each entry and evaluated for plant height, branch angle, and hypocotyl diameter.

Directional selection for high versus low seed weight

The population derived from the cross N84004 x P89405 was studied to evaluate the effect of selecting for large or small seed size. Adams (1967) defined yield as the product of three components; X, the average number of pods; Y, the average number of seeds per pod; and Z, the average weight per seed. Five percent of the total number of F_2 plants analyzed for architectural traits, were randomly selected for both large (>15 g/50 seeds) and small (<12 g/50 seeds) seed size for a total of 20 $F_{2:3}$ families. The only restriction for inclusion in this investigation was that the F_2 plants produced 60 or more seeds.

Twenty seeds derived from an F_2 plant were planted at a 20 cm spacing within the row and replicated three times in a randomized complete block design at East Lansing, Michigan, 1991. Each family row was rated for plant architecture. Five plants with uniform interplant competition were randomly selected from each entry and evaluated for the total number of pods, the total number of seeds, and the weight of 100 seeds.

RESULTS AND DISCUSSION

Heritability of upright plant architecture

Twelve F_2 populations derived from a partial diallel were rated for plant architecture on a scale of 1 to 9. In addition, architectural traits (branch angle, hypocotyl diameter, and plant height) were measured to substantiate the architecture rating. In the F_2 generation, branch angle most frequently correlated to architecture rating. Three exceptions were crosses between type I and type III plants (Table 1.2). The crosses did not involve the architectural plant types (N84004 and P89405) therefore, the exceptions support the importance of branch angle, as a trait generally associated with narrow plant profile, and a key component of type II growth habit. The remaining architectural traits, hypocotyl diameter and plant height, were less important contributors to architecture rating in these particular populations.

Similar trends were observed in the plant architecture directional selection studies but, branch angle constituted an even greater portion of the architecture rating. The higher association is attributed to the lack of intermediate architectural ratings which may confound branch angle with other architectural traits.

Broad-sense heritability estimates for plant architecture were exceptionally high indicating the environment has little effect on the expression of plant architecture (Table 1.3). A large portion of the genetic variation is heritable and can be selected as evident by the narrow-sense estimates. Using parent-offspring regression of $F_{2:3}$ progeny means on an F_2 parent, architecture rating was estimated to be moderately high to highly heritable. The realized heritability estimates indicate that greater architectural differences occurred in

Table 1.2. Correlation coefficients (r) for architecture rating with three architectural traits in F_2 and F_3 generations (E. Lansing, MI 1990 and 1991).

			Trait		
Population	Cross†	Gen.	Branch Angle‡	Hypocotyl Diameter	Plant Height
Seafarer x Michelite	I,N x III,N	F_2	.06	-.24***	-.53***
Seafarer x UI-114	I,N x III,P	F_2	-.20**	.02	.15*
Michelite x Ouray	III,N x I,P	F_2	-.12	-.12	-.31**
Ouray x UI-114	I,P x III,P	F_2	.13	.03	.04
Seafarer x N84004	I,N x II,N	F_2	-.44***	.22***	.44***
Ouray x P89405	I,P x II,P	F_2	-.39***	-.17*	.03
N84004 x Michelite	II,N x III,N	F_2	-.45***	-.06	.03
P89405 x UI-114	II,P x III,P	F_2	-.35***	-.33**	-.24***
Seafarer x P89405	I,N x II,P	F_2	-.34***	.20**	.34***
		F_3	-.79***	-.01	.01
N84004 x Ouray	II,N x I,P	F_2	-.29***	.03	.04
		F_3	-.76***	-.14	-.17
N84004 x UI-114	II,N x III,P	F_2	-.18**	.10	.03
		F_3	-.71***	-.14	.18
Michelite x P89405	III,N x II,P	F_2	-.25***	-.03	-.05
		F_3	-.88***	-.26*	-.32*

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

† I-determinate bush, II-indeterminate upright, III-indeterminate prostrate.
P and N designate pinto and navy commercial classes, respectively.

‡ Actual means and ranges for plant architecture rating and branch angle are reported in Table A.1.

Table 1.3. Broad-sense (H), narrow-sense (h^2), and realized heritability (H_R) estimates for architecture rating and branch angle from four dry bean crosses.

Trait	Cross	H	h^2	H_R
Architecture Rating	Seafarer x P89405	.99	.76	.46
	N84004 x Ouray	.87	.79	.55
	N84004 x UI-114	.98	.85	.63
	Michelite x P89405	.92	.60	.44
Branch Angle	Seafarer x P89405	.43	.43	.43
	N84004 x Ouray	.53	.07	.80
	N84004 x UI-114	.35	.28	1.45
	Michelite x P89405	.62	.30	.84

the F_2 generation than in the F_3 generation. In a study by Acquaah (1987) plant architecture remained stable across environments as heritability estimates were obtained from generations grown in two different seasons. Plant architecture was also relatively environmentally stable when grown in East Lansing, Michigan and Chimaltenango, Guatemala.

The cross N84004 x UI-114 is typical of crosses made to combine plant architecture with medium seed size, therefore, gain from selection was estimated for the population N84004 x UI-114. Using a 10% selection intensity, average architecture rating of the progenies is predicted to be 31.3% greater than the mean of the unselected F_2 generation. Selection for plant architecture can be effectively conducted in early generations as indicated by the heritability estimates and the G_s. Erect plant architecture was recovered in the original cycle of recurrent selection and enhanced in subsequent cycles (Kelly and Adams, 1987).

Narrow-sense heritabilities calculated from the Warner backcross method were inconsistent. Due to time constraints, BC_1F_1 plants from the backcrosses were evaluated rather than BC_1F_2 plants. BC_1F_2 plants would have provided more accurate and reliable estimates of the nonheritable components of variance, and therefore, more valid narrow-sense heritability estimates. For this reason, Warner backcross heritability estimates will not be presented.

Plant architecture appears to have a relatively simple mode of inheritance although it is classified as a quantitative trait because of its complex interactive morphological features. The fact that progress for upright plant architecture was made in the F_2 generation implies that major genes govern the trait. The minimum number of genes controlling plant architecture was estimated according to the Castle-Wright equation (Wright, 1934) which only detects genes for which the parents differ. The estimated number of genes governing plant architecture was 2.2 for the Seafarer x P89405 population, 3.9 for the N84004 x Ouray population, 4.7 for the Michelite x P89405 population and 6.3 for the N84004 x UI-114 population. The Seafarer x P89405 and N84004 x Ouray populations were derived from crosses between type I and type II growth habits which have more similar architectural characteristics than type II and type III growth habits (Singh, 1982). The estimated number of genes governing plant architecture provides evidence that type I and type II growth habits are also genetically more similar.

Frazier et al. (1958) investigated upright and sprawling, prostrate bush growth habits of snap bean. They found that three major recessive genes may be responsible for the upright bush habit. In other studies, a few major genes have likewise accounted for a substantial portion of the variation of quantitative traits. Sullivan and Bliss (1983) suggested that one or a few genes were responsible for enhanced levels of phaseolin in near-homozygous inbred-backcross lines of common bean. Also in common bean, Vallejos and Chase (1991) identified a gene, *Ssz-1*, that exhibited additive gene action and accounted for 30-50% of the seed size differences between parents which had a two-fold difference in seed weight. In oats, as few as two or three major genes may have a large effect on oat mosaic virus resistance, a quantitative trait with relatively simple inheritance (Uhr and Murphy, 1992). However, large populations are necessary to detect a significant departure from the normal distribution characteristic of traits influenced by many polygenes (Thoday and Thompson, 1976).

The architectural complex, in addition to being controlled by few genes, has a moderately high heritability estimate, and can be easily and effectively selected in early generations. These attributes characterize plant architecture as a suitable trait for a backcross breeding scheme. However, in a backcross breeding scheme, the intensity of plant architecture may be effected as desirable alleles for plant architecture are lost in each backcross. As a result, large populations would have to be developed in order to ensure that favorable alleles are maintained in the population and the subsequent recovery of architecturally desirable plants.

Phenotypic recurrent selection allowed for the recovery of the major architectural genes in the initial cycle whereas minor genes were accumulated in later cycles. In addition, medium seed size was recovered without affecting the intensity of plant architecture. Seed size is an additive trait that may be governed by as many as ten effective factors in broad crosses between wild and cultivated *P. vulgaris* (Motto et al., 1978). The cyclic breeding scheme was necessary to gradually accumulate all of the seed size genes as well as minor architectural genes.

