

INHERITANCE OF SEVERAL AGRONOMIC CHARACTERS
AND ASSOCIATIONS AMONG THEM IN SOYBEAN
(GLYCINE MAX (L.) MERRILL)

By

GHOLAM ABBAS RANJBAR

Licentiate

Tehran University

Karadj, Iran

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Thesis Approved:

James S. Kirby

Thesis Adviser

J. W. Lynch

Dale E. Weibel

Ronald W. McJewer

Norman N. Durham

Dean of the Graduate College

967642

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CHAPTER I

INTRODUCTION

The soybean (Glycine max (L.) Merr.), a native of eastern Asia, has become one of the most important crops in the United States. This plant of the century, soybeans, with normal percentages of 40% protein and 20% oil is a valuable source of protein and oil for human consumption and animal feed as well as being important for industrial uses.

The soybean is a member of the Leguminosae family and the sub-family Papilionoideae. It is an erect, bushy or branching summer annual plant. Flowers are borne on racemes in the axils of the leaves, and each axil, whether on the main stem or on a branch, appears to be a site for flowers and pods. There is a great amount of genetic variability for agronomic characters in soybeans. Attempts have been made to recognize and extract lines with desirable characters. The objectives of this study were to investigate inheritance of flowering and maturity time, height, yield, weight of 100 seed, pubescence, pubescence color, seed coat color, and hilum color, and to determine associations among these characters in a soybean cross, Davis X T145.

CHAPTER II

REVIEW OF LITERATURE

Morphology, Genetics, and Physiology of Pubescence

Commercial varieties of soybeans are covered by hairs (pubescence) on stems, leaves (petioles and leaflets), pods, and calyx. Only a few Japanese varieties are hairless.

An individual normal hair is an elongated and cylindrical apical cell (1-3 mm) on one, two, or three basal cells. It tapers gradually at the end joining the basal cell, and then tapers abruptly at the tip (31).

Much variation exists among varieties of soybeans with respect to size, shape, durability and distribution of plant hairs. Bernard and Singh (5) mentioned five types of pubescence: glabrous, curly, dense, sparse, and puberulent besides normal type. Hairs of the dense and sparse types are similar to normal type; however, hairs of curly type are similar initially to normal, but they become flat, curl, and tend to fall off. Singh et al. (31) in studying the effect of pubescent types on vigor of the plant with isogenic lines of Clark and Harosoy varieties found that dense isolines of soybeans had approximately four times as many hairs per unit area as normal, and the normal types three to four times more than sparse. There are only a few stubby

hairs on glabrous leaflets, and they tend to fall off in early stages of the growth. Each stubby hair is made up of one to seven nearly isometric cells. Hairs of the puberulent type consist of a single elongated (0.1 mm) apical cell with one or two basal cells (31). Hair density on the lower surface of the leaf is higher than on the upper surface of the leaf for each type (17).

A single locus (P_1, p_1) controls glabrousness over pubescence, with complete dominance of P_1 . Four single-gene controlled traits affect shape and density of pubescence and are designated as p_c (curly vs. normal), p_2 (puberulent), P_d (dense vs. normal), and P_s (sparse vs. normal). These are independently inherited, but P_1 is epistatic over them. p_2 and p_c affect hair shape. P_2 is completely dominant over p_2 and causes normal pubescence; however, there is no dominance of P_c or p_c and the heterozygote is semi-curly. P_d and P_s genes have opposite functions. P_d controls the high density of pubescence and is completely dominant over its allele (p_d) which in turn controls normal density of pubescence; however, P_s is a nearly dominant gene and controls low density of pubescence, and its nearly recessive allele (p_s) controls normal density of pubescence. These two loci (P_d and P_s) interact with each other in additive fashion in controlling hair density. Different combinations of alleles at these two loci produce different hair densities from very dense ($P_d-p_s p_s$) to very sparse ($p_d p_d P_s P_s$) according to Bernard and Singh (5).

A review of literature pertaining to the effect of pubescence on plant vigor is presented by Singh et al. (31), indicating that the glabrous gene (P_1) suppresses the vigor of the plant by either its direct effect or its close linkage with factors affecting plant vigor.

They found marked growth differences between the different pubescence types in the field associated with differences in infestation by the potato leafhopper (Empoasca fabae (Harris)). They reported significant differences of height in the order of glabrous, curly, sparse, normal, and dense with the glabrous shortest and dense tallest in all stages of growth; however, yields of normal, dense, and sparse were reported to be similar and superior to yields of curly and glabrous.

Pubescence affects photosynthesis and light absorptance. Gausman and Cardenas (17) reported that hairs diffuse and entrap incoming near-IR light and increase its absorptance and decrease its reflectance. Ghorashy et al. (18), in a study concerning effect of leaf pubescence on transpiration, photosynthesis rate, and seed yield of three near-isogenic lines of soybeans, found that seed yield and apparent photosynthesis rates were not affected by pubescence, but the dense pubescent line had lower transpiration rates than the normal or glabrous isolines. They concluded that water use might be reduced without reducing apparent photosynthesis or yield of soybeans by increasing pubescence.

Genetic Nature of Color Pigments

in Soybean

Bernard and Weiss (6) summarized literature pertaining to inheritance of color pigments in soybeans. Regardless of green parts of the plant, color pigments occur in flowers, pods, pubescence, seed coat and hilum. Flower colors are white and purple, controlled by a single gene pair (W_1, w_1) with purple (W_1) completely dominant over white (20,43). Some other loci which cause variation between purple

and white flower colors have been reported. These are designated as (W_2, w_2) , (W_3, w_3) , and (W_4, w_4) . According to Hartwig and Hinson (19) the allele W_1 is considered essential for the production of purple coloration, but in the absence of W_3 or W_4 , color is indistinguishable or only a tinge is produced. The W_4 allele with W_1 results in purple flowers. The W_3 allele with W_1 causes pigment development only at the base of the standard and with W_1W_4 it intensifies normal purple pigmentation.

Pods at maturity are black, brown or tan. According to Bernard (1), two gene pairs (L_1, l_1) and (L_2, l_2) control pod colors so that L_1 causes black pigment while l_1 produces brown with L_2 and tan with l_2 .

Pubescence color in soybean is either tawny or gray. Woodworth (42) found that a single locus controls color of pubescence with tawny (T) completely dominant over gray (t). This locus has a major effect on seed coat and hilum color. Recently, Bernard (4) discussed the presence of another major locus designated as T_d-t_d which causes the occurrence of near-gray or light tawny, medium tawny, and dark tawny; whereas, no variation in gray color, produced by homozygous tt , is observed. This locus has no effect on seed coat and hilum color.

Four main colors of green, yellow, black, and brown occur in seed coats. Inheritance of green and yellow is completely independent of black and brown. A single gene pair controls green vs. yellow seed coat with green (G) completely dominant over yellow (g). Cases of maternal inheritance of green seed coat have also been discussed (34). The loci (T, t) and (R, r) interact with each other to produce black (RT), brown (rT), and buff (rt), and interact with the locus controlling flower color (W_1, w_1) to produce buff (Rtw_1) and imperfect

black (RtW_1) pigments according to Woodworth (42), Williams (40), Johnson and Bernard (20), and Bhatt and Torrie (7). A gene designated as r^m , which is allelic to R, r (recessive to R and dominant over r), causes black and brown semi-circular stripes around the hilum (39). Johnson and Bernard (20) and Weiss (39) found that a locus (O, o) affects brown pigment in recessive allelic form and changes it to reddish brown.