The major contributor to plant architecture in both the F_2 and the F_3 generations was branch angle and therefore, one would expect high to moderately high branch angle heritabilities. Broad-sense heritabilities were of similar magnitude as those estimated by Acquaah et al. (1989) and provide evidence of genetic variation for branch angle (Table 1.3).

Branch angle heritabilities calculated from parent-offspring regression were low relative to the estimated plant architecture heritabilities (Table 1.3). Branch angle may have lower heritability estimates because there is less initial variability. The narrow-sense heritability estimate in the N84004 x Ouray population was considerably lower than the estimates for the remaining three populations. The low estimate (h^2 = 0.07) may indicate that the N84004 x Ouray population is more responsive to environmental differences. It is possible, however, to differentiate between high and low architecture ratings as indicated by the realized heritability estimate. The narrow-sense heritability estimates suggest that a component of the genetic variance for branch angle is due to additive genetic variance.

The narrow-sense heritability estimates for branch angle may be biased because branch angle was not directly selected in the F_2 generation nor was it randomly sampled in the F_2 generation. Furthermore, environmental differences can effect the magnitude of the regression coefficients when parents and offspring are not grown in the same season (Bartley and Weber, 1952). Variable environmental conditions decrease heritability estimates, whereas, uniform conditions increase heritability estimates (Falconer, 1960).

For all crosses realized heritability estimates for branch angle exceeded parent-offspring heritability estimates and were comparable or somewhat higher than the broad-sense estimates (Table 1.3). For the N84004 x UI-114 population, the realized heritability estimate exceeded the theoretical limit indicating that greater branch angle differences occurred in the F_3 generation than in the F_2 generation. Although realized heritability estimates may be biased by environmental effects, inbreeding, maternal effects (Falconer, 1960), or limited sampling, the estimates do signify that narrow branch angle selected in the F_2 generation is expressed in the F_3 generation.

$F_{2:3}$ families selected for desirable plant architecture had significantly narrower profiles than did those selected for undesirable plant architecture (Table 1.4). This supports

Table 1.4. Mean response of branch angle, hypocotyl diameter, and plant height to directional selection for high and low architecture ratings. $F_{2:3}$ families grown at E. Lansing, MI 1991.

Trait	$F_{2:3}$ Family	Architecture Rating		P
		High	Low	
Branch Angle (degrees)	Seafarer x P89405	30.4	33.0	.001
	N84004 x Ouray	27.0	33.0	.004
	N84004 x UI-114	32.6	38.4	.001
	Michelite x P89405	29.8	35.5	.03
	Trait Average	30.0	35.0	.001
Hypocotyl Diameter (mm)	Seafarer x P89405	7.7	7.6	NS
	N84004 x Ouray	7.2	7.4	NS
	N84004 x UI-114	6.8	7.2	NS
	Michelite x P89405	7.9	7.9	NS
	Trait Average	7.4	7.5	NS
Plant Height (cm)	Seafarer x P89405	39.5	38.3	NS
	N84004 x Ouray	34.0	35.3	NS
	N84004 x UI-114	34.0	36.2	NS
	Michelite x P89405	40.4	42.9	NS
	Trait Average	37.0	38.2	NS

NS = Not significant at the 0.05 level.

the realized heritability estimates and indicates that selection for branch angle can be effectively conducted. In fact, Acquaah (1987) showed that desired branch angle was recovered after C_1 of recurrent selection and was improved in subsequent cycles. It seems evident, however, that progress for erect plant architecture can be made when selection is based on narrow plant profile of which branch angle is the major contributing factor.

$F_{2:3}$ family means for hypocotyl diameter and plant height did not vary due to directional selection based exclusively on architectural rating (Table 1.4.). Both traits increased in magnitude from the original cycles to the advanced cycles of recurrent selection (Acquaah, 1987). Even though significant differences were not observed in response to directional selection, the traits may be emphasized and modified in subsequent generations. Selection for either trait would influence the other because they are highly correlated (correlation coefficients range from r=0.30 to r=0.71 in the $F_{2:3}$ families).

Relationship between upright plant architecture and seed weight

Six F_2 populations; Seafarer x P89405, Seafarer x UI-114, N84004 x Ouray, N84004 x UI-114, Michelite x Ouray, and Michelite x P89405; were evaluated for plant architecture and seed weight. In five of the six populations, architecture rating and seed weight were nonsignificantly correlated. The exception was the population Seafarer x P89405. The significant but low positive correlation between seed weight and architecture ($r=0.157$, $P<.02$) indicates that upright erect plant architecture associates with increased seed weight. This association is not unexpected because the donor of medium seed size is also the improved architectural type. Overall, the F_2 data provide evidence that architecture and seed weight are not negatively linked.

In the architecture directional selection studies, architecture rating and seed weight were nonsignificantly correlated in the N84004 x UI-114 $F_{2:3}$ families and in the N84004 x Ouray $F_{2:3}$ families. The Michelite x P89405 $F_{2:3}$ families had a significant but low negative correlation ($r=-0.26$, $P<.05$) between architecture rating and seed weight. However, the mean seed weight of $F_{2:3}$ families originally selected for high architecture rating (27.9 g/100 seeds) was not significantly lower than the mean seed weight of $F_{2:3}$ families selected for low architecture rating (29.9 g/100 seeds). Seed weight and architecture were significantly correlated ($r=0.41$, $P<.001$) in the Seafarer x P89405 $F_{2:3}$ families. A significant positive correlation also existed in the F_2 generation.

Interrelationship of yield components

A directional selection study was conducted with the population N84004 x P89405 to investigate why medium-seeded, upright beans were not recovered in the initial cycles of Kelly and Adams' (1987) recurrent selection. N84004 and P89405 possess type II growth habit so progeny segregated only for yield components X, average number of pods; Y, average number of seeds per pod; and Z, average weight per seed (Adams, 1967).

$F_{2:3}$ families selected for high seed weight had a significantly higher mean seed weight than families selected for low seed weight (Table 1.5). Regression of the $F_{2:3}$ progeny means on an F_2 parent provided narrow-sense heritability estimates for seed weight. The estimates were r=0.70 (P<.001) for Seafarer x P89405, r=0.70 (P<.001) for N84004 x Ouray, r=0.69 (P<.001) for N84004 x UI-114, and r=0.54 (P<.01) for Michelite x P89405. The high to moderately high seed weight heritabilities agree with other heritability estimates (Nienhuis and Singh, 1988; Motto et al., 1978).

Directional selection for high versus low seed weight did not result in significant differences in seed yield (Table 1.5). When compared to the navy ideotype of equal yield potential, the pinto ideotype essentially represents a two-fold increase in the Z component for seed size. Therefore, one or both of the remaining yield components must be compensating to maintain yield.

Table 1.5. Mean response to directional selection for high and low seed weights. N84004 x P89405 $F_{2:3}$ families grown at E. Lansing, MI 1991.

Trait	Seed Weight			
	High	Low	LSD	P
Seed Weight (g/100 seeds)	30.9	25.2	2.0	.007
Yield (grams)	36.9	35.1	3.5	NS
Number of Pods	29.5	30.7	1.9	NS
Number of Seeds per Pod	4.1	4.6	0.4	.04
Number of Seeds	120.1	140.7	6.6	.005

NS=Not significant at the 0.05 level.

The average number of pods, yield component X, did not significantly differ due to directional selection. However, yield component Y, the average number of seeds per pod, was significantly different in response to directional selection (Table 1.5). The average number of seeds per pod had a significant negative correlation with seed weight ($r=-0.45$, $P<=.001$), signifying that as seed weight is increased, the average number of seeds per pod decreases. In the N84004 x P89405 population, the yield component seeds per pod compensated for lower seed weight to maintain yield.

Directional selection for high or low seed weight also resulted in significant differences in the mean number of seeds (Table 1.5). Correlations between seed number and the yield components were all significant. The correlation coefficients for seed number with the average number of seeds per pod and with the average weight per seed were $r=0.47$ ($P<.001$) and $r=-0.30$ ($P<.001$), respectively. Pod number was highly correlated to seed number at $r=0.82$ ($P<.001$), therefore, number of pods could also compensate for yield. Indeed, the pinto ideotype developed through recurrent selection (Kelly and Adams, 1987) had larger and fewer pods than did the navy ideotype (Acquaah et al., 1991). Yield component compensation is also present in barley where selection for an increased number of heads results in lower kernel weight or fewer kernels per head (Benbelkacem et al., 1984).

Due to yield component compensation, the pinto ideotype differs from the architype defined for the navy bean (Adams, 1982). Selection based on the pinto ideotype should be successful in recovering medium-seeded, type II plants. Our results provide evidence that medium seed size and plant architecture are inherited independently and can be combined based on the pinto ideotype.

The balanced pinto ideotype

A strong association between seed size and growth habit exists in common bean. In fact, naturally occurring medium-seeded materials with type II architecture are rare as evident from evaluation of accessions at the CIAT germplasm bank (Kelly and Adams, 1987). Singh et al. (1991) used the association between growth habit and seed weight in combination with other morphological and molecular traits to classify races within *P. vulgaris*. The lack of recombination between type II growth habit and seed size may be attributed to the lack of adequate breeding systems to combine the desirable traits of two diverse germplasm pools. Recurrent selection however, allowed for the gradual recombination of traits from the architectural germplasm pool with the seed-size germplasm pool. The use of recurrent selection in self-pollinated crops is limited by the time and expense necessary to make a large number of crosses (Avey et al., 1982). Recurrent selection has been successfully used for increased phaseolin in common bean (Delaney and Bliss, 1991), early heading in winter wheat (Avey et al., 1982), kernel weight in spring wheat (Busch and Kofoid, 1982), and seed size in soybean (Tinius et al., 1991).

The architectural germplasm pool of the common bean is characterized by acute lower branches, stiff stem, fruiting on basal and upper nodes, small seeds, and 6-8 seeds per pod. In contrast to the architectural types, the seed-size germplasm has prostrate branches, weak stem, fruiting concentrated in basal nodes, medium sized seeds, and 4-5 seeds per pod (Singh, 1989; Singh et al., 1991). The structural characteristics related to yield in both germplasm pools belong to three developmental patterns: size (weight), number, and architectural factors (Denis and Adams, 1978). The pinto ideotype resulting from recurrent selection was balanced for all three factors where source was balanced against sink. There are many different combinations which would constitute a genotypic balance for such morphological and physiological characteristics (Denis and Adams, 1978). A cyclic breeding scheme such as recurrent selection was necessary to rearrange the balanced constituents of the parental germplasm into a new order of balance. The pinto ideotype represents the most balanced combination of the desired morphological and physiological components of the architectural and seed-size germplasm pools.

CONCLUSION

Plant architecture is a complex trait that appears to have a relatively simple mode of inheritance. Desirable plant architecture was recovered *in-toto* in the initial cycles of recurrent selection (Kelly and Adams, 1987) and our data show that plant architecture is a highly heritable trait.

The data also indicate that architecture and seed weight are not negatively linked, in contrast to the evidence of Kelly and Adams (1987). A negative linkage would appear to exist if selection were based visually for the pod traits of the navy architype. The navy architype pod traits, which include a large number of pods per plant and many seeds per pod, may visually appear to favor increased yield. When in fact, selection for increased number of seeds per pod or pods per m^2, results in reduced seed weight (Nienhuis and Singh, 1986). Selection on this basis would therefore result in the development of small-seeded architypes.

Early generation (S_1) F_2 recurrent selection was an appropriate method to combine the architectural traits of the navy germplasm with the seed size, shape and color of the pinto germplasm. Backcross breeding, as an alternative to phenotypic recurrent selection, would not have been an efficient method to introduce plant architecture into pinto bean germplasm.

A cyclic breeding scheme such as recurrent selection was necessary to increase the frequency of favorable alleles governing seed traits. The seed color and mottle traits of the pinto commercial class were recovered as early as C_1, whereas, the major genes for seed size were not recovered until later cycles (Kelly and Adams, 1987). The additional cycles were necessary to maintain upright plant architecture while increasing seed size. Coyne (1968) showed that seed size is an additive trait that may be governed by as many as ten effective factors in broad crosses with large differences in seed size (Motto et al., 1978). The number of cycles necessary to combine erect plant architecture and medium seed size in a balanced relationship may have been reduced if selection were based on the pod traits of the pinto bean ideotype in earlier recurrent selection cycles.

Selection for medium-seeded, upright plants should be based on the pinto ideotype which is physically different from the navy architype (Figure 1.1). Due to yield component compensation, the pinto ideotype proposed for the humid midwestern United States exhibits fewer seeds per pod and fewer pods per plant than the navy architype. Both traits can be visually selected, allowing for the rapid recovery of medium seed size in combination with desired type II plant architecture.

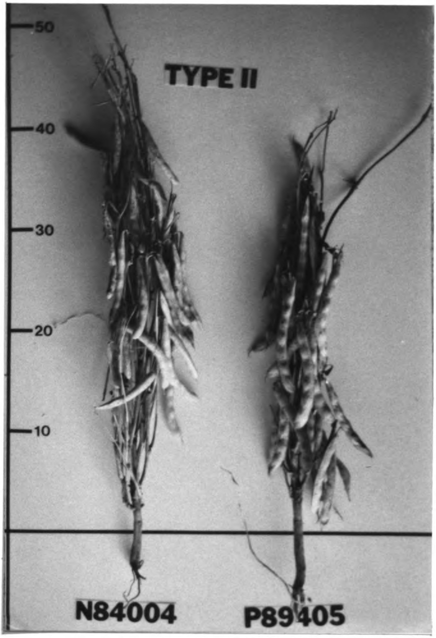

Figure 1.1. Comparison of the navy architype, N84004, and the pinto ideotype, P89405. P89405 displays modified pod traits, allowing for the recovery of medium seed size.

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CHAPTER TWO

ALLOZYME EVALUATION OF UPRIGHT PLANT GENOTYPES

ABSTRACT

Advanced navy, pinto and great northern breeding lines and cultivars with upright type II plant architecture were analyzed for an allozyme variant of the enzyme diaphorase (DIA). The *Diap-2*^{105} allele, characteristic of the Unique DIA zymotype, was present in 71% of genotypes with type II plant architecture. The genetic relationship between upright plant architecture and the *Diap-2*^{105} allele was further investigated in F_2 populations derived from crosses between navy and pinto bean parental lines differing for type I, II, and III growth habit and DIA genotype. The *Diap-2*^{105} allele associated with upright plant architecture was not linked to the architectural complex or the architectural traits of branch angle, hypocotyl diameter, and plant height. Directional selection for *Diap-2*^{105} did not result in significant architectural differences. Due to random drift, the *Diap-2*^{105} allele, initially associated with type II architecture through founder effect, may be maintained in such genotypes without providing greater fitness or without being associated with a locus or linked loci governing upright plant architecture.

INTRODUCTION

Allozyme variants have been used extensively to: assess genetic variability (Brown et al., 1978; Kesseli and Michelmore, 1986; Weeden, 1983), provide information on evolutionary and genetic relationships (Bassiri and Adams, 1978a; Bassiri and Adams, 1978b; Koenig and Gepts, 1989b; Singh et al., 1991b; Wall and Wall, 1975), determine linkage groups (Douches and Quiros, 1989; Koenig and Gepts, 1989a; Muehlbauer et al., 1989; Smed et al., 1989), and create linkage maps (Tanksley and Rick, 1980; Weeden and Marx, 1984). Allozyme variants of six isozyme systems separate the common bean (*Phaseolus vulgaris*) into small-seeded Mesoamerican and large-seeded Andean gene pools (Sprecher, 1988b; Koenig and Gepts, 1989b). In addition, allozyme variants also provided indications of gene flow from wild to cultivated *P. vulgaris* and supported the separation of five subgroups within the Mesoamerican gene pool and four subgroups within the Andean gene pool (Singh et al., 1991b).

Sprecher (1988a) reported that an allozyme variant of the enzyme diaphorase (DIA) is associated with tropical black upright genotypes of race Mesoamerica of the Mesoamerican gene pool (Singh et al., 1991a). She determined that DIA is a tetrameric enzyme coded by two tightly linked loci, *Diap-1* and *Diap-2*, with four and three alleles, respectively. Allelic variability at the *Diap-1* locus separated *P. vulgaris* into Mesoamerican (*Diap-1*^{95}) and Andean (*Diap-1*^{100}) gene pools.