A locus with four alleles (I, i^1, i^k, i) controls distribution of these pigments from the hilum over the entire seed coat on a green or yellow background. The I and i^1 alleles restrict different pigments only to the site of the hilum. The gene i^1 restricts the pigment produced by other genes; however, I affects pigments and makes them lighter in intensity in a manner that black and imperfect black become gray (26). Some other variations related to the effect of I on pigments are discussed by Bernard and Weiss (6). Restriction of pigments to the site of the hilum is not complete when the allele i^k is present, and pigments are distributed in a saddle pattern on the seed coat near and including the hilum. The hilum color is the same as the seed coat in the presence of homozygous ii . The order of dominance is $I > i^1 > i^k > i$, but some reverse variations may occur as discussed by Bhatt and Torrie (7). Bernard and Weiss (6), based on work of Williams (41), recalled another locus (k) which distributes black and brown pigments in a saddle pattern shape similar to that of i^k .

Flowering and Maturity of Soybeans

in Relation to Photoperiod

Garner and Allard (16) were the pioneers who recognized that the

soybean plant is sensitive to daylength. This photoperiodic response is based on the fact that soybean plants, depending on their genotype, require a critical number of hours of darkness to initiate flowering, according to Parker and Borthwick (29).

Van Schaik and Probst (36) found that development of 'Clark' and 'Midwest' soybeans was delayed at long daylength. Fisher (15) observed that time of flowering in 'Harosoy 63', 'Hawkeye', and 'Lincoln' soybean varieties was delayed considerably under a 20-hour daylength in a greenhouse. Johnson et al. (21) found that time from flowering to pod set increased under long daylength. Lawn and Byth (24) observed that long daylength increased the time from flowering to termination of flowering. Criswell and Hume (12), in an experiment with 12 varieties of soybeans, found that the number of days from planting until first flower was increased by long photoperiods in all but 1 of the 12 varieties. Thomas and Raper (35) studied the interaction between photoperiod and morphological stage of development in soybeans and found that (a) actual pod production was significantly affected by both duration of photoperiodic treatment and the morphological stage of plant development at the onset of photoperiodic treatment and that (b) potential pod production vastly exceeded actual pod production. Costa and Pendleton (11) reported that photoperiod and temperature interactions greatly affect soybean growth and development. Major et al. (25) found that the most obvious difference among genotypes of soybeans in sensitivity to daylength was at the flowering period. Nagata (27) suggested that daylength sensitivity of soybeans differed in each growth stage.

Based on photoperiodic response, soybean varieties are developed adaptive to different latitudes (different in daylength). Soybean cultivars adapted to lower latitudes (shorter summer days) are more sensitive to daylength than are those adapted to higher latitudes (longer summer days) as Major et al. reported (25). According to response to daylength, ten maturity groups of soybean varieties have been recognized from least to most sensitive, namely early to late-maturing variety groups, designated as 00, 0, I, II, III, IV, V, VI, VII, and VIII. A maturity range of 10 to 15 days exists within each maturity group. Recently, Nissly et al. (28) in field screening observed that lines of group III maturity exhibited wide variation in sensitivity to daylength. Attempts for development of day-neutral soybeans have been made. Polson (30) screened 400 strains from maturity groups 00 and 0 for daylength neutrality by growing plants at various photoperiods in a greenhouse. He found some daylength-neutral strains, but some of these strains were delayed in maturity more than the others by long photoperiods.

Genetic Mechanisms of Flowering and Maturity

In comparison to physiology of flowering and maturity, limited research has been done on the genetic mechanisms of these traits. Most research indicates that time of flowering and maturity is regulated by one, two or three genes; however, the variation for these traits is continuous, indicating quantitative trends. Woodworth (43) reported a gene pair (S,s) to affect maturity and plant height with late and tall dominant over early and short. Bernard (2) reported that two

independent gene pairs, designated as (E_1, e_1) and (E_2, e_2) , affect time of flowering and maturity in soybeans. At each locus lateness was observed to be partially dominant. Buzzell (8) studied the inheritance of flowering time of soybeans in a greenhouse under fluorescent light and found a gene pair (E_3, e_3) to affect flowering time. Sensitivity to fluorescent light was due to the dominant allele (E_3) which delayed flowering considerably under a long fluorescent photoperiod. Bernard and Weiss (6) confirmed the hastening effect of e_3 on flowering and maturity of soybeans under field conditions. Kilen and Hartwig (22) conducted a similar experiment, involving two crosses of soybean varieties (Dorman X Hill-insensitive to light quality and Arksoy X Lee-sensitive to light quality), in which daylength was extended to 15 hours by fluorescent light. Progeny of the two crosses segregated in the F_2 generation at approximately 3 delayed:1 early when grown under fluorescent lamps alone, indicating that the light-quality sensitive character acts as a monogenic recessive under these conditions. Bernard and Weiss (6) suggested that this was probably the same gene that Buzzell (8) reported. This suggestion was confirmed by the work of Buzzell and Bernard (9), in a study which also confirmed that E_2 and E_3 were at different loci. Drissi (13), in a cross between two varieties of soybeans (Lee 74 X Bonus), studied the inheritance of time of flowering and maturity. Results from parental and F_2 populations indicated that inheritance of time of flowering and maturity were each regulated by a single pair of alleles operating with a degree of dominance in the direction of lateness. The results correspond to the findings of Bernard (2).

Weiss (38) found genetic linkage between e_1 and two other genes, y_{12} conditioning chlorophyll deficiency in seedlings and t determining gray color of pubescence, in the order of $y_{12} e_1 t$. The linkage between e_1 and t was very close.

Inheritance of Height

Veatch (37) stated that soybean plant height is a function of two variables: number of nodes and average length of internodes. He said because nodes are sites of flowering and pod set, a greater number of nodes may cause an increase in yield. Woodworth (44) stated that plant height in soybean is not independent of type of growth; indeterminate stems are usually longer with more nodes than determinate stems. Growth type is controlled by a single gene (D_t, d_t) which also affects number of nodes. Earlier, Woodworth (43) stated that a single gene (S, s) affects plant height and maturity with tall and late dominant over short and early. Bernard (3) found two gene pairs (Dt_1, dt_1) and (Dt_2, dt_2) affecting growth habit. $Dt_1 dt_1$ is the same gene found by Woodworth (44) but Bernard concluded dt_1 to be partially recessive to Dt_1 and the heterozygote $Dt_1 dt_1$ to be semi-determinate. A completely dominant gene, Dt_2 , is found in a few varieties, and causes a semi-determinate type of stem similar to the heterozygote $Dt_1 dt_1$. In crosses between the two types Bernard observed dt_1 to be epistatic over Dt_2, dt_2 . The main effect of both dt_1 and Dt_2 is hastening the termination of apical stem growth which decreases both plant height and number of nodes, but dt_1 has a much greater effect according to Bernard (3). Stewart (33) observed that in a cross between normal (tall) and dwarf (short) soybean types, the F_2 generation segregated 3 normal:1 dwarf.

Caviness and Prongsirivathana (10), in the cross 'Lee' X R 61-900, found the number of nodes and plant height to follow the same pattern of genetic inheritance. Both were monogenic with a high degree of phenotypic dominance for tallness and for a large number of nodes, although minor and/or modifying genes also affected these characters. They found no evidence for any type of discrete segregation for average length of internodes. Recently, Kilen and Hartwig (23), in a study concerning inheritance of a short internode character, concluded that this trait is probably determined by a single recessive gene.

CHAPTER III

MATERIALS AND METHODS

The soybean material used in this study, composed of two parental lines (Davis and T145) and their F_1 and F_2 generations, was obtained from Dr. Curtis Williams, Department of Agronomy, Louisiana State University.

Seeds of the parental lines, F_1 's, and F_2 's were space-planted 75 cm apart in rows which were 75 cm apart in the field at the Agronomy Research Station, Perkins, Oklahoma, in the summer of 1975 on a Teller loam soil.

The field layout corresponded to a completely randomized design in which the experimental units were individual plants 75 cm apart from each other.

Table I displays some characteristics of the parental lines and F_1 studied in this cross.

A total of 784 seeds, consisting of 110, 111, 12, and 551 seeds of P_1 , P_2 , F_1 , and F_2 , respectively, were planted. F_2 seeds were derived from three different individual F_1 plants and were labeled as F_{2-1} , F_{2-2} , and F_{2-3} which contributed 172, 177, and 202 seeds, respectively, to the total of 551 F_2 seeds. Attempts were made to provide optimum conditions for plant growth; however, poor field emergence conditions, severe stem breakage of spaced plants, and other environmental hazards

caused the loss of about 310 plants during the different stages of growth.

TABLE I
SOME CHARACTERISTICS OF PARENTAL
LINES AND THEIR F₁

Character	Davis (P ₁)	T145 (P ₂)	F ₁
Maturity group	VI	III	-
Flowering and Maturity	Late	Early	-
Growth habit	Determinate	Determinate	-
Hair	Gray pubescent	Glabrous	-
Height	Tall	Short	-
Seed coat color	Yellow	Brown	Yellow
Hilum color	Buff	Brown	Black

All seeds were planted on June 19, 1975. The data were collected on a single plant basis. The following characters were measured and recorded.

Flowering date. Number of days from planting date (June 19, 1975) to appearance of the first flower on the plant.

Maturity date. Number of days from planting date to the date when 95% of the pods were ripe.

Plant height. Plant height was recorded in centimeters as the distance from the ground surface to the tip of the main stem.

Grain yield/plant. Yield was determined by threshed grain weight in grams.

Weight of 100 seed. Weight was recorded as grams per 100 seeds.

Pubescence. Plants were recorded as either pubescent or glabrous in the field.

Pubescence color. Pubescent plants were determined as either tawny or gray near maturity in the field.

Seed coat color. Seeds were classified for their testa color into yellow, black, brown, and buff classes by visual observation.

Hilum color. Seeds were classified for their hilum color into black, brown, and buff classes by visual observation.

Analytical Procedures

Means, ranges, and variances were analyzed for each quantitative character.

Homogeneity of variances of P_1 , P_2 and F_1 populations were tested by Bartlett's test (32).

The minimum number of genes controlling each quantitative character was estimated by the formula:

$$K = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8\sigma_G^2}$$

where \bar{P}_1 = mean of Davis parent, \bar{P}_2 = mean of T145 parent, and σ_G^2 = genetic variance. The assumptions were equal gene effect, no dominance,

no epistasis, and no linkage (14). The genetic variance was computed as:

$$\sigma_G^2 = \sigma_{F_2}^2 - \frac{\sigma_{P_1}^2 + \sigma_{P_2}^2 + \sigma_{F_1}^2}{3}, \text{ where}$$

$\sigma_{P_1}^2$, $\sigma_{P_2}^2$, $\sigma_{F_1}^2$, and $\sigma_{F_2}^2$ were phenotypic variances of P_1 , P_2 , F_1 , and F_2 , respectively.

Chi-square tests were used to study inheritance of qualitative characters such as pubescence, pubescence color, hilum color, and seed coat color.

Analyses of variance were conducted to determine whether any differences for agronomic characters existed among pubescent classes.

Correlations among five agronomic characters were computed as

$$r = \frac{\text{Cov}(X,Y)}{\sigma_X \cdot \sigma_Y} \text{ where}$$

$\text{Cov}(X,Y)$ was the covariance between characters X and Y, and σ_X and σ_Y represented the standard deviation of X and Y, respectively.

CHAPTER IV

RESULTS AND DISCUSSION

Means and Variances

Means, ranges, and variances of flowering, maturity, height, yield, and 100 seed weight for parental lines, F_1 's, and F_2 's are presented in Tables II, III, IV, and V. Analyses of variance in Tables VI, VII, VIII, IX, and X indicate highly significant differences between P_1 (Davis), P_2 (T145) and F_1 populations. P_2 (T145) was earlier than P_1 (Davis) about 15 days in flowering and 26 days in maturity. P_2 (T145) was shorter in height and lower in yield and weight of 100 seed. The F_1 was intermediate for flowering, maturity, and height and superior for yield and weight of 100 seed to both parents. Statistical analysis in Table XI indicates equality of variances of parental lines and F_1 for flowering, maturity, yield and weight of 100 seeds, and inequality of variances of P_1 , P_2 , and F_1 for height. Perhaps this is due to different environmental responses of P_1 , P_2 , and F_1 for this character. Stem breakage was more frequent in the pubescent parent (P_1) than in the glabrous parent (P_2) and F_1 and could contribute to the differences of environmental responses.

Inheritance of Agronomic Characters

Table XII presents estimates of the minimum number of genes controlling flowering, maturity, height, yield and weight of 100 seeds.