(Allozyme loci and alleles are designated as in Koenig and Gepts, 1989b.) Allelic variability at the *Diap-2* locus differentiated within the Mesoamerican gene pool. The allele, *Diap-2*^{100}, commonly exists in both Andean and Mesoamerican materials however, the *Diap-2*^{105} allele is present only in race Mesoamerica (Sprecher, 1988a; Koenig and Gepts, 1989b; Singh et al., 1991b). Furthermore, both *Diap-2*^{100} and *Diap-2*^{105} alleles are present in cultivated *P. vulgaris* whereas, wild materials possess only the *Diap-2*^{100} allele (Koenig and Gepts, 1989b; Singh et al., 1991b). The *Diap-2*^{105} allele which is associated with tropical black/upright genotypes (Sprecher, 1988a) possibly resulted from a mutation during or after domestication of such genotypes (Singh et al., 1991b).

The genotype *Diap-1*^{95}/*Diap-2*^{105} produces the 'Unique' zymotype and may have evolutionary significance because of its close association with race Mesoamerica of *P. vulgaris* (Sprecher, 1988b). Included within this race are the tropical black genotypes (Singh et al., 1991a) used for the architectural improvement of dry beans (Kelly and Adams, 1987). In an isozyme survey of upright type II beans, Sprecher (1988b) reported that 75% were homozygous for the *Diap-2*^{105} allele. A linkage with upright plant architecture is suggested because the *Diap-2*^{105} allele was maintained through indirect selection.

The objectives of this investigation were (1) to determine the genetic relationship between the *Diap-2*^{105} allele and upright, erect plant architecture and (2) if the *Diap-2*^{105} allele is not linked to any component of the architectural complex, determine why the allele is associated with type II plant architecture.

MATERIALS AND METHODS

Genetic relationship between erect plant architecture and the *Diap-2*^{105} allele

Plant materials

Advanced Michigan State University (MSU) breeding lines and cultivars representing navy, pinto, and great northern commercial classes were surveyed for DIA to determine the frequency of the *Diap-2*^{105} allele among advanced Mesoamerican genotypes. The lines evaluated in this investigation exhibited mainly type II plant architecture but some type I and type III lines were also included (Kelly personal communication). Two plants were analyzed for each pinto and great northern line, whereas, four plants were evaluated per navy line.

Eight F_2 populations segregating at the *Diap-2* locus were evaluated to study the genetic relationship between upright plant architecture and the *Diap-2*^{105} allele. The bean lines used to generate the populations represent both navy and pinto bean commercial classes and differed in type I, II, and III growth habit and DIA zymotype (Table 2.1). The populations studied were crosses between zymotypes and included:

Seafarer x N84004	(Type I, Slow x Type II, Unique)
Seafarer x P89405	(Type I, Slow x Type II, Unique)
N84004 x Michelite	(Type II, Unique x Type III, Slow)
N84004 x Ouray	(Type II, Unique x Type I, Slow)
N84004 x UI-114	(Type II, Unique x Type III, Slow)
Michelite x P89405	(Type II, Slow x Type II, Unique)
Ouray x P89405	(Type I, Slow x Type II, Unique)
P89405 x UI-114	(Type II, Unique x Type III, Slow)

Approximately 320 seeds per F_2 population were planted at a 20 cm spacing within rows and a 51 cm spacing between rows at East Lansing, Michigan, 1990. Where emergence was poor a type I kidney bean, Isabella, was hand planted two weeks later to ensure uniform interplant competition. Parental lines were included as checks on each side of the F_2 populations.

Isozyme analysis

Young, fully expanded leaves sampled from 16-42 day old field grown plants were analyzed for DIA. All steps were carried out on ice or at 4°C unless otherwise specified. Two leaf disks, 1.0 cm in diameter, were placed in 1.5 ml eppendorf tubes. Potassium phosphate grinding buffer (0.35 ul) modified from Weeden (1984) was added to each eppendorf. Specifically, 0.25% Triton X-100, a detergent

Table 2.1. Characteristics of small-seeded (20 g/100 seeds) navy and medium-seeded (40 g/100 seeds) pinto bean parental lines.

Bean Line	Commercial Class	Seed Size	Growth Habit	Architecture Rating	Diaphorase Genotype	Diaphorase Zymotype
UI-114	Pinto	Medium	III	1	$\textit{Diap-1}^{95}$ $\textit{Diap-2}^{100}$	Slow
Michelite	Navy	Small	III	2	$\textit{Diap-1}^{95}$ $\textit{Diap-2}^{100}$	Slow
Seafarer	Navy	Small	I	4	$\textit{Diap-1}^{95}$ $\textit{Diap-2}^{100}$	Slow
Ouray	Pinto	Medium	I	5	$\textit{Diap-1}^{95}$ $\textit{Diap-2}^{100}$	Slow
P89405	Pinto	Medium	II	8	$\textit{Diap-1}^{95}$ $\textit{Diap-2}^{105}$	Unique
N84004	Navy	Small	II	9	$\textit{Diap-1}^{95}$ $\textit{Diap-2}^{105}$	Unique

added to enhance the release of enzymes from membrane bound organelles (Kephart, 1990), was added rather than Weeden's (1984) recommended 0.5% concentration. The 0.08 M potassium phosphate grinding buffer also contained 20% sucrose (w/v), 5% PVP-40 and 14 mM 2-mercaptoethanol. The Triton X-100 and 2-mercaptoethanol were added just prior to use.

To release enzymes, tissue was macerated using a 'Con-Torque' mechanical grinder. Following homogenization, extracts were centrifuged in a refrigerated microfuge (2-4°C) at 12,000 rpm for 5 minutes to remove cellular debris and produce zymograms with sharper resolution and less streaking (Wendel and Weeden, 1989). The purified homogenate was absorbed into 3 mm x 10 mm chromatography paper wicks and stored at -15°C for 24 to 48 hours prior to use.

The electrophoresis buffers used were modified from Sprecher and Vallejos' (1989) lithium borate/tris citrate (Li-Bo) discontinuous system. Diaphorase was resolved on a 10% (w/v) starch gel prepared 18 to 36 hours in advance using Buffer A (29 mM lithium hydroxide and 192 mM boric acid, pH 8.1) and Buffer B (6 mM citrate and 51 mM lithium hydroxide, pH 8.4) in a 1:9 ratio. Twenty-two grams of starch in combination with 20 ml of Buffer A and 200 ml of Buffer B produced a gel of adequate thickness to obtain three slices. The buffer reservoirs were filled with Buffer A.

Wicks from 18 segregating samples along with two parental samples were inserted into a vertical slice 4 cm from the base of the gel. Electrophoresis was carried out at 45 mA for ten minutes to load the proteins into the gel. The wicks were then removed and electrophoresis resumed at 38 mA for 4.5-5.5 hours at 2-4°C.

The DIA assay contained in 50 ml: 100 mM Tris-HCl pH 8.5, 14 mg beta-NADH, 20 mg MTT (3-[4,5-Dimethylthiazol-2-yl]-2,5 diphenyltetrazolium bromide) and 1.0 mg 2,6-dichlorophenol indophenol (Weeden, 1984). Both anodal and cathodal sections of a gel slice 1.5 mm thick was placed in a plastic tray along with the staining solution. The gel was incubated in the dark at 37°C and scored after two hours. The second most abaxial slice of the three slice gel produced the most scorable and repeatable results.

Agronomic evaluation

All plants analyzed for DIA were rated at maturity for plant architecture on a 1 to 9 scale and evaluated for traits contributing to plant architecture as described in Chapter 1. The weight of 50 seeds was also determined.

Directional selection for the *Diap-2*^{100} allele versus the *Diap-2*^{105} allele

Four populations derived from the crosses N84004 x UI-114, Michelite x P89405, Ouray x P89405 and P89405 x UI-114 were selected for inclusion in a directional selection experiment. The cross N84004 x UI-114 is typical of crosses initially made by Kelly and Adams (1987) to combine the plant architecture of the navy architype with the seed size of the prostrate, type III pinto. The Michelite x P89405 cross is the reciprocal, a prostrate, type III navy crossed to the pinto ideotype. The Ouray x P89405 and P89405 x UI-114 were included based on the results of the F_2 data. For each population, eight F_2 plants, or approximately 5% of the plants analyzed for DIA, were selected for both the *Diap-2*^{105} and the *Diap-2*^{100} alleles for a total of 16 $F_{2:3}$ families. The only restriction for inclusion in the study was that the F_2 plants produced 60 or more seeds.

Twenty seeds derived from a single F_2 plant were spaced planted (20 cm spacing) in a row and replicated three times in a completely randomized block design at East Lansing, Michigan, 1991. Plant architecture and 100-seed weight were determined for each family row.