TABLE II
 MEANS, RANGES, AND VARIANCES OF
 CHARACTERS FOR P₁ (DAVIS)

Character	N	Mean	Range	Variance
FLWR	80	59	56-69	7.41
MATUR	69	121	108-139	40.24
HT (cm)	63	57	22-79	232.63
YIELD (gm)	62	98	20-192	1552.68
W100SD (gm)	64	14	9-18	2.06

TABLE III
 MEANS, RANGES, AND VARIANCES OF
 CHARACTERS FOR P₂ (T145)

Character	N	Mean	Range	Variance
FLWR	17	44	39-54	16.14
MATUR	17	94	84-105	32.74
HT (cm)	17	21	10-31	46.97
YIELD (gm)	17	38	2-75	571.15
W100SD (gm)	15	12	10-13	0.95

TABLE IV
 MEANS, RANGES, AND VARIANCES OF CHARACTERS
 FOR F₁ (DAVIS x T145)

Character	N	Mean	Range	Variance
FLWR	4	53	50-54	3.58
MATUR	4	113	110-114	3.00
HT (cm)	4	39	31-48	50.00
YIELD (gm)	4	105	59-136	1218.34
W100SD (gm)	4	15	14-17	1.83

TABLE V
 MEANS, RANGES, AND VARIANCES OF CHARACTERS
 FOR F₂ (DAVIS x T145)

Character	N	Mean	Range	Variance
FLWR	369	50	38-65	26.94
MATUR	366	111	85-132	42.85
HT (cm)	367	41	11-71	112.12
YIELD (gm)	342	108	9-216	1585.89
W100SD (gm)	342	14	9-22	7.13

TABLE VI
ANALYSIS OF VARIANCE OF DATA FROM P₁, P₂,
AND F₁ FOR FLOWERING

Source	d.f	M.S.S.
Entry	2	1557.15**
Residual	98	8.72

**Significantly greater than the error mean square at P = 0.01

TABLE VII
ANALYSIS OF VARIANCE OF DATA FROM P₁, P₂,
AND F₁ FOR MATURITY

Source	d.f	M.S.S.
Entry	2	4770.59**
Residual	87	37.58

**Significantly greater than the error mean square at P = 0.01

TABLE VIII
ANALYSIS OF VARIANCE OF DATA FROM
 P_1 , P_2 , AND F_1 FOR HEIGHT

Source	d.f	M.S.S.
Entry	2	8675.90**
Residual	81	189.19

**Significantly greater than the error mean square at $P = 0.01$

TABLE IX
ANALYSIS OF VARIANCE OF DATA FROM
 P_1 , P_2 , AND F_1 FOR YIELD

Source	d.f	M.S.S.
Entry	2	24718.89**
Residual	80	1343.84

**Significantly greater than the error mean square at $P = 0.01$

TABLE X

ANALYSIS OF VARIANCE OF DATA FROM P_1 , P_2 ,
AND F_1 FOR WEIGHT OF 100 SEED

Source	d.f	M.S.S.
Entry	2	32.87**
Residual	80	1.86

**Significantly greater than the error mean square at $P = 0.01$

TABLE XI
 RESULTS OF BARTLETT'S TEST FOR HOMOGENEITY
 OF VARIANCES OF P₁, P₂, AND F₁
 POPULATIONS

	Variances			Chi-square (X ² ₂)
	P ₁	P ₂	F ₁	
FLWR	7.41(80)†	16.14(17)	3.58(4)	5.30
MATUR	40.24(69)	32.72(17)	3.00(4)	4.80
HT (cm)	232.63(63)	46.97(17)	50.00(4)	17.01***
YIELD (gm)	1552.68(62)	571.15(17)	1281.34(4)	4.86
W100SD (gm)	2.06(64)	0.95(15)	1.83(4)	3.05

***Significant at P = .005

†Number of observations on which variances are based in parentheses.

TABLE XII

MINIMUM NUMBER OF GENES INVOLVED IN INHERITANCE
OF FLOWERING, MATURITY, HEIGHT, YIELD
AND WEIGHT OF 100 SEED

Character	Parental Means		K*
	P ₁ (Davis)	P ₂ (T145)	
FLWR	59	44	2
MATUR	121	94	5
HT (cm)	57	21	70
YIELD (gm)	98	38	1
W100SD (gm)	14	12	0

*Minimum number of genes involved in inheritance of character

Genotypes of the two parents for the last trait seemed not to be different in this particular cross and observed variability was completely due to environment. The highly significant difference for weight of 100 seeds between the two parents probably was a result of more vigorous plants of the pubescent parent (Davis) and weaker plants of the glabrous parent (T145). Parental genotypes for yield seemed to be monogenically different. The pubescent parent yielded about 60 grams per plant more than the glabrous parent, while the mean yields of F_1 and F_2 plants were greater than both parents.

Height seemed to be controlled by a large number of genes (Table XII). Figure 1 shows the frequency distribution of heights of P_1 , P_2 , and F_2 plants. Distribution of F_2 plant heights is a normal one which indicates multigenic control of height. These results are quite contradictory to previous reports which all indicated monogenic control of height, number of nodes and length of internodes (10,23,33, 43).

Length of time from planting to flowering appeared to be a digenic trait; however, maturity time appeared to be controlled by several genes. Figures 2 and 3 display frequency distributions, which resemble normal distributions for these two traits, especially for maturity. These results are completely different from those of Bernard (2) and Drissi (13). Bernard mentioned two dominant genes E_1 and E_2 which both postpone flowering and maturity time; however, Drissi reported two genes, one controlling flowering and the other maturity time. He did not mention coeffect of these two genes on flowering and maturity as Bernard did. Nevertheless, Drissi found a highly significant genotypic correlation between these two traits. Not much research has been done