Use of anthracnose reaction as a non-linked locus

Twenty $F_{2:3}$ families from the cross N84004 x UI-114 were initially selected for high (10 $F_{2:3}$ families) and low (10 $F_{2:3}$ families) architecture rating (Chapter 1). The $F_{2:4}$ progenies were screened in the greenhouse for resistance to the alpha race of anthracnose (*Colletotrichum lindemuthianum*). Dominant genes at the *A* locus in N84004 confers resistance to race alpha (Cardenas et al., 1964). In a normally segregating population approximately 56.3% of the N84004 x UI-114 $F_{2:4}$

progenies would be expected to be resistant to race alpha. However, selection for plant architecture may maintain a greater frequency of non-linked loci from the architectural germplasm pool. Detection of a significantly higher frequency of the *A* locus in architecturally desirable lines may be used as an indication of the representative contribution of the architectural germplasm pool in the final progeny.

Five to ten $F_{2:4}$ plants per N84004 x UI-114 family were inoculated ten days after emergence with race alpha of *C. lindemuthianum* and placed in a mist chamber for 48 hours. The plants were evaluated for disease reaction after uniform symptoms developed on UI-114, the susceptible parental check. N84004, the navy architype, is resistant to race alpha. Reaction to anthracnose was classified as resistant, intermediate, or susceptible.

RESULTS AND DISCUSSION

The diaphorase zymograms

Diaphorase isozymes are most clearly expressed in root tissue, however, in this investigation, leaf tissue was used for the DIA analysis. Leaf and root tissues produce zymograms with slightly different expression of isozymes, but it is possible to distinguish between isozyme variants. Zymograms exhibited by random samples of root tissue were in concordance with their corresponding leaf tissue extract.

The three DIA zymograms observed with greatest frequency were the 'Slow,' the 'Unique,' and the heterozygote between the Slow and Unique banding patterns (Figure 2.1). Fast and Unique/Fast heterozygous zymograms were additionally observed in breeding lines surveyed for DIA. Zymograms produced by root tissue sampled from genotypes homozygous at both loci display five dark staining bands. Genotypes heterozygous only at the *Diap-2* locus (Slow x Unigue heterozygote) produce 15 bands which is in agreement with Shaw's (1964) formula to predict the number of isozymes formed by multimeric enzymes.

Leaf tissue zymograms do not produce banding patterns characteristic of a tetrameric enzyme coded by two alleles. Homotetramers produced by the *Diap-2* locus appear after staining whereas homotetramers produced by the *Diap-1* locus cannot be visualized (Figure 2.1). Genotypes heterozygous at the *Diap-2* locus exhibit additional bands intermediate to the *Diap-2*^{105} and the *Diap-2*^{100} allozymes. Characterization of the DIA genotype was based on the intensely staining bands with relative migration distances (Rf, as calculated by Sprecher, 1988b) of -0.20, 0.05, 0.10, and 0.30.

The interpretation of shoot zymograms was verified in some cases by the clearer reaction from the root tissue extracts. In addition, leaf extracts from known root DIA genotypes were included as checks in each gel. Although leaf and root zymograms differ, they represent the same DIA genotype as was verified by root and shoot protein extracts

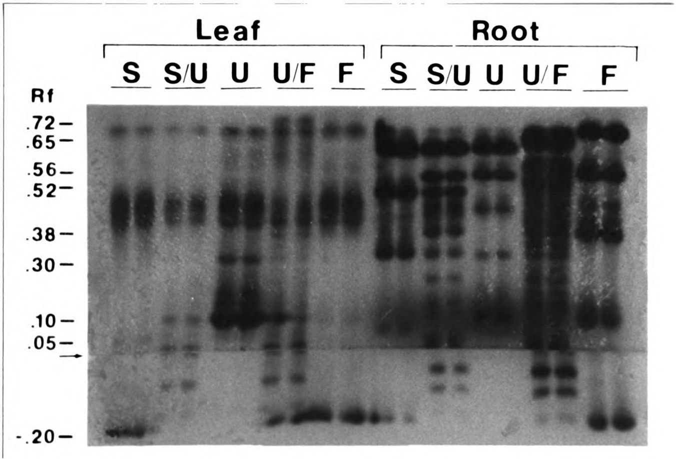

Figure 2.1. Diaphorase zymograms from leaf (L) and root (R) tissue extracts. Migration distances (Rf) as calculated by Sprecher (1988b) are given on the left. Origin is located at the arrow. *Diap-1*^{100} homotetramer located at Rf=0.72; *Diap-1*^{95} homotetramer, Rf=0.65; *Diap-2*^{105} homotetramer, Rf=0.10; *Diap-2*^{100}, Rf=-0.20. (S - Slow; S/U - Slow/Unique; U - Unique; U/F - Unique/Fast; F - Fast)

from the same plant. Bands with relative migration distances less than or equal to 0.38 have corresponding mobilities in leaf and root tissue (Figure 2.1).

In leaf tissue, the activity of isozymes produced by the faster migrating DIA subunits is insufficient to detect after staining. Presuming *Diap-1* and *Diap-2* gene products have the same subcellular distribution, the gene products may have different rates of synthesis and degradation to the extent that one gene product increases and the other decreases or disappears. Scandalios (1974) noted such a change in expression of two catalase loci in maize. Degradation of *Diap-1* gene products may account for the absence of the faster migrating isozymes composed mainly of *Diap-1* subunits. The *Diap-2* gene products may be more efficient in leaf tissue and subsequently visualized in the zymograms. The absence of the most anodal isozymes does not effect leaf physiology but these isozymes may be important in root physiology as indicated by the tissue specificity of DIA. Tissue specificity of isozymes has also been reported in other crops (Scandalios, 1964; Upadhya and Yee, 1968; Pedersen and Simonsen, 1987; Murray and Ayre, 1987).

Monomorphic bands were observed in addition to the major DIA isozymes in zymograms produced from leaf and root tissues. The monomorphic bands were located between bands with Rf values of 0.38 and 0.52 and they were of lesser staining intensity in root tissue extracts than in extracts from leaf tissue. A third invariant band migrated slightly farther than 0.65. Coinciding bands were also noted by Sprecher (1988b). The absence of heteromeric bands suggests that the invariant isozymes do not interact with subunits produced by *Diap-1* and *Diap-2*. The isozymes may be forms of structurally different DIA enzymes which are developed by the nonspecific staining protocol used in this investigation (Sprecher, 1988b).

The frequency of the *Diap-2*^{105} allele in type II plants

In a survey of Mesoamerican navy, pinto, and great northern bean lines, the *Diap-2*^{105} allele existed in 71% of genotypes with type II growth habit, whereas the *Diap-2*^{100} allele, in combination with *Diap-1*^{95}, was present in only 24% of the Mesoamerican type II lines (Appendix tables B.1, B.2, B.3). The Fast zymotype (*Diap-1*^{100}/*Diap-2*^{95}) was observed in 16% of the type II navy, pinto, and great northern bean lines. This zymotype is associated with the Andean gene pool and differs from the Mesoamerican DIA genotypes at the *Diap-1* locus. The Fast DIA lines have, in their pedigrees, *Diap-1*^{100}/*Diap-2*^{95} genotypes derived from Kelly and Adams' (1987) recurrent selection program. The Andean allele, *Diap-1*^{100}, originated from 79-1515 (Sprecher, 1988b), a single stem plant type that was used in the initial cycle of recurrent selection to develop the pinto bean ideotype.

The Fast great northern and pinto bean lines represent introgression of the Andean *Diap-1*^{100} allele into Mesoamerican germplasm. Genetic recombination between the Andean gene pool and the Mesoamerican gene pool is limited by two complementary genes: Dl_1 and Dl_2 (Singh and Gutierrez, 1984). Small-seeded Mesoamerican germplasm carry Dl_1, whereas large-seeded Andean germplasm carry Dl_2. The Fast DIA lines can potentially be used as a genetic bridge between Andean and Mesoamerican materials because they did not exhibit the abnormal developmental characteristics (Shii et al., 1981) typical of incompatible crosses between the gene pools.

The results of our survey indicate that the *Diap-2*^{105} allele is present in 71% of advanced navy, great northern, and pinto bean lines with type II plant architecture. A low frequency of the type II bean lines examined had the DIA genotype *Diap-1*^{95}/*Diap-2*^{100} or *Diap-1*^{100}/*Diap-2*^{100}. In addition, the *Diap-2*^{105} allele was present in only one type III line and three type Ia lines which had parents homozygous for the *Diap-2*^{105} allele. The determinate type Ia growth habit is characterized by strong and upright branches and mainstem in contrast to type Ib which has weak branches and mainstem (Singh, 1982).

The association between upright plant architecture and the *Diap-2*^{105} allele

Although the *Diap-2*^{105} allele is frequently present in upright plant types, the allele segregates normally and independent of plant architecture. Segregation at the *Diap-2* locus followed the expected 1:2:1 ratio in all eight F_2 populations and when pooled across F_2 populations (Table 2.2).

The *Diap-2*^{105} allele was nonsignificantly correlated to high architectural ratings with the exception of two populations, Ouray x P89405 ($r=0.18$, $P<.03$) and P89405 x UI-114 ($r=0.21$, $P<.005$). However, segregation ratios in low (architecture ratings 1, 2, and 3), intermediate (ratings 4, 5, and 6), and high (ratings 7, 8, and 9) architectural categories did not deviate from the expected Mendelian ratio suggesting independent assortment in each of the architectural categories (Table 2.3). If a linkage relationship did exist between plant architecture and the *Diap-2*^{105} allele, the allele of interest would have occurred with greater frequency in the high architectural category.

Significant correlations between the *Diap-2*^{105} allele and the architectural traits branch angle, hypocotyl diameter, and plant height were infrequent. Therefore, it did not appear that the allozyme was linked to either the architectural complex as a whole or any of the architectural traits evaluated.

Table 2.2. Allelic segregation at the *Diap-2* locus from crosses of *Diap-1*^{95,95}/*Diap-2*^{100,100} genotypes with *Diap-1*^{95,95}/*Diap-2*^{105,105} genotypes. E. Lansing, MI, 1990.

F_2 Population	*Diap-2* Alleles			Total	X^2 (1:2:1)	P† (2 df)
	100-100	100-105	105-105			
Seafarer x N84004	46	92	34	172	2.51	>0.2
Seafarer x P89405	48	88	39	175	0.93	>0.5
N84004 x Michelite	49	88	38	175	1.39	>0.5
N84004 x Ouray	51	76	46	173	2.84	>0.2
N84004 x UI-114	44	82	47	173	0.56	>0.9
Michelite x P89405	36	90	49	175	2.07	>0.3
Ouray x P89405	37	90	43	170	1.01	>0.5
P89405 x UI-114	41	82	53	176	2.45	>0.2
Pooled across F_2 populations	352	688	349	1389	0.14	>0.9

† Probability (goodness of fit by X^2 test)

Table 2.3. Allelic segregation at the *Diap-2* locus of *Diap-1*^{95,95}/*Diap-2*^{100,105} genotypes for Low (1, 2, and 3), Intermediate (4, 5, and 6), and High (7, 8, and 9) architectural categories of four F_2 populations. E. Lansing, MI 1990.

		Diap-2 Alleles					
F_2 Population	Architectural Category	100-100	100-105	105-105	Total	X2 (1:2:1)	P† (2 df)
Ouray x P89405	Low	0	1	0	1	0.50	>0.7
	Intermediate	30	80	36	146	1.84	>0.3
	High	4	5	4	13	0.80	>0.5
P89405 x UI-114	Low	18	34	13	36	0.91	>0.5
	Intermediate	23	47	37	107	5.24	>0.05
	High	0	1	3	4	4.50	>0.1
N84004 x UI-114	Low	4	6	4	14	0.29	>0.8
	Intermediate	36	65	40	141	1.09	>0.5
	High	4	8	3	15	0.20	>0.9
Michelite x P89405	Low	8	13	8	29	0.31	>0.8
	Intermediate	21	68	37	126	4.86	>0.05
	High	2	3	1	6	0.33	>0.8

† Probability (goodness of fit by X^2 test)

Linkage between the *Diap-2*^{105} allele and loci determining the quantitative trait (QTL), plant architecture, was also investigated. Analysis of variance of plant architecture rating for different *Diap-2* genotypic classes (*Diap-2*^{105,105}, *Diap-2*^{105,100} and *Diap-2*^{100,100}) was significant for only one population, P89405 x UI-114 (Table B.4). Orthogonal contrasts as described by Osborn et al. (1987) were conducted to compare the mean architectural rating of the *Diap-2*^{105,105} homozygous genotypic class with the mean of the *Diap-2*^{100,100} homozygous genotypic class and to compare the mean architectural rating of the two *Diap-2* homozygous classes combined, with the mean of the *Diap-2*^{105,100} heterozygous class. Both contrasts were significant in all but one of the F_2 populations (Table B.4). However, the genotypic class with the highest average plant architecture rating was not consistent throughout all eight F_2 populations. In only two populations, P89405 x UI-114, and Ouray x P89405, the *Diap-2*^{105,105} homozygous genotypic class had the highest average architecture rating, whereas, in four populations the *Diap-2*^{100,100} homozygous class had the highest average architecture rating. Therefore, because a consistent trend was not present, the contrasts, although significant, did not indicate a linkage between the *Diap-2*^{105} allele and a locus or group of linked loci governing plant architecture.

Directional selection for the *Diap-2*^{105} allele versus the *Diap-2*^{100} allele did not result in significant architectural differences. In all four populations, the average architectural ratings for the *Diap-1*^{95}/*Diap-2*^{105} $F_{2:3}$ families was not significantly higher than the average architecture rating of the *Diap-1*^{95}/*Diap-2*^{100} $F_{2:3}$ families. The results of our directional selection study confirm that type II plant architecture and the *Diap-2*^{105} allele segregate independently.

The crosses N84004 x Ouray, Seafarer x N84004, Ouray x P89405, and Seafarer x P89405 were further evaluated for linkage associations between the *Diap-2*^{105} allele and indeterminate versus determinant growth habit. In the four F_2 populations, allelic segregation at the *Diap-2* locus in combination with growth habit indicated that *Diap-2*^{105} was independent of growth habit (Table 2.4).

Our results indicate that *Diap-2*^{105} is not linked to plant architecture or any of the three architectural traits evaluated. The association between the *Diap-2*^{105} allele and type II plant architecture may be due to founder effect and subsequent selection for a larger portion of race Mesoamerica parentage needed to refine upright plant architecture. The major constraint to founder effect is that a relatively small number of individuals, or colonizers, are involved in the establishment of a new population (Mayr, 1942). The genetic variability of the resulting population is limited to the alleles introduced by the colonizing individuals (Schwaegerle and Schaal, 1979). A mutation occurring simultaneously with

Table 2.4. Joint F_2 segregation of *Diap-2* alleles with plant growth habit.

	Observed Phenotypes†								
F_2 Population	S/I	S/D	H/I	H/D	U/I	U/D	Total	X^2	P‡
Seafarer x N84004	34	10	71	21	26	8	170	2.74	>0.7
Seafarer x P89405	32	8	67	21	38	9	175	2.41	>0.7
N84004 x Ouray	39	12	56	19	33	13	172	3.46	>0.5
Ouray x P89405	28	8	66	23	32	9	166	1.53	>0.9
Pooled across F_2 populations	133	38	260	84	129	39	683	1.11	>0.95

† S, H, U; homozygous for *Diap-2*^{100}, heterozygous, and homozygous for *Diap-2*^{105}, respectively. I and D signify indeterminate and determinate growth habits.

‡ Probability, 5 df (goodness of fit to the expected 3:1:6:2:3:1 Mendelian ratio)

the founding event leads to novel variability in the resulting population (Ladizinsky, 1985).

In order for founder effect to account for the association between *Diap-2*^{105} and erect plant architecture, the colonizing plant(s) would have had to possess unique, upright plant architecture. The plant architecture could allow for the establishment of areas previously unoccupied, giving rise to race Mesoamerica of the Mesoamerican gene pool. If the appearance of the *Diap-2*^{105} allele arose initially in the few colonizing individuals, the association between upright architecture and *Diap-2*^{105} may be explained. The *Diap-2*^{105} allele would have resulted from a mutation during or shortly after the founding event as the allele is not present in wild *P. vulgaris* (Koenig and Gepts, 1989b; Singh et al., 1991b).