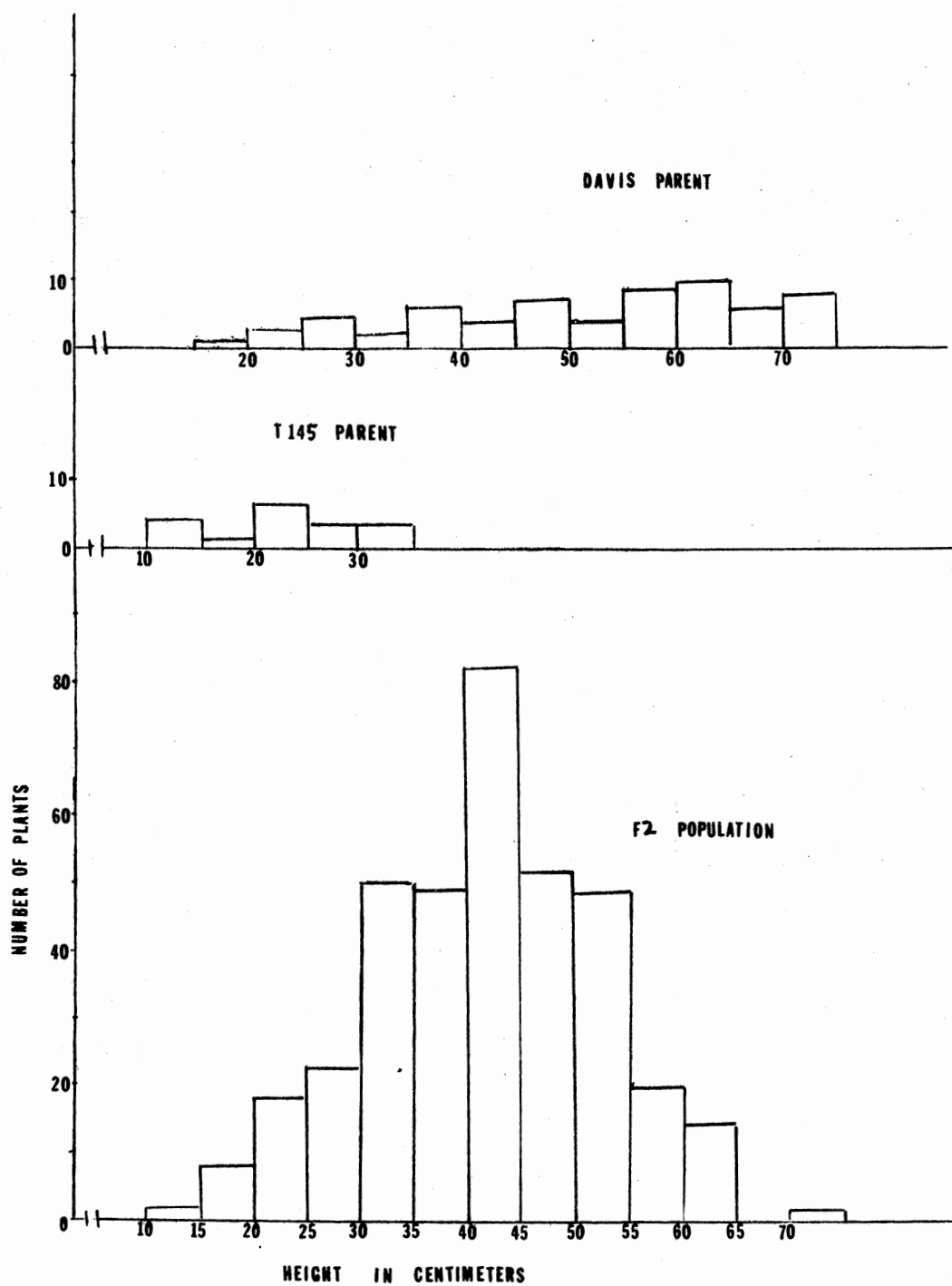


Figure 1. Frequency Distributions of Parental and F₂ Populations for Plant Height.

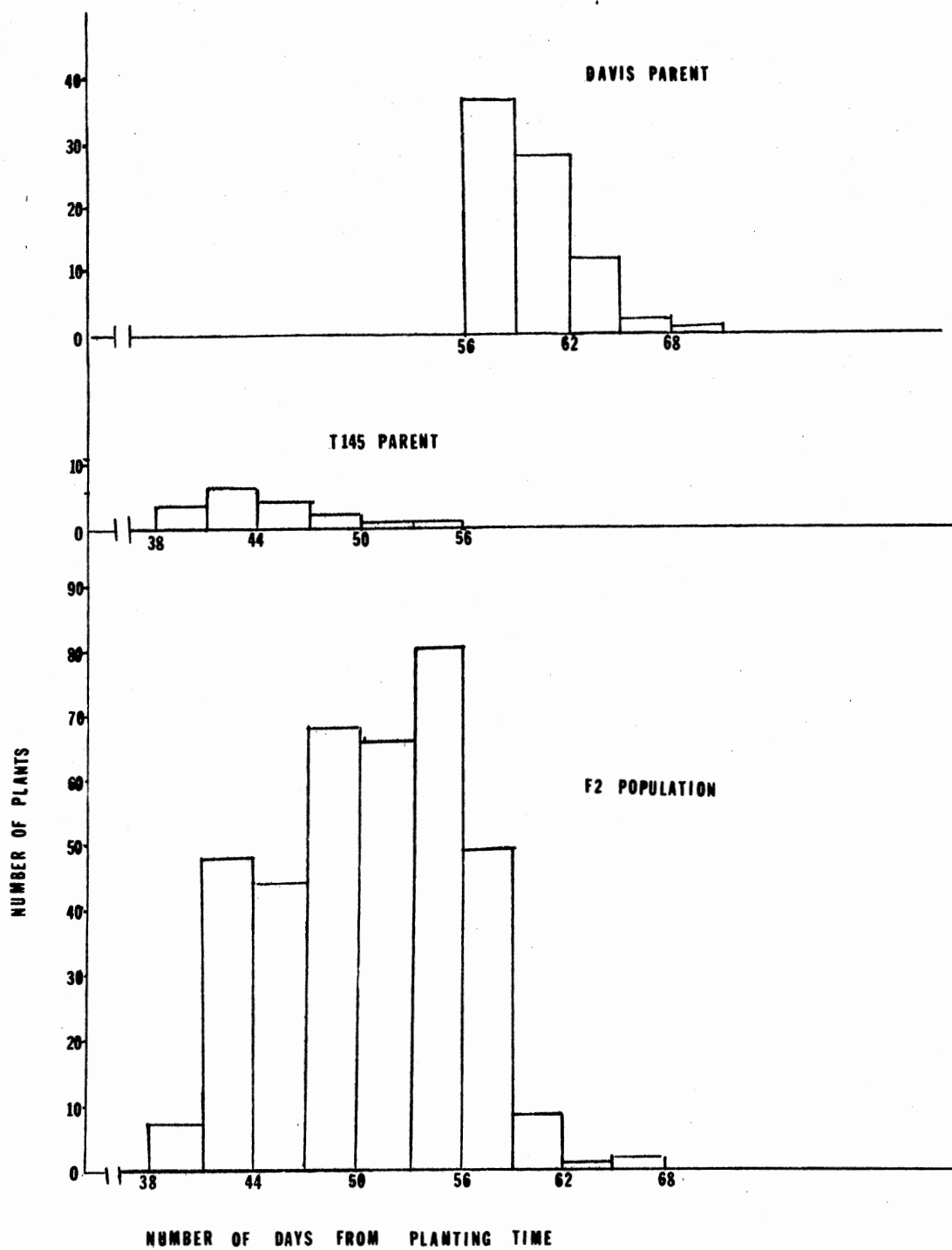


Figure 2. Frequency Distributions of Parental and F₂ Populations for Flowering

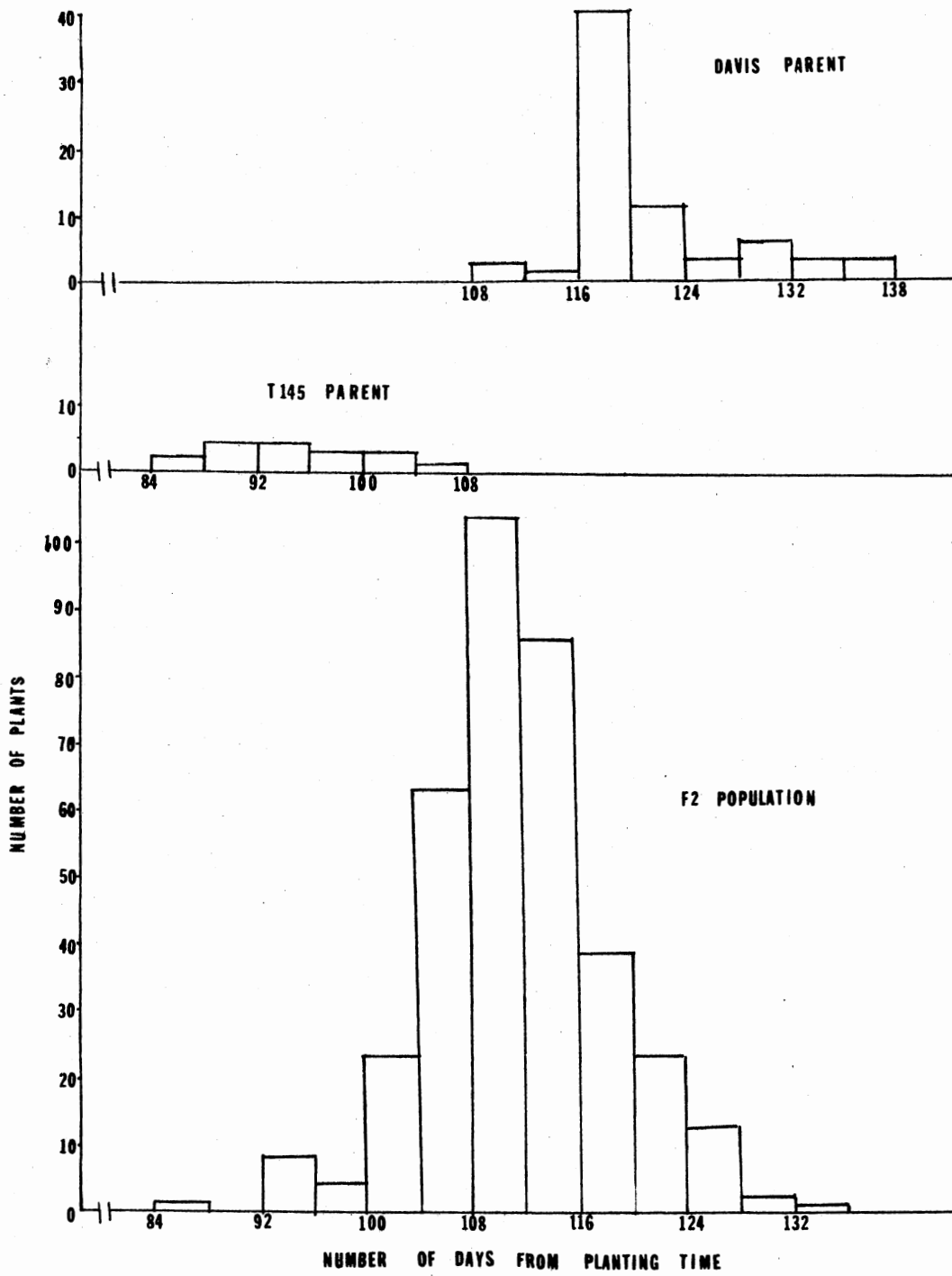


Figure 3. Frequency Distributions of Parental and F₂ Populations for Maturity

on the genetic nature of flowering and maturity time of the soybean plant, and these few studies cannot establish a clear mode of flowering and maturity inheritance.

Inheritance of Other Characters

Pubescence and Pubescence Color

Observed and expected frequencies of pubescent and glabrous plants in the F_2 population are presented in Table XIII. In Table XIV pubescent plants of the F_2 population are classified for their hair colors. Statistical analyses of the data in these tables indicate that pubescence and pubescence color are both monogenic with glabrous (P_1) and tawny (T) dominant over pubescent (p_1) and gray color (t), respectively. These results confirm previous studies (5,20,42) related to genetic mechanism of pubescence and pubescence color.

Bernard (4) recently proposed digenic nature of pubescence color with regard to tawny, near gray, and gray colors. In our experiment only the two colors of tawny and gray were distinguished.

Seed Coat and Hilum Color

Classifications and analyses related to hilum and seed coat color are presented in Tables XV, XVI, and XVII. Table XVII indicates absolute association of tawny pubescence (T) with black or brown hilum and/or seed coat, and gray pubescence (t) with buff color of hilum and/or seed coat. Thus, the locus which controls pubescence color (T,t) also affects hilum and seed coat color. In Table XV seeds are classified into black, brown, and buff for their hilum color. Since

TABLE XIII

OBSERVED AND EXPECTED NUMBER OF GLABROUS
AND PUBESCENT PLANTS IN THE
F₂ POPULATION

Plant Type	Observed	Expected (3:1)	Chi-square
Glabrous	284	276.75	0.19
Pubescent	85	92.25	0.57
Total	369	369.00	$X^2_1 = 0.76$ n.s.

n.s. - not significant

TABLE XIV

OBSERVED AND EXPECTED NUMBER OF TAWNY
AND GRAY PUBESCENT PLANTS IN
THE F₂ POPULATION

Pubescence Color	Observed	Expected (3:1)	Chi-square
Tawny	64	63.75	0.001
Gray	21	21.25	0.003
Total	85	85.00	$X^2_1 = 0.004$ n.s.

n.s. - not significant

TABLE XV

OBSERVED AND EXPECTED NUMBER OF PLANTS
WITH BLACK, BROWN, OR BUFF SEED
HILUM IN THE F₂ POPULATION

Hilum Color	Expected Genotype	Observed	Expected (9:3:4)	Chi-square
Black	R_T-	191	207	1.24
Brown	rrT-	72	69	0.13
Buff	rrtt or R_tt*	105	92	1.84
Total	----	368	368	$X^2_2 = 3.21$ n.s.

n.s. - not significant

*Buff hila with genotypes rrtt and R_tt could not be separated and were, therefore, classified together to give a total expected frequency of 4/16.

TABLE XVI

OBSERVED AND EXPECTED NUMBER OF PLANTS
IN WHICH SEED COAT AND HILUM COLOR
WERE 1-DIFFERENT 2-SAME

Seed Coat and Hilum Color	Expected Genotype	Observed Number	Expected Number (3:1)	Chi-square
Different	i^i	279	276	0.03
Same	i	89	92	0.10
Total	--	368	368	$X^2_1 = 0.13$ n.s.

n.s. - not significant

TABLE XVII

ASSOCIATION OF PUBESCENCE COLOR
AND HILUM COLOR

Hilum Color	Pubescence Color	
	Tawny	Gray
Black or Brown	64	--
Buff	--	21

the number of plants with black hilum and/or seed coat over brown ones fits a ratio of 3:1, and with regard to the black hilum observed in F_1 seeds, it is assumed that one major gene pair (R,r with complete dominance of R) controls inheritance of black (R) over brown (r) pigment in association with the dominant allele of the locus controlling pubescence color (T), while the recessive allele (t) associating with the (R,r) locus causes production of buff pigment. In other words, the following combinations of two loci cause production of related pigments as black (RT), brown (rT), and buff (rt and Rt). Buff hila with genotypes $r r t t$ and $R - t t$ could not be separated and are, therefore, classified together to give a total expected frequency of $4/16$, while expected frequencies for black and brown hila are $9/16$ and $3/16$, respectively (Table XV). In Table XVI plants are classified for their seed coat color into two classes of self-colored coats in which seed coat and hilum color were the same (black, brown, or buff), and the class in which seed coat color was different from hilum color (yellow seed coat with black, brown, or buff hilum). Our intention was to check the mechanism of inheritance of restriction and distribution of pigments produced in the hilum over the entire seed coat. Statistical analysis in Table XVI indicates the presence of a single gene pair controlling distribution of pigments, the dominant allele (i^1) restricts pigment to the site of the hilum, so the seed coat is yellow as in the F_1 and P_1 seeds, and the recessive gene (i) distributes pigments from the hilum over the entire seed coat as in the P_2 seeds. Apparently these are two of the four in the allelic series described by Bernard and Weiss (6). As we recall Terao's work (34) on yellow and green seed coat in which he suggested a single gene pair (G,g) with

green completely dominant over yellow, it should be mentioned that in our experiment the female parent (Davis) and the F_1 seeds had yellow seed coats, and there was no segregation other than black, brown, and buff colors as described above. It is assumed that both parents possessed the same allele (g) for color of seed coat as far as yellow and green colors are concerned.