A founding event coupled with the *Diap-2*^{105} mutation could have led to the allelic differences between race Mesoamerica and the remaining races of the Mesoamerican gene pool. However, the question remains as to why the *Diap-2*^{105} allele is present in the majority of advanced bean lines and cultivars bred to exhibit type II architecture. Some of the lines were developed through recurrent selection, a cyclic breeding scheme which would dissociate unlinked traits. $F_{2:4}$ families from the N84004 x UI-114 population were screened for the presence of the independent *A* locus to investigate why the *Diap-2*^{105} allele was recovered in a high frequency of plants with type II architecture. The *A* locus, also present in the navy architype, N84004, confers resistance to race alpha of anthracnose (*C. lindemuthianum*). The $F_{2:4}$ families screened were derived from a directional selection study based on plant architecture (Chapter 1). A greater frequency of the *A* locus in the architecturally desirable lines would provide an indication of the representative contribution of the architectural germplasm pool.

$F_{2:4}$ individuals were rated resistant, intermediate or susceptible in comparison to the anthracnose reaction on the parental lines. N84004 was absent of lesions and flecking 14 days after inoculation with race alpha. UI-114, the susceptible parental check, had numerous lesions on both stem and leaves. The intermediate class, in comparison to UI-114, had fewer lesions especially on the main stem. For purposes of segregation analysis, the intermediate reactions were considered susceptible.

The presence of the *A* locus was not significantly different from the expected frequency in the $F_{2:4}$ families originally selected for poor plant architecture. Segregation in the $F_{2:4}$ families with high architecture rating also fit the expected frequency of a dominant resistant trait in the F_4 generation. If the frequency of the *A* locus was significantly higher than 56.3%, selection for plant architecture indirectly maintained the dominant resistant trait in the population. However, resistance to race alpha cannot be used to estimate the contribution of the architectural germplasm pool to upright plant genotypes. Anthracnose reaction does not provide information regarding the association between upright plant architecture and *Diap-2*^{105}.

The *Diap-2*^{105} allele may be associated with upright plant architecture through linkage with the root system. Tissue specificity of DIA indicates that the DIA isozyme variants may effect root physiology. The *Diap-2*^{105} allele may be linked to an enhanced feature of root providing greater fitness and contributing to productivity, an indirect aspect of plant architecture (Kelly et al., 1987) but a feature of major breeding importance.

However, The *Diap-2*^{105} allele may be present in 71% of type II navy, great northern, and pinto bean lines because of random drift. Although many of the bean lines were developed through recurrent selection, the number of parents used to initiate the C_0 base population was limited. When the number of individuals selected to initiate a new population is limited, genetic drift could have a greater effect on changing gene frequencies than the effects of selection alone (Helms et al., 1989).

If the initial parents contributing plant architecture carried the *Diap-2*^{105} allele then, through random drift, the allele may have become fixed in the population. As a result, less genetic variation was present at the *Diap-2* locus and the *Diap-2*^{105} allele existed in a higher frequency of type II genotypes. Due to random drift, the *Diap-2*^{105} allele may have a skewed distribution without help from selection for greater fitness or an association with upright plant architecture (Simmonds, 1979).

CONCLUSION

The *Diap-2*^{105} allele is present in 71% of genotypes with type II plant architecture which suggests the allele associates with the architectural complex. However, contrary to the indication of association, the *Diap-2*^{105} allele cannot be used as a marker for plant architecture because the allele segregates independent of the architectural complex. *Diap-2*^{105} is also not linked to any of the architectural traits including branch angle, hypocotyl diameter, and plant height. Quantitative trait loci (QTL) analysis also indicated that the *Diap-2*^{105} allele was not linked to a locus or group of linked loci governing plant architecture. The *Diap-2*^{105} allele was originally associated with type II architecture through founder effect and, due to random drift, may be indirectly maintained in upright genotypes without providing greater fitness or without being associated with a locus or linked loci governing upright plant architecture.

Previous research suggested that the architectural complex has a simple mode of inheritance and is governed by a relatively few number of genes. Heritability estimates indicated that plant architecture can be easily and effectively recovered in early generations (Chapter 1). Therefore, an indirect marker is not necessary to aid breeders in the selection of upright plant architecture.

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SUMMARY

The success of the ideotype concept in the small-seeded (20 g/100 seeds), navy bean market class (Kelly et al., 1984) prompted the architectural improvement of the medium-seeded (40 g/100 seeds), pinto bean class. Architectural improvement based on the navy ideotype was limited in the pinto bean class by the proposed negative linkage between seed size and upright plant architecture (Kelly and Adams, 1987). Using phenotypic recurrent selection, Kelly and Adams (1987) developed a pinto ideotype by combining the upright architectural traits of the navy and black bean germplasm with the seed size of the prostrate pinto. Allozyme variability of upright genotypes was later investigated (Sprecher,1988) and a diaphorase (DIA) allozyme variant governed by *Diap-2*^{105} was frequently present in plants with upright architecture. A linkage with upright plant architecture is suggested because the *Diap-2*^{105} allele was maintained through indirect selection in such genotypes.

In the first part of this thesis, linkage relationships between architectural traits, plant architecture and seed size were analyzed in F_2 populations derived from crosses between type I, II, and III *Phaseolus vulgaris* lines from small-seeded (20 g/100 seeds) navy bean and medium-seeded (40 g/100 seeds) pinto bean market classes. The architectural trait branch

angle was the most significant contributor to upright plant architecture, which was estimated to be moderately high to highly heritable. The data also indicate that seed size and upright plant architecture were not negatively linked, in contrast to the evidence of Kelly and Adams (1987). A negative linkage would appear to exist if selection for a medium-seeded pinto ideotype were based visually on the pod traits of the navy ideotype. The research we conducted was important in defining the pinto bean ideotype which is physically different from the navy architype due to the interrelationship of yield components. The proposed pinto ideotype emphasizes fewer seeds per pod or fewer pods per plant.

The objective of the second chapter was to investigate the genetic relationship between upright plant architecture and the DIA allozyme variant characterized by the allele, Diap-2^{105}. The *Diap-2*^{105} allele was present in approximately 71% of navy, pinto, and great northern genotypes with type II plant architecture. The genetic relationship between upright plant architecture and the *Diap-2*^{105} allele was further investigated in F_2 populations derived from crosses between navy and pinto bean parental lines differing for type I, II, and III growth habit and DIA genotype. The *Diap-2*^{105} allele was not genetically linked to the architectural complex as a whole or to any of the architectural traits investigated. The *Diap-2*^{105} allele was initially associated with type II architecture due to founder effect and, through random drift, may be maintained in such genotypes without providing greater fitness or without being associated with a locus or linked loci governing upright plant architecture.

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APPENDIX A

Table A.1. Means and ranges for plant architecture rating and branch angle in the F_2 and F_3 generations (East Lansing, MI 1990 and 1991).

		Architecture Rating		Branch Angle (degrees)	
Population	Gen.	Mean	Range	Mean	Range
Seafarer x Michelite	F_2	3.1	2-4	39.6	30-50
Seafarer x UI-114	F_2	2.6	1-4	41.8	38-55
Michelite x Ouray	F_2	3.4	2-5	41.4	30-60
Ouray x UI-114	F_2	2.5	1-5	45.5	30-85
Seafarer x N84004	F_2	5.6	4-8	39.0	20-70
Ouray x P89405	F_2	5.3	3-7	30.3	15-70
N84004 x Michelite	F_2	4.7	2-8	36.9	25-50
P89405 x UI-114	F_2	4.0	1-8	39.5	23-60
Seafarer x P89405	F_2	5.6	4-8	36.2	20-50
	F_3	5.6	4-8	33.0	19-44
N84004 x Ouray	F_2	6.1	4-8	37.4	20-50
	F_3	6.5	5-9	30.0	18-43
N84004 x UI-114	F_2	5.1	2-8	35.5	23-50
	F_3	4.6	1-7	35.5	18-46
Michelite x P89405	F_2	4.4	2-8	37.6	30-53
	F_3	5.3	3-9	32.7	18-46

APPENDIX B

Table B.1. Advanced navy bean lines and cultivars evaluated for DIA genotype.

			Alleles	
Bean Line	Plant Type†	Zymotype‡	*Diap-1*	*Diap-2*
N90540	Ia	U/S:U:U/S:U	95	100,105
N90573	Ia	U:U:U:U	95	105
N90590	Ia	S:S:S:S	95	100
N90598	Ia	U:S:U:S	95	100,105
N90599	Ia	S:S:S:S	95	100
Laker	Ia	S:S:S:S	95	100
Seafarer	Ib	S:S:S:S	95	100
Tuscola	Ib	S:S:S:S	95	100
Cygnus	Ib	S:S:S:S	95	100
Fleetwood	Ib	S:S:S:S	95	100
Midland	Ib	S:S:S:S	95	100
Mitchell	Ib	S:S:S:S	95	100
Sprint	Ib	S:S:S:S	95	100
Sanilac	Ib	S:S:S:S	95	100
N84004	IIa	U:U:U:U	95	105
N90402	IIa	U:U:U:U	95	105
N90410	IIa	U:U:U:U	95	105
N90426	IIa	U:U:U:U	95	105
N90523	IIa	U:U:U:U	95	105
N90605	IIa	U:U:U:U	95	105
N90609	IIa	U:U:U:U	95	105
N90614	IIa	U:U:U:U	95	105
N90616	IIa	S:S:S:S	95	100
N90618	IIa	S:S:S:S	95	100
Mayflower	IIa	U:U:U:U	95	105

† Ia=upright determinate bush; Ib=determinate bush with weak branches; IIa=indeterminate upright with short vine; IIb=indeterminate upright with long vine; III=indeterminate prostrate (Singh, 1982).

‡ Four samples per line. F=Fast, U=Unique, S=Slow, U/S=heterozygous zymotype.

Table B.1 (cont'd).

Bean Line	Plant Type†	Zymotype‡	Alleles	
			Diap-1	*Diap-2*
Northstar	IIa	U:U:U:U	95	105
Avanti	IIa	U:U:U:U	95	105
Neptune	IIa	U:U:U:U	95	105
Swan Valley	IIa	U:U:U:U	95	105
C-20	IIa	S:U:S:U	95	100,105
Schooner	IIb	U:U:U:U	95	105
Centralia	IIb	S:S:S:S	95	100
Crestwood	IIb	S:S:S:S	95	100
Gryphon	IIb	U:U:U:U	95	105
Michelite	III	S:S:S:S	95	100

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† Ia=upright determinate bush; Ib=determinate bush with weak branches; IIa=indeterminate upright with short vine; IIb=indeterminate upright with long vine; III=indeterminate prostrate (Singh, 1982).

‡ Four samples per line. F=Fast, U=Unique, S=Slow, U/S=heterozygous zymotype.

Table B.2. Advanced pinto bean lines and cultivars evaluated for DIA genotype.

Bean Line	Plant Type†	Zymotype‡	Alleles	
			Diap-1	*Diap-2*
Ouray	Ib	S:S	95	100
P89405	IIa	U:U	95	105
P89414	IIa	U:U	95	105
P89423	IIa	U:U	95	105
P90507	IIa	U:U	95	105
P90522	IIa	U:U	95	105
P90523	IIa	U:U	95	105
P90539	IIa	U:U	95	105
P90541	IIa	U:U	95	105
P90545	IIa	U:S	95	100,105
P90557	IIa	U:U	95	105
P90558	IIa	U:U	95	105
P90559	IIa	U:U	95	105
P90561	IIa	U:U	95	105
P90562	IIa	S:S	95	100
P90563	IIa	S:S	95	100
P90564	IIa	F:F	100	100
P90565	IIa	F:F	100	100
P90566	IIa	F:F	100	100
P90567	IIa	U:U	95	105
P90568	IIa	U:F	95,100	100,105
P90569	IIa	S:S	95	100
P90570	IIa	U:U	95	105
P90571	IIa	S:S	95	100
P90573	IIa	U:U	95	105

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† Ib=determinate bush with weak branches; IIa=indeterminate upright with short vine; III=indeterminate prostrate (Singh, 1982).

‡ Two samples per line. F=Fast, U=Unique, S=Slow, U/F=heterozygous zymotype.

§ Sprecher, 1988.

Table B.2 (cont'd).

Bean Line	Plant Type†	Zymotype‡	Alleles *Diap-1*	 *Diap-2*
P90574	IIa	F:F	100	100
P90577	IIa	U:F	95,100	100,105
P90578	IIa	U:U	95	105
P90579	IIa	S:S	95	100
P90580	IIa	F:F	100	100
P90581	IIa	U:U	95	105
P90582	IIa	U:U	95	105
P90583	IIa	U:U	95	105
P90587	IIa	F:F	100	100
P90588	IIa	F:F	100	100
P90589	IIa	F:F	100	100
P90591	IIa	F:F	100	100
P90592	IIa	F:F	100	100
P90593	IIa	U:U/F	95,100	100,105
P90594	IIa	U:U	95	105
P91101	IIa	S:S	95	100
P91102	IIa	U:U	95	105
P91103	IIa	U:U	95	105
P91104	IIa	F:S	95,100	100
P91105	IIa	S:U	95	100,105
P91106	IIa	S:S	95	100
P91107	IIa	U:U	95	105
Sierra	IIa	U:U	95	105
Aztec	IIa	U:U	95	105
I90219 (NDSU)	IIa	S:S	95	100
Arapaho	III	U:S	95	105,100
Olathe	III	S:S	95	100

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† Ib=determinate bush with weak branches; IIa=indeterminate upright with short vine; III=indeterminate prostrate (Singh, 1982).

‡ Two samples per line. F=Fast, U=Unique, S=Slow, U/F=heterozygous zymotype.

§ Sprecher, 1988.

Table B.2 (cont'd).

Bean Line	Plant Type†	Zymotype‡	Alleles	
			Diap-1	*Diap-2*
Othello	III	S:S	95	100
Pindak	III	S:S§	95	100
UI-114	III	S:S	95	100

† Ib=determinate bush with weak branches; IIa=indeterminate upright with short vine; III=indeterminate prostrate (Singh, 1982).

‡ Two samples per line. F=Fast, U=Unique, S=Slow, U/F=heterozygous zymotype.

§ Sprecher, 1988.

Table B.3. Advanced great northern bean lines and cultivars evaluated for DIA genotype.

Bean Line	Plant Type†	Zymotype‡	Alleles *Diap-1*	 *Diap-2*
Alpine	IIa	U:U	95	105
G90101	IIa	U:U	95	105
G90102	IIa	U:U	95	105
G90103	IIa	U:U	95	105
G90104	IIa	U:U	95	105
G90105	IIa	S:S	95	100
G90106	IIa	U:U	95	105
G90107	IIa	U:U	95	105
G90124	IIa	S:S	95	100
G90125	IIa	S:S	95	100
G90126	IIa	S:S	95	100
G90127	IIa	U:U	95	105
G90128	IIa	U:U	95	105
G90129	IIa	U:U	96	105
G90130	IIa	U:U	95	105
G90131	IIa	U:U	95	105
G90135	IIa	U:U	95	105
G90136	IIa	U:U	95	105
G90137	IIa	U:U	95	105
G90138	IIa	U:U	95	105
G90139	IIa	U:U	95	105
G90151	IIa	U:U	95	105
G90155	IIa	U:U	95	105
G90162	IIa	U:S	95	100,105
G90164	IIa	U:U	95	105

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† IIa=indeterminate upright with short vine; III=indeterminate, prostrate (Singh, 1982)

‡ Two samples per line. F=Fast, U=Unique, S=Slow, U/S=heterozygous zymotype.

$ Sprecher, 1988.

Table B.3 (cont'd).

Bean Line	Plant Type†	Zymotype‡	Alleles *Diap-1*	*Diap-2*
G90171	IIa	S:S	95	100
G90180	IIa	F:F	100	100
G90188	IIa	F:F	100	100
G91201	IIa	U:U	95	105
G91202	IIa	U:U	95	105
G91203	IIa	U:U	95	105
G91204	IIa	U:U	95	105
G91205	IIa	U:U	95	105
G91206	IIa	U:U	95	105
G91207	IIa	S:S	95	100
G91208	IIa	U:U	95	105
G91209	IIa	U/S:S	95	100,105
G91210	IIa	U:S	95	100,105
G91211	IIa	U:S	95	100,105
G91212	IIa	U:U	95	105
G91213	IIa	U:U	95	105
G91214	IIa	F:F	100	100
UI-59	III	S:S§	95	100
Starlight	III	S:S§	95	100
Beryl	III	S:S§	95	100
Valley	III	S:S§	95	100
Harris	III	S:S§	95	100

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† IIa=indeterminate upright with short vine; III=indeterminate, prostrate (Singh, 1982)

‡ Two samples per line. F=Fast, U=Unique, S=Slow, U/S=heterozygous zymotype.

§ Sprecher, 1988.