It should be mentioned that the above findings are nothing but confirmation of works by pioneers such as Woodworth (42), Williams (40), Johnson and Bernard (20), Bhatt and Torrie (7), and Mahmud and Probst (26).

Agronomic Characters in Relation to Pubescence and Pubescence Color

In Table XVIII F_2 plants are classified as glabrous, tawny pubescent and gray pubescent, and in each class the averages for flowering time, maturity time, height, yield, and weight of 100 seed are displayed. Analyses of variance of the data in Table XVIII indicate no difference between glabrous, tawny pubescent, and gray pubescent groups for the characters mentioned above except that weight of 100 seed for the glabrous group was lower than for the pubescent classes, although the pubescent parent in the cross was taller, yielded more, flowered and matured later, and had a heavier weight of 100 seed than did the glabrous parent. These results in some aspects disagree with those obtained by Singh et al. (31) where glabrous and pubescent isolines were compared. They reported that glabrous isolines were shorter and weaker in all stages of growth, and yielded less than the pubescent isolines; however, the pubescent vs. glabrous isolines gave

TABLE XVIII

ANALYSES OF VARIANCE OF MEANS OF DIFFERENT
CHARACTERS IN GLABROUS, TAWNY PUBESCENT,
AND GRAY PUBESCENT F₂ CLASSES

Character	Pubescence Classes			M.S.S.		F
	Glabrous	Tawny Pubescent	Gray Pubescent	Among Classes	Within Classes	
FLWR	50(284)‡	50(64)	50(21)	2.60	27.07	0.10
MATUR	111(281)	110(64)	111(21)	53.54	42.80	1.24
HT	41(283)	41(63)	41(21)	8.37	112.69	0.10
YIELD	110(283)	102(58)	97(21)	2789.41	1578.80	1.77
W100SD	14b(283)	16a(58)†	15a(21)	85.17	6.67	12.78***

***Significant at 0.001 level of probability

†For weight of 100 seed different classes bearing the same letter are not significantly different

‡Number of observations on which means are based in parentheses

differences in maturity and seed weight depending on the specific genetic background. Results obtained by Ghorashy et al. (18) indicated that seed yield was not affected by pubescence which corresponds to our findings. Our results reveal that the glabrous gene per se does not suppress the plant vigor and yield. The weakness of the glabrous parent in comparison to the pubescent one should be due to some other factors not linked or not closely linked with glabrous gene since in the F_2 population these suppressing factors were randomly inherited. So, we should conclude that at least in our experiment the glabrousness was not a cause of plant weakness and was not linked with factors suppressing plant vigor. Also, no significant effect of pubescence color on flowering, maturity, height, yield, and 100 seed weight was observed.

Correlations Among Agronomic Characters

Coefficients of linear correlations among five agronomic characters are presented in Table XIX. Flowering time was positively correlated with height and maturity time which indicates that early flowering phenotypes were shorter and matured earlier. Also, yield and 100 seed weight exhibited positive correlations with maturity time indicating that late maturing plants had higher yield and heavier seeds. Height was positively correlated with yield, and negatively correlated with 100 seed weight, implying that shorter plants yielded less but had heavier seeds. These results were obtained under a space-planted experiment where different genotypes were involved and cannot be generalized to normal field conditions.

TABLE XIX
 PHENOTYPIC CORRELATION COEFFICIENTS OF FIVE
 AGRONOMIC CHARACTERS IN F₂ POPULATION
 OF DAVIS X T145 CROSS

Character	W100SD	YIELD	HT	MATUR
FLWR	0.02	0.07	0.33****	0.74****
MATUR	0.39****	0.12**	0.09	
HT	-0.40****	0.31****		
YIELD	0.04			

****Significantly different from zero at P = 0.0001

**Significantly different from zero at P = 0.025

CHAPTER V

SUMMARY AND CONCLUSION

The purpose of this study was to investigate the genetic nature of flowering, maturity, height, yield, weight of 100 seed, pubescence, pubescence color, seed coat color, and hilum color as well as to determine the relationship and association among the characters in a cross of Davis X T145, two cultivars of soybean (Glycine max (L.) Merrill). Davis was a gray pubescent, late-maturing, yellow seed coat, and buff hilum parent, while T145 was a glabrous, early-maturing, brown seed coat, and brown hilum parent. The parents, F_1 , and F_2 generations were space-planted in a completely randomized design in which experimental units were single plants 75 cm apart.

Analysis of data from parents, F_1 , and F_2 generations gave estimates of number of genes which indicated that the two parents differed for flowering, maturity, and height by 2, 5 and 70 genes, respectively, and their frequency distributions resembled normal ones. Parental lines differed monogenically for yield, while they appeared identical for any genes controlling weight of 100 seeds in this cross.

Pubescence and pubescence color were each controlled by a single gene in which glabrous (P_1) and tawny (T) color of pubescence were completely dominant over pubescence (p_1) and gray color of pubescence (t), respectively. The gene controlling pubescence color also affected pigmentation of hilum and seed coat. A single locus (R,r) in

association with the gene (T,t) produced black, brown, or buff pigments in different combinations. The allele producing black pigment (R) was completely dominant over the one producing brown pigment (r). Another locus seemed to control distribution of pigment from hilum over the entire seed coat. The allele which restricted pigment to the site of the hilum (i^1) was completely dominant over the one which distributed pigment over the entire seed coat (i).

Pubescence and color of pubescence seemed to have no significant effect on flowering, maturity, height, and yield; however, the weight of 100 seed of the glabrous group was lower than that of the gray and tawny pubescence classes.

Maturity and height were positively correlated with flowering, and in the same manner yield and 100 seed weight were correlated with maturity. Height had a positive correlation with yield, and a negative correlation with 100 seed weight.

LITERATURE CITED

1. Bernard, R. L. 1967. The inheritance of pod color in soybeans. *J. Heredity*. 58:165-168.
2. _____. 1971. Two major genes for time of flowering and maturity in soybeans. *Crop Sci.* 11:242-244.
3. _____. 1972. Two major genes affecting stem termination in soybeans. *Crop Sci.* 12:235-239.
4. _____. 1975. The inheritance of near-gray pubescence color. *Soybean Genet. Newsl.* 2:31-33.
5. _____, and B. B. Singh. 1969. Inheritance of pubescence type in soybeans: glabrous, curly, dense, sparse, and puberulent. *Crop Sci.* 9:192-197.
6. _____, and M. G. Weiss. 1973. Qualitative genetics. IN: B. E. Caldwell (ed.) *Soybeans: improvement, production, and uses.* Amer. Soc. Agron., Madison, Wis. p. 117-154.
7. Bhatt, G. M., and J. H. Torrie. 1968. Inheritance of pigment color in the soybean. *Crop Sci.* 8:617-619.
8. Buzzell, R. I. 1971. Inheritance of soybean flowering response to fluorescent-daylength conditions. *Canad. J. Genet. Cytol.* 13:703-707.
9. _____, and R. L. Bernard. 1975. E₂ and E₃ maturity gene tests. *Soybean Genet. Newsl.* 2:47-49.
10. Caviness, C. E., and C. Prongsirivathana. 1968. Inheritance and association of plant height and its components in a soybean cross. *Crop Sci.* 8:221-224.
11. Costa, J. A., and J. W. Pendleton. 1975. Temperature and light effects in soybeans. *Agron. Abstracts.* Amer. Soc. Agron. p. 79.
12. Criswell, J. G., and D. J. Hume. 1972. Variation in sensitivity to photoperiod among early maturing soybean strains. *Crop Sci.* 12:657-660.

13. Drissi, N. M. 1976. Inheritance of flowering and maturity and their association with other agronomic characters in soybean (Glycine max (L.) Merrill). M.S. Thesis. Oklahoma State University.
14. Falconer, D. S. 1964. Long term results of selection. Introduction to quantitative genetics. The Ronald Press Company, New York. p. 217-219.
15. Fisher, J. E. 1963. The effects of short days on fruit set as distinct from flower formation in soybeans. *Canad. J. Botany* 41:871-873.
16. Garner, W. W., and H. A. Allard. 1920. Effect of relative length of day and night and other factors of the environment on the growth and reproduction in plants. *J. Agr. Res.* 18:553-606.
17. Gausman, H. W. and R. Cardenas. 1973. Light reflectance by leaflets of pubescent, normal and glabrous soybean isolines. *Agron. J.* 65:837-838.
18. Ghorashy, S. R., J. W. Pendleton, R. L. Bernard, and M. E. Bauer. 1971. Effect of leaf pubescence on transpiration, photosynthetic rate, and seed yield of three near-isogenic lines of soybeans. *Crop Sci.* 11:426-427.
19. Hartwig, E. E., and Kuell Hinson. 1962. Inheritance of flower color of soybeans. *Crop Sci.* 2:152-153.
20. Johnson, H. W., and R. L. Bernard. 1962. Soybean genetics and breeding. *Advance Agron.* 14:149-221.
21. _____, H. A. Borthwick, and R. C. Leffel. 1960. Effects of photoperiod and time of planting on rates of development of the soybean in various stages of the life cycle. *Bot. Gaz.* 122:77-95.
22. Kilen, T. C., and E. E. Hartwig. 1971. Inheritance of a light-quality sensitive character in soybeans. *Crop Sci.* 11:559-561.
23. _____, and _____. 1975. Short internode character in soybeans and its inheritance. *Crop Sci.* 15:878.
24. Lawn, R. J., and D. E. Byth. 1973. Response of soya beans to planting date in South-Eastern Queensland. I. influence of photoperiod and temperature on phasic development patterns. *Aust. J. Agr. Res.* 24:67-80.
25. Major, D. J., D. R. Johnson, J. W. Tanner, and I. C. Anderson. 1975. Effect of daylength and temperature on soybean development. *Crop Sci.* 15:174-179.

26. Mahmud, I., and A. H. Probst. 1953. Inheritance of gray hilum color in soybeans. *Agron. J.* 45:59-61.
27. Nagata, T. 1958. Studies on flowering and fruiting of summer vs. autumn soybean types. *Crop Sci. Soc., Japan, Proc.* 27:87-90.
28. Nissly, C. R., C. N. Hittle, and R. L. Bernard. 1975. Variation in daylength sensitivity in soybean germplasm of group III maturity. *Agron. Abst., Amer. Soc. Agron.* p. 74.
29. Parker, M. W., and H. A. Borthwick. 1951. Photoperiodic responses of soybean varieties. *Soybean Digest* 11(11):26-30.
30. Polson, D. E. 1972. Day-neutrality in soybeans. *Crop Sci.* 12:773-776.
31. Singh, B. B., H. H. Hadley, and R. L. Bernard. 1971. Morphology of pubescence in soybeans and its relationship to plant vigor. *Crop Sci.* 11:13-16.
32. Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. The McGraw-Hill Book Company, Inc. p. 347-349.
33. Stewart, R. T. 1927. Dwarfs in soybeans. *J. Heredity.* 18:281-284.
34. Terao, H. 1918. Maternal inheritance in the soybean. *Amer. Nat.* 52:51-56.
35. Thomas, F. Judith, and C. David Raper, Jr. 1975. Interaction between photoperiod and morphological stage of development in soybean. *Agron. Abst., Amer. Soc. Agron.,* p. 76.
36. Van Schaik, P. H., and A. H. Probst. 1958. Effects of some environmental factors on flower production and reproductive efficiency in soybeans. *Agron. J.* 50:192-197.
37. Veatch, C. 1930. Vigor in soybean as affected by hybridity. *J. Amer. Soc. Agron.* 22:289-310.
38. Weiss, M. G. 1970. Genetic linkage in soybeans: linkage group I. *Crop Sci.* 10:69-72.
39. _____. 1970. Genetic linkage in soybeans: linkage group II and III. *Crop Sci.* 10:300-303.
40. Williams, L. F. 1952. The inheritance of certain black and brown pigments in the soybean. *Genetics* 37:208-215.

41. Williams, L. F. 1958. Alteration of dominance and apparent change in direction of gene action by a mutation at another locus affecting the pigmentation of the seedcoat of the soybean (Abs.). Tenth Int. Cong. Genet. Proc. 2:315-316.
42. Woodworth, C. M. 1921. Inheritance of cotyledon, seed-coat, hilum, and pubescence colors in soy-beans. Genetics 6:487-553.
43. _____. 1923. Inheritance of growth habit, pod color, and flower color in soybeans. J. Amer. Soc. Agron. 15:481-495.
44. _____. 1933. Genetics of soybeans. J. Amer. Soc. Agron. 25:36-51.

VITA

Gholam Abbas Ranjbar

Candidate for the Degree of

Master of Science

Thesis: INHERITANCE OF SEVERAL AGRONOMIC CHARACTERS AND ASSOCIATIONS
AMONG THEM IN SOYBEAN (GLYCINE MAX (L.) MERRILL)

Major Field: Agronomy

Personal Data: Born in Darab, Iran, October 13, 1947.

Education: Graduated from Hekmat High School, Shiraz, Iran in May,
1966; received a degree of Licentiate in Agronomy from the
Tehran University, Karadj, Iran in 1970.

Experience: Served in Extension Corps as a part of Military Service in
1970-1972. Employee of Extension Organization, Ministry of
Agriculture, as Agronomy Affairs Expert from 1972-1974.

Member of: Honor Society of Phi Kappa Phi, American Society of
Agronomy, and Crop Science Society of America.